ECOLOGY AND BEHAVIOR OF THE MANATEE (*Trichechus manatus*) IN FLORIDA

HARTMAN

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ECOLOGY AND BEHAVIOR OF THE MANATEE (*Trichechus manatus*) IN FLORIDA

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FOREWORD

MANATEES are members of an obscure order of aquatic mammals known as the Sirenia and are believed to be descendants of the same ancestor from which the elephants evolved. Living representatives of the Sirenia include three species of manatees (West Indian, *Trichechus manatus*; Amazonian, *T. inunguis*; and West African, *T. senegalensis*) and their marine relative, the dugong (*Dugong dugon*). A fifth species, a toothless 25-foot kelp-feeder from the Bering Sea named Steller's sea cow (*Hydrodamalis gigas*), was exterminated by fur sealing expeditions within a quarter century of its discovery in 1741.

Present-day sirenians are tropical or subtropical in distribution. Esteemed for their succulent flesh, they are harpooned and netted wherever unprotected and, as a result, have been reduced to rare or endangered status throughout most of their range (Bertram and Bertram, 1973).

Little is known of the ecology and behavior of sirenians. The paucity of information on their natural history can be attributed to their phlegmatic, retiring habits and to their inaccessibility in coastal shoals and turbid rivers. Most of the literature on the behavior of manatees and dugongs is founded on studies of captive animals. Field reports are mostly speculative and fragmentary, being limited to observations from above the surface of the water.

Manatees have been effectively used as agents of aquatic weed control (Allsopp, 1960, 1961, 1969; Anonymous, 1961, 1964, 1973, 1974; Sguros, 1966; MacLaren, 1967). They also have been suggested as a potential source of protein to help alleviate world food requirements (Anonymous, 1917; Pirie, 1967; C. Bertram and G. Bertram, 1968). Until more data are available on the reproductive physiology and population dynamics of manatees, however, it is premature to envision managing and utilizing them on a large scale for weed clearance or meat production.

In the United States, sirenians are represented by a single species of manatee (*Trichechus manatus* Linnaeus) confined, with rare exceptions, to peninsular Florida and the coast of Georgia. The behavior of these manatees, apparently isolated in the North Temperate Zone, is distinguished by seasonal cold-induced congregations in warm-water refugia. Some of these refugia are fed by limpid springs, the only places in the world, to my knowledge, where sirenians can be observed underwater with relative ease. It was this consideration that prompted my research.

This study is a contribution of the New York Cooperative Wildlife Research Unit and is based on a doctoral dissertation submitted to Cornell University. I am grateful to my former advisor, James N. Layne, for the idea of the study and to the members of my graduate committee at Cornell, Daniel Q. Thompson, William C. Dilger, and David Pimentel, for their suggestions and criticisms. In addition, I would like to thank Joseph C. Moore for reviewing my original proposal; Daniel B. Ward, Dana Griffin, David Hall, Joanne Gaudsmith, Jack van Breedveld, J. Stephen Davis, and Harold Humm for identifying aquatic plants; Stephen G. Zam for analyzing a manatee fecal sample; Carter R. Gilbert for identifying a species of shark; and David K. Caldwell, Earl S. Herald, and Kenneth S. Norris for their counsel.

Among the many Florida residents who contributed information or donated their time to work directly with me, I am particularly obligated to Harold Watson, Ed Collinsworth, Charlie Barnes, Bonnie Bonsall, Brownie Searle, Sharell and Richard Howze, and the late Gary Morrison. I wish especially to acknowledge the cooperation and friendship of Jim Macbeth, Margaret Cole, Violet Stewart, and Tom McQuarrie. I am also indebted to Robert M. Ingle who placed the services of the Florida Board of Conservation at my disposal and to Rudi Wolter who generously provided me with an outboard-powered runabout for the duration of my work. Buddy Powell who assisted me throughout the study deserves separate thanks.

Lastly, my greatest debt is to my wife, Maggie, whose continuous encouragement and good cheer made research bearable under the often merciless West Florida sun.

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INTRODUCTION

THIS study was conducted primarily in Citrus County on the central west coast of Florida. Research was focused on the headwaters of the Crystal and Homosassa rivers where clear springs of constant temperature afforded ideal conditions for above- and underwater observations of periodic cold-induced congregations of manatees during the winter months. The study was conducted from 1 October 1967 to 31 March 1969.

Following completion of the study, I returned twice to Florida to engage in further manatee research. In the winter of 1970–71, I spent a month at Crystal River and a month at Blue Springs Park on the St. Johns River, Volusia County. From November 1972 to January 1974, I conducted a study of the manatee's distribution and status in the United States, operating from headquarters at Crystal River. Many new discoveries relating to the ecology and behavior of manatees were made during these subsequent visits to Florida. These discoveries, most of which were made outside Citrus County, have been incorporated in the present paper.

HABITATS

CITRUS County lies within the terraced Coastal Lowlands subdivision of the Coastal Plain Province (Vernon, 1951). The immediate coastal belt consists of relatively undisturbed mangrove keys, salt marsh islets, and labyrinthine waterways. The region is underlain by Tertiary limestones and is a discharge area of the artesian ground water system of central Florida.

The general study area extended from the Chassahowitzka River on the south to the Withlacoochee River on the north, and lay roughly between latitudes 28°40′ and 29°00′ N (Fig. 1). The floor of the Gulf of Mexico in this area is a gently rolling shelf that slopes gradually seaward. At low water, depths of less than 2 meters occur as far as 10 kilometers offshore. The floor is broken by oyster reefs, shell deposits, limestone outcrops, and sandbars (Vernon, 1951). Although many bars are exposed at low tide, depths of up to 3 meters occur in the interbar waters and in the cuts through the oyster reefs (Dawson, 1955). In contrast, the inshore or "back-swamp" waters that flow through the network of islands are exceptionally shallow, averaging approximately 0.5 meter in depth at mean low tide (Dawson, 1955).

According to the Tide Tables of the U.S. Coast and Geodetic Survey, the diurnal tidal range is 1 meter. Maximum tidal fluctuations of more than 2 meters have been recorded. Tides tend to be higher in summer under prevailing west and southwest winds, and lower in winter when east and northeast winds predominate.

Salinity values within the study area range from 0.0 parts per thousand (ppt) in the rivers to normal sea water (35.0 ppt) offshore. At the mouths of rivers salinity characteristics are, of course, estuarine. Dawson (1955) recorded a mean salinity of 16.0 ppt in Crystal Bay at the mouth of the Crystal River over the period September 1951 through August 1952.

The coastal waters off Citrus County support extensive submarine meadows of the seagrasses *Thalassia testudinum, Syringodium filiforme,* and *Ruppia maritima. Halophila engelmanni* and *Diplanthera wrightii* occur in lesser abundance (Phillips, 1960*a*). In addition, Phillips (1960*b*) found 46 taxa of algae, of which 25 were epiphytic. Thorne (1954) cited *Acetabulum, Caulerpa, Gracilaria, Halimeda, Hypnea, Penicillus, Polysiphonia, Sargassum,* and *Udotea* as typical associates of the marine spermatophytes and *Melobesia farinosa* as a common epiphyte on *Thalassia.* The distribution of the seagrasses seems to depend primarily on salinity. *Thalassia, Syringodium,* and *Halophila* favor offshore marine conditions; *Diplanthera* and *Ruppia* thrive in inshore bays and estuaries of diluted salinity (McNulty *et al.,* 1972).

The coastline of Citrus County consists of an intricate maze of thousands of islands, which, like the margin of the mainland, are part of a vast salt marsh that extends along the coast well beyond the confines of the study area. The flora of the marsh is dominated by needle rush (*Juncus roemerianus*), cordgrass (*Spartina patens*), and saw grass (*Cladium jamaicense*). Frequent hardwood hammocks characterized by cabbage palm (*Sabal palmetto*), red-bay (*Persea borbonia*), magnolia (*Magnolia virginiana*), wax-myrtle (*Myrica cerifera*), swamp holly (*Ilex cassine*), yaupon holly (*Ilex vomitoria*), and red-cedar (*Juniperus silicicola*) interrupt the flat monotony of the land. The marsh is dissected by many shallow coves, small lagoons, and meandering tidal creeks.

A few kilometers inland, coastal flatwoods replace the savannah.

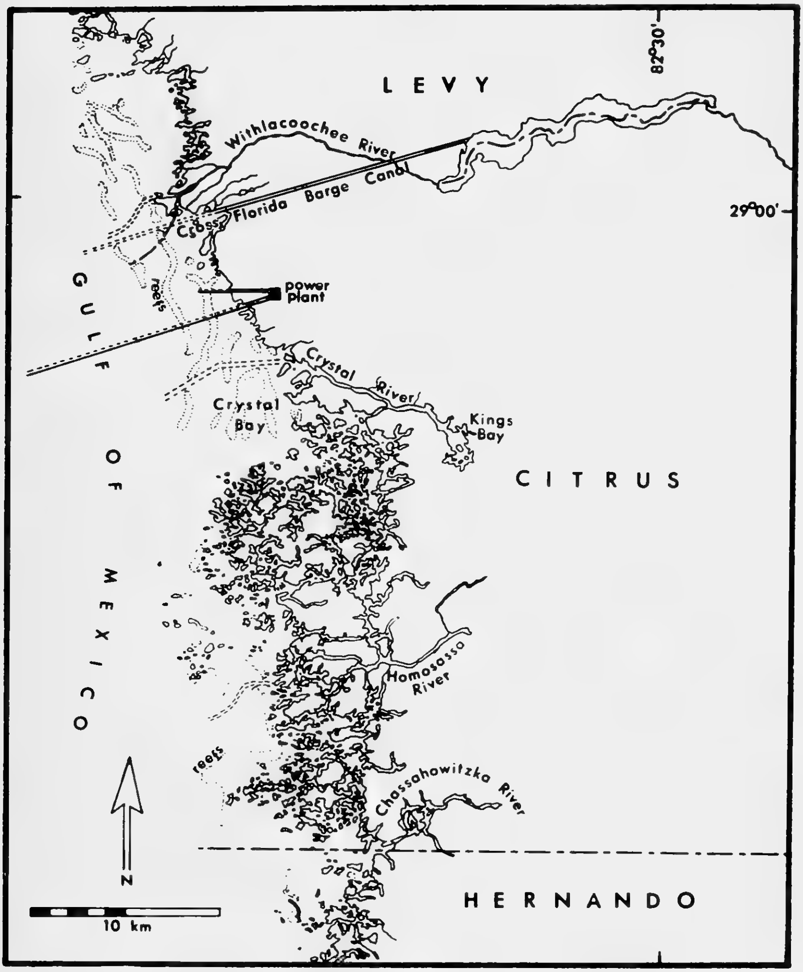


FIG. 1. Map of the study area.

This forest surmounts a limestone escarpment that is directly connected with the artesian water of the Floridan aquifer (Vernon, 1951). From the escarpment arise three spring-fed rivers—from north to south, the Crystal, the Homosassa, and the Chassahowitzka (Figs. 1 and 2).

The physical, chemical, and biological properties of the large springs feeding these rivers have been analyzed by Furguson *et al.*

FIG. 2. Aerial views of manatee habitats in Citrus County: A, headwaters of the Crystal River (arrow indicates site of Main Spring).

(1947), Odum (1957), Wetterhall (1965), and Mann and Cherry (1969). The total daily output of the springs fluctuates with the tides and with seasonal rainfall. Of the three artesian rivers, the Crystal discharges the greatest volume of water. The combined output of its springs averages 2.25 million kiloliters (600 million gallons) of water per day, more than four times that of the Homosassa's waters and more than six times the flow of the Chassahowitzka (Mann and Cherry, 1969).

The northern boundary of Citrus County is formed by the Withlacoochee River, which flows into the Gulf 10 kilometers north of the Crystal River. Midway between the mouths of the two rivers the Florida Power Corporation has dredged an intake and a discharge canal for a generating plant. An uninterrupted spoil bank bordering the intake canal projects 4 kilometers into the Gulf from the mainland. The entrance to the Cross Florida Barge Canal lies a kilometer south of the mouth of the Withlacoochee.

Fig. 2 (cont.) B, headwaters of the Homosassa River. Coastal forest is dominated by cabbage palm (*Sabal palmetto*), bald cypress (*Taxodium distichum*), live oak (*Quercus virginiana*), red maple (*Acer rubrum*), red-cedar (*Juniperus silicicola*), magnolia (*Magnolia virginiana*), red-bay (*Persea borbonia*), and wax-myrtle (*Myrica cerifera*).

Of the five major stream types in Florida recognized by Beck (1965), spring-fed rivers such as the Crystal, Homosassa, and Chassahowitzka are classified as calcareous streams, as distinct from sand-bottomed streams like the Withlacoochee. The Withlacoochee, in fact, differs strikingly from the other rivers in Citrus County. Whereas the Crystal, Homosassa, and Chassahowitzka rivers are all less than 13 kilometers in length, the Withlacoochee reaches more than 100 kilometers into the Florida interior and is fed as much by surface runoff as by artesian water. Also, whereas the three spring-fed rivers of the study area are mostly broad, straight, and shallow, the Withlacoochee is comparatively narrow, winding, and deep. It averages 25 to 30 meters in width and has a controlled depth of 3 meters at mean low water. A channel for small craft has been cut through the bars from its mouth to offshore waters. Twenty kilometers upstream from the Gulf, a flood control dam presents an insurmountable barrier to manatees. Unlike the relatively clear waters of the spring-fed rivers, those of the Withlacoochee are darkened by tannic acid. Nonetheless, aquatic vegetation grows profusely along the banks of the river below the dam. The dominant species of submerged vascular plants found in the Withlacoochee were *Hydrilla verticillata, Elodea densa, Ceratophyllum demersum, Myriophyllum spicatum,* and *Ruppia maritima. Potamogeton pusillus* and *P. illinoensis* occurred in isolated patches. Natant vegetation on the Withlacoochee consisted principally of *Eichhornia crassipes* and *Salvinia rotundifolia.*

Of the three spring-fed rivers in Citrus County, the Chassahowitzka is the smallest, shortest (9 kilometers), and shallowest. Except for a channel 2 to 3 meters in depth in its lowest reaches, it is exceedingly shoal, with depths rarely greater than 1 meter at low tide. No access channel has been dredged from offshore waters to the mouth of the river.

The Homosassa River is longer (12 kilometers) and deeper than the Chassahowitzka. It consists of a chain of bays linked by narrows. Before reaching the Gulf its waters merge with a series of branch waterways that are actually tidewater extensions. A natural offshore channel 2 to 5 meters deep leads to its mouth. The depth of the river at mean low water ranges from 1 to 3 meters. The main boil at the river's headwaters is the feature of a tourist attraction. The Halls River, a spring-fed tributary entering 1 kilometer downstream, is unnavigable.

The Crystal River enters the Gulf of Mexico 15 kilometers north of the Homosassa. The Crystal varies in breadth from 100 to 200 meters and flows 11 kilometers from its headwaters to the Gulf. From its mouth a channel 18 meters wide has been dredged through the oyster bars offshore to permit the passage of small craft. The channel's controlled depth at mean low water is 2 meters. Maximum depths of the river range from 2 to 4.5 meters at low tide. Six-and-a-half kilometers upstream, a shallow tidal creek, the Salt River, diverts a portion of the Crystal River's backflow to the southwest and connects circuitously with the Homosassa River. At its head, the Crystal River expands into Kings Bay.

During normal tidal cycles, maximum flow in the main channel of the Crystal River is approximately 112 cubic meters per second (m^3/s) (Mann and Cherry, 1969). Velocities higher than 6 kilometers per hour (km/hr) have been recorded in gaps at the mouth of the Crystal and in the Salt River (Dawson, 1955). During hurricanes, the Crystal River's flow has been estimated at more than 280 m^3/s (Mann and Cherry, 1969).

The mineral content of water in the Crystal River is subject to wide variation. The concentration of dissolved solids, principally sodium chloride, is dependent on both seasonal and diurnal tidal cycles. During a two-and-a-half year period from 1964 to 1966, the concentration of dissolved minerals in the river fluctuated between 300 and 15,000 milligrams per liter (mg/l) (Mann and Cherry, 1969).

The focus of my study was on Kings Bay, the headwaters of the Crystal River (Fig. 2A). The bay, an area of roughly 165 hectares, is bordered by the town of Crystal River. Commerical fishermen and charter boatmen have operated out of Crystal River for more than 60 years. It is only within the last 15 to 20 years, however, that the shorelines of Kings Bay and the river itself have been altered by canal excavations, landfills, and the building of sea walls.

The center of the town is situated near the northeast corner of Kings Bay. Much of the remainder of the bay is surrounded by real estate subdivisions. During the study, dredges were often at work somewhere on the bay or up one of its canals. In some places silt produced by dredging reduced underwater visibility to 1 meter, whereas, in the larger springs, visibility normally exceeded 30 meters. The consensus of local residents was that the bay and river were much clearer before housing development.

The floor of Kings Bay is permeated by hundreds of springs (Fig. 3), the largest of which, the Main Spring, is the principal site of the manatee congregations. Where limestone is not exposed, the bay floor is of sand and muck, with a mean depth of between 2 and 3 meters.

The shallow, relatively clear waters of Kings Bay are conducive to the growth of submerged aquatics. Species identified included *Ceratophyllum demersum, Myriophyllum spicatum, Potamogeton pectina-*

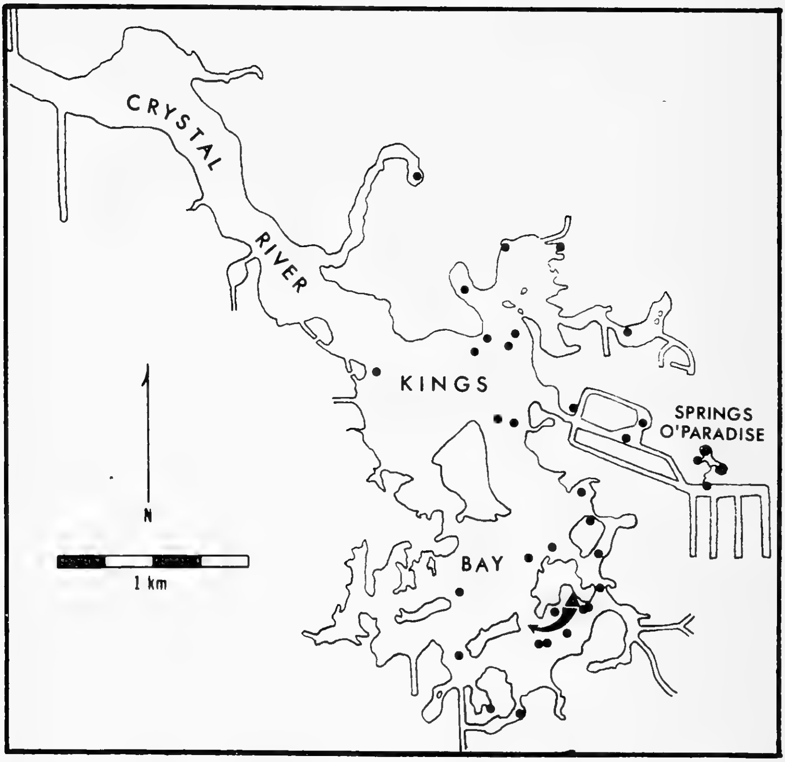


FIG. 3. Map of Kings Bay and the upper reaches of the Crystal River showing the locations of the Main Spring (solid triangle) and other major springs (solid circles). Arrow indicates course of Main Spring run.

tus, P. pusillus, Ruppia maritima, Zannichellia palustris, Najas guadalupensis, Vallisneria neotropicalis, Elodea densa, and *Hydrilla verticillata.* Of these, *Hydrilla, Myriophyllum,* and *Vallisneria* were most abundant. Their distribution is shown in Fig. 4.

To determine the percentage frequency of occurrence of the dominant species of submerged aquatics in the Crystal River headwaters, the floor of Kings Bay was systematically sampled during the last two weeks of October 1968. The bay was divided into a grid with 493 coordinates. At each coordinate a pole was dropped perpendicularly to the bottom and the species of aquatic(s) touching the pole recorded. Percentage frequency of occurrence of the

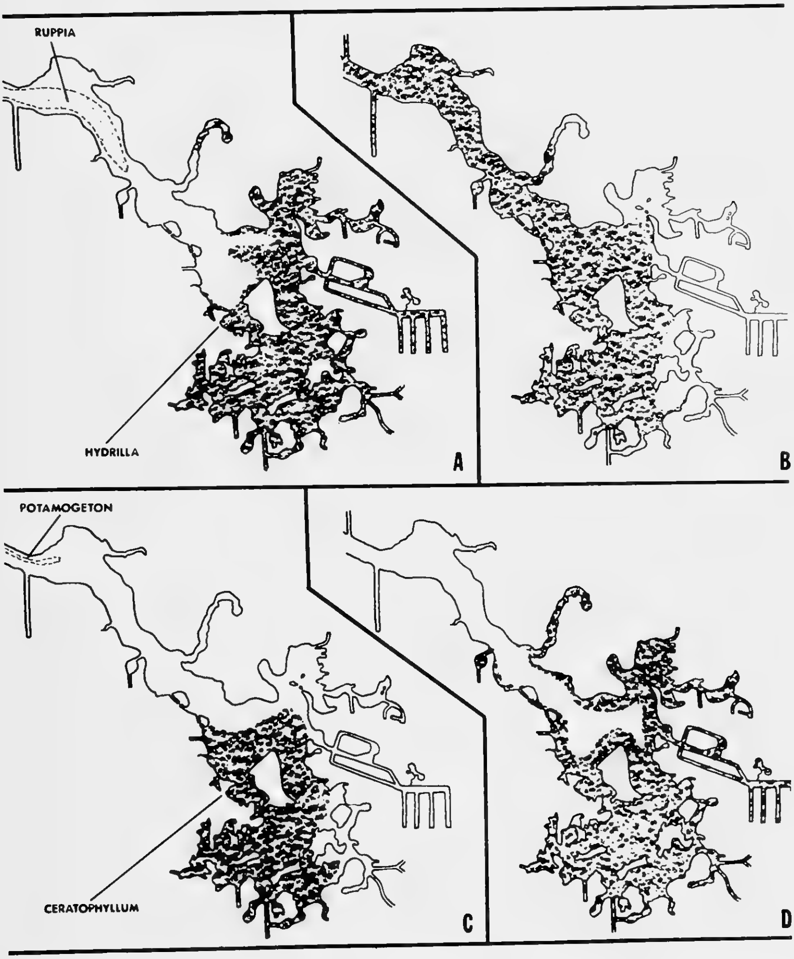


Fig. 4. Distribution of important submerged aquatic plants in Kings Bay and the upper reaches of the Crystal River: A, elodea (*Hydrilla verticillata*) and widgeongrass (*Ruppia maritima*); B, Eurasian water milfoil (*Myriophyllum spicatum*); C, coontail (*Ceratophyllum demersum*) and sago pondweed (*Potamogeton pectinatus*); D, wildcelery (*Vallisneria neotropicallis*).

six most important species are given in Table 1. The results indicated that *Hydrilla* had by far the greatest biomass. *Myriophyllum, Vallisneria,* and *Ceratophyllum,* although nearly as ubiquitous as *Hydrilla,* occurred in more widely scattered stands.

TABLE 1

PERCENTAGE FREQUENCY OF OCCURRENCE OF THE SIX MOST IMPORTANT SPECIES OF SUBMERGED AQUATICS IN KINGS BAY AS DETERMINED FROM 493 SAMPLING POINTS.

Species	Per cent
Hydrilla verticillata	40
Myriophyllum spicatum	14
Ceratophyllum demersum	14
Vallisneria neotropicalis	5
Najas guadalupensis	<1
Potamogeton pectinatus	<1

The submersed vegetation of the bay and river is in a state of flux. Both *Hydrilla* and *Myriophyllum* were introduced and have erupted to nuisance levels within the last 20 years. They appear to be gradually replacing *Vallisneria.* No explanation for the sudden eruption of "weeds" has been accepted, although it is known that nutrient enrichment from septic tank seepage is fertilizing the bay. The Citrus County Health Department has found coliform bacteria concentrations higher than 2,400/100 ml only 200 meters from the Main Spring. Throughout Kings Bay, muck and silt from dredging and from the decomposition of the adventive vegetation are rapidly covering the sandy floor.

During the peak of annual growth in August and September, *Hydrilla* formed virtually impenetrable walls that wove upwards in the spring runs from depths as great as 4 meters. At the surface, rafts of detritus, filamentous algae, and floating aquatics collected in its canopies. Beds of *Hydrilla* often created a false bottom on the bay floor, lending a deceptive impression of the true depth.

Myriophyllum is more tolerant of brackish water and predominated in the river. It, too, grew to heights of 4 meters and in areas of dense growth presented a formidable jungle of stems. During summer, its floral bracts were emersed and trapped mats of surface vegetation. *Myriophyllum* seemed to be encroaching slowly into fresher water. Specimens were found throughout the bay.

Ceratophyllum was confined to Kings Bay and also appeared to be increasing. Local residents reported that it was absent or scarce in the bay prior to 1960. At the time of the study, it grew as high and as densely as *Hydrilla* in some areas.

Vallisneria was found scattered over the bay floor in association with other rooted aquatics. It was supposedly the dominant species before the invasion of *Hydrilla* and *Myriophyllum.*

Of the remaining six species of submerged aquatic plants, none contributed significantly to the total biomass of the bay's flora. *Najas guadalupensis* was most prevalent but was highly restricted, whereas *Potamogeton pectinatus, P. pusillus, Ruppia maritima, Zannichellia palustris,* and *Elodea densa* were scarce.

In the upper reaches of the river, submerged aquatic vegetation, particularly *Myriophyllum,* grew at all depths. *Najas* and *Potamogeton pectinatus* were more abundant there, and pastures of *Ruppia,* invading from the Gulf, extended almost to Kings Bay. Below its confluence with the Salt River, the Crystal River deepens, and vascular aquatic vegetation becomes exclusively littoral. The lower reaches of the river supported only *Ruppia* and *Myriophyllum.*

Water hyacinth (*Eichhornia crassipes*) was the dominant floating aquatic and was present in nuisance proportions on Kings Bay and the river. Rafts of hyacinths, subject to the vicissitudes of winds and tides, littered the bay, choked inlets, and piled up along the shore in all seasons. Other natants included *Pistia stratiotes, Lemna perpusilla,* and *Azolla caroliniana.*

Algae were abundant in the bay and river. Planktonic and filamentous species proliferated through the summer. A superficial survey of the filamentous *aufwuchs* community of Kings Bay yielded four dominant genera—*Enteromorpha, Cladophora, Oscillatoria,* and *Spirogyra.* Clumps of bottom-dwelling *Hydrodictyon reticulatum* were discovered beside the Main Spring. In the river, there was an annual turnover of species. During winter, cold-tolerant *Ectocarpus* invaded the upstream waters as the warm-water green algae died off.

Aquatic plants from the other two spring-fed rivers in Citrus County corresponded to the flora of the Crystal River. A small cluster of *Nymphaea mexicana* in the Homosassa River was anomalous. Nonvascular vegetation was not sampled in the Homosassa and Chassahowitzka rivers.

PROCEDURES

In winter, the focus of my attention was on the Crystal River headwaters where I snorkeled with manatees approximately three hours every day and spent the remainder of my time observing them from vantage points on land or patrolling for them in an outboard-powered runabout. These procedures were sometimes followed at night.

Underwater observations were conducted with the use of simple snorkel gear (snorkel, face mask, and flippers). For insulation I wore a rubber dry suit over a full wet suit. At all times I carried a 35-mm Nikonos camera and a waterproof chronometer. Notes were made with pencil on a sheet of opaque polyethylene plastic and later transcribed.

Snorkeling was usually conducted from the boat. I would locate manatees, anchor nearby, and swim to them. Occasionally I waded into the water directly from the shore.

When on patrol in the boat, I surveyed the river from its source to its mouth but concentrated my search in the spring-fed headwaters. When located, manatees were approached close enough to

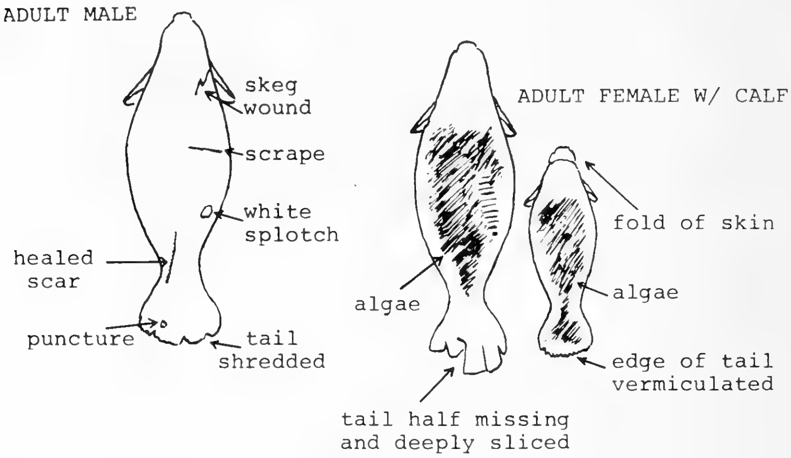


FIG. 5. Sample page from field notes illustrating method of recording identifying marks on manatees.

FIG. 6. Adult male recognizable by pattern of propeller scars on his back (photo by James Powell, Jr.).

be identified through a glass-bottomed bucket, then followed at a distance so as not to interfere with their behavior. A small aluminum punt was used to patrol waters beyond the Crystal River. At least once a week, I surveyed the headwaters of the Homosassa River.

An attempt was made to recognize all manatees encountered underwater. For this purpose, size, shape, and marks of the kind used by Moore (1956) for above-water identification were most helpful (Figs. 5 and 6). These included notches and tears in the tail and scars on the body inflicted by the propellers and skegs of outboards. Algal growth and barnacles, tumors and lesions, and incrusted areas on the epidermis were also useful in recognizing individual animals. Identification often was facilitated by the coloration of animals, which ranged from gray to brown. Recognition of most individuals was reinforced by behavioral traits. There was wide variation in individual temperaments, and a few animals could be identified exclusively by their behavioral idiosyncrasies.

During summer, I shifted my interest from the Crystal River headwaters to the Gulf of Mexico and to the activities of manatees outside fresh water. Surveys by boat and airplane and over a hundred interviews were conducted along the coasts of Citrus, Hernando, and Levy counties. In 1973 the aerial surveys and interviews were expanded to encompass all of peninsular Florida and the coast of Georgia. More than 150 hours were spent in the air reconnoitering manatee habitat, and nearly 1500 persons were interviewed.

In the course of the study, approximately 900 hours were spent in contact with manatees. Of this total, 330 hours involved underwater observations.

Efforts to tag a manatee with an ultrasonic transmitter failed. I had hoped to attach a pinger to at least one animal and follow its movements day and night from a fishing boat. I experimented with latex "armbands" slipped over the flippers and with foam-rubber "belts" attached around the juncture of tail and torso. I conducted these trials on five of the tamer manatees—three adults, a juvenile, and a calf. In each instance the animal became irritated by the encumbrance and removed it by scratching, rubbing, or thrashing.

CHARACTERISTICS OF THE WINTER POPULATIONS IN THE HEADWATERS OF THE CRYSTAL AND HOMOSASSA RIVERS

Numbers

SIXTY-THREE manatees were identified in the Crystal River headwaters during the winters of 1967–68 and 1968–69. Thirty-five of these animals appeared in both winters. Of the remaining 28 manatees, 15 were present only during the winter of 1967–68 and 13 showed up only during the winter of 1968–69. At least 16 manatees identified during the winters of 1967–68 and 1968–69 were present in Kings Bay during the winter of 1972–73. Seven manatees were identified in the Homosassa headwaters in 1968–69.

Local guides and fishermen unanimously agreed that manatees were more numerous in Citrus County than at any previous time. The findings of this study corroborated their claims of a high manatee count. The maximum number of manatees observed in a winter congregation in the headwaters of the Crystal River was 38 in 1967–68, 44 in 1968–69, 45 in 1972–73, and 44 in 1973–74. The maximum number seen in the headwaters of the Homosassa River was seven in the winter of 1968–69, 13 in 1972–73, and 17 in 1973–74. The cow-calf ratio was also indicative of a healthy population: out of a total of 21 adult females identified at Crystal River, eight were accompanied by calves, five gave birth, and at least four were pregnant in the course of the study.

The growth of the Citrus County population is correlated with the recent eruption of aquatic vegetation, although it has not been proved that an increase in manatees has resulted from this factor. Dredging of canals for housing developments on the Crystal and Homosassa rivers has created new travel routes that, when colonized by aquatic plants, provide additional grazing grounds for manatees. The waterways of Citrus County currently supply manatees with a surfeit of food.

Age Composition and Sex Ratio

In the absence of more precise aging criteria, animals were divided into three simple age classes: calf, juvenile, and adult. A calf was defined as any animal associating with its mother. By this definition, it is possible for calves to be older and larger than precocious juveniles. Calves seen at Crystal River ranged in length from 1.4 meters (±one week old) to approximately 2.4 meters (±20 months old). Any independent animal was considered a juvenile or an adult. Juveniles were separated from adults on the basis of size and sexual behavior. Walker (1964) suggested that manatees less than 2.5 meters long are "probably sexually immature." My own observations and measurements support this suggestion, but I would emphasize that the 2.5-meter length is arbitrary. The transition from juvenile to adult is gradual; thus assignment of "borderline" individuals to a particular age class was, in the absence of behavioral observations, subjective. Three juveniles measured underwater had an average length of 2.3 meters with a range of 2.2 to 2.4 meters. The average length of three adults was 2.9 meters with a range of 2.7 to 3.0 meters. It appears that the transition from juvenile to adult is usually made at a length of from 2.5 to 2.7 meters. Females less than 2.6 meters in length never were observed in estrus and lacked the distended teats characteristic of postpartum females, all of which were longer than 2.6 meters. Males less than 2.6 meters tended to have a weaker appetitive drive toward estrous females than did mature males. In play, furthermore, females seemed to allow juvenile males liberties that were denied adult males (see section on social behavior).

Although adult females tended to be bulkier than adult males, there was no significant variation in their respective lengths as best I could judge from observations of animals resting abreast.

During the winter of 1967–68, six calves, 13 juveniles, and 31 adults were present at one time or another in the Crystal River headwaters. In the winter of 1968–69, 11 calves, 11 juveniles, and 26 adults appeared. The seven manatees observed in the Homosassa River in 1968–69 all were adults.

The population of manatees in the Crystal River had a sex ratio of 25 females to 25 males in the winter of 1967–68 and 25 females to 23 males in the winter of 1968–69. The sexes of manatees in the Homosassa River were not determined.

COLD-INDUCED CONGREGATIONS

By inhabiting waters in a temperate zone, Florida manatees are subject to a risk not shared by their tropic-dwelling congeners. Periodically, manatees face harsh winter temperatures in Florida. Reports of dead animals washing ashore in the wake of severe freezes are evidence that manatees succumb to extreme cold (Bangs, 1895; Cahn, 1940; Hamilton, 1941; Gunter, 1942; Krumholz, 1943; Moore, 1951*a,* 1956; Layne, 1965). It is interesting that all manatee deaths attributed to freezes have been reported from areas that lacked warm-water refugia.

When possible, manatees seek refuge from cold in springs or in the warm waters discharging from factory cooling systems (Moore, 1951*b,* 1956; Layne, 1965; Hartman, unpublished manuscript). Loose congregations of manatees gather in these sanctuaries and remain for the duration of the cold spell.

Headwaters of the Crystal and Homosassa Rivers

Congregations that form at the head of the Crystal and Homosassa rivers are illustrative of this phenomenon (Figs. 7, 8, and 9). According to local residents, the gathering of manatees in the headwaters of these rivers is an annual winter event. The head of the Crystal River, in fact, appears to be the principal congregating site for manatees along the central part of the west coast of Florida. During a prolonged freeze, Kings Bay would provide ideal circumstances for survival. The Homosassa River headwaters, by comparison, are narrow and shallow, and attract comparatively few manatees (Fig. 9).

The Chassahowitzka headwaters are inaccessible to manatees because of the shallow depth. Individuals present at the mouth of the Chassahowitzka in summer did not overwinter there.

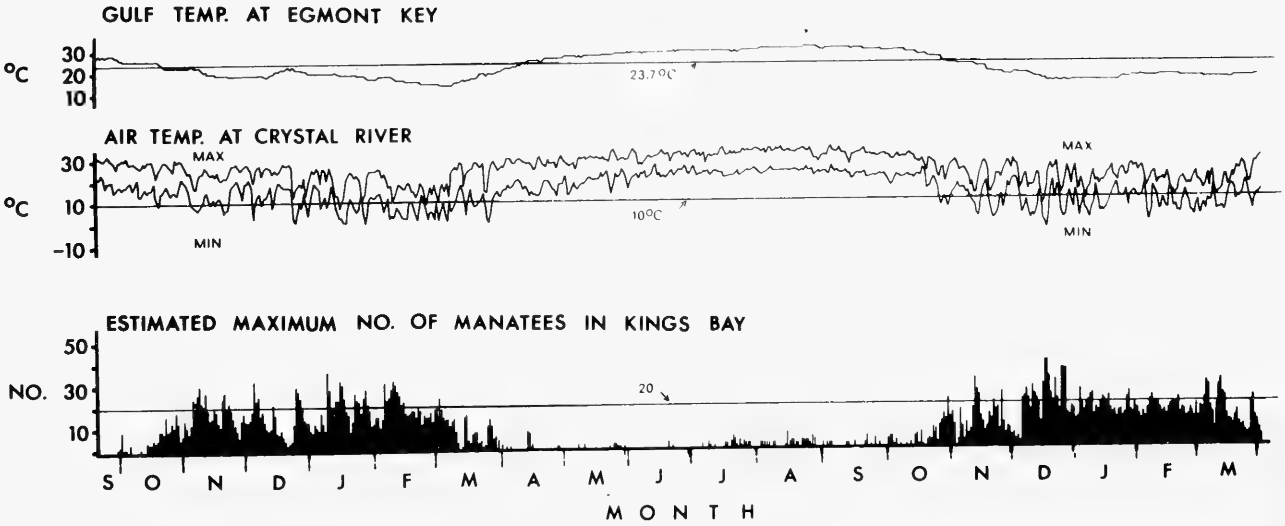
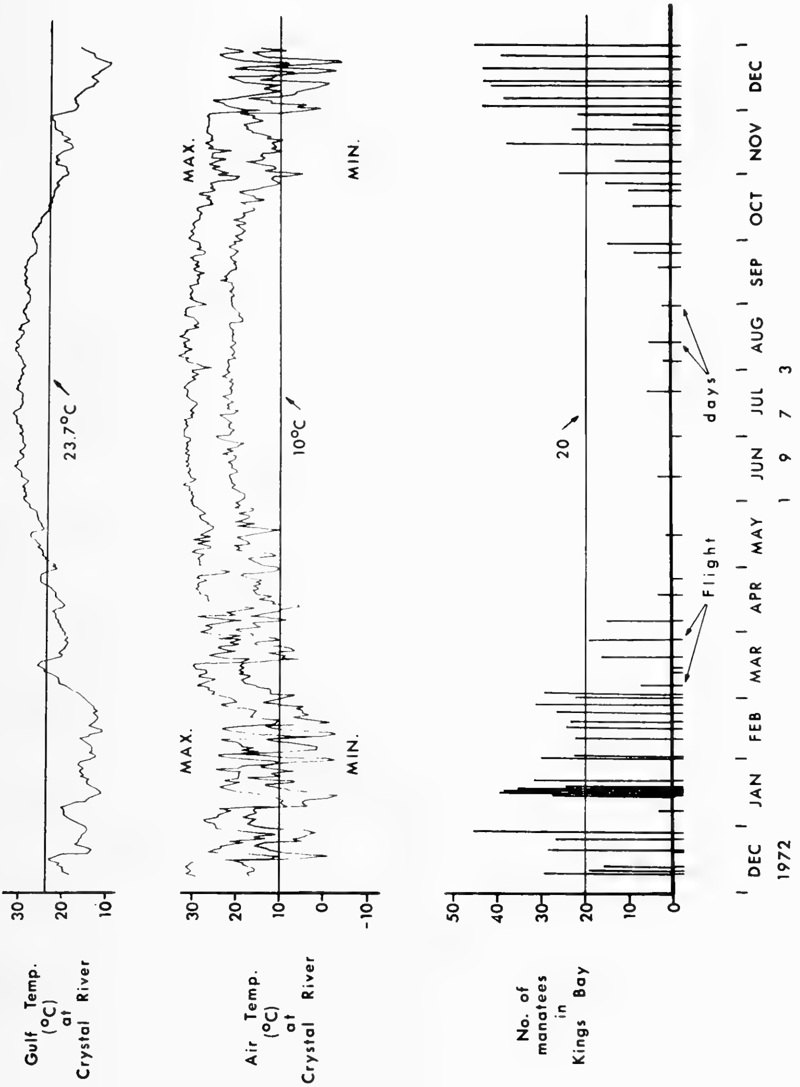


FIG. 7. Relation of number of manatees in Kings Bay to water temperatures of the Gulf of Mexico at Egmont Key and air temperatures at Crystal River during the period 21 September 1967 to 1 April 1969.


Gulf Temp. (°C) at Crystal River
30
20
10
23.7°C
Air Temp. (°C) at Crystal River
30
20
10
0
-10
MAX.
MIN.
MAX.
MIN.
10°C
No. of manatees in Kings Bay
50
40
30
20
10
0
20
Flight days
DEC
1972
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
1 9 7 3

On the other hand, manatees have started to capitalize on the warm waters in the new outflow canal of the Florida Power Corporation generating plant just north of the Crystal River. From time to time, fishermen and company employees reported manatees in the discharging waters at the head of the canal.

Manatees began to appear regularly in Kings Bay with the arrival of cold weather in October and November. At that time the temperature of the Gulf coastal waters gradually fell from summer highs near 30°C to lows below the constant 23.7°C of the Crystal River springs. The presence of manatees in Kings Bay corresponded with this drop in the Gulf temperature (Figs. 7 and 8). The correlation coefficient (*r*) between numbers of manatees in Kings Bay and Gulf temperatures during the winters of 1967–68 and 1968–69 was .49 which is significant at the .01 level.

Inshore waters of the Gulf are prone to rapid and extreme temperature fluctuations. Winter temperatures of the coastal waters at the mouth of the Crystal River varied from 13 to 21°C in the course of the study. In shoals removed from the warmer estuarine waters, temperatures as low as 7°C (16 December 1968) were recorded. It was the conviction of many commercial fishermen on the west coast of Florida that manatees cannot be found on shallow salt-water flats in the winter but must be sought in deep coves and bays where low temperatures are less extreme.

Throughout the winter, the number of manatees in Kings Bay on a given day is generally proportional to the air temperature. It appears that a drop in the air temperature below a certain threshold induces manatees to take refuge in warmer waters; the subsequent drop in water temperature serves only to reinforce this primary stimulus. The manatee probably becomes aware of temperature changes in the air when its nose is exposed above the surface to breathe.

Moore (1956) found that manatees congregated at a power plant in the Miami River whenever the air temperature dropped below 10°C. My own findings at Crystal River tended to agree with this figure, but is should be mentioned that air temperatures of 15°C have been known to induce congregations at a power plant in Fort Lauderdale (Fran Perlmutter, personal communication).

During the two winters of the study, the air temperature dropped below 10°C on 37 occasions. Congregations of 20 or more manatees in Kings Bay coincided with 81 per cent of these tem-

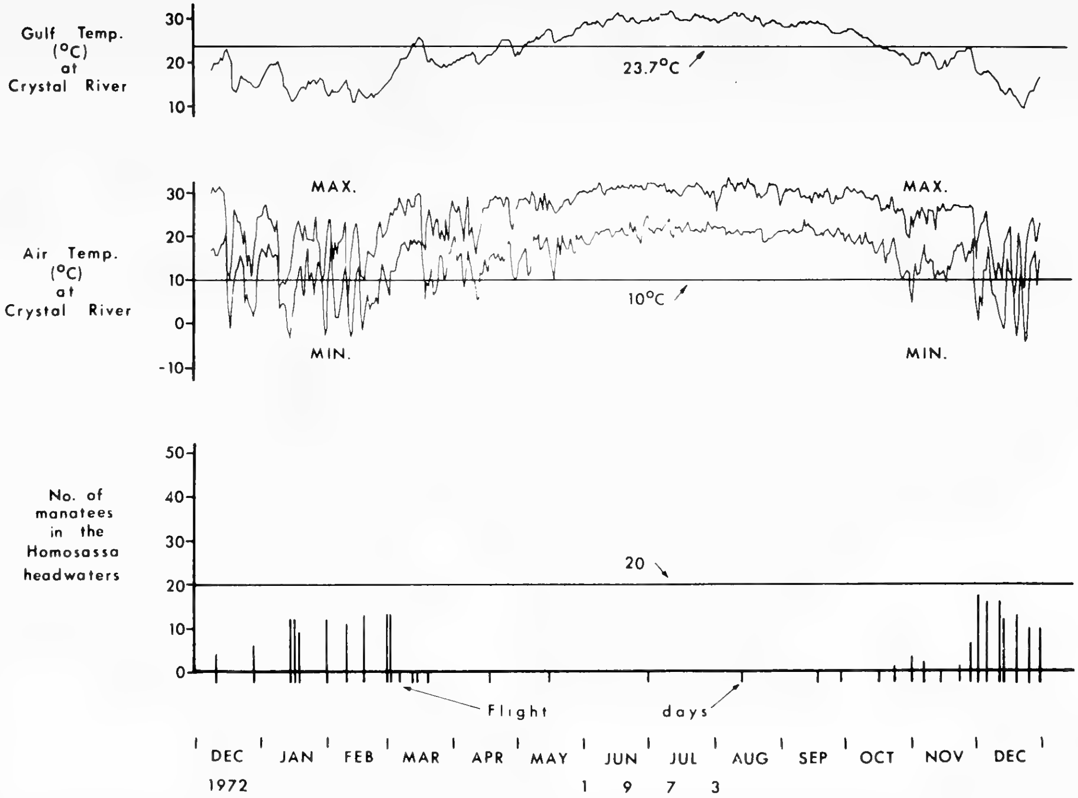


FIG. 9. Relation of number of manatees in the Homosassa headwaters to water temperatures of the Gulf of Mexico and air temperatures at Crystal River during the period 8 December 1972 to 1 January 1974.

perature lows. The manatees may acclimate to cold water as the winter progresses; whereas air temperatures of 10°C prompted congregating in November, by March, temperatures closer to 5°C were necessary to insure large manatee concentrations in the headwaters.

What is a manatee's physiological threshold of cold tolerance? Five animals were found dead in Charlotte Harbor after the water temperature dropped from 20 to 8°C during a freeze in 1940 (Cahn, 1940). According to Allsopp (1961), the manatee cannot live at ease where the water temperature is less than 21°C. This figure is not supported by my observation of manatees feeding casually in lower Tampa Bay in water as cold as 19°C. Sguros (1966) cited 16–18°C as the minimum water temperature tolerable to manatees. This estimate also strikes me as high. In January of 1973, after a week of freezing or near-freezing nights, an estrous cow accompanied by seven bulls descended the Crystal River to a point where the water temperature was 15.7°C, hesitated, then doubled back upstream. Three times during this study manatees were followed into water with a temperature of 15°C and once into water as cold as 13.5°C. Each instance involved adult animals that had left the headwaters of the Crystal or Homosassa rivers in the middle of a cold spell and were moving downriver toward yet colder water (11–13°C) in the Gulf when they were lost from sight. These manatees, all of whose identities were known, eventually returned to the headwaters in apparent good health; one reappeared several weeks after descending the river, one within two days, and two the same evening.

The attendance records of known individuals in the congregations at Crystal River provided additional evidence that the manatee's tolerance to cold is greater than has been supposed. The same complement of animals was rarely present in Kings Bay on consecutive days. Although a majority remained in the bay during cold weather, there was a constant exchange of animals between the river and the Gulf. For example, on the coldest morning of the two winters, when the air temperature dropped to −5°C, a record number of 40 manatees was counted in Kings Bay from the air. This number, however, did not constitute the full complement of animals known to occur in the area in winter, which suggests that the remainder had found sanctuary elsewhere or that they were in coastal waters. There is cause to believe that at least some were in the Gulf, for after absences of up to four weeks, often during the coldest periods in winter, manatees returned to the Main Spring covered with barnacles and marine algae, proof that they had been passing time in salt water. One adult female, for instance, was absent from Kings Bay from 21 January to 4 March 1968, during which time there were six major drops in the air temperature to below 10°C, including two consecutive nights of freezing weather. In her absence, two of the cold snaps (defined here as days with minimum temperatures below 10°C) lasted for periods of more than a week. The female finally returned to the Main Spring covered with barnacles but obviously in good condition. An adult male was not seen in Kings Bay from 4 December to 23 December 1968. Temperatures were subfreezing on the nights of December 14 through 16. He eventually returned coated with a marine algal scum. He remained at Crystal River only a few days before again disappearing for nearly two weeks.

In February 1973, after two nights of freezing temperatures, I journeyed to Gibsonton on the Alafia River (Hillsborough County) to observe the cold-induced congregation of manatees at the mouth of the "hot water" discharge (35.5°C) from the Cities Service phosphate plant. Eight to 10 animals were bottom-resting just above the discharge canal in water where the temperature fluctuated between 15.8 and 19.0°C. One kilometer above and below the discharge canal water temperatures as low as 12.3°C were recorded. Any manatee joining or leaving the congregation would have to traverse these cold waters.

It would seem, then, that manatees can endure water temperatures at least as cold as 13.5°C. Heat produced metabolically while cruising may enable the animals to tolerate water temperatures that would be unendurable were they less active. This might account for their ability to migrate in cold coastal waters during the winter. My general impression is that sensitivity to cold has been exaggerated and that, except during unseasonably cold weather, manatees bask in tepid springs less out of thermoregulatory necessity than for the salubrious sensation. The value of springs and other warm-water sources as refuges from cold is probably restricted to protracted periods of freezing or near-freezing temperatures, which are uncommon in Florida.

The mechanisms of thermoregulation in cetaceans have been studied (Tomilin, 1951; Kleinenberg *et al.*, 1964; Kanwisher and

Sundnes, 1966; Irving, 1969), but heat regulation in the Sirenia has not been investigated. In Citrus County, bottle-nosed dolphins (*Tursiops truncatus*) inhabited the same environment as did manatees but appeared to have a much broader temperature tolerance. Both manatee and dolphin have an insulating layer of blubber, but it seems only the latter is adapted to protracted stays in water colder than 15°C. The principal reason for this may be that dolphins have a higher metabolic rate and generate more heat than do manatees.

There is evidence that manatees raise their metabolic rate to increase heat production when resting in critically cold water (see section on breathing). Irving (1973) recorded a similar phenomenon among young harbor seals (*Phoca vitulina*).

A rise in the minimum daily air temperature to above 10°C usually heralded an exodus of manatees from Kings Bay. Within a day or two of the onset of a warm spell, the Crystal River headwaters were apt to be vacated by a large proportion of the congregating manatees. At such times, manatee sightings outside Kings Bay increased as the number of animals in the bay declined. In the course of one warm period (19 to 22 February 1969), animals were seen in the outlet canal of the Florida Power Corporation generating plant, at the entrance to the Cross Florida Barge Canal, and in the Withlacoochee River, 20, 25, and 30 kilometers from Kings Bay, respectively.

To account for the irregular attendance records of manatees in the Miami River congregations, Moore (1956) proposed that ". . . the number of aggregations attended by a manatee may be inversely proportional to the amount of time or energy required to reach the aggregation site from its range . . . . Beyond the maximum distance from which the cold stimulus motivates these sirenians to come to the . . . aggregation site, it seems likely that they may be stimulated to aggregate in other places." This hypothesis seems basically valid in light of findings at Crystal River. It should be noted, nonetheless, that extremely low temperatures induced the largest congregations in Kings Bay with no corresponding increase in animals in alternate congregating sites in Citrus County.

A temperature gradient exists from the Gulf to the springs of Kings Bay; the colder the Gulf, the steeper the gradient. Manatees surely follow this gradient, among other cues, in locating the Crystal River from the Gulf and in locating springs once in the river.

Even within Kings Bay, a temperature range as wide as 7°C has been recorded between the Main Spring (23.7°C) and the junction of the bay with the river.

Manatees that gathered in Kings Bay in response to low temperature concentrated their activity about the Main Spring. On a cold day, the limestone shelves and sand slopes around the Main Spring were littered with resting animals. Manatees presumably preferred the Main Spring to the myriad of lesser springs in the bay because its greater discharge maintains the surrounding water at a more uniform warmth. On cold mornings, differences of as much as 5°C were recorded between the surface and bottom waters in the run. This prompted some animals to bask suspended at the surface. Where manatees had been active, however, there was unavoidable mixing of cold bottom waters with the warmer surface layers.

Manatees habitually arrived at the Main Spring in the early daylight hours, apparently driven in by the predawn temperatures. The animals remained around the spring until disturbed by the first appearance of boats and SCUBA divers who daily dove in the cave at the source of the spring. As a result of this harassment, most of the animals would move to more sequestered reaches of the bay. As the day progressed and boating activity picked up, many left the headwaters for the river and Gulf. They returned upstream in the quiet of the night and repeated the cycle the next day.

Perhaps in response to harassment by divers, manatees sometimes frequented the major boil in the secluded Springs O'Paradise canal network (Fig. 3). A few unusually shy animals avoided the Main Spring altogether.

Blue Springs Run

In addition to the headwaters of the Crystal and Homosassa rivers, favorable conditions for viewing cold-induced manatee congregations also are found at Blue Springs Park on the upper St. Johns River, 4 kilometers west of Orange City, Volusia County. Each winter manatees take refuge here in the warm (22.2°C) waters of Blue Springs Run near its confluence with the St. Johns. In contrast to the turbid river, the clear spring-fed waters of the run provide excellent circumstances for underwater study. Cursory observations of manatees in the vicinity of Blue Springs Park were made for three consecutive weeks in December and January of 1970–71 and from mid-November 1971 to mid-March 1972.

According to park personnel, manatees appear sporadically in Blue Springs Run throughout the year, but are most likely to be seen between October and April when the temperature of the river is colder than that of the run. Virtually every morning during the winters of 1970–71 and 1971–72, at least one or two manatees were found resting in the spring-fed waters. During the day the animals tended to disperse and leave the run in order to feed in the river. They usually returned in the evening or at night. It appeared that pestering by boats and SCUBA divers stimulated them to leave and may have been partly responsible for their absence from the run during daylight.

Once in the river, the manatees swam up or downstream to favored grazing areas. In the course of observations, animals were followed by boat to feeding sites as far as 5 kilometers from the run. There is reason to believe (see section on movements) that during warming trends the manatees move much farther afield.

A total of 11 animals was identified at Blue Springs Park in the winter of 1970–71. These included one yearling male calf, three juvenile males, two adult females, and five adult males. During the winter of 1971–72, 18 different manatees were seen at least once in Blue Springs Run. Seven of these were returnees from the previous year. The group included one yearling male calf, one juvenile female, three juvenile males, two adult females, and 11 adult males.

Precisely the same group of animals was rarely present in the run on successive days. As was found at Crystal River, the number of manatees attending a congregation appeared to be directly influenced by the temperature of the air. During two days of unusually warm weather at Christmas 1970, the air temperature did not drop below 15°C, and only two manatees showed up in the run. Five days later, however, following two nights of freezing temperatures, 11 animals were present. Latecomers arrived two days after the onset of the freeze, suggesting that they had sought asylum elsewhere in the river or that they had migrated more than a day's journey from Blue Springs Park.

The 18 manatees observed during the winter of 1971–72 had highly irregular attendance records. Manatees congregated in the run in the wake of cold spells (minimum daily air temperature below 10°C), but the complement of animals in each congregation varied unpredictably from cold spell to cold spell. A manatee that appeared in the run during one cold spell was often absent during the next. For instance, two manatees that were originally present in November never returned after the first warming trend of the winter, indicating they were transients in passage up or down the river. A major exodus of manatees from the run coincided with the onset of warm weather (minimum daily temperature above 10°C). Rarely were there more than five or six animals remaining or returning from the congregation formed during the previous cold snap. Only the cow with calf stayed in the vicinity of Blue Springs Park throughout the winter, a tactic, perhaps, to reduce the chance of the offspring being caught in a freeze far removed from sanctuary in warm water.

During the winter of 1971–72, the temperature of the St. Johns River at Blue Springs Park dropped from 30°C in October to a low of 13°C on 21 February. By May, the temperature had climbed back to 30°C. In general, when the water temperature of the St. Johns was lower than 16°C, manatees resting in the run seemed reluctant to seek sanctuary in the river in order to escape harassment from boats or divers. Even on weekends with exceptionally heavy boat traffic, the animals would mill around the mouth of the run in agitation rather than flee into the colder waters of the river.

The manatees rested in the lower reaches of the run and were generally found in a group, facing the current. If the weather grew uncommonly cold and the temperature of the lower run dropped to 20°C, they moved farther upstream and, during severe cold snaps, have been reported to swim the length of the run to the boil at its source. To reach the boil which is located 650 meters from the St. Johns River, manatees must buck a stiff current in a channel that, in sections, is as shallow as a meter.

MOVEMENTS

Manatees appear to be resident along the central part of the west coast of Florida in semiisolated populations that are concentrated in rivers and estuaries that are of suitable depth and provide an adequate source of food and fresh water. These populations are concentrated in three regions—the mouth of the Suwannee River (lat. 29°15′), the spring-fed rivers of Citrus County (lat. 28°40′–29°00′), and the Little Manatee and Manatee rivers (lat. 27°30′–27°45′). It appears that animals tend to favor estuarine areas, periodically moving along the coast from one river mouth to the next. Manatees seem to reside only temporarily in a particular estuary or river before returning to familiar surroundings or moving on to yet another area.

Migrations

Although I was unable to obtain positive proof that there is an intermixing of animals between populations, I strongly suspect that such an exchange takes place and that it is effected by long-range migrations. Migrations, moreover, appear to be both seasonal, in response to changes in the air temperature, and nonseasonal. These suspicions are founded on the following grounds:

1. Calves excluded, 52 manatees were identified in the headwaters of the Crystal River during the winters of 1967–68 and 1968–69. Twenty nine of these animals were present at one time or another during both winters. Of the remaining 23 animals, 13 were only seen the first winter and 10 appeared for the first time in the second winter. These data indicate that some manatees overwintered outside Citrus County and suggest that the animals have no permanent home range but take up temporary residence wherever favorable conditions are encountered.

2. Manatees never before encountered in the winter congregations at Crystal River appeared sporadically in Kings Bay, sometimes to remain, sometimes to disappear as suddenly as they had arrived. These animals were presumably transients moving north or south along the coast when attracted by the warmth of the river.

3. A severely scarred manatee that was identified in the Chassahowitzka River in summer failed to seek refuge in the Crystal or Homosassa headwaters the following winter. I assume the animal moved south because the Chassahowitzka sheltered no manatees during the winter.

4. All evidence points to the conclusion that once freed from the restrictions of winter cold snaps, manatees leave the Crystal River headwaters in spring and range along the coast in summer. The major exodus of manatees from Kings Bay began in late March and early April.

By the end of April, the headwaters were colder than the coastal waters and virtually deserted by manatees. On their departure from the Crystal River, a few animals remained temporarily in the estuarine waters at its mouth, but most migrated north or south without pause. During summer, occasional manatees visited Kings Bay in the course of their movements along the coast, but the majority of animals did not return until the autumn (Figs. 7 and 8). No animals were sighted at the head of the Homosassa River between March and November (Fig. 9).

Manatees observed in Kings Bay were positively identified outside the Crystal River on four occasions. Last seen in Kings Bay on 26 March and 14 April (1968), respectively, a juvenile male and adult female were recorded on 2 July in the Withlacoochee River, 40 kilometers away. To reach the Withlacoochee from the Crystal River, manatees must circumnavigate a spoil bank that projects 4 kilometers into the Gulf. The female had returned to the Crystal River by 25 July and was found regularly in Kings Bay until the end of August when she disappeared for a month and a half. She returned to the bay for the winter on 17 October. The juvenile was absent from Kings Bay from 26 March to 3 October. Another juvenile male that appeared in Kings Bay at intervals in July, August, September, and October of 1968 was discovered on 13 November in the Homosassa headwaters, 45 kilometers from Kings Bay. To avoid shoals between the Homosassa and Crystal rivers, manatees must migrate around St. Martins Keys at least 8 kilometers offshore. The young male returned to the Crystal River on 23 November. An adult male seen in the Crystal River on 31 January 1973 was identified in the Homosassa headwaters 10 days later. He did not reappear in the Crystal River until the following winter. On 3 July 1968, a juvenile female from Crystal River was identified at the mouth of the Chassahowitzka River, 55 kilometers from Kings Bay. She failed to appear in Kings Bay from March to October. She was accompanied by a prominently scarred adult that had been seen in the same location 24 days earlier.

5. Commercial fishermen questioned at Crystal River claimed to have seen manatees as far as 5 kilometers offshore. In every

instance animals were reported to be swimming with definite bearing. Offshore sightings were recorded throughout the year.

6. Manatees are periodically seen in locations where food resources are lacking and where their appearance is regarded as an anomaly by local residents. On rare occasions, for example, manatees turn up on the Gulf Coast of Pinellas County where turbid water discourages the growth of seagrasses. According to interviewees, the animals are usually on the move, which suggests to me that they are in transit between the rivers of Citrus County and the rivers of lower Tampa Bay.

7. In December 1973, a SCUBA diver photographed a manatee near Western Sambo Reef, 8.5 kilometers off Key West. This sighting lends credence to rumors of manatees turning up in the Dry Tortugas and is additional evidence of long-range migrations.

8. Aerial surveys in 1973 found manatees on the move at all times of year throughout peninsular Florida (Hartman, unpublished manuscript). Statewide interviews confirmed my impression that, except when compelled to seek warm water in winter cold, most manatees are nomadic, their wanderings embracing hundreds of kilometers of coastline.

9. Sightings and speculation in the literature suggest that major movements of manatees south and north along the Gulf and Atlantic coasts coincide with the beginning and end of winter respectively (Gunter, 1941, 1942; Moore, 1951*b*; Caldwell and Golley, 1965; Hartman, unpublished manuscript). In the course of this study, 15 of the 17 manatee sightings reported from Gulf waters north of Citrus County took place outside of the winter months.

In considering the migrations of manatees within the study area, it is important to remember that offshore waters are only 2 to 4 meters in depth and that scattered beds of spermatophytes occur on the bottom. Rather than cruise uninterrupted, it is likely that migrating manatees dawdle to rest and feed as they journey.

I doubt that manatees return to the same summer range year after year or that the movements of each individual follow a repetitive pattern. It appears that the animals are acquainted with the entire coast of Citrus County and beyond and that their movements, although locally delimited by shallows and the availability of food, are casual and unpredictable. The animals apparently migrate up and down the central part of the Florida west coast, pausing for days, weeks, months, or seasons in those estuaries and

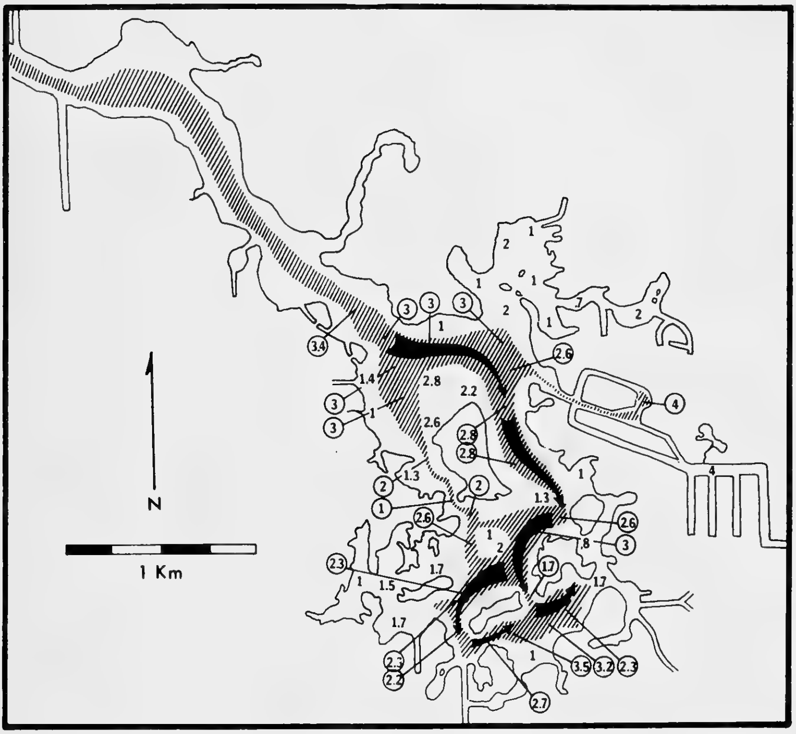


FIG. 10. Manatee thoroughfare from the Crystal River to the Main Spring in Kings Bay (arrows). Hatching indicates areas regularly utilized by manatees for normal activities. Depths in meters at mean low tide.

rivers that supply their needs. In summer, the Crystal River assumes no more importance to manatees than the Withlacoochee, Homosassa, or Chassahowitzka rivers. All four rivers harbor small, constantly fluctuating manatee populations from April to October.

In coastal waters, manatees presumably navigate by means of submarine landmarks, currents, and/or salinity and thermal gradients. Their presence in the West Indies (Miller, 1918; Ray, 1960; Erdman, 1970) suggests that they are capable of traversing waters of the bathyal zone. Manatees have been caught by fishermen up to 15 kilometers off the coast of Guyana (W. H. L. Allsopp, personal communication). Bertram and Bertram (1973) cited evidence of dugongs "island hopping" across wide expanses of sea. This would, of course, necessitate open-ocean navigation, but by what

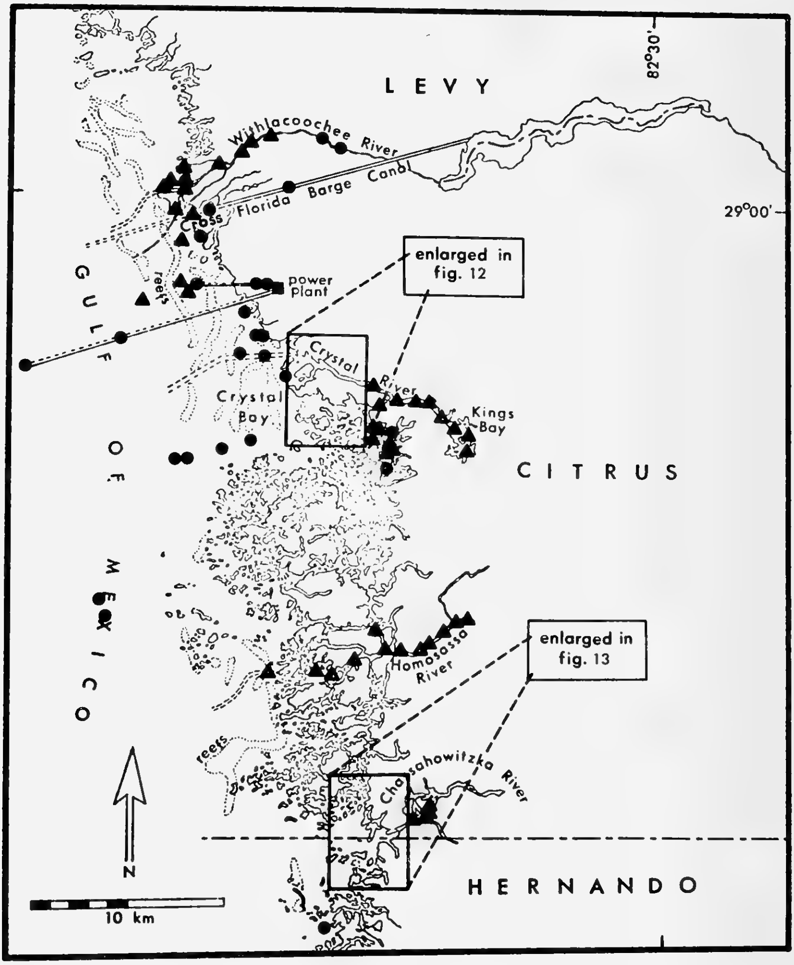


FIG. 11. Manatee sightings on the coast of Citrus County. Solid triangles represent sightings by author; solid circles, sightings by interviewees.

means sirenians orient themselves in the open sea, whether by chemoreception or other cues, is unknown.

Travel Routes

According to Jarman (1966), dugongs cruise along well-established pathways in shallow water. The first indication that manatees travel via specific routes was provided by the movements of animals in the headwaters of the Crystal River. To reach the Main Spring

FIG. 12. Manatee sightings at the mouth of the Crystal River. Solid triangles represent sightings by author; solid circles, sightings by interviewees. Depths in meters at mean low tide.

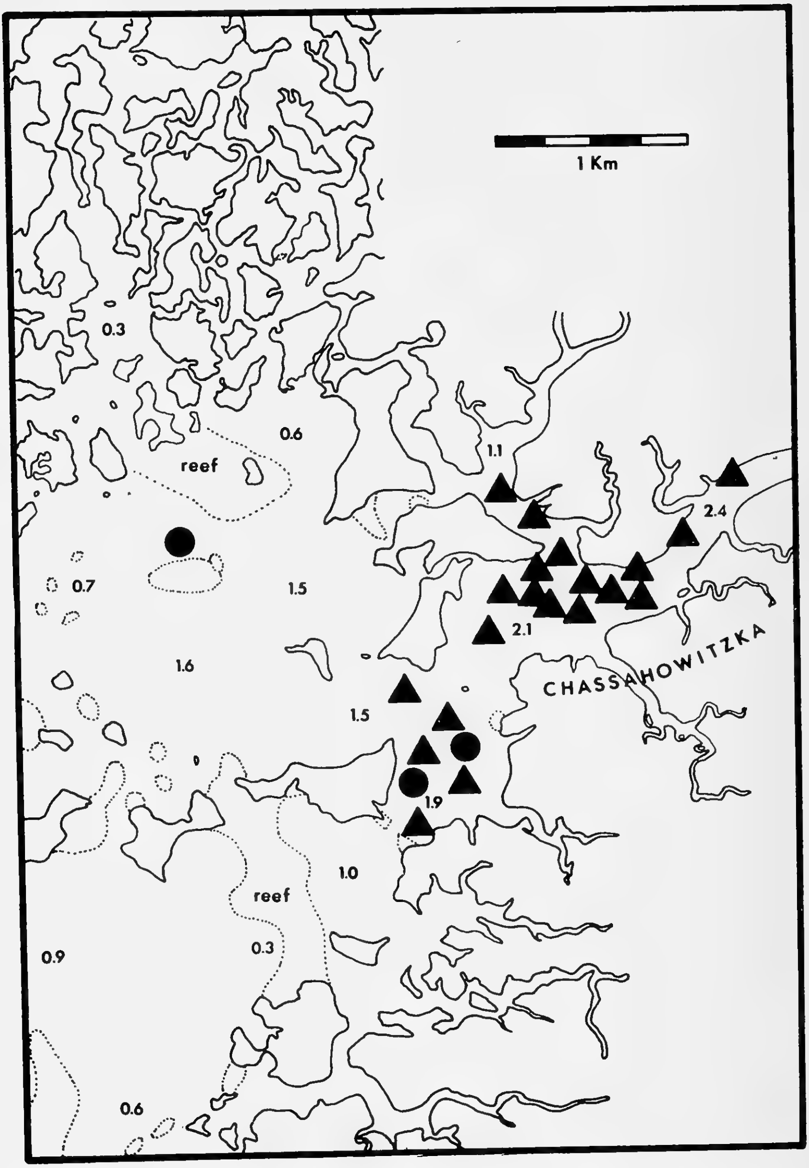


FIG. 13. Manatee sightings at the mouth of the Chassahowitzka River. Solid triangles represent sightings by author; solid circles, sightings by interviewees. Depths in meters at mean low tide.

from the river, manatees followed the deepest channels in Kings Bay (Fig. 10). These channels averaged 2 to 4 meters in depth but were as shallow as 1 meter at "bottlenecks." The major thoroughfares were served by secondary routes that, in turn, branched into smaller arteries less frequented by manatees. In the shoal coastal waters at the mouth of the river, manatees repeatedly followed the same channels among the oyster reefs and sand bars. Throughout the inshore waters of Citrus County, animals were almost always sighted in the deepest channels (Figs. 11, 12, and 13).

During their migrations along the coast, it appears that manatees also proceed via established routes determined by depth. Off shallow, low energy coastlines, migrants tend to remain well away from shore. On the coast of Citrus County, for example, all sightings of migrant manatees have been several kilometers offshore in water no less than 3 meters deep. Three migrants were seen off Indian Rocks Beach (Pinellas County) swimming 180 meters from shore. Off high energy beaches, on the other hand, manatees were always seen to swim just outside the breakers, 50 to 100 meters from the shore. If a reef was present offshore, the animals generally swam between the reef and the breakers. In calm weather, manatees were occasionally seen directly over reefs. Jetties were circumnavigated. One animal was observed 250 meters offshore heading around a jetty at Ft. Pierce Inlet (St. Lucie County). In shallow sections of the Intracoastal and Okeechobee waterways, manatees migrate via the channel dredged for boats.

Exploratory Activity

At Crystal River it was not uncommon for manatees to leave familiar routes to explore less frequented reaches of their habitat. It would appear that the young especially profit from exploration; calves accompanying their mothers are exposed to the shoals, cul-de-sacs, and other limits of their environment. A highly disproportionate surplus of males in cold-induced congregations at Blue Springs Park, near the terminus of the species range in the St. Johns River, suggests that male manatees may roam farther than do females, and thus are more likely to be encountered in peripheral habitat.

Remote canals and inlets were often the foci of exploratory activity. One interviewee claimed to have followed a manatee as it cruised 32 kilometers round-trip from the Gulf to the first dike on the Cross Florida Barge Canal. Occupants of housing developments that front on the less accessible canal networks at Crystal River reported seeing manatees off their seawalls two or three times a year. Animals have been seen to cruise up a trunk canal exploring each successive branch canal to its end. Sometimes it seemed that a manatee was scouting for other animals when, for example, it would systematically visit one favored area of activity after another in Kings Bay.

In most areas of Florida, I suspect that manatees undertake migrations simply in response to a strong exploratory drive. It is otherwise difficult to explain their propensity to leave choice habitat. For instance, ample food and fresh water are available to manatees the year around on the coast of Citrus County, yet evidence indicates a major exodus of animals coincident with the onset of spring and a perpetual shifting of attention from river to river throughout the year. Males are perhaps stimulated to migrate in search of estrous females.

HABITAT DETERMINANTS

It was among the aims of this study to discover how various habitat factors influence the movements of manatees. The importance of climate on the behavior of these animals in Florida already has been discussed, but it was not known if manatee activity was affected by depth, tides, salinity, currents, storms, sun, turbidity, and dense vegetation. The findings of this study suggest that most of these factors modify manatee behavior.

Depth.—As indicated above, the travel routes followed by manatees are mostly dictated by the depth of the water. In the Crystal River headwaters, manatees carried on most of their activities in water 2 to 3 meters deep and normally travelled via waterways that were at least 2 meters in depth. Flats and shallows less than a meter deep were avoided unless immediately adjacent to deeper water. In Citrus County as a whole, manatees generally confined their movements to rivers, canals, and deep channels. Shallow tidal creeks that are drained at low tide were altogether ignored. In the backwaters of Everglades National Park, manatees range throughout estuarine bays averaging 1.2 to 1.8 meters in depth. In the lower St. Johns River, manatees were followed from the air as they moved along the shoreline in water 1.2 to 1.5 meters deep. In Tampa Bay, manatees were observed from the air to cruise along the declivities on the margins of shoals, favoring water 1.5 to 2 meters deep. Manatees were also seen to swim along the margins of shoals following the bottom contour and avoiding depths less than 1.5 meters on the east shore of Cape Haze (Charlotte County) and in the Indian River (Brevard County). Animals migrating along beaches swam in water 3 to 5 meters deep, apparently discouraged from entering shallower water by the turbulence of breaking waves.

Much of the range of the manatee on the east and west coasts of Florida is delimited by shallow water. On the Atlantic seaboard, the nearshore waters of the Indian River (Brevard, Indian River, St. Lucie, and Martin counties) are prohibitively shoal. Most of Mosquito Lagoon (Volusia and Brevard counties) is inaccessible to manatees for the same reason. On the Gulf coast, inshore waters are notoriously shallow, especially north of Tampa Bay. Off Pasco, Hernando, and Citrus counties, shoals confine manatees to offshore waters as much as 5 kilometers from the mainland. Shallow waters also may be a deterrent to occupancy of Florida Bay (Monroe County).

There are exceptions to the avoidance of shoals by manatees. Estrous females have been known to take shelter from pursuing bulls in waters as shallow as 60 centimeters and may even strand themselves intentionally (see section on sexual behavior). Feeding manatees have been observed to move onto flats as shoal as 50 centimeters, but always with immediate access to deeper water.

Aversion to shoals by manatees was demonstrated by their wary behavior in shallow passages. To reach the major springs in the headwaters of the Homosassa and Crystal rivers, manatees must funnel through bottlenecks in the channels. Maximum depths in the bottlenecks are between 1 and 1.8 meters. Animals approached such areas furtively and with hesitancy. Only when they had safely passed the "squeeze" did they accelerate into deep water. The slightest disturbance, such as the sound of an outboard motor, caused them to balk and turn back from their approach to a bottleneck. From a bridge over one such narrows, I once witnessed a cow and her calf balk and double back five times in four hours (during which time the tide rose 50 centimeters) before cautiously passing through. On her initial approach to the bottleneck, the cow was deterred by a fisherman who tried to hook her with a large rubber lure held dangling in the center of the passage. The cow "spooked" and fled back into deep water with her calf and two accompanying juveniles.

In deep water, manatees cruised at depths of 1 to 3 meters, usually around 2 meters. The greatest depth at which I observed a manatee was 8 meters. This was in the Main Spring where an animal dove to escape from a motorboat overhead. Water pressure may discourage the animals from descending to greater depths. In areas where depths did not exceed 3 meters, animals preferred to swim near the bottom or midway between the bottom and the surface. Venters of several bore extensive longitudinal gashes, doubtless received as the animals glided over oysters or other sharp objects.

Tides.—Tides strongly influence the movements of manatees. Low tide often denies animals access to channels that serve as thoroughfares at high tide. For instance, manatees capitalized on high tides to exit from the Salt River via a gap that was prohibitively shoal (<1 meter) at low tide. In addition, manatees took advantage of high tides to feed on the margins of shoals that were otherwise inaccessible. High tides also permit manatees to approach the shore to reach bank growth. In the turbid Intracoastal Waterway of northeastern Florida where bank grasses are the staple food of manatees, high tides dictate the hours during which animals may feed.

Stranding in the wake of an ebbing tide is extremely rare. I am aware of only two strandings that may not have been deliberate. On the east side of Sanibel Island (Lee County), a group of manatees failing to retreat with the outgoing tide were landlocked in tidal backwaters until the next high tide (Charles LeBuff, Jr., personal communication). An extraordinary incident of stranding occurred in 1969 when an adult male was found trapped in a meter-wide storm sewer in North Miami Beach.

Salinity.—Moore (1951*a*) wrote that manatees favor ". . . shallow salt-water bays and the fresh or brackish waters of sluggish, coastal rivers." The results of this study indicate that, although manatees move freely from fresh to salt water, their preferred habitats are rivers and estuaries (<25 ppt salt). During flights over the coast of Citrus County, I sighted manatees 68 times (not counting animals seen in cold-induced congregations), but only two sightings were made over salt water. On the Gulf Coast of Florida, manatee populations are concentrated in and around the major rivers from the Suwannee (Dixie and Levy counties) to Everglades National Park. On the Atlantic Coast, manatees are found in the lagoons that extend the length of the peninsula but are most often seen at the mouths of rivers or in proximity to a source of fresh water (Hartman, unpublished manuscript). Sightings of manatees off coastal beaches were comparatively rare except in the vicinity of inlets. Moreover, the majority of manatees seen in the ocean or Gulf appeared to be migrating. It seems that manatees undertake excursions into salt water primarily to move from one estuary to another. Their apparent need for fresh water is discussed in the account of feeding ecology.

Currents.—Currents have some effect on the activities of manatees. Animals bottom-resting in Blue Springs Run (Orange City, Volusia County) tended to orient along the axis of flow facing the current. In Guyana, resting manatees are reported to lie in eddies at the elbows of rivers to avoid being disturbed by the current (Datakaran Jeetlall, personal communication). In combination with other deterrents, fast currents (>5 km/hr) probably discourage manatees from occupying certain tributaries of the St. Johns River. Aerial reconnaissance revealed that, in regions where tidal waters funnel through narrow channels, fast currents pose a navigational problem for manatees. Animals migrating via the Intracoastal Waterway on the Atlantic seaboard were never seen swimming against currents that exceeded 6 km/hr. In the Intracoastal Waterway north of the Haulover Canal (Brevard County), a manatee was clocked swimming 1.5 km/hr against a current estimated at 4 to 5 km/hr.

Most of the drawbridge tenders on the Intracoastal Waterway felt that manatees were more disposed to swim along the shore than in the center of a channel, especially when faced with a swift current. Sightings from the air substantiated this opinion. In the Sebastian Inlet (Brevard and Indian River counties), currents in excess of 11 km/hr have been recorded (McCall *et al.,* 1970). Currents of such velocity surely deter manatees or force them to crowd the shore when swimming against the tide. Perhaps the animals wait for a change in the tide to slip in or out between the ocean and the Intracoastal Waterway.

At Crystal River the activities of manatees were little affected by the generally modest flow of the waters. The current in the river

(2 to 3 km/hr) was not sufficient to influence the course set by an animal. Manatees, for example, did not hug the shoreline where the rate of flow is reduced. Nor was there any indication that manatees increased their swimming efforts when countering a current; they simply took longer to cover a given distance when competing against a current than when cruising with it. Off Shell Island at the narrow mouth of the Crystal River where tidal flow was swiftest (6 km/hr), guides claimed to have seen manatees buck the current as they entered or left Crystal Bay; more often the animals chose alternate gaps where flow was reduced (4 to 5 km/hr).

If undeterred by swift currents, manatees will apparently ascend rivers as far as the depths will allow. Within the study area, manatees have been spotted as much as 20 kilometers up the Withlacoochee River. According to Moore (1951*b*), animals have also been seen 100 kilometers from the Gulf at the junction of the Suwannee and Santa Fe rivers (Gilchrist, Lafayette, and Suwannee counties). Manatees in the upper St. Johns River (Volusia, Lake, and Putnam counties) are 230 kilometers from the ocean. In Nicaragua, manatees have been observed 130 kilometers up the larger waterways (Townsend, 1904).

Storms.—Wind and rain had no significant effect on manatee activity in Kings Bay. During storms of exceptionally high winds and heavy rain, animals conducted their daily routines uninterrupted. They never responded to strong surface turbulence by seeking shelter on the leeward side of land masses. In more exposed coastal regions, however, water turbulence may play a role in the movements of manatees. According to Kingdon (1971), shelter from rough conditions is a factor determining the distribution of dugongs on the coast of East Africa. There may be a similar relation between turbulence and the predilection of manatees for inshore areas where they find protection from the heavy wave action engendered by storms. Out of 61 sightings made from the air over coastal waters, 92 per cent were on the inshore side of mainland or barrier beaches and only eight per cent on the seaward side. That storms can prove fatal to manatees was confirmed in 1972 when a live calf washed up on shore at Vanderbilt Beach (Collier County) during a strong northwester.

Sun.—It was suggested by a resident of Crystal River that the sun influences the choice of resting sites. My observations did not support this theory. On sunny afternoons a difference in water temperature existed between the bottom and the surface, but this difference was minimized by the intermixing of currents generated by surfacing manatees. Furthermore, animals bottom-rested in precisely the same location regardless of whether it was sunny or overcast and usually in the midst of silt churned up by their tails.

While observing cold-induced congregations of manatees in the turbid Miami River, Moore (1951*a*) noted that animals remained longer at the surface with backs exposed as the sun warmed the air. At Crystal River, however, there was no evidence that manatees resting suspended with backs awash were sunbathing, for this activity occurred as often on cloudy days or at night as during sunny days.

Turbidity.—Manatees showed no preference for murky or limpid water. Animals were never seen to seek camouflage or protection in turbidity of their own making.

Vegetation.—The activities of manatees in Kings Bay were considerably influenced by vegetative growth. In many sections of the bay, the animals were forced to detour around dense clumps of *Hydrilla, Ceratophyllum,* and *Myriophyllum.* Near the Main Spring animals roamed under galleries formed by *Hydrilla,* sometimes plunging headlong through walls of the waterweed and occasionally becoming deeply enmeshed. At the head of the river, animals ranged through the margins of the *Myriophyllum* beds, emerging bedecked with stalks. Normally, manatees did not hesitate to surface under mats of vegetation, respiring through the debris. Unusually dense mats of *Hydrilla,* however, discouraged manatees from surfacing and compelled them to seek openings to breathe.

DAILY ACTIVITY

THE results of this study indicate that manatees are essentially arhythmic. Individual animals observed in the headwaters of the Crystal River failed to manifest a predictable periodicity of activity. The frequency of feeding, resting, and other activities showed no consistent differences related to time of day, as suggested by the behavior of the manatees in Fig. 14. The activities of these animals was observed without interruption for periods ranging from 10.5 to 12 hours. The movements of the animals over the same period are traced in Fig. 15. Total distances covered

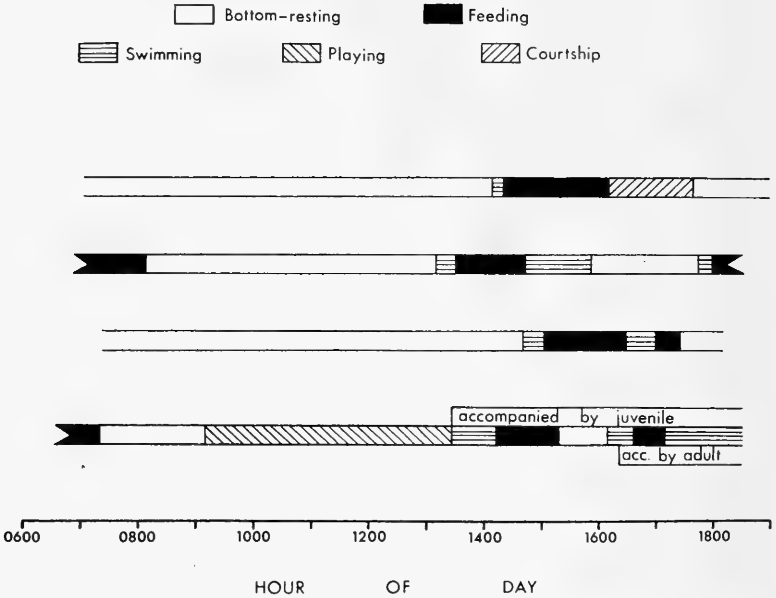


FIG. 14. Diurnal activities of manatees in Kings Bay and the upper reaches of the Crystal River: A, estrous female between 0704 and 1900 hours on 9 February 1969; B, adult female with calf between 0654 and 1832 hours on 14 January 1969; C, adult female between 0724 and 1813 hours on 6 January 1969; D, juvenile male between 0638 and 1828 hours on 23 January 1969.

in Figs. 15A through 15D are 1.5, 4, 5.5, and 12.5 kilometers, respectively. Night observations of manatees revealed no change in their activities.

Manatees occupied most of their time feeding, resting, idling, cruising, and socializing. Adult animals tended to feed six to eight hours a day in sessions that usually lasted from one to two hours. Resting consumed as few as two and as many as 12 hours a day. During cold snaps, animals were known to have spent the time from dawn to dusk resting on the bottom at the Main Spring. However, six to 10 hours resting, distributed through a 24-hour period in sessions of two to four hours, was more typical. The amount of time spent in social interactions was highly variable. In summer, solitary animals may go for days without coming in contact with other manatees. In contrast, social encounters within win-

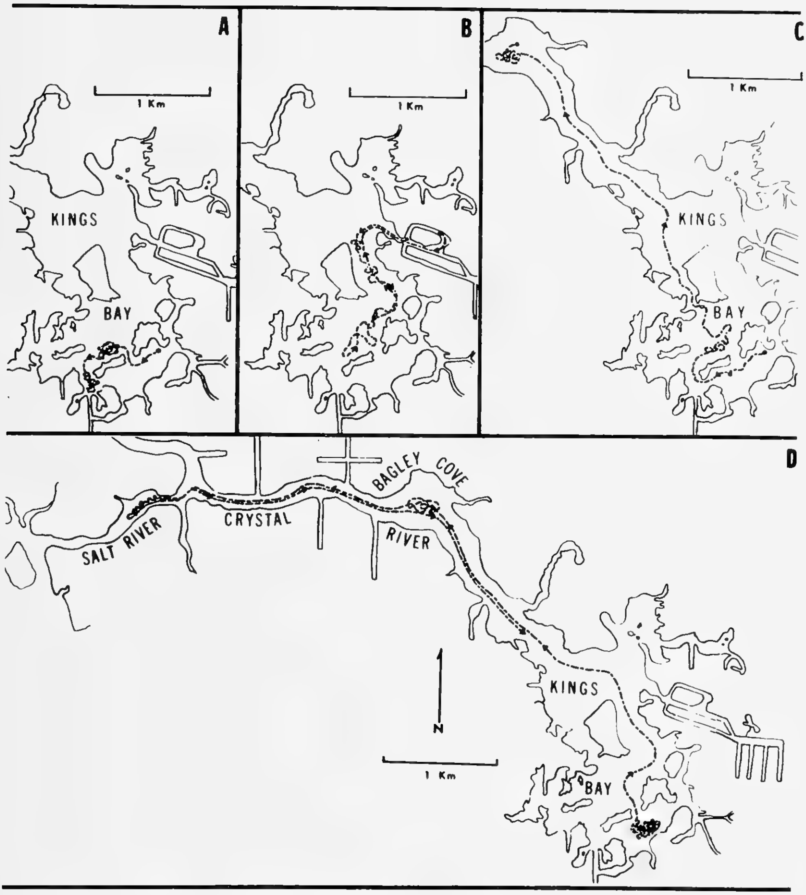


Fig. 15. Movements of manatees in Kings Bay and the upper reaches of the Crystal River: A, estrous female between 0704 and 1900 hours on 9 February 1969; B, adult female with calf between 0654 and 1832 hours on 14 January 1969; C, adult female between 0724 and 1813 hours on 6 January 1969; D, juvenile male between 0638 and 1828 hours on 23 January 1969.

ter congregations were frequent. From the shore I have watched manatees play for as long as three and a half hours, feed and rest for six hours, then resume playing. Sociality peaks in an estrous herd where a cow and her male escorts may remain together for more than a month.

FOOD HABITS

THE preceding discussion indicated that the movements of manatees in Florida are influenced by several factors, including depth, salinity, tides, currents, and access to warm water during winter cold spells. The distribution of manatees is also determined by the availability of food (Hartman, unpublished manuscript). Manatees are opportunistic feeders and have been observed grazing on a wide variety of plants both aquatic and terrestrial, fibrous and nonfibrous, vascular and nonvascular. They are even known to feed on fish. This section considers food preferences and feeding ecology.

Food Plants and Preferences

Vascular vegetation.—Captive and semicaptive manatees have been known to consume many types of vascular aquatic plants (Table 2). In addition to aquatic vegetation, captive animals have been fed lawn grass (*Poa* sp.); dandelions (*Taraxacum officinale*); sow-thistles (*Sonchus oleraceus*); palmetto fronds (*Sabal palmetto*); most of the garden vegetables, cultivated legumes, and pasture grasses; and many commercial fruits (Chapman, 1875; Murie, 1880; Crane, 1881; Coates, 1940; Gunter, 1941; Allsopp, 1961; personal observations). Bread, fish, and meat also are consumed (Crane, 1881; Mohr, 1957; Powell, 1978).

In the wild, manatees, as other herbivores, probably select plants for their palatability, digestibility, and nutritional value (Heinsohn and Birch, 1972). Allsopp (1969) found that manatees used for weed control in Guyana generally preferred submerged, floating, and emergent vegetation in that order. I found a similar tendency among manatees in Florida. Crystal River manatees fed almost exclusively underwater, virtually ignoring natant and emergent plants as a source of food. In more turbid rivers, manatees fed on submerged plants when available and, in their absence, on floating vegetation, mostly water hyacinth (*Eichhornia crassipes*). In those waterways that were destitute of aquatic spermatophytes, manatees resorted to grazing on algae and bank growth.

Within the study area, manatees were relatively indiscriminate in selection of food and generally ate whatever submerged vege-

TABLE 2

VASCULAR AQUATIC VEGETATION CONSUMED BY TRICHECHIDS UNDER CAPTIVE AND SEMICAPTIVE CONDITIONS.

Genera	Source
Submergents	
Cabomba	Allsopp, 1969
Ceratophyllum	Chapman, 1875; Allsopp, 1969
Elodea	Allsopp, 1969
Myriophyllum	Allsopp, 1969
Najas	Browder, 1967
Nitella	Allsopp, 1969
Potamogeton	Brown, 1878; Townsend, 1904; Allsopp, 1969
Ruppia	Allsopp, 1969
Utricularia	Browder, 1967; Allsopp, 1969
Vallisneria	Chapman, 1875; Allsopp, 1969
Zostera	Townsend, 1904
Natants	
Azolla	Allsopp, 1969
Eichhornia	Allsopp, 1969
Lemna	Allsopp, 1969
Mimosa	Allsopp, 1969
Nelumbium	Allsopp, 1969
Nelumbo	Allsopp, 1969
Neptunia	Allsopp, 1969
Nymphaea	Allsopp, 1969
Paspalum	Allsopp, 1969
Pistia	Allsopp, 1969
Salvinia	Allsopp, 1969
Victoria	Allsopp, 1969
Emergents	
Alternanthera	Allsopp, 1969
Hymenachne	Allsopp, 1969
Ipomoea	Allsopp, 1969
Leersia	Allsopp, 1969
Luziola	Allsopp, 1969
Montrichardia	Allsopp, 1969
Panicum	Browder, 1967
Sagittaria	Brown, 1878; Browder, 1967; Allsopp, 1969
Typha	Browder, 1967; Allsopp, 1969

tation was at hand. In fresh and brackish waters of the Crystal, Homosassa, and Withlacoochee rivers, manatees fed on the six dominant species of submerged plants—*Hydrilla verticillata, Vallisneria neotropicalis, Ceratophyllum demersum, Myriophyllum spicatum, Ruppia maritima,* and *Diplanthera wrightii.*

Hydrilla comprised the bulk of the diet in the Crystal River headwaters but was not necessarily preferred to its associates *Vallisneria* and *Ceratophyllum.* In areas where *Ceratophyllum* and *Myriophyllum* both grew, the animals showed a predilection for *Ceratophyllum.* Manatees also preferred *Ruppia* and *Myriophyllum* where they grew in association with *Potamogeton pectinatus. Potamogeton,* however, was occasionally grazed. *Najas guadalupensis,* highly localized in the rivers, was ingested incidentally. *Potamogeton illinoiensis, P. pusillus,* and *Zannichellia palustris* were found in traces in the waterways of Citrus County, but were never seen to be cropped by manatees. From interviewees it was learned that manatees fed on *Elodea densa,* which was largely restricted to the Withlacoochee River.

In salt water, manatees have been alleged to feed on seagrasses (Barrett, 1935; Krumholz, 1943; Charnock-Wilson, 1968). This was confirmed during aerial surveys over the Gulf and Atlantic coasts of Florida. I observed manatees from the air feeding on *Syringodium filiforme, Thalassia testudinum,* and *Diplanthera wrightii* (Table 3). Animals appeared to favor *Syringodium* where it grew in mixed stands with *Thalassia.* For the most part, *Diplanthera* prefers intertidal water and was not found in association with *Thalassia* and *Syringodium,* which occur only below low water levels. *Diplanthera* usually was consumed near the shore of turbid waterways that did not support beds of *Thalassia* or *Syringodium.*

There are two additional species of seagrasses in Florida, *Halophila baillonis* and *H. engelmanni.* Both are strictly limited in distribution (Phillips, 1960*a*). *Halophila engelmanni* was found growing in association with *Thalassia* at three manatee feeding sites, but it occurred only in traces close to the substrate and was apparently ignored by manatees.

Floating vegetation held little attraction for manatees in Citrus County, although I found that water hyacinth was their staple food in many rivers that lack submerged plants. At Crystal River, manatees were observed feeding on water hyacinth less than a half dozen times. All other natant vegetation, including water lettuce

TABLE 3

DEPTH, SALINITY, AND LOCATION OF SITES AT WHICH MANATEES WERE OBSERVED FEEDING ON MARINE SPERMATOPHYTES.

Plant	Water depth (meters)	Salinity (ppt)	Body of water	County
Thalassia	1.0–1.6	31	Tampa Bay	Hillsborough
	0.9–1.0	26	Charlotte Harbor	Charlotte
	1.0	29	Turtle Bay	Charlotte
	1.2–1.5	31	San Carlos Bay	Lee
	0.9–1.2	27	Lostmans River	Monroe
	1.0–1.4	34	Norris Cut	Dade
Syringodium	1.0–1.6	31	Tampa Bay	Hillsborough
	1.1	30	Indian River	Brevard
	1.4	23	Indian River	Brevard
	1.4	19	Indian River	Brevard
Diplanthera	0.8–1.0	8	Withlacoochee River	Citrus
	0.7	11	Salt River	Citrus
	0.9–1.2	31	San Carlos Bay	Lee
	0.5	35	Indian River North	Volusia

(*Pistia stratiotes*), water lilies (*Nymphaea mexicana*), and water ferns (*Azolla caroliniana*), was disregarded by the animals.

In the St. Johns River, manatees were seen to feed regularly on water hyacinth and alligatorweed (*Alternanthera philoxeroides*), but showed no interest in water lettuce. Water ferns (*Salvinia rotundifolia*) were consumed only accidentally while manatees were feeding on water hyacinth.

Citrus County manatees completely ignored emergent vegetation and bank growth. Animals observed in the St. Johns River near Blue Springs Park (Volusia County) paid no attention to spatter-dock (*Nuphar advena*), shunning even its tender submerged seedlings. At other locations, however, manatees have been known to graze on littoral aquatics and phraetophytes (Barrett, 1935; Moore, 1951*a*; C. Bertram and Bertram, 1968; Hartman, unpublished manuscript). Table 4 lists the bank grasses and forbs that manatees have been seen to feed upon in Florida. Apparently the foliage of mangroves does not appeal to manatees. Bangs (1895) reported that they fed on mangrove leaves when other food was unavailable, but no one interviewed during this study had seen manatees eating mangrove leaves. One interviewee claimed that the animals occasionally ate the floating seedlings of red mangrove

TABLE 4

BANK GRASSES AND FORBS COLLECTED FROM SITES AT WHICH MANATEES HAVE BEEN OBSERVED FEEDING.

Type	Body of water	County
Typha domingensis (young shoots)	Tomoka River	Volusia
Distichlis spicata	Tomoka River	Volusia
	Hillsboro Canal	Palm Beach
	Dania Cut-off Canal	Broward
Panicum purpurascens	St. Johns River	Volusia
Panicum sp.	Imperial River	Lee
Paspalum vaginatum	Little Manatee River	Manatee
	Eau Gallie River	Brevard
Paspalum sp.	Intracoastal Waterway	Volusia
	Earman River	Palm Beach
Spartina alterniflora	St. Johns River	Duval
	Tolomato River	St. Johns
	Intracoastal Waterway	Flagler
Vigna repens	Eau Gallie River	Brevard

(*Rhizophora mangle*). It is noteworthy that manatees in the vicinity of Blue Springs Park never were seen to feed on the leaves of overhanging trees and shrubs or on Spanish moss (*Tillandsia usneoides*).

Although manatees generally avoid fibrous vegetation, those that congregate in the discharge of a power plant in Palm Beach County have eaten the fronds of coconut palms (*Cocos nucifera*) fed to them by local residents. The death of a young manatee at the Miami Seaquarium was attributed to an impacted intestine, the result of eating palm fronds (Warren Zeiller, personal communication).

Algae.—In captivity, manatees have been reported to accept both fresh-water and marine algae, including *Chara, Spirogyra,* and *Ulva* (Chapman, 1875; Coates, 1939; Allsopp, 1969). In the wild, however, it appears that algae do not figure significantly in the diet of manatees unless vascular vegetation is unavailable. In the Crystal River headwaters, manatees seldom fed on nonvascular plants and then only incidentally while foraging on the bottom for detritus. At such times, animals devoured clumps of *Enteromorpha, Oscillatoria,* and *Navicula.* At the mouth of the Crystal River, manatees showed no interest in *Sargassum,* and from the air I never saw animals feeding on beds of marine algae. There is evidence that,

TABLE 5

ATTACHED ALGAE COLLECTED FROM MARINAS, DOCKYARDS, AND JETTIES WHERE MANATEES HAVE BEEN OBSERVED FEEDING.

Type	Body of water	County
Chlorophyceae (green algae)		
Caulerpa prolifera	Ft. Pierce Inlet	St. Lucie
Caulerpa racemosa	Ft. Pierce Inlet	St. Lucie
Caulerpa sertularioides	Ft. Pierce Inlet	St. Lucie
Chaetomorpha brachygona	Intracoastal Waterway	Broward
Enteromorpha sp.	Intracoastal Waterway	Flagler
Halimeda tuna	Ft. Pierce Inlet	St. Lucie
Ulva lactuca	Matanzas River	St. Johns
	Tolomato River	St. Johns
	San Sebastian River	St. Johns
Rhodophyceae (red algae)		
Agardhiella tenera	Ft. Pierce Inlet	St. Lucie
Botrycladia pyriformis	Ft. Pierce Inlet	St. Lucie
Champia parvula	Ft. Pierce Inlet	St. Lucie
Gracilaria mammillaris	Matanzas River	St. Johns
Grateloupia filicina	Matanzas River	St. Johns
Hypnea cervicornis	Ft. Pierce Inlet	St. Johns
Hypnea spinella	Ft. Pierce Inlet	St. Lucie
Laurencia microcladia	Ft. Pierce Inlet	St. Lucie
Wrangelia argus	Ft. Pierce Inlet	St. Lucie
Cyanophyceae (blue-green algae)		
Lyngbya sp.	Indian River	Brevard
Xanthophyceae (yellow-green algae)		
Vaucheria sp.	Matanzas River	St. Johns

under normal conditions, dugongs also shun algae and feed exclusively on spermatophytes (Gohar, 1957; Jarman, 1966; Heinsohn and Birch, 1972). However, Heinsohn and Spain (1974) found that dugongs began to supplement their diet with brown algae following severe damage to their sea grass pastures by a cyclone.

In turbid waterways with impoverished vascular flora, manatees supplement their diet by feeding on algae. On the east coast of Florida, it is well known that manatees graze on algae that grow on jetties, pilings, floats, docks, mooring lines, and the hulls of boats. Table 5 presents a list of attached algae collected from marinas, dockyards, and jetties where manatees have been seen feed-

TABLE 6

ALGAL ASSOCIATES AND EPIPHYTON OF MARINE AND ESTUARINE SPERMATOPHYTES GRAZED BY MANATEES AT OBSERVED FEEDING SITES.

Type	Body of water	County
Non-epiphytes		
Chlorophyceae (green algae)		
Caulerpa paspaloides	Crystal Bay	Citrus
Caulerpa prolifera	Tampa Bay	Hillsborough
	Crystal Bay	Citrus
Spirogyra sp.	Salt River	Citrus
Ulva lactuca	Turtle Bay	Charlotte
	San Carlos Bay	Lee
Rhodophyceae (red algae)		
Acanthophora muscoides	Indian River	Brevard
Acanthophora spicifera	Turtle Bay	Charlotte
Chondria littoralis	Tampa Bay	Hillsborough
Chondria sedifolia	Crystal Bay	Citrus
Dasya sp.	Turtle Bay	Charlotte
Gracilaria compressa	Tampa Bay	Hillsborough
	Turtle Bay	Charlotte
	Indian River	Brevard
Gracilaria verrucosa	Crystal Bay	Citrus
	Tampa Bay	Hillsborough
	Turtle Bay	Charlotte
Hypnea cervicornis	San Carlos Bay	Lee
Hypnea musciformis	Tampa Bay	Hillsborough
Polysiphonia spp.	Salt River	Citrus
Spyridia filamentosa	Turtle Bay	Charlotte
Phaeophyceae (brown algae)		
Dictyota dichotoma	San Carlos Bay	Lee
Cyanophyceae (blue-green algae)		
Lyngbya sp.	Indian River	Brevard
Epiphytes		
Rhodophyceae (red algae)		
Ceramium subtile	Crystal Bay	Citrus
Ceramium sp.	Indian River	Brevard
Polysiphonia macrocarpa	Indian River	Brevard
Phaeophyceae (brown algae)		
Ectocarpus sp.	Crystal River	Citrus
Cyanophyceae (blue-green algae)		
Lyngbya sp.	Indian River	Brevard
Bacillariophyceae (diatoms)		
Anhnanthes longipes	Indian River	Brevard
Amphora spp.	Indian River	Volusia
Grammatophora marina	Indian River	Brevard
	Indian River	Volusia

TABLE 6 (Continued)

Type	Body of water	County
Licmophora sp.	Tampa Bay	Hillsborough
Mastogloia sp.	Indian River	Volusia
Melosira nummuloides	Indian River	Volusia
Navicula sp.	Tampa Bay	Hillsborough
Nitzschia sp.	Indian River	Brevard
Rhabdonema adriaticum	Indian River	Volusia
Striatella sp.	Tampa Bay	Hillsborough
Synedra hennedyana	Indian River	Brevard
Synedra sp.	Indian River	Brevard

ing. The animals seem to prefer green algae. They have been seen to feed on mixed associations of red and green algae but have only been found eating green algae where colonies consisting of a single species occur. In Everglades National Park, manatees may eat the alga *Chara hornemanni* that, according to Tabb *et al.* (1962), flourishes in the quiet removes of Whitewater Bay when the salinity is less than 30 ppt.

Manatees cannot avoid ingesting epiphytic algae when feeding on spermatophytes. Nonepiphytic algae appear to be taken only accidentally while animals graze. In the fresh waters of the study area, the dominant algae associated with submerged spermatophytes were *Enteromorpha, Spirogyra, Cladophora,* and *Oscillatoria.* Manatees made no effort to avoid feeding on such *Aufwuchs.* In estuarine and marine waters, manatees adventitiously consume a wide variety of algae associated with the seagrasses *Ruppia, Diplanthera, Thalassia,* and *Syringodium* (Table 6). In addition to the algae listed, a number of unidentified diatoms and dinoflagellates as well as a red and a blue-green alga were found on blades of *Thalassia* collected from manatee feeding sites.

Feeding methods.—Manatees feed in a variety of manners depending on the growth form of the food source and the part of the plant being consumed. When feeding on submerged plants that produce simple leaves from basal clusters or rhizomes, such as the seagrasses and *Vallisneria,* manatees behave as grazers. In these circumstances, the body is generally tilted cephalad, the mouth and flippers often touching the substrate, especially when short growth is being cropped.

It appears that manatees eat only the leaves of *Thalassia, Syringodium, Diplanthera,* and *Ruppia,* and there was no evidence that they preferred young to mature plants. When feeding on *Vallisneria,* however, they seemed to prefer the leaf bases, basal sheaths, and young shoots to the mature blades. The rhizomes were not touched.

Where food plants attained considerable height in the water or floated on its surface, manatees tended to act more like browsers. In many areas of Kings Bay, for example, *Myriophyllum* and *Hydrilla* formed dense "jungles" of stalks that reached 2 to 4 meters to the surface. Manatees fed haphazardly on these stems, attacking them at any point from crown to base. Stems, leaves, and flowers were consumed indiscriminately.

Manatees routinely fed on *Hydrilla* by cropping marginal growth or by immersing themselves in clumps. Animals sometimes became buried in masses of *Hydrilla,* hollowing out a cave as they fed. In such cases they were forced to back out in order to surface but usually returned to the same hole to continue feeding. Occasionally they had difficulty disengaging themselves from the tangle of vegetation and had to plunge through it to escape. Manatees also fed on rafts of floating *Hydrilla* uprooted by their activity.

Feeding manatees normally concentrated on a particular clump of *Hydrilla* but sometimes roved from one to the next. Strands of vegetation often dangled from the mouths of animals making their rounds. I once watched four manatees drift in tandem out of a canal snatching at *Hydrilla* as the current swept them along.

The animals "browsed" *Ceratophyllum* from the top of one clump to another, favoring the dense, young, uppermost "coontails." A juvenile male once fed with nose awash on the uprooted, broken, decaying stems and leaves of *Ceratophyllum* that had collected near the surface in a mat of *Hydrilla.*

Observations of manatees feeding on water hyacinth were made chiefly on the St. Johns River at Blue Springs Park (Volusia County). Here, rafts of water hyacinth collect beside the shore or among beds of spatterdock. Manatees fed on these rafts, often working their way slowly along the banks of the river. The animals grazed at the periphery of a raft or fully immersed in the tangle of roots and stalks. Upon surfacing under a "ceiling" of plants, their heads covered with hyacinths, animals sometimes gave the impression of exhaling with added force in an apparent effort to clear their nostrils of obstructing vegetation. When small clumps of water hyacinth broke free from the rafts and were carried across the water by wind or current, manatees often intercepted them as they drifted overhead.

Manatees approached water hyacinths from below the surface or with their heads and backs awash. Reaching a plant, they would evert their lip pads, grasp a stalk or blade above the surface, then pull the whole unit underwater. Occasionally an animal projected its entire head above water in order to seize a leaf. While feeding, manatees either remained exposed at the surface or submerged, sometimes sinking to the bottom to finish eating. In several instances, two or three animals were seen sharing the same plant below the surface.

Underwater, the manatee held the water hyacinth in front of its mouth with the tips of its flippers and delicately cropped each leaf. In general, only the leaves were consumed. They were clipped just above the inflated portion of the petiole. Stalks and roots were normally rejected. When an animal had eaten all of the leaves, it released the plant and rose to the surface to grasp another. On occasion, entire plants, roots included, were consumed.

In those few instances when manatees were observed to feed on water hyacinth at Crystal River, they appeared first to investigate the clumps by nibbling, then dragged them under water and devoured them completely—leaves, petioles, and roots. A few times manatees were seen investigating and nibbling clumps of moribund water hyacinth without actually eating the plants.

When feeding on floating mats of alligatorweed in the St. Johns River, manatees usually remained at the surface chewing with their heads awash. The stems, leaves, and roots of this plant were eaten indiscriminately.

Additional sources of food.—Manatees consume a variety of invertebrate periphyton when feeding in fresh or salt water. The invertebrate fauna associated with manatee food plants includes: amphipods; isopods; tiny shrimp, crayfish, and crabs; insect larvae; bivalves; snails; leeches; nematodes; platyhelminths; polychaete worms; tunicates; hydroids; bryozoans; anemones; and brittle stars. Gammarid and caprellid amphipods were found to be particularly common in aquatic vegetation. Arthropods occur in the vegetation in such abundance as to suggest that they contribute an important source of protein to the manatee's diet.

Manatees were occasionally observed to forage on the bottom, nibbling the surface of the substrate and pausing to chew detritus.

TABLE 7

DAILY FOOD CONSUMPTION OF CAPTIVE MANATEES, *TRICHECHUS MANATUS* AND *TRICHECHUS INUNGUIS*.

Manatee			Food		
Species	Weight (kilograms)	Length (centimeters)	Plant	Amount consumed per day (kilograms)	Source
T. manatus	—	198	wildcelery	10	Chapman, 1875
T. manatus	—	240	lettuce	40–50	Murie, 1880
T. inunguis	—	145	lettuce endive	7	Crane, 1881
T. inunguis	—	140	lettuce endive	7	Crane, 1881
T. manatus	590	460	—	27–45	Gunter, 1941
T. manatus	42	135	escarole hyacinth	12	Hartman, personal observation
T. inunguis	83	—	lettuce	8	E. S. Herald, personal communication

It often appeared that they were feeding not only on decaying organic matter but also on a mixture of sand and mud, perhaps in quest of trace elements or other essential minerals. Several times I saw animals ingest manatee feces. More often, they simply nuzzled and chewed the dung, then allowed the mash to filter out of their mouths.

Most extraordinary is the recent documentation of piscivorous behavior in manatees on the northern coast of Jamaica (Powell, 1978). It appears that sirenians in that area systematically visit gill nets set by local fishermen and deflesh the small scaled fish (carangids and scombrids) caught in the mesh.

Daily food consumption.—During each of the winters of the study, manatees gradually denuded whole stands of *Hydrilla, Ceratophyllum,* and *Myriophyllum* in Kings Bay, but, because the attendance of animals in the bay was irregular and because other vegetation-removing factors (for example, herbicides, weed harvesters, dredges, anchors, outboard propellers, and waterfowl) constantly intruded, it was impossible to quantify daily food consumption per animal. The only available data on daily food consumption are from captive individuals (Table 7). Captives have been recorded to eat up to one fourth their body weight per day in wet greens or as much as 1 kilogram of vegetation per 5 centimeters of body length. For comparison, a pair of captive dugongs daily ate 1 kilogram of seagrasses (wet weight) per 7 centimeters of body length (Jones, 1967).

Feeding Ecology

Feeding sessions.—Manatees fed in discrete sessions during which they concentrated on one species of plant. Feeding sessions normally lasted between 30 and 90 minutes but continued for more than two hours if animals were exceptionally hungry. From the shore I once clocked a bull who fed for 75 minutes of which 70 were spent feeding and the remaining five surfacing and stationing himself in front of the food. Calves fed with less concentration and for shorter periods than did adults. They often had to wait for their mothers to finish feeding. As animals became sated, they frequently interrupted feeding to rest. Eventually they would cease feeding altogether and move off to other pursuits.

Depths.—The depths at which manatees feed are determined by tides, by the depth at which plants grow, and by the growth forms of the food species. Table 3 includes the depths at which manatees were seen feeding on various seagrasses. In Kings Bay, animals were observed feeding from the surface to a depth of 4 meters. In the lower river where submerged vegetation is strictly littoral, manatees fed on the narrow bank close to shore at depths of approximately a meter. In the Salt River and neighboring estuarine waters, animals occasionally grazed on flats as shoal as 80 centimeters. In the St. Johns River, near Blue Springs Park (Volusia County), manatees normally fed on water hyacinth in water a meter or more in depth, but were occasionally observed feeding near the shore in water only 50 centimeters deep. In Guyana, manatees were observed to feed on bank growth in water shallower than 50 centimeters (Datakaran Jeetlall, personal communication).

Animals cropped *Thalassia, Syringodium, Diplanthera, Ruppia,* and *Vallisneria* on or near the bottom, depending on the size of the plants. At manatee feeding sites, *Thalassia* and *Syringodium* were found growing to heights of 60 centimeters, *Diplanthera* and *Ruppia* to 20 and 15 centimeters, respectively, and *Vallisneria* to 50 centimeters. Manatees usually fed on *Ceratophyllum* and *Myriophyllum* at middle depths of 1 to 3 meters in Kings Bay. They grazed on *Hydrilla* from the bottom to the surface, sometimes with their backs awash. Animals never descended below 4 meters to feed on *Hydrilla,* although it grew at depths of 10 meters in the Main Spring.

There are vast areas of manatee habitat in which shallow water renders potential food plants inaccessible. *Syringodium* and *Diplanthera* grow profusely in the Indian River north of Titusville (Brevard County), but only *Syringodium* is found at depths accessible to manatees; *Diplanthera* grows from the shoreline to a depth of only 26 centimeters (Kerry Clark, personal communication). In the St. Johns watershed, *Ruppia, Zannichellia, Najas,* and the algae *Chara* and *Nitella* are normally found in water 20 to 60 centimeters deep, unavailable to manatees.

Selection of feeding sites and timing of movements.—Although at one time or another manatees were seen feeding in every accessible corner of Kings Bay, they were generally selective in their choice of feeding sites. It was not unusual for an animal to return repeatedly to a preferred feeding area until its resources had been depleted or until another site had found favor. For example, an adult female returned to Kings Bay at least four times within two weeks to feed on precisely the same patch of *Vallisneria.* During one week in October, two cows with calves returned daily to feed on a single bed of *Hydrilla.* A bait-house owner on the Withlacoochee River reported that a group of manatees appeared daily for three weeks to feed below his dock on *Elodea.* From the air, manatees were repeatedly seen feeding in the same general coastal areas, further suggesting that they have preferred feeding sites.

There is evidence that manatees time their movements to coincide with the availability of food. In the Banana River (Brevard County), I have seen 10 or more manatees congregate in a cove to feed on floating mats of *Syringodium* and *Diplanthera* blown inshore by the wind. During the rainy season in southern Florida, manatees move up the canals to the flood control dams to feed on water hyacinth and other vegetation pouring through the gates (Hartman, unpublished manuscript). Similar behavior has been reported in the Demerara River of Guyana where manatees collect at the outlets of drainage canals to intercept floating plants sluiced through the locks (W. H. L. Allsopp, personal communication). It has even been recorded that Amazonian manatees congregate to feed on fruit that drops to the water from overhanging trees (Nunes Pereira, *in* G. Bertram and C. Bertram, 1973).

In some areas the feeding habits of manatees are dependent on the season. In the winter, growth of aquatic vegetation is terminated or much reduced. Leaf kill of *Thalassia* and *Syringodium* in the offshore waters of Citrus County was not determined, but in inshore waters *Diplanthera* suffered extensive leaf kill in winter. *Ruppia* generally survived in the rivers, and there was always an adequate supply of submerged plants in the warm headwaters. In many segments of the Intracoastal Waterway, however, algae die off each winter, and manatees must find alternative sources of food.

In estuarine waters, the distribution and abundance of *Ruppia* and *Diplanthera* fluctuate seasonally with the rains (Phillips, 1961*a*; Tabb *et al.,* 1962). During periods of high salinity, *Diplanthera* replaces *Ruppia,* and manatees presumably shift feeding from one to the other.

Heinsohn and Spain (1974) reported that the diet and movements of dugongs were influenced by cyclone-induced damage to seagrass beds. Although a reasonable possibility, no comparable influence on the feeding behavior of manatees has been documented.

Freshwater needs.—There is growing evidence that manatees require fresh water. They may seek it to rid themselves of barnacles and marine ectoparasites, but their attraction to hyposaline water seems more directly related to osmoregulation. Their apparent need for fresh water was first noticed in 1681 by William Dampier who wrote: "Manatees that live in the sea do commonly come once or twice in 24 hours to the mouth of any freshwater river that is near their place of abode" (Dampier, 1906). A need for fresh water also may have been shared by Steller's sea cows, which were drawn to the mouths of brooks on Bering Island (Steller, 1751). Phillips (1964) reported that a captive manatee housed in a saltwater tank drank fresh water regularly from a hose. (All captive manatees, to my knowledge, have been kept in fresh water or provided with a source of fresh water.) Phillips also proposed that manatees travel up rivers specifically to drink fresh water. This theory may account for the overwhelming prevalence of manatee sightings in freshwater and estuarine habitats. Many interviewees claimed that heavy rains often are followed by the appearance of manatees at the heads of tidal rivers.

In the canals of southern Florida, manatees are commonly seen just below the flood control dams, presumably drinking the fresh water sluiced through the spillways. Groups of manatees are found almost daily below the spillway on the Fakha Union Canal (Collier County). In Ft. Lauderdale, I once watched a manatee swim up to the base of a flood control dam and fan its mouth as if drinking.

It appears that manatees are drawn to virtually any source of fresh water. They have been observed drinking sulfur water flowing from a pipe into the Tolomato River (St. Johns County). They were attracted to the fresh water discharging from a high pressure hose used at a construction site on the Intracoastal Waterway (St. Johns County). In years past, manatees focused their activity around a storm drain at the City Yacht Basin in Daytona Beach. They were also known to gather around the discharge of the municipal sewer in St. Augustine. At least a dozen interviewees had observed manatees drink fresh water from hoses hanging off piers. One of the few manatees recently seen in the Lower Keys turned up near a source of fresh water at a marina in Key West. According to a report in the November 1972 issue of *Conservation News* (Florida Department of Natural Resources), manatees in the Titusville Yacht Basin are attracted to boats that are being washed in order to drink the freshwater runoff. Manatees also may drink from artesian springs at their point of discharge into salt or brackish waters. It may not be far-fetched to suggest that manatees drink fresh water at the surface during heavy downpours.

I have personally observed manatees feeding in fresh water and in water as salty as 35 ppt (Table 3). This feat is most singular when one considers that the vascular vegetation on which manatees graze contains over 85 per cent water (Rickett, 1924; Phillips, 1960*a*). Feeding in both fresh and salt water must place considerable demand on the water balance mechanisms of manatees. The manatee kidney, in fact, bears little resemblance to the kidneys of other mammals, including the dugong (Owen, 1838; Murie, 1874; Beddard, 1897; Petit, 1925; Hill, 1945; Quiring and Harlan, 1953; Batrawi, 1957), but it is not known if manatees excrete less water under conditions of hypersalinity.

INTERACTIONS WITH OTHER ANIMALS

MANATEES paid little heed to the indigenous fauna of Kings Bay. They took no interest in crabs (*Callinectes sapidus*), cooters (*Chrysemys floridana*), sting rays (*Dasyatis sabina*), or large species of fish such as longnose gar (*Lepisosteus osseus*), sharp-nosed sharks (*Rhizoprionodon terraenovae*), and tarpon (*Tarpon atlanticus*) and passed unperturbed through dense schools of migratory marine fish. On occasion, however, manatees were startled by commotions at the surface. The animals were sometimes frightened by jacks (*Caranx hippos*) splashing after needlefish (*Strongylura marina*), by coots (*Fulica americana*) taxiing directly overhead, or by pelicans (*Pelecanus occidentalis*) plunging nearby. Ordinarily the reaction was to flee a few meters, then return to investigate the source of the disturbance.

Manatees resting on the bottom were pestered by fish, which pecked their hides apparently in quest of microorganisms. The manatees rarely reacted when their backs were pecked by smaller fish such as gray snappers (*Lutianus griseus*), pinfish (*Lagodon rhomboides*), and bluegills (*Lepomis macrochirus*), but winced whenever such fish pecked in their orbits. They flinched and slapped ineffectually with their flippers when pecked by large fish such as jacks and sheepshead (*Archosargus probatocephalus*). One morning a single sheepshead molested a group of seven manatees who, in their efforts to avoid being pecked, rolled on their sides and upside down but were finally forced to leave their resting site. At the same location the next day, however, a sheepshead pecked but failed to irritate a young cow.

Manatees also encountered otters (*Lutra canadensis*) and bottlenosed dolphins (*Tursiops truncatus*) at Crystal River. I watched such encounters from the runabout. Only one otter-manatee confrontation was observed. Three otters crossed the path of a bull as it was cruising through a cut; neither otters nor manatee hesitated or changed course. Dolphin-manatee encounters were seen on four occasions. Each time, two or more dolphins passed casually through a group of manatees and were apparently ignored by the sirenians.

The reaction of manatees to alligators (*Alligator mississippiensis*) was never observed. Alligators, particularly larger individuals, had been all but exterminated in Citrus County at the time of the study.

INTEREST IN INANIMATE OBJECTS

MANATEES frequently reconnoitered the bottom, pausing to nudge and nibble rocks and organic debris as well as bottles, cans, and other foreign articles. An animal often satisfied its curiosity by taking an object into its mouth and tonguing it or gently grinding on it with its teeth. The following incidents at the Main Spring exemplify the interest of manatees in inanimate objects.

An adult male picked up an 8-centimeter piece of palmetto bark and carried it for a few meters. An old bull picked up an 18-centimeter forked piece of waterlogged driftwood, swam with it for a short distance, then let it fall. A cow nudged a 40-centimeter log along the sand. Her calf rolled a beer can with his muzzle and later pushed a piece of sunken wood across the bottom for several meters before losing interest. The same calf was also seen to pick up a piece of limestone and carry it to the surface before releasing it. A gravid cow chewed briefly on a small rock, audibly sloshing it in her mouth.

Animals were also seen nibbling and transporting odds and ends of glass, plastic, and rubber found on the bottom. A juvenile male chewed on the head of a Coca Cola bottle, eventually picked it up by its neck and dropped it. Another young male chewed on my rubber flippers for five minutes as I stood on a ledge overlooking the spring. A juvenile cow once nibbled the edge of my polyethylene clipboard as it lay on the ledge. On another occasion a young male picked my thermometer up from the bottom, munched on it momentarily, then dropped it. Once when I dangled the thermometer on a string in front of a juvenile male, he approached it, everted his lip pads, tucked the thermometer end-first into his mouth and chewed on it until I jerked it free.

The manatees responded with curiosity to a 4-meter steel reinforcing rod that I dangled with strings from the surface in an effort to measure them. The more inquisitive animals nibbled and rubbed on it. Eventually a cow caught one of the strings under a flipper and broke the line.

When my runabout was anchored at the Main Spring, manatees often nudged and nibbled the anchor and anchor rope. An inordinately tame young female regularly investigated the boat by nuzzling its hull and the propeller on the outboard (Fig. 27). Occasionally she grasped the anchor rope to her belly with her flippers, nibbling and rubbing on it (Fig. 19I). Another tame female had a habit of chewing on the hydrophone cable.

Manatees occasionally nuzzled floating objects such as buoys, branches, palmetto fronds, beer cans, dead coots, and pieces of paper. A juvenile female once nudged a strip of floating facial tissue and surfaced with it on her nose.

PARASITES AND COMMENSALS

Endoparasites

According to Jones and Johnson (1967), sirenians are parasitized by digenetic trematodes and ascarid nematodes. Dailey and Brownell (1972) listed 10 species of trematodes and two species of nematodes found in the stomach, intestines, and caecum of dugongs. The paramphistomid fluke *Chiorchis fabaceus* has been obtained from the intestines of *Trichechus manatus, T. senegalensis,* and *T. inunguis* (Sokoloff and Caballero, 1932; Price, 1932; Baylis, 1936). Another fluke, *Opisthotrema cochleotrema,* has been found in the alimentary system of *T. manatus* (Dailey and Brownell, 1972). Numerous intestinal roundworms (*Plicalolabia hagenbecki*) were found in a young male *T. manatus* that died in 1969 at Busch Gardens in Tampa (Radhakrishnan and Bradley, 1970).

Hill (1945) found a small fish inside the prepuce of a male dugong and suggested a commensal association.

As no fresh manatee carcasses were available for autopsy during this study, examination for endoparasites was confined to fecal analysis. A single fecal sample from the floor of Kings Bay was subjected to three standard techniques—iodine-stained direct smear, formol-ether sedimentation, and zinc sulphate flotation. A number of unidentifiable nematode eggs were present.

External Associates

The hide of manatees supports an assortment of plant and animal associates. Many are difficult to categorize as parasites or commensals. The only previously identified sirenian ectoparasite is a copepod, *Harpacticus pulex,* discovered on two captive manatees at the Miami Seaquarium (Humes, 1964). Local bacterial and fungal infections are encountered among captive animals (personal observations), but there is no evidence that the organisms involved infest manatees in the wild. The Crystal River animals were without visible infections other than occasional pus-filled tumors. Water mold grew harmlessly in minor wounds.

The hides of some individuals bore incrusted patches, the cause of which was perhaps a parasite. The crusts did not seem to irritate the animals but, once acquired, remained despite the constant epidermal sloughing characteristic of manatee hide. The incrusted areas were ridged and grooved and seemed to shelter a greater number of organisms than the smooth surfaces of the skin.

A few animals supported extensive growths of a blue-green alga (*Lyngbya martensiana*) on their backs, suggesting that they had spent most of their time in rivers and estuaries. A red alga (*Compsopogon coeruleus*) grew from the tips of hairs and vibrissae on some manatees. The backs of animals arriving in Kings Bay from the Gulf were often coated with a brown scum composed largely of the diatoms *Zygnema* and *Navicula.* In fresh water the diatoms died, and the scum eventually wore off. The presence of the scum indicates that some manatees pass considerable time outside rivers.

Occasionally animals arrived in the Crystal River headwaters with balanid barnacles on their backs and tails. The barnacles gradually died in fresh water and dropped off, leaving their hosts temporarily mottled. That barnacles settle and mature on manatees is another indication that the animals spend protracted periods away from fresh water. It was on the basis of barnacles and algal growth that Moore (1956) believed manatees living predominantly in the Miami River could be distinguished from those living in Biscayne Bay.

During the summer and autumn, manatees arriving from the Gulf were often accompanied by remoras (*Echeneis naucrates*). One animal was seen hosting over 20 fish. The remoras tended to remain with the same individual, avoiding manatees that had been in fresh water longer. The fish are evidently intolerant of hyposalinity for they abandoned their hosts a few days after entering fresh water, presumably to return to the Gulf. The remora-manatee association is further evidence that manatees make extensive use of marine environments.

Epidermal organisms were collected by scraping the hides of manatees with the open ends of plastic vials. Scraping was concentrated on the back and tail and in the folds and recesses under flipper and chin. No lice or mites were found. Smooth-skinned manatees were free of all but microscopic protozoans, nematodes, copepods, and ostracods. Samples from backs covered with *Lyngbya* were more productive, yielding, in addition to the above, amphipods, isopods, and dipteran larvae. Tiny gastropods and small leeches, churned up from the bottom, appeared on manatees from time to time but soon disappeared.

In general, the macroscopic associates of manatees seem to be free-living and ectophoretic rather than parasitic. Incrusted and algae-covered hides provide them with transport and a suitable microhabitat. The microscopic inhabitants of the skin apparently range from casual commensals to obligate parasites. The euryhaline habits of manatees may be responsible for the comparative scarcity of parasites and commensals; potential associates would be subjected to rigorous osmotic stresses.

MAINTENANCE BEHAVIOR

Locomotion

The manatee's aquatic stability seems to stem from the elongate shape and dorsal position of its lungs and from the pachyostotic condition of its skull and ribs. The heavy bone structure apparently serves as ballast and contributes to the animal's neutral buoyancy. Virtually weightless underwater, the manatee swims with agility and grace. Its movements are ponderous only when compared with those of the Cetacea. Manatee hydrobatics and body postures include somersaults, half gainers, back dives, head and tail stands, barrel rolls, and upside-down gliding. These antics, however, are incidental to routine locomotion and will be dealt with individually under later headings. The present section considers the locomotory processes manifested in normal swimming and maneuvering.

Use of the tail.—The hydrodynamics of swimming in the Sirenia are virtually unstudied. A cruising manatee propels itself by undulating its tail dorsoventrally like a cetacean (Figs. 16 and 17). The propulsive forces in cetacean locomotion are discussed and diagrammed by Slijper (1962), Lang (1966), Gray (1968), and Hertel (1969). In the Cetacea, thrust is developed by movement of both the tail and the body; the body is flexible and undulates with each stroke of the tail. I observed no such body motion among manatees, although it may occur at high speeds. It is apparent, however, that each stroke of the tail displaces the body vertically, the degree of pitch increasing with the power of the stroke (Fig. 17).

There are also basic structural differences between manatees and cetaceans, the outcome of which is that manatees are comparatively inefficient swimmers and are unable to reach or sustain high speeds. Manatees are less streamlined than cetaceans, which undoubtedly results in reduced laminar flow and increased drag

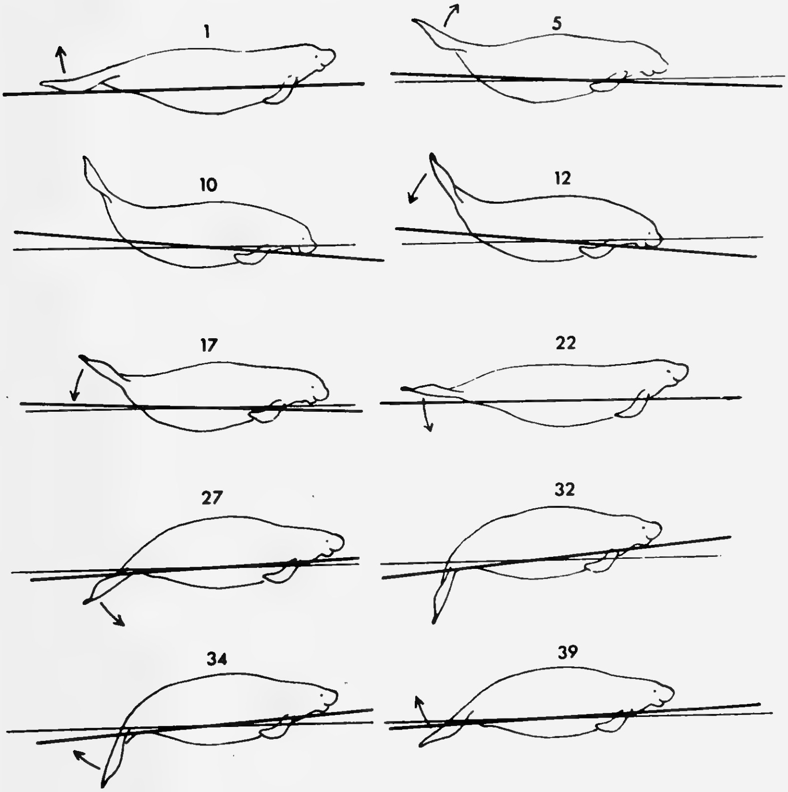


FIG. 16. Lateral view of a cruising manatee. Drawings are from an 8-mm film sequence and encompass one complete undulation of the tail. Arrows indicate direction of movement. The heavy lines passing through the animal's approximate center of gravity represent the long axis of the body and illustrate the slight deviation from the horizontal plane (light lines) engendered by each stroke. Numbers refer to the number of the film frame.

during swimming. Manatees also lack the peduncular musculature found in the Cetacea and cannot generate comparable thrust. Manatees seem to beat the tail about a pivotal point near its base compared with cetaceans, in which the fulcrum of thrust appears to be above the anal aperture. In full stroke the tip of a manatee's tail describes an arc of only 130 degrees as opposed to an arc of over 200 degrees described by the fluke of a dolphin (pictured in Slijper, 1962). Moreover, the manatee's tail is flexible and has a

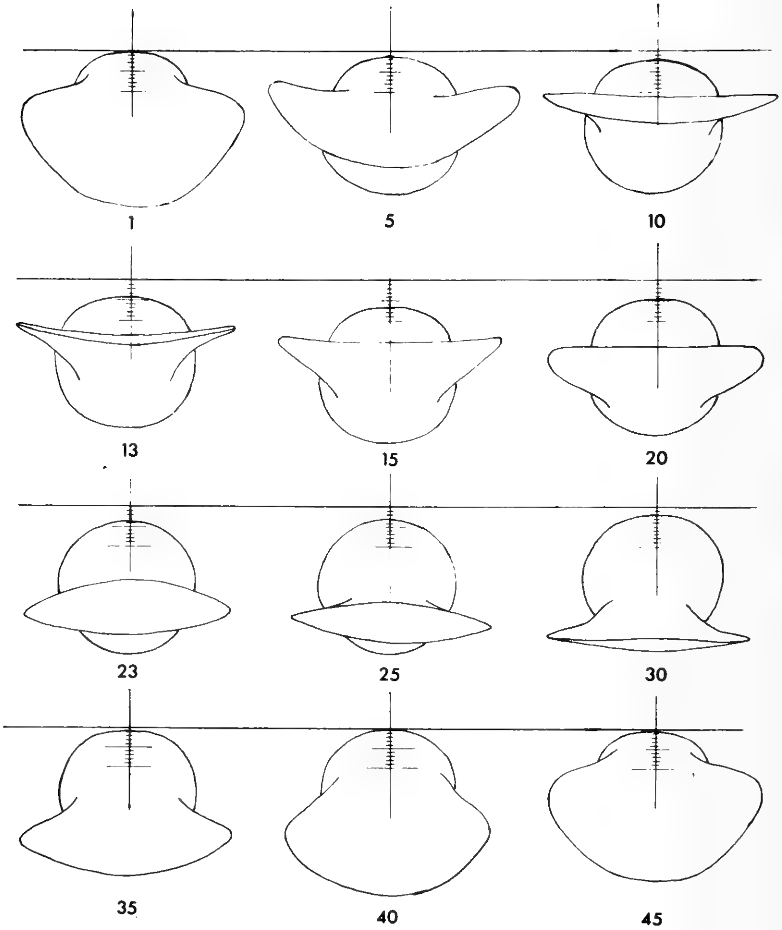


FIG. 17. Posterior view of a cruising manatee. Drawings were made from an 8-mm film sequence and encompass one full undulation of the tail. Coordinates illustrate body's relative displacement along a vertical axis. Number indicates number of film frame.

slight positive dihedral, which results in deflection of the caudal and lateral margins during downswings. Manatees initiate movement from a stationary position by an upswing of the tail followed by a downswing, repeated until the undulatory rhythm is established.

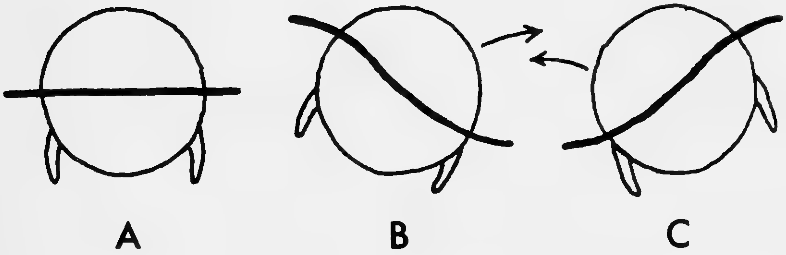


Fig. 18. Diagrammatic representation of the use of the tail as a rudder. Posterior view of a cruising manatee in forward glide (A), preparing to turn to the right (B), and preparing to turn to the left (C). Roll does not always accompany a turn.

It should be mentioned here that dugongs are more streamlined than are manatees and show other structural modifications, including a fluke, that suggest a greater specialization for aquatic life than is found in trichechids.

The tail of the manatee also serves as a rudder (Fig. 18). According to Kinzer (1966), the tail may be at an angle as great as 45 degrees to the long axis of the body when a manatee is turning in a circle. Cruising animals can steer, bank, and roll by means of the tail alone. Immobile or idling manatees frequently adjust the angle of the tail to counteract roll and, to some degree, yaw. At the same time, the tail may be elevated or depressed to adjust the longitudinal axis of the body.

Stroke rate.—Stroke rate and the amplitude of undulations of the tail vary with the state of activity. Defining a stroke as one complete undulation of the tail, I determined the stroke rates of adult and subadult manatees while idling, cruising, and fleeing. Adult manatees were seen to stroke 18 to 20 times per minute when idling and 24 to 36 times per minute while cruising. Idling involves several moderate strokes followed by a glide. Idling manatees swim with less regular strokes than when cruising and either dangle their flippers or adduct them at the wrists under their chests. When cruising, in contrast, manatees tend to maintain a constant rhythm of even strokes, the tail moves through a greater arc, and the flippers are held back flush against the body. Maximum stroke rate and amplitude are associated with flight. Fleeing manatees were observed to stroke their tails 45 to 50 times per minute.

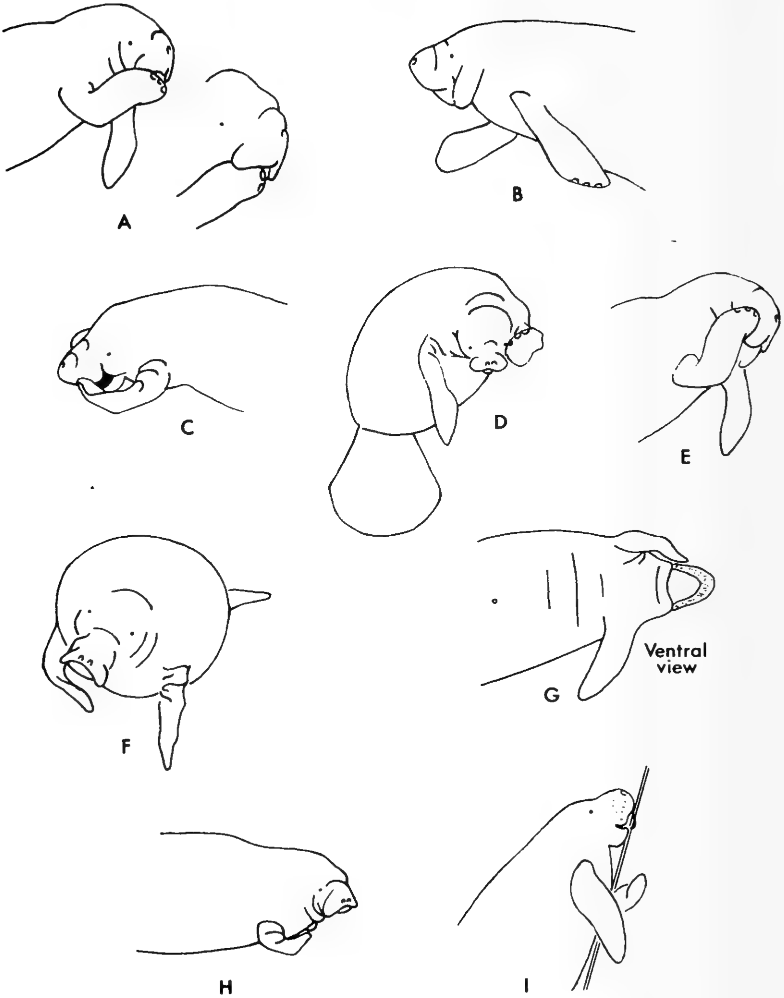


Fig. 19. Selected manatee attitudes illustrating various uses of the flippers (drawn from photographs).

Stroke rate also varied with size. Calves were found to have a higher stroke rate than did older animals engaged in the same activity. The number of strokes per minute for cruising calves ranged from 36 to 44 as compared with 24 to 36 for adults. To keep pace, calves must maintain a higher stroke rate than their mothers. The cruising speeds of cows with calves were clocked at Crystal River, and it was discovered that mothers, apparently to accomodate their offspring, swim more slowly than do other adults. One cow with a pre-yearling calf was clocked cruising approximately 1 km/hr slower than a cow with a yearling calf.

Speeds.—Fishermen from British Honduras claim that manatees attain speeds up to 48 km/hr (Charnock-Wilson, 1968). Jarman (1966) estimated that cruising dugongs swam at 9.6 km/hr. At Crystal River, I clocked manatee speeds with a stopwatch while following animals in the runabout over a 30-meter course. This clocking method, although crude, involved 10 different manatees and suggested that swimming velocities range from 2 to 25 km/hr, depending on the activity. Idling manatees swam at 2 to 3 km/hr, cruising animals at 3 to 7 km/hr, and animals in flight at 18 to 25 km/hr. The sprints of fleeing manatees were short, usually 20 to 30 meters and never more than 100 meters. I obtained one estimate of manatee speeds from the air; three animals moving along the beach at Sanibel Island (Lee County) cruised at approximately 3.5 km/hr.

Use of the flippers.—The manatee flipper is a highly maneuverable appendage (Fig. 19). Only the forearm and hand are free from the torso, but the elbow and wrist permit remarkable flexion (Flower and Lydekker, 1891). Davilliers (1938) stated that the manus can be rotated 180 degrees in a parasagittal plane. Lateral reach, on the other hand, is limited by the downward displacement of the forelimb.

Manatees differ strikingly from the cetaceans in the use of their flippers for locomotion. While cruising, manatees do not utilize their flippers as hydrofoils as is typical of cetaceans (Felts, 1966). Instead, the flippers are normally held motionless against the sides. Moore (1956) noted an adult manatee that occasionally swam using flippers as well as tail, alternately stroking with right and left flipper. I did not observe such use of the flippers during my study.

It should be noted that, unlike manatees, cruising dugongs may use their flippers. Prater (1928) claimed that when swimming, dugongs employ the flippers to turn and to maintain balance.

Newborn manatees are reported to swim exclusively with their flippers (Moore, 1956, 1957). The youngest calf observed at Crystal River was two to three months of age, and it swam entirely with its tail.

The flippers are normally used only for precise maneuvering and for minor corrective movements to stabilize, position, and orient an animal while it is feeding, idling, investigating, or socializing. In such situations, the flippers may be worked simultaneously or independently.

On the bottom, the flippers function as the sole source of motion. Manatees use the tips of their flippers to balance on the bottom and to propel themselves forward or backward, barely grazing the substrate with their bodies. Animals "walk" on the bottom with alternate movements of the flippers. When greater speed is required, the flippers are manipulated in unison, pulling the animal ahead in a series of lunges until enough momentum is gained to launch off the bottom into a full cruise.

Off the bottom, the flippers are usually used in conjunction with the tail during such activities as feeding or cavorting. In maneuvering to the surface, the flippers are feathered to complement the rudder action of the tail; in turning, they themselves may be employed as rudders (Fig. 19F). Flippers and tail also coordinate as a unit to control pitch.

The flippers sometimes serve as the only instruments of locomotion, initiating or retarding forward or backward movement. By means of forward or reverse feathering of the flippers, manatees can approach or back away from objects.

The primary use of flippers is to turn an animal to the right or left on its longitudinal axis. Due to the structure and rigidity of the manatee's spinal column and, in particular, of its cervical vertebrae, the head cannot be turned to the side. An animal must resort to "coming about" with the aid of its flippers in order to face whatever has drawn its attention. To turn abruptly to the left, for example, a manatee paddles backward with its left flipper while pulling forward with the right.

Flippers are always feathered to present maximum surface area on the power stroke and minimum surface area on the return. Figure 20 diagrams a forward stroke. The flipper is brought forward from the neutral or resting position, its leading (radial) edge exposing the least surface to water resistance. At its fullest extension the flipper is rotated 90 degrees so that its broad palmar surface delivers the stroke. On a backward stroke, the flipper is drawn back with its ulnar edge leading, but again rotated so that the palmar surface draws water.

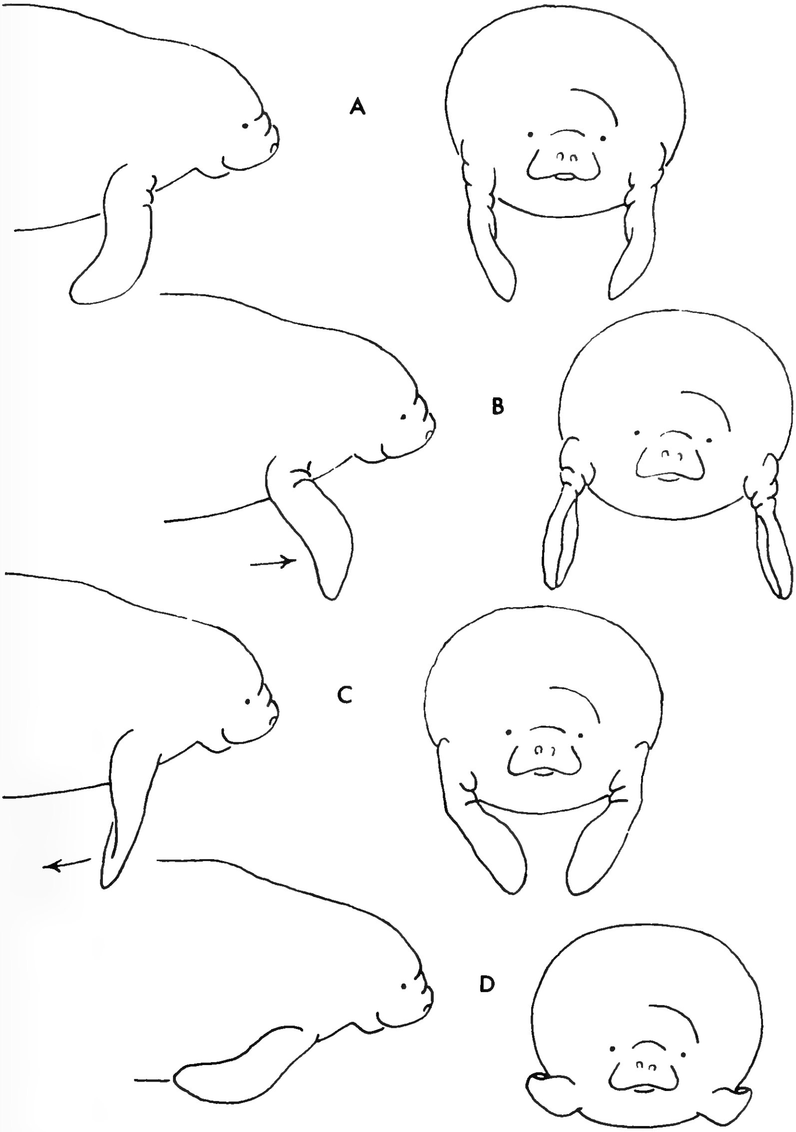


FIG. 20. Lateral and frontal views of flipper positions during suspended resting (A) and during a typical forestroke (B, C, D). Arrows indicate direction of movement. Drawings are from an 8-mm film sequence.

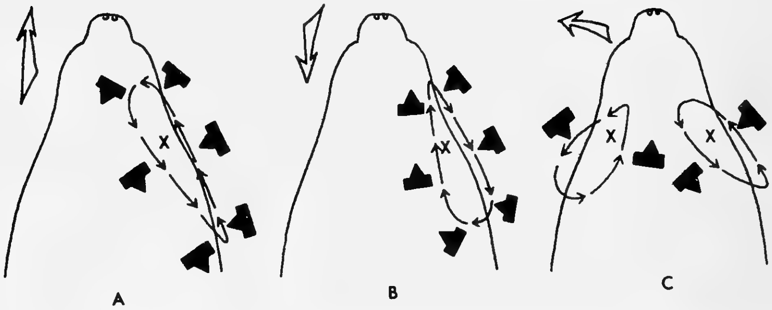


FIG. 21. Ellipse patterns described by the flippers during various movements as seen from above: A, forward stroke; B, backward stroke; C, coming about. Rectangles symbolize flipper cross sections and show orientation of forearm at various points in the orbit; triangles indicate palmar surfaces. Arrows indicate direction of movement. "×" indicates the approximate point of emergence of flipper from the torso.

The path of a flipper during either a forward or backward stroke describes a narrow ellipse (Fig. 21). Power strokes are delivered closer to the body than return strokes. The shape of the ellipse varies depending on an individual's reach, on the strength of the stroke, and on the use to which it is being put. When an animal is coming about, the flippers tend to describe wider, more erratic ovals than during direct forward paddling.

Propelled only by their flippers, manatees are capable of surfacing perpendicularly from the bottom. This, in fact, is the ordinary mode of ascent for young calves, which rise to the surface at a steep angle by working the flippers synchronously or, as observed by Moore (1956), by alternating strokes. Young calves seem to have a buoyancy problem and must make a considerable effort to rise and dive. Unlike more mature animals, resting calves depend almost entirely on their flippers for the climb to the surface and return to the bottom. Normally, resting manatees rise and descend in the water in a horizontal position with little motion of tail or flippers. The flippers are occasionally used to aid the lift off from the bottom. G. Bertram and C. Bertram (1964) suggested that resting manatees are able to ascend and descend effortlessly by means of muscular compression and relaxation of the lungs; rising is effected by expanding the air space in the lungs and sinking by compressing it.

Breathing

The breathing behavior of manatees is probably a conditioned reflex dating from the day of birth when a mother, calf on back, is reputed to introduce her offspring to a breathing rhythm by dunking it into the water (Moore, 1951*a*). Except during the social ritual of "kissing," only one breath is taken during a surfacing. The manatee opens its nostrils for air at the exact moment of reaching the surface and closes them on submersion with equally precise timing. Exhalation is followed instantaneously by inhalation. Occasionally, a manatee starts to exhale before its nose breaks water, but no animal was ever seen to blow out air as it submerged. This agrees with the observations of Scholander and Irving (1941), who reported that a large captive manatee always dove with full inspiration. Scholander and Irving also found that at rest an adult manatee exchanges about 50 per cent of the air in its lungs as opposed to 80–90 per cent in the bottle-nosed dolphin and 10–20 per cent in man.

When disturbed in the act of breathing, manatees interrupted the respiratory sequence and dove, apparently without filling the lungs with air. In such situations animals were always observed to resurface immediately.

From time to time manatees experienced difficulty breathing and surfaced with a snort. Wheezing inhalations often accompanied the snorts and suggested that the respiratory tracts were partially obstructed. It seemed that the hoarse "blows" were made in an effort to clear the nasal passages. Snorts were frequently repeated in successive surfacings until the congestion was relieved.

During snorts or forceful exhalations, spouts of spray 1 to 2 meters high were sometimes visible. It appeared that these vapor plumes resulted simply from water being blown off the nostrils.

Variation in surfacing behavior.—When resting, idling, or feeding, manatees tended to surface gently and to breathe quietly. The sequence of a typical surfacing from the bottom is portrayed in Fig. 22. Approaching the surface, the manatee elongates its body and elevates its nostrils above the water. Inhalation is accompanied by a slight upthrust of the tail, which arches the back and commences the descent while the nose is still exposed. The animal then sinks slowly to the bottom, usually to the very spot from which it

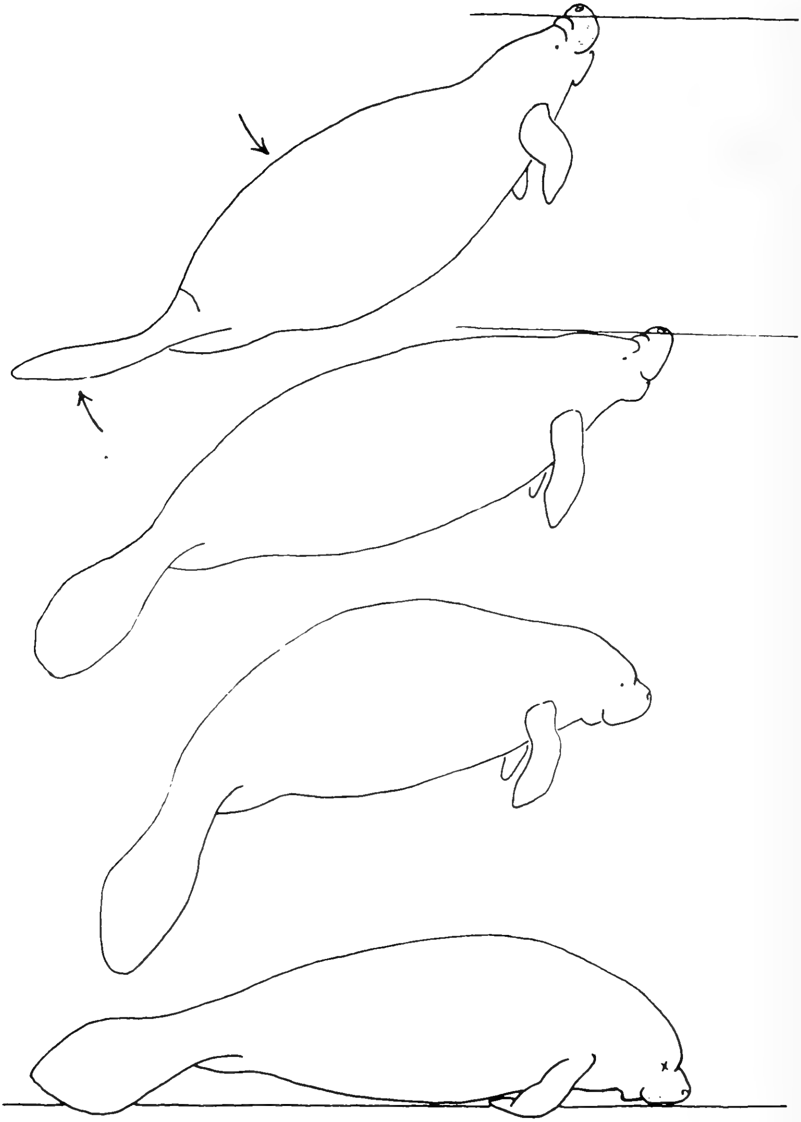


Fig. 22. Surfacing sequence from bottom-resting position. Inhalation (top drawing) is accompanied by a slight upstroke of the tail, which arches the back and commences the descent while the nose is still exposed above the surface.

rose. Sometimes a manatee followed a quiet surface with a stretch and/or steep dive before settling to the bottom.

The upthrust of the tail has the additional advantage of tilting back the head and raising the nostrils higher above the surface during inhalation. This would reduce the chance of inhaling water, especially under turbulent conditions. Manatees do, in fact, expose more of the head above the water line when surfacing in rough water, as first observed by Moore (1951*a*). Young calves appear to be positively buoyant at the surface and expose not only the nostrils but the crown of the head and sometimes the back.

On occasion, a manatee lifted its entire head out of water during a surfacing. The purpose of this peculiar behavior was not clear, but it was decidedly not a means of surveying the above-water surroundings (see section on sight).

Cruising or socially active manatees surfaced in a fashion that bore no resemblance to the surfacing behavior of less active animals. Stages in the surfacing of a cruising manatee are diagrammed in Fig. 23. As can be seen, a swimming manatee climbs gradually to the surface, momentarily ceases its rhythmic tail strokes, exposes its nostrils, then plunges head-first to lower depths, normally breaking water with its back and tail. When surfacing, cruising manatees elevated their noses particularly high in order to clear their own wake.

The breathing of active manatees was forceful and distinctly audible. Respirations during sexual interactions were especially noisy.

Ventilative breathing.—Rhythmic patterns in the breathing of captive manatees and dugongs have been described by Parker (1922), Scholander and Irving (1941), and Kenny (1967). Parker found that upon rising for air after a protracted submergence, manatees would remain near the surface and breathe two to four times in comparatively rapid succession before sinking to the bottom. Scholander and Irving noted a similar phenomenon in an adult manatee whose respiratory frequency increased from less than one breath per minute after submergences of one to two minutes to two to three breaths per minute following submergences of 12 to 15 minutes. In Everglades National Park, Moore (1951*a*) found that the respiration of an adult manatee was characterized by relatively short "breathing periods" between "long, submerged resting periods."

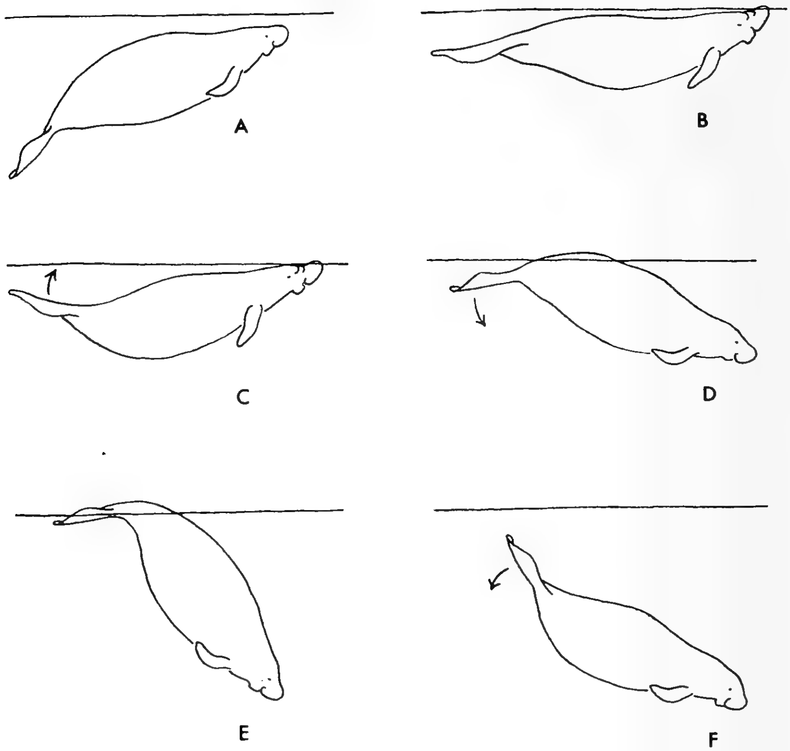


FIG. 23. Sequence of a surfacing while cruising. Arrows indicate direction of tail's movement.

The rhythmic respirations that accompany bottom-resting are apparently a means of recovering oxygen depleted by prolonged submergence and of replenishing air in preparation for the next dive. According to Kooyman (1973), it is typical of all slow-breathing marine mammals to remain at the surface after a dive and to ventilate several times to eliminate carbon dioxide and to renew oxygen.

Figure 24 illustrates the ventilative breathing of manatees observed bottom-resting at Crystal River. Generally two to three breaths are taken in less than a minute when ventilating. The data

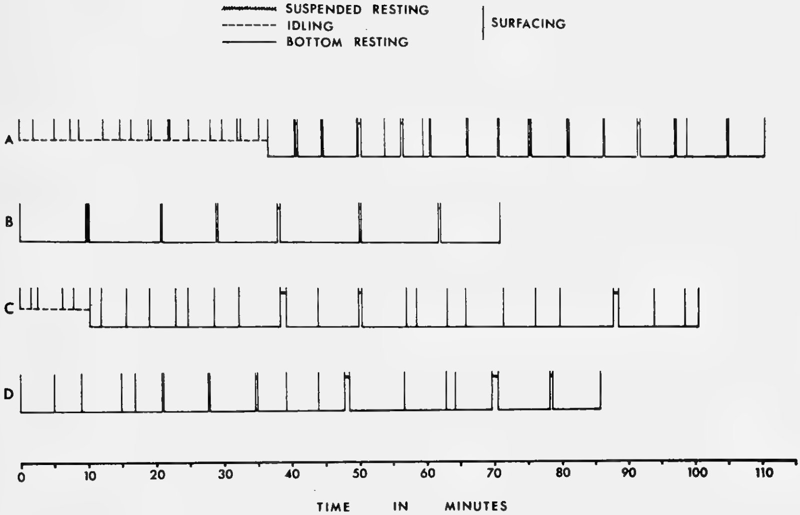


FIG. 24. Consecutive submergence periods of four resting manatees: A, male calf approximately 2 meters long; B, juvenile male approximately 2.4 meters long; C, adult female approximately 3 meters long; D, adult male approximately 3.1 meters long.

contradict Parker (1922), who concluded that the larger the manatee the more breaths it takes while ventilating.

Ventilative breathing was observed only when manatees were resting on the bottom or feeding under dense mats of vegetation. Prolonged submergence characterized both activities. Normally manatees did not compress their breathing into discrete bouts; rather they took single breaths at relatively equal intervals over a period of time. Notice, for example, how the respiratory sequence of the calf (A) changes when it stops idling and begins to bottom-rest (Fig. 24). When involved in social interactions, manatees did not have a respiratory rhythm but tended to breathe irregularly whenever their activity brought them to the surface.

Synchronous surfacing.—When two or more manatees were resting or swimming together, they usually surfaced synchronously to breathe. According to Jarman (1966), groups of dugongs also break water in unison. Synchronous surfacing also occurs among many species of cetaceans (Slijper, 1962; Caldwell, Caldwell, and Rice, 1966; personal observations).

TABLE 8

Frequency and Synchronization of Breathing of Cows and Accompanying Calves While Idling and Resting.

Individuals	Hours observed	Mean number of breaths per hour	Mean number of synchronous breaths per hour	Percentage of calf's breaths in unison with its mother's breaths
cow I	2	21.5	20.0	92
calf I		23.5		
cow II	2	21.0	19.5	92
calf II		23.5		
cow III	3	18.7	15.3	82
calf III		31.0		
cow IV	3	26.7	23.0	86
calf IV		31.0		
cow V	1	20.0	18.0	90
calf V		30.0		

The functional value of synchronous surfacing is conjectural. Among manatees, it appears to be more than a manifestation of social facilitation. It surely does not afford an advantage in procuring food nor in discouraging predators. It is possible that surfacing in unison is an extension of behavior learned at birth when a mother synchronizes her movements with those of her newborn calf or in some manner impresses her offspring to remain at her side. The incidence of synchronous surfacing between mothers and their calves is shown in Table 8. Eighty two to 92 per cent of a calf's breaths are in unison with the breathing of its mother. Whatever its function or motivation, synchronous surfacing ensures closer side-by-side contact between animals, decreasing the odds of accidental separation, a constant hazard in turbid water, especially for a calf.

Length of respiration.—From studies of captive manatees, Parker (1922) found that larger animals took longer breaths than did smaller manatees. Data collected at Crystal River support this finding and indicate that not only a manatee's size but also its state of activity have direct bearing on the duration of breathing (Table 9). Length of respiration was 0.1 to 0.7 seconds shorter for calves than for juveniles and 0.1 to 0.5 seconds shorter for juveniles than for adults. Moore (1951*a*) estimated that the average respirations of

TABLE 9

LENGTH OF RESPIRATION (IN SECONDS) IN RELATION TO BODY SIZE AND STATE OF ACTIVITY. AVERAGES ARE WEIGHTED. "LIGHT ACTIVITY" INCLUDES RESTING AND IDLING; "MODERATE ACTIVITY" INCLUDES FEEDING, CRUISING, AND PLAYING; "STRENUOUS ACTIVITY" INVOLVES FLEEING.

	Light activity			Moderate activity			Strenuous activity		
Age group	Number of observations	Mean	Range	Number of observations	Mean	Range	Number of observations	Mean	Range
Calves (1.8–2.3 meters)	46	2.5	2.0–2.8	14	2.1	1.9–2.4	9	1.9	1.4–2.8
Juveniles (2.3–2.7 meters)	51	3.2	2.6–4.2	21	2.3	1.3–2.6	6	2.0	1.7–2.8
Adults (2.7–3.1 meters)	167	3.8	2.5–5.2	74	3.3	2.6–4.0	9	2.5	2.3–2.7

a resting calf a meter long lasted two seconds, half a second less than the average recorded for calves at Crystal River. The difference can perhaps be explained by the small size of Moore's animal, almost a meter shorter than the smallest calf encountered at Crystal River.

Due to their smaller lung capacity, calves undoubtedly exchange less air when breathing than do larger manatees. When a cow and calf surfaced synchronously, the full breathing cycle of the calf was sometimes completed before its mother had begun to inhale.

Table 9 shows that the length of each breath is reduced as a manatee increases its activity. Manatees at rest may take over a second longer to breathe than animals in flight.

Length of exhalation and inhalation.—The relation of exhalation and inhalation times to size and state of activity is shown in Table 10. The data indicate that it takes adult manatees roughly 0.5 seconds longer than calves to exhale and 0.5 seconds longer than calves to inhale. The exhalation and inhalation times of juveniles fall midway between those for calves and adults. Analyses of variance (significant at the .10 level) suggested that the breathing of active manatees is shortened as a result of quick, forceful exhalations and that the length of inhalation is little affected by an increase in activity. Exhalation occupies approximately 55 per cent of total breathing time when manatees are at rest but only 43 per cent when they are in flight.

TABLE 10

Length of Exhalation and Inhalation (in Seconds) in Relation to Body Size and State of Activity. Averages Are Weighted. "Light Activity" Includes Resting, Idling, and Feeding; "Moderate Activity" Includes Cruising and Playing; "Strenuous Activity" Involves Fleeing.

	Light activity			Moderate activity			Strenuous activity		
Age group	Number of observations	Mean	Range	Number of observations	Mean	Range	Number of observations	Mean	Range
Exhalation									
Calves (1.8–2.3 meters)	20	1.3	0.9–1.8	10	1.0	0.7–1.6	2	0.7	0.6–0.7
Juveniles (2.3–2.7 meters)	19	1.9	1.5–2.3	14	1.5	1.1–2.0	5	1.2	0.8–1.5
Adults (2.7–3.1 meters)	65	2.1	1.3–3.0	14	1.8	1.3–2.1	4	1.2	1.0–1.3
Inhalation									
Calves (1.8–2.3 meters)	14	1.0	0.5–1.3	8	0.9	0.6–1.3	4	0.9	0.6–1.1
Juveniles (2.3–2.7 meters)	19	1.5	0.9–2.1	16	1.2	0.8–1.9	3	1.3	0.8–1.5
Adults (2.7–3.1 meters)	65	1.6	1.0–2.3	12	1.5	1.0–2.2	3	1.5	1.4–1.6

Intervals between breaths.—According to Parker (1922), large manatees can remain submerged longer than small animals. The average submergence period of a captive calf less than 2 meters long was approximately four and a half minutes as compared to 12 minutes for an adult 3 meters long. Data from the present study corroborate these findings but indicate that the size of a manatee is related to the length of time it remains submerged only when comparing calves with older animals (Table 11). Juveniles do not appear to remain submerged for briefer periods than adults, at least while bottom-resting or idling.

There is evidence that the submergence periods of very young calves are exceptionally short. In Everglades National Park, Moore (1951*a*) observed a resting calf approximately 1 meter in length and found that the intervals between its breaths averaged less than a minute. This compares with an average submergence period of 3.4 minutes recorded at Crystal River for resting calves, the smallest of which was nearly 2 meters long.

D. Caldwell (1955) found that the frequency of breathing in the

TABLE 11

Length of Submergence (in Seconds) in Relation to Body Size and State of Activity. Averages Are Weighted. "Light Activity" Includes Idling, Feeding, and Rooting; "Moderate Activity" Involves Cruising.

	Resting											
	On bottom			Suspended			Light activity			Moderate activity		
Age group	Number of observations	Mean	Range	Number of observations	Mean	Range	Number of observations	Mean	Range	Number of observations	Mean	Range
Calves (1.8–2.3 meters)	48	201	84–325	17	20	9–42	81	114	7–260	36	88	32–110
Juveniles (2.3–2.7 meters)	59	313	85–650	34	26	14–53	19	185	19–328	14	104	89–134
Adults (2.7–3.1 meters)	88	232	61–470	41	30	12–59	64	160	53–338	71	112	49–200

spotted porpoise (*Stenella plagiodon*) increased as its activity increased. It appears that the same is true of sirenians. Moore (1951*a*) clocked the intervals between breaths of a young manatee during a 10-minute pursuit by speedboat and found that the animal was submerged for substantially shorter times than those recorded for an adult that was resting on the bottom. Jarman (1966) found that dugongs surface every three minutes when cruising in contrast to every five to 10 minutes when feeding. A direct correlation between length of submergence and state of activity was also observed among manatees at Crystal River (Table 11). The data indicate that manatees remain submerged for progressively shorter periods as their activity becomes more strenuous. For lack of sufficient data, submergence periods during flight or at the culmination of intense social interactions are omitted from the table. It is fair to predict, however, that intervals between breaths during these most strenuous of activities would be even briefer than those recorded for cruising manatees.

It seems that manatees also increase respiration in response to cold. In the Alafia River (Hillsborough County), bottom-resting animals were observed to breathe every minute or thereabouts in water 16 to 19°C—four to five times as often as their Crystal River counterparts, which rest in water 22 to 24°C. I am tempted to conclude that the reduced submergence intervals of the manatees in the Alafia River were a reflection of increased oxygen expenditure in the face of cold stress.

The longest submergence time recorded during the study was 11 minutes 46 seconds for a juvenile male resting on the bottom. The briefest intervals between breaths occurred when manatees were ventilating after a protracted dive (Fig. 24) and while engaged in "kissing" at the surface (Fig. 32). I have seen manatees breathing as often as eight times per minute while kissing but feel that this behavior should be divorced from the present discussion, inasmuch as I consider that respiration during kissing is an involuntary response not directly related to metabolic needs.

Resting

Two basic resting postures were employed by manatees observed in this study: 1) hanging suspended near the surface and 2) lying prostrate on the bottom. In both positions, the animals lapsed into

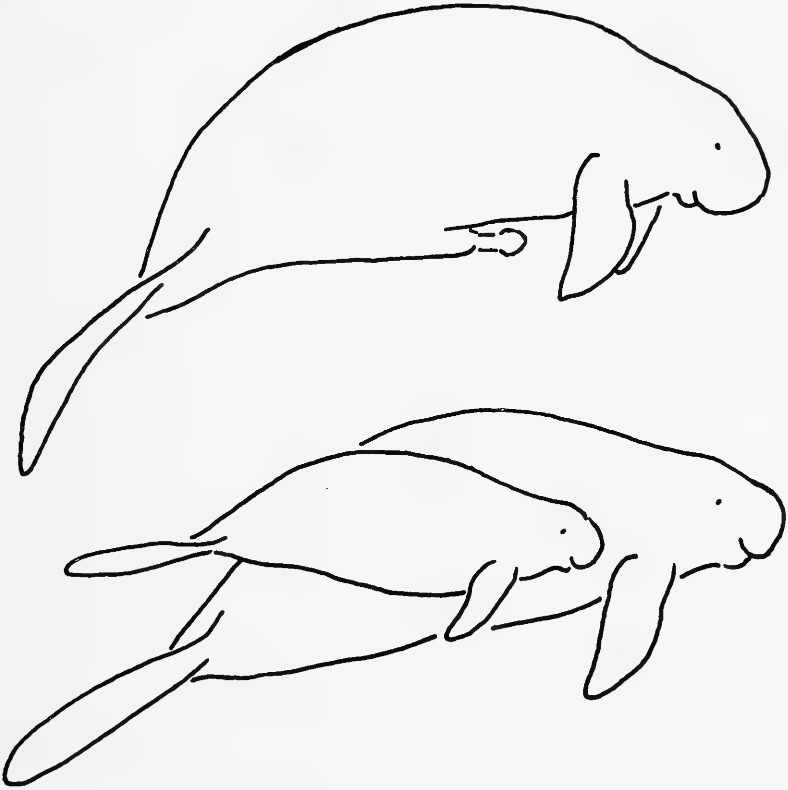


Fig. 25. Suspended-resting postures (drawn from photographs). Above, adult male with extruded penis. Below, preyearling calf beside its mother.

a somnolent state with their eyes closed and their bodies motionless. The eyes were opened only to surface.

Manatees allow the tail and flippers to dangle in typical suspended resting (Fig. 25). Animals usually adopted this posture just below the surface but occasionally broke water with their backs. While lolling at the surface, animals were sometimes seen to roll on their backs to bask for a moment with chest and flippers projecting above the water.

Young calves evidently lack proper ballast and have a unique suspended resting posture that suggests the center of gravity is shifted cephalad (Fig. 25). Moore (1951*a*) observed a meter-long calf that appeared to have positive buoyancy and difficulty maintaining its equilibrium.

When resting suspended, manatees are liable to drift and must regularly compensate for their displacement by making minor corrective movements with tail and flippers. Turbulent water tended to discourage suspended resting, the animals opting for the bottom where conditions were more placid.

Suspended resting was frequently interspersed with idling and was a more transitory activity than bottom-resting. It sometimes served as a substitute for bottom-resting on cold days when the upper layers of water were warmer than those at the bottom. Suspended resting was often a prelude to bottom-resting. A special case of suspended resting is found among bottom-resting animals when they take ventilative breaths at the surface between rests (see section on breathing).

When resting on the bottom, manatees are supported on the muzzle, stomach, and tail (Fig. 22). The flippers are held along the sides or flexed at the wrists and adducted under the chest. The tail usually rests flat on the bottom but may be curled under at its tip. It was common for bottom-resting manatees to roll on their sides or backs momentarily. One juvenile male was seen to lie immobile on his back for periods exceeding a minute. When alerted by a disturbance, bottom-resting manatees poised themselves on the tips of their flippers, ready to shove off at the least provocation.

Animals were seen to bottom-rest, apparently without preference, on a variety of substrates (including sand, mud, limestone, oyster bars, and beds of aquatic plants). I have even observed them "asleep" burrowed into clumps of dense vegetation. Resting calves sometimes lay on the backs or tails of their mothers. I once observed a bull resting on a limestone ledge supported by his muzzle and tail with his midsection suspended over a wide crevice. The swollen bellies of cows in advanced pregnancy forced them to rest at an angle to the bottom so that their heads or tails were off the substrate. One gravid female was seen resting on a clump of *Hydrilla* tilted forward at a 45-degree angle to the bottom.

Manatees generally chose shoals of 1 to 3 meters for bottom-resting, but occasionally rested at greater depths. At the site of a large spring in one canal, they bottom-rested at a depth of 4 meters. In the vicinity of the Main Spring, animals showed a predilection for two sandy areas kept free of vegetation by their activity.

Feeding

Use of the mouth.—The upper lips of a manatee are bilobed and covered with stiff bristles. Their use in feeding has been described by Chapman (1875), Garrod (1879), Mohr (1957), and Allsopp (1961). The lobes are everted, projecting the bristles into the food source, then closed laterally, forcing the bristles to grasp the vegetation, tuck it into the cleft between the lobes and funnel it to the mouth. The process is rapidly repeated and suggests fanning (Chapman, 1875).

Manatees chew incessantly while they manipulate their lip pads. The sound of their teeth grinding is audible underwater. The masticatory rate is approximately two chews per second. Feeding animals masticate as they rise to surface, pause to breathe, then resume chewing on the descent. Occasionally at Crystal River a manatee would begin its ascent to breathe by jerking its head back to break rooted plant stalks in its mouth.

Use of the flippers.—Use of the flippers to facilitate feeding depends upon the type of vegetation being consumed. In the St. Johns River where water hyacinth is the principal food, manatees were observed to pull the plants below the surface with their lips, then to hold the hyacinth in front of their mouths with the tips of their flippers. At Crystal River where the preferred food is submerged and rooted, manatees did not use their flippers to convey food to their mouths or to assist ingestion in any way. Feeding animals employed their flippers solely to position themselves and to sweep encumbering vegetation away from their heads.

Manatees normally raise themselves on their flippers to feed on bank growth. Bangs (1895) wrote of animals dragging their bodies partially out of water with the flippers to reach mangrove leaves. At the Crandon Park Zoo (Dade County), manatees have been seen to raise their heads and shoulders above the surface to crop lawn grass (Gordon Hubble, personal communication). Many interviewees in Florida had seen manatees feeding on the banks of rivers with heads and backs awash and supported on the flippers. In Guyana, manatees regularly graze on phraetophytes with their bodies half out of water and their flippers exposed on the mud (Datakaran Jeetlall, personal communication).

Gohar (1957) reported that for feeding purposes dugongs use their flippers to dig out and collect seagrasses into little piles on the bottom, but I observed no evidence of comparable behavior among manatees.

Comfort Activities

Stretching.—The bodies of manatees are remarkably supple, as reflected in their stretch postures (Fig. 26). In one, the back is arched concavely and in another, convexly. Variant postures combining elements of both the convex and concave arches also are illustrated. In all stretch postures the eyes were closed, the chin drawn in on the chest, and the flippers adducted tightly across the chest. Animals usually uttered a prolonged groan while stretching.

Stretching was closely associated with resting. Resting sessions were regularly interrupted or terminated by stretches. Animals stretched on the bottom or on rising to or descending from the surface. Manatees usually arched their backs convexly then concavely in sequence.

A stereotyped stretch-roll often followed the stretching sequence. The animal rolled on its back in a concave arch, then backdived to the bottom, often plunging headfirst into the sand or silt where it lay momentarily, its muzzle buried, in a partial headstand or upsidedown.

While arching their backs convexly, males sometimes extruded the penis. Doubled over thus, they occasionally stroked the penis with one or both flippers in what looked to be incipient masturbation. Stroking, however, was awkward and unrhythmic and rarely lasted more than a few seconds. Ejaculation was never observed. Extrusion and retraction of the penis was often repeated several times in succession. Occasionally, males swam about and rested with the penis extruded (Fig. 25). In one instance a bull's penis, extruded during a stretch, remained tumescent and pulsing for nearly five minutes of suspended resting and was only retracted when the animal finally sank to the bottom. In another case a young male maintained an erect penis for 16 minutes during which time he alternately bottom-rested and courted passing cows. The erect penis was always directed craniad and did not deviate from the longitudinal axis of the body.

Scratching.—Manatees make use of their flippers to scratch but are restricted by the limited reach of the appendages and must confine scratching to the chest, ventral neck, and head regions.

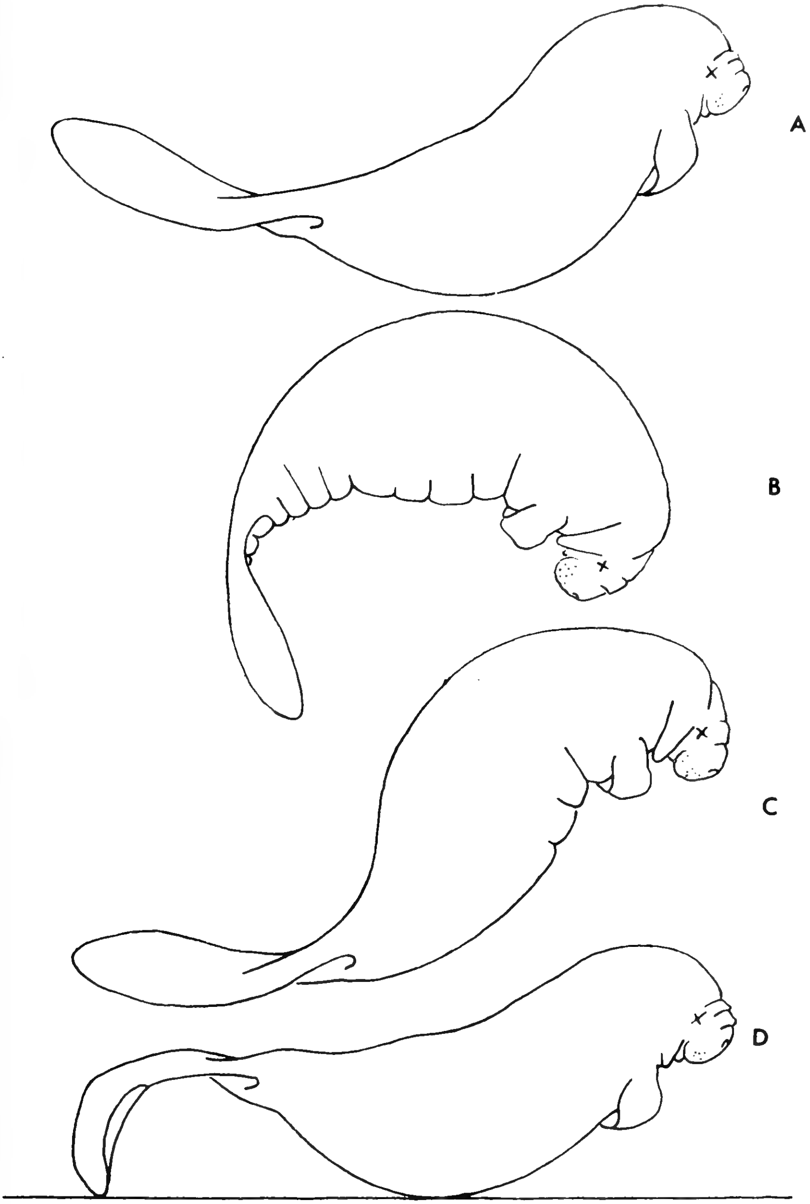


FIG. 26. Various stretch postures.

Irritations on the remainder of the body are relieved by rubbing on objects.

The manatee operates its flippers singly or in unison when scratching. The radial edge of the flipper is normally used to rub the creases under the chin and the tip and palmar surface to rub the head, chest, opposite flipper, and axil. I once saw a bull use the tip of his right flipper to scratch at a hook caught in his left flipper.

Scratching tended to be concentrated in the axils of the flippers, in the folds under the chin, and in the orbits of the eyes (Fig. 19D). Microorganisms may have been responsible for the itch; epidermal scrapings from afflicted areas yielded microscopic nematodes.

In Kings Bay, manatees regularly rubbed on logs, poles, cement blocks, and limestone outcrops. Sandy areas bared by manatee activity surrounded these objects. A broken milk bottle firmly implanted in the sand was used for rubbing and may have cut the bellies of some animals. Local crabbers complained that manatees rubbed on their crab traps, turning them over or imbedding them in the mud.

Manatees also rubbed on buoy lines and anchor ropes, making repeated passes that recalled a cat brushing against a person's leg. Once, several manatees rubbed along the string suspending a thermometer hung in their midst. One especially tame young cow used to swim up to my boat to nibble and rub her head on the anchor, anchor rope, hull, and propeller blades (Fig. 27). At times she grasped the anchor rope to her chest and rubbed awkwardly on it (Fig. 19I). At a yacht basin in Palm Beach County, manatees have been seen to rub their backs on the hulls of boats (to remove barnacles, it was claimed by those who made the observation).

The limestone ledges at the Main Spring were a favorite rubbing site for some animals. One mature bull was particularly fond of rubbing there. He was once seen to spend an hour rubbing on the rock, slamming into it, rebounding, tumbling, turning, and twisting to make contact with all parts of his body, and working himself into a ferment. On another occasion, a young cow rolled sideways, wedged herself in a limestone crevice, and rubbed back and forth on her side.

A log below the Main Spring was another popular rubbing site. Manatees gathered here to rub, wallow in the sand, and scratch on a cement block nearby. Usually the animals dragged their bellies

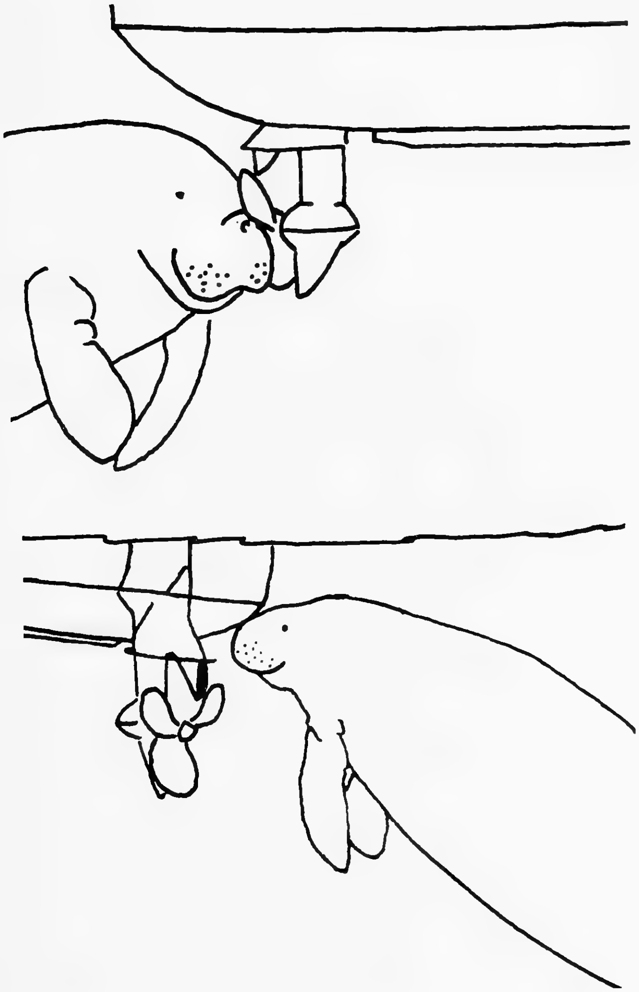


Fig. 27. Juvenile female nuzzling propeller and hull of runabout (drawn from photographs).

and tails to and fro across the log. Among males there was one instance of possible masturbation during such behavior. A juvenile bull with penis extruded courted a cow near the log but was thwarted; in an apparent displacement reaction, the young male rubbed his genital region briefly against the wood. One bull stroked the surface of his tail to the right and left across the log for more than five minutes, then rolled over and repeated the act. At the cement block manatees rubbed their noses, chins, and orbits. Bottom-resting animals occasionally rubbed their muzzles in the sand and rolled on their sides to rub their heads. A young male once lay on his back rubbing in the sand for almost a minute.

An adult female was once discovered standing on her head at the foot of an iron signpost, rubbing the underside of her tail on the pole. Other animals were frequently observed rubbing their bellies, sides, backs, heads, and tails at the base of the same pole. Rust smears on the hide were a telltale indication that an individual had recently engaged in this activity.

Mouth cleaning.—Prominent among the self-care activities of the manatee is mouth cleaning. The animal opens its mouth wide, wrinkles back its nose, and everts the lobes of its upper lips in an apparent effort to free irritating particles of vegetation lodged in the mouth (Fig. 28). Sometimes the mouth was closed so that the lower lip protruded over the upper lobes. If this manipulation failed to loosen entrapped particles, the animals resorted to the fanning, masticatory movements of feeding, and/or to rubbing the tip of a flipper back and forth across the gums. The flipper on the side of the irritation was usually used, although on rare occasions, both flippers were employed simultaneously. If the annoyance persisted, the manatee was apt to rub frantically and even swat its lip pads (Fig. 19C). I once watched a bull become almost frenzied in its attempts to extricate plant debris from its mouth.

Mouth cleaning took place at any time, interrupting any activity. It was not more prevalent during or after feeding sessions and was observed in calves as well as adults. Mouth cleaning was generally engaged in for only a few seconds, although occasionally it occupied an animal for several minutes. Often during the cleaning process broken bits of vegetation could be seen falling from the mouth.

In behavior evidently unrelated to mouth cleaning, manatees sometimes nibbled the tips of their flippers in a manner suggesting that the irritation was on the manus.

Rooting.—Manatees sometimes paused to root in the sand or mud while reconnoitering the bottom. They appeared to "chew" the substrate, drawing a mixture of sand and water into their

FIG. 28. Mouth cleaning. Above, adult male everting lips; note bristles. Below, adult female rubbing mouth parts with her flipper (photos by Russ Kinne and James Powell, Jr.).

mouths, then expelling it. The activity, audible underwater and reminiscent of feeding, sounded as if sand was being sifted through the mouth. In the process, the flippers made abortive movements to push sand away from the mouth. The flippers were sometimes flailed about so violently as to stir up clouds of sand around the head. Eventually the action of mouth and flippers scooped a pit out of the sand.

A juvenile cow was once observed "standing" on her head while she rooted in a pit; her muzzle was buried up to the eyes in the loosened sand. After surfacing she would return to the same depression and start rooting again. This continued for 20 minutes. On another occasion I observed a calf rooting for more than an hour.

One juvenile cow that was rooting along the sand collided head on with a bull that was rooting in the opposite direction. Both then wallowed in the silt they had kicked up. Shortly thereafter, the cow wedged herself into a wide limestone crevice and rooted in the sand at its base.

The function of rooting is not clear. It may be a means of cleaning the mouth or perhaps simply affords a pleasurable sensation. If silt and sand are ingested, rooting may provide manatees with ballast or with needed minerals.

Sneezing.—Twice in the course of the study manatees appeared to sneeze. In each instance the animal opened its mouth and recoiled, exploding a mass of bubbles from the nostrils and startling its companions. The sneezes were followed at once by a surfacing.

Eliminative Behavior

Micturition and defecation.—Manatees have no special postures or behavior associated with urination and defecation. The elimination of waste took place at any time, even while resting. The frequency of urination was not determined. Defecation was practically continuous. Feces are passed slowly and often trail partially extruded from the anal aperture.

Manatee feces are soft, mealy, ochroid cylinders that are sometimes grooved. They are tapered at the ends if not broken (Fig. 29). One fecal specimen was 28 centimeters long, an unusual length because the cylinders usually break on discharge before

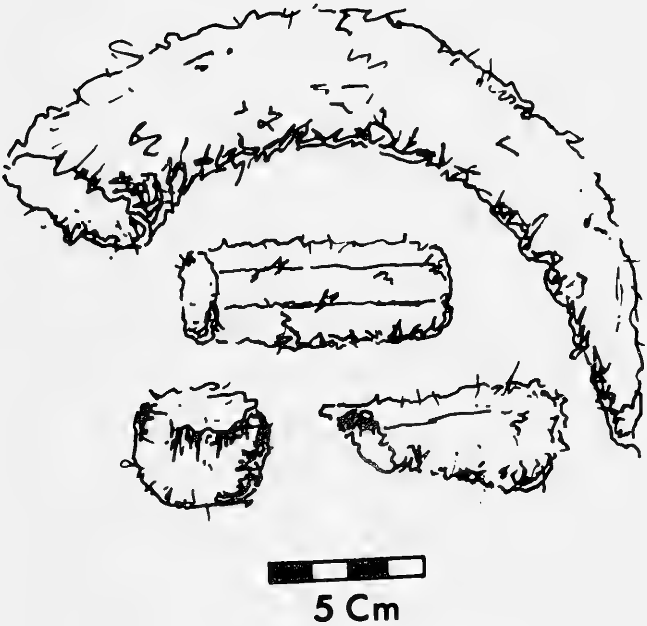


Fig. 29. Manatee fecal specimens.

reaching that size. The diameter of most feces is 5 to 7 centimeters, the maximum diameter observed being 7.3 centimeters.

Manatee excrement was not consumed by fish or other animals and lay on the bottom until it disintegrated, usually within a day or two.

Flatus.—The herbivorous diet of manatees generates considerable gas in the alimentary tract, and the animals were constantly relieving flatulence. Apparently gas is never expelled through the mouth.

Regurgitation.—Manatees periodically regurgitated a yellow-green mash composed of partially digested plant material. Animals often chewed while the mash was being brought up and passed through the mouth. Neither eructation nor visible stomach contractions were seen to accompany regurgitation. Calves regurgitated as well as adults.

Regurgitation occured preponderantly during resting, at least

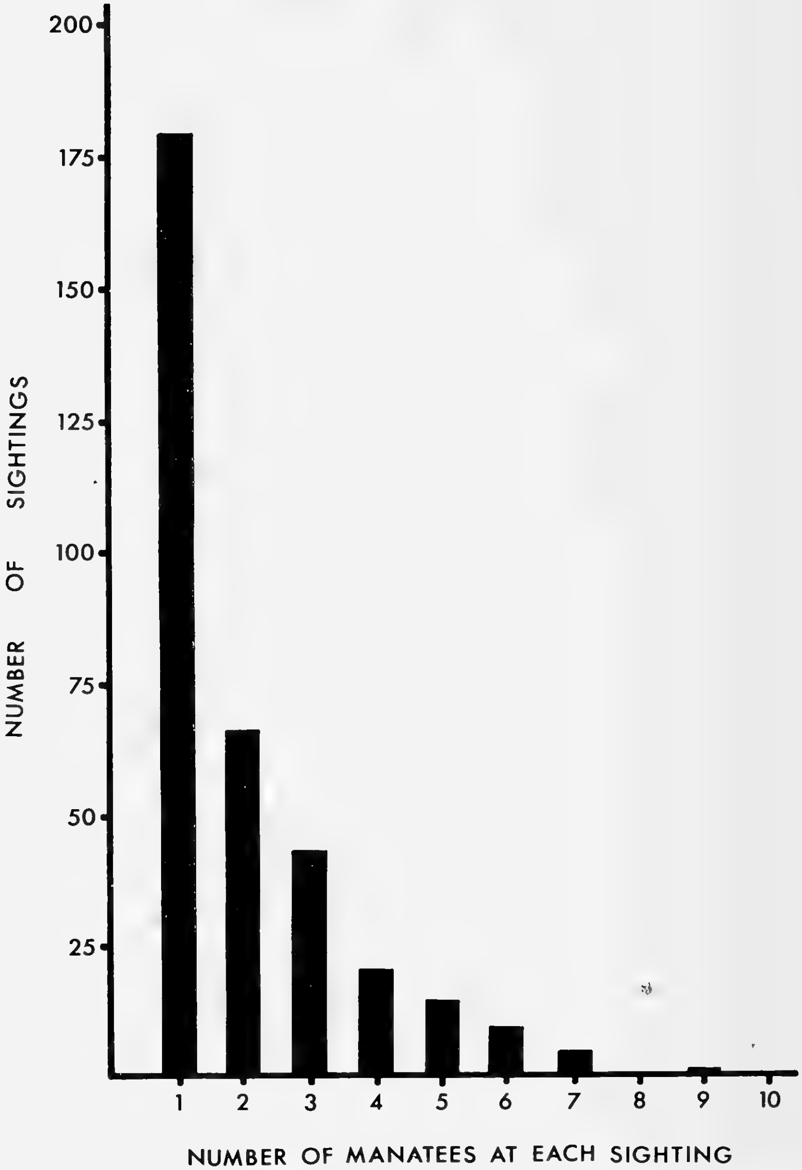


FIG. 30. Frequency distribution of sightings of single and various-sized groups of manatees (a cow with calf is considered a single animal). Data are from 335 aerial sightings outside the cold-induced congregations.

an hour after the last feeding session. Once, a juvenile cow regurgitated after ingesting manatee excrement, but there appeared to be no correlation between the two acts.

SOCIAL BEHAVIOR

The manatee is a mildly social, essentially solitary animal. Results of tracking manatees on their daily rounds indicated that each animal was fully independent and generally passed its time alone. Outside the cold-induced congregations, 53 per cent of all manatee sightings from the air were of solitary individuals; groups of two, three, and four were seen 17 per cent, 13 per cent, and 6 per cent of the time, respectively (Fig. 30). These statistics are contradicted by more recent data from aerial surveys conducted by the National Fish and Wildlife Laboratory. According to Howard Campbell, leader of the project, groups of two or more manatees were seen more often than single animals, suggesting that manatees are not "essentially solitary."

I found the only firm association among manatees to be that between a cow and its calf, which comprises the manatee family unit. All other associations, (with the exception of the estrous herd) were casual, temporary groupings. Groups consisted randomly of juveniles and adults of both sexes. Animals grouped to cavort, migrate, rest, or feed, but the social bond was highly unstable, sometimes lasting only minutes. Few animals were known to have remained together so long as a day.

Bulls were more active socially than cows and were responsible for most intraspecific contact. Cows were generally passive, limiting their social overtures to nonsexual situations. Gravid cows were exceptionally sluggish and generally nonsocial. Resting manatees that preferred to be left undisturbed rolled or swam away from solicitous companions. Bottom-resting animals occasionally cuffed intruders with their flippers.

Social interactions occurred in both sexual and nonsexual contexts. The distinction was not sharply defined because the patterns of all intraspecific contact were basically the same. These included mouthing, nuzzling, nudging, and embracing. There were no displays. The preponderance of mouthing (here defined as any caress with the mouth or lip pads) suggested that manatees possess a

FIG. 31. Juvenile male mouthing and embracing peer. Adult female in foreground (photo by James A. Sugar, (c) National Geographic Society).

chemoreceptive sense (see section on taste). Mouthing was concentrated on the backs and sides of a recipient and was often accompanied by an embrace with the flippers (Fig. 31). Nuzzling and nudging were minor variations of mouthing. Muzzle to muzzle contact was generally restricted to stereotyped "kisses" at the surface (Fig. 32). For lack of a better understanding of their function, kissing and related forms of nonsexual interaction are discussed beyond in the section on play.

Manatees exhibited social facilitation when in groups. Responses were mutually stimulating. If one animal fed or rested, its associates often did likewise. The herd instinct, however, appeared to be vestigial. Flight reactions, communicated vocally, generally produced a response from other manatees in the vicinity, but the vocalizations of an alarmed animal seemed less group-oriented than simply a reflection of its own emotional state. At the approach of potential danger, squeals that might be interpreted as warnings or alerts were not always emitted. The only predictable alarm response was between a cow and her calf and this rarely attracted the attention of other manatees in the area.

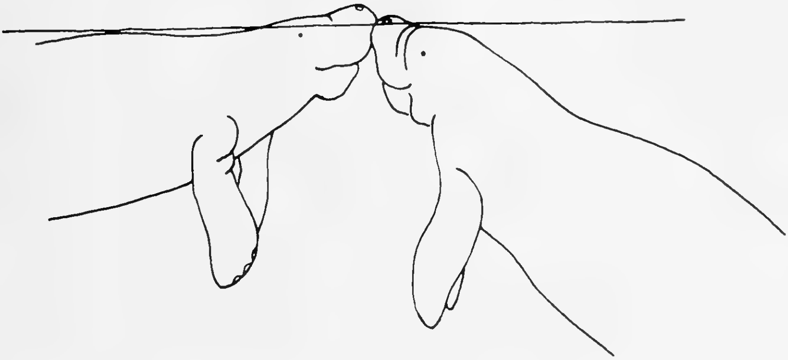


Fig. 32. Two juvenile females "kissing" at the surface (drawn from photograph).

Cruising manatees, furthermore, did not maintain formations. Animals sometimes swam temporarily in eschelons, abreast of one another or in tandem, but these formations did not appear to be intentional.

As far as is known, manatees do not assist distressed or wounded individuals. Within groups at Crystal River, there was no evidence of communal defense or mutual aid. The behavior of a mother toward her calf may be an exception. Frank Rivell, an old guide on the Tomoka River (Volusia County), told me of having seen a cow butt her dead calf for two days in an apparent effort to keep it above the surface.

I never witnessed the reaction of manatees to an afflicted companion although Steller (1751) wrote of harpooned sea cows being accompanied in their struggles by fellow animals. During the present study a local resident fishing in Kings Bay inadvertently hooked a manatee. He told me that a second individual remained close by the hooked animal until the line was cut. In the absence of more conclusive proof, this activity is, to me, as much an indication of curiosity as it is of succorant behavior.

Aggression in manatees was confined to collisions between bulls for a position next to an estrous female. Agonistic contact was never observed outside the estrous herd, but there were occasional hints of an age-dependent hierarchy. For example, on one occasion a juvenile male that I was scratching seemed to flee at the approach of an adult bull. Normally, however, animals seeking my attention underwater never competed for priority. At rubbing stations, animals of the same size tolerated one another, but subadults usually yielded to adults.

There appears to be no territoriality among manatees. I obtained no evidence of an animal defending or guarding an area or exhibiting agression toward conspecifics in a territorial context. My observations support Moore's (1956) conclusion that manatees have independent, overlapping, often identical ranges.

Vocalizations

Manatee vocalizations were first recorded by Schevill and Watkins (1965), who found most of the calls to be squeaky and ragged, lasting 0.15 to 0.5 seconds and composed of two or more frequencies that were not harmonically related. Most fundamental tones were between 2.5 and 5 kHz. Evans and Herald (1970) found that the sounds produced by a young male Amazonian manatee were basically similar, but of higher fundamental frequency (6 to 8 kHz).

Manatee calls heard underwater at Crystal River consisted mostly of high-pitched squeals, chirp-squeaks, and screams. These noises were produced with mouth and nostrils closed and with no accompanying escape of air. According to Phillips (1964), manatees also vocalize out of water; a captive female squeaked as she was being hoisted from one tank to another at the Miami Seaquarium.

Manatees were normally silent at Crystal River, even in groups. Hours of recordings with a hydrophone gave the impression that manatees have an impoverished vocabulary. They seemed to convey information by varying the intensity and duration of their calls rather than by emitting mood-specific, harmonically distinct noises. They apparently make sounds only under conditions of fear, aggravation, protest, internal conflict, male sexual arousal, and play. Unlike cetacean phonations, manatee vocalizations appear to be nonnavigational; to lack ultrasonic signals, pulsed emissions, or directional sound fields; and to be more impulsive than communicative.

The relative importance of vocalizations in intraspecific communication is unclear. To what extent, for example, are individual vocalizations a monologue or a dialogue? The human ear cannot pinpoint the source of a phonation, so in most social interactions it was impossible to attribute a sound to a specific animal. In some cases, however, I was able to identify the individuals producing sounds and to speculate on their function.

Frightened animals generally screamed in alarm. I gained the impression that juvenile manatees vocalized more often than adults under conditions of stress, perhaps because juveniles still retain the tendency, acquired as calves, to call repeatedly for mother (see below). Older manatees were rarely heard to emit an alarm call.

Occasionally bottom-resting animals squealed in apparent irritation when disturbed by other manatees. Cows often squealed in seeming annoyance when embraced by bulls. Bulls thwarting the homosexual overtures of other males squealed in what appeared to be vexation.

At the height of sexual frenzy in an estrous herd, vocalizations were almost constant from cow and bulls alike. It is possible that the bulls' squeals were rivalry signals emitted in a competitive context. Bulls also squeaked in homosexual embraces, appearing to reinforce the abnormal pair bond.

Manatees also vocalized during play. I presume that many of the calls associated with this activity were expressions of pleasure and inducements to further contact.

Manatees occasionally emitted sounds when alone. From time to time animals chirp-squeaked and squealed in apparent pleasure while rubbing on logs or other objects. A few squealed when I caressed their backs. One animal emitted a single, high, almost inaudible squeak while being scratched. Manatees generally investigated divers with caution, sometimes emitting "snort chirps" or squeals that I interpreted to be displacement vocalizations resulting from approach-avoidance conflicts.

In addition to squeaking and squealing, manatees groaned, particularly while stretching. Bulls interspersed groans with squeaks during collisions in pursuit of estrous cows. Animals that approached me to be caressed emitted soft, barely audible grunts.

The only predictable vocal exchange between manatees was the alarm duet between a cow and her calf. The appearance of a boat or divers ordinarily threatened a cow with offspring. She would react by calling the calf to her side with repeated screams. Each scream triggered an immediate reply from the calf. Once together, the pair usually fell silent and investigated the source of danger.

The cows resumed vocalizations only as they prepared to flee, presumably to insure that their calves remained close beside them.

Recordings indicated that calves called more often than their mothers. Calves vocalized even when undisturbed and in close proximity to their mothers. The cows usually responded unless resting. The distress squeals of startled calves always brought their mothers to investigate. Mothers and calves also appeared to increase vocalizations in turbid water. I was impressed by the frequency of sound emission whenever I dove with cows and their young in water in which visibility was a few meters or less. This suggests that animals maintain contact under conditions of impaired vision by becoming more vocal.

I believe that manatees are able to recognize one another by sound—that is, by subtle variations in the pitch, frequency, and timbre of individual vocalizations. It was obvious, for example, that cows were selectively responsive to the calls of their calves and vice versa. Bottle-nosed porpoises have been found to discriminate between the whistles of various conspecifics, and sonagraphic analysis of the calls has revealed minor differences unique to the individual (Caldwell *et al.,* 1972). It seems reasonable to assume similar "voice prints" characterize individual manatees.

Sexual Behavior

Estrous herd.—The only cohesive association between manatees, besides the cow-calf family unit, is found in the estrous herd composed of a cow in heat accompanied by courting bulls. These groups may remain together for periods ranging from a week to more than a month. As many as 17 bulls once were observed following an estrous cow—virtually the entire male population of Kings Bay at the time. Juvenile males joined and left the herd constantly, but a nucleus of mature bulls was always present and in persistent pursuit of the cow.

The urgency of male courtship within an estrous herd waned when the cow was not in motion—when feeding or bottom-resting, for example. At such times, bulls themselves were induced to feed or rest, only resuming their sexual overtures when the cow was again active. Courting bulls had a tendency to huddle around an estrous cow that was bottom-resting and to face in the same direction as she.

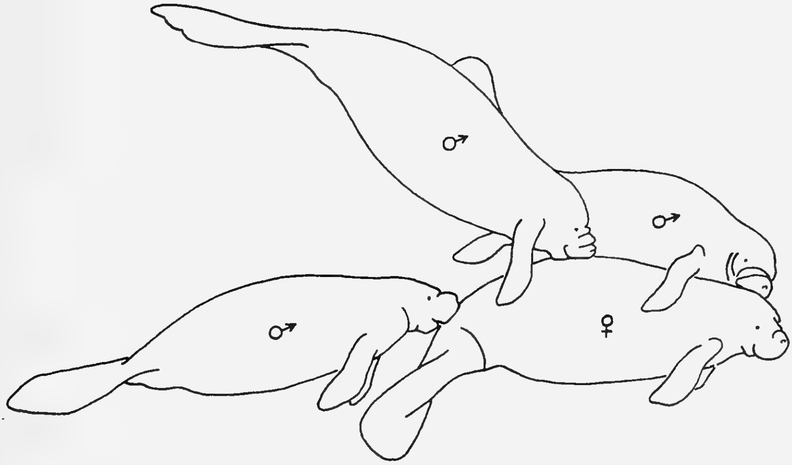


FIG. 33. Courtship activity. Three adult males mouthing and embracing estrous female (drawn from photograph).

For the most part, the courtship of bulls was relentless, forcing the cow into continuous flight. The bulls mouthed and embraced her back (Fig. 33), rode her when she surfaced (Figs. 34 and 35), and rolled upside down in an effort to approach her abdomen. The cow invariably rolled away from them, presenting her back to their advances. If a bull succeeded in nibbling or grasping her underside, she escaped with a violent jackknife, which usually incited her escorts to more frenzied embraces. I have seen bulls knocked to the surface by the powerful thrusts of a cow's tail. I myself was once thrown clear of the water when a cow directly below me jackknifed in response to a bull mouthing her genital region. Sexually aroused bulls sometimes left the herd momentarily to court passing anestrous cows or to transfer their sexual drive to homosexual encounters.

At the peak of courtship, estrous herds are frequently observed in shallow water a meter or less in depth. It is a popular conception in Florida that under these circumstances manatees are mating. It appears that, to the contrary, estrous cows seek shoals to evade their male escorts. A cow is less vulnerable in shallow water because it is more difficult for bulls to approach her underside. I have reason to believe that cows in estrus may even resort to stranding

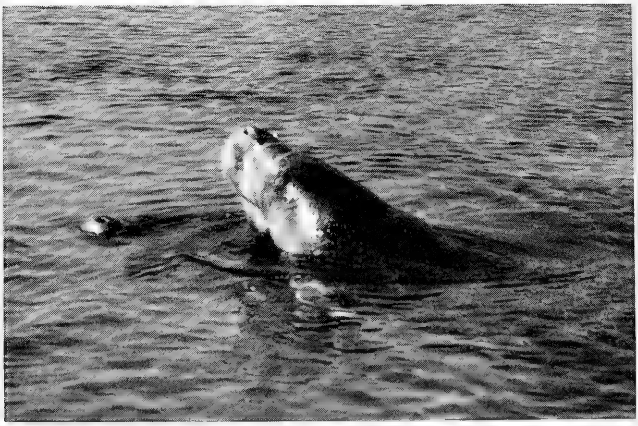


FIG. 34. Male riding back of female during surfacing (photo by Russ Kinne).

in an effort to escape the unrelenting pursuit of the bulls. Once, during frenetic sexual activity in shallows off a sand bar in Kings Bay, a member of an estrous herd beached momentarily on the bar with its back awash. I was unable to identify the beached animal, but the following incidents lead me to think it may well have been the cow. From the air my pilot and assistant saw an adult manatee beached in 20 centimeters of water on the shore of a spoil island in the Indian River (Brevard County). In the shallow water beside the stranded animal were at least five other manatees milling about. There was little question that the group was an estrous herd, and it appeared that the beached manatee was the female driven in to shore by the accompanying bulls. As the plane circled, the stranded manatee lifted itself on its flippers, floundered around, reversed direction, and headed toward the water. The New Smyrna Beach News (13 September 1973) reported the stranding of a mantee on an outgoing tide and its rescue by local residents. The Marine Patrol Officer who supervised the rescue operation said the beached animal was an adult female and that 10 to 15 manatees had been seen beyond the surf just before the stranding.

To my knowledge, copulation never took place in shoals. I have been reliably informed, however, that in Belize a pair of copulating manatees was found awash on their sides in knee-deep water (Colin Bertram, personal communication). The one copulation I observed

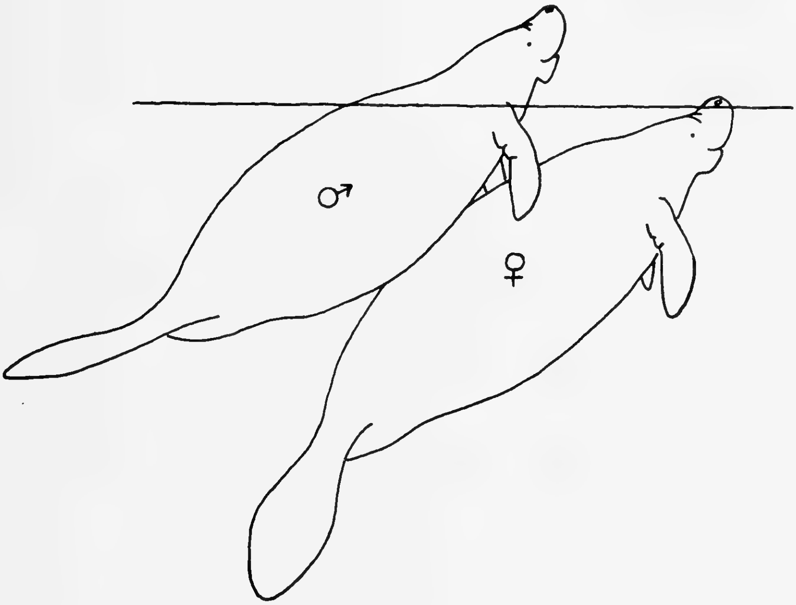


FIG. 35. Male riding back of female during surfacing. This posture is sometimes assumed by two males engaged in homosexual activity.

occurred near the bottom in water 2.5 meters deep. Immediately before this observation, the cow in question was sexually active over a "deep" and may have mated at a depth of 4–5 meters. Her activity at that time was obscured by silt.

The parallels between the mating behavior of manatees and elephants (*Loxodonta africana* and *Elephas maximus*) are striking and possibly reflect their common origin. Elephant cows are promiscuous and cow-bull associations are transitory (Buss and Smith, 1966; Elapata, 1969; McKay, 1973). According to Short (1966), intervals of sexual inactivity are intermixed with periods of intense activity when as many as four matings may take place within two hours. Manatees exhibit similar sexual behavior; while receptive, estrous cows are polyandrous.

I observed copulatory behavior on 7 December 1968. For 45 minutes a female, pursued by five bulls (three adults and two juveniles), engaged in intense reproductive activity in a 5-meter

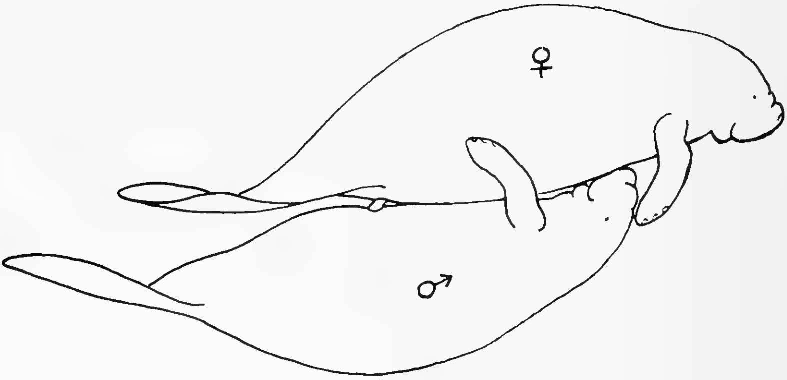


FIG. 36. Copulatory embrace.

"deep" near the Main Spring in Kings Bay. Although interactions were obscured by the roiled water, mating probably took place. When the herd finally emerged in clear water, the cow paused in flight to allow successive copulations by two of the adult and one of the juvenile bulls. The nearest male would roll on his back, swim up from the rear, mouth the genital area of the cow, then slide fully under her, firmly grasping her from beneath, extruding his penis and effecting intromission (Fig. 36). Pelvic thrusts were not evident. During copulation, the other bulls mouthed and embraced the cow from above and from the side. The cow was passive throughout and sank to the bottom in each embrace so that the males lay on their backs while mating. Between copulations the cow swam short distances before again pausing. Intervals between matings lasted less than a minute. The copulatory embraces lasted 15 to 30 seconds. Postcopulatory behavior among the bulls was identical to precopulatory behavior. They continued to embrace and pursue the cow. Within 10 minutes of the final mating, the cow made vigorous but unsuccessful attempt to evade her escorts. In her efforts to escape, she plunged headlong into clumps of *Hydrilla*. The males continued to pursue the female in the same area of the bay for most of the day, and the herd was there again the next morning.

With the exception of the above instance, estrous cows were never seen to make receptive gestures to their male escorts. It appears, therefore, that a particular stage of the estrous cycle is responsible for a cow's receptivity and that the intensity of male courtship is of lesser importance. Perhaps cows are receptive only during estrus proper but engage the attention of bulls during the other phases of the cycle. Among elephants, multiple copulations suggested to Buss and Smith (1966) that proboscideans may have successive periods of estrus leading to conception. Like the elephant, the manatee may be a monovular, polyestrous species that undergoes a number of sterile estrous cycles before conceiving (Short, 1966). The fact that estrous herds sometimes involve cows with calves supports this hypothesis, assuming that ovulation does not occur during lactation. The actual duration of estrus in manatees is unknown.

Male aggression.—Male competition for the nearest position to an estrous cow appears to be the sole cause of aggression among manatees. As courtship activity intensified in an estrous herd, the mature bulls maintained closer station to the cow and, rolling on their sides, collided belly-to-belly with one another, briefly embraced, then thrashed apart in violent contortions. Bulls turning to embrace the cow sometimes collided sideways with oncoming rivals. Squeaks and groans accompanied the collisions.

As the pitch of sexual activity heightened, the frequency of collisions increased. In their excitement, bulls often tore through submerged vegetation, causing mats of uprooted plants to float to the surface. Competition eventually reached a peak, irrespective of the cows receptivity, then gradually subsided. Juvenile males tended to remain at the periphery of the herd and rarely competed with older bulls.

Collisions never resulted in injury. In the long run, the strongest, most aggressive bull is presumably closest to the cow during her receptive period and thus first to inseminate her. Clashes between bulls over anestrous cows were short-lived and infrequent.

Social interactions outside the estrous herd.—Sexual interactions between male and female manatees were not limited to the estrous herd. In fact, sexual encounters outside estrous herds were habitual. These encounters also appear to be characteristic of dugongids. Describing social interactions of the now-extinct northern sea cow, Steller wrote that the females turned away from the males and fled from their incessant pursuit (translation in Goodwin, 1946).

Sexual encounters among manatees were invariably initiated by bulls, both juveniles and adults, but always thwarted by cows. Bulls appear to have strong sexual appetites and spent much of their time courting any anestrous cows fortuitously encountered. The bulls were indescriminate in their overtures and mouthed and embraced subadult and adult females as well as cows with calves. Bulls often devoted attention to several cows at a time. Sometimes several bulls converged simultaneously on a single cow. Anestrous cows rebuffed and fled from all sexual advances. Like estrous females, they were particularly defensive of the venter and presented the dorsum to every male overture. This behavior was first described by Moore (1956), who wrote of an adult female that predictably turned her genital aperture 180 degrees away from an aggressive male. In response to a male rolling fully on his back to mouth her underside, a cow would roll upside down, discouraging a belly-to-belly embrace. Once, a bull, nudging a cow that had rolled on her side to avoid his embrace, pushed her into a limestone ledge.

The majority of bull-cow encounters outside of the estrous herd were casual and brief. On a few occasions, however, sexually aroused males persisted in their overtures for hours and even drove cows into hiding. I once watched two juvenile males pester an adult cow for three hours until she stymied them by concealing herself in a massive clump of *Hydrilla.*

The excitement generated by sexually aroused males was pervasive and stimulated other males in the immediate area to sexual activity. The pursuit of cows became more intense and was frequently interspersed with homosexuality. Groupings dispersed and reformed in a variety of male-male and male-female combinations. At the height of sexual activity, cows in flight from bulls were seen to tear through vegetation and plunge into the mud. The general agitation subsided in time as the animals dispersed to feed or rest.

Homosexuality.—Homosexual and masturbational activities have been seen among captive male manatees (Earl Herald, personal communication; personal observations). In the wild, manatees also engage in mutual masturbation. In typical homosexual behavior, two bulls embrace, merge genital apertures, then extrude and rub penes. It is likely that ejaculation occurs although I never saw emission of semen. Homosexual activity was never observed among females.

Homosexual embraces in no way resembled the copulatory em-

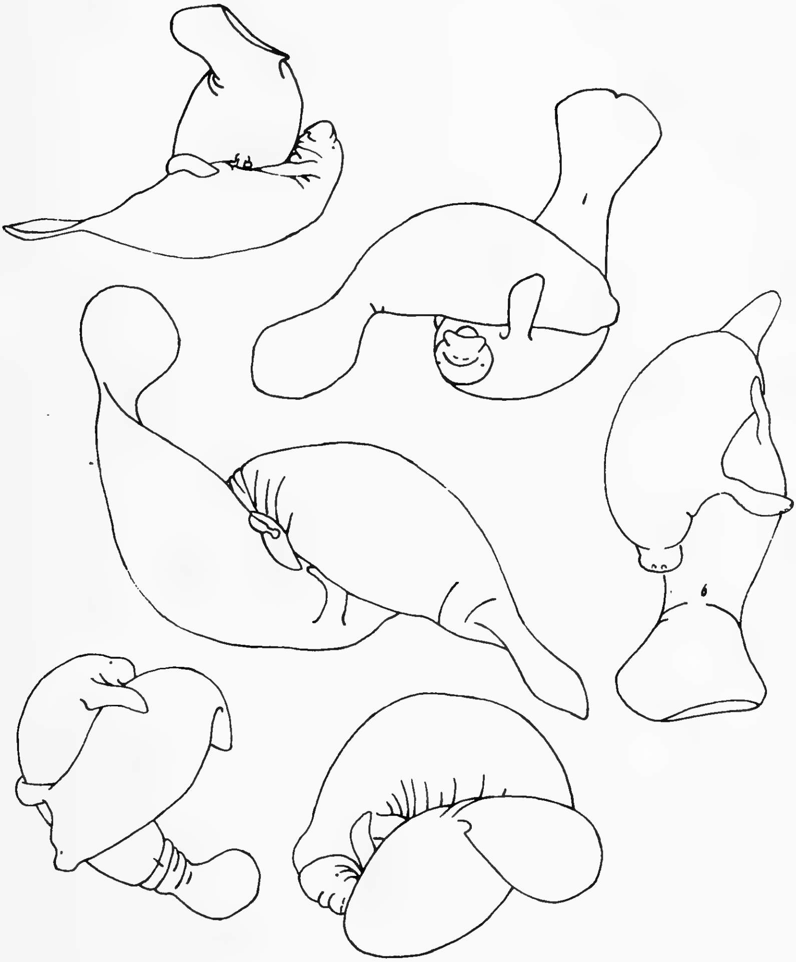


Fig. 37. Male homosexual embraces (drawn from photographs).

brace. Males embraced one another head to tail or from the side (Fig. 37). No bull ever assumed the position of a receptive female. In the embrace, frequently preceded by "kisses" at the surface, the two males tumbled to the bottom where they remained tightly clasped, thrusting and wallowing. Homosexual embraces lasted up to two minutes before the participants disengaged to surface.

Often more than two bulls were involved simultaneously in a homosexual match. I once watched four adult males as they kissed at the surface, then firmly interlocked in a group embrace. The two outside males clasped the central participants and rubbed their genitalia against any exposed abdominal surface. One of the central bulls, constrained by the embraces of the three other males, eventually jackknifed out of their grasp.

Homosexual behavior was contagious and persisted sometimes for hours as more and more males were drawn into the activity. The individuals involved in the homosexual embraces constantly changed as new groups formed, dissolved, and reformed. Eventually, with the masturbational drive presumably consummated, the excitement of homosexual activity tapered off.

Aroused by homosexual encounters, bulls were apt to mouth and embrace any other individual in the vicinity, whether a male or a female. Other males, however, were not always receptive to these advances and might only engage in a perfunctory embrace or flee, squeaking in apparent annoyance. I once saw a bull embrace the back of another only to be walloped by the latter's tail as it fled.

Juvenile males engaged in homosexual embraces with both adult and other juvenile bulls. Two young males were once observed nibbling each other's venters before embracing, but in their embrace there was less penis-to-penis contact than awkward thrusting against the side and belly of the other animal. Additional males arrived, made incipient gestures of joining the embrace, then swam away.

Sometimes homosexual behavior occurred spontaneously. A young bull that was feeding on *Hydrilla* finally yielded to the persistent overtures of another juvenile. The two embraced, sinking into the vegetation. On disengaging, the juvenile returned to feed but the other pressed his advances. The first individual plunged into the *Hydrilla* and became temporarily enmeshed in an attempt to evade the other. Most often, homosexual behavior resulted from the frustration of repeated thwarting by cows. Competitive belly-to-belly collisions while jockeying for position next to an estrous cow were apt to evolve into homosexual embraces.

Play

Several types of behavior occur in manatees that may tentatively be defined as play in the context of Loizos (1966). Juvenile males occasionally exhibited behavior suggestive of sexual activity but lacking the full complement of patterns found in adult reproductive interactions. Young males gathered to mouth and embrace accommodating cows, either juveniles or adults, who, instead of thwarting their advances, appeared to welcome them, allowing belly-to-belly embraces and even tolerating mouthing of the genital regions. For their part, the males neither extruded their penes, clashed competitively, nor engaged in more than incipient homosexuality. Some of these play sessions lasted for hours during which activity gained momentum, reached a peak, then gradually subsided.

Day after day in the main boil of the Springs O'Paradise, I watched juvenile males caress cows in this playful manner. As many as six juveniles were seen to mouth and embrace a cow simultaneously. Two cows accepting caresses at once came together from time to time to kiss one another. Cows with calves were also caressed. The calves "stood by" or exchanged random kisses with their mothers or other cows. One mother that had consistently thwarted all advances by young males, finally succumbed to their caresses and was drawn into the play. The arrival of mature bulls usually disrupted the "games," provoking the cows to abandon play in their effort to rebuff the more serious intentions of the bull.

Sexual undercurrents did not appear to run through all manatee play. Much intraspecific contact consisted of gentle nibbles, kisses, and embraces that were reciprocal, age and sex independent, and decidedly nonsexual. In such encounters, cows accepted the advances of bulls but still remained intolerant of contact with their venters. For example, I once observed an adult cow mouthing the back and sides of an old bull lying on the bottom. The bull reciprocated, but whenever he mouthed the cow's underside, she thrashed away.

Typically, two or three animals were involved in nonsexual exchanges, although larger groups sometimes formed for mutual kissing, mouthing, embracing, bumping, nudging, and chasing. Calves also participated, frolicking with older manatees as well as with their peers. Once a calf "charged" an idling juvenile from the rear, riding up on its back and causing it to thrust away in surprise. Calf and juvenile then rolled upside down and swam briefly on their backs with muzzles and flippers protruding above the surface.

Several times I observed what appeared to be play intention movements. A juvenile cow seemed to be inviting bottom-resting companions to play as she rolled on her back and grazed their sides. Similarly, a young bull swimming on his back made several lazy approaches to bottom-resting cows. Another young male chewed on the tip of a cow's tail as she bottom-rested but elicited no response.

Occasionally manatees played by themselves. An adult bull broke from the playful embraces of two juvenile males, slid along the bottom on his belly, then rolled on his back, skimming the sand and plunging through vegetation. Calves amused themselves by twisting, tumbling, and barrel-rolling through the water. While its mother was resting 20 meters away, one calf completed several minutes of play by "rocketing" to the surface so that his chest and flippers broke water.

The function of manatee play remains unclear. Moore (1956) suspected the kiss to be relict behavior inherited from terrestrial ancestors and involving odor of breath. He proposed that it was a form of greeting, perhaps assisting in individual recognition. Yet, when two or more manatees meet, there is no greeting ritual. The animals give little more than a passing glance at one another or approach head-on only to veer aside at the last instant without contact.

I believe manatee play may serve as social reinforcement. The reciprocal nibbles and embraces of play may serve to solidify a rudimentary social bond between animals. Undoubtedly the high incidence of tactile contact in play provides the animals with pleasurable sensations. In so far as I could tell, play only occurred when the animals were fully fed and rested and free of environmental pressures such as human harassment.

Mother-Young Behavior

Probably to reduce the danger of predation, a cow about to give birth apparently seeks the safety and seclusion of a sheltered backwater where she bears her calf and nurses it through its vulnerable first days. Evidence for this was my discovery of a dead newborn calf whose carcass washed ashore at the end of a narrow canal 3 kilometers long.

Shelter-seeking behavior among cows that are nearing their time of delivery may be characteristic of female sirenians in general.

According to a dugong fisherman in Mozambique, calves are born in estuaries and not in offshore waters (Hughes and Oxley-Oxland, 1971).

Parturition in the manatee has never been witnessed. A head-first presentation, like that of cetaceans, is the likely mode of delivery. The heavy head of the foetus probably settles in the lower front of the uterus and the tail toward the cervix (Slijper, 1962). Support for this theory is MacMillan's (1955) observation of a dugong cow giving birth to a calf head-first on a sand-bank at low tide. This is the only record of a sirenian giving birth out of water.

The behavior of captive manatee cows toward newborn calves has been described by Barbour (1937), Moore (1951*a*, 1957), and Phillips (1964). Immediately after delivery the mother is reported to lift her calf above the surface on her back and then to dunk it repeatedly until it has established a breathing rhythm of its own. Within half a day of birth calves are apparently capable of swimming and surfacing under their own power, unassisted by their mothers. For the first days of its life the newborn calf of a captive cow swam entirely with its flippers and rode occasionally on the back of the female (Moore, 1957).

Calves normally suckled when their mothers were idling or resting. Cows made no movements to accomodate their nurslings. Cows suspended near the surface often raised their heads to breathe while being suckled. Calves nursed suspended or on the bottom or as their mothers sank from the surface to the bottom (Fig. 38). One calf was observed to grasp its mother's teat as she slowly cruised.

To suckle, a calf approaches its mother's side from the rear, rolls toward her, and grasps the axil of a flipper in its mouth. Not infrequently one can see the lips of a nursing calf move with a slight, regular sucking action. Nursing periods lasted about two minutes. The mean length of 16 nursing intervals involving six different calves was 126 seconds with a range of 106 to 146 seconds. Pre-yearling calves, even the younger ones, showed no tendency to grasp the teat longer than did yearlings. Calves sometimes released their grasp momentarily to breathe. One mother was seen to break away from her nursing calf but immediately allowed it to resume feeding. On another occasion three cavorting manatees bumped a cow and calf, interrupting nursing.

Manatee cows evidently lactate as long as they are accompanied

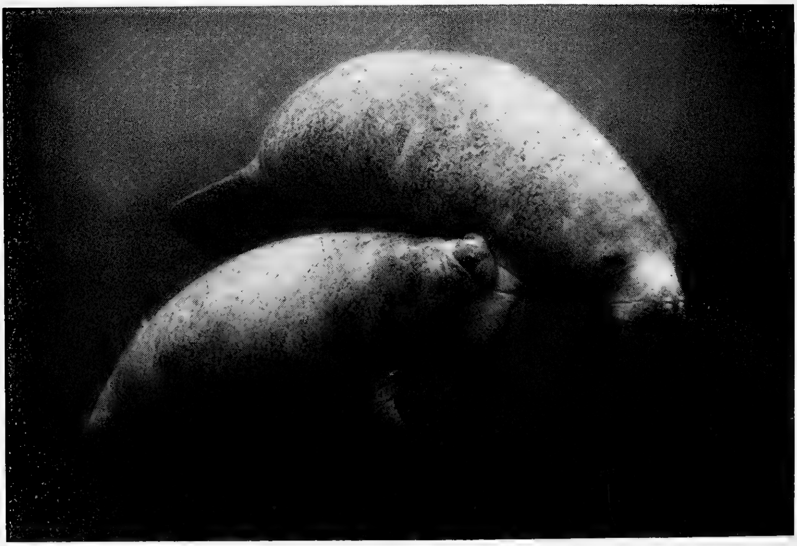


FIG. 38. Cow suckling yearling calf (photo by James A. Sugar, (c) National Geographic Society).

by offspring. As they mature, however, calves become less dependent on their mothers for milk and increasingly turn their attention to grazing. In six hours of continuous observation I saw one yearling nurse only three times at intervals of 96 and 132 minutes. Sometimes yearlings go even longer without feeding, then, as if to compensate, suckle and graze several times within a few minutes. In the space of five and a half hours a yearling male devoted eight and a half minutes to suckling and 17 minutes to grazing, interspersing the two activities at intervals of 262, 14, 6, 11, and four minutes.

It appears that sirenian calves begin to nibble on vegetation at an early age. According to Heinsohn (1972), young dugongs start grazing by three months of age. Kenchington (1972) found the stomach of a newborn dugong calf distended with seagrasses. Moore (1957) recorded a 38-day-old captive manatee feeding on lettuce. The youngest calf observed at Crystal River, known to be no more than three months of age, was both nursing and grazing when first encountered.

Apparently cow and calf maintain intimate contact for a period of one to two years. The calf constantly reinforces the bond by mouthing and kissing its mother. As previously noted, a conspicuous feature of mother-young behavior is synchronous surfacing. Only when one wandered away from the other did a cow and calf fall out of unison in their surfacing. In the absence of its mother, a calf sometimes fell into the breathing rhythm of a neighboring animal.

The cow-calf association is markedly close while the pair is cruising, when the risk of becoming separated is undoubtedly the greatest. The calf swims beside its mother, just behind a flipper, crossing occasionally above or beneath her to swim on her opposite side. At no time were mothers seen to assist their young in swimming as has been reported among cetaceans (Tavolga and Essapian, 1957), although this behavior may occur between a mother and a newborn calf.

When not cruising, cow and calf showed less intimate association. The calf still tended to follow the lead of its mother—resting when she rested, feeding when she fed—but they were more apt to wander away from each other for short periods. While their mothers bottom-rested, calves sometimes ventured to explore, feed, or bottom-rest independently for periods up to an hour. Calves also "played" with other manatees, mouthing and grazing the sides of juveniles and adults who, in turn, responded with gentle nibbles, nudges, and embraces.

There is little evidence that the cow and calf ever separate beyond the range of effective communication. One six- to eight-month-old calf was extremely independent and strayed afield as much as 50 meters, yet cow and calf managed easily to locate one another, apparently by means of vocal cues. Another female moved more than 60 meters away from her calf but returned to it quickly when alerted by its squeals. I feel certain that manatees communicate underwater over even greater distances than those involved in the above observations.

The defensive behavior of a menaced cow with calf was restricted to alarm calls and flight. A cow answered scream for scream any distress calls from its calf, hurried to it, and led it away from the source of anxiety. For example, on one occasion a cow called her calf to her side as it was about to surface too near a boat. In another case, a bull rising from the bottom collided accidentally with a calf who screamed in surprise, igniting a duet with its mother and bringing her to investigate.

Cows with calves never were seen to engage in agonistic displays. Mothers never threatened divers that were frightening their calves. Once, however, a cow appeared to dissuade her calf from investigating a diver by turning it aside with gentle nudges. When a cow with calf was the focus of an estrous herd, the position of the calf beside its mother was frequently usurped by courting males, forcing the calf to keep station beside peripheral bulls. During intense courtship, the calf was apt to drop far behind the herd into the company of straggling escorts. If a calf became isolated in the imbroglio of sexual activity, its mother, perhaps alerted by loss of vocal contact with her offspring, doubled back to find it. A cow persistently pestered by bulls sometimes fled without summoning her calf to her side. The deserted calf either waited until called by its mother or swam squealing in the direction of her departure.

When cows with calves consorted together, calves often had to wait for their mothers to finish feeding or resting. At such times calves milled around and occasionally amused themselves by embracing, nudging, kissing, and lazily pursuing one another.

With the exception that they did not indulge in the sexual interactions typical of older animals, calves exhibited much the same behavior as adults. They rooted in the sand, toyed with inanimate objects, rubbed on logs and ledges, and cavorted with other manatees. Their hydrobatics were replicas of adult behavior and included basking at the surface upside down. Male calves even extruded their penes from time to time in what seemed to be an involuntary response relating to stretching and not to sexual excitation.

SENSES

THE following description of manatee sensory capacities is based largely on circumstantial evidence. Findings relating to the senses of whales and porpoises are included to illustrate the convergent adaptations of sirenians and cetaceans.

Hearing

Sound appears to be the principal sensory modality of both sirenians and cetaceans (Evans, 1967). At Crystal River, there was no question but that manatees have exceptional acoustic sensitivity and that sound was a major directional determinant in social interactions. Guided apparently by vocal cues alone, lagging bulls tended to swim directly toward estrous herds that were beyond visual range. Manatees were also extremely efficient at localizing surface noises. Even in highly turbid water, animals arrived at once to investigate the splashing of divers.

Keeping in mind that sound pressure is 60 times greater in water than in air, the manatee's actual range of effective audibility underwater is uncertain. From the shore I attracted animals 15 meters away by gently splashing the water with my hand. One animal, passing roughly 40 meters from my boat, altered its course to investigate the banging of an oar against the gunwale. From the air, manatees were seen to change bearing and "zero in" on other manatees from distances as great as 50 meters. As noted above, a cow responded to the squeals of her calf from a distance of more than 60 meters.

Reflex actions induced by different man-made sounds provided additional proof of the manatee's sensitive hearing. The click of a camera shutter within a few meters of their heads caused manatees to wince. Once, a bull that was lolling beside me flinched when I blew water out of my snorkel. Not infrequently animals were irritated by the high-pitched wheezing of regulators on SCUBA divers. The sharp sound of an outboard motor changing gears 10 meters away caused several animals to wince in unison. I once saw a cow flinch at the splash of a diver entering the water 30 meters from her.

On the other hand, an ultrasonic transmitter, beeping at a frequency of 70,000 cycles per second (c/sec) did not elicit reactions from animals even when held next to their external ear openings.

It is possible that the manatee cannot hear such high-pitched sounds. The fundamental tones of manatee vocalizations range from 600–5000 c/sec with the highest conspicuous harmonic at 16,000 c/sec (Schevill and Watkins, 1965). Cetaceans seem to be sensitive to a wider range of tones than manatees and have responded to sounds between 150 and 153,000 c/sec (Slijper, 1962).

Sirenians are also able to detect above-water sounds. Oke (1967) described the conditioned response of a captive dugong to a gong. I have witnessed a captive manatee respond to its keeper's voice by swimming in the direction of the sound. At Crystal River, the roar of a low-flying jet fighter caused a resting male to flinch violently and dive from the surface to the bottom. A group of manatees bottom-resting at 3 meters was frightened out of the Main Spring by the voices of fishermen whose boat drifted 10 meters away. On a number of occasions I was able to distract manatees from their activities with shouts from the shore a few meters away.

Sight

The manatee's vision, used by its early ancestors for a terrestrial existence, has become adapted to life under water. The orbits are lined with oil glands that bathe the corneas, possibly protecting the eyes from the harmful effects of brine. Strands of mucus sometimes accumulate in the orbits but do not seem to bother the animals. The manatee blinks frequently to keep its eyes lubricated. The nictitating membrane closes, followed by contraction of the muscular walls of the orbit.

It is apparent from the behavioral reactions of captives that many of the smaller toothed whales use vision extensively (D. Caldwell and M. Caldwell, 1972). Like cetaceans, manatees make use of their eyes in clear water, but their vision is presumably of little value under murky conditions. According to Walls (1967), sirenians have made fewer ocular modifications for aquatic life than cetaceans: the eyes are highly sensitive but visual acuity is poor and visual stimuli of no consequence.

The findings of this study contradict Walls. In Kings Bay, the preferred method of environmental exploration by manatees was visual. The animals typically reacted to an unfamiliar auditory stimulus by investigating its source with their eyes. The animals either rose to face the source head-on or balanced on the bottom with their bodies cocked to the side so they could look up. In the latter case they repeatedly shifted position so that first one eye was exposed and then the other.

Manatees approached objects head-on without moving their heads from side to side, suggesting that they posses binocular stereoscopic vision. It is obvious, at least, that the visual fields of the two eyes overlap. The rigid neck structure prevents a manatee from turning the head from side to side to scan and forces it to "come about" with its flippers to confront an object.

Visual signals alone sufficed to alert manatees. While I lay motionless on the surface, resting animals were often oblivious to my presence, noticing me only when they opened their eyes to surface. Their visual range underwater is as great as a diver's through a face mask. Under exceptionally clear conditions, animals saw and approached me from distances of up to 35 meters. This refutes the supposition that manatees are myopic. In fact, poor depth perception at close range is evidenced by their tendency to bump heads and eyes, causing them to wince, while rubbing on cement blocks and other objects.

There is no reason to suspect that the vision of manatees at night is poorer than that during the day. Their *tapeta lucida* shine pink in the dark, indicative of good vision in low light intensities (Walls, 1967). The animals rarely shied from a flashlight beam.

Kellogg and Rice (1966) found that the bottle-nosed dolphin was sensitive to above-water movements but could not discriminate visual forms from water to air. It is questionable whether the manatee has the same capacity. At times I was convinced that manatees investigating my boat were alerted by my movements to and fro, but my motion was betrayed by auditory stimuli, which may have been responsible for their attention. As evidence that manatees are either disinterested in or unable to detect above-water motion, no amount of gesticulation from the shore perturbed animals in a canal 3 meters away.

Several species of odontocetes are thought to have good vision out of water (Kritzler, 1952; Slijper, 1962; Kellogg and Rice, 1966). The behavior of captive manatees in the Botanic Gardens of Georgetown, Guyana, provide evidence that they also can see with their heads out of water. These animals, accustomed to accepting handouts of plants, raise their heads above the surface at the feet of visitors, then swim with obvious discrimination towards persons that proffer grass or other herbage. At Crystal River, on the other hand, there was no indication that manatees gained information by raising their heads above water. They never raised their eyes above the surface in response to an above-water stimulus.

Touch

A high incidence of body contact and mouthing in social interactions is characteristic of both manatees and dolphins and suggests that the sense of touch is very important to both (Tavolga and Essapian, 1957; D. Caldwell and M. Caldwell, 1972). The propensity of manatees to rub on objects and to solicit caresses from divers is further evidence that the epidermis is highly sensitive to touch. The scattered dorsal hairs seem to be sensitive to currents in the water and are conceivably receptive to low frequency vibrations or pressure waves. Layne and Caldwell (1964) suggested that the Amazon dolphin (*Inia*) may use the hairs on its rostrum to locate food. Assuming a subminimal auditory cue is not involved, the stimulus for bottom-resting manatees to surface in near unison appears to be tactile; nearby manatees, often faced in the opposite direction, appear to "feel" the slight currents produced by the ascent of a lead animal and are thus stimulated to rise. In turbid water manatees cruising in tandem or in eschelon formation may follow a lead animal by means of the currents generated by its undulations.

The bristles on the lip pads serve a tactile function when manatees feed, when they mouth one another, and when they explore the bottom by nibbling.

Taste

The prevalence of mouthing in social encounters suggests that manatees have specialized sense receptors on their tongues and respond to gustatory cues. The sophistication of their taste apparatus, however, is purely conjectural. Do manatees, for example, possess a chemical sense by which they can recognize odor gradients in the water? Can they obtain directional information from salinity gradients? Do males differentiate anestrous from estrous cows by a change in the taste of their hides? Is a waterborne pheromone involved in sexual identity? Is there a smell-taste basis to individual recognition?

The fact that odors dissipate more slowly in water than in air would tend to favor evolution of a chemoreceptive sense. Furthermore, there is growing evidence that toothed whales perceive odors in water. Yablokov (1957, 1961) discovered preanal glands in male belugas (*Delphinapterus*) and sperm whales (*Physeter*) and found "olfactory pits" on the surface of the tongue of several odontocetes. D. Caldwell *et al.* (1966) suggested that sperm whales "lay a trail" in the water, imparting chemical information to other whales and maintaining contact between members of a pod. D. Caldwell and M. Caldwell (1972) cited evidence of a strong gustatory sense among captive odontocetes and suggested that taste centers on the tongue may function in chemoreception. It seems reasonable to assume that a communication system utilizing chemoreception also exists among sirenians.

Smell

Observations at Crystal River indicate that the manatee's sense of smell, if still functional, is less important than was formerly assumed. Sirenians have a fairly well-developed olfactory organ which, it has been contended, may be used for smelling above the surface (Allsopp, 1961; Slijper, 1962; Harrison and King, 1965). Moore (1956) suggested that the manatee's habit of "kissing" at the surface involved ritual smelling of one another's breath or other source of odor. My own observations do not support this interpretation. The increased frequency of breathing associated with kissing seemed to me to be a reflex stimulated by exposure of the nose above water. Furthermore, kissing occasionally took place underwater where the nostrils were tightly closed at all times. Whatever manatees recognize or communicate while kissing at the surface, I suspect that the message is transmitted predominantly, if not exclusively, through the mouth, not through the nose.

One incident suggests that airborne odors may be relevant to manatees. Within a period of 15 seconds, I once saw an adult male take five breaths where bubbles of flatus from a female were breaking on the surface. This behavior may not have been related to smell, however, since on no other occasion were animals ever seen "scenting" or making any smelling gestures at the surface. When I was stationed directly upwind of them in my boat, there was no indication that the animals were ever alerted to my presence as a result of smell. Flight reactions could always be traced to auditory and visual signals.

Sirenians seem to be similar to cetaceans in having a poor or absent olfactory sense. It is claimed that the sense of smell is completely lacking in odontocetes and rudimentary in mysticetes (Howell, 1930; Slijper, 1962). Yablokov (1961) regarded the unreduced olfactory region in the cerebral cortex of the common dolphin (*Delphinus*) as evidence of a functional "sense of smell" probably associated with chemoreception.

POPULATION DYNAMICS

Birth Rate

It appears that manatees in Florida breed year-round. As evidence for this, Moore (1953, 1956) cited the fact that young calves have been seen at all times of year. Births at Crystal River provided further evidence that manatees are nonseasonal breeders. Five cows calved during the study, three in spring or summer and two in winter. The dates between which births occurred were as follows: 3 February to 26 February; 14 March to 20 July; 25 March to 21 September; 25 May to 26 August; and 20 November to 2 December. Howard Campbell (personal communication) recently has gathered data, based on the recovery of newborn calf carcasses, which suggest there may be an increase in natality in the spring. Perhaps manatees in Florida, confronted with winter temperatures potentially dangerous to their calves (see section on mortality factors), are gradually evolving a reproductive cycle in tune with the North Temperate climate.

The gestation period of manatees is not certain. A captive cow calved 152 days after her capture, indicating a gestation of at least five months (Moore, 1951*a*). Harrison and King (1965) suggested a gestation interval of 12 months. The following observations made at Crystal River during this study indicate an even longer gestation.

On 20 October 1967, an adult female became the focus of an estrous herd. She was escorted by bulls until 5 November 1967. Between 20 November and 2 December 1968, she delivered a female calf whose carcass was eventually found by the shore of a canal. Assuming that conception took place during her period of estrus in 1967 and that her calf was born about 25 November 1968, gestation lasted from 385 to 400 days, or approximately 13 months. Weight and measurements (in centimeters) of the dead calf were as follows: weight, 42.0 kg; total length, 139.7; navel to genital aperture, 22.9; genital aperture to anus, 5.6; length of flipper, 26.7; maximum width of flipper, 8.4; maximum width of tail, 33.5.

The postpartum-preconception interval for manatees evidently varies from one to two years, the time required to wean a calf. Cows with calves come into estrus but may not be impregnated (see section on estrous herd). However, females that loose their calves may breed soon after. One cow, for example, which lost her calf shortly after its birth was in estrus 10 to 15 days later.

Thus, barring infant mortality, females breed no less than every two years and more likely every two and a half years. In support of this contention, a cow that lost her calf on 25 November 1968 was seen with a new preyearling calf on 11 November 1970 and with another preyearling on 4 December 1972. A cow's fertile life span and total reproductive capacity are unknown.

Norris (1960) and Jarman (1966) stated that dugongs occasionally have twins. An incident at Crystal River confirmed that the manatee is not always uniparous. During the winter of 1970–71, a female provided evidence of both twinning and foster parenthood among manatees. On 11 November, I encountered a cow accompanied by two preyearling calves of identical size. The family was met again a week later. On 19 December, I came upon the same cow accompanied by three preyearlings. The new calf was slightly larger than the twins. Apparently the cow had not only given birth to twins but had also adopted an orphaned calf. I followed the foursome underwater for half an hour during which each of the twins suckled once. Interactions between the orphan and the cow were similar to those between the cow and its own offspring, leading me to suspect that the orphan was also being nursed.

Since it is believed that a cow with a newborn calf immediately raises her offspring above the water on her back to prevent its drowning, there would have to be an interval between delivery of twins that would allow the mother time to introduce the first calf to a surfacing rhythm before the birth of the second.

Age at Weaning

Mohr (1957) proposed that, with teeth well developed at birth, calves could feed on plants at birth and tolerate separation from their mothers at an early age. Captive calves have been known to nibble algae and grass when only a few weeks old (Phillips, 1964). One calf born and raised in captivity was eating lettuce within 38 days of birth (Moore, 1957). At Crystal River, a calf that was born in July or August was feeding extensively on vegetation the following October, but it is not known precisely when it began this behavior.

The literature suggests that sirenian calves accompany and are suckled by their mothers from one to two years (MacMillan, 1955; Norris, 1960; Walker, 1964; Harrison and King, 1965; Heinsohn, 1972). Evidence accumulated at Crystal River supports this claim. Of six calves present in Kings Bay the first winter of this study, the two youngest accompanied their mothers for at least a year and a half. The size or age of a calf, however, is an unreliable indication of impending separation from its mother. At the conclusion of the study, one yearling calf (±20 months old) was only 35 centimeters shorter than its mother yet less independent than another calf that was six to eight months old.

Age at Sexual Maturity

According to Heinsohn (1972), male and female dugongs attain reproductive maturity at approximately two years of age. The age of the manatee at sexual maturity has been estimated at three to four years (Walker, 1964; Harrison and King, 1965). At Crystal River, observations of the size, growth rate, and behavioral attributes of juveniles suggested that sexual maturity is not reached before three and possibly as late as five years. This is strictly an estimate as the study was too brief to follow the maturation of a calf to adulthood.

Longevity

There is no information on the length of life of sirenians in the wild, although Betz (1968) thought that manatee longevity might exceed 50 years. Reports of captive manatees throw little light on the subject. An anecdote in True (1884) mentions a manatee confined in a pond by Spanish colonists for 26 years. The longevity record among recent captives is held by a manatee born in captivity 28 years ago and presently housed in Bradenton, Florida.

Mortality Factors

Although there is, as yet, no concrete evidence to substantiate the claim, it has been postulated that sirenians are preyed upon by aquatic predators. MacMillan (1955) stated that dugongs panic when killer whales (*Orcinus orca*) are near. According to several sources (Allsopp, 1961; G. Bertram and C. Bertram, 1968, 1973; Datakaran Jeetlall, personal communication), manatees in the rivers of South America may be vulnerable to attack from piranhas (*Serrasalmo*). Sharks and crocodilians also have been implicated as potential enemies of manatees and dugongs, especially of calves at parturition (MacMillan, 1955; Jarman, 1966; G. Bertram and C. Bertram, 1968, 1973; Kingdon, 1971). However, natives from Mafia Island (Tanzania) insist that crocodiles never attack dugongs and point out that the sirenians are regularly found in shark-infested waters (Dollman, 1933). In Florida, crocodiles (*Crocodylus acutus*), alligators, and several species of large shark occur in manatee habitat, but no manatees were seen to bear scars suggesting attacks by any of these predators. From South America there is a report of jaguars (*Panthera onca*) preying on the Amazonian manatee (Nuñes Pereira, *in* G. Bertram and C. Bertram, 1973).

Pleurisy and bronchial pneumonia from cold exposure have been held responsible for the deaths of captive manatees (Beddard, 1897; Townsend, 1904; Sguros, 1966) and may be the cause of fatalities in the wild during unusually low temperatures. I believe the death of a newborn calf found washed ashore at Crystal River after two nights of subfreezing temperatures was the result of cold exposure. Young calves have a comparatively large surface to volume ratio and are poorly insulated, rendering them more susceptible to cold than are older animals.

Complications during birth may also result in death. In January 1973, the carcasses of a cow and newborn calf were found together on Sewall Point in the Indian River (Martin County). According to Don Rodgers of the Fish and Wildlife Service, the afterbirth was still intact and protruding from the cow's genital opening and the calf appeared to have drowned or died of starvation. Measurements (in centimeters) of the cow were as follows: total length, 305; navel to genital aperture, 68; genital aperture to anus, 26; length of flipper, 48; maximum width of flipper, 17; maximum width of tail, 66. Measurements of the calf (female) were: total length, 111;

navel to genital aperture, 18; genital aperture to anus, 5; length of flipper, 18; maximum width of flipper, 6; maximum width of tail, 20.

Two unusual incidents of mortality among sirenians are worthy of mention. The deaths of seven manatees in the Fort Myers area in the spring of 1963 coincided with the deaths of other aquatic animals and with an outbreak of red tide in the vicinity (Layne, 1965). However, there was no conclusive relation between these events. On the coast of India, Jones (1967) reported the discovery of a dead dugong with the tail of a sting ray imbedded in its underside, although death could not with certainty be attributed to the sting.

By far the most serious threat to the survival of manatees is man. In Florida, the propellers of power craft are the major cause of manatee deaths. Half of the 14 manatee carcasses reported to me from across the state bore severe propeller wounds on the back or head. Virtually all of the animals in Citrus County carried scars inflicted by propellers and skegs.

Other important sources of mortality to manatees in Florida are vandalism, poaching, and habitat alteration (Hartman, unpublished manuscript). John Reynolds (personal communication) has also called attention to flood control gates which have been known to crush and drown manatees and are a particularly serious threat to the animals in the canal network of southeastern Florida.

At least two chemicals have been implicated in the deaths of sirenians: Oke (1967) cited copper sulphate as the possible killer of a captive dugong, and arsenic was discovered in the tissues of a calf found dead in the Crystal River headwaters in 1976 (James Powell, Jr., personal communication). In the St. Johns River, manatees are presumed to feed on water hyacinth coated with the herbicide 2,4-D, but long-term effects are unknown. During my study, various herbicides, notably copper sulfate and sulfuric acid, were dumped in the rivers of Citrus County in experiments to control aquatic weeds. Manatees were exposed to only dilute concentrations, and no immediate effects were observed.

Polluted water may be responsible for a peculiar condition recently noticed among Florida manatees. In June, 1973, residents of Everglades City (Collier County) reported seeing manatees so bloated they could not submerge. The Miami Herald (1 March 1974) carried an article on a bloated manatee found in Broward

County and transferred to the Miami Seaquarium for study. The cause of the bloat has not been diagnosed, but if similar to bloat in ruminants, it may have resulted from the ingestion of bacteria, the fermentation of which in the stomach produced a froth that blocked the alimentary canal preventing the escape of gas. The bacteria were presumably in the water or in plants that were eaten. Bloat evidently offsets the manatee's neutral buoyancy and prevents the animals from diving. I was unable to establish a relationship between the appearance of bloated manatees and local water contamination.

Another potential source of peril to manatees is the accidental ingestion of hooks, spinners, or other fishing lures caught in the vegetation on which the animals are feeding. Lodged in the digestive tract, barb and hook could cause a severe, possibly fatal, ulcer or blockage. No such cases have been documented; that manatees encounter fishing devices, however, was evidenced by hooks and tears in the skin of several animals.

It also appears that manatees occasionally drown after becoming entangled in fish or turtle nets. In Guyana, the greatest threat to manatees is accidental capture in fishing nets and subsequent slaughter for food (W. H. L. Allsopp, personal communication). In Florida, I encountered several commercial fishermen who claimed to have had manatees drown in their mullet nets.

Entanglement in buoy lines, anchor ropes, underwater cables, and monofilament is another danger for manatees. In the winter of 1971–72, a mother manatee attending the cold-induced congregations in Blue Springs Run (Volusia County) was found to have a trotline looped tightly around the axil of her left flipper (James Powell, Jr., personal communication). The flipper had begun to atrophy, and her calf was never seen to suckle from the left teat. Otherwise, the line in no way seemed to handicap the animal or hinder its normal motor patterns. The previous summer, personnel of the Lake Woodruff National Wildlife Refuge reported a manatee towing a pole in the Norris Dead River (Volusia County). A manatee trailing a lobster buoy and line was seen on several occasions in Palm Beach County during the fall of 1973.

MAN-MANATEE RELATIONS

Response of Man to Manatees

Floridians living in contact with manatees tend to have a dispassionate or benign attitute toward them. The animals are unobtrusive and interfere little with man's activities. The general attitude toward manatees is reflected in the views of Citrus County residents, most of whom accept the animals with interest and gratitude. Manatees are among the attractions that draw divers to the Crystal River springs, thus contributing to the tourist economy of the community. More importantly, their usefulness as agents of aquatic weed control in the spring-fed rivers is welcomed. On the other hand, guides and fishermen complain of breaking propellers on the backs of manatees, and mullet fishermen begrudge manatees the holes torn in their gill nets. However, the incidence of such cases is rare and is not treated too seriously.

Maliciousness toward manatees does occur. Attacks by vandals, especially in canals on the east coast of Florida, have increased substantially in recent years (Hartman, unpublished manuscript). The following incidents in Citrus County illustrate the problem. In the winter of 1966–67, an animal was observed passing up a little-used canal off Kings Bay with the head of a garden rake imbedded in its back. Several years ago a manatee was shot through the head as it surfaced in the Withlocoochee River. I have personally seen bored fishermen hook animals intentionally and "play" them for sport.

The most constant sources of harassment to the Crystal River manatees were power boats and divers. The travel routes utilized by manatees were also the principal thoroughfares for boats. The approach of boats often caused animals to interrupt activities or alter their course. Boat traffic was especially heavy on weekends and harassment was compounded by tourists and divers patrolling in search of manatees. Divers daily invaded the Main Spring with SCUBA and snorkel equipment and when manatees were present, bothered the animals by trying to "ride" them. Invariably the manatees were chased from the spring. The activity of divers, however, was generally restricted to the spring and rarely disrupted the activities of manatees elsewhere in Kings Bay. Turbid water at the head of the Homosassa River discouraged divers, and the manatees there remained unmolested.

Response of Manatees to Man

Manatees are inquisitive animals. They were frequently seen to investigate boats that were anchored or drifting nearby. On several occasions during dredging operations at the mouth of the Suwannee River, workmen watched manatees investigate their barge, attracted to it, no doubt, by the noise. Stories of extraordinarily tame manatees are legion. At a marina in Miami there was a famous manatee that would roll over to have its belly scratched with a deck brush. At the City Yacht Pier in St. Augustine, the dockmaster uses a paint scraper to clean barnacles off the back of a large manatee that appears regularly. Frank Rivell, captain of a "jungle cruise" on the Tomoka River (Volusia County), claims to have petted manatees over the gunwales of his tour boat.

Response to boats.—In general, manatees reacted to a boat under power as to a potential danger. The sound of an approaching motor usually sent animals that were near the surface diving to the bottom. If surprised in shallows (2 meters or less in depth), animals escaped to deeper water. Once they reached the bottom in deep water, they were not as easily intimidated and were more likely to watch a boat pass over than to flee. I have motored over animals bottom-resting at 3 meters barely disturbing them.

Manatees that were overtaken unawares at the surface by a boat "spooked," thrashing the surface with their tails and churning up the water in flight. In their panic animals frequently plunged headlong through vegetation. I once surprised a cow and calf who became momentarily separated in flight. On another occasion I saw a fleeing juvenile collide with a calf.

The alarm of a manatee scared by a boat was often contagious. One afternoon as I was chasing a juvenile male in order to clock his flight speed, the surface erupted suddenly with frightened manatees, some as far as 100 meters from my boat.

When pursued by boat, manatees usually accelerated to a fast cruising speed but were slow to change course until about to be overtaken at which time they were apt to veer sharply away from the boat or somersault to reverse direction. Manatees sometimes demonstrated exceptional furtiveness in evading pursuit. Twice

FIG. 39. Author scratching juvenile female (photo by James A. Sugar, (c) National Geographic Society).

during the study animals apparently resorted to concealment tactics. An adult cow fled into a dense stand of *Hydrilla* and rested on the bottom under cover. A cow with calf that I had pressed for 10 minutes sought seclusion in the heart of a bed of *Myriophyllum.* While in hiding, manatees seemed to breathe with unusual stealth, but there was no indication that they remained submerged for abnormal lengths of time.

On a few occasions, I managed to follow manatees closely in the runabout without disturbing them. The animals seemed unaware of the boat and the sound of its motor. One cow even collided with the bow on surfacing. Perhaps the noise of a motor at close range interferes with or disrupts sound exchange between animals or in some way disorients them.

Response to divers.—The manatees at Crystal River exhibited wide variation in their response to divers. Most were wary and would not permit close approach. A few of the older animals, evidently accustomed to divers, paid them little heed. Manatees that were unfamiliar with divers tended to investigate them with cautious curiosity, then fled. Timid animals were often torn between flight

FIG. 40. Above, juvenile female "kissing" author; below, juvenile female nibbling author's hand (photos by James A. Sugar, (c) National Geographic Society).

and curiosity. This approach-avoidance conflict resulted in intention movements and ambivalence. The animals would rise from the bottom to within arm's length of a diver, then dive in retreat, squealing constantly and repeating the performance several times before swimming away.

A handful of Crystal River animals were attracted to divers and actively solicited caresses from them. At times as many as a half dozen manatees sought my attention and followed me wherever I swam. Manatees remained immobile, often with closed eyes, when caressed by a diver. Some uttered intermittent squeaks. A few rolled on their backs and presented their bellies to be scratched (Fig. 39). Animals routinely resisted caresses in the region of their mouths and noses and tended to evade two-handed embraces, which they seemed to identify with the clasps of their own species.

One exceptionally tame juvenile cow gave the impression that she returned to the Main Spring as much to be scratched by divers as to linger in the warm water. I once saw her lolling under the caresses of seven divers. She was also attracted to my runabout as I motored into the spring. More than once, she swam to the boat, nudged the hull at the waterline, and allowed me to pet her from over the gunwale.

In my encounters with her underwater, she was extremely forward in her attentions. At the surface she nuzzled my face mask in a manner suggesting the manatee kiss (Fig. 40). She also nibbled my dry suit and fingers (Fig. 40) and clutched my body with her flippers, drawing me below the surface. Once she embraced my head and tore off my mask. Throughout these encounters she uttered faint grunts audible only when my head was next to hers.

Cows with calves were no more cautious of divers than other manatees. One mother regularly sought the attention of divers in the Main Spring. Her calf, at first unapproachable, gradually followed its mother's example and within a few days was responding to caresses. Once while the pair were feeding at the surface on water hyacinth, they accepted some from my hand underwater. Similar behavior was witnessed in Blue Springs Run on the St. Johns River (Volusia County) where several manatees, including mothers and their calves, were persuaded to accept water hyacinth, alligatorweed, coontail, and para grass (*Panicum purpurascens*) when offered to them underwater by divers.

I felt that in time many of the manatees at Crystal River grew accustomed to my presence and showed an acceptance of me that was not apparent with other divers, but whether they could distinguish me or whether my quiet approaches simply made them less apprehensive was never clear.

The aversion of manatees to the average diver stemmed from thoughtless harassment by divers. They startled animals with their sudden motions and loud splashing. Manatees were especially frightened when divers left the surface and plunged to the animals' level in the water. SCUBA divers were generally given a wide berth, the manatees evidently associating the sound of a regulator with being pestered. Animals that were being chased or "ridden" by divers turned their backs and jackknifed away when constrained. No manatee ever made a threatening gesture toward a diver.

A few animals accepted abuses by divers as the price for resting in the Main Spring. In late winter of 1969, an estrous herd appeared daily at the spring regardless of the commotion caused by divers. Members of the herd, seemingly in anticipation of disturbance by divers and in preparation for a fast escape, faced their exit route when bottom-resting. The tamer animals, however, were quick to respond to considerate treatment and would allow close approach. One day a bull rubbed against the dangling legs of a friendly diver.

The number of divers visiting Crystal River is increasing every year, and the appearance of manatees in the Main Spring is becoming less frequent. In the winter of 1972–73 manatees were seen in the spring only on mornings of subfreezing temperatures and fled at the arrival of the first boat.

DISCUSSION

Sirenians are fully aquatic mammals, a distinction shared only with the Cetacea. The two orders have separate phylogenetic origins but show a basic convergence in morphological and locomotory adaptations. There also appear to be similarities in their diving physiology (Scholander and Irving, 1941; Irving, 1966; Harrison and Kooyman, 1971; Blessing, 1972) and, as mentioned earlier, in their sensory capacities. A comparison of the behavioral repertoire of manatees and whales in relation to their ecology and evolution provides, I feel, an appropriate conclusion to this study.

Sirenians are believed to share a common subungulate origin with the proboscideans (Simpson, 1932; Romer, 1966). Fossil evidence suggests that the Sirenia evolved from primitive terrestrial herbivores early in the Tertiary. The Cetacea are also products of early land mammals and appear to have originated at about the same time as the Sirenia. The ancestry of the cetaceans is obscure, but they seem to have derived from insectivore-creodont stock just before the divergence of the carnivore and ungulate lines (Kulu, 1972). According to Howell (1930), the sedentary, herbivorous life of the Sirenia has not stimulated rapid evolutionary change, with the result that manatees and dugongs retain certain terrestrial features and are less specialized for aquatic life than cetaceans.

Their widely separate lineages are reflected in the basic habits of sirenians and cetaceans. Manatees and dugongs are sluggish herbivores that require neither speed nor "intelligence," because they have no need to catch prey. Most cetaceans, by comparison, are lively carnivores that, to obtain food, must constantly confront problem-solving situations that require some measure of insight. In general, carnivores tend to have a wider range of behavioral capacities than do herbivores, as will be evident in the following comparison.

Relatively little is known about the natural history of cetaceans, but it appears that a full spectrum of social organization may be found among members of the order ranging from the solitary lives and small family groups of *Balaenoptera musculus, B. borealis, Balaena, Kogia, Inia,* and *Platanista* to large schools of *Balaenoptera physalus, Eubalaena, Delphinus, Prodelphinus, Lagenorhynchus, Orcaella, Sousa, Stenella, Steno,* and *Tursiops* that at times number in the hundreds or thousands (Layne, 1958; Slijper, 1962; Pilleri, 1970; Saayman and Tayler, 1973). The size of many cetacean groupings seems to fluctuate with the breeding season and the availability of food. There is little doubt, however, that social ties among cetaceans are stronger than those among manatees. The herd instinct seems fundamental to most whales, dolphins, and porpoises but appears vestigial in manatees. Social facilitation is highly evolved in most cetaceans (M. Caldwell and D. Caldwell, 1972) but rudimentary in manatees. Formation swimming has been observed in the narrow-snouted porpoise (*Stenella*) and beluga (*Delphinapterus*)

(Kleinenberg *et al.,* 1964; Evans and Bastian, 1969) but does not occur in manatees. Hump-backed dolphins (*Sousa*) perform courtshiplike interactions in a greeting context (Saayman *et al.,* 1973), whereas manatees appear to have no greeting ceremony.

Another indication that the Cetacea are more tightly social than the Sirenia is evident in epimeletic (care-giving) behavior. Reports of mysticetes and odontocetes supporting injured, distressed, or dead companions and especially of mothers raising dead or afflicted calves to the surface are not uncommon (McBride and Hebb, 1948; McBride and Kritzler, 1951; Hubbs, 1953; Moore, 1955; Brown and Norris, 1956; Slijper, 1962; Andersen, 1969; Pilleri and Knuckey, 1969). In most instances the mother was joined in her efforts by other animals. Pilleri (1971*b*) presented evidence of a female La Plata dolphin (*Pontoporia*) attempting to free her calf from a net. It should be mentioned, though, that cases of cetaceans failing to give aid to wounded companions have also been recorded (Slijper, 1962). Among manatees there is only one report of assistance given to a distressed individual—that of a lone cow butting her dead calf to the surface.

According to Slijper (1962), male leaders are found in schools of pilot whales (*Globicephala*) and bottle-nosed whales (*Hyperoodon*). Conversely, several species of cetaceans (*Eschrichtius, Delphinapterus, Delphinus, Orcinus,* and *Monodon*) are believed to consort in leaderless schools of mixed age and sex at certain times of the year and in separate age and sex-differentiated schools at other times (Tomilin, 1935; Kleinenberg *et al.,* 1964; Rice and Wolman, 1971). There is also evidence that, like manatees, at least some cetaceans may not form stable or cohesive groups. Saayman and Tayler (1973) found that hump-backed dolphins (*Sousa*) consort with different companions in temporary associations.

According to Evans and Bastain (1969), territoriality probably does not exist among wild cetaceans, which is in keeping with the behavior of manatees. However, social dominance, virtually absent in manatees, has been observed in both captive and free-ranging cetaceans. In captivity, bottle-nosed and white-beaked dolphins (*Lagenorhynchus*) have established microterritories and peck orders based largely on size, and there is evidence for social hierarchies among wild whales (Slijper, 1962; Tavolga, 1966; M. Caldwell and D. Caldwell, 1972; Tayler and Saayman, 1972). In *Tursiops aduncus,* it appears that dominant males cooperate in their behavior to coordinate group activities (Tayler and Saayman, 1972). Slijper

(1962) hypothesized that violent interactions among cetaceans occur more in contexts of social dominance than in contexts of sexual competition. In manatees, sexual rivalry appears to be the only stimulus for aggression. Visual signals related to threat and submission have been observed in dolphins (D. Caldwell and M. Caldwell, 1972) but evidently do not occur among manatees.

Fundamental differences in the behavioral attributes of cetaceans and sirenians also are obvious in their play. The antics of porpoises and dolphins, both captive and free, suggest a sense of play far more refined than the stereotyped, sex-oriented play sessions of manatees. Play in dolphins appears to be an integral part of their behavior, consummating an important psychological need. Many of the smaller toothed whales occupy hours of each day engaging in hydrobatics and chasing and playing with one another. *Tursiops* has even been known to direct play toward other animals (Tayler and Saayman, 1972). Manatees seem to engage in intraspecific play only coincidentally when the right combination of animals happens to meet. At such times young males chase and embrace females in a near replica of sexual behavior. Manatees have never been observed to play with other animals.

Various species of cetaceans are known to ride waves, leap free of the water, spin and somersault in midair, and lobtail (Slijper, 1962; Evans and Bastian, 1969). Manatees have never been seen to breach with the exception of one occasion when an animal is reported to have jumped completely out of water to escape capture in a net (Scholander and Irving, 1941).

Many of the odontocetes appear to be not only playful but imitative and inventive. In captivity they are highly responsive to training and have learned a complex variety of tricks, games, and behavioral sequences, many of which they perform without reinforcement and seemingly for pleasure (McBride and Hebb, 1948; McBride and Kritzler, 1951; Kritzler, 1952; Brown and Norris, 1956; Norris and Prescott, 1961; Layne and Caldwell, 1964; Caldwell and Caldwell, 1964, 1966, 1968; Caldwell *et al.,* 1965; Brown *et al.,* 1966; Tavolga, 1966; M. Caldwell and D. Caldwell, 1972; Tayler and Saayman, 1973). Captive manatees, on the other hand, have shown no evidence of perceptual learning and are only known to perform a few simple conditioned responses in anticipation of feeding (personal observations). The behavior of a captive male that would roll over and slap his flipper on his chest for a reward was typical. Dolphins have been known to amuse themselves for hours playing with floating objects while the manatee's interest in toying with floating or submerged objects is perfunctory.

Both manatees and cetaceans appear to have strong investigative and exploratory drives. However, scouting behavior which has been observed in *Tursiops* (Caldwell *et al.*, 1965) does not seem to occur in manatees.

Manatee vocalizations were compared briefly with those of cetaceans (page 98). Manatees are normally silent and evidently have no need for ultrasound. Their vocal repertoire of squeaks and squeals appears remarkably simple when compared with the wide range of clicked, burst-pulsed, and pure tone signals produced by cetaceans for purposes of echo-ranging and communication (Norris, 1969; Busnel and Dziedzic, 1966). There is evidence that *Tursiops truncatus* can discriminate frequencies from 1 to 36 kHz (Herman and Arbiet, 1972), whereas the spectrum of recorded frequencies for manatees is only 0.6 to 16 kHz (Schevill and Watkins, 1965). It seems that whales and dolphins produce both sonic and ultrasonic emissions in connection with procuring prey, maintaining contact within pods, and expressing a wide variety of emotional states (Evans and Bastian, 1969). Manatee phonations seem basically emotive and less socially oriented than the calls of cetaceans. The supracranial air sinuses appear to play an important role in the production of sound by cetaceans (Lawrence and Schevill, 1956; Kellogg, 1961), but there is no suggestion that sirenians produce noise through the nasal passages.

Mass panic and strandings, notably among pilot whales (*Globicephala*), killer whales (*Orcinus*), false killer whales (*Pseudorca*), and sperm whales (*Physeter*), are believed to be related to disruption of sonar and subsequent disorientation in shallow water (Dudok van Heel, 1966). Stranding in manatees appears to result from failure to retreat with an outgoing tide or from evasive action intentionally undertaken by an estrous female to escape pursuit by male escorts.

Among the Cetacea there appear to be both arhythmic and rhythmic species. Captive Amazon and bottle-nosed dolphins have been found to intersperse sleep and activity throughout a 24-hour period, although in the latter there is evidence for a periodicity in the frequency of vocalizations (M. Caldwell *et al.*, 1966; Powell, 1966; M. Caldwell and D. Caldwell, 1972). In the wild, Amazon dolphins seem to be active day and night (Layne, 1958), and it appears that gray whales do not rest at night, at least while migrating (Cummings *et al.,* 1968). There is also evidence that sperm whales are equally active day and night (Slijper, 1962). However, Saayman *et al.* (1973) discovered that the feeding of free-ranging *Tursiops aduncus* was influenced by a diel cycle and that social interactions and whistle phonations in captive *Tursiops* showed a daily rhythm with peaks in early morning and late afternoon. Manatees, it will be recalled, have shown no evidence of a circadian rhythm.

All cetaceans on which reproductive data have been accumulated appear to have breeding cycles (McBride and Kritzler, 1951; Tavolga and Essapian, 1957; Kleinenberg *et al.,* 1964; Tavolga, 1966; Evans and Bastian, 1969; M. Caldwell and D. Caldwell, 1972). According to Slijper (1962), seasonal breeding in whales and dolphins often is timed with the end of migrations and the availability of food. It also seems that dugongs have a mating and calving season (Anderson, 1902; Phillips, 1927; MacMillan, 1955; Heinsohn, 1972). However, there is little indication of an annual breeding cycle in manatees. The reason for this is obscure, but it may have to do with the fact that manatees always have access to food and, in the tropics at least, are not subject to seasonal changes in environmental stress.

Prolonged courtship evidently precedes copulation in both cetaceans and sirenians. Only in the Cetacea, however, does courtship appear to be characterized by tenderness and active participation of the female (Slijper, 1966). Saayman *et al.* (1973) found that during courtship in *Tursiops aduncus* the behavioral roles of male and female were interchangeable. Moreover, courtship behavior in the hump-backed whale (*Megaptera*), gray whale (*Eschrichtius*), and certain odontocetes seems to involve more activity and ritual than is found in manatees (Tavolga and Essapian, 1957; Slijper, 1962; Sauer, 1963; Evans and Bastian, 1969). Precopulatory behavior in captive bottle-nosed dolphins includes mutual posturing, stroking, rubbing, nuzzling, mouthing, jaw clapping, and yelping (Tavolga and Essapian, 1957). By comparison, courtship activity in manatees is limited to chasing, mouthing, and embraces that are initiated by males and never reciprocated by females. It appears that male manatees do not direct their vocalizations as much to the female as to other males; the female, in turn, squeals mostly in annoyance.

Tayler and Saayman (1972) found that mating in *Tursiops adun-*

cus is a system of rotating consort relationships that does not involve the formation of permanent pair bonds. Manatees do not pair up to mate; rather, estrous females are escorted by many males and are promiscuous. Harems and bachelor herds are reported in sperm whales (Slijper, 1962) but are not found in manatees.

A strong sexual drive among males seems to be characteristic of both the Sirenia and Cetacea. This may be related to the difficulty of broadcasting the occurrence of estrus in water. In manatees at least, it appears as if male sexual appetite has evolved in conjunction with an extended estrous period to increase the chance of a female being accompanied while in heat. Homosexual behavior has been observed among wild manatees and masturbation in captive manatees and bottle-nosed dolphins (M. Caldwell and D. Caldwell, 1972; personal observations).

Horizontal copulation is apparently the rule among cetaceans; however, vertical copulation has been observed in mysticetes and the sperm whale (Slijper, 1962; D. Caldwell *et al.,* 1966), and above-water copulation has been recorded in the Gangetic dolphin (*Platanista*) (Pilleri, 1971*a*). As far as known, manatees mate only in a horizontal position. Intromission in the bottle-nosed dolphin lasts 2 to 10 seconds (Tavolga and Essapian, 1957) as compared with 15 to 30 seconds in the manatee.

Sirenians and cetaceans are generally uniparous. Slow maturation of the young and a strong tie between mother and calf are characteristic of both manatees and whales. In both groups, mothers bear and suckle their young underwater and raise the newborn to the surface for air. In certain dolphins, however, the care of a young animal is sometimes shared by other cows or "aunts" (Slijper, 1962). There is no evidence of comparable behavior in manatees; the mother raises her offspring unassisted. There is reason to believe that cetacean cows are aggressive in defense of their calves (Slijper, 1962), whereas manatee mothers react passively in times of danger.

Manatee calves pump milk from the pectoral teats of their mothers by sucking for periods up to two minutes. Cetacean mothers squirt milk into the mouth of the calf from pelvic nipples. In *Tursiops* the calf has been seen to suck one to nine times per feeding session, each suckling lasting for only a few seconds (Tavolga and Essapian, 1957).

The reason for behavioral differences in manatees and cetaceans are speculative, but it appears that manatees have less need for tight sociality than do pelagic mammals. Manatees live within the confines of rivers and coastal channels where there are more opportunities to find mates, where the dissemination of odor and sound is more restricted, where the chance of becoming lost is reduced, and where the risk of predation is lessened. Statements in Tate (1947) and Jarman (1966) suggest that dugongs are as loosely organized as manatees and have not evolved stronger social bonds as an adaptation to life in coastal shoals. It is also worth noting that river dolphins (*Inia, Lipotes, Platanista,* and *Pontoporia*) and harbor porpoises (*Phocoena*) tend to be solitary or to live in much smaller groups than their pelagic relatives.

Cetaceans that inhabit the open ocean seem to have evolved a highly developed social life as a means to facilitate capture of prey and to counteract the threats of separation and predation. It is known that schooling functions in cooperative fishing (Slijper, 1962; Kleinenberg *et al.,* 1964; Saayman *et al.,* 1973). Coordinated herding of food fish has been reported in a number of delphinids, and I have observed such behavior in *Tursiops.* A tight communal organization also seems to play a role in defense against predators (Slijper, 1962). Hostile interactions between sharks and dolphins have been reported (Wood *et al.,* 1970; Irvine *et al.,* 1973) and instances recorded of sharks (*Carcharodon*) and killer whales (*Orcinus*) preying on cetaceans (Kleinenberg *et al.,* 1964; Rice and Wolman, 1971; Arnold, 1972; Baldridge, 1972). Manatees, on the other hand, appear to lack predators and have no need for cooperation in the procurement of food, obviating the need for mutual aid in times of stress and accounting in part, it seems, for their relatively unstructured social life.

SUMMARY

THE ecology and behavior of the manatee, *Trichechus manatus* Linnaeus, were studied in Florida from October 1967 through March 1969, during the winter of 1970–71, and from November 1972 to January 1974. Research was focused on the coast of Citrus County in west-central Florida, particularly on the headwaters of the Crystal River, where clear springs of constant temperature (23.7°C) provided convenient conditions for above-

and underwater observations of periodic cold-induced congregations of manatees during the winter months. Summers were mostly devoted to interviews and aerial surveys and to observations of manatees in salt water. The following were among the major findings of the study.

1. Seventy manatees were identified in Citrus County in the winters of 1967–68 and 1968–69. The population consisted of 13 calves, 15 juveniles, and 42 adults, and included 31 males and 32 females among animals of known sex.

2. Drops in the air temperature below 10°C induced congregations of manatees in the headwaters of the Crystal and Homosassa rivers. A concomitant drop in the temperature of the Gulf coastal waters apparently reinforced this primary stimulus. Manatees were observed in water as cold as 13.5°C.

3. Populations of manatees appear to be concentrated in select estuarine and riverine habitats on the central west coast of Florida. There is evidence of long-range offshore migrations between population centers. Migrations appear to be both seasonal, in response to changes in the air temperature, and nonseasonal.

4. The activities of manatees seem to be arhythmic.

5. In their movements manatees followed established travel routes. They preferred channels that were 2 meters or more in depth and generally shunned waterways less than a meter deep. The animals usually swam at depths of 1 to 3 meters. Salinity, tides, and currents affect the activity of manatees.

6. In the rivers and estuaries of Citrus County, manatees fed almost entirely on submerged vascular plants. Their staple food species were *Hydrilla verticillata, Vallisneria neotropicallis, Ceratophyllum demersum, Myriophyllum spicatum, Ruppia maritima,* and *Diplanthera wrightii.* In salt water, manatees preferred *Syringodium filiforme* and *Thalassia testudinum.* In the absence of submerged vascular vegetation, manatees were seen to feed on *Eichhornia crassipes.* In waterways devoid of submerged or floating spermatophytes, manatees turned to algae and bank growth. Manatees usually fed in discrete sessions during which they focused their attention on one species of plant. There is evidence that the animals time their movements to coincide with the availability of food. They also appear to require fresh water for osmoregulation.

7. The manatee uses its tail not only as an organ of propulsion but as a rudder by means of which it is able to control roll, pitch,

and yaw. The flippers are used in precise maneuvering and in minor corrective movements to stabilize, position, and orient the animal. Cruising manatees do not utilize their flippers as hydrofoils. Cruising speeds ranged from 3 to 7 km/hr; fleeing manatees reached speeds of 25 km/hr.

8. Lengths of breaths and the intervals between breaths are correlated with age and state of activity. The surfacing behavior of resting manatees bore no resemblance to that of cruising animals. Manatees tended to surface synchronously when in groups.

9. Manatees rested by hanging suspended near the surface or lying prone on the bottom. In both positions animals lapsed into a somnolent state with eyes closed and bodies motionless.

10. Comfort activities included stretching, scratching, rubbing, mouth cleaning, and rooting.

11. Manatees periodically regurgitated a yellow-green mash composed of partially digested plant material.

12. The manatee is a weakly social, essentially solitary animal. The family unit consists of a cow with a calf. All other associations, with the exception of an estrous herd, are temporary and loosely organized. Groups are randomly made up of juveniles and adults of both sexes. Social interactions occur in both sexual and nonsexual contexts. The repertoire of intraspecific contact includes mouthing, nuzzling, nudging, and embracing. There are no displays. Manatees exhibit social facilitation, but there is no evidence of communal defense or mutual aid. There was virtually no indication of a social hierarchy.

13. Manatees were normally silent but emitted high-pitched squeals, chirp-squeaks, and screams under conditions of fear, aggravation, protest, internal conflict, male sexual arousal, and play. Their vocalizations seem to be nonnavigational; to lack ultrasonic signals, pulsed emissions, or directional sound fields; and to be more impulsive than communicative. The only predictable vocal exchange between manatees was the alarm duet between a cow and her calf.

14. A cow in heat was accompanied by courting bulls for periods of less than a week to more than a month. During this time the courtship of bulls was relentless, but the cow appeared to be receptive only at brief intervals. While receptive, the cow was promiscuous. Copulation was effected when a bull rolled on his back and grasped the cow to his belly from underneath. Male compe-

tition for the position next to an estrous cow seemed to be the sole source of aggression among manatees. Bulls also made sexual advances toward anestrous cows but were invariably thwarted. Male manatees engaged in various types of homosexual behavior.

15. Manatees indulged in what appeared to be play. The animals exchanged gentle nibbles, kisses, and embraces that were age and sex independent and decidedly nonsexual. Juvenile males occasionally instigated interactions with cows that suggested sexual activity, but lacked the full complement of patterns found in adult reproductive behavior.

16. Presumably to reduce the danger of predation, cows are believed to seek the safety of a sheltered backwater to give birth. Nursing periods lasted approximately two minutes. The defensive behavior of a menaced cow with a calf was restricted to alarm calls and flight.

17. Manatees in Florida appear to have no definite breeding season. Barring the death of an infant, cows probably breed every two to two and a half years. Gestation apparently lasts about 13 months. A cow suckles her calf from its birth to the dissolution of the parent-offspring bond, a period of one to two years. One cow at Crystal River provided evidence of both twinning and foster parenthood.

18. The greatest dangers to the manatee in Florida are the propellers of power boats and attacks by vandals. There was no evidence of manatees being preyed upon by aquatic predators.

19. Manatees have exceptional acoustic sensitivity; sound is doubtless the major directional determinant in social interactions. Manatees also make extensive use of their eyes; in clear water their preferred method of environmental exploration is visual. The prevalence of mouthing in social encounters suggests that manatees possess a chemoreceptive sense by which they can recognize odors in the water.

20. Manatees usually dove from the surface to avoid being hit by power boats. Most of the animals at Crystal River were wary and would not allow close approach by divers. A handful of animals, however, had become inured to the presence of divers and actively solicited caresses from them.

21. Members of the Sirenia and Cetacea are fully aquatic and show convergence in morphology, locomotion, and diving physiology. The behavioral attributes of the two orders, however, are

largely divergent. Manatees are lethargic littoral herbivores, subject to minimal environmental stress. Without need for association in obtaining food or defense against predators, they manifest a rudimentary sociality. The majority of cetaceans, on the other hand, are animated carnivores whose activities demand insight, group cooperation, and the production of ultrasound. Porpoises and whales, especially pelagic species, appear to have structured societies whose organization is reflected in intricate vocal repertoires and in highly developed patterns of play, courtship, herding, and defense. Behavioral similarities between manatees and cetaceans (at least certain species) include lack of territoriality and absence of a diel rhythm.

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