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INFLUENCE OF POWER PLANTS AND OTHER WARM-WATER REFUGES ON FLORIDA MANATEES

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ABSTRACT

Because of limited tolerance to cold, most Florida manatees survive cold winter periods by aggregating at warm-water discharges from power plants and natural springs in central and northern Florida. Many power plants used by manatees may soon be retired. When this occurs, some people assume manatees will move to warmer areas in southern Florida; others fear they will stay near retired plants and sustain high levels of cold-related deaths causing a decline in abundance. To assess these possibilities, we examine warm-water habitats, population structure and movement, cold-related deaths, and information on possible historical manatee distribution. Winter water temperatures even in southernmost Florida periodically fall below manatee tolerance levels. To survive such periods, manatees use two types of warm-water refuges: warm-water discharges, and passive thermal basins that cool slowly, thereby temporarily retaining warm temperatures. During the coldest periods, perhaps 60% of all manatees use 10 power plants and 15% use four natural springs; most others use thermal basins in southern Florida. Site fidelity to these refuges appears to be the principal factor segregating manatees into at least four subpopulations. Since 1986, rates of cold-related deaths in southernmost Florida (10.0%) have exceeded those in areas with natural springs in central and northern Florida (8.8%). Our findings suggest that warm-water springs in northern Florida offer better winter habitat than thermal basins in southern Florida and are better able to support large numbers of manatees. Although evidence is scant, we suggest that manatees historically overwintered principally at northern springs, but that Pre-Columbian and European hunting restricted their winter range to southernmost Florida by the early 1900s. We also suggest that southernmost Florida may not be able to sustain a large influx of displaced of manatees in the absence of power plants, and that warm-water springs in northern Florida should be considered the most important source of natural warm-water habitat.

Key words: Florida manatees, *Trichechus manatus latirostris*, habitat protection, warm-water refuges, Florida springs, power plants, zooarcheology, conservation, risk assessment.

Florida manatees (*Trichechus manatus latirostris*), a subspecies of West Indian manatee (Domning and Hayek 1986), occupy the northern limit of the species' range and occur only in rivers and coastal habitats in the southeastern United States. Because of a limited tolerance to cold (Irvine 1983, Bossart *et al.* 2002), water temperature is a critical factor determining their distribution. Their current winter range is limited almost exclusively to the lower two-thirds of the Florida Peninsula. As water temperatures fall below 18°–20°C in winter, most manatees retreat to confined warm-water refuges formed by thermal discharges from power plant cooling systems or natural warm-water springs that typically remain ≥20°–22°C. As temperatures rise in spring, manatees disperse throughout Florida, with some ranging north along the Atlantic coast to Georgia and the Carolinas, and west along the Gulf of Mexico coast as far as Texas (Lefebvre *et al.* 2001).

Based on archeological and historical evidence, O'Shea (1988) concluded that Florida manatees are as widespread now as they ever were. However, it also is widely accepted that thermal discharges from power plants built on Florida's east and west coasts before the early 1970s caused a northward expansion in their winter range, which was previously limited to southernmost Florida. Assessments of their historic winter range have relied largely on the first detailed accounts of Florida manatees by Moore (1951*a*, *b*) before most power plants were built. He concluded that their winter range did not extend north of Sebastian Inlet on the Atlantic coast (about halfway down the Florida Peninsula), or Charlotte Harbor on the Gulf of Mexico coast (about two-thirds of the way down the peninsula). An understanding of the availability of natural winter habitat for manatees both at present and historically is a crucial management issue, because large numbers of manatees now rely on power plants in central Florida that are reaching the end of their planned operational lives (Laist and Reynolds, in press). Some people believe that, without those outfalls, manatees would simply move farther south to warmer parts of the state where their assumed historical winter range, as described by Moore, occurs. However, if natural winter habitat in southern Florida is not adequate to sustain large numbers of manatees and alternative warm-water habitats are not available, then the elimination of power plant outfalls could drastically reduce their available winter habitat and precipitate a substantial decline in manatee abundance. In addition, even if such habitat was available, it is not clear manatees would be able to find and move to alternative sites. In this regard, Laist and Reynolds (in press) have reviewed information on manatee responses to past shut-downs of industrial outfalls used as warm-water refuges and concluded that many manatees now accustomed to overwintering at power plants may remain near those sites after discharges are terminated and sustain high levels of cold stress-related deaths.

The availability of natural warm-water habitat and the extent to which power plant closures could affect manatee abundance is directly relevant to ongoing deliberations about the level of protection Florida manatees should receive under state and federal law. The Florida Fish and Wildlife Conservation Commission currently is considering the merits of down-listing Florida manatees from "endangered" to "threatened" under state law (Marine Mammal Commission 2003) and similar action is possible at the federal level based on the results of a Florida manatee status review planned by the U.S. Fish and Wildlife Service under provisions of the Endangered Species Act. Given the fundamental importance of warm-water habitat for winter survival of manatees, it is essential that such decisions carefully consider the availability of winter habitat and the effects of impending power plant closures on future manatee abundance. Decisions to relax protection efforts would be short sighted at best and possibly seriously set back recovery efforts.

With the potential loss of major warm-water refuges imminent and decisions on responsive management actions likely to be determining factors affecting the long-term distribution and status of Florida manatees, a careful examination is needed to assess assumptions that southernmost Florida comprises the core of historical winter manatee range and that the large numbers of manatees now using power plants would be able to find and survive in that area. The key questions we address here include:

(1) What is the historical evidence for manatees occupying their current winter range? Is the current distribution a recent, or perhaps artificial phenomenon?
(2) If power plants are shut down or spring flows are lost or significantly reduced, will manatees move to warmer areas in south Florida? If so, will there be adequate warm water and other resources to support them. If not, what are the possible or likely impacts to Florida's manatees? What are some possible mitigation options?

To help examine these questions and assess the availability of natural warm-water habitat for manatees as power plant discharges disappear in coming years, we review information on (1) manatee thermoregulatory needs, (2) available warm-water habitat, (3) cold-related manatee deaths, (4) manatee movement patterns and population structure, and (5) possible past effects of human exploitation and climate on historical manatee distribution and winter habitat.

Methods

To determine manatee thermoregulatory needs, we examined published literature on manatee thermal tolerances and effects of cold on manatee health. We then examined water temperatures in winter manatee habitats. Water temperatures in southernmost Florida were obtained from U.S. Geological Survey temperature probes established at three sites along Florida's southern tip as part of the Comprehensive Everglades Restoration Program. Two sites were along coastal mangrove habitat in water about 1.5–1.8 m deep—one in the North River off Whitewater Bay on the western side of Florida's southern tip; the other in Joe Bay on the eastern side. The third site was in a lake along the Taylor River 3.2 km up stream of the coastal mangrove fringe in Joe Bay in water about 1.4 m deep. Temperature probes at the first two sites were 0.6–0.8 m below the surface and the probe at the Taylor River site was about 0.5–0.6 m below the surface. Although the probes recorded water temperatures at 15-min intervals year-round, we limited our examination to hourly temperatures recorded from early December through the end of February. We obtained data for the winters of 2001–2002 and 2002–2003, which included a year with some of the coldest water temperatures recorded since the first probes were deployed in 1995.

Winter water temperatures at power plant outfalls used by manatees were obtained directly from utility operators. Power plant operators are required to record outfall temperatures at 15-min intervals. Outfall temperatures at individual sites can vary greatly depending on physical configuration of outfall basins, the location and number of temperature probes, variable cooling water intake temperatures, variable plant heat outputs, and other factors. Because we were interested in the general temperatures that attract and support manatees over time, we asked plant operators to provide us with typical outfall temperatures in the core of the area used by manatees between December and March. Because detailed systematic efforts to characterize thermal plumes over time have not been undertaken and were beyond the scope of this review, reported values are only crude indicators of outfall temperatures and not comparable between sites. We also asked plant operators whether their electric generating units ran continuously or intermittently through winter months. Temperatures of natural springs used by manatees were obtained from published literature based on temperature probes in the spring discharge vents.

To assess the number of manatees using warm-water habitats, we reviewed published and unpublished counts at individual warm-water discharges and thermal basins to determine the maximum single count at major overwintering sites. We also reviewed unpublished data from a statewide manatee count by the Florida Fish and Wildlife Research Institute on 5–6 January 2001. This survey produced the highest single manatee count in Florida to date. To avoid double counting individual manatees during this survey, east coast habitats were counted on 5 January and west coast habitats were counted on 6 January. The data examined had been aggregated into total counts for specific warm-water habitats by county. We calculated the percentage of the total count obtained at individual power plants, warm-water springs, and all other areas for both the east and west coasts of Florida, and also summed the counts and percentages by type of winter habitat.

To compare the ability of different types of warm-water habitats to sustain manatees in winter, we reviewed unpublished data on cold stress-related manatee deaths recorded by the manatee salvage and necropsy program operated by the Florida Institute. We summed the number of deaths ascribed to cold-stress and total deaths due to all causes for the months of December through March from 1986 through 2003 in counties where manatees rely exclusively or principally on natural springs, power plants, and thermal basins. For selected counties, we calculated the percentage of total manatee mortality caused by cold stress during winter months.

To determine manatee population structure and site-fidelity to particular warm-water habitats, we reviewed published literature and government agency reports from studies of manatee movements based on telemetry and photo-identification studies. We also considered published results of studies to assess genetic diversity within the Florida manatee population and genetic variation among regions of Florida to assess manatee movements between Florida regions and look for possible signs of past population depletion.

To assess historical trends of manatee distribution and winter habitat use patterns, we examined published and unpublished information on the occurrence of manatee remains at archeological sites and published descriptions of paleoclimatic conditions.

Results

Thermoregulatory Requirements

Manatees are poorly adapted for survival in cold environments for several reasons (O'Shea 1988); they have a low basal metabolism, they subsist on low-energy food, they have a limited capacity for thermogenesis, and they have a high thermal conductance (Irvine 1983). Extended exposure to cold temperatures causes a cascade of clinical signs and chronic disease processes called "cold-stress syndrome" that can be lethal (O'Shea *et al.* 1985, Bossart *et al.* 2002). These signs and processes include emaciation, depletion of fat reserves, skin lesions, and degeneration of heart tissue. Calves and juveniles, which have a greater surface-to-volume ratio and lose heat more rapidly than larger adults, are more susceptible to cold stress (O'Shea *et al.* 1985, Bossart 2001). However, the frequency of cold stress-related calf deaths is low compared to juveniles. High rates of cold stress among juveniles compared to calves may be due to one or a combination of physiological and behavioral factors that could include a calf's access to energy-rich milk during nursing, thicker subcutaneous fat layers around the umbilical area, or the accompaniment of calves with mothers, who are more experienced than recently independent juveniles in finding and using warm-water habitats.

Both absolute temperature and the length of time exposed to cold are important factors in causing cold-related manatee deaths. Exposure to severe cold can cause rapid death due to acute hypothermia, whereas sustained exposure to somewhat higher temperatures can bring about death more slowly.[1] Hartman (1979) observed that manatees can survive short periods of time (*e.g.*, less than an hour) in water as cold as 13°C, but O'Shea *et al.* (1985) noted that prolonged exposure to temperatures of 15°C can be lethal. Although it is believed that manatees require water warmer than about 20°C to survive (Irvine 1983, Shane 1984, O'Shea 1988), some manatees can survive relatively long periods in water 17°–18°C (Glaser and Reynolds 2003). Deutsch (2000) reports an adult female and calf tracked over a two-week migration south in Georgia and northeastern Florida through waters colder than 15°C. The female survived but the calf did not. As temperatures decline below 17°–20°C, survival times presumably decrease; however, precise estimates of the length of time manatees can survive at different temperatures are not available and likely vary by size, age class, and perhaps acclimation to cold.

Warm-Water Habitats

Throughout Florida, river and estuarine water temperatures routinely drop below 19°–20°C in winter (Irvine 1983). This is true even in southernmost Florida. Hartman (1974) reported minimum winter water temperatures of 14°C and 13°C at Miami and Key West, respectively, with mean minimum winter temperatures of 18°C in both areas (Hartman 1979). Temperatures recorded more recently at three typical manatee habitats on the peninsula's southern tip in the winters of 2001–2002 and 2002–2003 reveal even colder temperatures. Although up to 40 km apart, temperatures at all three sites (Fig. 1) dropped below 20°C on most days between mid-December 2001 and early February 2002, remained below 17°C for all but a brief period over 12 d in late January 2002, and fell to a minimum 11°–15°C on six days during the latter period. To survive cold periods, most manatees retreat to warm-water refuges that generally remain $\geq$19°–20°C. Manatees appear to use two distinct functional types of warm-water refuges: warm-water discharges and passive thermal basins.

[1] Worthy, G. A. J., T. A. Miculka and S. D. Wright. 2000. Manatee response to cold: how cold is too cold? *In* Florida manatees and warm water: Proceedings of the warm-water workshop. Jupiter, Florida, 24–25 August 1999. U.S. Fish and Wildlife Service. Jacksonville, FL. Multi pp.

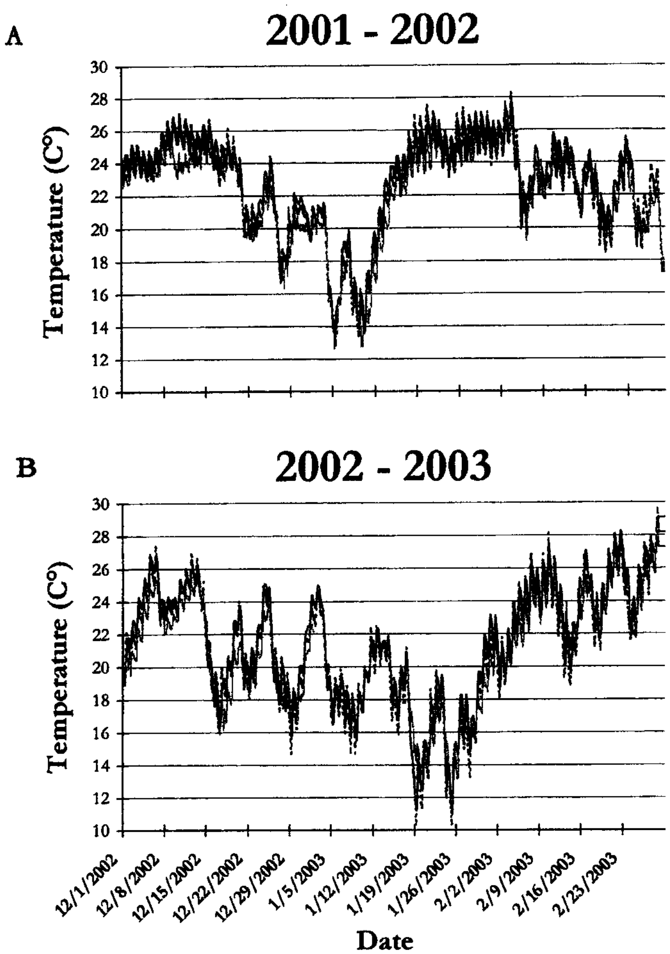

Figure 1. Hourly water temperatures at three sites in southernmost Florida (North River in Whitewater Bay = solid gray, Taylor River upstream off Joe Bay = solid black, and Joe Bay = dotted) between 1 December and 28 February during the winters of 2001–02 (a) and 2002–03 (b) (U.S. Geological Survey, unpublished data).

Warm-water discharges—Warm-water discharges are localized areas rarely larger than a few acres in size and often covering only a few hundred square meters where water usually warmer than 19°–20°C continuously flows from natural springs or industrial outfalls (usually power plants). Currently, there are 14 warm-water discharges with winter counts of at least 50 manatees; all are in Florida and most are in the central third of the Florida Peninsula (Table 1; Fig. 2). Four are natural warm-water springs and 10 are power plant outfalls. The discharges used by the largest number of manatees include natural springs in Kings Bay at the head of the Crystal River, with recent maximum counts of about 300, two power plants with maximum counts exceeding 400, and one power plant with a count exceeding 500. In January 2001, when a record high statewide manatee count of 3,276 manatees was made, nearly three-fourths of all animals were

Table 1. Warm-water refuges in Florida with information on location by county, date built, maximum one-day winter counts of 50 or more manatees as of August, 2003, and typical winter water temperatures.

Warm water refuge	Location (county)	Date built	Maximum 1-d count # (year)	Typical winter water temperature[a]
East Coast				
Blue Spring	Volusia	—	144 (2004)[d]	22.5°C
Reliant Energy Power Plant	Brevard	1959	241 (1997)[e]	14–22°C[b]
Cape Canaveral Power Plant	Brevard	1965	510 (1998)[e]	19–20°C
Vero Beach Power Plant	Indian River	1961	65 (1999)[f]	14–23°C[b]
Fort Pierce Power Plant	St. Lucie	1945[c]	99 (1996)[f]	15–20°C[b]
Riviera Beach Power Plant	Palm Beach	1946	409 (2001)[f]	26°C
Fort Lauderdale Power Plant	Broward	1926	221 (2003)[e]	26°C
Port Everglades Power Plant	Broward	1960	290 (2001)[f]	25°C
West Coast				
Crystal River Springs	Citrus	—		
Homosassa Springs	Citrus	—		
Bartow Power Plant	Pinellas	1958	301 (2000)[g]	23.7°C
Big Bend Power Plant	Hillsborough	1970	123 (1999)[g]	22.2°C
Warm Mineral Springs	Sarasota	—	102 (1999)[e]	18–23°C[b]
Fort Myers Power Plant	Lee	1958	333 (2003)[e]	21–27°C
			74 (2003)[h]	24–27°C
			434 (1996)[f]	20°C

[a] Temperatures of power plant outfalls were provided by plant operators. Outfall temperatures vary depending on weather, plant operating levels, and other factors that vary within and between years. The temperatures listed here reflect typical temperatures provided by utility operators, rather than maximum or minimum limits and are only broadly indicative of outfall temperatures, Temperatures of warm-water springs are from Rosenau *et al.* 1977.

[b] Power plant operates intermittently during winter months.

[c] The H. D. King Power Plant at Ft. Myers was initially built in 1912, but operation of the once-through cooling system discharging heated water was not added until 1945.

[d] Personal communication from Wayne Hartley and Richard Harris, Park Rangers, Blue Spring State Park, 2100 West French Avenue, Orange City, FL 32763.

[e] Unpublished data from state-wide aerial manatee surveys, 1991–2003, Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute, 100 8th Ave., SE, St. Petersburg, FL 33701.

[f] Reynolds III, J. E. 1983 to 2003. Distribution and abundance of Florida manatees (*Trichechus manatus latirostris*) around selected power plants following winter cold fronts. A series of annual survey reports for the winters of 1982–83 to 2002–03. Prepared for Florida Power & Light Co., Environmental Services Department, Juno Beach, FL.

[g] Personal Communication, Joyce Kleen, Biologist, Crystal River National Wildlife Refuge, U.S. Fish and Wildlife Service, Crystal River, FL 34429.

[h] Personal communication from Lucy Keith, Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute, 100 8th Avenue, SE, St. Petersburg, FL 33701.

found at these 14 discharges, including 59.3% at the ten power plants and 14.8% at the four natural warm-water springs (Table 2).

There are also numerous secondary warm-water discharges used by small numbers of manatees (*i.e.*, usually fewer than 10 at any one time). Some of these

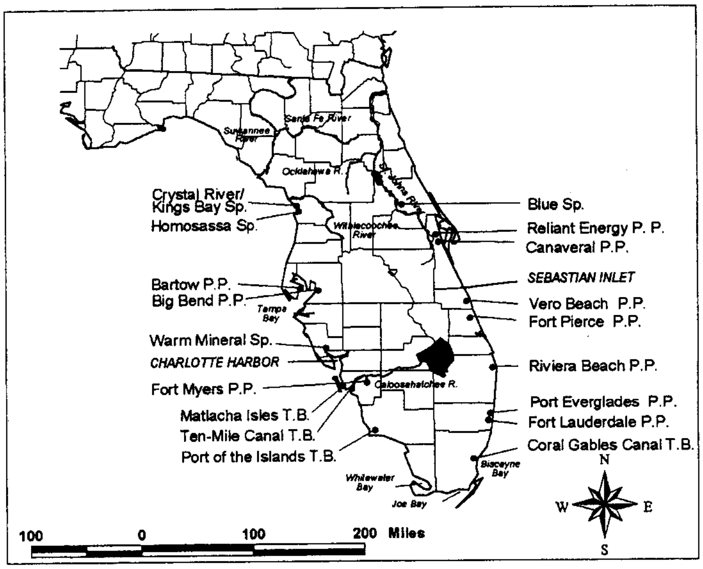

Figure 2. Location of major warm-water discharges (power plants = P.P. and springs = Sp.) and passive thermal basins (T.B.) with at least one winter count of 50 or more or more manatees (Marine Mammal Commission 2003 and Florida Wildlife Research Institute, unpublished data), and the northern boundaries of winter manatee distribution in the early 1950s (Moore 1951*a*).

refuges are natural springs; others are industrial outfalls, principally power plants and paper mills, with small discharges. Manatees also occasionally use sewage outfalls, whose effluents are not heated but may be slightly warmer than surrounding waters. Most secondary refuges appear to be temporary stopover points used during spring and fall migrations to and from major warm-water refuges (Deutsch *et al.* 2000, 2003).

Florida has 33 first-order magnitude artesian springs (*i.e.*, discharges >100 ft^3/s [2.83 m^3/s]) and about 200 second-order magnitude springs (*i.e.*, discharges between 10 and 100 ft^3/s [0.28 and 2.83 m^3/s]) (Scott *et al.* 2002). They typically discharge water at nearly constant temperatures year round. Temperatures vary from spring to spring depending on factors, such as the amount of solar radiation water receives before filtering through porous rock into the aquifer, and the aquifer's depth, volume, and flow rate. In general, springs in the northern, central, and southern Florida discharge water at 10°–23°C, 22°–26°C, and 27°–31°C, respectively (Rosenau *et al.* 1977). Although all of Florida's first-order springs discharge water between 19° and 23°C, those now used by large numbers of overwintering manatees are at least 22°C. In addition to the three first-order springs now used as major warm-water refuges by manatees, there are 17 other first-order springs, all in north-central Florida, with water temperatures of ≥22°C (Fig. 3). Most springs in southern Florida are water-table springs whose flow rates and temperatures are more variable than those of artesian springs and depend largely on seasonal rainfall and soil saturation.

Although only four springs are now used regularly by large numbers of overwintering manatees, human modifications have limited or precluded manatee

Table 2. Counts of manatees at major warm-water discharges on the East and West coasts of Florida during a statewide survey 5–6 January 2001 (Florida Fish and Wildlife Research Institute, unpublished data)[a].

Location	# of Manatees count	Percent of coastal count	Percent total count
East Coast			
Blue Spring	112	7.4	3.4
Reliant Energy Power Plant	0	0	0
Cape Canaveral Power Plant	457	30.0	13.9
Vero Beach Power Plant	3	0.2	0.1
Fort Pierce Power Plant	19	1.3	0.6
Riviera Beach Power Plant	409	26.9	12.5
Fort Lauderdale Power Plant	144	9.5	4.4
Fort Everglades Power Plant	148	9.7	4.5
Total: All major East Coast discharges	1,292	85.0	39.4
Total: Other East Coast areas	228	15.0	7.0
Total: East Coast	1,520	100.0	46.4
West Coast			
Kings Bay	296	16.9	9.0
Homosassa Springs/Blue Waters	50	2.8	1.5
Bartow Power Plant	10	0.6	0.3
Big Bend Power Plant	316	18.0	9.7
Warm Mineral Springs	30	1.7	0.9
Fort Myers Power Plant	434	24.7	13.3
Total: All major West Coast discharges	1,136	64.7	34.7
Total: Other West Coast areas	620	35.3	18.9
Total: West Coast	1,756	100.0	53.6
TOTALS			
Total: All major discharges	2,428	—	74.1
Total: All other areas	848	—	25.9
Total count	3,276	—	100.0

[a] Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute, 100 Eighth Avenue, S.E., St. Petersburg, FL 33701.

use of other springs that may have been used more frequently in the past. Constraints on current use include locks, dams, fences, and silted in spring runs that prevent or restrict manatee access. For example, Silver Spring on the Oklawaha River (a tributary of the St. Johns River) is blocked by a downstream dam, Rainbow Spring on the Withlacoochee River is obstructed by a downstream dam and lock, and the main boil at Homosassa Springs is blocked by a fence across the spring run. Other springs no longer exist because of ground water pumping for domestic, agricultural, and industrial purposes or simply being capped to allow development (Rosenau *et al.* 1977). The average annual flow rate at Blue Spring declined by 13% between the periods 1932–1975 and 1985–1994,[2] and Vergera (1994) predicted it

[2] Suczy, P., R. Hupalo and R. Freeman. 1998. Minimum flow determination for Blue Spring, Volusia County: The relationship between ground water discharge and winter refuge for manatees. St. Johns River Water Management District. Palatka, FL. 73 pp.

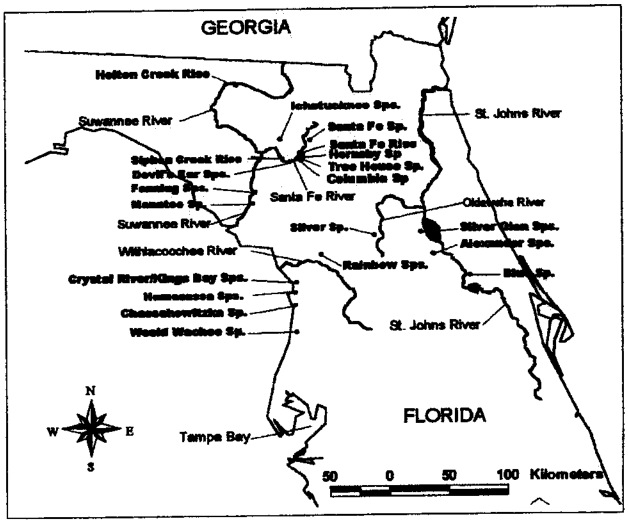

Figure 3. Location of Florida's first-order magnitude (*discharges* >100 ft^3/s [2.83 m^3/s]) artesian springs with water temperatures 22°C or higher (Scott *et al.* 2002).

could decrease another 16% by 2010 if expected increases in ground water use are not controlled.

Still other springs may have been available to manatees several thousand years ago when sea levels were lower. Rosenau *et al.* (1977) list 16 submarine springs, most of which are in the Gulf of Mexico off Wakulla and Taylor counties in northwestern Florida and between Tampa Bay and Crystal River; two are located along the Atlantic coast off St. Augustine in northeastern Florida. Those farthest off shore include Mud Hole Spring 24 km northwest of Naples in water 13 m deep off southwestern Florida, Ray Hole Spring 37 km southeast of Apalachee Bay in water 12 m deep off northwestern Florida, and Red Snapper Sink 35 km southeast of St. Augustine in water 27 m deep.

Passive thermal basins—Passive thermal basins are confined areas that retain heat from direct solar radiation or biodegradation of organic deposits (Smith 2000). They usually include dredged basins or naturally deep holes where circulation patterns and thermoclines delay cooling and thereby create temporary pockets of relatively warm water (Smith 2000). Passive thermal basins differ from warm-water refuges in that they lack a steady inflow of warm water. As such, their ability to retain elevated temperatures during long or intense cold periods is far more limited than warm-water refuges.

In the central third of the Florida Peninsula, manatees tend to use thermal basins as migratory stopover sites during relatively brief or mild cold periods (Deutsch *et al.* 2000, 2002, 2003). However, in the southern third of Florida where winter temperatures are milder, thermal basins can serve as functional equivalents to warm-water discharges. At least four of these sites have had winter counts of 50 or more manatees (Fig. 2). The site with the highest winter count of manatees is a dredged canal at Port of the Islands on Florida's southwestern coast, where up to 240 manatees have been counted during cold periods (Florida Marine Research Institute, unpublished data). The other three thermal basins include Matlacha Isles,

Table 3. Proportion and number of cold-related deaths in winter months for selected counties in Florida from December 1986 through March 2004 (Florida Fish and Wildlife Research Institute, unpublished data).

	Percentage of cold-stress deaths (no./total deaths)				
County	December	January	February	March	Four month total
Counties with major springs					
Citrus	10% (1/10)	10% (1/10)	17% (3/17)	0% (0/21)	9% (5/58)
Volusia (St. Johns R. only)	0% (0/0)	0% (0/3)	33% (1/3)	0% (0/4)	10% (1/10)
Counties with power plants					
Brevard	8% (4/52)	40% (37/93)	17% (11/63)	6% (4/67)	20% (56/275)
Palm Beach	15% (2/13)	0% (0/22)	7% (2/28)	9% (1/11)	7% (5/74)
Broward	13% (1/8)	10% (2/20)	0% (0/18)	8% (1/12)	7% (4/58)
Hillsborough	23% (3/13)	0% (0/11)	0% (0/7)	0% (0/18)	6% (3/49)
Pinellas	0% (0/6)	57% (4/7)	29% (2/7)	12% (2/17)	22% (8/37)
Lee	4% (2/52)	24% (20/85)	15% (10/66)	1% (1/124)	10% (33/327)
Southernmost counties with no springs or power plants					
Dade	0% (0/16)	5% (1/20)	0% (0/18)	0% (0/18)	1% (1/72)
Monroe	8% (1/13)	19% (4/21)	0% (0/22)	0% (0/15)	7% (5/71)
Collier	9% (4/44)	22% (8/37)	32% (12/38)	3% (2/59)	15% (26/178)

a canal system off Matlacha Pass in Lee County with a count of 125 (Mote Marine Laboratory, unpublished data), the so-called "Pit," a 12-m deep basin along Ten-mile Canal off the lower Caloosahatchee River also in Lee County with a count of 50 (Mote Marine Laboratory, unpublished data), and Coral Gables Canal south of Miami in Dade County with a count of 56 (Florida Wildlife Research Institute, unpublished data). During the January 2001 manatee survey, 6.5% of the total count was made in two southernmost Florida counties (*i.e.*, Dade and Monroe), where thermal basins are the primary available warm-water habitats. Because the locations of thermal basins are poorly known and because manatees using them may spend most of their time at depth beneath cold surface water layers in turbid water, the overall percentage of manatees seen using thermal basins during aerial surveys almost certainly underestimates the actual percentage using them.

Cold-Related Deaths

Necropsies of manatee carcasses recovered in winter suggest that thermal basins in southernmost Florida provide somewhat less protection against cold stress than natural warm-water springs in more northern parts of the state (Table 3) . In the three southernmost counties which lack warm water discharges formed by power plants or major warm water springs (*i.e.*, Dade, Monroe, and Collier), cold stress is listed as the cause of death for 10.0% of total mortality (32 of 321) during winter months from December 1986 through March 2004. In the two northern counties with natural warm-water springs (*i.e.*, Citrus and the St. Johns River portion of Volusia), cold stress accounted for 8.8% of all winter deaths (6 of 68 deaths) over the same period even though water temperatures outside the discharge areas are much colder than waters in southernmost Florida.

These rates of cold stress were comparable to or lower than counties with major power plant outfalls. In the southernmost counties with power plants used by manatees (*i.e.*, those in Broward, Palm Beach, and Lee) the proportion of cold-stress related deaths averaged 9.2% of total winter mortality (42 of 459 deaths). However, in more northerly areas, such as Tampa Bay on the west coast where manatees rely on power plant outfalls in Hillsborough and Pinellas Counties, cold stress accounted for 12.8% (11 of 86 deaths) of all winter deaths. The county with the highest number (57) and proportion (20.4%) of cold-related deaths was Brevard, where coastal waters are colder than other counties with power plants, and the two power plant outfalls used by manatees sometimes fall below 18°C.

The high proportion of deaths in Brevard County was strongly influenced by deaths during the winter of 1989–1990 when a severe cold front in the last week of 1989 caused an unusually high number of deaths. Between December 1989 and March 1990, 31 of 49 deaths in this county were attributed to cold stress. If these deaths are excluded from the long-term average, the proportion of winter cold stress-related deaths between 1986 and 2004 declines to 11.1% (25 of 226 deaths), which is only slightly greater than the proportions of cold stress in southernmost Florida and counties with major warm-water springs. The effects of this cold front on manatees were far less significant in other parts of Florida. For example, between December 1989 and March 1990 there were no deaths recorded due to cold or any other causes in the three southernmost counties and only one death unrelated to cold was recorded in the two counties with warm water springs used by manatees.

Manatee Movements and Population Structure

Resightings of identified individuals (Moore 1951*b*, Hartman 1979, Reid *et al.* 1991, Beck and Reid 1995) and telemetry studies (Beeler and O'Shea 1988; Rathbun *et al.* 1990; Weigle *et al.* 2001; Deutsch *et al.* 2002, 2003) show manatees to be highly independent in their behavior and movement patterns, but have a high degree of site fidelity to individual refuges or groups of refuges. Other than cow-calf pairs that remain together for one or two years, and mating groups (*e.g.*, 2–18 animals) that persist for periods of a few hours to a few weeks (Rathbun *et al.* 1995), the formation of pairs or small groups is usually ephemeral.

Studies also suggest that manatees are remarkable navigators exhibiting a high degree of site fidelity. Most manatees return annually to specific warm-water refuges or groups of refuges (Rathbun *et al.* 1990; Reid *et al.* 1991; Deutsch *et al.* 2000, 2003). They also return repeatedly to other aquatic features (*e.g.*, feeding areas, resting areas, freshwater sources, and travel corridors) spread over hundreds of kilometers of intricate coastal waterways. Based on their movements and seasonal ranges, Florida manatees have been divided into four relatively discrete subpopulations for management purposes (Fig. 4)—two on Florida's east coast and two on the west coast (U.S. Fish and Wildlife Service 2001).

East coast subpopulations—Two manatee subpopulations have been identified along Florida's east coast. The upper St. Johns River subpopulation (currently numbering about 165 manatees) relies on a single major warm-water refuge (*i.e.*, Blue Spring). Telemetry studies reveal that these animals generally remain in the St. Johns River system year-round (Bengtson 1981). During winter, manatees at Blue Spring undertake routine feeding excursions to nearby grassbeds along the river and in Lake Beresford, about 10 km downstream.

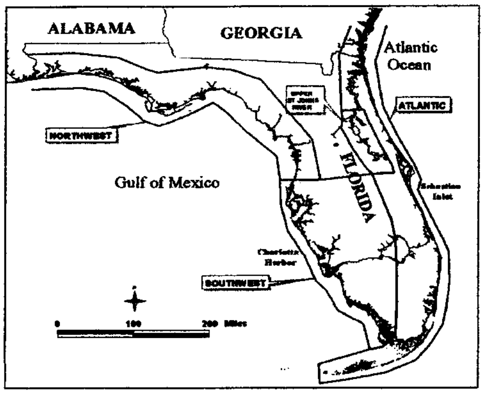

Figure 4. Approximate geographic boundaries of four identified Florida manatee subpopulations (U.S. Fish and Wildlife Service 2001).

In contrast to manatees in the St. Johns River, the Atlantic coast subpopulation, which numbers about 1,500 animals (Craig and Reynolds 2004), relies principally on five power plant outfalls spread over 260 km of shoreline between Cape Canaveral and Fort Lauderdale. Telemetry studies (Deutsch *et al.* 2000, 2003) document a wide variety of seasonal movement patterns within this subpopulation. Some East Coast animals appear to be year-round residents that return to the same outfall each winter and remain within a few tens of kilometers of the outfall throughout the summer. Others rely principally on a single outfall, but migrate hundreds of kilometers north in summer. For the most part, those using northern outfalls near Cape Canaveral move farthest north in summer, while those using southern outfalls may migrate only as far north as Cape Canaveral. Still other manatees use two or more outfalls, with the northern refuges serving as spring or fall stopover sites and the southern refuges used in mid-winter. Interestingly, among nearly 80 animals tracked between 1986 and 1998 (Deutch *et al.* 2000, 2002), none overwintering at power plant outfalls moved farther south than northern Biscayne Bay. Also, no animals captured for tagging south of Miami moved north to use power plant oufalls.

During winter, manatees at warm-water refuges along the Atlantic coast undertake regular feeding forays to grassbeds located within a few tens of kilometers of plant outfalls (Marine Mammal Commission 1989, Deutsch *et al.* 2002, 2003). Sightings of animals known to overwinter at refuges along the Atlantic Coast are very infrequent at Blue Spring in winter. Similarly, animals known to overwinter at Blue Spring are almost never seen at Atlantic Coast refuges in winter. Such a pattern supports the separation of Atlantic Coast and upper St. Johns River populations into two groups.

West coast subpopulations—Two separate subpopulations also have been identified on Florida's the west coast, although movements between them may be more frequent. The northwestern subpopulation, numbering at least 400, overwinters at warm-water springs at the head of the Crystal and Homosassa Rivers, while the southwestern subpopulation, numbering at least 1,300 animals, relies principally on power plant outfalls in Tampa Bay and the Caloosahatchee River. At least some of the rapid growth of the northwestern Florida subpopulation over the past 30 yr has been attributed to the immigration of animals from the south (Powell and Rathbun 1984).

Manatees at the Crystal and Homosassa rivers feed in a network of creeks and marshes running about 11 km downstream to the coast (Marine Mammal Commission 1984, Rathbun *et al.* 1990). Those using power plants in Tampa Bay forage in grassbeds scattered around the Bay (Weigle *et al.* 2001), and those at the Fort Myers power plant move downstream to San Carlos Bay, Pine Island Sound, and Charlotte Harbor about 15–25 km away.[3] Manatees often follow a diel foraging pattern. At Blue Spring (Bengtson 1981) and Crystal River (Rathbun *et al.* 1990), they tend to stay near spring vents in early morning, disperse to nearby grassbeds in late morning and afternoon as temperatures rise, and return to the spring discharges in the evening or at night as temperatures drop. At other sites, such as the Big Bend power plant in Tampa Bay and the Matlacha Isles thermal basin, the reverse seems to occur with animals feeding away from refuges at night and returning during the day (Barton and Reynolds,[4] Deutsch *et al.* 2002).

Genetic exchange—Some interbreeding likely occurs among the four regional groups. This is supported by studies that reveal no clear genetic differences among the four subpopulations (Garcia-Rodriguez *et al.* 1998). Genetic studies also show that Florida manatees have remarkably low genetic diversity indicative of either a founder effect or a major bottleneck of evolutionary significance (Garcia-Rodriguez *et al.* 2000). The latter could result from (1) the relatively recent arrival of a small founding population, (2) reducing a population to very low numbers (*e.g.*, a few tens of animals), or (3) maintaining a somewhat larger group at a low level for an extended period of time (Frankel and Soule 1981, Amos and Harwood 1998, Waldick *et al.* 2002).

Prehistoric and Historic Human Exploitation and Climate

Fossil remains document the presence of modern manatees, *T. manatus*, in Florida since the early Pleistocene about 1.1–1.5 million yr ago (Morgan and Hulbert 1995, Domning[5]). Whether they have been present continuously since then is less clear. About eight glacial-interglacial cycles have occurred over the past 800,000 yr, each lasting about 100,000 yr (Williams *et al.* 1993, Roberts 1998). It is unclear whether glacial phase temperatures in Florida fell to levels that could have prevented manatee survival. Crowly and North (1991) suggest that, during the last glacial maximum 20,000–14,000 B.P., average annual temperatures south of the Laurentide ice sheet, which extended south to present day Illinois and Ohio, were about 10°C cooler then present, but that winter temperatures, made more severe by polar fronts flowing south over the ice sheet, were perhaps 15°–20°C cooler in Tennessee and South Carolina. Differences between current and glacial period temperatures decline towards the tropics. While it is unclear how much colder it was in Florida, sparse estimates for the tropics during the last glacial maximum are

[3] Lefebvre, L., and K. Frohlich. 1986. Movements of radio tagged manatees in southwestern Florida, January 1985–March 1986. U.S. Fish and Wildlife Service and Florida Department of Natural Resources. Unpublished report 1-87.

[4] Barton, S. L., and J. E. Reynolds, III. 2002. Manatee use of Matlacha Isles, a secondary winter refuge site in southwestern Florida. Technical Report No. 849. Mote Marine Laboratory. Sarasota, FL. 33 pp.

[5] Daryl P. Domning, Department of Anatomy, College of Medicine, Howard University, Washington, DC, December 2003.

about 4°–5°C cooler (Crowley and North 1991). During the previous interglacial period (*i.e.*, the Eemian interglacial that occurred 125,000 B.P. and lasted about 11,000 yr) temperatures may have reached within 2°C of the current interglacial phase (*i.e.*, Holocene), with sea level rising to within a few meters of the present (Roberts 1998). Many species shifted their geographic distribution thousands of kilometers north and south in response to these climatic cycles (Bennett 1997).

Also unclear is the condition of Florida's artesian springs during past geologic periods. Since the beginning of the Holocene (about 11,000 B.P.), the geological structure supporting artesian springs has likely changed little, with springs concentrated in central and northwestern Florida and nearly absent in southern Florida. However, flow rates, temperature, and their accessibility to open rivers may have changed significantly in response to climate cycles. During particularly dry periods, some Florida springs may have been reduced to isolated waterholes. Pending better information on spring conditions at different times throughout the Holocene, assessments as to their possible use by manatees must remain speculative. Nevertheless, manatee fossils dating from uncertain time periods between the late Pleistocene and early Holocene (126,000–10,000 B.P.) have been recovered throughout northern Florida in areas where warm-water springs are now prominent features. Among these are sites along the Oklawaha, Santa Fe, Waccasassa, and Withlacoochee rivers; from Rainbow, Rock, Wekiva, and Poe springs; and in Taylor County (Florida Museum of Natural History Vertebrate Paleontology Collection, www.flmnh.ufl.edu/databases/mammals).

Paleoindian period (12,500–9,500 B.P.)—When humans first arrived in Florida during the final phase of the last ice age, Florida temperatures likely averaged several degrees cooler (Roberts 1998), sea level was perhaps 40–60 m lower (Crowley and North 1991), and the peninsula was twice its current width with the western shoreline roughly 160 km farther west, and the northeastern shoreline up to a few tens of kilometers farther east near what is now the continental shelf break (Milanich 1994). The northern half of the peninsula was an arid upland interspersed with more hospitable river drainage systems (Milanich 1994, Dickel and Doran 2002), while the southern half (*i.e.*, what is now the Everglades and Florida Bay) was a dry, treeless savanna (Griffin 1988).[6]

Between 11,500 and 10,000 B.P., an abrupt increase in global temperatures marked the dawn of the Holocene. In many locations temperatures rose to levels a few degrees warmer than those of today and persisted through a long, climatically stable period called the "hypsithermal interval" (Deevey and Flint 1957). Although the beginning (11,000–7000 B.P.) and end (5500–2600 B.P.) of this period are equivocal (Deevey and Flint 1957, Crowley and North 1991, Roberts 1998), it is widely recognized as the Holocene's warmest, and by 9000 B.P. most of the Laurentide Ice Sheet had disappeared (Crowley and North 1991). Precipitation trends were more variable and warmer temperatures in northern Florida would have increased the temperature of water percolating into aquifers to levels above those of the present. Southern Florida, however remained a dry savanna without apparent rivers to provide manatee habitat.

There is evidence that Florida's earliest Paleoindians hunted manatees. The vertebrate paleontology collection of the Florida Museum of Natural History in Gainesville includes a "modified" manatee rib (UF 156808) from an Oklawaha River site and two others with "cut marks" (UF 135791) from a Withlacoochee

[6] Griffin, J. W. 1988. The archeology of the Everglades National Park: A synthesis. Prepared for the National Park Service by the Southeast Archeological Center, Tallahassee, FL.

River site, all dating *ca.* 10,000 B.P. Waller (1970), as cited in Cumbaa (1980), also describes large quantities of cut and worked manatee bone mixed with Paleoindian and later archaic period artifacts in river bottoms below shallow stream fords on the Chipola (Gulf County), Santa Fe (Gilchrist County,) and Withlacoochee (Citrus County) rivers. Waller concluded that these bone accumulations reflected kill sites used by early hunters over long periods of time. Whether Paleoindians hunted manatees at springs is unclear; however, there is evidence they used springs and shallow river crossings to ambush big game. Mammoth bones with butchering marks (Waller 1970) and a chert projectile point embedded in an extinct bison skull (Webb *et al.* 1984) have been found at shallow river crossings in Florida and studies at Wakulla Spring, Honsby Spring, Ichetucknee Springs, and the Wicassa River show that Paleoindians were living around springs and hunting extinct species of megafauna in those areas (Scott *et al.* 2002).

Archaic periods (9500–2400 B.P.)—The beginning of the archaic period is marked by a change from nomadic big-game hunting traditions to a more sedentary life style dominated a diet of fish, mollusks, and other aquatic species (Milanich 1994, Dickel and Doran 2002). In the early archaic (9500–6900 B.P.), encampments were established at various springs (Scott *et al.* 2002) and along waterways such as the St. Johns River, Oklawaha River, and Florida's southwestern coast (Milanich 1994). The exploitation of manatees during this period, however, remains enigmatic. The only well-dated evidence we found of manatee use was a manatee rib fashioned into an unusually large atlatl weight/handle recovered from an early archaic (7400 B.P.) human burial pit (the Windover site) near Titusville between the Atlantic Coast and the St. Johns River (Penders 2002). To the authors' knowledge, this is the earliest and only manatee bone found in a clearly dated archeological context in Florida that was fashioned into a tool by Pre-Columbian natives.

During the middle (*ca.* 6900–4000 B.P.) and late (4900–2400 B.P.) archaic periods, rainfall in both southern and northern Florida increased. By 5500–4500 B.P. both Lake Okeechobee and the Everglades assumed a recognizable form and rapidly melting glaciers had elevated sea level to within a few meters of current levels in Florida.[6] With average temperatures above those of today and solar-heated water flowing through the Florida Everglades, winter habitat in southern Florida may have become even more suitable for manatees than it is today. Water temperatures and discharge rates at major springs in northern Florida also were likely higher and better able than today to support overwintering manatees.

These conditions likely continued into the late archaic period (4900–2400 B.P.) as human populations continued increasing and regionally distinctive cultural traditions evolved. Major population centers developed along coastal and river wetlands that are today considered prime manatee habitat, including the central St. Johns River, southwestern coast from Charlotte Harbor to the Ten Thousand Islands (Milanich 1994). During this period, fine mesh nets were developed to catch fish, and perhaps also manatees, in tidal creeks of southwestern Florida (Marquardt 1999), where Milanich (1994) concluded "late archaic villagers . . . apparently ate nearly everything that was available along the coast."

Although middens on major Florida rivers and springs, such as Blue Spring,[7] attest to human presence during archaic periods, very few have yielded manatee

[7] Sassaman, K. E. 2003. St. Johns archeological field school 2000–2001: Blue Spring and Pontoon Island State Parks. Technical Report 4. Laboratory of Southeastern Archaeology. Dept. of Anthropology. University of Florida. Gainesville, FL. 213 pp.

remains. Cumbaa (1980) cites reports of manatee remains in middens at the Belle Glades site near Lake Okeechobee (Willey 1949), at Crystal River, and at the Tick Island and Bluffton sites on the St. Johns River (Florida State Museum archeology collection); however, the reports do not identify the number, context, or age of the manatee bones and some or all could have been from post archaic midden levels.

Post Archaic (400 B.C.–A.D. 1550)—From the end of the late archaic period (*ca.* 2400 B.P.–400 B.C.) to the arrival of the first Europeans in the late 1500s, climatic conditions became less stable. Short-term (*e.g.*, decadal) climate variations were superimposed on longer term cycles, such as the "Medieval Optimum" (*ca.* A.D. 1100–1300) with warm temperatures comparable to the present, and the "Little Ice Age" (*ca.* A.D. 1300–1850) when temperatures averaged one or two degrees Centigrade cooler, sufficient to stop and even reverse glacial retreat in some areas (Fagan 2000). During this period human populations may have reached several thousand in locations now important to manatee, including Crystal River,[8] the Charlotte Harbor-Pine Island Sound area of southwestern Florida (Marquardt 1992, 1999), and the St. Johns River (Milanich 1994).

A few manatee bones have been recovered from shell middens dating from the end of the late archaic up to the 1500s, but they are rare. A few manatee bones have been found in middens in the Crystal River area, including one from a midden dating between A.D. 500 and 1300.[8] Griffin,[6] citing Wing (1984) also notes manatee remains at post-archaic sites in the Big Cypress National Preserve in the Everglades, but does not identify specific locations, numbers of bones, or the context in which they were found. It also is possible that the manatee remains referenced by Cumbaa (1980) were from this period rather than archaic periods. Given the rarity of manatee remains in shell middens, Hartman (1979) concluded that manatees were not a dietary staple, but rather an opportunistic supplement to more common foods.

Post Spanish contact (A.D. 1550–1900)—Arrival of Spanish explorers in the mid-1500s and the establishment of St. Augustine in 1565 ushered in a new and likely more intensive phase of manatee hunting. At the beginning of this period, global climates were still in the grip of the "Little Ice Age," with its long sequence of short-term changes from colder to warmer winters and back again (Fagan 2000). This would have made Florida less suitable for manatees than it is now. Southern Florida, with its near absence of artesian springs, may have become marginal winter habitat.

During the 1700s at least some manatees used northern springs as warm-water refuges, Bartram (1791), in one of the earliest accounts mentioning manatees in Florida, describes the skeleton of a manatee he saw on the bank of Manatee Spring in the summer of 1774 that his guide told him had been killed by Indians earlier that winter. His guide also informed him that he ". . .saw three of them (manatees) at one time in the spring." This is the first and only report prior to the 1900s providing an actual count of manatees at a warm-water spring. In the 1800s European and native hunters apparently killed "hundreds" of manatees for food (*e.g.*, Brinton 1869 as cited in O'Shea 1988), with manatee numbers in various parts of Florida declining to a point that left "no doubt that the manatee (was) fast becoming extinct" (*e.g.*, Canova 1885 as cited in O'Shea 1988). They apparently were absent from the Crystal and Homosassa rivers (Hallock 1876 as cited in Powell and Rathbun 1984) where they

[8] Gary D. Ellis, Director, Gulf Archaeology Research Institute, 5990 N. Tallahassee Road, Crystal River, FL, January 2004.

are now abundant. Other records, however, conflict with the view that manatees were nearing extirpation in the late 1800s. True (1884) as cited in O'Shea (1988), refers to reports of large numbers of manatees in the Indian River on the Atlantic Coast and in southwestern Florida, and concluded that "the Florida manatee cannot yet be considered as threatened with extinction." Nevertheless, concern that manatee numbers had been severely reduced led the nascent state of Florida to enact a ban on all manatee hunting in 1893.

Modern era (A.D. 1900–present)—During the first half of the 1900s, reports persist of manatees being taken for food or caught incidentally in fishing nets (Moore 1951*a*, *b*; O'Shea 1988). Although at least a few manatees apparently overwintered at Blue Spring and Crystal River by the early 1900s (Hartman 1974, 1979; O'Shea 1988), most manatees appear to have been concentrated in rivers and estuaries in the Everglades in southernmost Florida where Moore (1951*b*) concluded "that manatees have survived their persecution best." In Biscayne Bay (southeastern Florida) an airship officer reportedly saw "some 30 animals in a day" during an overflight on an unspecified date in the 1930s or 1940s (Barbour 1944 as cited in O'Shea 1988).

By the mid-1960s the nuclei of current manatee subpopulations in the Crystal River and upper St. Johns River were already in place (Hartman 1979). In the winters of 1967–1968 and 1968–1969, when the first manatee counts were made at Crystal River, Hartman identified 63 individuals, 35 of which were seen both years. At that time local guides and fishermen unanimously advised that manatees were far more numerous in the area than at any previous time. At Blue Spring in the winters of 1970–1971 and 1971–1972, 11 and 18 manatees, respectively, were identified, seven of which were seen both years (Hartman 1979). Although great improvements have been made in manatee survey techniques since early surveys in the 1970s, recent counts (Table 1), suggest manatee abundance at both sites may have increased nearly tenfold over the past three decades.

In hindsight, Glaser and Reynolds (2003) concluded that the late 1980s and early 1990s may have been a relative "golden age" for manatee recovery. Despite a lack of reliable abundance estimates for all but the small St. Johns River subpopulation (where each animal is known individually), other demographic indicators (*e.g.*, Langtimm *et al.* 1998, Craig *et al.* 1997, Craig and Reynolds 2004, Runge *et al.* 2004) suggest that the total number of Florida manatees increased by some uncertain amount during this period, but that the two largest populations may have stabilized or declined slightly during the mid-1990s.

Discussion

Historical Winter Habitat

Although Moore (1951*a*) concluded that Florida manatees were limited to the southern third of Florida in winter before power plants influenced their distribution, we suggest his observations are not necessarily inconsistent with the hypothesis that natural springs in northern and central Florida were major, if not the principal winter habitats for manatees. A more northerly winter range seems consistent with evolving, although still very limited, understanding of manatee habitats in the prehistoric Holocene. It also seems possible that a long history of hunting pressure may have restricted manatees to southernmost Florida by the time Moore conducted his studies.

As noted above, data are not sufficient to determine if manatees were present in Florida throughout the last ice age; however, archeological evidence places manatees in northern Florida *ca.* 10,000 B.P. in areas where warm-water springs now occur. Although reduced rainfall and lower water tables at that time would have reduced spring discharges and perhaps left some springs as isolated water holes, other springs along major river systems may have remained accessible to manatees. Some springs now inundated by higher sea levels on the western Florida continental shelf (Scott *et al.* 2002) also may have been available to manatees. Based on their rapid adoption of industrial outfalls as far north as Georgia to survive winter cold, it seems possible that manatees could have quickly learned to use available warm-water springs as winter refuges if they were accessible. Current winter use of Blue Spring now more than 140 mi upstream from the mouth of the St Johns River demonstrates that manatees could have reached current spring sites even though they may have been more than a hundred miles farther inland when sea levels were lower.

With few natural predators and a diet encompassing many aquatic plants, it also seems possible that subpopulations numbering in the hundreds, and perhaps even a thousand or more, could have developed in a few hundred years or less around networks of warm-water springs on major river systems in northern Florida, such as the upper St. Johns, Oklawaha, Santa Fe, Withlacoochee, Homosassa, and Crystal rivers. If new information on spring temperatures and flow rates at various periods in the Holocene becomes available, the potential use of these habitats by manatees should be reassessed. Conversely, with a near absence of warm-water artesian springs in southernmost Florida, cooler winters at the dawn of the Holocene and even more recently during the Little Ice Age between 1300 and 1850 B.C. may have made southern Florida less suitable for overwintering manatees than it is today.

The rare occurrence of manatee bones in middens of the period could be due at least in part, to a reduction in manatee numbers by hunters before midden formations began in the early archaic (*ca.* 9500 B.P.). Also, as noted by O'Shea (1988), their rarity in middens may reflect a practice of leaving heavy manatee bones at kill sites, such as springs, where they could be carried off by alligators and other scavengers.

With virtually all Paleoindian sites found to date located north of present-day Tampa Bay, Florida's first human inhabitants apparently occurred principally in northern parts of the peninsula or perhaps along more southerly coastal areas now submerged by higher sea levels. Given colder winters and few artesian springs and rivers in the southern part of the peninsula (*i.e.*, south of what is now Key West and the Dry Tortugas), southernmost Florida may have provided poorer winter habitat for manatees than it does today. Thus, if warm-water springs north of present-day Tampa Bay were accessible to manatees and discharges were above 20°C, they may have supported a large proportion of Florida manatees.

During post-archaic periods, human populations increased in key manatee habitats, such as the St. Johns River, along the Crystal River, and in the Charlotte Harbor area. The development of fishing nets during this period (Marquardt 1999) and an extensive reliance by pre-Columbian Indians on fish and shellfish in seagrass meadows for food (Walker 1992, Milanich 1994) suggests that post-archaic hunters had both an improved ability and opportunity to catch manatees. With arrival of European hunters in the middle of the Little Ice Age, we suggest that manatees numbers in southern Florida remained small or declined—perhaps to the low hundreds. By the late 1800s or early 1900s, the combined take of manatees by Indians and Europeans may have eliminated at least some subpopulations dependent on springs in northern Florida, while reducing other spring groups to perhaps a few tens of animals or less.

The remarkably low genetic diversity in present-day Florida manatees could reflect the combined effects of a small founding group of manatees arriving in Florida from the West Indies at the end of the last ice age, coupled with the maintenance of subpopulations at low numbers by hunting over many millennia followed by further reductions by European hunters.

Thus, the winter range of manatees through the mid-1900s may have been artificially restricted to southern Florida by persistent hunting through the 1800s and continued poaching into the mid-1900s. As poaching ended towards the mid-1900s and power plants were built along Florida's east and west coasts, we suggest that migrating manatees from southernmost Florida quickly learned to use those outfalls as they provided warmer, more reliable winter habitat than thermal basins in southernmost Florida. This, in turn, reduced exposure to cold stress, enhanced their survival rates, and facilitated a recovery that continues for at least some subpopulations to this day. Their more northerly winter location also could have facilitated their reoccupation of natural springs located still farther north.

If power plants are shut down or spring flows are lost or significantly reduced, will manatees move to warmer areas in south Florida? If so, what are the likely impacts?

With cold stress-related deaths in southernmost Florida comparable to or lower than those in northern counties with power plants, one might expect a greater proportion of Florida manatees to overwinter in southernmost Florida than statewide manatee counts would indicate. The reason why this is not the case is unclear. It may be that cold-related deaths in southernmost Florida are not lower and they are underestimated because carcasses are hard to find in dense Everglades vegetation, or because a disproportionate number are too badly decomposed to determine the cause of death by the time they are found. It also is possible that manatee abundance in southernmost Florida is already near its carrying capacity and greater abundance is constrained by various factors, including a limited ability of available thermal basins or food resources necessary to support manatees through cold periods.

Winter water temperatures even in southernmost Florida fall below potentially lethal levels for some manatees (*i.e.*, below about 18°C) for periods of two weeks or more during cold winters, so manatees throughout Florida require localized areas where water remains warmer than 18°–20°C and preferably warmer than about 22°C. Although two types of habitat meet this need—warm-water discharges and passive thermal basins—most manatees use the former.

Site-fidelity patterns in manatees are likely transferred from generation to generation as calves learn to use those refuges while accompanying their mothers (Reid *et al* 1991). Similar site fidelity patterns ingrained in calves of humpback whales, as they accompany their mothers from tropical calving grounds to northern feeding areas, have been cited as the reason why humpback whales in the North Pacific and North Atlantic Oceans form similar discrete subpopulation units that return repeatedly to particular feeding areas (Clapham *et al.* 1993, and Calambokidis *et al.* 2001).

Perhaps 75% or more of all Florida manatees rely on 14 warm-water discharges (10 power plant outfalls and 4 natural springs), most of which are located in the central third of the Florida Peninsula. All 10 plants are at least 30 yr old. Two of the 10 power plants (the Fort Myers and Fort Lauderdale plants) were recently repowered, thereby extending their expected operational lives for another 25–30 yr. Many of the others may be retired within the next 10–20 yr. This could eliminate nearly half of the major warm-water discharges now used by manatees.

Although major and minor power plant outfalls are used to varying degrees by perhaps two-thirds of all Florida manatees, fluctuating discharge temperatures and intermittent operations at some plants cause outfalls to periodically dip below 19°C during severe and prolonged cold periods. As a result, cold-related deaths can be common in counties with major power plant refuges, particularly in northern areas, such as Brevard County. However, with outfall temperatures remaining above 20°C through most winter periods, manatees are attracted to and appear to use them more than thermal basins.

Temperatures of springs now used by large numbers of manatees fluctuate far less than power plant outfalls and remain at or above 22°C even in the coldest weather. Despite spring locations at the northern end of manatees' winter range, cold-related deaths at Crystal River and Blue Spring have been nearly absent even in the coldest, most prolonged periods of winter weather. Winter manatee survival may therefore depend on the availability of areas that stay unfailingly at or above 22°C. Although other factors may be involved, the only two subpopulations clearly increasing in size at present are those dependent on warm-water springs. Manatees also appear to be in the process of reoccupying other warm-water springs in central and northern Florida, although this is impeded by human alterations that prevent or limit manatee access to some spring discharges.

Southernmost Florida appears to offer somewhat less optimal winter habitat used by smaller numbers of animals than natural springs. Regional water temperatures can fall below 18°C for weeks at a time and the area has no natural warm-water artesian springs. Although as yet unknown thermal basins used by small numbers of animals (*e.g.*, <10) may occur, extensive radio-tracking and aerial survey studies over the past 20 yr indicate that undetected thermal basins used by large numbers of manatees are highly unlikely. Better information on the number and location of thermal basins and their temperature fluctuations in winter would help clarify the extent to which this region might support manatees.

We suggest that the greater winter use of warm-water springs and power plant outfalls by manatees in central and northern Florida reflects a greater level of protection against winter cold stress compared to coastal waters at Florida's southernmost tip. As such, warm-water springs and power plant outfalls appear to be better able to sustain large numbers of overwintering manatees. We also note that, because of strong site fidelity patterns, manatees tend to remain near industrial outfalls when their discharges are terminated or interrupted in winter (Laist and Reynolds, in press). Thus, the gradual loss of major power plant outfalls could result in a substantial decline in manatee abundance along the Atlantic Coast and in southwestern Florida. We believe few manatees now using power plants would move north to natural springs outside of their familiar range. If they moved to southernmost Florida, which also seems questionable, thermal basins may not be adequate to support large numbers of displaced manatees through especially cold winters.

Conclusions

The current winter distribution of manatees is similar to the species' likely historical winter distribution. Coastal power plants currently serve as functional equivalents to natural springs for purposes of providing habitat for manatees in winter. Perhaps two-thirds of all Florida manatees depend to varying degrees on 10 plants located in areas where alternative, natural warm-water refuges are either not available or are rare. If these plants are retired, manatees will become increasingly dependent on natural warm-water springs in central Florida and thermal basins in southernmost Florida. Human development, however, now obstructs manatee access to some springs, and other springs face threats of reduced flow rates due to expanding human withdrawals of water from aquifers. In addition, habitats in southernmost Florida have been radically altered by channelization of the Everglades, agricultural runoff, and other factors affecting water quality, and it currently may be unable to support larger numbers of manatees in winter.

In light of this situation, there is an urgent need to develop a forward-looking research and management strategy aimed at identifying and maintaining a long-term network of warm-water refuges to meet the thermoregulatory needs of overwintering Florida manatees. Possible alternative actions include efforts to enhance manatee access to natural warm-water springs currently unused or little used, and to create alternative warm-water habitats.

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