NATURAL HISTORY OF THE RAYS OF THE GENUS *MOBULA* IN THE GULF OF CALIFORNIA

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ABSTRACT

Mobulid rays, which abound during summer in the southern Gulf of California, southern Baja California, Mexico, were monitored for a period of four years during a study of their biology. A total of 262 specimens belonging to four species of *Mobula* were examined. *Mobula thurstoni* was the most abundant (58% of the catch), followed by *M. japanica* (30%), *M. munkiana* (9%), and *M. tarapacana* (3%). The study area served as a nursery ground for *M. thurstoni*, a summer feeding and mating ground for *M. thurstoni* and *M. japanica*, and a wintering ground for *M. munkiana* and young *M. thurstoni*; *M. tarapacana* was rare. Data on size, weight, sex ratio, life history, seasonality, feeding habits, behavior, habitat, and symbionts are presented for each species. Size segregation was a common feature of *M. thurstoni*, *M. japanica*, and *M. munkiana*; sex segregation was not evident. An extreme degree of feeding specialization was noted: summer prey were almost exclusively the euphausiid *Nyctiphanes simplex*; the mysid *Mysidium* sp. dominated in the winter. A key to the genus *Mobula* in the Gulf of California is presented as an aid for species identification.

This paper reports on natural history aspects of rays of the genus *Mobula* (Mobulidae), a poorly known group of elasmobranchs commonly called manta rays or devil rays, frequent in the Gulf of California. A good early overview of the family Mobulidae was given by Gill (1908). Cadenat (1960) described the natural history of the mobulids of tropical west African waters, based on specimens which were occasionally captured by the local fishermen. However, with the exception of observations carried out with some regularity by Coles (1910, 1913, 1915, 1916a, 1916b) of *Mobula olfersi* (= *M. hypostoma*) and *Manta birostris* off North Carolina, most of the available literature is purely anecdotal and deals with occasionally encountered or harpooned specimens. Long-term field investigations of devil ray ecology and behavior are wanting. As a result, mobulids are among the least known of the batoid taxa. This was recognized by Bigelow and Schroeder (1953) in their comprehensive review of the knowledge of this family. No major contribution to the understanding of any aspect of mobulid biology has since been published.

Regular fisheries for mobulids were not known to exist, because mobulid meat is generally considered of little market value. However, in 1981, during a reconnaissance trip to the southern Gulf of California (Mexico), in the vicinity of La Paz, Baja California Sur, a regular, seasonally important fishery was discovered. This activity afforded the opportunity to study several aspects of the natural history and the ecology of these batoids.

Preliminary oral interviews revealed that local fishermen in the Gulf of California knew of, and routinely captured, four species of devil rays, in addition to the well-known giant manta ray, *Manta birostris*. This information contrasted with the scientific literature, where only two mobulid species, *Manta birostris* and *Mobula lucasana*, were reported for the area (Beebe and Tee-Van 1941; Fowler 1944; Castro-Aguirre 1965). The confusing state of mobulid taxonomy demanded a revisionary work of the genus *Mobula* (Notarbartolo-di-Sciara 1987), and a discussion of the systematics of *Manta* in the eastern Pacific (Notarbartolo-di-Sciara in press). Such effort permitted designation of names for all species of *Mobula* found in the Gulf of California: *M. thurstoni* (Lloyd 1908), of which *M. lucasana* Beebe and Tee Van (1938) is a junior synonym; *M. japanica* (Müller and Henle 1841); *M. tarapacana* (Philippi 1892); and *M. munkiana* Notarbartolo-di-Sciara (1987), which had not been described before. Many of the reports of *M. lucasana* (= *M. thurstoni*) from Central and South America (Beebe and Tee-Van 1941; Fowler 1944; Nichols and Murphy 1944; Barton 1948; Castro-Aguirre 1965; Chirichigno 1974; Pequeño 1983) undoubtedly refer to other species of *Mobula*. A key to the genus *Mobula* in the Gulf of
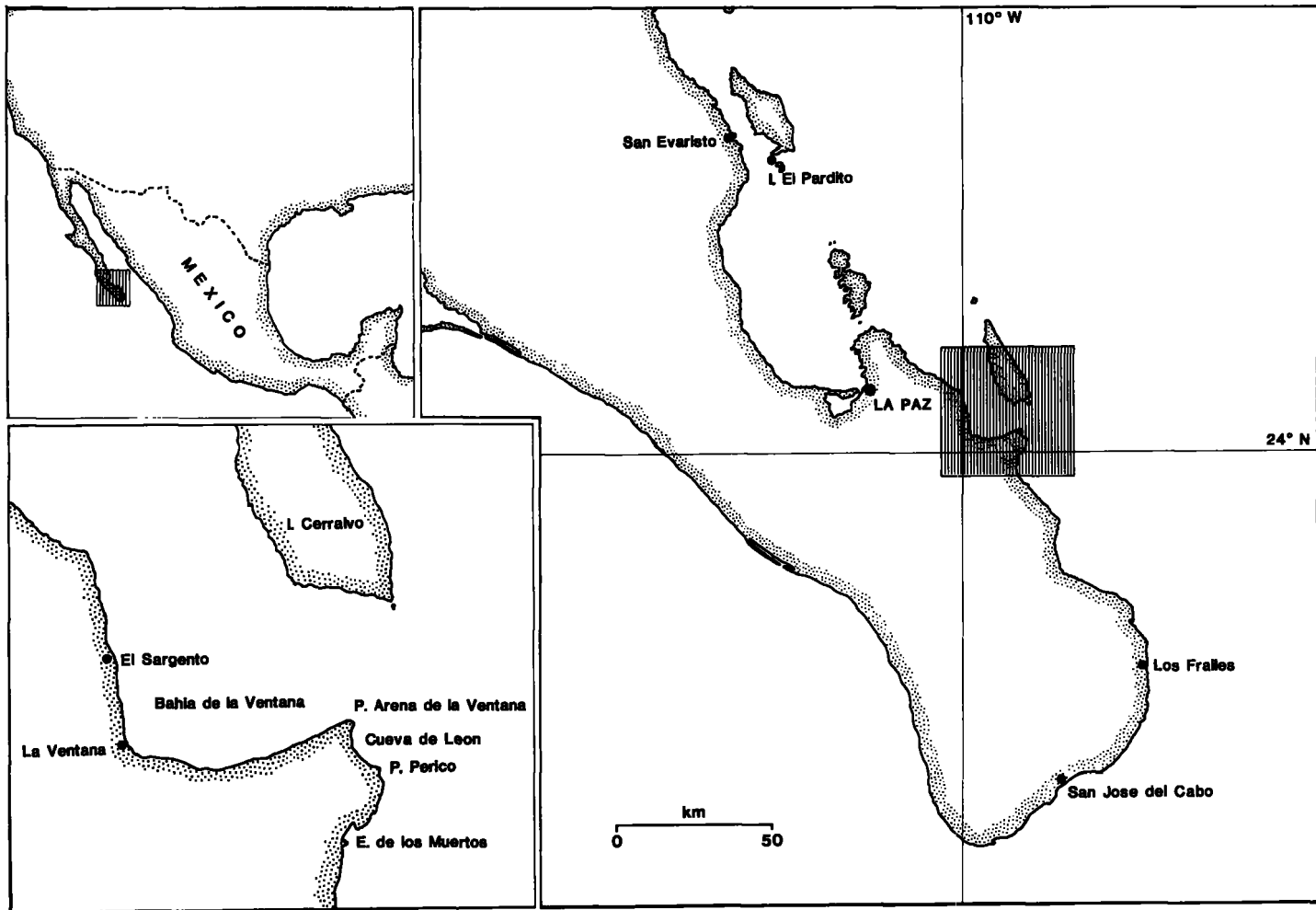
FIGURE 1.—The study area.

California is presented as an aid to future studies of mobulids from this region.

Working relationships were established with the local fishing communities, and their activities were intermittently monitored between 1981 and 1984. Captured rays were examined and measured before their pectoral fins were filleted; stomach contents and reproductive organs were examined later. Information was gathered on size, weight, sex ratios, life history, seasonality, feeding habits, habitat, behavior, and symbionts of four species of rays belonging to the genus *Mobula* (*M. thurstoni*, *M. japanica*, *M. munkiana*, and *M. tarapacana*). Detailed descriptions and morphometrics of those species are given by Notarbartolo-di-Sciara (1987). The manta ray, *Manta birostris*, was also occasionally captured (Notarbartolo-di-Sciara in press), but is not treated in the present study.

METHODS

Although mobulids are locally said to be abundant on both sides of the southern Gulf of California, for logistic convenience collecting trips were made only to the peninsular coast (Fig. 1). The fishing cooperative based at Punta Arena de la Ventana was selected as the prime collecting site, because mobulids were caught there more consistently than at other localities. Fishing camps on Isla El Pardito, at Cueva de Leon, Ensenada de los Muertos, and Bahia de los Frailes were also sources of study material. Other fishing communities, such as Juncalito, San Evaristo, El Sargento, La Ventana, and San Jose del Cabo were occasionally visited, but yielded no data because mobulids were not specifically sought by the fishermen. Seven field trips were made. Six were short-term (24 January–8 February 1981, 25 November 1981, 16–21 December 1981, 20–23 December 1982, 19–26 January 1984, and 28 October–1 November 1984); one lasted almost six months (26 January–15 July 1983).

Mobulids of all available species and sizes are caught with nets and harpoon; their meat is filleted out of the pectoral fins for human consumption and used as shark bait. Gill nets are either strung just under the surface or are set on the bottom perpendicular to shore, usually at depths between 10 and 200 m. Fishing vessels were 5–7 m fiberglass launches, locally called "pangas", powered by an outboard engine. Fishing occurred within a radius of about 15 km from a base camp. Nets are checked once a day, early in the morn-

ing. Rays weighing up to approximately 100 kg were hauled on board, larger specimens were towed ashore. Rays that were dead in the nets, after several hours (i.e., three unsexed specimens of *Mobula thurstoni*), were often partially destroyed by gammarid amphipods (locally called "plaga"), and were unmarketable.

Specimens were weighed and measured before being processed by the fishermen. Weights (WT) were taken with calibrated spring-scales. Rays lighter than 20 kg were weighed to the nearest pound with a 50-lb scale; weights were subsequently converted to kg. Heavier rays were weighed to the nearest kg with a 150 kg scale. Specimens which exceeded 150 kg (all postnatal *M. tarapacana*) were cut in four pieces and weighed separately. Ten percent was then added to the total weight to compensate for body fluid loss. All the specimens could not be weighed, as occasionally a large number of rays were beached simultaneously, and because of the intense heat the fishermen could not delay their processing.

A set of 29 measurements was taken for morphometric analysis and systematic purposes. Methods and results are presented in Notarbartolo-di-Sciara (1987). Measurements relevant to the present paper were disc width (DW), greatest dimension between outermost tips of pectoral fins, pelvic fin length, from anterior margin of vent to tip of pelvic, and clasper length, from anterior margin of vent to tip of clasper. Most specimens were discarded after measuring and sampling. All preserved specimens were deposited in the Marine Vertebrate Collection of the Scripps Institution of Oceanography. Raw data listing all specimens examined and preserved can be found in Notarbartolo-di-Sciara (1985).

The size and shape of the testes were inspected in male specimens, and the ducti deferentes were cut slightly above the genital papilla. Presence or absence of seminal fluid was determined by running a finger in the caudal direction over the ducts anterior to the cut. Clasper length in thousandths of disc width (DW) was plotted against DW to determine size at maturity, and the presence or absence of seminal fluid was noted. Relative size and contents of uteri and nidamental glands were examined in female specimens, and right and left ovaries were compared. The diameter of the largest ovum was plotted against DW to determine size at maturity of female *Mobula*. Eggs were extracted from the germinative epithelium and their greatest di-

ameter was measured to the nearest 0.1 mm with a steel dial caliper.

Stomach contents, if not larger than approximately 200 cc, were sampled whole; otherwise, the bolus was made homogeneous by stirring, and about 200 cc were preserved. Stomach content samples were fixed and preserved in 10% buffered formalin. The stomach content of each sample was thoroughly agitated, separated with a plankton strainer (mesh size 0.5 mm), rinsed of formalin in deionized water, and blotted for 30 seconds on blotting paper. The lump was then molded into a cylindrical shape, and a portion of one end was separated to make up 1 g of wet weight, measured to the nearest 0.1 g. The subsample was then placed with water in a gridded tray, and examined under a dissecting microscope. Contents of the spiral intestine were discarded, because the small crustacean prey was rapidly digested.

Feeding habits were analyzed quantitatively by computing the Index of Relative Importance (%IRI) (Pinkas et al. 1971; Hyslop 1980) for each prey species. The IRI combines percentage by number (N), mass (M), and frequency of occurrence (F) in the formula:

$$IRI = (\%N + \%M) \times \%F$$

Prey items were identified, when possible, to lowest taxa or species, then the %N of all prey species within each subsample was calculated. When more than one species was present, all items were individually counted. To obtain the %M term of the equation, mean mass was calculated for each species by measuring the length of each item contained in five randomly selected squares on a tray, calculating the average length of each prey species, and obtaining mass values from Miller's (1966) Plankton Conversion Tables, where mass is related to length for all main planktonic taxa. The %N from all subsamples were summed, and the percent from the new sum was calculated, to calculate %IRI for each prey species. The same procedure was applied to %M and %F. The total %N was then added to the total %M, and that sum was multiplied by the total %F, to obtain total IRI for each prey species, from which the %IRI was calculated. When few items (e.g., copepods) were found among a large amount of partially digested euphausiid or mysid shrimps, the possibility of reconstructing the shrimp number within the subsample by counting the digestion-resistant eye pairs was discarded to avoid bias in favor of the shrimp frac-

tion. The following method was adopted instead: all odd prey items were counted and measured, and their total mass was obtained from Miller's tables; this was subtracted from the total weight (1 g) of the subsample. The remaining weight was divided by the mean weight of each individual item, calculated by averaging the lengths of all available intact specimens, and obtaining the corresponding weight in Miller's tables. A potential biasing factor existed, when only a few prey remains were found (e.g., when a relatively uncommon item occurred alone in a stomach, therefore contributing a value of 100 %N and %M to the total IRI). This factor was avoided by considering, for quantitative treatment, only those stomachs which contained more than 1 g (wet weight) of recognizable food. All stomachs that had <1 g of contents were in fact virtually empty, and the few items found in them were treated only qualitatively.

Remoras were fixed in 10% formalin, preserved in 50% isopropanol, and deposited in the Marine Vertebrate Collection, Scripps Institution of Oceanography. Parasitic copepods were fixed and preserved in 50% isopropanol and sent to the Long Beach State University for taxonomic identification and study.

RESULTS AND DISCUSSION

A total of 262 mobulid rays, belonging to four species (*Mobula thurstoni*, *M. japanica*, *M. munkiana*, and *M. tarapacana*) were examined between 1981 and 1984. Of these, *M. thurstoni* was the most abundant species, constituting 58% of the total catch, followed by *M. japanica* (30%), *M. munkiana* (9%), and *M. tarapacana* (3%).

KEY TO THE SPECIES OF *MOBULA* IN THE GULF OF CALIFORNIA

Mobula can be distinguished from *Manta* by the mouth on the lower surface of the head rather than being subterminal, and by the presence of toothbands in both jaws. Moreover, *Manta* grows to a greater size, and the size of its head, relative to the body, is much greater than in *Mobula*.

1a. Branchial filter plates fused .... *M. tarapacana* (Spiracle in an elongated longitudinal slit, dorsal to plane of pectoral fins. Teeth tessellated, surface of crown pitted, buccal edge comblike. Thick cover of acumi-

nate denticles. Large adult size, often exceeding 3 m in width. Dorsal side greenish brown. Ventral side anteriorly white, posteriorly gray).

1b. Branchial filter plates separate 2

2a. Spine on base of tail .... *M. japanica* (Tail very long with a line of white tubercles on both sides. Spiracle a short transversal slit, dorsal to plane of pectoral fins. Teeth not in contact with each other, at least twice as high as the crown is wide; crown subtriangular in apical view. Medium-large adult size, approaching 2.5 m in width. Dark blue to black on dorsal side, apex of dorsal fin white; ventral side white. Skin rough to the touch).

2b. No spine on base of tail .... 3 (Spiracle small, subcircular, ventral to plane of pectoral fins. Skin smooth to the touch).

3a. Base of tail dorsally depressed ....*M. thurstoni* (Double curvature of anterior margin of pectoral fin. Surface of tooth crown rugose. Medium adult size, exceeding 1.8 m of width. Dark blue to black on dorsal side, apex of dorsal fin white; ventral side white, with a dark greenish patch near the posterior margin of each pectoral fin, and with a pattern of dark and shiny silvery pigmentation on distal half of pectorals).

3b. Base of tail laterally compressed .... *M. munkiana* (Anterior margin of pectoral fin straight to weakly convex. Surface of tooth crown smooth. Small adult size, barely exceeding 1 m of width. Dorsum mauve gray; ventral side white, tips of pectoral fins gray).

Mobula thurstoni (Lloyd 1908)
Local name: cubana de lomo azul

Eighty one males (disc width range 630–1,770 mm), 69 females (210–1,801 mm), and three specimens of undetermined sex (941–1,494 mm), were caught at four stations (Punta Arena de la Ventana, Cueva de Leon, Ensenada de los Muertos, and Isla El Pardito) and their adjacent waters, between 7 February 1981 and 30 October 1984. Overall and seasonal size-frequency distributions

for *M. thurstoni* are given in Figure 2. Mean size varied with season, smaller rays being dominant in winter catches, medium sizes prevailing in the summer. The difference between mean disc width (DW) in winter and overall mean DW is highly significant (T-value = 5.189, df = 169, $P \ll 0.001$). There were no significant differences between male and female DWs (T-value = 0.3767, df = 145, $P > 0.5$), with the exception of the November to February period, when females were larger (T-value = 2.331, df = 12, $P < 0.05$).

A total of 105 specimens (210–1,770 mm DW) were weighed. The WT/DW relationship is best described by the equation:

$$WT = 4.817 \times 10^{-8} \, (DW)^{2.78}$$

$$r = 0.99$$

WT is given in kg, DW in mm. The largest specimen in the sample was a female; DW was not measured because the fishermen had already started filleting the pectoral fins. Calculated DW, regressed from disc length, cranial width, and upper toothband length, was 1,801 mm (multiple correlation coefficient = 0.99). The second largest specimen was also a female, 1,799 mm DW. The largest male had a DW of 1,770 mm and weighed 53 kg. The smallest freshly caught specimen was 876 mm DW and weighed 6.4 kg. The smallest postnatal specimen was a male, the carcass of which was found drying on the beach in Ensenada de los Muertos. Its calculated DW, regressed from toothbands length, was 864 mm (multiple correlation coefficient = 0.99).

Overall ratio of males to females caught was 1.18 ($N = 148$). Catch sex ratios varied with season. Females appeared to be dominant in winter (ratio of males to females 0.27; $N = 14$). The reverse was true in March, in favor of males. A significant difference from a 1:1 ratio (chi square test $P > 0.05$) was not noted. Geographical segregation, either of sex or size, was not apparent for *M. thurstoni* during the warmer months when a wide array of size classes and both sexes were found in the same fishing area. Males and females were occasionally harpooned from the same group basking at the surface. This fact argues against behavioral sex segregation. Winter data, however, were suggestive of size segregation at that time of year. It was common knowledge among local fishermen that during the winter months all *M. thurstoni* caught are small. The bimodal size-frequency distribution for early
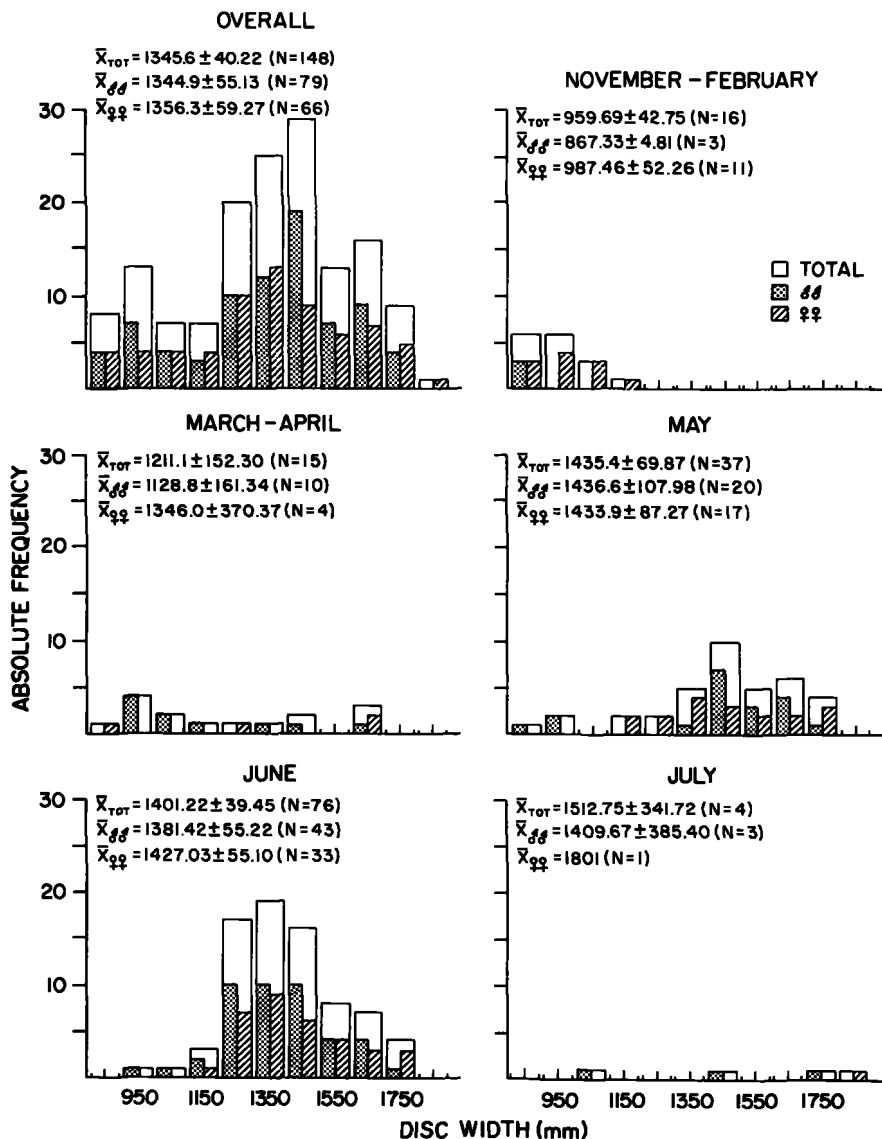
FIGURE 2.—Size-frequency distributions of *Mobula thurstoni* (means ±2 SE).

spring (Fig. 2) suggested that larger rays began to move into the area in the spring from their unknown wintering grounds.

Mature testes are large, elongated structures attached by the mesorchia to the upper anterior wall of the pleuroperitoneal cavity, on either side of the vertebral column. A large epigonal organ is associated with each testis. Both testes appeared to be functional. They were usually about the same size, although occasionally the left testis was nearly 25% larger. The paired ducti deferentes remain separated from each other through-

out their length and open into the cloaca at the tip of the urogenital papilla through two distinct pores, rather than merging in the urogenital sinus, as in most elasmobranchs (Daniel 1934), including *Manta ehrenbergi* (Gohar and Bayoumi 1959). Clasper length was plotted against DW for 43 *M. thurstoni* (Fig. 3), to determine the onset of male maturation. Rapid increase in relative size of the claspers, beginning at a DW of about 1,500 mm, was concomitant with the incipient presence of abundant seminal fluid in the lower portion of each ductus deferens. The pelvic fin area, and

especially the tissue at the bases of claspers, of the larger males appeared swollen and congested in May and June, and some of the skin had assumed a pink coloration. Similar observations in carcharhinid and odontaspid sharks have been linked with mating activities (Springer 1960; Gilmore et al. 1983).

The ovaries in *M. thurstoni* are paired, elongated organs located inside the pleuroperitoneal cavity, analogously to the testes, and are connected to a large epigonal organ. Eggs are produced within the germinative epithelium. The largest eggs were found at the anterior end of the ovary. Only the left ovary develops and is functional, whereas the size and aspect of the right ovary remains comparable with those of the immature stage. Asymmetry is also present in the oviducts, the left uterus being usually the largest in mature females. It consists of a voluminous, thick-walled expansion of the lower tract of the oviduct; its lumen is lined with a highly devel-

oped epithelium consisting of elongated, flattened villi (trophonemata), a well-known mobulid (Gill 1908; Setna and Sarangdhar 1950; Wourms 1977) and rhinopterid (Schwartz 1966; Smith and Merriner 1986) feature. In several instances both uteri were found to contain a viscous, whitish or greenish substance. Oviducts open separately into the cloaca. A progression of sexual maturity in female mobulids was evident from the examined ovary's developmental condition. In the immature female the germinative epithelium is a narrow, leaf-shaped band, tapering at both ends, located opposite to the mesovarium (facing the center of the cavity) along the ovary's longitudinal axis. In mature females the germinative epithelium takes over most of the ovary's ventral side, making room for the mature ova. To determine the size at maturity of female *M. thurstoni*, the diameter of the largest ovarian egg was plotted against DW (19 specimens, Fig. 4). An egg growth plateau was not evident, because data on

FIGURE 3.—Relationship between clasper size and body size in *Mobula thurstoni*.
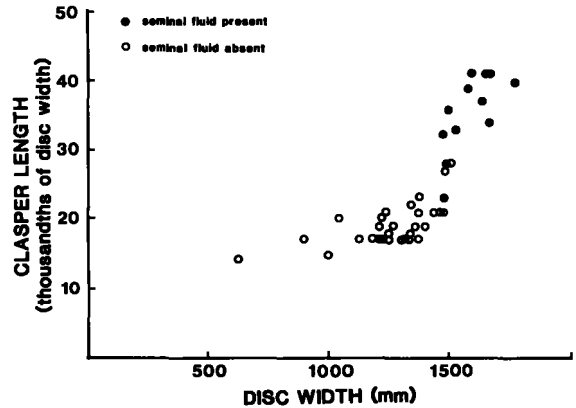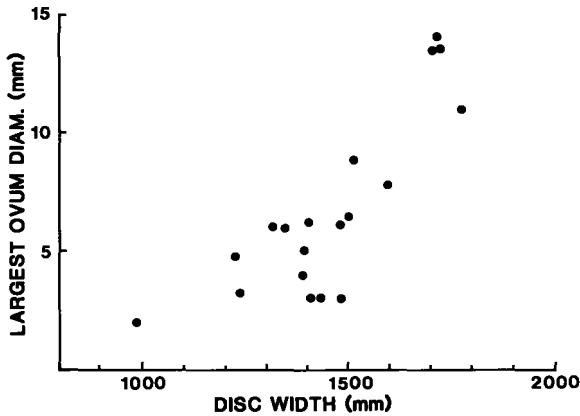

FIGURE 4.—Relationship between size of largest ovum and body size in *Mobula thurstoni*.

the larger sizes were insufficient, and therefore the maximum egg diameter was not known. It appears from the scanty available data that female *M. thurstoni* began to mature at a DW of about 1,500 mm (the point at which the slope of the curve becomes steeper).

Mobula thurstoni, like all mobulids, is a viviparous matrotroph (Wourms 1981), the near-term embryo being three orders of magnitude larger than the mature egg. Uteri and nidamental glands of 68 females were inspected. No adult female examined from March through June (*N* = 55) was pregnant. Embryos were found in July and October. Two embryos from females caught in July were near-term. Four embryos found in October were in an early stage of development. All females (*N* = 4) inspected in October were pregnant, and all embryos were in the same developmental stage, suggesting coordinated breeding activity. The largest female (DW 1,801 mm) had a single embryo, which appeared to be in the final stage of fetal development, fully pigmented, the yolk sac completely absorbed, and the umbilicus a mere scar (Fig. 5A). The embryo's DW was 630 mm; its WT, 3.4 kg. It occupied the left uterus with the rostrum pointed forward. Its pectoral fins were folded dorsally, the right pectoral on top. The cephalic fins were almost totally unrolled and extended ventrally towards the midline of the body. The uterus, with the embryo inside, occupied roughly one third of the female's pleuroperitoneal cavity. Lack of space inside the cavity and the distended skin on the abdomen made it apparent that no other embryo had been recently expelled or aborted. Uniparity appears to be a common pattern within the genus *Mobula* (Hill 1862; Gill 1908; Coles 1913, 1916b; Barnard 1925; Setna and Sarangdhar 1950; Cadenat 1960; Wallace 1967; Capapé and Zaouali 1976; Figueiredo 1977). Only Risso (1826) asserted that *Cephaloptera giorna* (= *M. mobular*) may have one or two young, but his statement was not documented. Since the smallest free-swimming specimen noted had a DW of 864 mm, the average size at birth for *M. thurstoni* is probably between 650 and 850 mm DW, and a WT of approximately 4.5 kg. The second largest female (DW 1,799 mm) had also only one embryo in her left uterus. The embryo was unpigmented, with disc 210 mm wide, and weighed 173 g. Like the term-embryo, its rostrum was pointing forward; unlike it, however, its pectoral fins were folded ventrally.

Mating, parturition, and early mobulid life history take place in the shallower portion of a population's range, not an uncommon elasmobranch feature. McLaughlin and O'Gower (1971) discussed inshore movements in the mating Port Jackson shark *Heterodontus portusjacksoni*, as did Springer (1960) for the sandbar shark *Eulamia milberti* (= *Carcharhinus plumbeus*). One-year-old gray reef sharks, *Carcharhinus amblyrhynchos*, were observed in French Polynesia in shallower waters than adults by Nelson and Johnson (1980). A similar result was reported for the hammerhead shark, *Sphyrna lewini*, by Clarke (1971) in Hawaii and by Klimley (1983) in the Gulf of California. Bullis (1967) hypothesized an upward movement to shallower depths for newborn marbled cat sharks, *Galeus arae*. There is likely an advantage for juveniles to remain in relatively protected areas during the earlier stages of their life, when they are most vulnerable to predation (Springer 1967).

Examination of 139 stomachs indicated that *M. thurstoni* was extremely specialized in its feeding habits. Eighty one (58.3%) stomachs were empty, or had only traces of food (<1 g wet weight). The remaining 58 stomachs (41.7%) had quantifiable contents. All recognizable prey items were planktonic crustaceans (with the exception of a few fish eggs, one nematod, and a small coleopteran, probably ingested accidentally when it was floating). They were listed, ranked by decreasing %IRI, in Table 1. *Mobula thurstoni*

TABLE 1.—Prey species found in 57 stomachs of *Mobula thurstoni*, ranked by decreasing Index of Relative Importance (IRI). *N* = percentage of prey species by number; *M* = percentage of prey species by mass; *F* = percent frequency of occurrence of prey species.

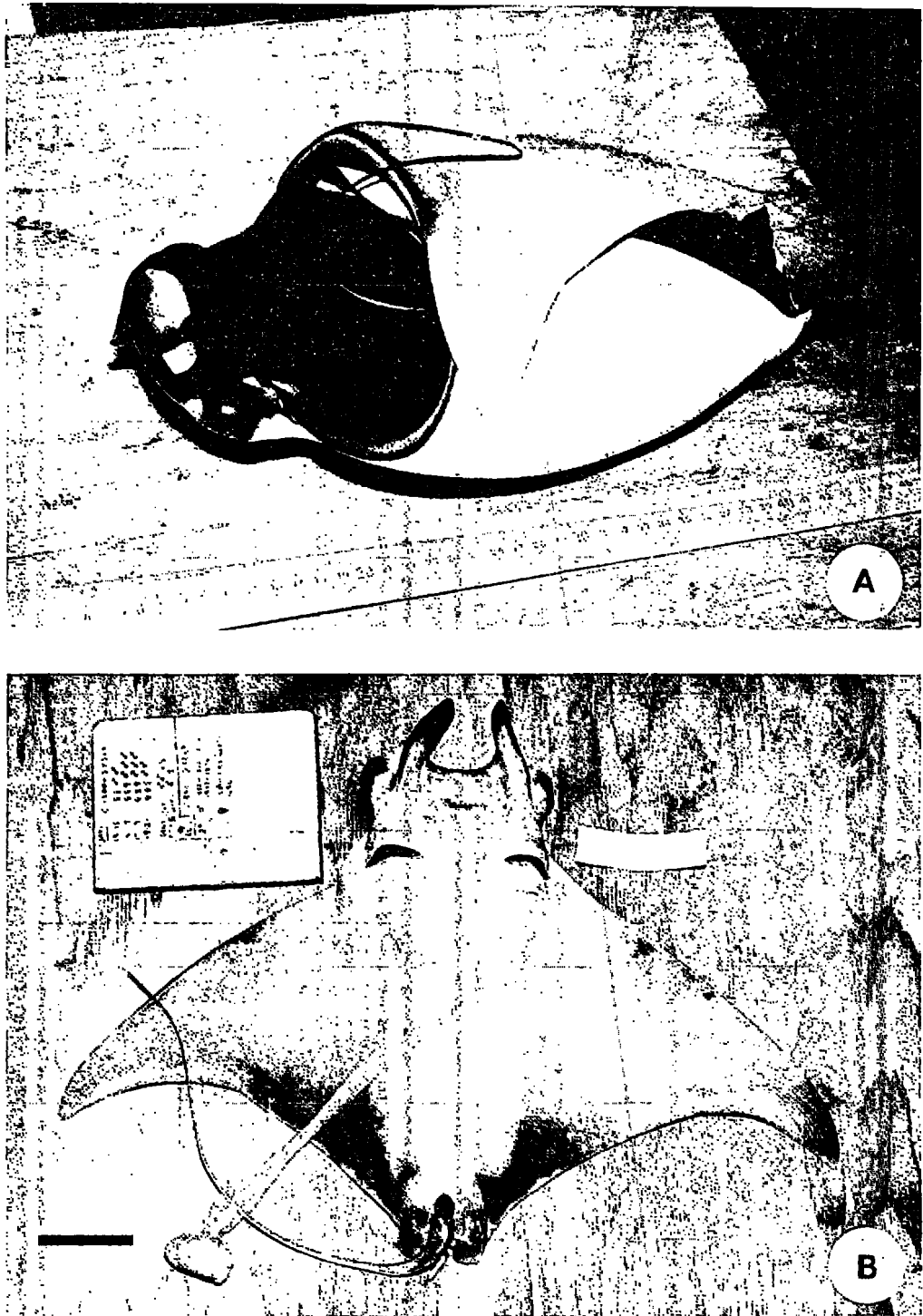| Prey species	N	%N	M	%M	%F	IRI	%IRI
Nyctiphanes simplex	4,940.8	86.70	4,982.0	87.40	87.7	15,268	97.90
Mysidium sp.	635.2	11.10	631.2	11.10	12.3	273	1.75
Copepoda	99.9	1.80	74.5	1.31	15.8	49	
Megalopa larvae	12.0	0.21	4.1	0.07	14.0	3.95	
Hyperiid amphipods	6.8	0.12	5.8	0.10	5.3	1.18	0.35
Fish eggs	1.4	0.03	1.8	0.03	5.3	0.302	
Nematoscelis diff.	0.5	0.01	1.1	0.02	1.8	0.050	
Stomatopod larvae	0.7	0.01	0.6	0.01	1.8	0.041	

FIGURE 5.—A: term-embryo of *Mobula thurstoni*. The scale in the photograph is in centimeters. B: embryo of *M. tarapacana*. The scale bar equals 5 cm.

fed mostly on adult and juvenile euphausiids, *Nyctiphanes simplex*. The mysid *Mysidium* sp. (underscribed, Thomas E. Bowman[2]) was second in order of importance. Mysids and euphausiids were never found together in the same stomach. The overall importance of the two food items differed by two orders of magnitude. All other prey species found in the stomachs were rare and probably fortuitously ingested. These included one zoea larva and the following copepod species: *Undinula vulgaris*, *Eucalanus subcrassus*, *E. subtenuis*, *Temora discaudata*, *Scolecithrix danae*, *Nannocalanus minor*, *Euchaeta remana*, *Euchaeta* sp., and *Labidocera diandra*. Diet varied with season (Fig. 6A), with mysids being dominant from December through March, and euphausiids during the warmer months. Diet varied with predator size (Table 2): smaller individuals fed both on euphausiids and mysids; the larger rays fed only on euphausiids. This result probably reflects the predominance of smaller rays during winter, when fewer euphausiids are available, rather than an ontogenetic change in food preferences.

TABLE 2.—Size differences in the diet of *Mobula thurstoni*.

	%IRI	
Prey species	DW < 1,300 mm (n = 21)	DW > 1,300 mm (n = 36)
Nyctiphanes simplex	79.04	99.91
Mysidium sp.	18.13	0
Other	2.83	0.09

Two remoras (Echeneididae) were occasionally found on large *M. thurstoni*: *Remora remora* (3 specimens; range: 98–200 mm SL), and *R. albescens* (3 specimens; 93–100 mm SL). Crustacean parasites were encountered: *Pupulina minor* (Copepoda: Caligidae), *Ecthrogaleus denticulatus* (Copepoda: Pandaridae) sparsely on the skin, and *Ecthrogaleus disciarai* (Benz and Deets 1987) in large patches on the dorsal surface, *Entepherus laminipes* (Copepoda: Cecropidae) from the branchial filter plates, *Eudactylina oliveri* (Copepoda: Eudactylinae) from the gill lamellae, and *Kroeyerina* sp. (Copepoda: Kroyeriidae) from the olfactory lamellae.

Mobula thurstoni was usually observed at the surface in coastal waters of Bahia de la Ventana, Cueva de Leon, and Bahia de los Muertos, often within a few hundred meters of land and occa-

sionally as far as 6 km. When sighted offshore, it was sometimes found over considerable depths (>500 m), although it appeared to be more abundant in shallower, neritic waters. *Mobula thurstoni* was always caught in the shallower part of the nets, usually at a depth of <100 m. The greatest part of the catch, however, was surface-dwelling rays. Beginning in mid-April, numerous *M. thurstoni* were consistently seen in the early morning hours cruising slowly at the surface. They would frequently pause, conspicuous on calmer days, with the tips of their pectoral fins protruding out of the water. This behavior is well known in mobulids (Norman and Fraser 1937); it has been observed also in connection with mating activities in *M. olfersi* (= *M. hypostoma*) by Coles (1910). During such occasions, fishermen could easily approach the rays and harpoon them, before startling them and causing them to dive. Repeated captures within the same aggregation revealed that rays of various sizes and both sexes could be found together. While at the surface, *M. thurstoni* was usually solitary or in small, nonpolarized groups (2–6), rather than in larger aggregations or schools. The species was frequently seen jumping out of the water in spectacular, often reiterated somersaults; it was recognized by the distinctive ventral markings.

It is not known to what extent mobulids make use of the sea bottom. Beebe and Hollister (1935) observed a group of 12 small devilfish (most likely *Mobula*) lying on the sandy substrate off Frigate Islet, in the British West Indies. Bigelow and Schroeder (1953) speculated that *Manta* spends much of its time resting quietly on the seafloor. During an experiment organized in conjunction with Sea World of San Diego, aimed at establishing whether *M. thurstoni* could survive in a confined environment, five young specimens were captured with gill nets and kept in a large pen (6 m in diameter) anchored in 2.5 m of water in Ensenada de los Muertos. None of the rays survived 24 hours of captivity; the reasons for their deaths were not clear, although the particularly stressful capturing method appeared as a likely cause. During that experiment the negatively buoyant rays (sinking tail-first as soon as they stopped swimming) spent a great deal of time resting on the bottom, and were able to circulate water through their gills while resting, by a synchronized maneuvering of the oral valve and of the gill covers (as judged from the flow made visible by the numerous particles suspended in the water). A frequent method of turning around

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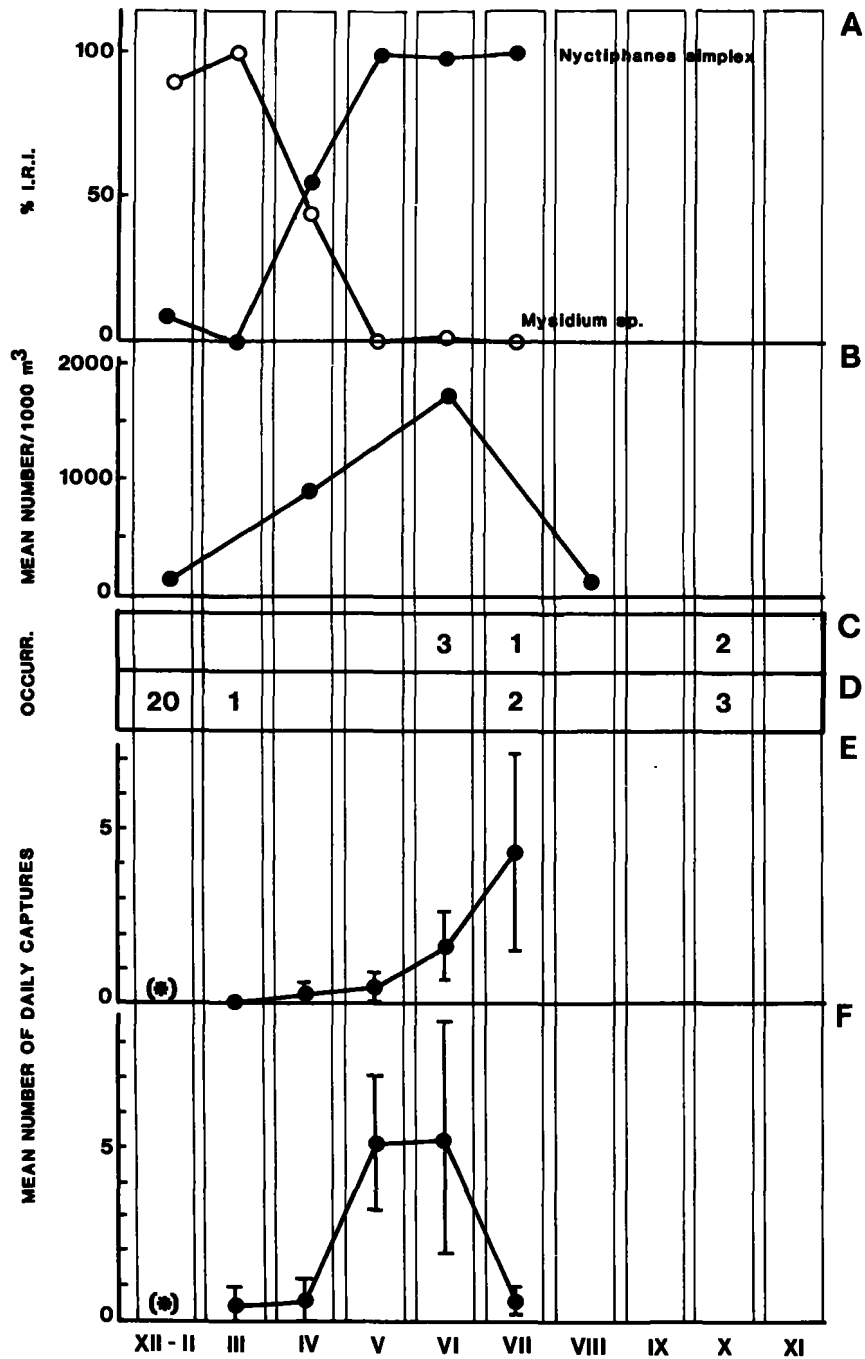[2]Thomas E. Bowman, Smithsonian Institution, Washington, D.C., pers. commun. 1984.

FIGURE 6.—A. seasonal variation of the relative importance of *Nyctiphanes simplex* and *Mysidium* sp. in the diet of *Mobula thurstoni*. B. seasonal variation of the abundance of adult and juvenile *N. simplex* in the coastal areas of the southwestern Gulf of California (modified from Brinton and Townsend 1980). C. captures of *M. tarapacana*. D. captures of *M. munkiana*. E. mean number of daily captures of *M. japanica*; bars represent 2 SE on either side of the mean. F. mean number of daily captures of *M. thurstoni*; error bars as in E. (*): although specimens were also captured between December and February, data are not comparable with spring and summer captures because catch effort was minor and inconsistent in the colder months.

(e.g., when swimming towards the wall of the pen) was to dive vertically in a tight circle until swimming in the opposite direction in an inverted position, and then spinning around the body axis to bring the dorsal side up, rather than turning by banking to the right or to the left.

An indication of the seasonal abundance of *M. thurstoni* in the surface waters of the study area was obtained by the mean number of rays caught daily from March to July 1983 (Fig. 6; Table 3). Mean daily catch should be taken as a rough indication of the relative abundance of *M. thurstoni* rather than as a precise index because the fishing effort was difficult to quantify. Mean effort, however, was roughly constant from March through July because the mean monthly number of working boats (about 20) and the number and size of the nets set then was constant. Furthermore, the fishermen would harpoon a ray every time they had the opportunity to do so. Peak of abundance was in June, a result which appears to be consistent with the fishermen's past experience, despite the 1983 abnormally high water temperatures (Cane 1983). In July the number of *M. thurstoni* caught had dropped drastically, and most of the catch consisted of *M. japanica*. No information was obtainable for the August–September period. Eighteen specimens were captured during six fall and winter field trips (24 January–8 February 1981; 25 November 1981; 16–21 December 1981; 20–23 December 1982; 19–26 January 1984; 28 October–1 November 1984), but that figure was not comparable with other data because part of the fishing cooperative migrated south to Los Frailes during the cooler months. It is common knowledge, however, among the local fishermen, that *M. thurstoni* in the colder season is present, but in fewer numbers than during the summer.

The study area constitutes a feeding, mating and nursery ground for *M. thurstoni*. The euphausiid *Nyctiphanes simplex*, the main diet item and the only food of the adults when in the area, is the most abundant and widespread euphausiid in the Gulf of California, and has been observed in dense swarms (Brinton and Townsend 1980). Although it is found in the study area year-round, its juvenile and adult stages are most abundant between February and August, peaking in June on the west side of the Gulf of California (Brinton and Townsend 1980). The seasonal abundance of *M. thurstoni* in the southern Gulf thus seems to be closely related to the seasonal abundance of its main prey. It is impossible to describe the general

TABLE 3.—Mean number of daily captures of *Mobula thurstoni*. *a* = total monthly number of captures; *b* = monthly number of days of monitoring; $\overline{X}$ = mean number of daily captures; SE = standard error of the mean; SD = standard deviation.

Month	a	b	$\overline{X}$	2SE	SD	range
March	6	16	0.38	0.54	1.1	0–4
April	9	13	0.69	0.69	1.3	0–4
May	35	7	5.00	1.95	2.6	1–9
June	77	15	5.10	3.32	6.4	0–23
July	5	9	0.56	0.34	1.0	0–3

movement and life history pattern of *M. thurstoni* in the Gulf of California from the fragmentary information available. The scanty data, however, suggest the following: 1) adult male and nonpregnant adult female *M. thurstoni* enter the area in spring to feed and to mate, 2) pregnant females segregate from the rest of the population in spring (as is also suggested by the slight predominance of males in spring and early summer), 3) gestation period is one year and females give birth to one young every two or more years, 4) the young are born in the study area or near it in midsummer and remain there throughout their early life, and 5) in late summer, when the numbers of adult and juvenile *Nyctiphanes simplex* decline due to intense heating of the water (Brinton and Townsend 1980), adult *M. thurstoni* leave the area, whereas the young switch their diet from euphausiids to mysids. Further investigations are needed for additional corroboration of these hypotheses.

Mobula japanica
(Müller and Henle 1841)
Local name: cubana de lomo blanco

A total of 78 specimens, 34 males (DW range 1,316–2,386 mm) and 44 females (1,470–2,302 mm), were caught at three stations (Punta Arena de la Ventana, Cueva de Leon, and Ensenada de los Muertos) and adjacent waters, between 16 December 1981 and 13 July 1983. Overall and seasonal size-frequency distributions for *M. japanica* are shown in Figure 7. With the exception of April, when females were larger (*T*-value = 4.697, df = 3, *P* < 0.02), there are no significant size differences between the sexes (*T*-value = 0.535, df = 76, *P* > 0.5). Most of the rays in the sample were large; only three were <1,900 mm DW.

Twenty-seven specimens (size range: 1,316–2,285 mm DW; 18.6–115 kg) were weighed. The WT/DW relationship is described by the equation:

$$WT = 4.29 \times 10^{-10} \ (DW)^{3.4}$$

$$r = 0.98$$

where WT is given in kg, DW in mm. The overall male to female ratio was 0.89 ($N = 78$). Females dominated the June through December period; males were predominant in April and May. Sex ratios, however, never significantly differed from 1 (χ^2 test $P > 0.05$). Sex segregation, behavioral or geographical, was never observed in *M. japanica* (both sexes were caught together in nets and by harpoon); sampling bias ($N = 3$) may explain why only males were caught in May. Geographi-

cal size segregation, by contrast, was an evident feature of sexually mature specimens in the Gulf of California (Fig. 7).

No pregnant females were found, although in some specimens the left uterus had a flabby and dilated appearance, suggesting recent delivery. Tissues at the base of the claspers of most of the larger males were swollen and reddened in June and July when the tips of the claspers were flexible and the rhipidion could be easily spread, and in doing so a white, viscous fluid would ooze from the hypophyle; all this suggested mating activity. The clasper length-DW relationship for *M. japanica* (Fig. 8) did not exhibit a clear pattern as in *M.*
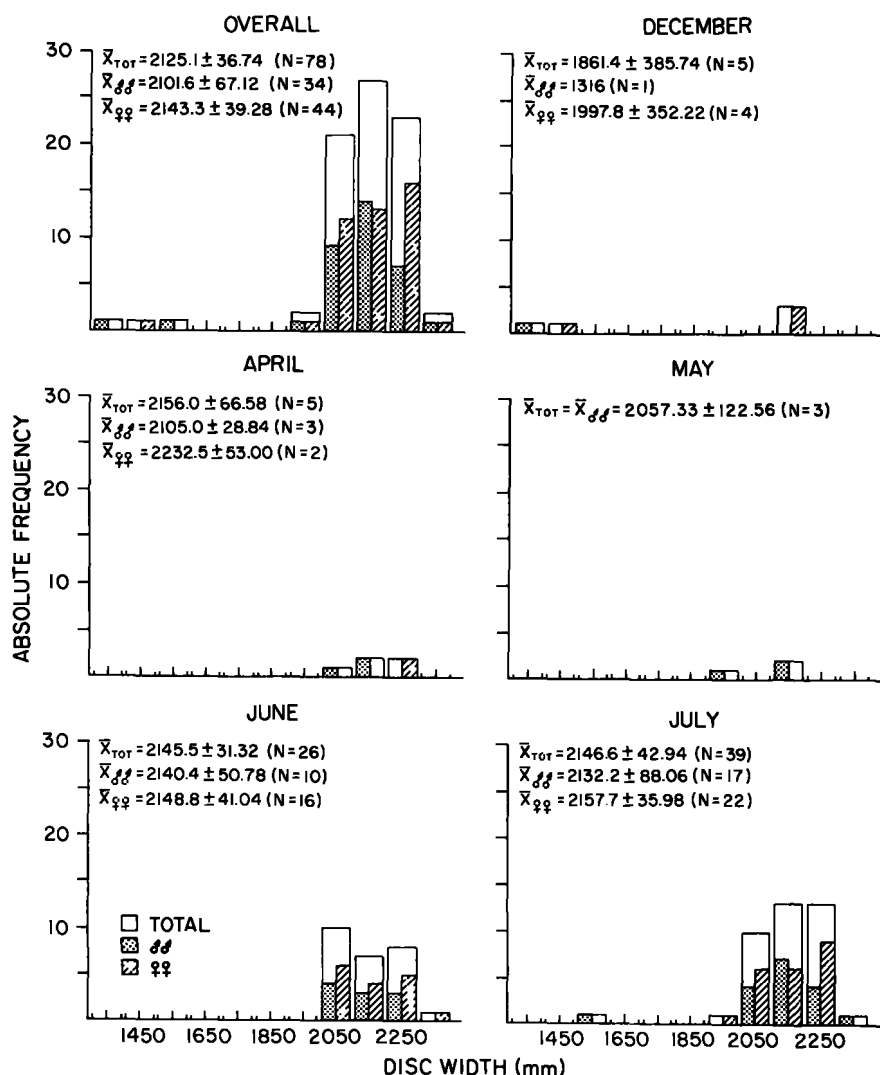

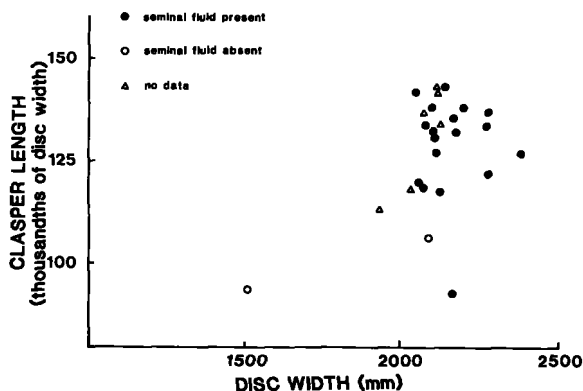FIGURE 7.—Size-frequency distributions of *Mobula japanica* (means ±2 SE).

FIGURE 8.—Relationship between clasper size and body size in *Mobula japanica*.

thurstoni, since most of the specimens of *M. japanica* were of larger size classes. It was apparent, however, that at a DW between 2,050 and 2,150 mm there is a high degree of variability in the relative size of claspers, which tended to stabilize at higher values (DWs >2,150 mm), indicating that male sexual maturity in *M. japanica* begins at a DW of 2,100 (±50) mm. Lack of information on smaller specimens prevented a clear understanding of the onset of female sexual maturity (Fig. 9). Large eggs were found in specimens as small as 2,070 mm DW, possibly indicating that female *M. japanica* began to mature at that size.

Only 19 (24%) of 78 specimens had quantifiable stomach contents (>1 g wet WT). The remaining 59 stomachs (76%) were empty or had only traces of food. All *M. japanica* fed largely on the euphausiid *Nyctiphanes simplex* (Table 4); no mysids were found. Other species occurring in the stomachs, including copepods, megalopa larvae, stomatopod larvae, hyperiid amphipods, caridean decapods (*Crangon* sp., *Pasiphaea* sp., and one alpheid decapod), and one cumacean, had an overall relative diet importance of only 0.38%. *Mobula japanica* were therefore very similar in feeding habits to large *M. thurstoni*. Information on the
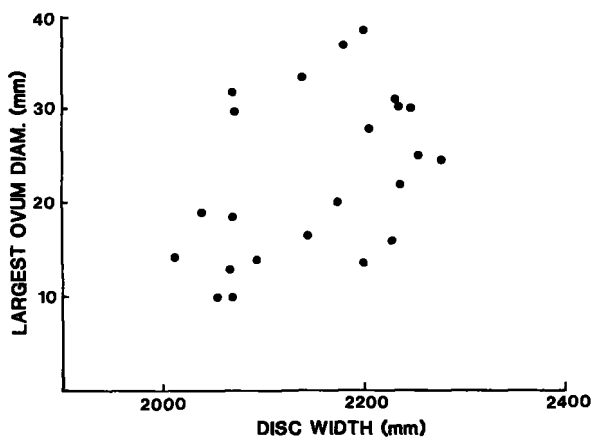

FIGURE 9.—Relationship between size of largest ovum and body size in *Mobula japanica*.

TABLE 4.—Prey species found in 19 stomachs of *Mobula japanica*, ranked by decreasing Index of Relative Importance (symbols as in Table 2).

Prey species	N	%N	M	%M	%F	IRI	%IRI
Nyctiphanes simplex	1,890.64	99.51	1,869.85	98.41	100.00	19,792	99.62
Copepoda	4.61	0.24	1.15	0.06	31.58	9.47	0.05
Other	4.74	0.25	29.00	1.53	36.84	65.58	0.33

winter diet of *M. japanica* was lacking, as four of the five specimens collected then had empty stomaches; the fifth, a large female, contained a small fragment of a partially digested fish carcass. Since quantifiable stomach contents were found only in large rays between April and July, no size or seasonal differences in the diet of *M. japanica* could be detected.

Mobula japanica was often found carrying *Remora remora*, usually seen clinging to the outside of body, but found once inside a spiracle. Six specimens of *R. remora* (range 109–217 mm SL) were collected from *M. japanica*. Only one specimen of *R. albescens* (97 mm SL) was found, in the mouth cavity of a *M. japanica*. A pilot fish, *Naucrates ductor* (Carangidae) also associated with *M. japanica*, swam alongside a harpooned ray that was being towed inshore and remained for some time at the water's edge, where the ray was beached. *Mobula japanica* was parasitized by the following crustaceans: *Nerocila acuminata* (Isopoda: Cymothoidae), *Pupulina brevicauda* and *P. minor* (Copepoda: Caligidae) on the skin; *Eudactylina oliveri* (Copepoda: Eudactylinae) in the gills; and *Kroeyerina* sp. (Copepoda: Kroyeriidae) among the olfactory lamellae. Unidentified trypanorhynch cestodes were occasionally found within the pleuroperitoneal cavity.

Habitat preference of *M. japanica* did not appear to differ from that of *M. thurstoni*. However, the use of the habitat differed seasonally: in April and May, when *M. thurstoni* was abundant at the surface, *M. japanica* was never seen, and few specimens were bottom gillnetted during those months. Conversely, *M. japanica*, in June and July, was seen in the late morning hours at the surface in groups of several individuals swimming parallel to the shore. Occasionally specimens were seen in water <1 m deep. *Mobula japanica* is not known to school, and I never observed schooling.

Coles (1910) reported that *M. olfersi* (= *M. hypostoma*) utters a "musical, bell-like bark" when dying. A similar account was given by Risso (1810) of *Cephalopterus massena* (= *M. mobular*). This information led subsequent authors (Norman and Fraser 1937; Bigelow and Schroeder 1953) to wonder whether mobulid rays are capable of producing sounds while in the water. Sound production is a fairly widespread phenomenon among bony fishes (Fish and Mowbray 1970; Tavolga 1971); however, elasmobranchs lack the traditional structures used by teleosts to generate sound, i.e., the swim bladder and bony skeletal parts (Marshall 1962), and recognizable sounds have not been recorded from these animals (Backus 1963). Sound production among elasmobranchs has been reported only for the Atlantic cownose ray, *Rhinoptera bonasus* (Myrberg 1981); in that case clicks and scraping sounds were presumably produced with the dental plates, elicited when strongly prodding three rays which were confined in a tank (Fish and Mowbray 1970). *Mobula japanica*, when beached alive, often emitted a distinctive noise which could have been the equivalent of Coles' "bark". This noise, however, was apparently caused by the periodic, spasmodic contractions of the mandibular, pharyngeal, and hypobranchial musculature of the asphyxiating ray, which forced air from the mouth cavity out of the gill openings through the meshlike branchial filter plates. Although underwater sonic recordings have never been made, it seems unlikely that under normal circumstances any audible sound could be produced in this fashion by submerged mobulids.

This area served as a spring and summer feeding and mating ground for adult *M. japanica*, rather than as a pupping or nursery ground, as indicated by the lack of small-sized specimens. Seasonal abundance of *M. japanica* in the surface waters was indicated by the catch data (Table 5) and is comparable to the seasonal abundance of *M. thurstoni* (Fig. 6). No *M. japanica* were observed in March; in April and May they occurred occasionally. By mid-June large numbers appeared in the nearshore surface waters near Punta Arena de la Ventana, and were easily harpooned. Most of the July mobulid catch consisted of *M. japanica*, when the numbers of *M. thurstoni* had declined. Data are lacking for the August–October period, therefore it was impossible to tell whether the peak of abundance occurred in July or later. Fishermen's reports were not clear, although there was agreement on an overall decline of mobulid abundance in late summer. *Mobula japanica* fed exclusively on the euphausiid *Nyctiphanes simplex*, and its numbers apparently declined concomitant with the late summer decline

TABLE 5.—Mean number of daily captures of *Mobula japanica* (symbols as in Table 1).

Month	a	b	$\overline{X}$	2 SE	SD	range
March	0	16	0	0	0	0–0
April	5	13	0.4	0.36	0.7	0–2
May	3	7	0.4	0.40	0.5	0–1
June	26	15	1.7	1.02	2.0	0–6
July	39	9	4.3	2.89	4.3	0–14

of abundance of their prey (Brinton and Townsend 1980). Some *M. japanica*, however, including individuals both large and small, were found in this region throughout December. Like *M. thurstoni*, winter catch data are not comparable because of differences in fishing effort, when *M. japanica* is apparently caught less frequently.

Mobula munkiana
Notarbartolo-di-Sciara 1987
Local name: tortilla

Twenty-four specimens, 10 males (DW range 686–900 mm) and 14 females (719–1,097 mm), were caught at four stations (Punta Arena de la Ventana, Ensenada de los Muertos, Bahia de los Frailes, and Isla El Pardito) and adjacent waters, between December 1982 and October 1984. Size-frequency distributions for *M. munkiana* (Fig. 10) revealed that female mean size was greater than male, although not significantly (*T*-value = 1.724, df = 22, $P > 0.1$). Seasonal differences in size-frequency distribution could not be examined because *M. munkiana* were only collected during the fall and winter. All 10 freshly captured specimens were weighed (size range: 686–1,097 mm DW; 4.1–11.8 kg). Their WT/DW relationship is described by the following equation:

$$WT = 1.041 / 10^{-6} (DW)^{2.34}$$

$$r = 0.95.$$

WT is given in kg, DW in mm.

The largest specimen in the sample, a female, was one of the largest "tortillas" ever seen. There are no data on size at birth, as no embryos were found. Lack of knowledge of the size of the young of the year also prevented insight on size segrega-
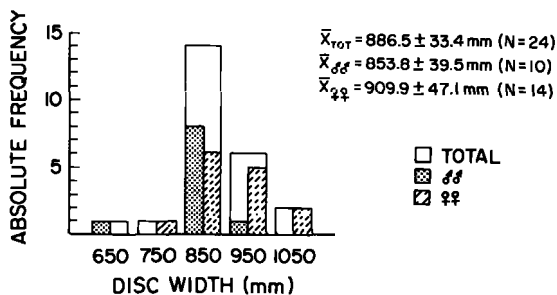
tion. Term-embryos in *M. rochebrunei*, a closely related, similar sized species from west Africa, were 340–350 mm wide (Cadenat 1960). Since *Mobula* at birth has a DW of about 1/3 of the adult, size at birth would be about 350 mm DW. This information argues in favor of size segregation in *M. munkiana*. Male to female ratio was 0.71 ($N = 24$), insignificantly different from 1 (χ^2 test $P > 0.05$). Both sexes were caught in the same net sets, indicating that males and females school together, and that there was no sex segregation, either geographic or behavioral.

A dried, twisted male carcass, for which morphometrics could not be obtained, with a calculated DW of 895 mm, had long, well-developed claspers, markedly protruding beyond the pelvic fins. Based on other mobulid species, this condition indicates sexual maturity. A second specimen, with a disc 686 mm wide, had small and pliable claspers, and the ratio between clasper length and pelvic fin length, both measured from tip to anterior margin of vent, was 0.88. At this ratio, both *M. thurstoni* and *M. japanica* are immature. Two *M. munkiana*, 871 and 872 mm DW, differed greatly in the relative size of their claspers: one possessed slightly longer claspers than the pelvic fins (ratio = 1.10), and an incipient hardening of the cartilage was apparent; in the other specimen the claspers were much shorter than the pelvics (ratio = 0.84), and still soft. This information suggested that male sexual maturity in *M. munkiana* began at about 870 mm DW.

The largest female specimen was sexually mature, as it had a large, flaccid left uterus, and the enlarged left ovary consisted mainly of about 30 macroscopic ova (size range 2–15.2 mm).

Ten stomachs were examined: four were empty, three contained unidentifiable whitish matter, and three were full of planktonic crustaceans. A list of prey species ranked by decreasing %IRI is given in Table 6. *Mysidium* sp. appeared to be the main staple of *M. munkiana*'s diet. *Mobula munkiana* is thus similar to the wintering young of *M. thurstoni*. One of the stomachs contained coarse coral fragments and small gastropod shells, perhaps ingested by the ray while foraging on mysids near a sandy substrate. The west African species *M. rochebrunei* appeared to have similar feeding habits, as Cadenat (1960) found mysids and a few larger postlarval stomatopods in the stomachs of several specimens.

I have no record of remoras associating with *M. munkiana*. The only parasitic crustacean

FIGURE 10.—Size-frequency distributions of *Mobula munkiana* (means ±2 SE).

found was *Pupulina* cf. *minor* (Copepoda: Caligidae) from the skin.

Among *M. munkiana*'s distinguishing features are its neritic preferences combined with its social habits. This is the only mobulid species in the Gulf of California that was consistently seen in schools. It is not known whether this is a seasonal behavior, or a permanent ethological feature of the species. Schools appear as a conspicuous dark patch, sometimes a few tens of meters in diameter, as they slowly cruise along the coastline in shallow water. The presence of the school is often also highlighted by the frequent, simultaneously leaping individuals, which betray its position from a long distance. Similar behavioral traits (schooling and leaping) have been reported for two closely related species from the Atlantic, *M. hypostoma* (Bancroft 1829; Coles 1910, 1916a) and *M. rochebrunei* (Cadenat 1960). During leaps, *M. munkiana* occasionally reached a height of about two DWs. Two types of leaps were observed: rising vertically head first and landing flat with the belly on the sea surface with a loud clap (breach), and spinning one to three times around the main transverse body axis (somersault).

A salient feature of *M. munkiana*'s ecology in this area is its winter occurrence when all other mobulids are absent or at their lowest numbers. *Mobula munkiana* apparently subsists then chiefly on the mysid shrimp, *Mysidium* sp., which is also the main food for young wintering *M. thurstoni*. However, *M. munkiana* frequents the area occasionally in summer: two specimens were caught by surface gill net in Bahia de la Ventana in July 1983. Even during the season in which it is most abundant, *M. munkiana* is seen in "pulses", as its occurrence at any particular location is spotty. It may occur in large numbers at one location for a few days, and then be absent for 1 or 2 weeks. This observation suggests the possibility that *M. munkiana* lives in large concentrations, perhaps composed by several schools, which travel along the coast. A similar phenomenon was observed off the Senegal coast by Cadenat (1960) in *M. rochebrunei*, a species which is closely related to *M. munkiana* both morphologically and ecologically.

It is conceivable that mobulids in the northern half of the eastern tropical Pacific mate and give birth in summer, based on the few term and near-term embryos found in summer in *M. thurstoni* and *M. japanica*, and from anatomical evidence of mating activity in adult males *M. thurstoni* and *M. japanica*. That such a hypothesis can also be extended to *M. munkiana* is supported by lack of reproductive activity in any of the specimens collected during the fall or winter, and that new-born and young-of-the-year are missing from the sample. This evidence corroborates the hypothesis that the local waters are a wintering ground for *M. munkiana*, which then migrates into an unknown area (perhaps the northern Gulf of California) during the warmer season for mating and pupping.

The possible causes of this ecological difference between *M. munkiana* and the other mobulids are many, and open to speculation. Mysid abundance may be declining in summer in the southern Gulf of California, and *M. munkiana* perhaps migrates to areas where this crustacean or related species abound during the warmer season. Alternatively, *M. munkiana* could be excluded from this region in spring by competition with the incoming, larger *M. japanica* and adult *M. thurstoni*. Finally, *M. munkiana* may be moving during the summer into an area which is more suitable for its reproductive needs. Unfortunately, this recently discovered species is very little known, and it has been reported only from the Gulf of California and Ecuador, although its distribution probably extends to other coastal areas of the tropical east Pacific (Notarbartolo-di-Sciara 1987).

TABLE 6.—Prey species found in three stomachs of *Mobula munkiana* ranked by decreasing Index or Relative Importance (symbols as in Table 2). Identifiable copepod species included *Undinula vulgaris*, *Rhincalanus nasutus*, and *Scolecithrix danae*. The stomatopods found were "erhithrus" larvae. One unidentified food item was a fragment of a larger crustacean, probably an euphausiid.

Prey species	N	%N	M	%M	%F	IRI	%IRI
Mysidium sp.	293.40	97.80	287.40	95.80	100.00	19,360	97.84
Stomatopod larvae	4.65	1.55	9.06	3.02	66.67	304	1.54
Copepoda	1.59	0.53	1.44	0.48	66.67	67.3	0.34
Other	0.37	0.12	2.10	0.70	66.67	54.7	0.28

Mobula tarapacana (Philippi 1892)
Local name: vaquetilla

Mobula tarapacana is not a common species in the study area. Seven specimens were collected, one of which, a premature male embryo, was expelled by a large female while she was being landed. Of the postnatal individuals, two were male (DW range 2,476–2,494 mm), and four were female (2,704–3,052 mm). All were caught in Bahia de la Ventana between 9 June and 30 October 1983. All but two of the specimens were weighed. The following equation describes the WT/DW relationship for *M. tarapacana* (where WT is given in kg, DW in mm):

$$WT = 2.378 \times 10^{-8}(DW)^{2.92}$$

$$r = 0.998.$$

Although all sampled postnatal *M. tarapacana* were large, smaller individuals are known from the area, as can be seen in photographs taken at Punta Arena de la Ventana in summer 1981 (courtesy Felipe Galvan Magaña, CICIMAR, La Paz, Mexico; also Greg B. Deets[3]). This information argues against geographical size segregation of *M. tarapacana*. Data on the embryo provide no indication of size at birth, since it was still far from term. Pale pigmentation was apparent only around the head and pelvic regions, and the external yolk sac was present (Fig. 5B). The embryo, expelled tail first, was alive at birth. Judging by its size it had filled the left uterus completely and must have been the sole developing embryo.

The small size of the sample does not permit any clear inference on size at sexual maturity for *M. tarapacana*. Some indication, however, can be obtained by comparison with similar species. Of the two postnatal males, the specimen with a disc 2,476 mm wide appeared to be immature: no seminal fluid was found in the ducti deferentes, the testes were small and apparently little developed, and the ratio between clasper length and pelvic fin length was 0.94. Conversely, the second postnatal male, with a disc of approximately the same width (2,494 mm), possessed claspers longer than pelvics (ratio = 1.14), and the testes were well developed. Thus, sexual maturity in male *M. tarapacana* begins around a DW of 2,400–2,500 mm.

The specimen with a DW of 2,704 mm, one of two nonpregnant females, had a bulky left ovary, containing numerous large eggs; the largest, 32 mm in diameter, weighed 12 g. Similar features appeared to be associated with sexual maturity in female *M. thurstoni* and *M. japanica*. The left ovary of another specimen, DW 2,831 mm, was smaller, and the diameter of the largest ovum was 18.6 mm, indicating that a DW of 2,700–2,800 mm denotes a transitional stage for female *M. tarapacana*, in which both mature and nonmature individuals can occur.

Twelve echeneidids were recovered from *M. tarapacana*. Three were *Remora remora* (size range: 108–229 mm SL), and nine were *R. albescens* (74–159 mm SL). The following crustacean parasites were also found: one cymothoid isopod (still in an unidentifiable aegathoid stage) and *Pupulina flores* (Copepoda: Caligidae) on the skin, *Entepherus laminipes* (Copepoda: Cecropidae) on the branchial filter plates, and *Eudactylina* sp. (Copepoda: Eudactylinae) in the gills.

Mobula tarapacana is strictly a summer and fall visitor to this region (Fig. 6C). This species is often found farther from the coast than *M. thurstoni* and *M. japanica*, and may have more pelagic habits. Four of the five stomachs examined (all from specimens caught in summer) were almost empty. Only traces of food were found among the folds of the stomach epithelium. Prey included four species of copepods (*Acartia* sp., *Pontella* sp., *Temora discaudata*, and *Undinula vulgaris*), hiperiid amphipods, one brachiuran (family Calappidae), one euphausiid, two caridean decapods (one of which belonged to the family Alpheidae), megalopa and stomatopod larvae, and a fish egg. The fifth stomach, from a late October capture, contained the remains of 27 fishes (probably carangids 15–30 cm long, and a smaller anchovy-like species). Small tetraodontids had been found before in the stomach of a *M. tarapacana* caught in Bahia de la Ventana (Felipe Galvan Magaña[4]). On this basis it is impossible to determine whether *M. tarapacana* is a specialized ichthyophagous ray, with the few crustacean items accidentally ingested while swimming, or a generalized feeder. The mesh size of this species' branchial filter plates is indeed greater than in other *Mobula* species (Notarbartolo-di-Sciara 1987). However, filter-

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[3]Greg B. Deets, Long Beach State University, CA, pers. commun. 1984.

[4]Felipe Galvan Magaña, CICIMAR, La Paz, Mexico, pers. commun. 1983.

feeding on planktonic crustacea still appears to be a feasible foraging technique for *M. tarapacana*, judging from the size of its branchial sieve as it compares with the average-sized crustacean prey.

SUMMARY AND CONCLUSIONS

Four species of *Mobula* were found in the southern Gulf of California. The most abundant species, *M. thurstoni*, was present year-round, but only the smaller individuals were seen during the winter. The bulk of the population, including the adults, appeared in early spring. Numbers began declining in July. *Mobula japanica*, the second most abundant species, was comprised of only large individuals; numbers progressively increased from March throughout July. Large *M. japanica* were rare in winter, but were occasionally caught then. *Mobula tarapacana* is the rarest mobulid in the area, yet its presence as a summer and fall visitor is well known and predictable; it is believed by the local fishermen to be more abundant farther offshore. All three species share a similar pattern of peak summer seasonal abundance. The reverse is true for *Mobula munkiana*, it being most abundant in winter, and almost totally absent during the rest of the year. It is not known where any species goes when not seen in the area. Seasonal migrations within the epipelagic habitat to different areas of the Panamic region are likely, but unverifiable because of the present lack of knowledge of the occurrence of identified *Mobula* species south of the Gulf of California. Alternatively, devil rays may spend part of the year in midwater, or near the sea bottom, therefore disappearing from sight and reach.

There is a striking similarity between the array of mobulid species found in the Gulf of California (and probably along the Pacific coast of tropical America) and the mobulid fauna from the tropical waters off west Africa. The family is represented in both areas by *Manta birostris* and by four species of *Mobula*: *M. thurstoni*; *M. japanica* (reported from west Africa as *M. rancureli* by Cadenat 1959); *M. tarapacana* (reported as *M. coilloti* for African waters by Cadenat and Rancurel 1960 and Stehmann 1981); and a small gregarious form, represented in the Gulf of California by *M. munkiana* and off west Africa by the closely related *M. rochebrunei* (Notarbartolo-di-Sciara 1987). Tropical coastal areas off west America and west Africa are known to be among

the most productive tropical waters in the world, because of comparable large-scale atmospheric and oceanographic circulation patterns (Sverdrup et al. 1942). It is conceivable that the ecological similarity between these two regions is reflected in similar faunal associations, especially as far as low levels of the tropic chain (e.g., plankton-feeding vertebrates) are concerned.

The Gulf of California presents a unique environment in the eastern Pacific Ocean, with extreme annual water temperature ranges, wind-induced mixing and upwellings, and subsequent great productivity (Roden 1964; Brusca 1980). Upwelling is caused along the peninsular coast by the southerly winds prevailing during the warmer months. This environment apparently creates optimal conditions for the existence of the euphausiid shrimp *Nyctiphanes simplex*, which is found in great abundance in the neritic habitat between spring and midsummer, before the intense August heat causes a decline in its numbers (Brinton and Townsend 1980). The following data are combined in Figure 6 to provide an overview of the possible relationship between the seasonality of predator and prey in the study area: a) the relative importance of *Nyctiphanes simplex* and *Mysidium* sp. in the diet of *M. thurstoni*; b) the relative abundance of *N. simplex*; the occurrence of *M. tarapacana* (c) and *M. munkiana* (d) in the catch; and the relative abundances of *M. japanica* (e) and *M. thurstoni* (f) (no data on the biology of *Mysidium* sp. are available).

Young *M. thurstoni* and all *M. munkiana* examined in winter appeared to subsist largely on *Mysidium* sp., whereas adult *M. thurstoni* and *M. japanica* caught during the warmer months fed exclusively on *N. simplex*. An extreme degree of feeding specialization was evident in all mobulid species in which quantitative analyses of the stomach contents was possible; most prey forms, other than *N. simplex* and *Mysidium* sp., were so rare that they were probably ingested accidentally. Stenophagy was linked to feeding specialization in another myliobatiform species, the mollusk-feeder *Rhinoptera bonasus* (Schwartz 1966; Smith and Merriner 1985). These results suggest that devil rays are highly efficient in locating and selecting their preferred food. They may be aided during this behavior by their prey's habit of swarming. Competitive interaction is to be expected between sympatric species-pairs which are closely related both taxonomically and ecologically. Food-resource partitioning is known to occur in sympatric species-pairs of skates

(McEachran et al. 1976). This condition, however, is not necessarily true when the sought-after resources are not in short supply (Zaret and Rand 1971). This may be the case of *M. thurstoni* and *M. japanica* feeding together on *N. simplex* when the abundance of euphausiids is at its peak. Competition should occur, however, in late summer, when prey numbers decline. It would be interesting to determine whether the slight morphological and behavioral differences between potentially competing species pairs (*M. thurstoni/ M. munkiana* in winter, *M. thurstoni/M. japanica* in spring and summer) influence or reflect partitioning of their habitat when food resources become limiting, as was described for both freshwater (Werner and Hall 1977) and marine teleosts (Hixon 1980; Larson 1980).

This overview of the ecology and natural history of mobulids in the Gulf of California is based on field investigations made chiefly in 1983, a year in which the El Niño perturbation was particularly severe (Cane 1983). Although in terms of fishermen's experience the year 1983 was not unduly different, as far as mobulid relative abundance and seasonality are concerned, the abnormally high water temperatures resulting from El Niño may have affected the devil rays studied in subtle ways; therefore this investigation should be repeated in a normal year.

According to the fishermen, the abundance of sharks (mostly carcharhinids and sphyrnids) on which their activity is based is declining. This decline will probably result in an increase of mobulid fishing effort. It is of concern that 72% of the specimens of *M. thurstoni* caught were immature (DW <1,500 mm).

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