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22 Status and Biogeography of the West Indian Manatee

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Abstract — We review historical and recent information on the distribution, status, and habitat associations of the West Indian manatee, *Trichechus manatus*, summarize threats to its continued survival, and discuss some biogeographical patterns of trichechids. Historical accounts indicate that manatees were once more common and that hunting has been responsible for declining numbers throughout much of their range. Small numbers occur throughout the Greater Antilles, where opportunistic taking by fishermen is a major source of mortality. Populations in Haiti, the Dominican Republic, and Jamaica are particularly vulnerable. Manatees have not been documented to occur in the Lesser Antilles since the 18th century, except for rare sightings in the Virgin Islands. Manatee sightings in the Bahamas are also rare; however, a recent dispersal from the northwest coast of Florida to the Bahamas has been documented. Manatees are relatively abundant in Belize compared with other countries of Central America. They persist in some of the large river systems of South America: the Río Magdalena in Colombia, Río Orinoco in Venezuela, and probably the Río Mearim in Brazil. They are absent or scarce along most of the South American coast, except in the extensive coastal wetlands of Guyana and Suriname. At present, there are only three regions in Mexico where manatees are still commonly found. Manatees are widely distributed on both coasts of Florida, and some venture westward along the Gulf coast and northward along the Atlantic coast of the southeastern United States, primarily during the warm season. Heated industrial effluents along both coasts have influenced manatee distribution and migratory patterns in the United States. Illegal killing continues to threaten the survival of manatees in many countries. Despite protective measures to regulate boating activity, collision with boats is still the major cause of human-related manatee mortality in Florida. Habitat alteration is a growing concern in all countries.

Manatees in the Greater Antilles and Central and South America belong to the same subspecies, *T. manatus manatus*. However, results of recent genetic analysis indicate greater similarity between the Florida manatee, *T. manatus latirostris*, and manatees in the Dominican Republic and Puerto Rico, than between the latter and manatees in South America. The highest genetic diversity is found along the northern coast of South America, at the core of the species' range; marginal populations (in Florida, Mexico, and Brazil) were each found to be monomorphic (only one haplotype apiece) although distinct from one another. Salinity, temperature, water depth, currents, shelter from wave action, and availability of vegetation are important determining factors of manatee distribution. The association of *T. manatus* with freshwater sources is a highly consistent pattern. Throughout most of their range, manatees appear to prefer rivers and estuaries to marine habitats. The Amazonian species, *T. inunguis*, may be restricted to the Amazon River because of intolerance of salinity. Cool winters and gaps in suitable habitat on the northern Gulf coast, and the Straits of Florida to the south, serve as geographical barriers that isolate the Florida subspecies. Manatees in northeastern Brazil, at the southern end of the species' range, may also be geographically isolated. Unlike the Florida subspecies, they no longer inhabit the subtropical to temperate portion of their historical range.

INTRODUCTION

There are four living species of the mammalian order Sirenia (sea cows): the dugong (*Dugong dugon*) and three manatees (*Trichechus* spp.). The dugong inhabits tropical and subtropical coastal waters in the Indian and western Pacific Oceans. The Amazonian manatee (*T. inunguis*) occurs only in fresh water in the Amazon River system, and the West African manatee (*T. senegalensis*) occurs in both freshwater and coastal marine habitats of tropical West Africa. The West Indian manatee (*T. manatus*) is the most widely distributed of the three trichechids. The common name "West Indian manatee" is not fully descriptive of the range of *T. manatus*, which includes the coasts and many of the rivers of Florida, the Greater Antilles, eastern Mexico and Central America, and northern and northeastern South America. The purpose of this chapter is to review historical and recent information on the distribution, status, and habitat associations of *T. manatus*, to summarize threats

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to continued survival of this species and conservation efforts throughout its range, and to discuss some of its biogeographical patterns. We incorporated much of the information presented in Lefebvre et al. (1989), rather than simply updating that work.

Two types of citations are used for unpublished communications: personal communication refers to a written communication (i.e., by letter) or a spoken communication between the cited individual and one of the authors, and unpublished reports appear in the Literature Cited section.

HISTORICAL DISTRIBUTION

Historical accounts indicate that manatees were once more common and that hunting has in part been responsible for declining manatee numbers throughout their range (Thornback and Jenkins, 1982). McKillop (1985) pointed out that early reports of manatee distribution and exploitation, such as Dampier's (1699), may demonstrate that manatees were previously more common and a reliable meat source, whereas current ethnographic accounts indicate that in many areas manatees are now scarce, difficult to capture, and not a major food source. Nevertheless, many of the areas where manatees were hunted prehistorically and historically still have manatees. The historical uses of manatee meat, oil, bones, and hide have been described by many authors, for example, True (1884), Allen (1942), Rouse (1964), Bertram and Bertram (1973), and Husar (1977) (see also Domning, 1996, for a comprehensive bibliography of this and other aspects of manatee biology). It is probably fair to say that if manatee meat had not been highly esteemed by pre-Columbian inhabitants and early explorers of the West Atlantic region, we would know much less about the former range and abundance of this species.

With the possible exception of Cuba, little historical evidence exists that manatees were ever very abundant in the Greater Antilles (Figure 1). In 1494 Columbus reportedly found freshwater springs in the Bahía de Cochinos, Cuba, which attracted "swarms" of manatees (Morison, 1942). Fernández de Oviedo, as reported by Cuní (1918), described the use of tethered remoras by Indians to locate and capture manatees on the coast of Cuba in 1520, and noted hunting of manatees by Spaniards with crossbows. Acosta also saw manatees in Cuba, as well as "St. Dominicke, Portrique and Jamaique" (Hispaniola, Puerto Rico, and Jamaica) in 1588, and ate manatee meat in Hispaniola (Baughman, 1946). Dampier (1699) saw manatees in Cuba and had heard of their occurrence on the north coast of Jamaica. According to Cuní (1918), manatees were abundant in the river mouths and estuaries of Cuba before 1866, but since then they have been reduced in numbers. Gundlach (1877) also described manatees in earlier times in Cuba as very abundant, but in his day as much reduced although not rare. Barrett (1935) optimistically concluded that manatees were once plentiful in estuaries on the central north coast of Puerto Rico because a town there was named Manatí by the Spanish. Evermann (1902) described the manatee in Puerto Rico as being "of very rare occurrence." Although Fewkes (1907) lists the manatee as one of many species that contributed to the Puerto Rican diet, he reported that fish, crabs, and small mammals were the most important food animals in the West Indies. Sloan (1725, quoted in Murray, 1991) said that manatees had formerly been frequent in Jamaica, but owing to overhunting they had already become rare by the time of his visit to the Caribbean in 1687–1689. Duerden (1901) did not mention manatees in his account of fisheries in Jamaica, the Bahamas, or the Leeward Islands (the northern Lesser Antilles), whereas he specifically mentioned them in his coverage of Trinidad and Tobago. Both Duerden (1901) and Neish (1896) reported that eight manatees had been captured in the vicinity of Old Harbour, Jamaica in the previous 7 to 10 years; Neish described them as uncommon, and Duerden seemed unimpressed with the manatee's potential for greater economic importance, noting that they are "very slow breeders."

A small number of manatee bones or bone fragments have been recovered at Amerindian sites in Jamaica (Wing and Reitz, 1982), Haiti (E. S. Wing, personal communication, 1987), the Dominican Republic (Miller, 1929), Puerto Rico (E. S. Wing, personal communication, 1987), and Vieques Island off Puerto Rico (Narganes-S., 1982). Rouse (1986:133) speculated that flint points crafted by Amerindians in Hispaniola 3,000 to 5,000 years ago were used as spear heads for hunting

manatees, since he assumed that large land mammals were absent. However, Rouse (1986) noted that early inhabitants of Cuba and Hispaniola were oriented primarily toward the land, and he may have overlooked ground sloths as an alternative prey species (Morgan and Woods, 1986). Manatees were commercially exploited in Suriname (de Jong, 1961; Husar, 1977), Guyana (de Jong, 1961; Bertram and Bertram, 1973), and Brazil (Domning, 1982a) for export to the West Indies during the 17th through 19th centuries, which suggests that manatees may not have been very abundant historically around these islands. In the Lesser Antilles, manatee remains have been identified at Amerindian archaeological sites on six islands: St. Croix, St. Kitts, Barbuda, Antigua, St. Lucia, and Grenada (Miller, 1918; Ray, 1960; Wing et al., 1968; Wing and Reitz, 1982; Watters et al., 1984; Steininger, 1986). Vertebrate remains collected at other excavation sites on St. Kitts, Antigua, St. Lucia, and Barbados did not include manatees (Wing, 1967; Wing et al., 1968; Wing and Scudder, 1980). Except for rare sightings in the Virgin Islands (e.g., D.W. Peterson, 1982, personal communication; Mignucci-Giannoni, 2000), manatees have not been documented to occur in the Lesser Antilles since the 18th century (Allen, 1942; Ray, 1960). Several 19th-century authors included the Islands of Marie-Galante and Martinique in the manatee's range, but gave no new documentation of their presence (Ray, 1960).

The evidence for recent large-scale reductions in Central and South American manatee numbers is stronger. Notable declines are thought to have occurred in Honduras (Klein, 1979; Rathbun et al., 1983), Costa Rica and Panama (Husar, 1977; O'Donnell, 1981), Venezuela (Bertram and Bertram, 1973; Mondolfi, 1974; O'Shea et al., 1986), and Brazil (Domning, 1982a). Dampier (1699) saw manatees along the coasts of Mexico and Central America, and heard of great numbers occurring in the rivers of Suriname. Historical accounts exist for manatees along the coast of Guatemala (Bradley, 1983). Barrett (1935) claimed that one of the best-known "herds" of manatees on the Caribbean coast inhabited the Indio River and its bayous in Nicaragua (Figure 2), where hunters took many. Von Frantzius reported manatees to be very common in several rivers in Costa Rica in 1868 (Allen, 1942). The Bahía Almirante and Bocas del Toro area were documented as a region where buccaneers were familiar with manatees and provisioned themselves with manatee meat during the 1600s (Dampier, 1699; O'Donnell, 1981). Although manatees currently persist in this region, their numbers have been severely depressed (Husar, 1977; O'Donnell, 1981). Maack reported in 1874 that manatees were frequently caught in the Atrato and Cacarica Rivers in Colombia (Figure 3) (Allen, 1942). True (1884) cited Brandt's 1868 literature review of manatee abundance in South America, which indicated that in many regions, particularly around river mouths or other places where shelter was lacking, manatees were disappearing or extirpated. In the upper reaches of rivers, however, Brandt concluded that hunting pressure may have been less severe (True, 1884). By the end of the 19th century, West Indian manatees disappeared from much of the east coast of Brazil (Whitehead, 1977).

Manatees historically occurred along the entire Mexican coast of the Gulf of Mexico and Caribbean Sea (Campbell and Gicca, 1978). Manatee meat contributed to the prehistoric diet in at least two sites in Mexico, near Alvarado and in northern Quintana Roo (Figure 2) (McKillop, 1985). Baughman (1946) cited several 16th- and 17th-century authors who reported manatees along the coast of Yucatan. Middens (A.D. 400–700) on Moho Cay near what is now Belize City have yielded the largest number of manatee bones of all greater Caribbean prehistoric sites thus far investigated (McKillop, 1985). Manatee remains have been reported from several other coastal and inland archaeological sites in Belize (Bradley, 1983), and manatees from Belize were provided to 17th-century privateers as a meat source (O'Donnell, 1981). Prehistoric evidence exists for the occurrence of manatees at the Islas de la Bahía in the offshore Caribbean near present-day Honduras (Strong, 1935), but they are no longer found in the region (Klein, 1979; Rathbun et al., 1983).

Hartman (1972, 1974) believed that hunting during the 17th through the 19th centuries reduced the number of manatees in Florida to a few relict groups, but he presented no evidence of their former greater abundance. Harlan (1824) cited Burrows' description of considerable numbers of manatees about the mouths of rivers near "the capes of East Florida" (according to Moore, 1956, the south end of Key Biscayne in the Miami area; Figure 4). Allen (1942) concluded that evidence

of manatees having once been much more abundant in Florida was subjective and unconvincing, although he stated, without reference to a specific source, that the manatee had become rather scarce in many parts of Florida by about 1890. He may have been overly influenced by information from Bangs (1895), who described the winters of 1894 and 1895 as exceptionally cold, resulting in freeze-related manatee mortality in the Sebastian River. Excessive drainage of wetlands has also been blamed for the manatee's disappearance from some regions of Florida (Trumbull, 1949).

Cumbaa (1980) determined that aboriginal use of manatees in Florida was almost exclusively restricted to inland and coastal riverine sites, and concluded that manatees were not abundant enough to supply a stable food resource to the Paleo-Indians of Florida. In 1773, Bartram (1791) found skeletal remains of a manatee that he thought had been killed by Indians at Manatee Spring on the Suwannee River. There are few other records of manatees using the Gulf coast of Florida from the Suwannee River south to the Chassahowitzka River before the mid-1900s (Powell and Rathbun, 1984). Allen (1942) attributed a slow increase in manatee numbers in Florida to an 1893 state law that prohibited their killing.

PRESENT DISTRIBUTION, STATUS, AND HABITAT ASSOCIATIONS

West Indies

Puerto Rico

Manatees occur along the entire coast of Puerto Rico, but are unevenly distributed (Figure 1). Aerial surveys flown during the late 1970s and mid-1980s documented the greatest concentrations along the south-central and eastern shores and none on the northwestern shore (Powell et al., 1981; Rathbun et al., 1985a). During 10 monthly surveys flown from June 1978 through March 1979, a mean of 22.6 ± 12.6 manatees was sighted, with a range of 11 to 51 (Powell et al., 1981). In 12 monthly surveys flown from March 1984 through March 1985, a mean of 43.6 ± 13.1 was sighted, with a range of 20 to 62 (Rathbun et al., 1985a). Both Powell et al. (1981) and Rathbun et al. (1985a) reported that slightly over one third of their sightings came from around the Roosevelt Roads Naval Station on the eastern end of the island, and the northwestern shore of neighboring Vieques Island (Figure 1). In both of these surveys, a similar proportion of calves were seen: 6.4 ± 4.9% (Powell et al., 1981) and 7.6% (Rathbun et al., 1985a).

The U.S. Fish and Wildlife Service's (USFWS) Caribbean Field Office conducted aerial surveys from 1984 through 1999 (Jorge Saliva, USFWS, personal communication, 2000). As in previous surveys, the greatest numbers of manatees were seen along the south-central and eastern coasts. Counts from these island-wide flights ranged from 43 to 101 individuals. Comparisons among these and earlier survey results may not be entirely valid because of differences in observers, methods, and survey conditions. However, the number of manatees in Puerto Rico probably has not declined, and may have increased, since 1978.

Except for Vieques Island, manatees are rarely reported from the islands offshore of Puerto Rico. A manatee was entangled in a fishing net off Culebra Island in 1982 (Jimenez, 1982), and one was reported there in 1999 (Caribbean Stranding Network, personal communication). Manatees have never been reported for Mona and Desecheo Islands (Powell et al., 1981).

A total of 79 manatee carcasses were recovered in Puerto Rico from 1974 through 1995, 35 since 1990 (Mignucci-Giannoni et al., 2000). Carcasses were recovered from all coasts, with the highest number of records from the north, northeast, and south coasts. The greatest concentrations occurred in the areas of Fajardo/Ceiba, Bahia de Jobos, Toa Baja, Guayanilla, Cabo Rojo, and Río Grande/Luquillo. The lowest numbers were in the northwest and extreme southeast coasts, Vieques Island, and Culebra Island. In 1998, a death was documented in St. Thomas, U.S. Virgin Islands; this animal was probably a stray from Puerto Rico.

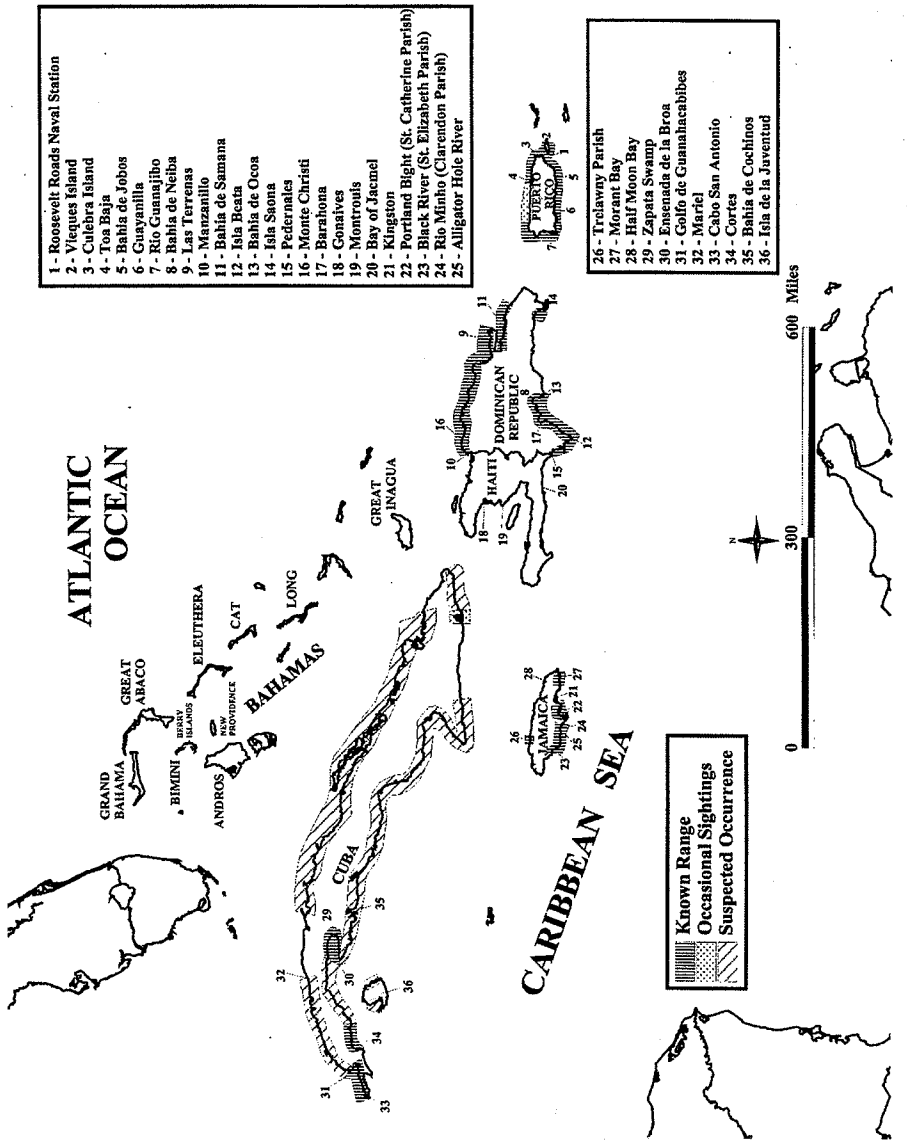

FIGURE 1 Distribution of the West Indian manatee (*Trichechus manatus*) in the Greater Antilles.

Of the 79 deaths recorded in Puerto Rico since 1974 (Mignucci-Giannoni et al., 2000), 39 (49%) were human-related, including 14 (18%) caused by watercraft collisions, two (2.5%) following accidental entanglement in fishermen's nets, and 19 (24%) illegally hunted and killed. A total of 17 cases (21%) involved dependent calves, and in 21 cases (27%) cause of death was not determined.

Manatees are protected by the U.S. Marine Mammal Protection Act and Endangered Species Act, as well as by several Commonwealth of Puerto Rico laws: La Ley de Pesca del Estado Libre Associado (1943), La Ley de Vida Silvestre (1977), and the Regulation to Govern the Management of Threatened and Endangered Species in the Commonwealth of Puerto Rico (1985) (D. Mignogno, personal communication, 1987). Although hunting pressures are believed to have subsided with the adoption of federal regulations and improvements in the island's economic status, poaching has been documented as recently as 1995.

As part of recovery efforts, the Caribbean Stranding Network has coordinated the rescue and rehabilitation of injured and orphaned manatees since 1990 (Mignucci-Giannoni, 1998). A successful public education campaign in the early 1990s to promote manatee conservation centered on an orphaned manatee named Moises that was rescued, rehabilitated, and release to the wild. Mortality studies and rescue and rehabilitation efforts have yielded additional life history information on manatees in Puerto Rico, including diet (Mignucci-Giannoni and Beck, 1998), population genetics (García-Rodríguez et al., 1998), parasitology (Mignucci-Giannoni et al., 1999), and hematology (Montoya-Ospina, 1994; Jiménez-Marrero et al., 1999).

Two recent radio-tracking studies of manatees in Puerto Rico have revealed regional movement patterns. From 1992 through 1996, the U.S. Geological Survey's Sirenia Project tagged seven manatees at the Naval Station Roosevelt Roads (NSRR), a known high-use area. Most remained near, or frequently returned to, the waters of NSRR; however, one individual swam 50 km south to Puerto Patillas and another individual ranged 40 km north to Luquillo. Four of the seven tagged manatees repeatedly traveled 9 km offshore to Vieques Island. The tagged manatees used specific areas, such as feeding sites in Pelican Cove and Ensenada Honda and the freshwater discharge at the Cape Hart sewage treatment plant. Although seagrass beds extend several kilometers offshore and to depths of over 20 m, most locations and documented feeding areas were close to shore and often in water only 1.5 to 3 m deep (Lefebvre et al., 2000).

The U.S. Geological Survey's Sirenia Project, U.S. Fish and Wildlife Service's Caribbean Field Office, and the Caribbean Stranding Network collaborated to radio-tag four manatees in western Puerto Rico from 1997 to 2000. These individuals were captured at the Río Guanajibo near Mayagüez, and primarily used the waters from Mayagüez south to Boquerón. Feeding areas were documented in shallow, nearshore waters, and in seagrass beds over 1 km offshore. One individual traveled 210 km north and east along the coast to just east of San Juan, where he remained for several weeks before returning to the Río Guanajibo.

Evermann (1902) recognized the association between animal distribution and the physical environment of Puerto Rico. He attributed the rarity of manatees "... to the absence of broad sluggish rivers in which it finds its favorite environment." Barrett (1935) related a decline in manatees along the north coast of Puerto Rico in part to "silting-up" of river mouths, which prevented manatees from grazing on shoreline grasses in river estuaries. Powell et al. (1981) also recognized that manatee distribution in Puerto Rico is influenced by the availability of fresh water. Almost all manatees seen during their nearshore surveys were in the ocean; however, 85.8% of the sightings were within 5 km of natural or artificial freshwater sources. Interviews indicated that manatees visit the mouths of the Loíza and Fajardo Rivers, and after heavy rains they may ascend these rivers for short distances. Powell et al. (1981) concluded that other Puerto Rican rivers are too shallow for manatees to ascend; however, manatees have been reported to swim about 1 km up the Río Loco, near Guanica (Jorge Saliva, USFWS, personal communication, 2000). Manatees have been observed by the third author on numerous occasions drinking fresh water flowing out of the mouth of the Río Blanco, Río Humacao, and Río Guanajibo. Rathbun et al. (1985a) did not

detect any dramatic seasonal shifts in distribution along the coast, nor was there a significant correlation between total monthly rainfall and the total number of manatees seen per month.

Powell et al. (1981) noted the association of manatee distribution and seagrasses, describing *Thalassia*, *Syringodium*, and *Halodule* as probably the most important manatee foods in Puerto Rico. Seagrass beds are relatively sparse along the northwest coast where no manatees were seen, and are extensive on the eastern and southern coasts of the island (Powell et al., 1981). Deep waters close to shore and a lack of embayments also result in less favorable manatee habitat along the north coast. Powell et al. (1981) first documented that manatees use the Cape Hart sewage treatment plant effluent at Roosevelt Roads Naval Station as a source of fresh water for drinking. Rathbun et al. (1985a) further documented the importance of these outfalls by demonstrating that manatees are likely to be present at any time, showing no seasonal, tidal, or diurnal changes in their preference for this site. Rathbun et al. (1985a) also noted the association of manatees and seagrass beds, and suggested that the higher incidence of cow/calf pairs observed at Roosevelt Roads Naval Station and northwestern Vieques Island may have been related to the abundance of seagrass beds at this site, the availability of fresh water at Cape Hart, and the protection from human harassment provided by security procedures at the naval base.

Jamaica

Manatees occur primarily along the southern coast, to the west of Kingston (Fairbairn and Haynes, 1982) (Figure 1). Between May 1981 and April 1982, 13 aerial surveys were conducted along the entire coastline, and manatees were observed primarily in Portland Bight, off the parishes of St. Catherine and Clarendon, and off St. Elizabeth and Manchester Parishes, between the Black River and the Rio Minho (Fairbairn and Haynes, 1982). Two were observed off St. Thomas Parish, on the eastern end of the island, and one off St. Ann Parish. The range in number of manatees seen during the monthly surveys was 1 to 13, with a mean of 6 (Fairbairn and Haynes, 1982). The average number of manatees seen per flight hour in Jamaica (1.27) was higher than the number seen per hour in Haiti (0.64), where only one entire-coast survey was flown, but much lower than the average number per hour seen in Puerto Rico (9.1) (Hurst, 1987). Powell (1976) conducted an aerial survey of the coast from St. Mary Parish clockwise to St. Elizabeth Parish in September 1976, and saw only one manatee, at Alligator Reef off Manchester Parish. Powell (1978) reported piscivory from fishermen's nets by manatees off St. Mary and Trelawny Parishes on the north coast, near Port Maria and Rio Nuevo.

The Natural Resources Conservation Authority (NRCA) conducted an aerial survey (5.5 h) on 10–11 April 1993. Eight manatees, all adults, were sighted, including three of four semicaptive manatees in the Alligator Hole River, Clarendon. A cavorting group of four manatees was observed at Fisherman's Bay, west of Port Morant, St. Thomas. The eighth manatee was sighted on the northeast coast, at Unity Bay, near the town of Port Antonio, Portland (NRCA, 1993). Four sightings were reported off the coast of Trelawny by Trelawny Environmental Protection Association in 1992 (NRCA, 1993). A 2-day aerial survey of the entire coast was conducted in June 1998 (J. A. Powell, personal communication, 2000). A total of 11 manatees were seen, including two calves. On the northern coast, a cow and calf were seen in Half Moon Bay near Falmouth, and three manatees were observed feeding in Turtle Crawle Harbour near Port Antonio. On the southern coast, a cow and calf were sighted in Galleon Harbour, in the northeastern portion of Portland Bight. A single manatee was seen near Macarry Bay, two adults near Great Pedro Bay, and one at Starve Gut Bay near the Black River.

Manatees in Jamaica are protected by the Wild Life Protection Act (1971), which prohibits hunting and possession of protected species (Shaul and Haynes, 1986). Law enforcement efforts, however, are inadequate (A. Haynes-Sutton, personal communication, 1987). Despite public education on the manatee's protected status, Jamaican fishermen continue to take and sell manatees illegally (Hurst, 1987; NRCA, 1993). Deliberate capture of manatees is most frequent in regions that are

economically depressed (A. Haynes, personal communication, 1986). At least three manatees were captured on the south coast of Jamaica in 1985; two were killed for meat and one was rescued by the Natural Resources Conservation Department and released in the Alligator Hole River (Hurst, 1987). In 1987, at least one manatee was killed illegally at Alligator Pond (A. Haynes-Sutton, personal communication, 1987). Hurst (1987) believed that fishermen are responsible for nearly all human-related manatee mortality in Jamaica. Manatees are captured following accidental entanglement in gill nets and beach seines; fishermen claim that manatees frequently drown before their presence is noted (Shaul and Haynes, 1986). Females and juveniles may be more susceptible to capture by beach seining (NRCA, 1993). Hurst (1987) attempted to estimate net entanglement losses from fishing boat statistics, and concluded that St. Elizabeth Parish has the greatest potential for fishing-related mortality. Interviews with local residents indicated that manatee numbers were generally believed to have declined in recent years (Crombie, 1975a; Powell, 1976). Major threats continue to include poaching for food and incidental taking in fishnets and other devices (A. Donaldson, NRCA, personal communication, 1993). There are approximately 12,000 registered full-time fishermen in Jamaica, and 23% of the total coastal catch is by gill nets and beach seines (NRCA, 1993). Gill nets were identified in every area considered good manatee habitat during the 1993 aerial survey (A. Donaldson, NRCA, personal communication, 1993). Destruction of mangrove swamps by commercial, agricultural, and residential development, most notably along the coast of St. Catherine, has also caused concern. Pollution from thermal and industrial discharge, siltation, and dredging operations have affected seagrass beds, thus threatening manatees' food source (NRCA, 1993).

The south coast of Jamaica has extensive areas of shallow water, numerous bays and other areas of calm water, freshwater sources, and seagrass beds, which create favorable habitat for manatees (Hurst, 1987). The north coast has a deep and rugged shoreline, but also has a number of river mouths. Manatees have been observed feeding on *Ceratophyllum* and the starchy root of *Phragmites* in the rivers of south Clarendon and Manchester Parishes (Shaul and Haynes, 1986). Several manatees in the Alligator Hole River were observed feeding on *Ceratophyllum*, *Potamogeton*, and *Phragmites*, and seemed to prefer the lower part of the river, where the undercut banks provide cover (Hurst, 1987; Domning, 1989).

Four manatees were impounded in the Alligator Hole River as part of an NRCA program, Operation Sea Cow, initiated in 1980 to publicize manatees and encourage research and conservation. However, these objectives have been difficult to accomplish because public access to the site is limited and the manatees, all female, are isolated from the already small free-ranging population (Domning, 1989). One of the manatees died and food in the river has become scarce. Plans have been made to radio-tag, release, and monitor the remaining manatees (Domning, 1998a).

Dominican Republic

Husar (1977) reported manatees to be distributed along the southwest and the entire north coasts of the Dominican Republic (Figure 1), with the greatest concentrations occurring in Bahía de Neiba and near Las Terrenas. Belitsky and Belitsky (1980) conducted six entire-coast aerial surveys every other month from February through December 1977. Manatees were sighted along the north coast from Manzanillo to Miches, and along the southwest coast from Isla Beata to Bahía de Ocoa; the only sighting outside of these areas was northwest of Isla Saona on the southeast coast. Belitsky and Belitsky's (1980) surveys indicated that manatees were more common around Monte Cristi than Las Terrenas on the north coast, and common in Bahía de Ocoa as well as Bahía de Neiba on the southwest coast, but in general, their findings conform to the report by Husar (1977). The mean number of sightings per survey on the north coast was 12.3 (range = 2 to 30), and the mean on the southwest coast was 7.5 (range = 1 to 11). Seasonal changes in distribution and abundance were not apparent. Interviews indicated that manatees occur in several other areas: on the east coast, from Boca de Yuma south to Isla Saona; near Nizao on the south coast; in coastal waters between

Isla Beata and the mainland; and near Pedernales (Belitsky and Belitsky, 1980). Local fishermen and residents also reported that manatees once ranged over more extensive areas of the coastline, and Belitsky and Belitsky (1980) attributed apparently reduced numbers to hunting pressure and degradation of habitat by land development.

Currently, the most important areas for manatees in the Dominican Republic are the coastal lagoons, estuaries, rivers, and creeks of the north coast, especially near Monte Cristi and in Samana Bay, and the southwest coast from Ocoa Bay to Barahona. Between August and December 1994, and December and July 1996, a systematic survey was conducted of coastal sites in the Dominican Republic (Ottenwalder and Leon, 1999). Researchers interviewed 418 people, predominantly fishermen (81% of sample), fish and wildlife inspectors, coast guards, park rangers, and people who buy and sell fish in the market. Although 90% of those interviewed knew what a manatee was, 83% believed that there were more manatees in the past. Many of those interviewed indicated that availability of fresh water and submerged vegetation is important in manatee distribution. Most (74%) reported that manatees are good to eat, although few claimed to know where meat could be obtained. A total of 95% knew that manatees are protected by law.

Manatees are still exploited for their meat and bones in the Dominican Republic, and they are currently considered one of the most endangered species on the island (Ottenwalder, 1995). The most significant source of mortality is illegal, opportunistic take by net capture. Approximately 5 to 15 manatees are captured annually along the coast of the island. Preliminary analysis of aerial survey data collected in 1995 (Ottenwalder, 1995) suggests that the number of manatees has decreased since the 1977 surveys conducted by Belitsky and Belitsky (1980). Ottenwalder (2000, personal communication) guesses that there are fewer than 200 manatees in the Dominican Republic.

Most of the river mouths in the Dominican Republic are periodically blocked by sandbars, and manatee habitat has been described as coastal marine rather than estuarine (Belitsky and Belitsky, 1980). Fishermen frequently report that manatees are attracted to springs and river mouths, to drink fresh water (J.A. Ottenwalder, 1987, personal communication). Interviews conducted in 1975 indicated that manatees frequent river mouths on the north coast during the rainy season, and are regular visitors to Río San Juan and Río Yasica (Campbell and Irvine, 1975). Manatees were seen within 1 km of springs northwest of Isla Saona (Tres Hermanas), in Bahía de Samaná (La Guázuma), and near Barahona (Playa de Saledilla) during at least one aerial survey (Belitsky and Belitsky, 1980). Manatees were reported to visit the Massacre, Yaque del Norte, San Juan, Bajabonico Isabela, and Yaque del Sur rivers; however, none was seen in aerial surveys or site visits to these rivers (Belitsky and Belitsky, 1980). Reports of manatees at other river mouths or springs include Playa Grande, northeast of Río San Juan; Playa de Rincón and Bahía de Rincón; Río Caño del Agua near Barahona; Río Cosón and Arroyo Cañada Salada, near Punta Cosón, Samaná; La Poza, east of Las Terrenas, Samaná; Bahía de Manzanillo; Los Patos y Bahía Regalada, Barahona; Estero Hondo y Punta Rucia, Puerto Plata; and Bahía de Yuma (J. A. Ottenwalder, personal communication, 1987). Crombie (1975b) conducted a helicopter survey of the coast between El Peñón and Boca de Yuma, including Isla Saona. He found the coast near Peñón (the site of Tres Hermanas springs), Bahía de Palmillas, and the south coast of Isla Saona to have the most suitable manatee habitat in this area (shallow, calm waters, with a few small *Thalassia* beds).

The sources of manatee mortality in the Dominican Republic are poaching and shark predation (the latter may actually be scavenging) (Belitsky and Belitsky, 1980). Five manatees were taken in 1976: three near Nizao, one east of Monte Cristi, and one near Pedernales (Belitsky and Belitsky, 1980). Manatees were frequently sighted by fishermen in Bahía de Samaná and occasionally caught accidentally in their nets (Mortensen, personal communication, 1975). Interviews conducted by Campbell and Irvine (1975) indicated that manatee meat is highly prized by fishermen in Bahía de Samaná, and that manatees are rarely seen on the north side of the bay, possibly because of fishing pressure.

The Dominican Republic has officially protected manatees since 1962 (Law No. 5914, Article No. 45) and is a signatory of CITES since 1987 (Secretaria de Estado de Agricultura, 1993).

However, law enforcement is not entirely effective (Ottenwalder, 1995). Commerce in polished and carved manatee bones and manatee oil in Santo Domingo markets may pose a significant threat to manatees (Mignucci-Giannoni, 1991). Infrequent boat strikes have been reported (Secretaria de Estado de Agricultura, 1993).

A nonprofit private organization, Prospectiva Ambiental Dominicana, has conducted research on manatees and produced and distributed educational materials. They have recommended measures to protect manatees, including enforcement of regulations to stop illegal taking; protecting preferred habitats by creating manatee sanctuaries; integrating coastal communities and fishermen into conservation efforts; conducting research to determine status, distribution, and exploitation of manatees and their habitats; and establishing a manatee rescue and rehabilitation program (Ottenwalder, 1995).

Haiti

One entire-coast aerial survey was conducted in May 1982, and eight manatees were observed (Rathbun et al., 1985b). Manatee sightings occurred within a very small portion of the western coastline, between Gonaïves and Montrouis (Figure 1). Interviews with coastal residents in 1982 and 1983 indicated that few people under 50 years old had firsthand knowledge of manatees, and the only other area where manatees were reported to have occurred recently was in the Bay of Jacmel in 1977 and 1978. Ottenwalder (1995) describes the manatee population along Haiti's coast as drastically reduced, and facing an uncertain destiny.

Manatees are caught opportunistically in beach seines; however, traditional hunting apparently is no longer practiced, probably because of a decline in manatee numbers over the past 50 years (Rathbun et al., 1985b). The status of manatees in Haiti is extremely tenuous because their known range is so restricted, and the areas where they occur are important to fishermen in this densely populated and economically depressed country. Several areas were identified as having shallow and protected waters, extensive submerged vegetation, and rivers (Figure 4), including the area where manatees were observed at the mouth of the Riviere de l'Arbonite. Woods and Ottenwalder (1992) recommended the establishment of a new national park at the delta of the Riviere de l'Arbonite, around the Baie de la Tortue and Baie de Grand Pierre, to increase protection of this endangered species. The extremely tenuous status of the manatee in Haiti heightens the need for manatee conservation efforts in the neighboring Dominican Republic.

Cuba

Manatees occur along both the north and south coasts of Cuba, and in 1978 were reported to be most frequently seen in the Río Hatiguanico in the Zapata Swamp and in Ensenada de la Broa (Figure 1) (Thornback and Jenkins, 1982). Fishermen were surveyed to determine manatee distribution and abundance in western Cuba between February 1984 and February 1985 (Estrada and Ferrer, 1987). Manatees reportedly occur from Mariel to Cabo San Antonio on the north coast and from Cortes to Bahía de Cochinos on the south coast (A. R. Estrada, personal communication, 1986). There are three areas where manatees are particularly abundant: Golfo de Guanahacabibes, between Cortes and La Coloma, and Ensenada de la Broa/Río Hatiguanico (Estrada and Ferrer, 1987). Sightings were most commonly of solitary manatees, groups of four or more, and pairs, in that order.

A comprehensive interview survey of 301 anglers was conducted countrywide in the late 1980s (except for the area between Jamainitas and Punta Hicacos) (A. R. Estrada, personal communication, 1993; L. T. Ferrer, personal communication, 1993). This survey indicated that manatees are distributed along both coasts, with greater concentrations in the Ensenada de la Broa–Río Hatiguanico–southern coast of Zapata Peninsula region (Matanzas Province). The 12 areas with a greater abundance of manatees were identified: Ensenada de Guadiana–Puerto Esperanza; Bahía de Cárdenas; Carahatas–Caibarién; Turiguanó; Nuevitas–Puerto Padre; Gibara–Cayo Saetía on the northern coast; Siguanea and Punta del Este (Isla de la Juventud); Ensenada de la Broa;

Casilda–Tunas de Zaza; Golfo de Ana María; Golfo de Guacanayabo–Ensenada de Mora; and Baitiquirí, on the southern coast.

Aerial surveys have been conducted over the Ensenada de la Broa–Río Hatiguanico–Zapata Peninsula region: four 80-min flights in November 1986 with a total of 25 manatee sightings; four 80-min (approx. 96-km) flights in July 1987 with 39 manatee sightings; and four 70-min (approx. 159-km) flights in July 1992 with 20 manatee sightings (A. R. Estrada, personal communication, 1993; L. T. Ferrer, personal communication, 1993). Eight 1-h (approx. 93-km) surveys were flown between October 1985 and January 1986 between the mouths of the rivers Jatibonico del Sur and Agabama-Manatí, south of Sancti Spíritus Province, with a total of 44 manatee sightings. Flights over Ensenada de la Broa and the southern coast of Sancti Spíritus Province between 1985 and 1987 resulted in 59 manatee sightings during 9.5 h (1425 km) in Ensenada, and 39 sightings during 5.75 h (990 km) in Sancti Spíritus (Wotzkow, 1990). All but two of the sightings were of adults.

Cuba has extensive areas of shallow, protected coastal waters and many rivers on both the north and south coasts. Cuni (1918) described the habitat of manatees in Cuba as more riverine than marine and noted manatees feeding on riverbank grasses with part of their bodies out of water. He also noted their use of freshwater springs. Estrada and Ferrer (1987) reported that manatees were most frequently sighted along sheltered coasts with extensive shallow areas offshore. They acknowledged that changes in riverine habitat, caused by damming, erosion related to deforestation, and pollution may have resulted in the manatee's shift to a more marine existence in Cuba. Estrada and Ferrer (1987) noted that almost no reports were received of animals in inter waters, and concluded that, like manatees in the Dominican Republic and Puerto Rico, Cuba's manatees occupy coastal marine habitat, where they feed in large meadows of aquatic plants. Interviews indicated that *Syringodium filiforme* and *Thalassia testudinum* are preferred by manatees (Estrada and Ferrer, 1987).

Varona (personal communication, 1975) described the status of the manatee in Cuba as rare and declining alarmingly, because of pollution and pursuit by humans for its flesh, fat, and hide. In contrast, Estrada and Ferrer (1987) reported that more than 50% of those interviewed had seen a manatee within the last year, and believed that manatees were abundant and had increased in number in the last 10 years. However, Estrada (personal communication, 1994) expressed concern about the manatee's status in more recent years. Interviews identified accidental drowning in fishing nets as the main cause of mortality of manatees in Cuba (Ferrer and Estrada, 1988). Underwater explosions related to petroleum extraction have also caused some manatee deaths.

Manatees in Cuba have been legally protected since 1936 by Decree 707, Article 39. The Fishing Law of 1955, Decree 2724, Article 75, also prohibits any taking of manatees. Manatees have been listed as a threatened species in Cuba since 1973 (A. R. Estrada, personal communication, 1993). In 1982, the Ministry of Fisheries permanently prohibited the capture of manatees in all national territory, with punishment including fines and loss of catch, fishing gear, and boat. However, no research, conservation, or management of the species has been implemented (A. R. Estrada, personal communication, 1993; L. T. Ferrer, personal communication, 1993).

Estrada and Ferrer (1987) recommended that studies be initiated in the areas of greatest manatee abundance to facilitate management and conservation efforts. From May 19 to 20, 1994, a National Workshop on the Protection and Management of Manatees was held in La Habana. Several governmental and nongovernmental institutions met for 2 days to discuss a draft National Plan for the Protection of Manatees in Cuba, which included a number of short-term and mid-term objectives and activities. It is unknown to what extent the plan has been implemented. In general, Cuba has only recently recognized the need to study and protect marine fauna and habitat (A. R. Estrada, personal communication, 1993).

Bahamas

Manatees rarely occur in the Bahamas. The first recorded sighting was in 1904 in the Bimini Islands (Allen, 1942). Odell et al. (1978) observed a manatee in a boat basin at West End, Grand Bahama

Island, in September 1975, and reported several other probable sightings on Grand Bahama Island between 1965 and 1977. A dead manatee, possibly the same one observed in September, was found at Freeport, Grand Bahama Island, in November 1975 (Odell et al., 1978).

Reports of manatees in the Bahamas increased in the 1990s. The Bahamas National Trust logged 25 reports of sightings throughout the islands from 1995 through 1999, many gathered by the Bahamas Marine Mammal Survey (Lynn Gape, Bahamas National Trust, personal communication). On 15 November 1995, a dead manatee was recovered from the intake of a pumping station on Great Inagua at the southern end of the Bahamas. Other reports were from the northern Bahamas, including Cat Island, Highbourne Cay and Staniel Cay (Exumas), Eleuthera Island, New Providence Island, Andros Island, Great Harbour Cay (Berry Islands), Bimini, and many of the Abaco Islands. Residents of Walkers Cay (Abaco Islands) and Andros Island claim manatees were not seen before the 1990s.

Between June 1997 and March 1998, sightings of one or two manatees were frequently reported in the Abaco chain of cays, including records from Tilloo Cay, Harbortown, Great Guana Cay, Man of War Cay, Little Abaco Cay, Black Sound Cay, and Walkers Cay. Two manatees, one with recent propeller scars, were given fresh water from hoses at the Man of War Marina on 15 February 1998. The same two manatees, identified by photographs of their scar patterns, appeared on 2 and 17 March at Walkers Cay and drank fresh water at the marina docks. These individuals may account for most of the recent sightings in the Abacos as they traveled among the islands. After the 17 March 1998 sighting at Walkers, no additional reports from the Abacos were received through December 1999.

A manatee was reported in Bimini on 21 March 1996. Also in Bimini, during late winter 1998, a manatee was seen almost daily for 6 weeks and given fresh water from the marina hoses. From 17 November 1998 to 17 December 1999, a manatee (nicknamed Gina) was routinely seen in the harbor of the U.S. Navy's Atlantic Undersea Testing and Evaluation Center (AUTEC) at Andros Island. This small adult female frequented the pier and boat ramp area, drank fresh water from hoses when it was provided, and approached divers. The longest documented period away from AUTEC was for 35 days between 10 April and 2 May. On 31 December 1999, residents on Great Harbour Cay in the Berry Islands observed a manatee in their marina (Reid, 2000). Sightings of this healthy and relatively tame, small adult female continued almost daily as she returned to drink fresh water from hoses at the marina. Using photographs of her distinctive scar patterns, she was identified as the same manatee that was seen at AUTEC in Andros during 1999. Her rate of travel, 145 km in 13 days, is similar to manatees in Florida. Several months after Gina was first sighted at Great Harbour Cay, an adult male manatee was frequently seen with her in the marina basin.

Based on an analysis of photographs (Beck et al., 1995), Gina, as a calf with her mother, was in the Homosassa River on the Gulf coast of Florida in winter 1993, and again as an independent juvenile during winter 1994. This provides the first documentation for the Florida origin of Bahamas waifs. The movements of another manatee in Florida suggest a mechanism and route for manatees getting to the Bahamas. In 1998, an orphaned manatee calf named Mo that had been raised in captivity was radio-tagged and released at Crystal River, just north of the Homosassa River. Mo soon wandered offshore and drifted south approximately 480 km (300 mi) with offshore currents and was rescued in deep water 20 mi northwest of the Dry Tortugas, well outside normal manatee distribution. Gina probably had a similar misadventure offshore of Florida's west coast, perhaps disoriented by a storm, eventually drifting into the Gulf Stream south of the Florida Keys and east onto the Great Bahama Bank. Because of the deep waters and strong currents separating Florida and the Bahamas, it is unlikely that manatees deliberately or repeatedly traveled between them.

Odell et al. (1978) described the habitat at West End as "ideal" for manatees because of the presence of extensive *Thalassia* beds, but noted the possibility that limited freshwater sources in the Bahamas could restrict the distribution and size of a resident group of manatees, if one existed there. Limited sources of fresh water are believed to have been the main factor restricting manatee numbers in the Bahamas. Due to the karst topography typical of most of the islands, there is little steam flow runoff accessible to manatees. Natural sources of fresh water do occur on Andros Island,

the largest in the Bahamas, but most fresh water is held inland as groundwater with no natural drainage to the marine waters. Fresh Creek may provide access to these inland fresh waters, provided manatees could navigate the uppermost reaches of this shallow tidal creek. Blue holes and submarine vents in shallow water off Andros are flushed with marine waters during tidal cycles but some may occasionally discharge fresh water.

Although reports of sightings have increased, manatee numbers in the Bahamas are quite low. Manatees seen in the Bahamas may be strays from Florida, as documented above. Likewise, the Greater Antilles is a likely source for manatees found at Great Inagua or other southeastern Bahamas cays. There are no recorded observations of young calves in the Bahamas so the small numbers may not have allowed for reproduction. The prospect exists for an increase in the numbers of manatees in the Bahamas due to the apparent absence of hunting, immigration of waifs from outside the region, and reproduction. As manatees become tolerant of human presence and begin to utilize artificial sources of fresh water at marinas, resident groups may become established at some locations.

Hunting of manatees for food has not been described for the Bahamas. Bahamas regulations, enforced by the Department of Fisheries, include protection for manatees. Manatees have not been recovered dead due to boat strikes, but some individuals bear scars and wounds typical of propeller injuries. Boat speed restrictions in selected areas used by manatees may be warranted.

Central America

Belize

Charnock-Wilson (1968, 1970) reported that aerial sightings of manatees were common in Belize (Figure 2), and that the outlook for the species was good there in comparison with other areas. In September 1977, Bengtson and Magor (1979) completed five aerial surveys of the shoreline, major rivers, prominent keys, and coastal and inland lagoons of Belize. They reported 101 sightings during 10 h of search time, which was the greatest rate of aerial survey sightings outside of Florida at that time. They reported 8.9% calves. In 1989 the major areas of manatee concentration, based on the 1977 survey, were flown again (O'Shea and Salisbury, 1991). A total of 102 manatees were sighted during 5.4 h of search time, with 10.6% calves (corrected for biases). In January and May 1994 and January 1995, aerial surveys of Belize and Chetumal Bay, Mexico, were completed (Morales et al., 2000). The analyses of these data did not use political boundaries, so the results are not easily compared with the earlier surveys of Belize. An average of 215 manatees per survey was seen, with 7.4% calves. In 1997, four surveys of Belize were completed in January, April, August, and December (Auil, 1998). The average number of sightings per survey was 272, with a range of 231 to 318. The average percentage of calves was 7.3%, with a range of 4.7 to 10.5%.

Manatees are seen all along the Belize coast, but particularly important areas (north to south) include the New River and Shipstern Lagoon area in southern Chetumal Bay; the Belize River and associated offshore keys near Belize City; the Southern Lagoon area; the Commerce Bight, and Freshwater Creek and Sapdilla lagoons south of Dangriga; the Placentia and Indian Hill lagoons area; and the Deep River and Port Honduras region (Bengtson and Magor, 1979; O'Shea and Salisbury, 1991; Auil, 1998; Morales et al., 2000). Manatees sighted from aerial surveys are associated (in decreasing order) with rivers, lagoons, cays, and open coast habitats (Morales et al., 2000). Several radio-tagged manatees in Southern Lagoon are currently being monitored via satellite and conventional ground-based methods (J. A. Powell, personal communication), which should contribute significant ecological and life history information.

O'Shea and Salisbury (1991) concluded that "... Belize remains one of the last strongholds for this species in this part of the world," which continues to be the case based on more recent information (Auil, 1998, Morales et al., 2000). In general, low human population densities, associated activities (Auil, 1998), and favorable manatee habitats contribute to these optimistic findings. The long offshore barrier reef shields most of the irregular coastline, which has numerous large

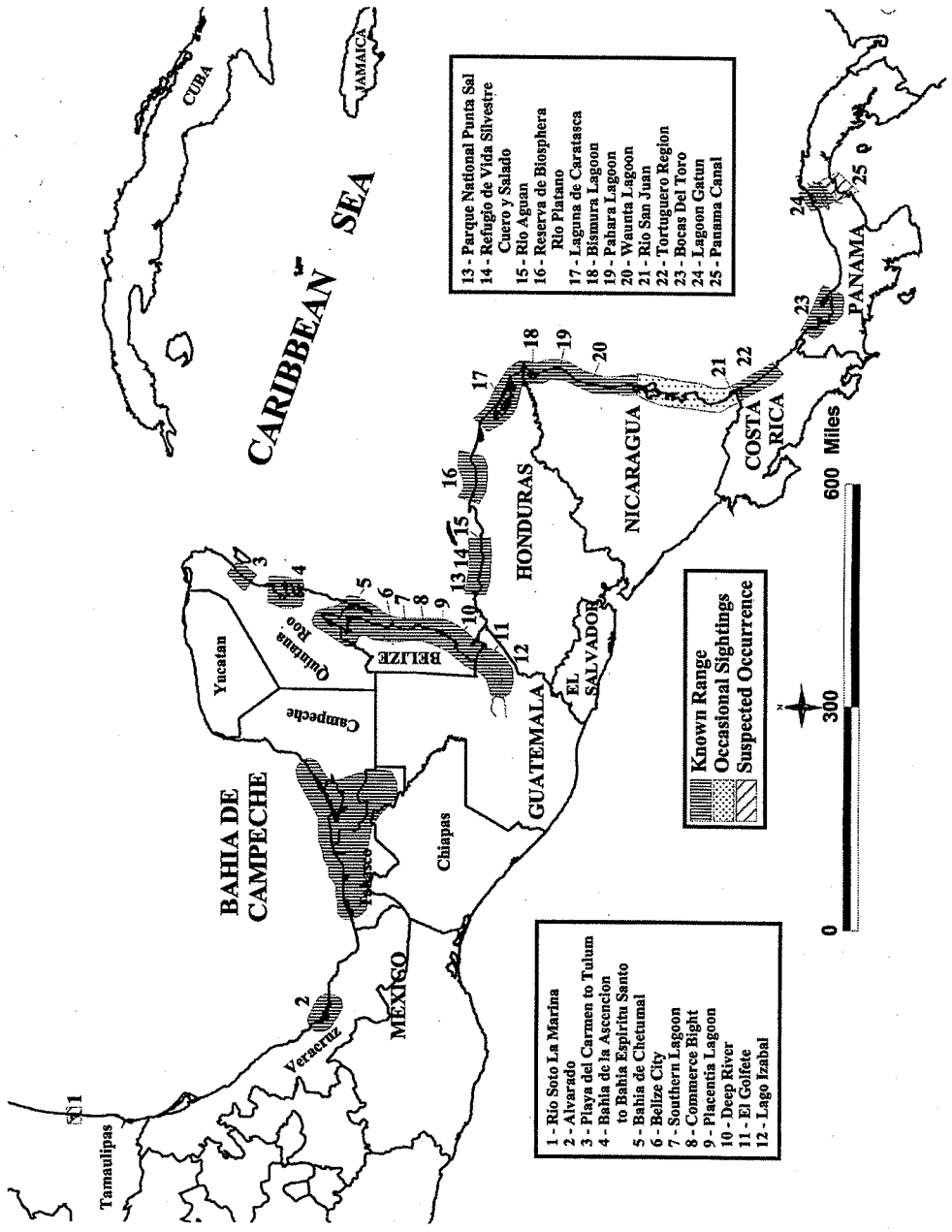

FIGURE 2 Distribution of the West Indian manatee (*Trichechus manatus*) in Mexico and Central America.

rivers and lagoons, from strong tidal currents and significant wave action. The southern coast of Belize, however, is less sheltered, and the rivers and creeks are faster flowing and rockier, which results in fewer manatees using this region (Charnock-Wilson, 1968; Auil, 1998).

Manatees have been protected in Belize since 1935 (O'Shea and Salisbury, 1991), and they have been listed as endangered under the Belize Wildlife Protection Act of 1981 (Auil, 1998). Considerable poaching activity, however, has apparently occurred during the entire period of protection. In addition, manatees are occasionally caught and killed incidentally in fishing nets and traps, and struck and killed by boats and barges (Auil, 1998). Poaching, however, appears to be the biggest source of human-caused mortality. During the 1960s through 1980s, it was believed that illegal killing had declined due to the loss of desire to hunt or eat manatees, or to their decline in abundance (Charnock-Wilson, 1968, 1970; Murie, 1935, cited in O'Donnell, 1981). However, Charnock-Wilson et al. (1974) reported 12 manatees killed at Ambergris Cay for sport and for the sale of meat at San Pedro. Matola (personal communication) observed that poaching attempts continued near Ambergris Cay in 1986, and that manatees were still being eaten along the Manatee River. In 1995, 11 separate butchering sites, with at least 35 manatee carcasses, were discovered in the Port Honduras area (Bonde and Potter, 1995). In 1997, five more recent carcasses were found in the Deep River area, and another "heap" of fresh bones was discovered near Punta Negra (Maheia, 1997; Domning, 1997a). Despite attempts to curtail the poaching (Auil, 1998), it continued into 1998, with additional evidence that the meat was being taken to Guatemala for sale, rather than being sold or consumed in Belize (Bonde, 1998).

The Belize Manatee Recovery Plan (Auil, 1998) is similar in structure and content to recovery plans for endangered species in the United States. It reviews the current status and biology of manatees in Belize, discusses in depth the known and potential conservation problems, and develops actions and funding mechanisms designed to effect long-term conservation solutions for manatees. In addition to human-caused mortality reviewed above, the plan focuses on several indirect potential problems, including coastal zone development for an expanding human population and the impacts of a rapidly increasing tourist industry. The recovery plan has been endorsed by the Belize Ministry of Natural Resources and the Environment, which is also committed to implementing many activities in the plan.

Guatemala

Guatemala (Figure 2) has the smallest Caribbean coastline in Central America and a small number of manatees. Within the Lago Izabal/Río Dulce system, the wetlands at the mouths of the Río Polochic and Río Oscuro on the western side of the lake were considered the best manatee habitat, although numbers there may have been greatly reduced by the late 1970s (Janson, 1978, 1980). Quintana (1993) conducted aerial surveys in five areas during January, March, April, and May 1992. The five areas surveyed represented most of the available manatee habitat in Guatemala: the Caribbean coast, inland lakes (Izabal and El Golfete), and three river systems (Dulce, Sarstún, and Motágua). During 40 h of total survey time, 73 manatees (66 adults and seven calves) were sighted. Calves were frequently observed in Cayo Padre. Group sizes ranged from 1 to 8 ($n = 24$), and Quintana (1993) estimated the manatee population in Guatemala to be 53 ± 44 (95% confidence interval).

Quintana (1993) also concluded that Lago Izabal provides the best habitat for manatees, particularly between Punta Chapín and Cayo Padre. This area was characterized by numerous shallow canals and lagoons (mean depth of 2 m), a mean water temperature of 29°C, freshwater aquatic vegetation including *Chara* sp., *Nymphaea ampia,* and *Pistia stratiotes*, and relatively little boat traffic. El Golfete may serve as a corridor between Lago Izabal and the coastal areas (Quintana, 1993). Presence of manatees in coastal areas tends to increase during the winter (May), when salinity declines. El Golfete has heavy boat traffic, and manatees are occasionally hit by boats (Quintana, 1993).

Manatees in Guatemala have been protected since 1959, and Guatemala is a signatory of CITES. Mortality caused by gillnets, hunting, and boat collisions has been reported (Quintana, 1993).

Shooting or hunting was reported from near Cayo Piedra in El Golfete and Laguna Perdida on the Río Motagua during 1986 (Grisko, personal communication), and three manatees (including a calf) were killed for their meat in Lago Izabal and Livingston in the early 1990s (Quintana, 1993). A manatee reserve, the Biotopa para la Conservación del Manatí Chocón-Machacas, was established in 1979, and encompasses the northeastern shore and surrounding habitat of El Golfete. This was the first manatee reserve designated anywhere in Central or South America, and is indicative of the desire of Guatemala to protect manatees. Given the reports of severely depressed numbers and continued hunting, the outlook for manatees in Guatemala is not good. Their more substantial numbers in neighboring Belize, however, could provide sources for natural recolonization should conditions become more hospitable in Guatemala through the continued existence of the Biotopa Chocón-Machacas reserve, stronger enforcement of laws, and increased educational efforts. Quintana (1993) further recommended more intensive surveys of Lago Izabal, determining the distribution of aquatic vegetation in Lago Izabal, and maintaining protection of El Golfete as a manatee travel corridor.

Honduras

Manatees are found in four regions along the coast of Honduras: the area between the Chamalecon and Punta Sal rivers, west of Bahia de Tela; the area between Río Colorado and Porvenir, west of La Ceiba; Laguna Bacalar, Laguna Ibans, Laguna Brus, and Río Platano in and near the Reserva de Biosfera; and Laguna de Karatasca (Klein, 1979; Rathbun et al., 1983; Cerrato, 1993) (Figure 2). The rivers and lakes of eastern Honduras provide the most extensive habitat for manatees (Klein, 1979), although relatively few sightings were made there during an aerial survey in 1979 (Rathbun et al., 1983). Rathbun et al. (1983) observed manatees 46 times in 16 h of aerial surveys in 1979 and 1980 at the following locations: the coast near Zambuco, Laguna de Boca Cerada, Laguna de Tansin, and mouths of the Río Lecan, Río Cuero, and Río Salado. Most of the sightings were not offshore, but at coastal lagoons and rivers. Reports of manatee sightings and killings during the mid-1970s also exist for the mouth of the Río Chamelecón near Puerto Cortés, and the Río Congrejal near La Ceiba (Klein, 1979). Cerrato (1993) guessed that the number of manatees in Honduras was approximately 120 to 140 individuals, based on direct counts from boats or planes, interviews with fishermen, and surveys conducted by Rathbun et al. (1983).

The regions where manatees occur are sheltered, have access to fresh water, and are characterized by abundant aquatic vegetation. The remainder of the Honduran coast is characterized by strong surf, steep shorelines, and a lack of broad, slow-moving rivers, and does not provide suitable habitat. Manatees that utilize the wetlands along the borders with Guatemala and Nicaragua may migrate seasonally (Cerrato, 1993).

Reports based on interviews made during the 1970s are unanimous in the conclusion that manatee abundance has declined markedly in Honduras (Klein, 1979; Rathbun et al., 1983). This decline is the result of widespread gillnetting, both incidental and intentional, and habitat degradation (Cerrato, 1993). Manatees have been protected by law in Honduras since 1959 (Article 49 of Fisheries Law, Decree No. 154), but enforcement has not been effective. Manatees may have become nocturnal in response to hunting pressure (Rathbun et al., 1983); nevertheless, a substantial illegal take has continued into the 1980s (G. Cruz, unpublished data). Small calves were observed during the 1979–1980 aerial surveys, and there is extensive remaining favorable habitat. Effective law enforcement is therefore a major key to the recovery of manatees in Honduras. A national program for environmental education and manatee conservation is lacking (Cerrato, 1993). Some local educational efforts have been conducted in Refugio de Vida Silvestre and Parque Nacional Punta Sal, west of Ceiba.

Nicaragua

Two aerial surveys were flown in 1992 over the main rivers and lagoons along the northern half of Nicaragua's coast (Carr, 1994) (Figure 2). A total of 71 manatee sightings were made, primarily

in Bismuna and Waunta lagoons (Carr, 1994). The sighting rate of four manatees/h is one of the highest for the Caribbean region, indicating good habitat and a healthy population (Carr, 1994). A study of manatee distribution along the southern half of the coast, based on boat surveys for feeding signs and interviews of local inhabitants, determined that manatees are widely distributed along the lower tracts (up to 60 km inland) of the region's waterways (Jiménez and Cateula, 1998; Jiménez, 2000a). Manatees appear to be currently absent from Lago de Nicaragua (Jiménez, 2000a), and have been described as scarce in or absent from areas they previously occupied (Nietschmann, 1979; Jiménez, 2000a). Nietschmann (1979) reported a manatee sighting off Set Net, one of the Pearl Cays.

The Caribbean coast of Nicaragua comprises some of the finest and most extensive habitat for manatees in Central America (Carr, 1994; Jiménez, 2000a). The Miskito lowlands stretch over nearly the entire eastern coast of the country, and consist of wetlands with numerous long, slow-moving rivers emptying into many interconnected coastal lagoons. The extensive floodplains of eastern Nicaragua are as wide as 100 km in some areas (Jiménez, 2000a). Large, estuarine lagoons and bays occur along the coast primarily in the northern half of the country. Manatees appear to migrate from one lagoon to another, and from lagoons into rivers during the dry season (Jiménez, 2000a). Shallow waters with lush seagrass beds extend far offshore (Phillips et al., 1982). Extremely high rainfall creates a corridor of brackish to fresh water parallel to the coast (Murray et al., 1982), which may attract manatees.

Human population density in coastal Nicaragua has been relatively low. Manatees have been protected in Nicaragua since 1956 under general hunting laws (Legislative Decree 306). However, manatees have been a traditional food source for indigenous people in this area, who hunt them using harpoons (Nietschmann, 1972; Loveland, 1976; Carr, 1994; Jiménez, 2000a). A small group of fishermen reported that nine manatees were killed in Waunta Lagoon in February 1992 (Carr, 1994), and Jiménez (2000a) estimated that over 30 manatees/year are taken by poachers in Nicaragua. Another threat is the use of gillnets in lagoons used by manatees, despite legal prohibition (Jiménez and Cateula, 1998; Jiménez, 2000a). Eastern Nicaragua lacks industrial or intensive agricultural activities; however, gold mining could contaminate river waters with toxic elements such as heavy metals and arsenic (Jiménez, 2000a). In 1998, the activities of a wood treatment plant of a logging company were discharging toxic chemicals into rivers, potentially harming manatee habitat downstream (Domning, 1998b).

In 1991, the federal government established the Miskito Coast Biological Reserve (Carr, 1994), a 5,000-ha protected area including vital coastal wetlands and lagoons. The Southeastern Nicaragua Biosphere Reserve was established in 1999, and is somewhat better protected than the Miskito Coast Reserve, especially on the San Juan and Indio rivers (Jiménez, 2000b). In general, law enforcement personnel are lacking in Nicaragua, and educational programs have been minimal (Jiménez, 2000a).

Costa Rica

Manatees probably continue to occur in reduced numbers in two areas of favorable habitat along the eastern coast of Costa Rica (Figure 2). The most extensive of these areas is the broad coastal plain of northeastern Costa Rica (Llanura de Tortuguero). A few manatees may also occur in southeastern Costa Rica, at the mouth of the Río Sixaola on the Panama border, at the mouth of the Río Estrella, and in Laguna Gandoca (O'Donnell, 1981). The area between Limón and Panama is generally less favorable habitat, with mountains reaching to the sea and few large rivers or lagoons. D. E. Wilson (1974) and O'Donnell (1981) conducted interviews and site visits in the 1970s, which suggested that few, if any, manatees occurred in this region. These investigators also made overflights in northeastern Costa Rica between Tortuguero and Barra del Colorado without observing manatees. Through interviews, however, they concluded that this area contained the last noteworthy but small group of manatees in Costa Rica. Wilson and O'Donnell agreed that much

of the habitat along the inland waterways and rivers of the Tortuguero region seemed to provide favorable conditions for manatees.

Sightings were made during the 1970s in Tortuguero National Park, Río Servulo, Laguna Penitencia, Laguna Yaqui, Laguna Coronel, the lower Río San Carlos, Río Sierpe, and around Parismina (O'Donnell, 1981). Manatees were thought to be absent or very rare in the Río Sarapiqui, Río Puerto Viejo, and the middle Río San Juan, although small numbers may exist in Lago Arenal far up the Río San Carlos (D. E. Wilson, 1974; O'Donnell, 1981). Evidence of a decline began to be apparent in the 1950s (O'Donnell, 1981).

Reynolds et al. (1995) concluded that manatees were rare in Tortuguero and along the northeastern coast, based on 60 h of boat surveys in 1984 and 6 h of aerial surveys in 1991. Interviews indicated that manatees had been common in the 1940s, but had declined precipitously since the 1950s (supporting O'Donnell's 1981 findings). Jiménez (1998) and Smethurst and Nietschmann (1999) indicate that manatees may be more abundant in Tortuguero than previously thought. The latter authors conducted more intensive boat surveys (3500 person hours) and interviews from 1996 to 1998, making 29 manatee sightings and documenting 61 others through interviews.

Anecdotal information suggests that manatees in Costa Rica migrate downriver in the dry season and upriver in the wet season, prefer quiet canals, have nocturnal or crepuscular activity peaks, prefer "grasses" as food, and are occasionally preyed upon by sharks (Reynolds et al., 1995). Smethurst and Nietschmann (1999) identified deep holes in the river around which manatees aggregate ("blowing holes") and suggested that manatees avoid areas of heavy boat traffic and favor areas where degradation is minimal. Manatees in Tortuguero occur especially in Caño Servulo and Agua Fria/Cuatro Esquinas, where environmental degradation has been minimal (Reynolds et al., 1995; Smethurst and Nietschmann, 1999).

The manatee is probably one of Costa Rica's rarest wildlife species because of past and present hunting pressure (Vaughan, 1983). Deforestation caused by logging, banana cultivation, and cattle ranches have greatly increased sedimentation in rivers and lagoons, making it difficult for manatees to enter the Tortuguero river system (Smethurst and Nietschmann, 1999). Other threats include heavy boat traffic, pollution, net entanglement, and ingestion of discarded plastic banana bags (Reynolds et al., 1995; Jiménez, 1998; Smethurst and Nietschmann, 1999). Habitat was destroyed by dredging and dynamiting in the construction of Tortuguero canals from 1963 to 1972 (Smethurst and Nietschmann, 1999).

Tortuguero National Park is the most important protected area for the manatee (Vaughan, 1983), although protection is less than ideal because many of its rivers extend outside of park boundaries (Smethurst and Nietschmann, 1999). Other protected areas include the Barra del Colorado Wildlife Refuge and the Gandoca-Manzanillo Refuge (A. Vásquez R., personal communication, 1993). Law 7317 (Ley de Conservación de la Fauna Silvestre) of October 1992 penalizes hunting and commerce in manatee products (Reynolds et al., 1995). Smethurst and Nietschmann (1999) point out that an integrated effort, involving local people, ranchers, logging companies, banana growers, and government entities, will be necessary to prevent further decline of Costa Rica's manatee population. In addition, public education, continued interviews with fishermen, characterization of habitat, and development of research and conservation plans are needed (Reynolds et al., 1995). A regional conservation effort with neighboring Panama and Nicaragua will ultimately be needed (Reynolds et al., 1995).

Panama

Panama has the longest Caribbean coastline of the Central American countries. Information on the present distribution and abundance of manatees in Panama is scant. The range is apparently fragmented by habitat discontinuities and possible depletion. Most of the current reports suggest that manatees continue to exist in regions of optimal habitat (lower reaches of large, slow-moving rivers and protected lagoons) but are seldom seen elsewhere.

The region from the Costa Rican border to Punta Valiente may constitute the most favorable habitat (Figure 2). O'Donnell (1981) received reports of manatees in the lower parts of the following rivers in this region: Río Sixaola, Río San San, and Río Changuinola. MacLaren (1967) reported on the capture of nine manatees from the Río Changuinola in 1963–1964 as part of a translocation project. Montgomery (1980) observed a few manatees in the lower Río San San during a series of brief overflights of this region, but did not observe them elsewhere in very limited surveys of the Changuinola area and the coast to the Río Guarumo, including the Laguna Chiriquí. Manatees observed feeding on seagrass beds in the Boca del Dragón area by fishermen are thought to move between that area and the Río Changuinola, rather than east to the Bahía Almirante (O'Donnell, 1981). No reports of manatees in the Laguna Chiriqui reached O'Donnell, although he was told that manatees persisted in the sparsely settled, heavily vegetated lower reaches of the Río Manatí.

The coastline east of Punta Valiente to Río Coclé del Norte lacks large lagoons, and the rivers are settled at their mouths and swifter than in the Bocas del Toro region. Manatees are currently only known from the relatively uninhabited Río Veraguas in this region (O'Donnell, 1981). Manatees apparently enter the Río Coclé del Norte and Río Miguel de la Borda only in the dry season, when they remain in the lower reaches. None has been reported from the Río Indio. Manatees occurred in the Río Chagres prior to the construction of the Panama Canal (MacLaren, 1967). The number occupying the canal system may have been augmented by the translocation of nine manatees from the Río Changuinola area to the Río Chagres in the 1960s, and manatees may now reach as far as the Pacific Ocean (MacLaren, 1967; Schad et al., 1981; Montgomery et al., 1982; Muizon and Domning, 1985). There is almost no information on the distribution of manatees over the long stretch of Caribbean coastline extending from Colón to the Colombian border. The mountains come close to the shore along this coast, which is marked by swift and shallow rivers and an absence of lagoons or extensive swamplands. This lack of information coupled with uncharacteristic habitat may indicate an absence of manatees.

Replicate aerial surveys were conducted during 1987 in the Bocas del Toro Province along the Caribbean coast (Mou Sue et al., 1990). A total of 70 manatee sightings (15.7% calves) were made in 22 surveys, in 54 h of flight time. The majority of sightings were made in the lower reaches of rivers, particularly Río San San, or in riverine lagoons. Sightings were also made in Río Mananti and Río Cana. The lack of sightings in other Bocas del Toro rivers is probably related to poor visibility rather than absence of manatees. For example, interviews indicated that manatees are relatively common in the turbid, vegetation-covered canals and lagoons of Río Changuinola, although none was seen in the 1987 surveys. Two adults and one calf were observed in Ensenada de Soropta, 10 km northeast of the mouth of the Río Changuinola (Mou Sou et al., 1990). This area is characterized by the presence of seagrass patches and coral reef.

During 5.5 survey hours, only one manatee was observed in Lago Gatun, but interviews suggested they occur in other areas of the lake and the Panama Canal (Mou Sue et al., 1990). Presence of manatees on the Pacific coast was not confirmed. Manatees were not observed in 11.5 survey hours along the Caribbean coast outside Bocas del Toro Province, between Punta Valiente and Ustopo. The authors concluded that the resident manatee population in Panama is centered in Bocas del Toro and in Gatun Lake and associated waters. True grasses (Poaceae) seem to be an important food for manatees in Panama's rivers. Interviewees reported observing manatees feeding on shore grasses, and Mou Sue et al. (1990) observed numerous patches of grazed shore grasses along the Río San San.

Panama is signatory of the CITES and Ramsar conventions, under which the San San area is listed as a wetland of international importance (Viquez, 1993). Despite protection by Executive Decree No. 23 of January 1967 and Resolution DIR-002-80 of the Department of Natural Resources, manatees are still killed by people in Panama and the meat illegally sold. Incidental drowning in gill nets does not seem to represent a major problem in Panama, so poaching may be the most crucial danger to manatees. Poaching has been reported in the Río San San, Sixaola, and probably

the Río Changuinola (Mou Sue et al., 1990). Occasional killing was also reported from western Gatun Lake and in rivers of the Veraguas and Colon provinces.

Future habitat degradation caused by operation of banana plantations and settlement following road construction for a new pipeline may put additional pressure on the manatee population (Mou Sue et al., 1990). The Changuinola region, between the San San and Changuinola rivers, is an area of intense cattle-ranching and banana plantation activities that degrade water quality. Other potential threats to manatees include the alteration of the San San wetlands (Bocas del Toro) for peat exploitation, the construction of a road connecting Isla de Colón to the continent to promote tourism, and the implantation of a hydroelectric project in the Teribe and Changuinola rivers (Viquez, 1993). Mou Sue et al. (1990) recommended that the small remaining manatee population in Panama be protected by providing reserve status to some of the unsettled rivers used by manatees, enforcing hunting regulations, promoting conservation education, reducing water pollution, and maintaining a ban on gill-net fishing in rivers. Education programs oriented to adult communities are lacking (Viquez, 1993).

South America

Colombia

Montoya-Ospina et al. (in press) conducted interviews from 1989 to 1995 and reviewed historical and recent information on manatee status, distribution, and causes of mortality in Colombia (Figure 3). Their findings generally support those of earlier researchers, who reported that the upper reaches of the Río Magdalena between Baranquilla and Bogotá, and the Río Atrato and its confluence with Bahía Candelaria appeared to have the largest remaining groups (Powell and Gicca, 1975; Husar, 1977). Although Husar (1977) reported small numbers of manatees within the Parque Naciónal Isla de Salamanca, there is no recent information on sightings or captures in the park (Montoya-Ospina et al., in press). A pair of captive manatees from the Río Magdalena was introduced to a pond in the park in March 1997 as part of a government education program.

Manatees in Colombia are in danger of extirpation because of hunting. Their skin, fat, and bones are currently used in a variety of products, including hammocks, candles, and asthma and snake bite cures (Montoya-Ospina et al., in press). They have been protected from hunting since 1969 under Resolution 574 of INDERENA, Colombia's natural resource agency. More recently, Colombia has adopted Law 17 (1981) and Law 165 (1994), and has become a signatory of CITES and the Biologic Diversity Treaty of 1992; however, funding continues to be inadequate for effective law enforcement, research, and education efforts. Law 99 (1993) allowed military and police corps personnel to enforce wildlife regulations, and established a central agency, the Ministerio del Medio Ambiente (MMA), to determine general policy for conducting wildlife management. The MMA prepared a National Recovery Plan in 1998, but a national agreement on the priorities for the conservation of manatees in Colombia has not yet been established (Montoya-Ospina et al., in press). In some cases, local communities enforce protection, for example, in Ciénaga de Paredes. Because of its geographical location, the city of Magangué may be a very important target for development of manatee education and research programs (Montoya-Ospina et al., in press). In 1991, the Corporación Autónoma Regional de los Valles del Sinu y del San Jorge (CVS) started a rescue and rehabilitation program for calves and adults, and educational programs.

Venezuela

There has been little research on manatees in Venezuela because of the remoteness of their habitat and poor visibility in the waters where they live (Delgado, 1995). Manatees occur in reduced numbers in parts of Lago de Maracaibo, and in greater abundance in the Orinoco River system and in drainages of eastern Venezuela along the Golfo de Paria (Mondolfi, 1974; O'Shea et al., 1986) (Figure 3). O'Shea et al. (1986) conducted interview and aerial surveys of potential manatee habitat

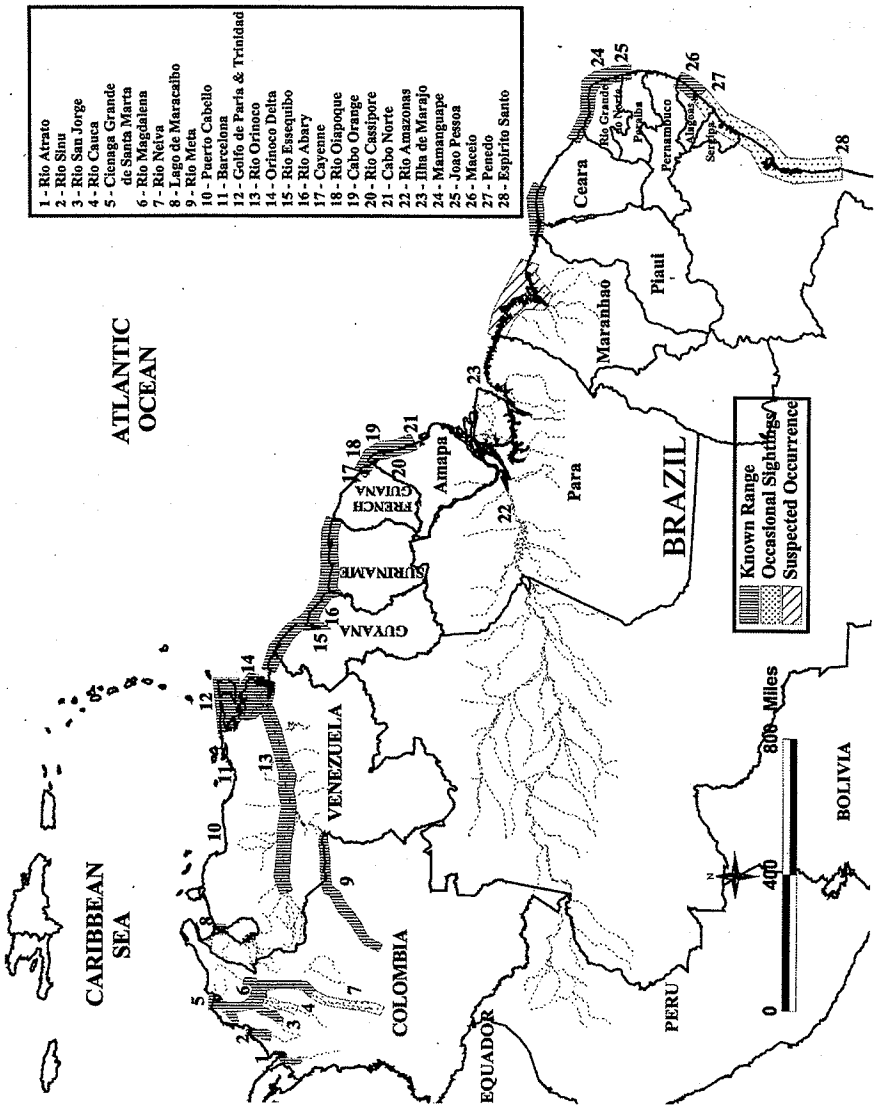

FIGURE 3 Distribution of the West Indian manatee (*Trichechus manatus*) in South America.

throughout Venezuela in early 1986. Aerial surveys yielded poor results in most areas because of water turbidity, and possibly because of low numbers and dry season inactivity. A small number of manatees exist in Lago de Maracaibo, centered northwest of Maracaibo City in the Río Limón/Laguna Sinamaica region and on the southwestern part of the lake bordering the extensive swamps of the Cienaga Juan Manuel de Aguas Claras y Aguas Negras.

O'Shea et al. (1986) concluded that there are no resident manatees along the Caribbean coast between Lago Maracaibo and the Boca del Dragón separating Trinidad and Venezuela, and that no historical evidence exists for their former occurrence on this coast. In 1990, however, a manatee accidentally drowned in fishing nets at the mouth of the Neverí River, in Barcelona (Anzoátegui State), and one was sighted in 1991 in the harbor of Puerto Cabello (Carabobo State) (Ojeda et al., 1993; Delgado, 1995). The northern coast of Venezuela is characterized by long, often desert stretches of rocky, mountainous coastline with high-energy beaches, deep water, and relatively cool sea surface temperatures; pockets of habitat that are suitable for manatees (sheltered lagoons and bays with freshwater input) have been settled by people for centuries (O'Shea et al., 1986). The general absence of manatees along the extensive Caribbean coast of Venezuela appears to be the result of habitat unsuitability, and represents a major discontinuity in the range of this species.

Eastern Venezuela provides a dramatic contrast to the Caribbean coastline, however, with frequent reports of continued manatee occurrence, numerous broad, slow-moving rivers, estuaries, mangrove swamps, and warmer waters. Mondolfi and Müller (1979) reported more than 30 locations inhabited by manatees in the states of Sucre, Monagas, and Delta Amacuro. Manatees continue to occur in most of the waterways of the extensive Orinoco delta and throughout the middle Orinoco and its tributaries as far as depths and currents allow (O'Shea et al., 1986; Correa-Viana, 1995). Strong seasonal fluctuations in rainfall and water levels may have a dramatic impact on manatee ecology in this region. Manatees have been reported to feed on 18 plant species in Venezuela, including mangrove (*Avicennia* and *Rhizophora*), grasses, sedges, *Montrichardia arborescens*, and *Eichhornia* (O'Shea et al., 1986).

In 1992, a group of English students associated with Project Mermaid recorded 11 sightings of manatees during a period of 19 days in Caño La Brea, a mangrove-lined tributary of the San Juan River running into Golfo de Paria (Sucre State, northeastern Venezuela) (K. Gotto, personal communication, 1993). In the same year, studies by PROFAUNA recorded two live and one dead manatee in Caño La Brea. PROFAUNA also reported three and two manatees in Laguna de Taguache (southern Anzoátegui State) in 1992 and 1993, respectively, and one where the Tigre River meets the Morichas Largo River, in Monagas State in 1993 (Ojeda et al., 1993).

Hunting for local markets in Venezuela was relatively heavy during the middle of the present century and resulted in a reduction in manatee abundance within their current range (Mondolfi, 1974; Mondolfi and Müller, 1979; O'Shea et al., 1986). Hunting activities appear to have declined substantially in recent years in response to laws protecting the species, education campaigns, and a general lack of interest in manatee hunting by the younger generations (O'Shea et al., 1986). Manatees are protected in Venezuela by Ley de Protección a la Fauna Silvestre of 1970 (Articles 11 and 77) and Resolución MARNR (Ministry of the Environment and Renewable Natural Resources) No. 127 of 1978 (Ojeda et al., 1993); however, illegal hunting by the indigenous Warao and some fishermen continues (Ojeda et al., 1993).

Four national parks encompass areas of known manatee occurrence: Ciénagas del Catatumbo (Zulia State), Mariusa (Delta Amacuro), Santos Luzardo (Apure State), and Turuépano (Sucre State). The park boundaries, however, have not been well defined, which has allowed the development of activities that are incompatible with the conservation of natural environments (Delgado, 1995). For example, seismic prospecting within Turuépano National Park has impacted habitat important to manatees and other aquatic mammals. Construction of dams, drainage of wetlands, development of the Orinoco–Apure region, construction of river ports, increase in river traffic, petroleum exploitation, deforestation (including exploitation of mangroves), and other habitat disturbance and destruction threaten the future existence of the manatee in Venezuela (Correa-Viana, 1995).

The waters of eastern Venezuela and the Orinoco system provide some of the largest continuous manatee habitat anywhere within the species' range. If hunting pressure and development impacts can be controlled, Venezuela has the potential to provide a major stronghold for manatees in the future. In 1992, during an International Symposium on Dolphins and other Aquatic Mammals of Venezuela, held in Caracas, an action plan for research and protection of manatees was written (Ojeda et al., 1993). Law enforcement, education, and research programs were recommended, as were formation of a group of experts to advise officials on aquatic mammal conservation issues and reevaluation of national park boundaries in light of their intended purpose (Delgado, 1995). Strict regulations on the use of nets and other fishing gear, particularly in the Orinoco River basin, education of fishermen, and monitoring of habitat important to manatees have also been recommended (Correa-Viana, 1995).

Trinidad

Information on manatees in Trinidad was obtained by Bindernagel in the early 1980s (Garrett, 1984; Hislop, 1985), and more recently by Boyle and Khan (1993). A survey of accessible locations and discussions with local residents indicated that there are possibly 25 to 30 manatees in Trinidad, located in rivers and along the eastern coast of the island (Boyle and Khan, 1993). A small number of manatees are present in Nariva Swamp, a large, freshwater swamp extending about 20 km north from Guataro Point to Manzanillo Bay. During the dry season, much of the swamp becomes inaccessible to manatees, which may become trapped in ponds. Manatees in Nariva Swamp are reported to feed upon water hyacinth (*Eichhornia crassipes*), water lettuce (*Pistia stratiotes*), cascadura grass (*Leersia hexandra*), Kharmi bhaji (*Ipomoea aquatica*), and pennywort (*Hydrocotyle umbellata*) (Boyle and Khan, 1993). Manatees have also been reported in the North Orepouche, Charamel, and Otoire Rivers.

Although poaching is occasionally reported, the primary threat to manatees in Trinidad is loss of habitat through agriculture and development (Boyle and Khan, 1993; Amour, 1993). Quarrying, dredging, and logging along the North Orepouche River have resulted in heavy siltation. All of Trinidad's east coast is vulnerable to oil pollution from ocean freighters, and oil can be seen on many of the beaches along this coast. Red tides have occurred along the east coast, and could potentially cause mortality in Trinidad's small manatee population, as it has in Florida.

Although not specifically named, manatees in Trinidad can be viewed as a protected species under the Conservation of Wildlife Act Chapter 67:01, the Fisheries Act Chapter 67:51, and the Archipelagic Waters and Exclusive Economic Zone Act No. 24 (Toppin-Allahar, 1993). Protection of habitat is provided under the Forest Act Chapter 66:01. The Nariva Swamp was named as a Ramsar site in April 1993. While the Ramsar Convention on Wetlands of International Importance for waterfowl habitat also affords some protection for manatee habitat, law enforcement efforts and habitat protection are generally inadequate, and manatees in Trinidad are still threatened with extinction (Amour, 1993). The Manatee Subcommittee of the Trinidad and Tobago Field Naturalist's Club was formed in 1991 to develop public education programs for schools (Boyle and Khan, 1993). A Trinidad and Tobago Conservation Trust Fund has been proposed to establish organized research, management, and conservation efforts for manatees and their habitat.

Guyana

Current information is lacking on manatees in Guyana (Figure 3), and a systematic survey is needed. Manatees occurred all along the coast, but were most frequently reported in river or canal mouths (Bertram and Bertram, 1973). The greatest concentrations occurred in the eastern region, on both sides of the border with Suriname (Husar, 1977). Considerable numbers of manatees were noted in the Canje and Abary Rivers, particularly in wet savannahs in their upper reaches (Bertram and Bertram, 1973). Manatees were also reported in the Courantyne, Berbice, Demerara, Essequibo, Pomeroon, Arapiako, Akawini, Waini, Barima, and Kaituma Rivers.

Manatees in Guyana apparently consume a wide variety of marine, estuarine, and freshwater vegetation; *Montrichardia arborescens*, an aquatic herb, was specifically noted by Bertram and Bertram (1964). Allsopp (1969) noted a wide variety of freshwater aquatic plants consumed by manatees in canals. Rivers with large masses of floating grass were described as providing the most suitable environment for manatees (Bertram and Bertram, 1964). Bertram and Bertram (1963) estimated that there were some thousands of manatees in Guyana, yet their numbers were generally believed to be much reduced from former times. Manatees have been protected in Guyana since 1956 (Fisheries Ordinance No. 30, Revised No. 13, 1961), and hunting no longer appeared to be a serious problem (Bertram and Bertram, 1973; Husar, 1977). Accidental entanglement in fishermen's nets may have resulted in some deaths, but manatees were not a welcome catch as they could cause considerable damage to nets (Roth, 1953). Motorboat strikes may have become an increasing problem in Guyana (Roth, 1953; Bertram and Bertram, 1964).

Manatees were used experimentally for biological weed control in Guyana since 1916 (Allsopp, 1960; Bertram and Bertram, 1963; National Science Research Council of Guyana and National Academy of Sciences, 1973). The establishment of an international center for manatee research and conservation in Georgetown was proposed in the early 1970s (National Science Research Council of Guyana, 1974).

Suriname

Little information exists on current manatee status and distribution. Manatees reportedly occurred in most of the coastal plain rivers of Suriname (Figure 3), usually not farther than 60 km inland (Bertram and Bertram, 1973; Husson, 1978). Duplaix and Reichart (1978) reported the greatest concentrations in Nanni Creek and the Coesewijne, Tibiti, and Cottica Rivers. However, they believed that manatees were easier to observe in these smaller creeks and rivers than in broader rivers such as the Corantijn, lower Saramacca, and Commewijne. Manatees have also been observed or reported in the Maratakka, Nickerie, Wayambo, Coppename, and Surinamee Rivers (Husson, 1978; Duplaix and Reichart, 1978). In 1966 and 1971, Dekker (1978) visited tidal areas of the Commewijne, Cottica, and Cassiwinica Rivers, and upstream, freshwater areas of the Coesewijne River and Nanni Creek. He recommended the Coesewijne River and Nanni Swamp as nature reserves for the manatee in Suriname.

Mangrove forests provided manatee habitat in the flat coastal regions and river estuaries of Suriname (Duplaix and Reichart, 1978). Husson (1978) stated that manatees had never been found in the open ocean off the coast of Suriname. Swamp forests behind the mangroves were also inhabited by manatees, which grazed on stands of *Montrichardia arborescens* along the banks at high tide (Duplaix and Reichart, 1978). Dekker (1974, 1978) believed that manatees in Suriname favored fresh water because of their preference for "Mokko mokko" *(Montrichardia)*, although many other plant species were also eaten. They could be heard grazing on bank plants, sometimes for hours at a time (Dekker, 1978). Savannah swamps, or floating savannahs, were found in upper river reaches, and were characterized by *Cyperus* and *Montrichardia*. Husson (1978) also noted *Montrichardia* as a manatee food in Suriname, as well as *Machaerium lunatum*, *Caladium arborescens*, and *Panicum*. In contrast to Bertram and Bertram's (1973) findings in Guyana, Duplaix and Reichart (1978) reported that manatees were not found in the floating savannahs, but in the small creeks transecting them. Seasonal flooding undoubtedly made vegetation in the floating savannahs accessible to manatees. Rapids in the upstream portions of Suriname's rivers prevented manatees from traveling farther upriver (Duplaix and Reichart, 1978).

Duplaix and Reichart (1978) interviewed 89 residents, primarily Amerindians, and found that although some people believed the manatee had become more common in recent years because it was no longer hunted, former hunters described the manatee as having disappeared from its usual haunts over the past 30 years. Manatees are still poached for food or for the alleged medicinal powers of the ear bones (Department of Nature Conservation, 1993).

Manatees receive some protection under Suriname's Nature Protection and Game Ordinances. Suriname ratified the CITES convention in 1981. Although no reserve has been created specifically for manatees, they were found in the estuary and mangrove swamps of the Coppename River Nature Reserve, covering 10,000 ha (Duplaix and Reichart, 1978). None of the manatees observed bore propeller scars, but commercial river traffic was heavy and the increasing use of outboard motors by fishermen and hunters was anticipated to eventually become a problem (Duplaix and Reichart, 1978). Some incidental taking in nets was also likely to occur. Duplaix and Reichart (1978) suggested that more vigorous enforcement of existing conservation laws and protection of areas with the highest manatee density, such as Nanni Creek, the upper Coesewijne River, and the Perica River, were needed to improve the status of the manatee in Suriname.

French Guiana

The absence of a broad coastal plain in French Guiana (Figure 3) led Bertram and Bertram (1964) to conclude that there was little suitable manatee habitat in this country. We know of no aerial survey or interview studies on manatee abundance or distribution in French Guiana. Brazilian hunters in the vicinity of Río Oiapoque on the Brazilian border reported manatees in the rivers Approuague, Mahury, Laughan, and Ouanary, as well as in some of the smaller rivers in eastern French Guiana (Best and Teixeira, 1982).

Brazil

Systematic survey data are generally lacking for Brazil (Figure 3), although interviews of fishermen and coastal residents have been conducted in some areas, particularly northeastern Brazil. On the north coast, *T. manatus* occurs along the coast of Amapá north of Cabo Norte, in the Rio Mearim in Maranhão (Domning, 1981a), and along the coast of Rio Grande do Norte. The species seems to have been exterminated from the coast of Pará, and may be absent from the Marajó region, where the presence of *T. inunguis* has been confirmed (Domning, 1981a, 1982a). Banks (1985), however, noted a 1983 report by Catuetê and Duarte of the coexistence of *T. manatus* and *T. inunguis* at the mouth of the Rio Amazonas. Borôbia and Lodi (1992) cite Albuquerque (1983) as suggesting that both species coexist in the mouth of the Amazon River, despite lack of supporting evidence. In an interview survey of Amapá, Best and Teixeira (1982) were able to positively identify only one *T. manatus* specimen, in the vicinity of the Rio Oiapoque. Hunter interviews indicated that manatees occur in the mouths of the rivers Oiapoque, Uaça, and Cassiporé. Interviewees reported that manatees are common along all of the Amapá coastline, whereas Domning (1981a) reported that the results of his interviews with Amapá residents, also conducted in 1978, were inconclusive. The seasonally flooded mangrove swamps of the Amapá coast have little or no submergent vegetation; thus manatees appear to depend upon floating and shoreline species such as mangrove (*Avicennia* and *Rhizophora*), aninga (*Montrichardia arborescens*), cai-seca (*Rhabdadenia biflora*), paratură (*Spartina brasiliensis*), and mururé (*Eichhornia*) (Domning, 1981a; Best and Teixeira, 1982).

Trichechus manatus has a disjunct distribution on the northeastern coast east of Maranhão, from the state of Piauí to Alagoas (Lima et al., 1992). Manatees were observed during 10 of 18 boat surveys or observations from reefs conducted in the Mamanguape estuary, Paraíba, from February through April 1986 (Borôbia and Lodi, 1992). A total of 20 manatee sightings were made during approximately 47 h of observation. Most of the sightings (70%) were made in March and April, inside the reefs that protect the Mamanguape estuary. No more than three manatees were observed in a single survey. Interviews with local residents and fishermen indicated that manatees frequent the mouth of the Rio Mamanguape from January through March, and also occur upriver to the Rio Tinto, where the water is much less saline. At high tide, manatees were sighted along the reef edges making repeated dives where seagrass beds were known to occur. Six manatees were sighted on the ocean side of the reefs, despite the continuous wave action (Beaufort 2). These observations differ from the general pattern of manatee preference for protected waters (Borôbia and Lodi, 1992).

An adult manatee was captured in nets at Bessa Beach in João Pessoa, Paraíba, in March 1982 (*O Norte*, 19 March 1982, p. 3). A total of 21 deaths and 12 strandings of dependent calves were recorded between 1988 and 1996 for the states of Paraíba, Pernambuco, Río Grande do Norte, and Ceará. Approximately 56% of the deaths were caused by fishing activities (nets or corrals) (Paludo, 1997). After interviewing coastal fishermen, Jackson (1975) concluded that manatees occurred as far south as Mangue Seca, Bahía, just south of Sergipe, but were no longer present in Espírito Santo, the historical (17th-century) southern limit of their range (Ruschi, 1965; Figure 3). Jackson believed that Alagoas provided the most favorable manatee habitat on the east coast because of numerous estuaries between Maceió and Penedo, and because inshore waters are protected by reefs running parallel to the coast. Banks and Albuquerque described beds of *Halodule wrightii* as natural pastures for *T. manatus* in Pernambuco (Banks, 1985).

After extensive surveys and interviews in northeastern Brazil from 1990 to 1991, Lima et al. (1992) confirmed the presence of manatees along 2000 km in three discontinuous coastal bands: from Piauí to western Ceará, from eastern Ceará to northern Pernambuco, and in Alagoas. The authors reported the lack of manatee records for the state of Sergipe, which they considered the recent southern limit of the species' distribution. Lima (1997) estimated the northeastern manatee population at 278 individuals, with the greatest concentrations around the Mamanguape estuary.

Best and Teixeira (1982) were unable to find any practicing manatee hunters south of Oiapoque, Amapá, and residents of Amapá interviewed by Domning (1981a) claimed that manatees were seldom captured, perhaps no more than two or three a year. Domning (1982a) reported evidence of exploitation of manatees, presumably for meat, in the states of Alagoas (in 1959) and Bahía (in 1964). Although occasional hunting for meat may still occur (Borôbia and Lodi, 1992), the last record of hunting with a harpoon is said to have occurred in 1987, in Barra do Mamanguape (Paludo, 1997). Currently, the stranding of calves along Río Grande do Norte coast, with subsequent intentional killings, is the main cause of death of manatees in northeastern Brazil (Lima, 1997).

Other threats include illegal hunting and incidental nettings. Industrial residues and residues from sugarcane plants (for production of sugar and alcohol as fuel) occur throughout the northeastern region, as well as silting and felling of mangrove swamps for agricultural and development purposes (R.T. de Almeida, personal communication, 1991; Borôbia and Lodi, 1992). The trend toward grand tourist development projects, with the construction of roads and haphazard occupation of the northeastern seashore, may cause detrimental effects to the manatee population (Paludo, 1997).

The Mamanguape Estuary was declared an Area of Environmental Protection in 1993, with the objective of protection and conservation of the manatee and its habitat. Likewise, the Paripueiras Marine City Park was established in Alagoas (Paludo, 1997). Domning (1981a) and Best and Teixeira (1982) recommended that a manatee reserve be established to include the Amapá coast near Cabo Norte and adjacent inland lakes, as this area may be the only place in the world where two sirenian species occur in close proximity (Domning, 1981a). Domning (1981a) also recommended that the lower Río Mearim in Maranhão be included in a reserve, because it provides large areas of undisturbed floating meadows in lakes and channels off the main river. Cabo Orange, Amapá, has been proposed as the site of a national park (Best and Teixeira, 1982). Both manatee species have been fully protected in Brazil since 1967 (under Lei No. 5.197, 1967, Portaria No. 3.481, 1973, and Portaria no. N-011, 1986); however, enforcement of these laws is almost impossible because of the lack of enforcement personnel and the large areas involved.

An educational and research program was started in 1980 by the then Brazilian department of environmental protection through the Manatee Center. The first buildings were in Barra do Mamanguape, but soon new bases were created in Paripueira (Alagoas), Sagi Beach and Natal (Grande do Norte), and Cajueiro da Praia (Piauí). Currently the headquarters are located on Itamaracá Island, in Pernambuco State. After 10 years the project became the Brazilian Institute of Renewable Natural Resources' (IBAMA) National Center for the Conservation and Management of Sirenians, or Manatee Center. A massive educational campaign conducted by the Manatee Project resulted in a change of attitude among manatee hunters. In Barra do Mamanguape, besides environmental

education, the project has invested in community development programs for fishermen and local inhabitants. In Itamaracá there is a rehabilitation center where stranded calves are raised for later release. The first pair of rehabilitated, captive-reared manatees was released in Alagoas in 1994, and their readjustment to the wild was successfully monitored by VHS and satellite telemetry (Paludo, 1997).

In late 1997 a workshop was convened in Barra de Mamanguape by the Manatee Center in order to review the status of knowledge and to plan strategic actions for research and conservation on manatees (Centro Nacional de Conservação e Manejo de Sirênios, 1997). Suggestions for specific projects were also included in the Brazilian aquatic mammal action plan (IBAMA, 1997).

North America

United States

The Florida manatee (*T. m. latirostris*) is a subspecies of the West Indian manatee. Although Florida was once considered to be the northern limit of the manatee's year-round range, sightings outside of Florida have increased in recent years, even during winter months. Manatees are frequently reported in the coastal rivers of Georgia and South Carolina in the warm season (Figure 4). Sightings on the Atlantic coast drop off markedly north of South Carolina, with the northernmost record from Rhode Island (Reid, 1996). The Suwannee River was previously described as the northern limit of the manatee's usual range on the Gulf coast of Florida (Powell and Rathbun, 1984); more recently, the Wakulla River has been described as the northwestern limit of the manatee's typical warm-season range on this coast (O'Shea and Kochman, 1990). Between 1992 and 1997, the number of manatee sightings west of Florida increased, particularly in Texas and Louisiana in 1995 (Schiro and Fertl, 1996). The 1995 warm season was a notably active one for major storms in the eastern Gulf of Mexico, which may have contributed to a broader distribution of manatees along the Gulf coast (C.A. Langtimm and C.A. Beck, personal communication, 2000). In recent years, sightings have also increased in rivers and along the coast of North Carolina, where they were first reported in 1919 (Schwartz, 1995). Schwartz (1995) and Schiro and Fertl (1996) noted that increased public awareness rather than an increase in the manatee population may account for this upward trend in sightings. Alternatively, storm events and a climatic trend of warmer winters and summers may help to explain increased extralimital movements by manatees on both the Gulf and Atlantic coasts.

Manatees occur along most of the Atlantic and Gulf coasts of Florida from April through October (the warm season). Warm season areas of abundance on the Atlantic coast are the St. Johns River, the Banana and Indian Rivers to Jupiter Inlet, and the rivers, canals, and western coast of upper Biscayne Bay (Bengtson, 1981; Shane, 1983; Kinnaird, 1985; Marine Mammal Commission, 1988). Manatees are most abundant on the Gulf coast in the lower Suwannee River and several other rivers in the Big Bend region, the Manatee and Little Manatee Rivers and east coast of Tampa Bay, Sarasota Bay to Lemon Bay, the Charlotte Harbor/Matlacha Pass/San Carlos Bay region, and in the creeks, rivers, bays, and coast of the Everglades and Ten Thousand Islands region (Moore, 1951; Hartman, 1974; Odell, 1979; Rose and McCutcheon, 1980; Irvine et al., 1982). Sightings and salvage records document manatee occurrence in Lake Okeechobee, particularly the Rim Canal (Beeler and O'Shea, 1988); however, relatively little is known about manatee use of this region. Manatees can access and exit the lake through the Caloosahatchee River on the western side and St. Lucie River on the east, and utilize canals that feed into and drain the lake.

When ambient water temperatures drop below about 20°C in autumn and winter, manatees migrate to natural or anthropogenic warm-water sources (Powell and Waldron, 1981; Irvine, 1983; Shane, 1983; Powell and Rathbun, 1984; Deutsch et al., 1998). Hartman (1979) believed that manatees began to frequent the headwaters of the Crystal and Homosassa Rivers in the early 1960s. Here their winter numbers have increased markedly over the last 20 years (Powell and Rathbun, 1984; Rathbun et al., 1995), with a record high count of 386, determined by aerial survey in

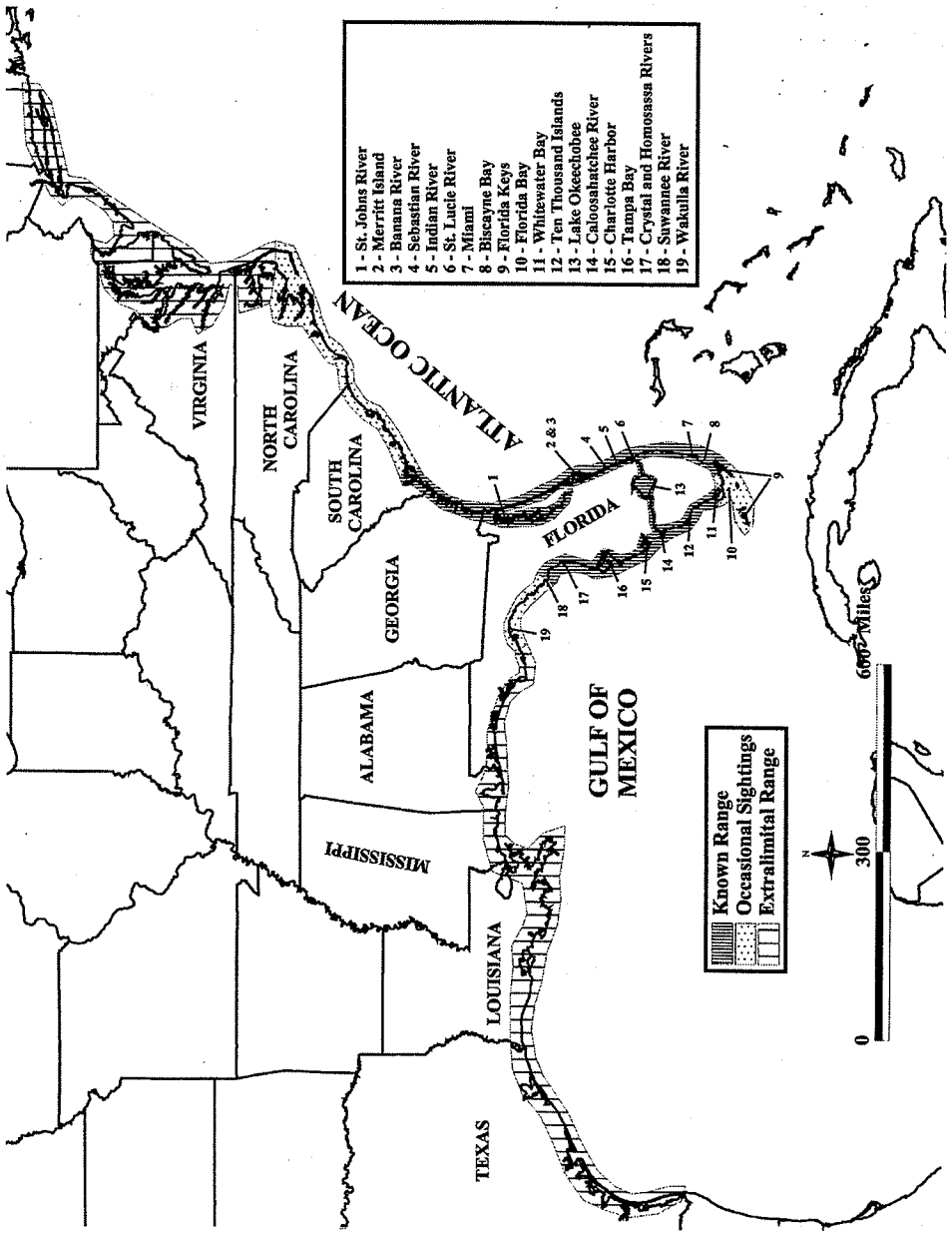

FIGURE 4 Distribution of the West Indian manatee (*Trichechus manatus*) in the United States.

November 2000 (Joyce Kleen, Chassahowitzka National Wildlife Refuge Complex, personal communication). Likewise, the number of manatees using Blue Spring on the St. Johns River has increased from fewer than 20 in the mid-1970s to a total count of 146 during the winter of 2000–2001 (Wayne Hartley, Blue Spring State Park, personal communication). Before the proliferation of coastal electrical-generating power plants in the 1950s to 1960s, Moore (1951) believed that the northern limit to the normal winter range of manatees was the Sebastian River on the Atlantic coast and Charlotte Harbor on the Gulf coast. Now, in addition to their use of warm-water springs, hundreds of manatees seek refuge from cold each winter in the warm-water discharges of power plants or other industrial sites (Reynolds and Wilcox, 1994; Reynolds, 2000). Manatees frequently return to the same winter ranges each year (Rathbun et al., 1983; Powell and Rathbun, 1984; Deutsch et al., 1998), and some also return to the same summer ranges (Bengtson, 1981; Shane 1983; Zoodsma 1991). Individual manatees may use different aggregation sites within winters, and use of sites as far as 850 km apart between winters has been documented (Reid and Rathbun, 1986). The highest statewide, aerial survey-based count of manatees was 3276 in January 2001 (Table 1).

On the Atlantic coast, 78 radio-tagged manatees were tracked over a 12-year period (1986–1998) to provide information for the development of effective conservation strategies (Deutsch et al., 2000). Most manatees migrated seasonally over large geographical areas between northerly warm-season regions and southerly winter ranges. Manatees were consistent in their seasonal movement patterns across years, showing strong site fidelity to warm-season and winter ranges. Seasonal movements of four immature manatees that were tracked with their mothers as dependent calves, and also after weaning as independent subadults, showed strong natal philopatry to specific warm-season and winter ranges and migratory patterns (Deutsch et al., 2000). Despite these conservative behavioral traits, manatees also exhibited considerable individual variation in movement patterns, and adaptability to human-altered habitats. Deutsch et al. (2000) concluded that, in addition to reduction of human-caused mortality, manatee population recovery depends on the ability to protect key habitats, and to keep the pace of habitat alteration within the manatee's ability to adapt.

The Florida manatee population shows genetic differentiation between the Gulf and Atlantic coasts, but not within coasts (Garcia, 2000). This finding differs somewhat from that of McClenaghan and O'Shea (1988), who found no differentiation among regions, within or between coasts. Both studies support the conclusion that the manatee's north–south seasonal migrations, promiscuous mating system, and wide-ranging movement patterns of individuals on both coasts contribute to the high rate of gene flow among regions within Florida (McClenaghan and O'Shea, 1988). However, in contrast to McClenaghan and O'Shea (1988), Garcia-Rodriguez et al. (1998) and Garcia-Rodriguez (2000) conclude that the low level of genetic variability observed in Florida manatees suggests that this population has been subjected to bottlenecks in population size that are characteristic of some endangered species.

Progress in research on manatee population biology was evaluated at a workshop held in Gainesville, Florida, in 1992. Six working groups discussed the topics of aerial survey and estimation of population size, reproduction, age structure, mortality, photoidentification, estimation of survival, and integration and modeling of population data (O'Shea and Ackerman, 1995). Long-term life history data obtained through documented sightings and resightings of individual manatees have formed the basis for estimates of adult survival, reproduction, and population growth (Beck and Reid, 1995; Eberhardt and O'Shea, 1995; Rathbun et al., 1995; O'Shea and Hartley, 1995; Langtimm et al., 1998). Estimated population traits of the Florida manatee are presented in Table 1. Although many valuable, long-term databases have been developed, gaps in information include age-specific estimates of reproduction characteristics, sampling effort for life history data, particularly in southwestern Florida from Tampa Bay through the Everglades, differences in characterization of some reproduction traits based on carcass examination and resightings of known individuals, reproductive physiology, and mating and social behavior (O'Shea and Ackerman, 1995). Another important gap is information on survival of juveniles and subadults (Langtimm et al., 1998).

TABLE 1
Estimates of Manatee Life History Traits and Other Statistics

Life History Trait	Source	Data
Maximum life expectance		60 years
Gestation		11–14 months
Litter size		1
% Twins	Blue Spring	1.79%
	Crystal River	1.40%
Sex ratio at birth		1:1
Calf survival	Blue Spring	60%
	Crystal River	67%
Annual adult survival	Atlantic coast	90%
	Blue Spring	96%
	Crystal River	96%
Age of first reproduction (female)		3–4 years
Mean age first reproduction (female)		5 years
Spermatogenesis (male)		2–3 years
Proportion pregnant	Salvaged carcasses	33%
	Blue Spring	41%
Proportion nursing first-year calves during winter season	Mean	36%
	Blue Spring	30%
	Crystal River	36%
	Atlantic coast	38%
Calf dependency		1.2 years
Interbirth internal		2.5 years
Highest number of births		May to September
Highest frequency in mating herds		February to July
No. verified carcasses in Florida[a]		4043 (1974–2000)
No. documented in ID catalog[b]		>1400 (1975–2001)
Highest count (aerial surveys)[a]		3276 in January 2001

Note: Except as noted, information was obtained from O'Shea et al., 1995.

[a] Data provided by the Florida Marine Research Institute, Florida Fish and Wildlife Conservation Commission.

[b] Data provided by the U.S. Geological Survey.

Regional and seasonal fluctuations in manatee abundance do not necessarily indicate changes in the statewide population trend, as manatees on both coasts of Florida migrate seasonally (Hartman, 1974) and are capable of moving great distances (Reid and Rathbun, 1986; Deutsch et al., 1998). Furthermore, the population size cannot be directly estimated because of environmental, survey-related, and manatee behavior-related factors (Lefebvre et al., 1995). Trend analyses of temperature-adjusted aerial survey counts show promise for providing insight to general patterns of population growth in some regions, although the estimated rates of change in counts may not be an accurate reflection of actual population rates (Garrott et al., 1994; Craig et al., 1997; Eberhardt et al., 1999). Strip-transect aerial survey methods have been applied to estimate the number of manatees in the Banana River during the warm season, and could be used to detect a 5% annual rate of change in <4 years with power ≥0.75 (Miller et al., 1998).

Models based on adjusted counts (Eberhardt et al., 1999) and survival and reproduction rate estimates (Eberhardt and O'Shea, 1995) indicate that population growth on the Atlantic coast has been marginal at best from the late 1970s through the early 1990s. In contrast, the smaller groups

of manatees that overwinter in the Crystal and Homosassa Rivers and at Blue Spring show higher rates of population growth (Table 1). Preliminary estimates of adult survival rates in southwest Florida (Tampa Bay to the Caloosahatchee River) are similar to those for the Atlantic coast (Holly Edwards and Bruce Ackerman, Florida Fish and Wildlife Conservation Commission, personal communication, 2000). Population viability analysis, based on reproduction and survival data from a sample of 1212 carcasses obtained in 1976–1991, projected a slightly negative population growth rate and unacceptably low probability of persistence over 1000 years (Marmontel et al., 1997). Thus, the fate of the Florida manatee population seems to hang in a delicate balance, with an ever-increasing number of carcasses recovered annually and the human population increase showing no signs of slowing down. "A turning point may soon be reached, if it has not already; ... no prudent alternatives exist to maintaining proactive, vigorous management aimed at mortality reduction" (O'Shea and Ackerman, 1995).

Hartman (1979) listed several factors that influence manatee distribution in Florida: (1) availability of aquatic vegetation; (2) proximity to channels of at least 2 m in depth; (3) recourse to warm water during cold weather; and (4) a source of fresh water. He concluded that the Florida manatee's preferred habitats are rivers and estuaries (<25 ppt salt). The rare occurrence of manatees in Florida Bay and in the area between Tampa Bay and the Chassahowitzka River may be related to shallowness and low freshwater input. Although manatees can tolerate a wide range of salinities (Ortiz et al., 1998), they prefer habitats where osmotic stress is minimal or where fresh water is periodically available (O'Shea and Kochman, 1990).

Manatees feed on a wide variety of freshwater aquatic plants, particularly *Hydrilla verticillata* in the Crystal River headwaters (Hartman, 1979) and *Hydrilla*, *Eichhornia*, *Vallisneria*, *Najas*, *Paspalum*, and floating grasses in the St. Johns River (Bengtson, 1981). The manatee's capacity for flexibility and opportunism in foraging is well illustrated by their use of live oak (*Quercus virginiana*) acorns in the St. Johns River during the winter (O'Shea, 1986). The coastal salt marshes from northeastern Florida to South Carolina provide abundant forage for manatees. They typically feed during the higher stages of the tide cycle on *Spartina alterniflora*, which lines the extensive network of tidal creeks and rivers (Baugh et al., 1987; Zoodsma, 1991). Radio-tracked manatees in Crystal and Homosassa Rivers typically left warm-water springs during the day and moved downriver at dusk to feed on submerged vegetation (*Ruppia maritima* and *Potamogeton pectinatus*), returning to a warm-water source by morning (Rathbun et al., 1990). Manatees seen during aerial surveys near the mouths of the Suwannee, Withlacoochee, Crystal, Homosassa, and Chassahowitzka rivers often feed on beds of *R. maritima* or *Halodule wrightii* growing adjacent to channels (Powell and Rathbun, 1984). Manatees frequently used those areas of a river that had shallow, vegetated shelves or sandbars next to a channel (Powell and Rathbun, 1984). Manatees radio-tracked in Charlotte Harbor, Matlacha Pass, and San Carlos Bay were frequently located along the edges of seagrass beds (Lefebvre and Frohlich, 1986), supporting Hartman's (1979) suggestion that manatees tend to stay close to deeper water while in shallow-water situations.

Because of their broad distribution and migratory patterns, manatees in Florida utilize a wider diversity of food items and are probably less specialized in their feeding strategies than manatees in tropical regions (Lefebvre et al., 2000). Nevertheless, seagrasses appear to be a staple of their diet in coastal areas (Ledder, 1986; Provancha and Hall, 1991; Kadel and Patton, 1992; Lefebvre et al., 2000), and manatees may return to specific seagrass beds to graze on new growth (Koelsch, 1997; Lefebvre et al., 2000). In Florida, as well as other countries within the manatee's range, seagrasses may be their most long-term, widely available, stable food resource, whereas freshwater vegetation can be more ephemeral (e.g., Terrell and Canfield, 1996; Mataraza et al., 1999) or limited in availability in local areas of high manatee use (Smith, 1993). Human-related impacts are concentrated along the coasts and rivers, and seagrass bed coverage has declined in some regions of Florida through human-related activities (Lewis, 1987; Busby and Virnstein, 1993; Fletcher and Fletcher, 1995).

From 1974 through 2000, 4043 dead manatees were recovered in Florida by the Florida Fish and Wildlife Conservation Commission and cooperators with the U.S. Fish and Wildlife Service,

University of Miami, University of Central Florida, and Kissimmee Diagnostics Laboratory. (Table 1). The major known cause of manatee mortality is collision with boats (Wright et al., 1995). Other human-related causes are entrapment in water-control structures and navigation locks, drowning in commercial fishing nets, infection resulting from entanglement in fishing gear, and vandalism (O'Shea et al., 1985). High winter mortality in 1977, 1981, and 1989 was related to exceptionally cold weather (O'Shea et al., 1985; Ackerman et al., 1995), and die-offs of manatees in southwest Florida in 1963, 1982, and 1996 were associated with red tide (*Gymnodinium breve*) outbreaks (Layne, 1965; Buergelt et al., 1984; O'Shea et al., 1991; Landsberg and Steidinger, 1998; Bossart et al., 1998). Manatees are thus vulnerable to both human-related and natural threats, and their vulnerability is increased in areas where large aggregations assemble.

Manatees in Florida have been protected by law since 1893. They are currently protected under the U.S. Marine Mammal Protection Act (1972) and are listed as endangered under the Endangered Species Act (1973). Manatee protection and conservation are primarily the responsibility of the U.S. Fish and Wildlife Service and the Florida Fish and Wildlife Conservation Commission. The U.S. Marine Mammal Commission provides guidance and oversight to the agencies involved in manatee research and management. Reynolds (1999) provided a comprehensive summary of the research and management activities of federal and state agencies, private organizations, and individuals involved in manatee conservation and recovery.

Reynolds (1995) divided the history of manatee conservation into three eras. From the late 1960s until 1980, various research and management activities were initiated, culminating in the first draft of the Florida Manatee Recovery Plan in 1980. From 1980 to 1989, cooperative state and federal research programs expanded, and management activities were coordinated by the U.S. Fish and Wildlife Service's Manatee Coordinator. The first revision of the Recovery Plan in 1989 marked the beginning of the third era, in which research and management activities became more focused, and interagency coordination efforts increased. The Recovery Plan was revised again in 1996, and is currently undergoing its third revision. The Florida Manatee Recovery Plans (1980, 1989, and 1996) have successfully guided the growing number of agencies, institutions, organizations, and individuals involved in manatee research, management, and conservation, and have served as models for development of manatee conservation plans in other countries.

The primary ways in which the State of Florida has addressed manatee protection are through the development of boat speed regulatory zones and county manatee protection plans (Reynolds, 1999). Unfortunately, some of the counties with the highest incidence of boat-related manatee deaths have also had the greatest difficulty developing effective management plans. Additional measures will clearly be required to achieve population recovery goals.

One of the alternative, recommended strategies is the creation of a system of reserves in the most essential habitat areas (Reynolds and Gluckman, 1988; Reynolds, 1999). Under the authority of the Endangered Species Act (1973), the U.S. Fish and Wildlife Service's Refuge Management Authority Act, and the Florida Manatee Sanctuary Act (1978), the Florida Fish and Wildlife Conservation Commission has established 23 no-entry and motorboat-prohibited zones, and additional sites are being evaluated for inclusion in a network of protected areas. Sanctuaries, which exclude boats and people, appear to be an effective way to protect manatees from mortality and harassment (Reynolds and Gluckman, 1988; Buckingham et al., 1999). Population and life history information indicates that the long-term prognosis for the Florida manatee could be good, provided that strong efforts are continued to reduce mortality, improve habitat quality, and prevent or minimize the impact of potential catastrophes (Lefebvre and O'Shea, 1995; Marmontel et al., 1997).

Mexico

Historically, manatees occurred along the entire eastern coast of Mexico (Figure 2) from Texas south to Belize (Colmenero-Rolón and Hoz-Zavala, 1986; Colmenero-Rolón, 1991). By the 1970s through the 1980s, however, they had largely disappeared from about Nautla, in the state of Veracruz, north to Texas (Colmenero-Rolón, 1986). However, as recently as 1985 sightings were reported

TABLE 2
Summary of Aerial Surveys in the State of Quintana Roo, Mexico

Region	Manatees/h	Ref.	Notes
Holbox to Tulum	0	Colmenero-R. and Zarate, 1990	1987–1988, n = 7 surveys
Holbox to Cancun	0	Morales-V. and Olivera-G., 1997	1993–1995, n = 3 surveys
Cancun to Tulum	2.7	Morales-V. and Olivera-G., 1997	1992–1996, n = 7 surveys; seen in or near springs at Xpuha, Xelha, and Tancah
Biosphere Sian Ka'an	1.4	Colmenero-R. and Zarate, 1990	1987–1988, n = 5/6 surveys; Ascension Bay = 11 of 14 sightings
Biosphere Sian Ka'an	2.3	Morales-V. and Olivera-G., 1994b	1992–1994, n = 5 surveys; Ascension Bay = 15 of 16 sightings
Punta Herrero to Bacalar Chico	0	Colmenero-R. and Zarate, 1990	1987–1988, n = 3 surveys
Chetumal Bay	11.6	Colmenero-R. and Zarate, 1990	1987–1988, n = 8 surveys
Chetumal Bay	12.3	Morales-V. and Olivera-G., 1994a	1990, n = 2 surveys
Chetumal Bay	20.4	Morales-V., 2000b	1992–1997, mean of 14 surveys

Note: For ease of comparison between surveys and areas, the number of manatees sighted per survey hour (pooled for all surveys, unless noted as averaged from all surveys) are presented.

from the Soto La Marina in the state of Tamaulipas (Lazcano-Barrero and Packard, 1989). At present, there are only three regions in Mexico where manatees are still commonly found. In decreasing order of importance, these are the vast wetland systems in the states of Tabasco, Campeche, and Chiapas; the southeastern Caribbean coast on the Yucatan Peninsula in the state of Quintana Roo; and the river, lake, and wetland system at Alvarado in Veracruz (Villa and Colmenero-Rolón, 1981; Colmenero-Rolón, 1984; Colmenero-Rolón and Hoz-Zavala, 1986). Historically, manatees occasionally were seen during the summer in Texas, and Gunter (1942) proposed that these were seasonal migrants from northern Mexico. During the 1970s and 1980s, sightings in Texas seem to have declined (Powell and Rathbun, 1984; Rathbun et al., 1990), which is probably due to their extirpation in northern Mexico (Alvarez, 1963; Colmenero-Rolón, 1984; Powell and Rathbun, 1984).

Once it was realized that the state of Quintana Roo had some of the more important manatee areas remaining in Mexico (Colmenero-Rolón, 1984; Colmenero-Rolón and Hoz-Zavala, 1986), several aerial surveys were completed that showed that they are common only in three regions of the state. In decreasing order of importance, these are the Chetumal Bay area next to Belize, the Biosphere Reserve Sian Ka'an, and the coast between the towns of Playa del Carmen and Tulum (Table 2). The trend along the eastern shore of the Yucatan Peninsula is for increasing abundance from north to south, culminating in Belize, where manatees are particularly abundant (Morales-Vela et al., 2000). The manatee population in Chetumal Bay is thought to be between 90 and 130 (Morales-Vela and Olivera-Gomez, 1994a; Morales-Vela, 2000b), while the number in the rest of Quintana Roo, based on Morales-Vela and Olivera-Gomez (1994b, 1997), Ortega-Argueta (1997), and Morales-Vela (personal communication) probably does not exceed 30 to 40 animals. However, estimating manatee abundance in Quintana Roo is difficult, not only because manatees are generally troublesome to count (e.g., Lefebvre and Kochman, 1991), but also because they undoubtedly travel freely between Belize and Mexico (Morales-Vela et al., 2000). Although manatees are common in coastal and inland areas of Tabasco, Campeche, and Chiapas, they are much more difficult to observe in complicated river, lake, and wetland systems (Colmenero-Rolón, 1986). No aerial surveys have been completed in this region, and there are no estimates of manatee abundance (Morales-Vela, personal communication).

Colmenero-Rolón (1986) suggested that ideal manatee habitat in Mexico is characterized by average water temperatures above 22°C, and average rainfall above 1000 mm. Manatee habitats in the southern Bahia de Campeche meet these criteria. Lluch-Belda (1965) and Colmenero-Rolón (1986) worked in this region, and they describe seasonal movements of manatees in relation to patterns of seasonal rainfall and food availability. During the dry season (February through mid-May) manatees are found in the lower parts of the major rivers and along the coast of Tabasco. When the heavy rains begin in late May the animals move upriver, but they are prevented from reaching the lakes and small tributaries farther inland by swift and turbulent water. When the rains moderate in November through January, the animals are able to move up into the lakes and streams and feed on the abundant emergent aquatic vegetation (i.e., *Paspalum* sp., *Chloris* sp., *Panicum* sp., *Eichhornia crassipes*) that becomes available during high water. As the water levels drop in these inland areas during the dry months, food becomes limited and the manatees move down toward the coast again. Although fishermen traditionally took advantage of the seasonal migrations, and captured manatees while they were in the shallow, restricted inland lakes and creeks (Lluch-Belda, 1965), Colmenero-Rolón (1986) reported that most fishermen now respect the laws protecting manatees.

In the area of Chetumal Bay, aerial surveys (Table 2; Morales-Vela et al., 2000) and radio-tagged manatees monitored by satellites and conventional ground-based observers (Morales-Vela et al., 1996; Morales-Vela, 2000a) show that animals are closely associated with shorelines, even in the bay, which has an average depth of only about 3 m. Manatees are particularly abundant in and around Laguna Guerrero on the western shore of the bay, in and near the Hondo next to the city of Chetumal, and in the area of Dos Hermanos south to Punta Calentura on the eastern shore of the bay. Six radio-tracked manatees in Chetumal Bay were each monitored between 73 and 1697 days, and none left the bay. Their movements, however, were variable, with the maximum distance between extreme locations for the single male being 51.0 km, and for the five females varying from 8.5 to 48.5 km (Morales-Vela, 2000a). Axis-Arroyo et al. (1998), using visual surveys from boats, found that manatee movements in Chetumal Bay were associated (in decreasing order of importance) with food distribution, wind intensity, other manatees, water depth, salinity, water and air temperature, and cloudiness. The relatively low importance of water and air temperatures is in contrast to the situation in Florida, but expected because the water temperatures in Chetumal Bay never dropped below 20°C (Axis-Arroyo et al., 1998).

The northeastern coast of the Yucatan Peninsula has few rivers because the region is relatively dry and low, with porous soils. Under these conditions, low manatee abundance would be expected because of their apparent need for fresh water (Lluch-Belda, 1965). The coast between Playa del Carmen and Tulum is unusual, however, in that manatees are attracted to fresh water from several artesian springs that occur just inland of the shore (*cenotes*) and in small inlets (*caletas*) (Lluch-Belda, 1965; Gallo-Reynoso, 1983; Morales-Vela and Olivera-Gomez, 1997). But these springs do not attract large manatee aggregations as similar sites do in Florida (Bengtson, 1981; Rathbun et al., 1990; Reid et al., 1991), because manatees in Quintana Roo do not need, and are not attracted to, warm water.

Manatees have a long history of legal protection in Mexico, starting in 1921 (Colmenero-Rolón, 1991). In the recent past, illegal poaching was thought to be among the more-pressing conservation problems facing manatees in Mexico (see reviews in Lefebvre et al., 1989; Colmenero-Rolón and Zarate, 1990). Although some poaching is still reported, problems characteristic of a more affluent and expanding human population are increasing in importance, including incidental entrapment in fishing gear and being struck and killed by motor boats (Morales-Vela et al., 1996). Habitat alteration is also becoming a major concern, as illustrated by the declining use of the *cenotes* and *caletas* in Quintana Roo by manatees as these sites are developed for the rapidly expanding tourist industry (Gallo-Reynoso, 1983; Morales-Vela and Olivera-Gomez, 1997; Ortega-Argueta, 1997). The need for conservation planning, however, has not gone unnoticed by Mexicans, and has resulted in an impressive array of actions. These include the creation of the biosphere reserve at Sian Ka'an in 1986 (López-Ornat and Consejo-Dueñas, 1988), a manatee recovery plan (Colmenero-Rolón, 1991), the

production of educational materials (e.g., Morales-Vela and Olivera-Gomez, 1992), numerous conservation recommendations (e.g., Morales-Vela et al., 1996, 2000), the establishment of the first manatee protected area in Mexico in Chetumal Bay (Morales-Vela et al., 2000), and the creation of the "Comite Consultivo para la Proteccion y Recuperacion del Manatí del Caribe en México" (Colmenero-Rolón, 1998). The goal of this committee is to define strategies and policies for manatee conservation and research in Mexico. At the same time, Mexicans are developing a conservation culture, as exemplified by the effort to rescue, rather than eat, manatees trapped in a drying lake in Chiapas during the drought of 1995 (Morales-Vela and Olivera-Gomez, 1996).

BIOGEOGRAPHICAL PATTERNS OF *TRICHECHUS*

Domning (1982b) pointed out that, although manatees comprise three of the four living species of the order Sirenia, their representation in the fossil record is minute compared to that of the family Dugongidae. Early sirenians had a "pan-Tethyan" distribution and gave rise to dugongids in the middle Eocene (Domning et al., 1982). Manatees do not emerge in the fossil record until the Miocene (Domning, 1982b, 1997b). Domning (1982b) speculated that early manatees arose in South America as coastal river and lagoon inhabitants in contrast to the more marine dugongids, their contemporaries in the New World. Manatees developed a unique process of tooth replacement, adapted to a more abrasive diet including true grasses (Gramineae), which may have allowed them to outcompete dugongids (Domning, 1982b). The latter disappeared from the western Atlantic at the end of the Pliocene. *Trichechus inunguis* probably evolved in isolation in the Amazon basin following the Miocene Andean orogeny, and exhibits more derived characters than the other two species of manatees (Domning, 1982b). Whether competition or some other factor maintains the apparent parapatry of *T. inunguis* and *T. manatus* at the mouth of the Amazon River is unknown (Domning, 1981a). The great similarity between *T. manatus* and *T. senegalensis* led Simpson (1932) and later Domning (1982b) to conclude that manatees dispersed between the South American and African continents relatively recently, in the Pleistocene or Pliocene. Simpson (1932), however, suggested that manatees dispersed from Africa to South America, whereas the present fossil record better supports dispersal in the opposite direction.

Fossil remains of *T. manatus* are known from the early Pleistocene of Florida (Hulbert and Morgan, 1989), and (especially) from the late Pleistocene of Florida and elsewhere in the southeastern and eastern United States (Domning, 1982b). The late Pleistocene records extend as far north as New Jersey (Gallagher et al., 1989), and even up the Mississippi River as far as Arkansas (Domning, unpublished data). Manatees have never been documented in the Mississippi or its tributaries in historic times; however, the New Jersey range record has recently been surpassed by a Florida manatee that was radio-tracked to Rhode Island and back in 1995 (Reid, 1996). The remainder of the species' range has thus far produced only one occurrence of possible Pleistocene age, in Jamaica (Domning, unpublished data).

The late Pleistocene manatees from the southeastern United States are morphologically distinct from any other known manatees, and are probably best regarded as a separate subspecies of *T. manatus* (Domning, 1982b, and unpublished data). This still unnamed fossil subspecies may have evolved from Antillean manatees that colonized Florida from the south at a time climatically similar to today; it presumably became extinct during the subsequent, end-Pleistocene glacial stage, which would have rendered Florida uninhabitable by manatees. Postglacial warming allowed this sequence of events to be repeated, resulting in the evolution of *T. m. latirostris*. Owing to the peculiar geographical configuration of southeastern North America, such ephemeral subspecies may have evolved several times during the Pleistocene on the northern margin of the species' range, as climatic zones shifted repeatedly north and south.

Although recent records of manatees from the Lesser Antilles are lacking, prehistoric and early historical evidence indicates that manatees have occurred there. Thus, it is possible that linkage between *T. m. manatus* in the Greater Antilles and in South America has been maintained by

wanderers that island-hopped across the Lesser Antilles. Dispersal may also occur between the Greater Antilles and Mexico and Central America. The North Equatorial Current, flowing from east to west through the Caribbean Sea and northward offshore of Yucatan, would tend to favor a Yucatan-to-Cuba crossing more than a Venezuela-to-Puerto Rico crossing, although manatees may not necessarily depend upon favorable currents to cross open ocean. An extensive area of shallow water (Miskito Bank) between the Honduras–Nicaragua border and Jamaica (Figure 2) might help to promote ocean crossing between Central America and the Antilles. Such a crossing is known for green sea turtles (Nietschmann, 1972; Carr et al., 1978). Allen (1942) suggested that manatees originally extended their range to the West Indies by way of the Yucatan Peninsula and the intervening shallows. Reynolds and Ferguson (1984) sighted two manatees 61 km northeast of the Dry Tortugas in the Gulf of Mexico, and suggested that they could be wanderers from Florida, Cuba, or Yucatan. Genetic studies do not yet provide decisive support for any of these scenarios, as data from Central American populations are lacking, and no mitochondrial DNA haplotypes are shared by manatee populations in the West Indies and South America (Garcia-Rodriguez et al., 1998; see below). West Indian haplotypes are more similar to ones from Colombia than from Venezuela, Guyana, or Brazil.

In addition to historical geography, physical and biological environmental factors such as salinity, temperature, water depth, currents, shelter from wave action, and availability of vegetation are important determining factors of manatee distribution. The rarity of offshore sightings of manatees in locations that apparently lack dependable freshwater sources, such as the Bahamas, suggests that their distribution is influenced by the availability of fresh water. Ortiz et al. (1998) report that "manatees may be susceptible to dehydration after an extended period if freshwater is not available." Seasonal shifts in manatee distribution and their use of available warm-water sources in Florida suggest that energetic requirements also influence the range limits of manatees (Irvine, 1983). The average lower limit of thermal neutrality is approximately 24°C (Irvine, 1983). Whitehead (1977) described the full range of *T. manatus* as falling within the northern and southern limits of the 24°C mean annual isotherm. The Florida manatee's low metabolic rate (15 to 22% of predicted weight-specific values) and high thermal conductance suggest that manatees could not survive in winter water temperatures in most of Florida (Irvine, 1983), much less farther north, without access to warm-water refuges. The cold Labrador Current, flowing southwest along the northeast Atlantic coast, meets the warm Florida Current in the area of Cape Hatteras; relatively few manatees are reported north of Cape Hatteras (Rathbun et al., 1982). Natural and artificial warm-water refuges ameliorate the effects of winter temperatures on manatees, and may have allowed a recent northward winter range extension in Florida (Hartman, 1979; Shane, 1983, 1984).

While it has long been clear that Florida is marginal habitat for manatees in regard to temperature, it is less noted that the same may be true in regard to an aspect of feeding ecology. The teeth of Florida manatees are typically far more heavily worn than those of Antillean manatees. This may be related to a less fibrous diet (more seagrasses than true grasses), resulting in slower tooth replacement, in combination with heavy tooth wear resulting from feeding on quartz sand bottoms rather than the softer calcareous sand prevalent in much of the Antilles (Domning, 1982b). Whether Florida manatees suffer any nutritional stress caused by tooth wear with age remains to be investigated. Surprisingly, the much more complex teeth of manatees were not demonstrated to be more efficient at masticating seagrasses than the simple, peglike teeth of dugongs (Marsh et al., 1999).

Extensive gaps in suitable habitat, such as the northern coast of the Gulf of Mexico and the Caribbean coast of Venezuela, may represent geographical barriers. The absence of manatees along the Caribbean coast of Venezuela may be related to cooler water temperatures, and the scarcity of sheltered lagoons and fresh water (O'Shea et al., 1986). Deep water and strong currents in the Straits of Florida may be effective barriers to gene flow between *T. m. latirostris* in Florida and *T. m. manatus* in the Antilles (Domning and Hayek, 1986). The geo-oceanography of the northern Gulf of Mexico, in addition to cool winters, may contribute to the scarcity of manatees in this region. From the Florida panhandle westward to northern Mexico, the regional coastal type is

alluvial: smooth shorelines with sandy beaches interrupted by deltas (Price, 1954). The Gulf shoreline in peninsular Florida is drowned karst or biogenous, and is characterized by mangrove swamps and marshes, with few sandy beaches (Price, 1954). Along much of the karst shoreline springs are common in streams and offshore, because of artesian groundwaters (Price, 1954). Although Louisiana has extensive salt marsh (dominated by *Spartina* and *Juncus*), Alabama and Mississippi have relatively little salt marsh. Discontinuity of suitable habitat along the northern Gulf of Mexico may discourage intentional manatee migration west of Florida; however, hurricanes and severe storms may promote accidental dispersal.

Domning (1981b) proposed that the lack of diversity among sirenians is a direct result of their coevolution with a relatively undiversified food base, the seagrasses. While the distribution of sirenians is clearly parallel to the distribution of seagrasses in tropical and subtropical regions (Brasier, 1975; McCoy and Heck, 1976), the origin and evolution of modern manatees is theoretically linked to their specializations for feeding on true grasses found in freshwater or estuarine systems (Domning, 1982b), and they are known to eat a wide variety of aquatic and semiaquatic macrophytes (Best, 1981). The relative contributions of freshwater and marine macrophytes to the geographical distribution of the West Indian manatee are unknown. The distribution of *T. manatus* is probably not influenced by the distribution of particular plant species, as the manatee is highly opportunistic in selecting foods, and many of the freshwater and marine plants consumed by the West Indian manatee have a wide distribution.

The newest tool in the study of manatee biogeography is the analysis of mitochondrial DNA (mtDNA). Garcia-Rodriguez et al. (1998) sampled the mtDNA of West Indian manatees and identified 15 distinct haplotypes among 86 individuals from Florida, Puerto Rico, the Dominican Republic, Mexico, Colombia, Venezuela, Guyana, and Brazil (Figure 5). These haplotypes were distributed in a complex pattern, but the following generalizations seem warranted. The highest genetic diversity is found along the northern coast of South America, at the core of the species' range; marginal populations (in Florida, Mexico, and Brazil) were found to be monomorphic (only one haplotype apiece) although distinct from each other. Manatees in Mexico, Colombia, and Venezuela share at least one haplotype, as do manatees in Guyana and northeastern Brazil. However, throughout the species' range, populations from neighboring areas show striking differences, indicating limited long-distance gene flow and significant efficacy of barriers such as stretches of open water and unsuitable coastal habitat. Three distinctive mtDNA lineages were identified within the species, corresponding approximately to (1) Florida and the West Indies; (2) the Gulf of Mexico and Caribbean mainland coasts and rivers; and (3) the Atlantic coast of South America. The Florida haplotype occurs also in the Greater Antilles, suggesting that the Florida population originated by colonization from that region, as proposed above. The Antillean subspecies would therefore be paraphyletic with respect to its derivative, the Florida subspecies, as these are currently defined. Further studies of this sort, and especially increases in the number and sizes of the samples analyzed, will no doubt add many details to the history of manatee distribution on both evolutionary and ecological timescales — a history that is more complicated than it has hitherto seemed.

CONCLUSIONS

Water temperature determines the northern limit of the West Indian manatee's range, while loss of suitable habitat appears to limit the southern range more than temperature. Manatees range well north of the tropical zone on the east coast of the United States, whereas none is known to occur today south of the State of Alagoas in Brazil, which lies within the tropical zone in the Southern Hemisphere. The winter range of manatees in temperate regions of the United States is generally restricted to areas with natural or anthropogenic sources of warm water (20°C).

The association of manatees with freshwater sources is an overwhelmingly consistent pattern, from Columbus' report of their attraction to springs in Bahía de Cochinos, Cuba to the recent distribution surveys in various countries throughout their range. Manatees in Florida and Central

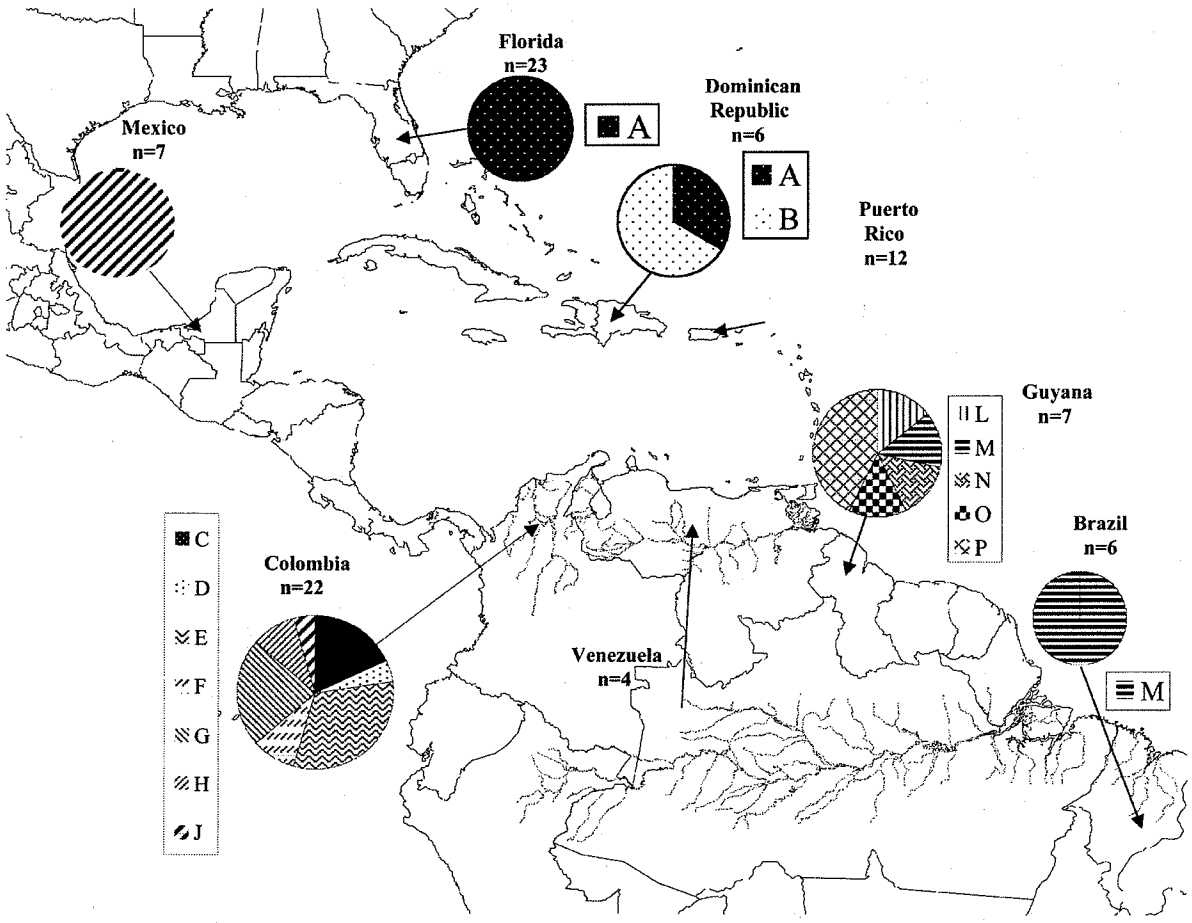

FIGURE 5 Distribution of 15 genetic haplotypes of the West Indian manatee. Three distinctive lineages were observed, corresponding approximately to Florida and the West Indies, the Caribbean coast and rivers of South America, and the Atlantic coast of South America. (Arrows indicate countries, not exact locations, from which samples were obtained for genetic analysis.) (From Garcia-Rodgriquez et al., Phylogeography of the West Indian Manatee (*Trichechus manatus*): How many populations and how many taxa? Mol. Ecol., 7: 1137–1149, 1998. With permission of Blackwell Scientific Ltd.)

and South America are frequently found in rivers and estuaries, while those in the Greater Antilles may of necessity occupy more marine environments. The association of manatees with shallow, protected coasts has also been noted by many authors. The occurrence of seagrasses and other submerged vegetation in shallow water accounts for part of this association. Extensive, unprotected coastlines with unvegetated sandy beaches or rocks may act as geographical barriers in some parts of the manatee's range.

Humans have undoubtedly influenced the distribution of manatees by depredation and alteration of habitat. Although hunting may have caused the manatee's disappearance from portions of its former range, the species persists in some regions despite a long history of exploitation by people. In these regions, for example, Guyana and Belize, the abundance of suitable habitat may have supported greater densities of manatees than areas where manatees have apparently been extirpated, such as the Lesser Antilles.

The West Indian manatee has fared better than the extinct Caribbean monk seal (*Monachus tropicalis*) (Kenyon, 1981; LeBouef et al., 1986), and the many species of land mammals in the West Indies that have become extinct since the late Pleistocene, largely as a result of human activities (Morgan and Woods, 1986; Woods and Ottenwalder, 1992). Manatees have adapted to hunting pressure by developing highly secretive behavior, and because they are totally aquatic and relatively far ranging, they have thus far been less susceptible to complete extirpation than many terrestrial species. Manatees are, however, increasingly vulnerable to human activities, and new sources of mortality may overshadow the former threat of hunting. The increased and widespread use of nylon and polyester gill nets is of particular concern because manatees may be unable to avoid nets in some locations, e.g., river mouths, and although incidentally caught they are often peremptorily slaughtered. The already high rate of boat-strike mortality in Florida may continue to increase with human population growth, and boat-strike deaths are now reported for other countries in the species' range. Only through strengthening of existing conservation efforts and improving enforcement of protective laws will manatees have a chance to endure.

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LITERATURE CITED

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1991. Pp. 223–258 *in* O'Shea, T. J., B. B. Ackerman, and H. F. Percival (eds.). Population Biology of the Florida Manatee (*Trichechus manatus latirostris*). Information and Technology Report 1, National Biological Service, Washington, D.C.

Allen, G. M. 1942. Extinct and Vanishing Mammals of the Western Hemisphere. American Committee for International Wildlife Protection, Special Publication No. 11. Intelligence Printing, Lancaster, Pennsylvania.

Allsopp, W. H. L. 1960. The manatee: ecology and use for weed control. Nature 188(4752):762.

Allsopp, W. H. L. 1969. Aquatic weed control by manatees — its prospects and problems. Pp. 344–351 *in* Obeng, L. E. (ed.). Man-Made Lakes. Ghana University Press, Accra.

Alvarez, T. 1963. The recent mammals of Tamaulipas, Mexico. University of Kansas Publication Museum of Natural History 14(15):363–473.

Amour, K. 1993. Status of the West Indian manatee (*Trichechus manatus*) in Trinidad and Tobago. Wildlife Section, Forestry Division, Ministry of Agriculture, Land and Marine Resources. Unpublished report.

Auil, N. 1998. Belize manatee recovery plan. UNDP/GEF Coastal Zone Management Project No. BZE/92/G31, United Nations Environmental Program, Caribbean Environment Program, Kingston, Jamaica.

Axis-Arroyo, J., B. Morales-Vela, D. Torruco-Gomez, and M. E. Vega-Cendejas. 1998. Variables asociadas con el uso de hábitat del manatí del Caribe (*Trichechus manatus*), en Quintana Roo, México (Mammalia). Revista de Biologia Tropical 46:791–803.

Bangs, O. 1895. The present standing of the Florida manatee, *Trichechus latirostris* (Harlan) in the Indian River waters. American Naturalist 29:783–787.

Banks, N. 1985. Sinopse cronológica dos estudos sobre o peixe-boi, no Brasil. Fifth Northeast Zoology Meeting, Natal, Río Grande do Norte, Brasil. Abstract.

Barrett, O. W. 1935. Notes concerning manatees and dugongs. Journal of Mammalogy 16:216–220.

Bartram, W. 1791. Travels through North and South Carolina, Georgia, East and West Florida. James and Johnson, Philadelphia. (Republished 1955, Dover Publications, Inc., New York.)

Baugh, T. M., J. A. Valade, and B. J. Zoodsma. 1987. Manatee use of *Spartina alterniflora* in Cumberland Sound. Marine Mammal Science 5(1):88–90.

Baughman, J. L. 1946. Some early notices on American manatees and the mode of their capture. Journal of Mammalogy 27:234–239.

Beck, C. A. and J. P. Reid. 1995. An automated photo-identification catalog for studies of the life history of the Florida manatee. Pp. 120–134 *in* O'Shea, T. J., B. B. Ackerman, and H. F. Percival (eds.). Population Biology of the Florida Manatee (*Trichechus manatus latirostris*). Information and Technology Report 1, National Biological Service, Washington, D.C.

Beeler, I. E. and T. J. O'Shea. 1988. Distribution and mortality of the West Indian manatee (*Trichechus manatus*) in the southeastern United States: a compilation and review of recent information. Vols. 1 and 2. National Technical Information Service, PB88-207980/AS, Springfield, Virginia.

Belitsky, D. W. and C. L. Belitsky. 1980. Distribution and abundance of manatees (*Trichechus manatus*) in the Dominican Republic. Biological Conservation 17:313–319.

Bengtson, J. L. 1981. Ecology of Manatees (*Trichechus manatus*) in the St. Johns River, Florida. Ph.D. thesis, University of Minnesota, Minneapolis.

Bengtson, J. L. and D. Magor. 1979. A survey of manatees in Belize. Journal of Mammalogy 60:230–232.

Bertram, G. C. L. and C. K. R. Bertram. 1963. The status of manatees in the Guianas. Oryx 7:90–93.

Bertram, G. C. L. and C. K. R. Bertram. 1964. Manatees in the Guianas. Zoologica (New York Zoological Society) 49:115–120.

Bertram, G. C. L. and C. K. R. Bertram. 1973. The modern Sirenia: their distribution and status. Biological Journal of the Linnean Society 5:297–338.

Best, R. C. 1981. Foods and feeding habits of wild and captive Sirenia. Mammal Review 11:3–29.

Best, R. C. and D. M. Teixeira. 1982. Notas sobre a distribuiçao e "status" aparentes dos peixes-bois (Mammalia: Sirenia) nas costas amapaenses brasileiras. Boletim Fundaçao Brasileira para a Conservaçao da Natureza, Río de Janeiro, 17:41–47.

Bonde, R. K. 1998. Poachers take more manatees in Port Honduras. Pp. 6–7 *in* Domning, D. P. (ed.). Sirenews, Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 30.

Bonde, R. K. and C. Potter. 1995. Manatee butchering sites in Port Honduras. P. 7 *in* Domning, D. P. (ed.). Sirenews, Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 24.

Borôbia, M. and L. Lodi. 1992. Recent observations and records of the West Indian manatee *Trichechus manatus* in northeastern Brazil. Biological Conservation 59:37–43.

Bossart, G. D., D. G. Baden, R. Y. Ewing, B. Roberts, and S. D. Wright. 1998. Brevetoxicosis in manatees (*Trichechus manatus latirostris*) from the 1996 epizootic: gross, histologic and immunohistochemical features. Toxicologic Pathology 26(2):276–282.

Boyle, C. and J. Khan. 1993. National report on the status of the West Indian manatee population in Trinidad and Tobago. Manatee Subcommittee, Trinidad and Tobago Field Naturalist Club. Unpublished report.

Bradley, R. 1983. The pre-Columbian exploitation of the manatee in Mesoamerica. Papers in Anthropology, University of Oklahoma 24:1–82.

Brasier, M. D. 1975. An outline history of seagrass communities. Palaeontology 18:681–702.

Buckingham, C. A., L. W. Lefebvre, J. M. Schaefer, and H. I. Kochman. 1999. Manatee response to boating activity in a thermal refuge. Wildlife Society Bulletin 27(2):514–522.

Buergelt, C. D., R. K. Bonde, C. A. Beck, and T. J. O'Shea. 1984. Pathologic findings in manatees in Florida. Journal of the American Veterinary Medical Association 185:1331–1334.

Busby, D. S. and R. W. Virnstein 1993. Executive summary. Pp. iii–viii *in* Morris, L. J. and D. A. Tomasko (eds.). Submerged Aquatic Vegetation and Photosynthetically Active Radiation. Special Publication SJ93-SP13, St. Johns River Water Management District, Palatka, Florida.

Campbell, H. W. and D. Gicca. 1978. Reseña preliminar del estado actual y distribución del manatí (*Trichechus manatus*) en México. Anales Instituto de Biologia, Universidad Nacional Autónoma de México, Serie Zoología 49:257–264.

Campbell, H. W. and B. I. Irvine. 1975. Manatee survey in Dominican Republic, Feb.14–25, 1975. U.S. Fish and Wildlife Service. Unpublished report.

Carr, A., M. H. Carr, and A. B. Meylan. 1978. The ecology and migrations of sea turtles, 7. The West Caribbean green turtle colony. Bulletin of the American Museum of Natural History 162:1–46.

Carr, T. 1994. The manatees and dolphins of the Miskito Coast Protected Area, Nicaragua. Marine Mammal Commission Report PB94-170354. Gainesville, Florida.

Centro Nacional de Conservação e Manejo de Sirênios 1997. Reunião de trabalho sobre pesquisa para a conservação do peixe-boi no Brasil, Barra de Mamanguape 6–8 Nov. 1997.

Cerrato, C. A. 1993. Estado del manati en Honduras. Report to Unidad de Coordinacion Ambiental, Programa Ambiental del Caribe del Programa de las Naciones Unidas para el Medio Ambiente. Cuidad Universitaria Tegucigalpa, Honduras. 14 pp.

Charnock-Wilson, J. 1968. The manatee in British Honduras. Oryx 9:293–294.

Charnock-Wilson, J. 1970. Manatees and crocodiles. Oryx 10:236–238.

Charnock-Wilson, J., C. K. R. Bertram, and G. C. L. Bertram. 1974. The manatee in Belize. Belize Audubon Society Bulletin 6:1–4.

Colmenero-Rolón, L. C. 1984. Nuevos registros del manatí (*Trichechus manatus*) en el sureste de México. Anales Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología 54:243–254.

Colmenero-Rolón, L. C. 1986. Aspectos de la ecología y comportamiento de una colonia de manatíes (*Trichechus manatus*) en el municipio de Emilia no Zapata, Tabasco. Anales Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología 56:589–602.

Colmenero-Rolón, L. C. 1991. Propuesta de un plan de recuperacion para la poblacion del manatí *Trichechus manatus* de México. Anales Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología 62:203–218.

Colmenero-Rolón, L. C. 1998. Manatee recovery committee established. P. 6 *in* Domning, D. P. (ed.). Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 29.

Colmenero-Rolón, L. C. and M. E. Hoz-Zavala. 1986. Distribución de los manatíes, situación y su conservación en México. Anales Instituto de Biología, Universidad Nacional Autónoma de Mexico, Serie Zoología 56:955–1020.

Colmenero-Rolón, L. C. and B. E. Zarate. 1990. Distribution, status and conservation of the West Indian manatee in Quintana Roo, Mexico. Biological Conservation 52:27–35.

Correa-Viana, M. 1995. El manatí: revisión de su distribución y abundancia actuales. Pp. 139–144 *in* Delfines y Otros Mamiferos Acuáticos de Venezuela. Academia de Ciencias Fisicas, Matamaticas, y Naturales and Fundacion para el Desarorollo de las Ciencias Fisicas, Matamaticas, y Naturales, Caracas, Venezuela.

Craig, B. A., M. A. Newton, R. A. Garrott, J. E. Reynolds III, and J. R. Wilcox. 1997. Analysis of aerial survey data on Florida manatee using Markov Chain Monte Carlo. Biometrics 53:524–541.

Crombie, R. I. 1975a. A report on the status and distribution of the manatee, *Trichechus manatus*, in Jamaica. U.S. Fish and Wildlife Service. Unpublished report. 9 pp.

Crombie, R. I. 1975b. Manatee survey of the southeastern tip of the Republica Dominicana. U.S. Fish and Widllife Service. Unpublished Report. 10 pp.

Cumbaa, S. L. 1980. Aboriginal use of marine mammals in the southeastern United States. Southeastern Archaeological Conference Bulletin 17:6–10.

Cuní, L. A. 1918. Contribución al estudio de los mamíferos acuaticos observados en las costas de Cuba. Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey" 3:83–126.

Dampier, W. A. 1699. A New Voyage Round the World. Vol. I, 4th ed. James Knapton, London.

Dekker, D. 1974. On the natural history of manatees (*Trichechus manatus*) from Suriname for the Amsterdam Zoo. Aquatic Mammals 2:1–3.

Dekker, D. 1978. Suriname, a last refuge for the manatee. Suralco Magazine 10(3):1–4.

Delgado, J. R. 1995. Status of the manatees in Venezuela. Pp. 159–165 *in* Delfines y Otros Mamiferos Acuáticos de Venezuela. Academia de Ciencias Fisicas, Matamaticas, y Naturales and Fundacion para el Desarorollo de las Ciencias Fisicas, Matamaticas, y Naturales, Caracas, Venezuela.

Department of Nature Conservation. 1993. National report of Suriname on the status of the West Indian manatee population in Suriname. Suriname Forest Service and Foundation for Nature Preservation in Suriname, Ministry of Natural Resources. Paramaribo, Suriname.

Deutsch, C. J., R. K. Bonde, and J. P. Reid. 1998. Radio-tracking manatees from land and space: tag design, implementation and lessons learned from long-term study. Marine Technology Society Journal 32(1):18–29.

Deutsch, C. J., J. P. Reid, R. K. Bonde, D. E. Easton, H. I. Kochman, and T. J. O'Shea. 2000. Seasonal movements, migratory behavior, and site fidelity of West Indian manatees along the Atlantic coast of the United States as determined by radio-telemetry. Work Order No. 163. Florida Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey and University of Florida. Unpublished report. 1–119 + appendices.

Domning, D. P. 1981a. Distribution and status of manatees *Trichechus* spp. near the mouth of the Amazon River, Brazil. Biological Conservation 19:85–97.

Domning, D. P. 1981b. Sea cows and sea grasses. Paleobiology 7:417–420.

Domning, D. P. 1982a. Commercial exploitation of manatees *Trichechus* in Brazil c. 1785–1973. Biological Conservation 22:101–126.

Domning, D. P. 1982b. Evolution of manatees: a speculative history. Journal of Paleontology 56:599–619.

Domning, D. P. 1989. Alligator Hole River Project. Pp. 6–7 *in* Domning, D. P. (ed.). Sirenews, Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 12.

Domning, D. P. 1996. Bibliography and index of the Sirenia and Desmostylia. Smithsonian Contributions to Paleobiology No. 80: iii + 611.

Domning, D. P. 1997a. More manatee poaching. Pp. 7–8 *in* Domning, D. P. (ed.). Sirenews, Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 28.

Domning, D. P. 1997b. Sirenia. Pp. 383–391 *in* Kay, R. F., R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.). Vertebrate Paleontology in the Neotropics: The Miocene Fauna of La Venta, Colombia. Smithsonian Institution Press, Washington, D.C.

Domning, D. P. 1998a. Status of captive manatees in the Alligator Hole River. P. 6 *in* Domning, D. P. (ed.). Sirenews, Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 29.

Domning, D. P. 1998b. Logging threatens coastal environment. Pp. 6–7 *in* Domning, D. P. (ed.). Sirenews, Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 29.

Domning, D. P. and L. C. Hayek. 1986. Interspecific and intraspecific morphological variation in manatees (Sirenia: *Trichechus*). Marine Mammal Science 2:87–144.

Domning, D. P., G. S. Morgan, and C. E. Ray. 1982. North American Eocene sea cows (Mammalia: Sirenia). Smithsonian Contributions to Paleobiology 52:1–69

Duerden, J. E. 1901. The marine resources of the British West Indies. West Indian Bulletin 2:123–127.

Duplaix, N. and H. A. Reichart. 1978. History, status and protection of the Caribbean manatee *Trichechus m. manatus* in Suriname. Rare Animal Relief Effort and United States Fish and Wildlife Service. Unpublished report. 1–23 + 10 appendices.

Eberhardt, L. L. and T. J. O'Shea. 1995. Integration of manatee life-history data and population modeling. Pp. 269–279 *in* O'Shea, T. J., B. B. Ackerman, and H. F. Percival (eds.). Population Biology of the Florida Manatee (*Trichechus manatus latirostris*). National Biological Service, Information and Technology Report 1:1–289.

Eberhardt, L. L., R. A. Garrott, and B. L. Becker. 1999. Using trend indices for endangered species. Marine Mammal Science 15(3):766–785.

Elizondo, C. L. H. 1993. El manati (*Trichechus manatus*) en Costa Rica. Base de Datos Conservación. Instituto Nacional de Biodiversidad-Convenio INBIO-TNC. Unpublished report. Pp. 94–95 + maps.

Estrada, A. R. and L. T. Ferrer. 1987. Distribución del manatí antillano, *Trichechus manatus* (Mammalia: Sirenia), en Cuba. I. Región occidental. Poeyana 354:1–12.

Estrada, A. R. and L. T. Ferrer. 1993. Informe sobre el estado del manati antillano en Cuba. Unpublished report prepared for UNEP. 1–4.

Evermann, B. W. 1902. General report on the investigations in Porto Rico of the United States Fish Commission Steamer Fish Hawk in 1899. Bulletin of the United States Fish Commission 20:24–25.

Fairbairn, P. W. and A. M. Haynes. 1982. Jamaican surveys of the West Indian manatee (*Trichechus manatus*), dolphin (*Tursiops truncatus*), sea turtles (Families Cheloniidae and Dermochelydae) and booby terns (Family Laridae). United Nations Food and Agriculture Organization Fisheries Report 278:289–295.

Ferrer, L. T. and A. R. Estrada. 1988. Primer record de mortalidad del manatí en aguas cubanas. Miscelanea Zoologica 41:1–2.

Fewkes, J. W. 1907. The aborigines of Porto Rico and neighboring islands. Annual Report of the Bureau of American Ethnology 25:48–50 and 192–193.

Fletcher, S. W. and W. W. Fletcher. 1995. Factors affecting changes in seagrass distribution and diversity patterns in the Indian River Lagoon complex between 1940 and 1992. Bulletin of Marine Science 57:49–58.

Gallagher, W. B., D. C. Parris, B. S. Grandstaff, and C. DeTample. 1989. Quaternary mammals from the continental shelf off New Jersey. Mosasaur: Journal of the Delaware Valley Paleontological Society 4:101–110.

Gallo-Reynoso, J. P. 1983. Notas sobre la distribución del manatí (*Trichechus manatus*) en las costas de Quintana Roo. Anales Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología 53:443–448.

Garcia-Rodriguez, A. I. 2000. Genetic Studies of the West Indian Manatee (*Trichechus manatus*). Ph.D. thesis, University of Florida, Gainesville.

Garcia-Rodriguez, A. I., B. W. Bowen, D. P. Domning, A. A. Mignucci-Giannoni, M. Marmontel, R. A. Montoya-Ospina, B. Morales-Vela, M. Rudin, R. K. Bonde, and P. M. McGuire. 1998. Phylogeography of the West Indian manatee (*Trichechus manatus)*: how many populations and how many taxa? Molecular Ecology 7(9):1137–1149.

Garrott, R. A., B. B. Ackerman, J. R. Cary, D. M. Heisey, J. E. Reynolds III, P. M. Rose and J. R. Wilcox. 1994. Trends in counts of Florida manatees at winter aggregation sites. Journal of Wildlife Management 58(4):642–654.

Gundlach, J. 1877. Contribución a la Mamalogia Cubana. Montiel y Compañía, Habana.

Gunter, G. 1942. Further miscellaneous notes on American manatees. Journal of Mammalogy 23:89–90.

Gunter, G. 1954. Mammals of the Gulf of Mexico. Fishery Bulletin of the United States Fish and Wildlife Service 55:543–551.

Harlan, R. 1824. On a species of Lamantin resembling the *Manatus Senegalensis* (Cuvier) inhabiting the coast of East Florida. Journal of the Academy of Natural Sciences of Philadelphia 3:390–394.

Hartman, D. S. 1972. Manatees. Sierra Club Bulletin 57:20–22.

Hartman, D. S. 1974. Distribution, status and conservation of the manatee in the United States. National Technical Information Service Publication PB81-140725, Springfield, Virginia.

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogists Special Publication 5:1–153.

Hatt, R. T. 1934. A manatee collected by the American Museum Congo Expedition, with observations on the recent manatees. Bulletin American Museum of Natural History 66:533–566.

Hislop, G. 1985. Trinidad and Tobago. P. 8 *in* Domning, D. P. (ed.). Sirenews, Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 3.

Hulbert, R. C., Jr. and G. S. Morgan. 1989. Stratigraphy, paleoecology and vertebrate fauna of the Leisey Shell Pit Local Fauna, Early Pleistocene (Irvingtonian) of southwestern Florida. Papers in Florida Paleontology No. 2:1–19.

Hurst, L. A. 1987. Review of the Status and Distribution of the West Indian Manatee (*Trichechus manatus*) in Jamaica, with an Evaluation of the Aquatic Vegetation of the Alligator Hole River. M.S. thesis, University of Florida, Gainesville.

Husar, S. L. 1977. The West Indian Manatee (*Trichechus manatus*). U.S. Fish and Wildlife Service, Wildlife Research Report 7. U.S. Government Printing Office, Washington, D.C.

Husson, A. M. 1978. The mammals of Suriname. Zoölogische Monographieën van het Rijksmuseum van Natuurlijke Historie No. 2:334–339.

IBAMA 1997. Mamíferos aquáticos do Brasil: Plano de ação. Brasília.

INDERENA 1993. Informe del estado actual del manati antillano (*Trichechus manatus*) en Colombia. Division de Fauna Terrestre. Santafé de Bogotá.

Irvine, A. B. 1983. Manatee metabolism and its influence on distribution in Florida. Biological Conservation 25:315–334.

Irvine, A. B., F. C. Neal, P. T. Cardeilhac, J. A. Popp, F. H. White, and R. L. Jenkins. 1980. Clinical observations on captive and free-ranging West Indian manatees, *Trichechus manatus*, in Florida. Aquatic Mammals 8:2–10.

Irvine, A. B., J. E. Caffin, and H. I. Kochman. 1982. Aerial surveys for manatees and dolphins in western peninsular Florida. Fishery Bulletin 80:621–629.

Jackson, J. F. 1975. Preliminary status survey of *Trichechus* in northeastern Brazil. Unpublished report for the U.S. Fish and Wildlife Service 1–6 + map.

Janson, T. 1978. Ecology and conservation of the Guatemalan manatee. Marine Mammal Information, Oregon State University:3. Abstract.

Janson, T. 1980. Discovering the mermaids. Oryx 5:373–379.

Jiménez, J. C. 1982. Letter to editor, San Juan Star Magazine, June 6, 1982.

Jiménez-Marrero, N. M., I. Méndez-Matos, R. A. Montoya-Ospina, E. H. Williams, L. Bunkley, and A. A. Mignucci-Giannoni. 1998. Rangos de referencia de immunoglobulina G en individuos de tres poblaciones des manatí (*Trichechus manatus*). Caribbean Journal of Science 34(3–4):313–315.

Jiménez Pérez, I. 1998. Ecology and Conservation of the West Indian Manatee in Northeastern Costa Rica. M.S. thesis in Wildlife Management and Conservation, submitted to Regional Wildlife Management Program for Mesoamerica and the Caribbean, Universidad Nacional, Costa Rica.

Jiménez Pérez, I. 2000a. Conservation status of the West Indian manatee (*Trichechus manatus*) in Nicaragua. Unpublished report.

Jiménez Pérez, I. 2000b. Los Manatíes del Río San Juan y los Canales de Torteguero: Ecología y Conservación. Asociación Comunidades Ecologistas la Ceiba, Amigos de la Tierra, Costa Rica.

Jiménez Pérez, I. and M. A. Cateula. 1998. Estado de conservación del manatí (*Trichechus manatus*) en la Gran Reserva Biológica Indio Maíz, Nicaragua. Unpublished report.

Jong, C. de 1961. Manatee hunters in Guiana in past centuries. Surinaamse Landbouw 9:93–100.

Kadel, J. J. and G. W. Patton. 1992. Aerial studies of the West Indian manatee (*Trichechus manatus*) on the west coast of Florida from 1985–1990: a comprehensive six year study. Mote Marine Laboratory Technical Report No. 246:1–17+ appendices.

Kenyon, K. W. 1981. Monk seals — *Monachus*. Pp. 195–220 *in* Ridgway, S. H. and R. J. Harrison (eds.). Handbook of Marine Mammals, Vol. 2 Seals. Academic Press, London.

Kinnaird, M. F. 1985. Aerial census of manatees in northeastern Florida. Biological Conservation 32:59–79.

Klein, E. H. 1979. Review of the status of manatee (*Trichechus manatus*) in Honduras, Central America. Ceiba 23(1):21–28.

Koelsch, J. A. 1997. The Seasonal Occurrence and Ecology of Florida Manatees (*Trichechus manatus latirostris*) in Coastal Waters near Sarasota, FL. Master's thesis, University of South Florida, Tampa.

Landsberg, J. H. and K. A. Steidinger. 1998. A historical review of *Gymnodinium breve* red tides implicated in mass mortalities of the manatee (*Trichechus manatus latirostris*) in Florida, USA. Pp. 97–100 *in* Raguera, B., J. Blanco, M. L. Fernández, and T. Wyatt (eds.). Harmful Algae. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO.

Langtimm, C. A., T. J. O'Shea, R. Pradel, and C. A. Beck. 1998. Estimates of annual survival probabilities for adult Florida manatees (*Trichechus manatus latirostris*). Ecology 79(3):981–997.

Layne, J. N. 1965. Observations on marine mammals in Florida waters. Bulletin Florida State Museum 9:131–181.

Lazcano-Barrero, M. A. and J. M. Packard. 1989. The occurrence of manatees (*Trichechus manatus*) in Tamaulipas, Mexico. Marine Mammal Science 5:202–205.

LeBouef, B. J., K. W. Kenyon, and B. Villa-Ramirez. 1986. The Caribbean monk seal is extinct. Marine Mammal Science 2(1):70–72.

Ledder, D.A. 1986. Food Habits of the West Indian Manatee *(Trichechus manatus latirostris)* in South Florida. M.S. thesis, University of Miami, Coral Gables, Florida.

Lefebvre, L. W. and R. K. Frohlich. 1986. Movements of radio-tagged manatees in southwest Florida, January 1985–March 1986. United States Fish and Wildlife Service and Florida Department of Natural Resources. Unpublished report: 1–87.

Lefebvre, L. W. and H. I. Kochman. 1991. An evaluation of aerial survey replicate count methodology to determine trends in manatee abundance. Wildlife Society Bulletin 19:298–309.

Lefebvre, L. W. and T. J. O'Shea. 1995. Florida manatees. Pp. 267–269 *in* Our Living Resources — Coastal and Marine Ecosystems. National Biological Service, U.S. Government Printing Office, Washington, D.C.

Lefebvre, L. W., T. J. O'Shea, G. B. Rathbun, and R. C. Best. 1989. Distribution, status and biogeography of the West Indian manatee. Pp. 567–610 *in* Woods, C. A. (ed.). Biogeography of the West Indies; Past, Present, and Future. Sandhill Crane Press, Gainesville, Florida.

Lefebvre, L. W., B. B. Ackerman, K. M. Portier, and K. H. Pollock. 1995. Aerial survey as a technique for estimating manatee population size and trend — problems and prospects. Pp. 63–74 *in* O'Shea T. J., B. B. Ackerman and H. F. Percival (eds.). Population Biology of the Florida Manatee (*Trichechus manatus latirostris*). Information and Technology Report 1, National Biological Service, Washington, D.C.

Lefebvre, L. W., J. P. Reid, W. J. Kenworthy, and J. A. Powell. 2000. Characterizing manatee habitat use and seagrass grazing in Florida and Puerto Rico: implications for conservation and management. Pacific Conservation Biology 5(4):289–298.

Lima, R. P. de 1997. Peixe-boi marinho (*Trichechus manatus*): distribuição, status de conservação e aspectos tradicionais ao longo do litoral nordeste do Brasil. M.Sc. dissertation, Universidade Federal de Pernambuco, Recife.

Lima, R. P. de, D. Paludo, R. J. Soavinski, K. G. Silva, and E. M. A. Oliveira. 1992. Levantamento da distribuição, ocorrência e status de conservação do peixe-boi marinho (*Trichechus manatus manatus*, Linnaeus, 1758) no litoral nordeste do Brasil. Peixe-boi – coletânea de trabalhos de consrevação e pesquisa de sirênios no Brasil 1(1):47–72.

Lluch-Belda, D. 1965. Algunas notas sobre la biología del manatí. Anales del Instituto Nacional de Investigaciones Biológico-Pesqueras, México 1:405–419.

López-Ornat, A. and J. J. Consejo-Dueñas. 1988. Implementación de un programa de conservación de los humedales de Quintana Roo (México): un proceso dinámico de cinco años. Pp. 351–356 *in* Anónimo (ed.). Ecología y conservación del Delta de los ríos Usumacinta y Grijalva. Memorias, INIREB-TABASCO.

Loveland, F. O. 1976. Tapirs and manatees: cosmological categories and social process among Rama Indians of eastern Nicaragua. Pp. 67–82 *in* Helms, M. W. and F. O. Loveland (eds.). Frontier Adaptations in Lower Central America. Philadelphia Institute for the Study of Human Issues, Philadelphia, Pennsylvania.

MacLaren, J. P. 1967. Manatees as a naturalistic biological mosquito control method. Mosquito News 27(3):387–393.

Maheia, W. 1997. Manatee poaching continues in Belize. Pp. 7–8 *in* Domning, D. P. (ed.). Sirenews, Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 27.

Marine Mammal Commission. 1988. Preliminary assessment of habitat protection needs for West Indian manatees on the east coast of Florida and Georgia. Marine Mammal Commission, Washington, D.C.

Marmontel, M., S. R. Humphrey, and T. J. O'Shea. 1997. Population viability analysis of the Florida manatee (*Trichechus manatus latirostris*), 1976–1991. Conservation Biology 11(2):467–481.

Marsh, H., T. J. O'Shea, and R. C. Best. 1986. Research on sirenians. Ambio 15:177–180.

Marsh, H., C. A. Beck, and T. Vargo. 1999. Comparisons of the capabilities of dugongs and West Indian manatees to masticate seagrasses. Marine Mammal Science 15(1):250–255.

Mataraza, L. K., J. B. Terrell, A. B. Munson, and D. E. Canfield, Jr. 1999. Changes in submersed macrophytes in relation to tidal storm surges. Journal of Aquatic Plant Management 37:3–12.

McClenaghan, L. R., Jr. and T. J. O'Shea. 1988. Genetic variability in the Florida manatee (*Trichechus manatus*). Journal of Mammalogy 69:481–488.

McCoy, E. D. and K. L. Heck, Jr. 1976. Biogeography of corals, seagrasses and mangroves: an alternative to the center of origin concept. Systematic Zoology 25(1):201–210.

McKillop, H. I. 1985. Prehistoric exploitation of the manatee in the Maya and circum-Caribbean areas. World Archaeology 16(3):337–353.

Mignucci-Giannoni, A. A. 1991. Outlook for manatee survival grim unless rapid action is taken. Pp. 7–8 *in* Sirenews, Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 15.

Mignucci-Giannoni, A. A. 1998. Marine mammal captivity in the northeastern Caribbean, with notes on the rehabilitation of stranded whales, dolphins and manatees. Caribbean Journal of Science 34(3–4):191–203.

Mignucci-Giannoni, A. A. and C. A. Beck. 1998. The diet of the manatee (*Trichechus manatus*) in Puerto Rico. Marine Mammal Science 14(2):394–397.

Mignucci-Giannoni, A. A., C. A. Beck, R. A. Montoya-Ospina, and E. H. Williams. 1999. Parasites and commensals of the West Indian manatee from Puerto Rico. Journal of the Helminthological Society of Washington 66(1):67–69.

Mignucci-Giannoni, A. A., R. A. Montoya-Ospina, N. M. Jimenez-Marrero, M. A. Rodriguez-Lopez, E. H. Williams, and R. K. Bonde. 2000. Manatee mortality in Puerto Rico. Environmental Management. 25(2):189–198.

Miller, G. S. 1918. Mammals and reptiles collected by Theodoor de Booy in the Virgin Islands. Proceedings U.S. National Museum 54(2244):507–511.

Miller, G. S. 1929. Mammals eaten by Indians, owls and Spaniards in the coast region of the Dominican Republic. Smithsonian Miscellaneous Collection 82(5):1–16.

Miller, K. E., B. B. Ackerman, L. W. Lefebvre, and K. B. Clifton. 1998. An evaluation of strip-transect aerial survey methods for monitoring manatee populations in Florida. Wildlife Society Bulletin 26(3):561–570.

Mondolfi, E. 1974. Taxonomy, distribution and status of the manatee in Venezuela. Memoria de la Sociedad de Ciencias Naturales La Salle 97(34):5–23.

Mondolfi, E. and C. Müller. 1979. Investigación y conservación del manatí en Venezuela. Vols. 1 (55 pp.) and 2 (88 pp.). Fundación para la Defensa de la Naturaleza. Unpublished report.

Montgomery, G. B., N. B. Gale, and W. P. Murdoch, Jr. 1982. Have manatee entered the eastern Pacific Ocean? Mammalia 46:267–258.

Montgomery, G. G. 1980. Status of the manatee (*Trichechus manatus*) in Bocas del Toro Province, Panama. Smithsonian Tropical Research Institute, Balboa, Panama.

Montoya-Ospina, R. A. 1994. Preliminary Blood Chemistry Reference Ranges for Antillean Manatees, *Trichechus manatus*, from Puerto Rico and Colombia. Master of Science thesis, Department of Marine Sciences, University of Puerto Rico, Mayagüez, Puerto Rico.

Montoya-Ospina, R. A., C. Caicedo-Herrera, S. L. Millán-Sánchez, A. A. Mignucci-Giannoni, and L. W. Lefebvre. In press. Status of the West Indian manatee, *Trichechus manatus*, in Colombia. Biological Conservation.

Moore, J. C. 1951. The range of the Florida manatee. Quarterly Journal of the Florida Academy of Sciences 14:1–19.

Moore, J. C. 1956. Observations of manatees in aggregations. American Museum Novitates 1811:1–24.

Morales-Vela, B. 2000a. Distribución, movimientos y reproduccion de manatí es radio-marcados en la bahia de Chetumal, México. Chapter in draft Ph.D. thesis: Distribución, abundancia y uso de habitat por el manatí en Quintana Roo y Belize, Facultad de Ciencia, Universidad Nacional Autónoma de México.

Morales-Vela, B. 2000b. Tendencia poblacional de manatíes es y su distribución en la bahia de Chetumal, Quintana Roo, México. Chapter in draft Ph.D. thesis: Distribución, abundancia y uso de habitat por el manatí en Quintana Roo y Belize, Universidad Nacional Autónoma de México.

Morales-Vela, B. and L. D. Olivera-Gomez. 1992. De sirenas a manatí es. Centro de Investigaciones de Quintana Roo (CIQRO), Chetumal, México.

Morales-Vela, B and L. D. Olivera-Gómez. 1994a. Distribución espacial y estimacion poblacional de los manatí es en las Bahia de Chetumal, Quintana Roo, México. Revista de Investigaciones Cientifica, Universidad Nacional Autónoma de México, Serie Ciencias del Mar 2 (No. especial SOMEMMA, 2):27–34.

Morales-Vela, B. and L. D. Olivera-Gómez. 1994b. Distribución y abundancia del manatí en la Reserva de la Biosfera Sian Ka'an, Quintana Roo, México: (1992–1994). Sian Ka'an Serie Documentos (2):55–59.

Morales-Vela, B. and L. D. Olivera-Gómez. 1996. Manatee rescue in Chiapas. P. 11 *in* Domning, D. P. (ed.). Sirenews, Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 25.

Morales-Vela, B, L. D. Olivera-Gómez, and P. Ramirez-Garcia. 1996. Conservacion de los manatíes en la region del Caribe de México y Belize. Informe técnico preparado por El Colegio del la Frontera Sur. ECOSUR Informe Técnico Numero MM01-CONACyT N9301-2017.

Morales-Vela, B. and L. D. Olivera-Gómez. 1997. Distribución del manatí (*Trichechus manatus*) en la costa norte y centro-norte del estado de Quintana Roo, México. Anales Instituto de Biologia, Universidad Nacional Autonoma de México, Serie Zoologia 68:153–164.

Morales-Vela, B., D. Olivera-Gómez, J. E. Reynolds III, and G. B. Rathbun. 2000. Distribution and habitat use by manatees (*Trichechus manatus manatus*) in Belize and Chetumal Bay, Mexico. Biological Conservation 95:67–75.

Morgan, G. S. and C. A. Woods. 1986. Extinction and the zoogeography of West Indian land mammals. Biological Journal of the Linnean Society 28:167–203.

Morison, S. E. 1942. Admiral of the Ocean Sea: A Life of Christopher Colombus. Little, Brown, Boston. 680 pp.

Mou Sue, L. L., D. H. Chen, R. K. Bonde, and T. J. O'Shea. 1990. Distribution and status of manatees (*Trichechus manatus*) in Panama. Marine Mammal Sciences 6(3):234–241.

Muizon, C. D. and D. P. Domning. 1985. The first records of fossil sirenians in the southeastern Pacific Ocean. Mammalia 46:257–258.

Murie, A. 1935. Mammals from Guatemala and British Honduras. Miscellaneous Publications of the Museum of Zoology University of Michigan 26:1–30.

Murray, J. A. (ed.). 1991. The Islands and the Sea: Five Centuries of Nature Writing from the Caribbean. Oxford University Press, New York.

Murray, S. P., S. A. Hsu, H. H. Roberts, E. H. Owens, and R. L. Crout. 1982. Physical processes and sedimentation on a broad, shallow bank. Estuarine, Coastal and Shelf Science 14:135–137.

Narganes-S., Y. M. 1982. Vertebrate Faunal Remains from Sorce, Vieques. M.S. thesis, University of Georgia, Athens.

National Science Research Council of Guyana and National Academy of Sciences, USA. 1973. Some prospects for aquatic weed management in Guyana. Workshop on Aquatic Weed Management and Utilization. Georgetown, Guyana.

National Science Research Council of Guyana. 1974. An international centre for manatee research. Georgetown, Guyana.

Natural Resources Conservation Authority. 1993. Jamaica — National report on the status of the West Indian manatee (*Trichechus manatus manatus*). Unpublished report prepared for UNEP. 1–8 + map.

Neish, W. D. 1896. The manatee, *Manatus australis*. Journal of the Institute of Jamaica 2:287–288.

Nietschmann, B. 1972. Hunting and fishing focus among the Moskito Indians, eastern Nicaragua. Human Ecology 1:41–67.

Nietschmann, B. 1979. Ecological change, inflation and migration in the far western Caribbean. Geographic Review 69:1–24.

Odell, D. K. 1979. Distribution and abundance of marine mammals in the waters of the Everglades National Park. National Park Service Biological Series 5:673–678.

Odell, D. K., J. E. Reynolds, and G. Waugh. 1978. New records of the West Indian manatee (*Trichechus manatus*) from the Bahama Islands. Biological Conservation 14:289–293.

O'Donnell, D. J. 1981. Manatees and Man in Central America. Ph.D. dissertation, Department of Geography, University of California, Los Angeles.

Ojeda C., M. M., J. Porras, H. Gonzalez, and J. Ojasti. 1993. Estado actual del manati antillano *Trichechus manatus* en Venezuela — informe nacional. Republica de Venezuela, Ministe del Ambiente y de los Recursos Naturales Renovables (M.A.R.N.R.). Unpublished report prepared for UNEP.

Ortega-Argueta, A. 1997. Uso de caletas y cenotes por el manatí del Caribe *Trichechus manatus manatus* (Linnaeus 1758) y el impacto del turismo en Quintana Roo, México. Tesis profesional, Facultad de Biología, Universidad Veracrusana, Xalapa, Veracruz, México.

Ortiz, R. M., G. A. J. Worthy, and D. S. MacKenzie. 1998. Osmoregulation in wild and captive West Indian manatees (*Trichechus manatus*). Physiological Zoology 71(4):449–457.

O'Shea, T. J. 1986. Mast foraging by West Indian manatees (*Trichechus manatus*). Journal of Mammalogy 67:183–185.

O'Shea, T. J. and B. B. Ackerman. 1995. Population biology of the Florida manatee: an overview. Pp. 280–288 *in* O'Shea, T. J., B. B. Ackerman, and H. F. Percival (eds.). Population Biology of the Florida Manatee (*Trichechus manatus latirostris*). National Biological Service, Information and Technology Report 1:1–289.

O'Shea, T. J. and W. C. Hartley. 1995. Reproduction and early-age survival of manatees at Blue Spring, Upper St. Johns River, Florida. Pp. 157–176 *in* O'Shea, T. J., B. B. Ackerman, and H. F. Percival (eds.). Population Biology of the Florida Manatee (*Trichechus manatus latirostris*). National Biological Service, Information and Technology Report 1:1–289.

O'Shea, T. J. and H. I. Kochman. 1990. Florida manatees: distribution, geographically referenced data sets and ecological and behavioral aspects of habitat use. Pp. 11–22 *in* Reynolds, J. E. III and K. D. Haddad (eds.). Report of the Workshop on Geographic Information Systems as an Aid to Managing Habitat for West Indian manatees in Florida and Georgia. Florida Marine Research Publications 49:1–57.

O'Shea, T. J. and C. A. Salisbury. 1991. Belize — a last stronghold for manatees in the Caribbean. Oryx 25:156–164.

O'Shea, T. J., C. A. Beck, R. K. Bonde, H. I. Kochman, and D. K. Odell. 1985. An analysis of manatee mortality patterns in Florida, 1976–81. Journal of Wildlife Management 49:1–11.

O'Shea, T. J., M. Correa-Viana, M. E. Ludlow, and J. G. Robinson. 1986. Distribution and status of the West Indian manatee in Venezuela. I.U.C.N. Contract Report 9132, Gland, Switzerland.

O'Shea, T. J., G. B. Rathbun, R. K. Bonde, C. D. Buergelt, and D. K. Odell. 1991. An epizootic of Florida manatees associated with a dinoflagellate bloom. Marine Mammal Science 7(2):165–179.

Ottenwalder, J. A. 1995. Situación del manatí en la República Dominicana. Dominican Business 32:41–44.

Ottenwalder, J. A. and Y. Leon. 1999. Resultados del análisis inicial de los surveys (entrevistas) de manatí conducidas en la costa de República Dominicana entre 1994 y 1996. Unpublished report.

Packard, J. M. 1981. Abundance, distribution and feeding habits of manatees (*Trichechus manatus*) wintering between St. Lucie and Palm Beach Inlets, Florida. U.S. Fish and Wildlife Service Contract Report No. 14-16-004-80-105.

Packard, J. M. 1983. Proposed Research/Management Plan for Crystal River manatees. Vol. I. Summary. Technical Report No. 7. Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville.

Packard, J. M. and P. M. Rose. 1985. Strategies for protection of non-exploited Sirenia populations. Fourth International Thelogical Congress. Abstract.

Packard, J. M. and O. F. Wetterqvist. 1986. Evaluation of manatee habitat systems on the northwestern Florida coast. Coastal Zone Management Journal 14:279–310.

Paludo, D. 1997. Estudos sobre a ecologia e conservação do peixe-boi marinho *Trichechus manatus manatus* no nordeste do Brasil. M.Sc. dissertation, Universidade Federal da Paraíba, João Pessoa, Brasil.

Phillips, R.C., R. L. Vadas, and N. Ogden. 1982. The marine algae and seagrasses of the Moskito Bank, Nicaragua. Aquatic Botany 13:187–195.

Powell, J. A. 1976. Jamaica trip report. U.S. Fish and Wildlife Service. Unpublished report.

Powell, J. A. 1978. Evidence of carnivory in manatees (*Trichechus manatus*). Journal of Mammalogy 59:442.

Powell, J. A. and D. F. Gicca. 1975. Colombia, South America trip report. U.S. Fish and Wildlife Service. Unpublished report.

Powell, J. A. and G. B. Rathbun. 1984. Distribution and abundance of manatees along the northern coast of the Gulf of Mexico. Northeast Gulf Science 7:1–28.

Powell, J. A. and J. C. Waldron. 1981. The manatee population in Blue Spring, Volusia County, Florida. Pp. 41–51 *in* Brownell, R. L. and K. Ralls (eds.). The West Indian Manatee in Florida. Florida Department of Natural Resources Tallahassee. Unpublished report. 155 pp.

Powell, J. A., D. W. Belitsky, and G. B. Rathbun. 1981. Status of the West Indian manatee (*Trichechus manatus*) in Puerto Rico. Journal of Mammalogy 62:642–646.

Price, W. A. 1954. Shorelines and coasts of the Gulf of Mexico. Pp. 39–65 *in* Galtsoff, P. S. (ed.). Gulf of Mexico — its origin, water and marine life. Fishery Bulletin of the Fish and Wildlife Service 89, Vol. 55:1–604.

Provancha, J. A. and C. R. Hall. 1991. Observations of associations between seagrass beds and manatees in east central Florida. Florida Scientist 54(2):87–98.

Quintana Rizzo, E. 1993. Estimación de la distribución y el tamaño poblacional del manati *Trichechus manatus* (Trichechidae-Sirenia) en Guatemala. M.Sc. thesis, Universidad de San Carlos de Guatemala, Facultad de Ciencias Quimicas y Farmacia, Guatemala. 80 pp.

Rathbun, G. B., R. K. Bonde, and D. Clay. 1982. The status of the West Indian manatee on the Atlantic coast north of Florida. Pp. 152–165 *in* Odom, R. R. and J. W. Guthrie (eds.). Proceedings of the Nongame and Endangered Wildlife Symposium. Georgia Department of Natural Resources, Technical Bulletin WL 5.

Rathbun, G. B., J. A. Powell, and G. Cruz. 1983a. Status of the West Indian manatee in Honduras. Biological Conservation 26:301–308.

Rathbun, G. B., J. A. Powell, and J. P. Reid. 1983b. Movements of manatees (*Trichechus manatus*) using power plant effluents in southern Florida. Florida Power and Light Co. Contract Report, Cooperative Agreement No. 14-16-0009-82-906.

Rathbun, G. B., T. Carr, N. M. Carr, and C. A. Woods. 1985a. The distribution of manatees and sea turtles in Puerto Rico. National Technical Information Service PB86-1518347AS, Springfield, Virginia.

Rathbun, G. B., C. A. Woods, and J. A. Ottenwalder. 1985b. The manatee in Haiti. Oryx 19:234–236.

Rathbun, G. B., J. P. Reid, and G. Carowan. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. Florida Marine Research Publications (48):1–33.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pp. 135–156 *in* O'Shea, T. J., B. B. Ackerman, and H. F. Percival (eds.). Population Biology of the Florida Manatee (*Trichechus manatus latirostris*). National Biological Service, Information and Technology Report 1.

Ray, C. E. 1960. The manatee in the Lesser Antilles. Journal of Mammology 41:412–413.

Reid, J. P. 1996. Chessie the manatee: from Florida to Rhode Island. Argos Newsletter No. 51:13.

Reid, J. P. 2000. Florida manatee now resident in the Bahamas. Pp. 7–8 *in* Domning, D. P. (ed.). Sirenews, Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 33.

Reid, J. P. and G. B. Rathbun. 1986. 1985 manatee identification catalog update. U.S. Fish and Wildlife Service and Florida Power and Light Co. Unpublished report.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

Reynolds, J. E., III. 1995. Florida manatee population biology: research progress, infrastructure and applications for conservation and management. Pp. 6–12 *in* O'Shea, T. J., B. B. Ackerman, and H. F. Percival (eds.). Population Biology of the Florida Manatee (*Trichechus manatus latirostris*). National Biological Service, Information and Technology Report 1:1–289.

Reynolds, J. E., III. 1999. Efforts to conserve manatees. Pp. 267–295 *in* Twiss, J. R., Jr. and R. R. Reeves (eds.). Conservation and Management of Marine Mammals. Smithsonian Institution Press, Washington, D.C.

Reynolds, J. E., III. 2000. Distribution and abundance of Florida manatees (*Trichechus manatus latirostris*) around selected power plants following winter cold fronts: 1999–2000. Florida Power and Light Company, Order Number: B93135-00139.

Reynolds, J. E., III and J. C. Ferguson. 1984. Implications of the presence of manatees (*Trichechus manatus*) near the Dry Tortugas Islands. Florida Scientist 47:187–189.

Reynolds, J. E., III and C. J. Gluckman. 1988. Protection of West Indian manatees (*Trichechus manatus*) in Florida. Final Report to the U.S. Marine Mammal Commission. NTIS Report PB88-222922/AS:1–85.

Reynolds, J. E., III and J. R. Wilcox. 1994. Observations of Florida manatees (*Trichechus manatus latirostris*) around selected power plants in winter. Marine Mammal Science 10(2):163–177.

Reynolds, J. E., III, W. A. Szelistowski, and M. A. Leon. 1995. Status and conservation of manatees *Trichechus manatus manatus* in Costa Rica. Biological Conservation 71:193–196.

Rose, P. M. and S. P. McCutcheon. 1980. Manatees (*Trichechus manatus*): abundance and distribution in and around several Florida power plant effluents. Florida Power and Light Co. Contract 31534-86626.

Rosen, D. E. 1975. A vicariance model of Caribbean biogeography. Systematic Zoology 24:431–464.

Roth, V. 1953. Notes and observations on animal life in British Guiana. Daily Chronicle, Ltd., Guiana Edition No. 3:69–73. Georgetown, British Guiana.

Rouse, I. 1964. Prehistory of the West Indies. Science 144:499–513.

Rouse, I. 1986. Migrations in Prehistory. Yale University Press, New Haven, Connecticut.

Ruschi, A. 1965. Lista dos mamíferos do estado do Espírito Santo. Boletim do Museu de Biología No. 24A:29.

Schad, R. C., G. Montgomery, and D. Chancellor. 1981. La distribución y frequencia del manatí en el Lago Gatun y en el Canal de Panama. ConCiencia 8:1–4.

Schiro, A. J., L. P. May, and D. C. Fertl. 1996. Manatee occurrence in the northwestern Gulf of Mexico. Journal of the American Cetacean Society 30(1).

Schwartz, F. J. 1995. Florida manatees, *Trichechus manatus* (Sirenia: Trichechidae) in North Carolina 1919–1994. Brimleyana 22:53–60.

Secretaria de Estado de Agricultura, Republica Dominicana 1993. El estado del manatí en l Republica Dominicana. Unpublished report to UNEP:1–36 + appendices.

Shane, S. H. 1983. Abundance, distribution and movements of manatees (*Trichechus manatus*) in Brevard County, Florida. Bulletin of Marine Science 33:1–9.

Shane, S. H. 1984. Manatee use of power plant effluents in Brevard County, Florida. Florida Scientist 47:180–187.

Shaul, W. and A. Haynes. 1986. Manatees and their struggle to survive. Jamaica Journal 19:29–36.

Simpson, G. G. 1932. Fossil Sirenia of Florida and the evolution of the Sirenia. Bulletin of the American Museum of Natural History 59:419–503.

Sloane, H. 1725. A voyage to the islands Madera, Barbados, Nieves, St. Christophers and Jamaica, with the natural history of the herbs and trees, four-footed beasts, fishes, birds, insects, reptiles, &c. of the last of those islands. Vol. 2. Printed by B. M. for the author, London.

Smethurst, D. and B. Nietschmann. 1999. The distribution of manatees (*Trichechus manatus*) in the coastal waterways of Tortuguero, Costa Rica. Biological Conservation 89:267–274.

Smith, K. N. 1993. Manatee habitat and human-related threats to seagrass in Florida: a review. Report of the Department of Environmental Protection, Tallahassee, Florida:1–38.

Steininger, F. F. 1986. Erste Ergebnisse über Untersuchungen zu Ernährungsstrategien des Arawaken-Siedlungsplatzes Pointe der Caille, NNW Vieux Fort, St. Lucia, West Indies. Mitteilungen der Prähistorischen Kommission Österreichischen Akademie der Wissenshaften 23:37–50.

Strong, W. D. 1935. Archaeological investigations in the Bay Islands, Spanish Honduras. Smithsonian Miscellaneous Collection 92:1–176.

Terrell, J. B. and D. E. Canfield, Jr. 1996. Evaluation of the effects of nutrient removal and the "Storm of the Century" on submersed vegetation in Kings Bay – Crystal River, Florida. Journal of Lake and Reservoir Management 12(5):394–403.

Thornback, J. and M. Jenkins 1982. Caribbean manatee. Pp. 429–438 *in* Red Data Book. Vol. 1. Mammalia. International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.

Toppin-Allahar, C. 1993. The law and the conservation of the manatee. Unpublished report for the Trinidad and Tobago Field Naturalists Club.

True, F. W. 1884. The Sirenians or seacows. The Fisheries and Fishery Industries of the United States, Sec. 1, Natural History of Useful Aquatic Animals, Part 1, Art. C, pp. 114–136.

Trumbull, S. 1949. Sea cows making comeback. Audubon Magazine 51:337.

Vaughan, C. 1983. A report on dense forest habitat for endangered wildlife species in Costa Rica. U.S. Department of Interior Contract No. 14-16-0009-79-055 and National University of Costa Rica Research Project No. 782085. Unpublished report.

Viquez, D. 1993. Situación del manati (*Trichechus manatus*) en la Republica de Panama – Informe Nacional. Ministe de Planificación y Política Económica. Comision Nacional del Medio Ambiente, Panama.

Watters, D. R., E. J. Reitz, D. W. Steadman, and G. K. Pregill. 1984. Vertebrates from archaeological sites on Barbuda, West Indies. Annals of the Carnegie Museum 53:383–412.

Whitehead, P. J. P. 1977. The former southern distribution of New World manatees (*Trichechus* spp.). Biological Journal of the Linnean Society 9:165–189.

Wilson, D. E. 1974. Status report on manatees of Costa Rica. U.S. Fish and Wildlife Service. Unpublished report.

Wing, E. S. 1967. Aboriginal fishing in the Windward Islands. Proceedings of the Second International Congress of Pre-Columbian Cultures of the Lesser Antilles:103–107.

Wing, E. S. and E. J. Reitz. 1982. Prehistoric fishing communities of the Caribbean. Journal of New World Archaeology 5:13–32.

Wing, E. S. and S. Scudder. 1980. Use of animals by the prehistoric inhabitants on St. Kitts, West Indies. Proceedings of the Eighth International Congress of the Pre-Columbian Cultures of the Lesser Antilles. Arizona State University Anthropological Research Papers No. 22:237–245.

Wing, E. S., C. Hoffman, and C. Ray. 1968. Vertebrate remains from Indian sites on Antigua, West Indies. Caribbean Journal of Science 8:123–139.

Woods, C. A. and J. A. Ottenwalder. 1992. The natural history of southern Haiti. Florida Museum of Natural History. Prepared for USAID/Haiti under contract number 521-0191-A-00-7107:1-211.

Wotzkow, C. 1990. Distribution and status of manatees in Cuba. Pp. 5–6 *in* Domning, D. P. (ed.). Sirenews, Newsletter of the IUCN/SSC Sirenia Specialist Group, No. 13.

Wright, S. D., B. B. Ackerman, R. K. Bonde, C. A. Beck, and D. J. Banowetz. 1995. Analysis of watercraft-related mortality of manatees in Florida, 1979–1991. Pp. 259–268 *in* O'Shea, T. J., B. B. Ackerman, and H. F. Percival (eds.). Population Biology of the Florida Manatee (*Trichechus manatus latirostris*). Information and Technology Report 1, National Biological Service, Washington, D.C. 1–289.

Zoodsma, B. J. 1991. Distribution and Behavioral Ecology of Manatees in Southeastern Georgia. M.S. thesis, University of Florida, Gainesville.