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**Manatee Habitat and  
Human-related Threats to Seagrass in Florida:  
A Review**

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# **Manatee Habitat and Human-related Threats to Seagrass in Florida: A Review**

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## **INTRODUCTION**

The West Indian manatee (*Trichechus manatus*) is a large aquatic mammal found predominantly in the Caribbean and throughout coastal waters and fresh-water systems with connections to the sea on both coasts of Florida in the United States. Manatees in Florida (*Trichechus manatus latirostris*, a subspecies of the West Indian manatee) are generalist herbivores whose ability to feed on virtually any vegetation in or near frequented waters, tolerance of variable levels of turbidity and conditions around urbanized areas, and euryhaline habits allow them to occur in a wide range of habitats. These animals favor near-shore marine, estuarine, or fresh waters which are shallow, warm, and calm (O'Shea and Kochman, 1990) and where aquatic vegetation is abundant. Human activities in and around manatee habitats in Florida have increased dramatically in recent years and represent an ever-increasing threat to this endangered species. Extensive development of coastal lands for housing, agricultural, and commercial purposes has altered much of the near-shore environment such that manatees may have altered their use of historically-important foraging sites. Other human activities contributing to manatee habitat alteration include recreational and commercial boating practices; dredge and fill operations; chenalization of rivers, streams, and other alterations of fresh-water flow; and industrial, agricultural, or civic effluent pollution. Such alterations have diminished the extent and environmental quality of much of the manatee's once pristine habitat and continue to do so at an alarming rate. While fatal encounters due to high speed and/or crushing collisions between manatees and boats remain high in areas of overlapping use, another critical threat to the continued survival of the manatee in Florida is the loss of required habitat resources.

Much of the information concerning the ecological components of manatee habitat has been gathered in recent years by researchers and regulatory agencies in an attempt to better identify the human threat to Florida's manatee population. This report provides an overview of the information regarding manatee habitat in Florida. The purpose of this report is to summarize the existing scientific information concerning: 1) the ecological requirements of manatees; 2) the behavior associated with manatee foraging; 3) the fresh-water and marine diet of the manatee; 4) the ecological impacts of manatees' feeding on seagrass communities; and 5) major threats to manatee habitat related to human activities. Discussions of habitat requirements for manatees are based on scientific and anecdotal information obtained from published sources.

## FACTORS AFFECTING MANATEE DISTRIBUTION

Temperature is the overriding factor in determining the geographic extent of suitable habitat available to West Indian manatees (*Trichechus manatus*). These large aquatic mammals have relatively low metabolic rates, a high level of thermal conductance typical of tropical animals, and lack of a thick blubber layer (Irvine, 1983). Because of this, manatees range from as far north as Cape Hatteras, N.C., on the east coast of the United States to as far south as the State of Bahia in Brazil (Lefebvre, et al., 1989). Both the northern and southern extremes of this range are visited infrequently by far-ranging individuals during the respective warm seasons of each hemisphere. A single manatee sighted in 1980 near the Georgetown Canoe Club in the Potomac River within Washington, D.C., represents the northern-most confirmed sighting for this species (Rathbun and Bonde, 1982). The manatee's limited ability to conserve heat in the aquatic environment restricts its year-round range to within the northern and southern limits of the 24°C mean annual isotherm (Whitehead, 1977; Irvine, 1983; O'Shea and Kochman, 1990). This placed the subpopulation of *T. manatus latirostris* in Florida at the cold season northern extreme of the West Indian manatee population confines. More recent information suggests that manatees may have extended their cold-season range into northeastern Florida with a few individuals venturing into southeast Georgia waters (Zoodsma, 1992; Valade, personal communication).

Before the extensive development of Florida's east and west coasts with the concomitant proliferation of coastal electrical generating stations and industrial effluents, which serve as artificial warm-water refuges for manatees, Moore (1951) suggested that the regular northern winter limit for manatees was Sebastian River on the Atlantic coast and Charlotte Harbor on the west coast. Current information suggests that manatees have extended their northern-most limits in Florida. *T. manatus latirostris* presently frequents Crystal and Homosassa Rivers on the west coast in large numbers (>250 animals) during the cold season. On the east coast of Florida, manatees regularly use Blue Spring (50-65 animals), along with several industrial warm-water effluents in the upper reaches of the St. Johns River during winter months (Beeler and O'Shea, 1988; FDNR GIS annual synoptic aerial survey data, 1990, 1991). Telemetry data obtained by Zoodsma (1991) during the winter months (January to March) identified small numbers of manatees using the warm-water effluents of the Gilman Paper Company facility on the North River in southeastern Georgia and those of the Container Corporation of America plant on the Amelia River on the northeast coast of Florida. These sites presently represent the northern-most cold-season limit for West Indian manatees. The apparent northward extension of the manatee's winter range is due in part to the use of warm-water refuges offered by natural spring systems and artificial sources during the passage of severe cold fronts in autumn and winter when ambient waters drop below 20°C (Figure 1) (Hartman, 1979; Rose and McCutcheon, 1980; Powell and Waldron, 1981; Rathbun and Bonde, 1982; Shane 1983, 1984; Powell and Rathbun, 1984; Reynolds and Wilcox, 1986; Lefebvre and Frohlich, 1986; Beeler and O'Shea, 1988; Lefebvre, et al., 1989; O'Shea and Kochman, 1990; Rathbun, et al., 1990; Reynolds, 1991; Reid, et al., 1991). Traveling manatees use warm-water refuges along their migratory routes during both the early spring and late fall in a "stepping stone" strategy, which may permit them to migrate north earlier in the spring than ambient temperatures would otherwise allow and also may permit them to remain at preferred northerly sites later into the fall (Reid, et al., 1991). The observed use of warm-water refuges probably

reduces the energetic costs of thermoregulation during passage of cold weather (Irvine, 1983). The metabolic need for warm water may override the manatee's energetic requirements for food (O'Shea and Kochman, 1990). Bengston (1981) found that manatees that use Blue Spring on the St. Johns River as a warm-water refuge would remain in warmer spring waters for up to a week without making feeding excursions into colder river waters. Irvine (1983) suggested that manatees will leave warm-water refuges to feed in 15-18°C waters only if they can shortly return to these refuges to digest their food. Rathbun and coworkers (1990) noted that several radio-tracked manatees that frequented Crystal River and Homosassa River warm-water refuges traveled up to 7 km downstream to feed on *Ruppia maritima* and *Potamogeton pectinatus* during late afternoon and dusk hours, but their study did not address ambient temperature variations. It is probable that these manatees left the warm spring waters only after air and adjacent water temperatures rose in the afternoon and only after cold fronts had passed. Manatees outfitted with buoyant satellite and VHF tags were tracked moving out of the thermal refuge of the Ft. Myers Power Plant outfall on the Orange River and traveling approximately 27 km down into Pine Island Sound and Matlacha Pass following the passage of cold fronts (Lefebvre and Frohlich, 1986). Lefebvre and Frohlich (1986) found that these animals moved rapidly to these areas (within several hours of leaving the power plant's effluent), where they remained associated with dense seagrass communities during warmer periods of the cold season. Manatees in this area would feed on seagrasses and remain close to the mouth of the Caloosahatchee River to facilitate return trips to the power plant during cold-weather events. Foraging resources and travel corridors used by manatees close to thermal refuges must be provided an extra measure of protection, as they are critical to a large percentage of the regional manatee population.

From spring to early autumn, manatees disperse from their winter refuge regions and range widely throughout coastal and riverine Florida and coastal Georgia. Manatees are typically observed from the Wakulla River to Cape Sable on the west coast and from coastal northeast Georgia to Biscayne Bay on the east coast during the warmer seasons (Beeler and O'Shea, 1988; O'Shea and Kochman, 1990; Rathbun, et al., 1990). Manatees travel long distances to reach preferred warm-season habitats. Reid and coworkers (1991) used photographic records of distinctively-scarred manatees to document an 850 km journey for an individual manatee from Blue Spring Run on the St. Johns River to Coral Gables near Miami. Manatees repeatedly return to habitual winter-aggregation and warm-season sites, the locations of which are presumed to be learned by individuals during the 12- to 24-month period of calf-cow dependency (Reid, et al., 1991). For instance, individual animals were observed moving between Jacksonville power plants on the St. Johns River and the Port Everglades Power Plant in Broward County on the east coast of Florida on an annual basis (Reid, et al., 1991). Zoodsma (1991) reported seasonal site fidelity for radio-tagged manatees that frequent southeastern Georgia waters. This information indicates that increased attention must be given to the protection of habitat resources throughout the manatee's travel corridors and summer dispersal areas in order to stabilize the population on both coasts of the State.

Although telemetry studies have provided information regarding the seasonal and long-term movements of manatees, information concerning the manatee's average home-range size and daily movements is not readily available. Both the range and daily movements of manatees vary according to each individual animal and are presumed to be determined by such factors as proximity to fresh-water sources, foraging habitat, and warm-water refuges, as well as reproductive status, ambient level of disturbance, and temperature (Brad Weigle, personal communication). Individual manatees may

remain within a 5 km<sup>2</sup> area of shallow seagrass beds for days at a time and suddenly move rapidly 30 or more kilometers to a river system with limited foraging resources (FMRI and USFWS telemetry data). Analysis of telemetry and observational data collected during tracking efforts may be capable of providing some insight into short-term and regional patterns of manatee habitat use. Such information is essential if determinations of home-range carrying capacity are to be made for manatee habitat protection efforts around the State.

Seasonal temperature fluctuations have probably acted as a strong selective pressure for the development of the manatee's migratory behavior. Such behavior may also have developed for other habitat-related reasons. Manatees may leave wintering sites because local food resources have been depleted to a suboptimal level (Zoodsma, 1991). By manatees' migrating away from preferred winter and summer sites, forage resources are provided adequate time to recover; and long-term exhaustion of these resources may be avoided (Bengston, 1981; Lefebvre and Powell, 1990; Provanha and Hall, 1991). Ample food resources are, therefore, secure at preferred sites for future winters and summers.

In addition to temperature, other factors, such as currents, shelter from wave action, water depth, proximity to fresh-water sources, and availability of vegetation, may determine manatee habitat and distribution (see Lefebvre, et al., 1989 for review). Campbell and Irvine (1977) found that manatees readily move between fresh-water and marine systems where the manatees graze on abundant submerged macrophytes. Manatees are sluggish by nature and avoid waters with swift currents or heavy surf; they show a distinct preference for large, slow-moving rivers as well as estuaries and lagoons or sounds protected by barrier islands (O'Shea and Kochman, 1990). Manatees must also surface frequently for air (every 3 to 5 minutes), and sustained dives in deep water have not been observed (Hartman, 1971; Bruce Ackerman and R. Kipp Frohlich, personal communication; personal observation.).

The availability of submerged aquatic vegetation (SAV) and its abundance influence manatee distribution and characterize preferred manatee habitat. These large herbivores are also limited to shallow, near-shore waters, as most aquatic macrophytes are restricted to waters less than 10 m in depth due to the rapid attenuation of sunlight in water (Zieman, 1982). Hartman (1979) also reported that tides determined manatee distribution on a local scale based on the accessibility of shallow seagrass beds and terrestrial vegetation. During high tides, manatees can feed on vegetation that would be inaccessible at low tides. During the low-tide cycle, manatees rest or cavort in deeper channels (Zoodsma, 1991), which in many areas are devoid of forage materials. Zoodsma (1991) also found that tidal cycles in southeastern Georgia dictated manatee feeding activity periods there; manatees ventured away from protective warm-water refuges they used during the cold season during early morning and probably nocturnal high tides to forage on nearby smooth cordgrass (*Spartina alterniflora*). During medium and low tides, when forage was unavailable, these same manatees returned to their respective warm waters to rest.

Lefebvre and Frohlich (1986) documented a pattern of manatee associations with the edges of seagrass beds in southwest Florida based on telemetry data obtained from radio-tagged animals. These authors suggested that the observed association of manatees and seagrass bed edges could be related to zonation of seagrass species by nutritive quality and/or density or a preference by manatees to remain in deeper waters adjacent to their forage source (presumably to allow for avenues of escape). More

recently, Kadal and Patton (1991) found that manatees may show a preference for specific areas which have healthy seagrass beds adjacent to relatively deep water with little boat traffic. These same areas may also have high nursery value, as disproportionately large numbers of cow-calf pairs were also observed there.

Manatee sightings are relatively infrequent in areas with little accessible fresh water (e.g., the Bahamas), which may indicate that availability of fresh water is important in determining manatee habitat as well (Odell, et al., 1978; Lefebvre, et al., 1989). Fresh water has been suggested to be critical for manatee osmoregulation (Moore, 1951; Hartman, 1974, 1979); and manatees in areas without natural fresh-water sources have been observed drinking from and aggregating near artificial sources, such as sewage or storm-water outfalls, drainage pipes, and private hoses (O'Shea and Kochman, 1990). The latter authors also identify that a disproportionate number of sightings occur in such locations, and tracking data show frequent movements by manatees towards sources of fresh water. Patton (personal communication) described an account of habitual manatee aggregation at the Port of the Islands Resort facility where manatees appear to follow a salinity gradient to a crack in a weir from which fresh water flows. He speculated that this breach in the fresh-water baffle may be in part responsible for attracting manatees to this area during the summer months, when this canal system has limited aquatic vegetation and experiences substantial boat-traffic disturbance. This system does serve as a minor thermal refuge during the cold season and provides some forage resources in the form of floating *Hydrilla* mats that accumulate below the weir during periods of high fresh-water flow (Kipp Frohlich, FDNR unpublished data).

O'Shea and Kochman (1990) speculate that manatees prefer to occupy locations with easy access to fresh water for "reasons of metabolic economy." Areas with fresh water available may minimize the osmotic stress experienced by resting or active manatees; however, it is possible that manatees may not require regular access to fresh water for physiological reasons. Reynolds and Ferguson (1984) reported sightings of two manatees northeast of the Dry Tortugas well away from fresh-water sources in uncharacteristically deep water. These researchers proposed that manatees, because of their renal morphology, may only require periodic consumption of fresh water for osmoregulation or that they may instead prefer occasional exposure to fresh water in order to rid themselves of stenohaline ecto- or endoparasites. Such individual migrations probably occur infrequently and for unknown reasons, although passage of an extreme cold front with a sudden drop in water temperature is known to stimulate manatee migration to warm-water refuges (in this case, perhaps Gulf Stream waters). Current research using deuterium as a tracer for metabolic osmoregulation in captive manatees held in salt water indicates that, while manatees do not actively drink salt water, they are capable of assimilating fresh water from their food sources (Ortiz and Worthy, unpublished data). These findings indicate that manatees may not require fresh water for survival, but, regardless of the reason, manatees are attracted to fresh-water outfalls and/or fresh-water systems (Lefebvre, et al., 1989).

Manatees are long-distance seasonal travelers, and individuals aggregate in areas where key resources (warm-water refuges, sources of fresh water, extensive seagrass meadows, etc.) are available along their migratory corridors (Hartman, 1971, 1974, 1979; Bengston, 1981; Beeler and O'Shea, 1988; Lefebvre, et al., 1989; O'Shea and Kochman, 1990; Reid, et al., 1991). Other locations, lacking obvious resources used by manatees, are also frequented by aggregating manatees. Bengston (1981)

referred to these areas as "traditional gathering sites." Patton (personal communication) suggests that there may be some physical or chemical characteristic (sediment composition, depth of the area relative to surrounding waters, or pH) which manatees preferentially seek out. Further research must be performed to more completely characterize and better understand the factors which influence manatee use of traditional gathering sites.

Habitat availability is presumed to have also influenced the development of the Florida subpopulation of manatees. Extensive gaps in suitable habitat in the Gulf of Mexico and Florida straits may limit the contact of Florida manatees with conspecifics in the Caribbean. These gaps are represented by a lack of fresh-water sources, sheltered lagoons, reduced seagrass availability, and seasonally cooler water temperatures (Lefebvre, et al., 1989). Manatees rarely cross these habitat voids. The resulting lack of genetic material exchange from other populations in the Caribbean has resulted in the isolation of the Florida subpopulation. Such deficiencies in habitat availability are also recognized along the Caribbean coast of Venezuela and between the islands of the Greater Antilles and Lesser Antilles, where extensive unprotected coastlines lacking vegetated near-shore shallows (some with rocky beaches) are commonplace (O'Shea, et al., 1988). Some isolation of manatee populations may also be caused by this lack of habitat, but information concerning manatee distribution in these areas is generally lacking.

## MANATEE FEEDING ECOLOGY

Manatees are generalist herbivores that feed on virtually all forms of aquatic macrophytes, including emersed, natant (floating), and submerged varieties, some terrestrial plants overhanging associated waters, accessible shoreline vegetation, and several species of algae (**Table I**) (Hartman, 1971 in Husar, 1978; Hurst and Beck, 1988). *Trichechus manatus* is also an efficient herbivore whose relatively slow food consumption and slow rate of digestion, combined with postgastric digestion of aquatic plants with low crude fiber content, permits digestive efficiencies approaching 80% for natural forage (Lomolino, 1977; Lomolino and Ewel, 1984; Burn, 1986). Anaerobic bacteria capable of cellulose fermentation have been identified in the hindgut of manatees (Odell, et al., 1993). Burn (1986) found that, with most digestion occurring in the cecum and proximal colon and long periods of plant material retention (146 hrs; Lomolino and Ewel, 1984), manatees have one of the highest digestibility coefficients for cellulose (80%) of any known mammalian herbivore. Slower rates of passage of food material allow for proportionately more microbial cellulose fermentation to occur in the intestinal tract of these animals (Parra, 1978 in Burn, 1986). Manatees differ from other herbivores in that protein and lipid digestion, although comparable in efficiency, occurs in this region of the large intestine rather than in the foregut (Burn, 1986). Even with this high level of digestive efficiency, manatees must on a daily basis consume large quantities of aquatic vegetation, which is high in crude fiber and low in protein, in order to meet their metabolic requirements.

**Table I**(continued)

<b>Submerged Freshwater Plants</b>		
<i>Cabomba australis</i>	Cabomba	1, 2
<i>Cabomba aquatica</i>	Fanwort	1, 2, 3
<i>Cabomba caroliniana</i>	Fanwort	1
<i>Ceratophyllum demersum</i>	Coontail	1, 2, 3
<b>Algae (continued)</b>		
<i>Egeria densa</i>	Brazilian Elodea	1, 2, 3
<i>Spirogyra sp.</i>	Spirogyra	3
<i>Hydrilla verticillata</i>	Florida Elodea (Hydrilla)	1, 2, 3
<i>Ulva lactuca</i>	Sea Lettuce	3, 4, 5
<i>Ludwigia repens</i>	Ludwigia	3
(1) <i>Myriophyllum aquaticum</i> in Ledder, 1986	Parrot's Feather	3
(2) <i>Myriophyllum spicatum</i> in Packard, 1981	Eurasian Watermilfoil	1, 2, 3
(3) <i>Najas guadalupensis</i> Hurst and Beck, 1988	Southern Naiad	1, 2, 3
(4) <i>Zizania, illinoensis</i> Lewis, et al., 1984	Illinois Pondweed	3
<i>Potamogeton pectinatus</i>	Sago Pondweed	1, 2, 3
<i>Potamogeton pusillus</i>	Grassleaf Pondweed	3
<i>Sagittaria kurziana</i>	Spring Tape	3
<i>Utricularia sp.</i>	Bladderwort	1, 2, 3
<i>Vallisneria americana</i>	Eelgrass	1, 2, 3
<i>Zannichellia palustris</i>	Horned Pondweed	3
<b>Natant (Floating) Plants</b>		
<i>Azolla caroliniana</i>	Water Fern	3
<i>Azolla sp.</i>	Water Velvet	1, 2
<i>Eichornia crassipes</i>	Water Hyacinth	1, 2, 3
<i>Lemna sp.</i>	Duckweed	1, 2, 3
<i>Luziola fluitans</i> ( <i>Hydrochloa caroliniensis</i> )	Southern Watergrass	3
<i>Nelumbo sp.</i>	Lotus	1, 2
<i>Nuphar luteum</i>	Spatterdock	3
<i>Nymphaea mexicana</i>	Yellow Waterlily	3
<i>Nymphaea sp</i>	Water Lily	1, 2

**Table I**(continued)

<b>Natant (Floating) Plants (continued)</b>		
<i>Pistia stratiotes</i>	Water Lettuce	1, 2, 3
<i>Salvinia rotundifolia</i>	Common Water Fern	1, 2, 3
<i>Salvinia sp.</i>	Water Fern	1, 2
<i>Victoria regia</i>	Giant Waterlily	1, 2
<b>Emergent/Terrestrial Plants</b>		
<i>Alteranthera philoxeroides</i>	Alligator Weed	1, 2, 3
<i>Avicennia germinans</i>	Black Mangrove	1
<i>Drosera rotiflora</i>	Butterfly	2

In fresh-water systems, manatees exhibit a preference for locally-abundant species of submerged aquatic macrophytes. In Florida, the most heavily utilized forage species include *Myriophyllum spicatum*, *Hydrilla verticillata*, *Ceratophyllum demersum*, *Vallisneria americana*, and *Sagittaria spp.* (Hartman, 1971 in Husar, 1978), among others (see Best, 1981; Ledder, 1986; and Hurst and Beck, 1988 for complete ingested species list). Hartman (1971) noted that manatees selectively foraged on the young leaf blades and root stalks of *Vallisneria* and on the young growing apices, termed "coontails," of *Ceratophyllum*. The same author observed manatees in groups foraging preferentially in areas with dense *Hydrilla* growth. Such feeding aggregations were observed to cause local reductions in aquatic plant density, and Hartman (1971) noted that caves and tunnels were eaten through thick clumps of *Hydrilla* by intense feeding activities of even a small number of manatees. More recently, Ledder (1986) found that *Hydrilla verticillata* constituted the highest percentage (12.7%) of any fresh-water macrophyte in gut samples obtained from 84 carcasses recovered from south Florida waters. Ledder also reported that, while assorted algae made up 6.0% of the manatee diet, it was found only in the digestive tracts of manatee carcasses recovered from the west coast of Florida. Hartman (1971, 1979) found that manatees ingested epiphytic algae (species of the genera *Enteromorpha*, *Spirogyra*, *Cladophora*, *Oscillatoria*, *Gracilaria*, and *Ectocarpus*) and epifaunal invertebrates (e.g., insect larvae, amphipods, mollusks, and shrimp). The latter dietary components may provide additional protein to a relatively protein-poor vegetarian diet. In more turbid fresh waters or in other areas where little, if any, submerged aquatic vegetation can grow, manatees feed primarily on floating macrophytes, such as *Eichhornia crassipes* (water hyacinth), *Pistia stratiotes* (water lettuce), *Lemna sp.* (duck weed) and *Salvinia rotundifolia* (water fern), and emergent vegetation, such as *Alteranthera philoxeroides* (alligator weed), (Hartman, 1971; Campbell and Irvine, 1977; Bengston, 1981; Ledder, 1986). Algae attached to boat hulls and crab pot buoy lines is also occasionally eaten when available (Hartman, 1979; personal observation).

Large numbers of manatees residing in a small area can quickly devour available forage and must often travel relatively long distances from aggregation sites to obtain sufficient food. Bengston (1983) found that manatees wintering in the St. Johns River and frequenting the Blue Spring warm-water refuge quickly devoured available vegetation in the refuge by late autumn. Manatees seeking thermal refuge in Blue Spring were then observed traveling into cooler river waters, requiring round-trip travel periods of 3 hours per day (excluding foraging time), to obtain sufficient food during the rest of the season. Manatees may also use alternate food resources when common forage materials are reduced or when their diets need supplementing. Frohlich and Lefebvre (personal communication) observed manatees browsing on bryozoans (*Bugula neritina*) encrusting a seawall in a thermal refuge on the Orange River and attributed this unusual feeding behavior to a lack of aquatic vegetation in the vicinity. Zoodsma (1991) observed a manatee mouthing a cannonball jellyfish (*Stomolophus meleagris*) in the warm-water discharge canal of the Container Corporation of America plant on the Amelia River in northeastern Florida. It could not be ascertained whether or not the manatee ingested the jellyfish, but this observation indicates that manatees may eat certain species of cnidarians when they are available in areas of limited forage. Although not generally considered coprophagic, manatees have also been observed consuming manatee feces on occasion (Hartman, 1971). This activity may allow manatees to obtain otherwise scarce essential vitamins produced by intestinal bacteria, as has been shown in other mammalian herbivores (Slade and Hintz, 1969; Anthony, 1974; Kornegay, et al., 1977), or it may be a means by which the guts of manatee calves are inoculated with essential cellulose digesting bacteria (Odell, et al., 1993).

On a daily basis, manatees spend prolonged periods of time feeding. Hartman (1979) first noted that manatees foraged on aquatic plants for 6 to 8 hours each day in 23°C waters. Bengston (1983) determined that manatees spent an annual average of 5.1 hours per day foraging on natant and submerged macrophytes. Etheridge and coworkers (1985), observing manatees on a continuous basis in the Crystal River, found that manatees spent approximately 5 to 6 hours feeding on hydrilla each day.

Bengston found that manatees spend more time foraging in late autumn (6.9 hours/day) than in early spring (3.2 hours/day). Autumnal foraging periods may be longer, because manatees must consume relatively lower-quality vegetation, in the form of senescent material, in preparation for the greater energy demands of the coming winter (Bengston, 1983). The decrease in spring foraging time may be due to the availability of higher-quality vegetation and more extensive production of plant material during this peak growth season.

Etheridge and coworkers (1985) found that free-ranging adult manatees can eat approximately 7.1% of their own body weight each day in wet-weight *Hydrilla*. Earlier estimates, based on Bengston's (1983) observations, indicated that manatees could consume between 4 to 9% of their body weight in wet-weight vegetation every day. A 700 kg adult manatee can, therefore, consume between 30 to 65 kg of vegetation per day in natural systems, which represents large areas of benthic coverage by aquatic plants (see **Table II** for study-specific summary). Studies estimating wet-weight vegetation consumption rates for captive manatees are comparable and indicate that these animals can consume between 8 and 11% of their body weight daily (Lomolino, 1977; Best, 1981).

Because manatees eat large quantities of submerged vegetation, qualitative research was performed during the 1960s to determine the effectiveness of manatees as a natural control for aquatic pest weeds like *Hydrilla* (Allsopp, 1960, 1961; Sgueros, 1966; MacLaren, 1967; all in Etheridge, et al., 1985). Inherent biological factors, such as metabolic requirements for year-round warm water, low total population numbers, relatively long digestive system retention time, and the target weed species' high levels of productivity in Florida waters, limit the manatee's capacity in this role. Etheridge and coworkers calculated that 18 manatees per hectare would be needed in Crystal River alone just to maintain the measured standing biomass of hydrilla at a constant level (Etheridge, et al., 1985).

**Table II Manatee Consumption Rate of Identified Aquatic Plants**

Estimated Area of Plant Standing Biomass Consumed (m <sup>2</sup> /day)	Mean Wet-weight Consumption Rate (kg/day)	Species Consumed in Referenced Study	Study	Year
-	80	-	*Severin	1955
-	9	-	*Crandall	1964
-	50	-	*Pinto da Silveria	1975
-	12	(see referenced text)	Hartman	1979
-	28	Lactuca lactuca (lettuce)	Best	1981
-	33.2	Panicum purpurascens Ceratophyllum demersum Vallisneria americana Najas guadalupensis Eichhornia crassipes Pistia stratiotes	^Bengston	1983
-	43-57.3	Lactuca lactuca (lettuce) Eichhornia crassipes	Lomolino and Ewel	1984
13.2	33.4	Hydrilla verticillata Vallisneria americana	^Etheridge, et al	1985
45.6	**33.2	Syringodium filiforme	^Provancha and Hall	1991

\*

in Bengston (1983)

\*\*

Authors used consumption rate value obtained from Bengston (1983) study.

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Values from these studies are for **free-ranging** manatees; all others are for

Seagrasses form the largest component of the West Indian manatee's diet in most areas throughout their coastal range in Florida and in the Caribbean (Ogden, 1976; Hartman, 1971, 1979; Zieman, 1982; Thayer, et al., 1984; Ledder, 1986). Hartman (1971, 1979) reported that the marine diet of manatees consists of *Thalassia testudinum* (turtle grass), *Syringodium filiforme* (manatee grass), *Halodule wrightii* (cuban shoal grass), *Ruppia maritima* (widgeon grass or ruppia), and *Halophila* spp. *Ruppia maritima* is also an important component of the manatee diet in brackish and marine waters and was shown to account for 7.4% of the manatee diet in one study (Ledder, 1986). *T. manatus* feeds predominantly on seagrasses in near-shore, shallow waters averaging approximately 1-3 m deep. For instance, manatees observed during the winter in Hobe Sound fed primarily on *Halodule* in water ranging from 0.4 to 1.6 m in depth (Lefebvre and Powell, 1990). These authors also noted that during the same season manatees that frequented Jupiter Sound fed on mixed seagrasses, including *Halodule*, *Syringodium*, and *Thalassia*. Preferred foraging depth for manatees is a function of not only their metabolic energy expenditure and physiological diving depth range but also seagrass availability, and that depth may be partially determined by the seagrass species sought. All species of seagrass found in Florida waters are available within the observed depth range associated with manatee foraging activities, but the species composition of seagrass communities is determined by local and/or regional conditions (e.g., ambient turbidity, sediment character, current velocity, etc.). *Halodule* is generally distributed along the shallow near-shore fringe of seagrass communities in waters shallower than 1 m, but it is often mixed with turtle grass and manatee grass; and cuban shoal grass may become the dominant, albeit sparse, seagrass in deep waters (between 15 and 20 m) where sufficient sunlight penetrates, such as in areas adjacent to Florida Bay (Zieman, 1982). Species within the genus *Halophila* (predominantly *Halophila decipiens*) are found throughout the depth distribution of other seagrasses from near-shore subtidal waters to waters 40 m in depth, depending on ambient water clarity (Josselyn, et al., 1986; Williams, 1988; Kenworthy, 1992; Kenworthy, personal communication). These seagrasses are diminutive relative to other seagrasses, form low canopies, rapidly expand through vegetative growth, are adapted to low light conditions, and in shallow waters are typically found in disturbed habitats or areas where water-column transparency limits the distribution and, hence, competition from other seagrass species (Williams, 1988). Manatee grass is often found in a dense narrow margin between dominant shoal grass (*Halodule*) and deeper turtle grass, but it is also found intermixed with both grasses in patches within dominant turtle grass meadows (personal observation) or in deeper waters (from 12 to 15 m) if overlying waters are clear enough (Zieman, 1982; Zieman and Zieman, 1989). Turtle grass is the dominant species found between 1 to 10 m in most areas of its range; however, on the east coast of Florida three seagrasses, along with species of *Halophila*, can be found either intermixed or singly within their relative depth distributions dependent upon local physical conditions (turbidity, sediment composition, salinity, temperature extremes, frequency of exposure, etc.) and levels of community disturbance. Ambient turbidity is critical to the attenuation of light and in many areas of Florida, such as the Indian River and Tampa Bay, restricts the majority of seagrass growth to waters less than 2 m deep (Zieman and Zieman, 1989; Penny Hall, personal communication). On the east coast of Florida cuban shoal grass and manatee grass tend to be codominant, especially in the Indian River and northern Biscayne Bay; and turtle grass is much less abundant in most areas (Lefebvre and Kenworthy, personal communication).

Some seagrass-associated invertebrates and algae are also incidentally consumed during

foraging activities. Hurst and Beck (1986) identified invertebrates in manatee ingesta, including a bryozoan (*Bugula neritina*) and unidentified hydroids and sponges, most probably incidentally ingested with seagrasses. In the spring of 1982, 41 manatee carcasses were recovered in the vicinity of the Caloosahatchee River estuary, most of which had consumed numerous tunicates of the species *Molgula occidentalis*, *M. manhattensis*, and *Styela sp.*, presumably while foraging on seagrass (O'Shea and Rathbun, 1982).

Husar (1978) noted that several marine algae genera have been recognized as being included in the manatee's diet, including *Acetabularia*, *Caulerpa*, *Gracilaria*, *Halimeda*, *Hypnea*, *Penicillus*, *Polysiphonia*, *Sargassum*, and *Udotea*. Ledder (1986) also reported the species of algae, either epiphytic on seagrasses or drift algae associated with seagrasses, that are most likely regularly ingested by manatees while foraging on seagrass. Algal species from all major algal classes were represented in her list.

Manatees have also been observed feeding on drift and attached macroalgae independent of seagrass association in marine systems. Lewis and coworkers (1984) observed manatees as they fed on red algae (*Gracilaria tikvahiae*) and on green algae (*Ulva sp.* and *Chaetomorpha linum*) adjacent to a shallow sandbar near the mouth of the Alafia River in Tampa Bay. This is an area characterized by poor water quality and high turbidity where seagrasses have been eliminated and can no longer grow. The authors of this study concluded that algae may be an important food source for manatees that frequent Tampa Bay (with an estimated loss of over 81% of its historical seagrasses). Hartman (1979) also stated that manatees that frequent turbid waters with "impoverished vascular flora" supplement their diet by feeding on algae, among other vegetation. Many species of algae, including *Ulva lactuca*, *Sargassum filipendula*, *Gracilaria cervicornis*, *G. verrucosa*, *Enteromorpha intestinalis*, *E. compressa*, *Chara zeylanica*, *Chaetomorpha brachygonia*, and *Caulerpa prolifera*, have also been identified in ingesta taken from recovered manatee carcasses (Hurst and Beck, 1988). Zoodsma (1991) recently reported that manatees that frequent south Georgia coastal waters routinely eat algae, including *Ulva lactuca*, *Gracilaria sp.*, and *Enteromorpha sp.* Coastal waters in southeast Georgia are devoid of seagrasses because of extreme turbidity and large tidal variations, so manatees are relegated to, and have been observed feeding on, algae and emergent or terrestrial vegetation in this region.

Evidence suggests that manatees feed both on seagrass shoots above the sediments and on the substantial seagrass rhizome-root biomass below the sediment surface (**Table III**). Hartman (1979) and Provancha and Hall (1991) observed manatees' feeding only on seagrass blades, while Packard (1981, 1984), Zieman (1982), and Lefebvre and Powell (1990) observed manatees' feeding on entire seagrass plants. The latter authors described a "rooting" foraging behavior, where manatees displaced sediments from around seagrass rhizomes, leaving feeding troughs 1 to several meters in length, with a mean width of 45 cm. Packard (1981 and 1984) also noted that manatees that were rooting for seagrass rhizomes used their forelimbs to dig into the sediment to help remove root material. Equipped with this adaptive behavior, manatees may graze on shoots and rhizomes in meadows with underlying firm sediments or in dense *Thalassia* beds (Lefebvre and Powell, 1990; Lefebvre, personal communication). Manatees may, however, be less capable of excavating root material from the tough and relatively deep (10 to 20 cm below the sediment surface) *Thalassia* rhizome mat, or hard sand-shell substrates, and may, therefore, prefer more sparsely covering forms with shallow roots (buried 3 to 5 cm below the sediment surface), such as *Syringodium* and *Halodule*. Under the latter circumstances, manatees pull shoot material up in long paths, decreasing blade height by as much as 80% (Provancha and Hall, 1991). Manatees that forage on seagrasses located in areas with loose, sand-silt sediments can more easily ingest rhizome material because of inherent morphological constraints associated with their feeding apparatus (**Table III**) (Zieman, 1982; Packard, 1984).

**Table III Manatee Consumption of Seagrass Plant Components**

Seagrass Species Consumed	Plant Parts Consumed	Mean % Biomass Consumed (Impacted Area m <sup>2</sup> )	Sediment Type	Region	Researcher	Year
* <i>H. wrightii</i> / <i>S. filiforme</i>	shoots and rhizomes	- -	loose sand and mud	Hobe Sound	Packard	1981
<i>H. wrightii</i> / <i>S. filiforme</i> / <i>T. testudinum</i>	shoots and rhizomes	- -	loose sand/silt (no rhizome removal from firm sediments)	South Florida	Zieman	1982
<i>H. wrightii</i> / * <i>S. filiforme</i>	shoots and rhizomes ("rooting")	46 to 65% 93 to 96% (179,000m <sup>2</sup> )	loose sand/silt	Jupiter Sound	Packard	1984
* <i>H. wrightii</i> / <i>S. filiforme</i>  <i>T. testudinum</i>	shoots and rhizomes  shoots	79 to 89% 46 to 67%  65% (grazed plots avg. 27m <sup>2</sup> )	loose sand/silt and compacted shell mash	Hobe Sound and Jupiter Sound	Lefebvre and Powell	1990
* <i>S. filiforme</i>	shoots only	30% **(1,755,000 m <sup>2</sup> )	firm sand/shell	Banana River	Provanca and Hall	1991

\* preferred component of manatee diet; most biomass removed by grazing activities

\*\* estimate based upon Bengston's (1983) consumption rate figure of 33.2 kg plant material/manatee/day (wet weight) and 60-day continuous manatee residence period/year

Zieman (1982; personal communication) and Thayer and coworkers (1984) have proposed that large herbivores, predominantly green turtles and manatees, could have been responsible for extensive regional foraging disturbance to seagrasses if former population levels were sufficiently high. It is not unreasonable to imagine that large herds of herbivorous manatees could cause detrimental effects on seagrasses on a local or even a regional basis. In fact, when large numbers of manatees aggregate in areas such as warm-water refuges and feed in groups of from 3 to 15 individuals, they can effectively denude accessible seagrass beds (Packard, 1981). Packard (1981) found that seagrass beds accessible to manatees (in waters greater than 1 m) in Lake Worth and Jupiter Sound and consisting predominantly of manatee and cuban shoal grass were denuded by heavy manatee foraging disturbances within two months of the start of the cold season. Lefebvre and Powell (1990) found that even small groups of manatees (2 individuals) in Hobe Sound and Jupiter Sound during a mild cold season fed extensively on both *Halodule wrightii* and *Syringodium filiforme*, causing dramatic reductions in plant biomass at sampled locations within preferred foraging areas (**Table III**). In this latter study, both seagrasses exhibited rapid growth and recovery during the spring and summer, a period of time when seagrass growth is at its seasonal peak and manatees disperse from this area. The recovery was such that no significant foraging effects were noted the following year prior to the return of manatee aggregations. Similar findings have been made using exclosures to protect seagrass beds from seasonal manatee herbivory in the upper Banana River (Lefebvre and Provancha, personal communication). The migratory nature of manatee behavior typified by the seasonal use of warm-water refuges apparently permits seagrass recovery in seasonally-impacted areas and may protect these areas from permanent damage caused by overgrazing.

Lefebvre and Provancha also found that manatees tended to feed on the edges of sparse seagrass beds and that, much like green turtles, manatees returned to formerly-grazed areas to feed from year to year. Increased nutritional value, shoots with fewer epiphytes, more available protein per kilogram of seagrass consumed, and altered substrate texture may contribute to regrazing of previously cropped seagrasses if the time period between foraging events is short (Thayer, et al., 1984). Repeated cropping of *Thalassia* by manatees, although not substantiated in any study to date, may cause damage to seagrass meadows if large numbers of manatees converge on a site where this seagrass is the primary constituent. Thayer and coworkers (1984) reported that intense grazing by green turtles combined with subsequent regrazing of *Thalassia* blades tends to cause measurable stress to the plants in terms of alterations in leaf width, leaf production, and rhizome storage capacity. These same researchers found that, if turtle grass blades are artificially cropped more than 6 times in a growing season, the rhizome exhausts stored nutrients, and turtle grass beds can be irreparably damaged or lost. Researchers have proposed that manatee grazing in turtle grass can, however, maintain seagrass community diversity. Packard (1984) proposed that manatee disturbance in *Thalassia* meadows would tend to maintain species diversity in seagrass communities by opening bare patches to colonization by pioneer species, such as *Halodule* and *Syringodium*. Shoal grass and manatee grass are probably poor competitors for space in manatee-grazed turtle grass plots, as recent observations indicate that at least in some locations manatees do not readily consume turtle grass rhizomes (Lefebvre and Powell, 1990). This indicates that manatees may not do as much long-term regional damage to *Thalassia* meadows as was previously proposed, although detrimental effects may be extensive in local areas where other forage species, such as cuban shoal grass or manatee grass, are unavailable.

Although studies have examined manatee foraging effects on seagrass systems, no research has

been performed that adequately addresses manatee digestive efficiency when these animals are subsisting on a diet of seagrass in marine systems. Estimates of the amount of seagrass consumed on a daily basis must be made by using information collected from feeding experiments on captive and free-ranging animals where manatees have been fed terrestrial and fresh-water vegetation (Lomolino, 1977; Lomolino and Ewel, 1984; Best, 1981; Bengston, 1983; Etheridge, et al., 1985). Burn (1986) postulated that, because seagrass has reduced quantities of lignin in the walls of the plant cells, the digestive efficiency of manatees that eat seagrass could be even higher than that measured in his and other studies. In combination with digestive efficiency and seagrass consumption information, previously-determined regional values for seagrass productivity can be used to calculate the carrying capacity of local systems (Zieman, 1982; Zieman and Zieman, 1989). The release of captive manatees into enclosed staging areas within seagrass beds may provide the opportunity to collect this needed information (Lynn Lefebvre and Bob Turner, personal communication).

Manatees show apparent feeding preferences in some areas. Hartman (1971) observed that manatees preferred *Ceratophyllum* in areas where it occurs with *Myriophyllum*. Ledder (1986) identified *Halodule wrightii* as comprising the largest portion (24.4%) of the manatee diet in south Florida. A possible preference for this species is further confirmed by the fact that manatee grass is equally abundant and available to manatees in this region and is probably higher in total available biomass than Cuban shoal grass (Lefebvre, personal communication). Lefebvre and Powell (1990) observed manatees' feeding on *Halodule*, while leaving adjacent *Syringodium* untouched at one site in Hobe Sound (see **Table III** for study-specific seagrass preference summary). *Halodule* rooted in sediments containing noticeable quantities of peat was also preferred over adjacent conspecific plants. It was speculated that this was due in part to some quality of the peat-grown plants, such as better taste or higher nutritive value, or perhaps it was because of the softness of the sediment, which made it easier for the manatees to consume root material. Manatees may also show preferred foraging strategies dependent upon a combination of factors, such as seagrass density and sediment character. Packard (1981, 1984) noted that manatees predominantly "rooted" seagrasses, eating entire plants in an area adjacent to the Loxahatchee River estuary. She proposed that this observed behavior would tend to favor the selective disturbance of more dense *Thalassia* and *Syringodium* meadows. Packard (1981) hypothesized that rooting versus grazing feeding behavior may be dependent upon seagrass density. She observed random grazing in sparse grassbeds and rooting in dense meadows; however, as mentioned above, Lefebvre and Powell (1990) observed extensive manatee foraging on the edges of previously-grazed, sparse seagrass beds. The effect of manatees' feeding on ungrazed, dense seagrasses by rooting may stimulate the generation of more nutritious shoots or growth from rhizomes left behind. It is also possible that this type of manatee foraging behavior may open substrate to colonization by more desirable vegetation and create higher-quality feeding sites in existing seagrass beds. This type of behavior has been shown for green sea turtles (*Chelonia mydas*) foraging on *Thalassia* in the Caribbean (Bjorndal, 1979; Mortimer, 1981). Bjorndal (1979) surmised that green turtles repeatedly crop patches of turtle grass in order to feed on the relatively protein-rich new growth of the trimmed shoots. Green turtles do, however, differ from manatees in that they have a higher degree of long-term home-site fidelity, so cropping of seagrass patches would provide greater realized benefits to *C. mydas* individuals. Preferences based on vegetation density are also reported in fresh-water systems for manatees. Hartman (1979) noted that manatees that feed on fresh-water macrophytes appear to actively seek and prefer foraging in areas with dense vegetative growth. The majority of Hartman's observations were made when manatees were feeding on hydrilla, which has a

92% water content (in Etheridge, et al., 1985). Manatees may need to consume larger quantities of *Hydrilla* relative to other, more nutritious aquatic macrophytes, such as eelgrass (*Vallisneria americana*), and thus use this observed high-density feeding strategy when eating *Hydrilla*.

Other studies have shown that manatees are flexible, opportunistic herbivores with no identifiable feeding preferences. Bengston (1983) determined that manatees showed no preference between *Eichhornia crassipes*, *Pistia stratiotes*, *Vallisneria americana*, or *Najas guadalupensis* when offered these plants from canoes in Blue Spring. When equally available, equivalent amounts of these macrophytes were consumed by manatees as they foraged in Blue Spring. Manatees also feed on emergent and/or terrestrial vegetation adjacent to or falling into inhabited waters. Hartman (1979) noted that observations were made of manatees in Georgia as they fed on smooth cord grass (*Spartina alterniflora*). Hardisky (1979) reported that manatees grazed on tidally-submerged beds of smooth cord grass which had been planted on dredge spoils in coastal Georgia, and Rathbun and Bonde (1982) reported manatees' feeding on emergent *Spartina* along the Hercules power plant effluent canal in the same area. Baugh and coworkers (1989) found indications of manatees' browsing on smooth cord grass along the shore of the Halifax River in Volusia County. They also observed manatees' foraging on *S. alterniflora* in fringing marshes along tidal creeks in Cumberland Sound during high tide and described their foraging habits and local impacts in this extensive system. O'Shea and Kochman (1990) suggested that manatees regularly traveled to estuarine areas where salt-marsh grass, accessible only at high tide, was the principal forage species available. Zoodsma (1991) observed manatees' foraging on smooth cord grass in southern coastal Georgia and examined stomach contents of specimens from this region; she reported that *S. alterniflora* is the predominant forage species eaten by manatees in this region. In some cases, manatees' feeding through high tide in flooded salt-marsh systems have become stranded as the tide recedes (Barb Zoodsma and Jim Valade, personal communication). Submerged vegetation is limited to green, red, and brown algae in marine and estuarine environments in both Georgia and South Carolina, so manatees that travel to these regions must rely on other available plant material for food. O'Shea (1986) observed manatees' wintering in Blue Spring, a natural spring maintaining sparse natant and submerged vegetation, feeding on Live Oak (*Quercus virginiana*) mast. In this study, 19 individual manatees were reported as periodically returning to acorn-filled, biogenic depressions in the sediment over which Live Oak canopies spread. Here, they sifted through the sediment and actively foraged on the abundant fruits. O'Shea calculated the nutritive value of the acorns based on estimated availability (the number that feeding grackles liberate from an oak tree which then fall into the spring) and their previously-determined caloric content. His findings indicate that mast can provide manatees with a significant, locally-dense food source during periods of Live Oak fruit production. Mast also contains large amounts of fat, sugar, starch, and protein relative to other vegetable material that manatees eat and may, therefore, augment seasonal dietary needs. Manatees have been observed feeding on the leaves and stems of such terrestrial vegetation as *Distichlis spicata* (salt grass), *Panicum purpurascens* (para grass), *Panicum hemitomon* (Maidencane), *Paspalum repens*, *Paspalum vaginatum*, *Phragmites australis* (giant reed), *Phragmites communis* (reed), *Alteranthera philoxeroides* (alligator weed), *Cocus nucifera* (coconut palm), *Sambucus canadensis* (common elder), *Scirpus californicus* (giant bullrush), and *Serenoa repens* (saw palmetto) (Hartman, 1979; Tiedeman, 1980; Reynolds, 1981; Bengston, 1981; Powell and Waldron, 1981; Zoodsma, 1991). The leaves of *Magnolia grandiflora* (southern magnolia), *Ficus sp.*, and exotic species [*Schinus brasiliense* (brazilian pepper) and *Casuarina equisetifolia* (australian pine)] along with native species, such as *Rhizophora mangle* (red mangrove), and those of other mangrove species have also been

found in the stomachs of dead manatees in Florida (Ledder, 1986; Hurst and Beck, 1988). Ledder (1986) noted that the leaves of shoreline vegetation, like mangroves, may enter into the manatee's diet via a detrital pathway as well as being directly consumed by these herbivores. Leaves that fall into adjacent waters are transported into areas with submerged vegetation and begin to deteriorate. Manatees that forage on seagrasses or other aquatic vegetation then incidentally ingest the decaying leaf matter. Ledder (1986) observed that, while mangrove leaf components were found in 92.9% of the sampled manatee intestines, the leaf components compose only 5.9% of the total measured ingesta. She also noted that most of the waxy-cuticled, highly-visible mangrove pieces included in the samples were small, composed of only several cells, thus indicating their detrital origin. There is also considerable anecdotal evidence that manatees browse lower mangrove leaves that overhang accessible waters (Lefebvre, personal communication). Grass trimmings from mowing or trimming activities may also be eaten by manatees after being cast upon surface waters and coalescing in mats. Manatees are also capable of pulling themselves at least partially out of the water to feed on terrestrial grasses in areas where vegetated lands are near waters accessible to manatees. Lefebvre (personal communication) has often seen manatees that forage by pulling themselves up to the shore to eat shoreline grasses in Brevard County waters.

Manatees have also been observed supplementing their protein-poor diets by eating fish captured in gill nets. Powell (1978) interviewed fishermen from the northern coast of Jamaica who observed manatees that habitually steal scombrid and carangid fishes caught in their nets. Powell himself observed manatees' cruising gill nets in a sequential circuit, apparently looking for entrapped fish. Sharon Tyson (personal communication) has also observed manatees' eating fish carcasses from waters adjacent to fish-cleaning tables in southeastern Florida. She noted that manatees select specific types of fish at these sites, eating only the carcasses of flounder (*Paralichthys sp.*), redfish (*Sciaenops ocellata*), and grouper (*Epinephelus sp.* or *Mycteroperca sp.*). Manatees probably ingest fish carcasses opportunistically, as live, fast-swimming fish are generally considered an inaccessible resource for a relatively slow-swimming animal with the jaw and mouth morphology of this herbivorous species. Some fish may, however, be occasionally captured by manatees. While Tyson was monitoring the activities of two manatees as they foraged in a basin congested from surface to bottom with free-floating seagrass blades, she observed one manatee surface with a live flounder in her mouth. The manatee had been able to capture the flounder, presumably because of the confining nature of the blind, sea-walled basin and the thick seagrass mat in the overlying water column, and was in the process of devouring it when a second manatee attempted to steal the meal from its mouth. Manatees have also been observed eating carcasses of terrestrial animals. Bonde (personal communication) reported that a dead rat that floated out from under a Brevard County dock was quickly devoured by a manatee that he was observing at the time.

## SEAGRASS HABITAT THREATS

Most recognized threats to manatees and their habitat are caused either directly or indirectly by human-related activities. Florida's human population has increased exponentially over the last 40 years, and further dramatic growth from immigration into the state will continue into the foreseeable future. Residents and huge numbers of seasonal tourists adversely affect coastal marine resources critical to the continued existence of the manatee. Development of coastal property for residential and

commercial purposes, storm-water runoff, upland agricultural activities, increased sewage discharge, and aquatic recreational and commercial activities decrease water quality and lead to a reduction in available foraging habitat for manatees and other marine herbivores, such as green turtles. With the loss of seagrass communities comes a loss of sediment and shoreline stability, faunal diversity, and primary productivity. After seagrasses have been eliminated from an area, sediments are more easily suspended, adding to increased turbidity and causing a situation that cannot easily be mitigated by planting new seagrass plants because of the reduced light levels and change in sediment character (Kenworthy and Haurert, 1990).

Clearing of upland vegetation for development and agricultural purposes, along with the channelization of meandering rivers and streams characteristic of water management practices in Florida, increases the rate of erosion and sediment transport into near-shore waters. This, in turn, increases turbidity in waters that overlie seagrass beds and in some areas drastically increases sediment deposition rates (Thayer, et al., 1975). Increased sediment loads can smother seagrasses, change the redox potential of rhizome-penetrated sediments, or cause increased water column turbidity, robbing seagrasses of the high levels of incident light required for metabolic functions (Zieman, 1982; Kenworthy and Haurert, 1990). Florida seagrasses require at least 15% to 25% of sunlight incident to the surface of overlaying waters (Kenworthy and Haurert, 1990; Kenworthy, Hobe Sound study, unpublished data). Such high light requirements mean seagrasses are affected by even minor increases in turbidity, which is now recognized as the predominant threat to seagrass communities.

Channelization of rivers and streams can alter the input of fresh water into a system such that seagrass species distributions are changed or even eliminated from a specified area (Thayer, et al., 1975; Zieman, 1982). This is especially true for halophilic turtle grass, which requires salinities of 20 to 35 ppt (Zieman, 1975). *Halodule wrightii* has a much broader salinity tolerance range (10 to 60 ppt) and often regional shifts in dominant community species occur when fresh-water input is either increased or decreased. Channelization of the fresh-water sheet flow above the Everglades has probably caused once dense meadows of shoal grass and *Ruppia maritima* to be largely replaced by turtle grass in Florida Bay (Zieman and Durako, personal communication). Increased runoff from developed land combined with channelized fresh-water systems can increase nutrient loading into waters overlaying seagrasses, promoting micro, epiphytic, and macroalgal growth, further limiting incident light penetration to seagrass blades. Increased chlorophyll levels caused by microalgal blooms caused by nutrient additions can increase attenuation of light in water and lead to seagrass disappearance from affected areas (Kenworthy, personal communication). Cultural eutrophication also has the potential of promoting extensive local growth of benthic macroalgae, such as *Dictyota spp.* and *Laurencia spp.*, which form dense meadows over existing seagrass beds that can persist for 6 months or more. Holmquist (1992) showed that ephemeral benthic macroalgae (*Laurencia sp.*) is capable of eliminating underlying turtle grass if the seagrass is covered for a period of 6 months, but deleterious effects to turtle grass, including root-rhizome deterioration, were observed over a much shorter period of coverage (Holmquist, personal communication). Recovery of turtle grass meadows progressed slowly and became apparent only after 18 months in this study. This algal competition is capable of "opening sizeable gaps in the seagrass canopy" through an interference mechanism which may include shading, preferential absorption of limited nutrients by overlaying algae, allelopathy, a shift in the pH of the sediments, and/or interference with dissolved gas exchange (Holmquist, 1992). These algae often detach from the bottom and form mobile, rolling fronts pushed along by currents, tidal forces, and

other turbulence that can potentially affect seagrass habitat kilometers distant from the site of original algal growth. Once openings are formed in the seagrass canopy, drift algae arriving in large clumps can be entrapped within the opening's perimeter "fence" of seagrass blades and limit the recovery of seagrass within the disturbed site for years.

The discharge of sewage into near-coastal waters has long been recognized as detrimental to seagrasses. An estimated 81% of Tampa Bay's historical seagrasses have been eliminated as a result of a combination of factors, which include shading effects from dock development and ephemeral algal growth in response to nutrient enrichment and near-shore buffering habitat loss (coastal development), but mostly from turbidity caused by nutrient enrichment from domestic sewage discharge and phosphate mining activities in Hillsborough Bay (Taylor, et al., 1973 in Zieman, 1982). Similar circumstances have led to an estimated 30% loss in seagrass habitat throughout the Indian River system (Brian Poole and Kalani Cairns, personal communication).

Petroleum product spills are recognized as having deleterious effects on seagrasses under special circumstances. *Thalassia* beds along the Bahia Sucia coast of Puerto Rico were decimated by a crude oil spill in 1973, when strong winds, extensive wave action, and shallow water combined to carry the oil down into the seagrass and overlaying sediments (Zieman, 1982; Zieman, et al., 1984). In most cases, however, where seagrass communities were examined both before and after a major oil spill, the seagrasses themselves showed little damage, but the faunal communities were usually severely affected (Mike Durako and Judd Kenworthy, personal communication). For example, recent surveys of Persian Gulf seagrasses off the coasts of Kuwait and Saudi Arabia showed minimal damage as a result of massive quantities of oil released into overlaying waters by Iraq during the Gulf War (Kenworthy, unpublished data, personal communication). Even highly-susceptible intertidal grass flats showed only minor blade density reductions there. Zieman and coworkers (1984) noted that most seagrasses are subtidal in nature, as they are susceptible to desiccation during prolonged periods of exposure, and have the bulk of their biomass (50-85%) underlying sediments. To a large degree, this insulates them from petroleum toxins, which remain suspended within the water column except when heavily mixed with sea water during storm events or when deposited on shallow grass flats during neap tides. Seagrass plants can rapidly deploy new blade growth from the starch reserves maintained in their rhizomes, and their blades grow out from a basal meristem. Significant damage to seagrasses via acute exposure to petroleum products is likely related to mean depth of overlaying waters and amount of sediment contamination and/or disturbance. Chronic effects on seagrasses from oil contamination may result from prolonged exposure, as in areas adjacent to marinas and to petroleum pumping, transport, drilling, and storage facilities. McRoy and Williams (1977, in Zieman, et al., 1984) found that sublethal levels of kerosene and toluene caused significantly reduced rates of carbon uptake in seagrasses, indicating decreased plant productivity. Chronic and acute effects of petroleum contamination may result in more dramatic damage in areas where seagrasses are at the extremes of their tolerance to particular physical parameters (i.e., salinity, temperature, turbidity, turbulence, desiccation, etc.). Seagrasses established in these areas would be under much greater stress than would those in areas with more optimal conditions, and petroleum product contamination could more easily exceed innate tolerance limits of the species in question (Zieman, et al., 1984).

One of the most severe direct adverse effects on manatee habitat is the damage done to seagrasses by boating activities in shallow coastal waters and estuaries (Zieman, 1976; Kenworthy, et

al., 1989). According to recent data maintained by the Florida Department of Environmental Protection, there were over 715,000 boats registered in Florida in 1992. Tens of thousands of out-of-state boaters also operate their vessels in state waters during vacations. First recognized in the late 1950s, the dredging of seagrass beds by the propellers of shallow-running vessels is the most obvious damage done to seagrasses by boaters (Phillips, 1960; Zieman, 1976). Zieman (1976) found that "prop scars" in Florida resulted from boats that run in waters less than 1 m deep at mean low water (MLW), and many of these scars were recognizable for as long as 5 years. In fact, Zieman noted that local fishermen used distinctive prop scars in turtle grass beds as navigational reference points from year to year. Propeller damage is most severe when *Thalassia* rhizomes are cut and excavated from sediments. Unlike manatee feeding scars in turtle grass, which tend to be small and distributed over a broad area, prop scars are often tens of meters in length, result in complete removal of rhizome and shoot biomass within the affected scar area, and can be locally abundant in areas of high boat traffic. Matthews and coworkers (1991) found that most areas in the Florida Keys had suffered losses of seagrass of between 10% to 20% due to repeated prop scarring and vessel groundings. Turtle grass is considered a "climax species" in terms of its successional ecological role. That is to say, *Thalassia* has a slow rate of rhizome elongation, low rate of population growth, few seeds, no seed reserve, poor seedling success, and low productivity relative to pioneer type species, such as *Halophila decipiens* and *Halodule wrightii*, which have some or all of the opposite characteristics (Williams, 1990 in Holmquist, 1992). As such, its root systems may not begin to grow until 1 to 2 years after the initial damage, by which time the character of the sediments surrounding the rhizomes may be dramatically altered and may not be able to support turtle grass growth without natural successional processes' first occurring (Zieman, 1976, 1982). Natural recolonization of prop scars may take 2 to 5 years or longer in some areas, but in other locations, such as the waters of Florida Bay or in areas exposed to high currents, recovery may never occur (Zieman, 1976; Durako, et al., 1992). Durako and coworkers (1992) working at Weedon Island in Tampa Bay have estimated that experimentally-produced prop scars in *Thalassia* beds will recover to natural short-shoot densities in approximately 3.6 to 6.4 years. Chronic disturbance to damaged seagrasses in areas of heavy boat traffic, such as around inlets or near channels, can lead to virtually immortal scars, which when added together over a large area can result in an extensive cumulative loss of manatee habitat. In a recent study performed in the Florida Keys, Kruer (unpublished data) determined that approximately 10,000 acres of seagrass have been damaged by prop scarring (Karen Steidinger and Frank Sargent, personal communication).

The effect of small-scale, direct disturbances, such as prop scarring, on shoal and manatee grass is less drastic. Both *Halodule* and *Syringodium* are fast-growing species with shallow, rapidly-expanding root systems which make them good colonizers of disturbed habitat through vegetative growth or possibly from seed (Zieman, 1976, 1982; Kenworthy, et al., 1988, 1989; Lefebvre and Powell, 1990). These characteristics allow rapid recolonization or primary colonization of disturbed sediments in a short period of time. Zieman (1976) noted that *Halodule* can "colonize an area in a few weeks when conditions are correct, and exists as an annual plant in many estuarine areas." Recovery of short-shoot densities in experimental prop scars adjacent to undisturbed *Halodule* beds estimated to require from 0.9 to 1.8 years in the interior of the bed (Durako, et al., 1992). Experimental prop scars around the less dense seagrass bed fringe were estimated to require from between 2.3 to 4.6 years to achieve the same density as that in the undisturbed interior bed (Durako, et al., 1992). This portion of the seagrass bed was, however, less dense than the interior region of the bed prior to experimental disturbance, making it unlikely that prop scars would ever achieve shoot densities similar to those of

the seagrass bed interior (Penny Hall, personal communication). It appears that prop-scar damage to shoal grass beds requires a relatively short recovery period when compared to the recovery time for turtle grass. After initial damage, long-term loss of seagrasses may result from continued heavy boat traffic or from strong current regimes. Under such circumstances, open sediments are regularly disturbed, causing a scouring effect that prevents recolonization of even pioneer seagrass species.

Boat traffic can also affect water-quality parameters critical to the maintenance of seagrass communities. Increased turbidity in the water column decreases the incident sunlight available to submerged plants for photosynthesis (Phillips, 1960; Odum 1963; Thayer, et al., 1975; Zieman 1982; Kenworthy, et al., 1988, 1989). Kenworthy and coworkers (1988, 1989) found that increased seasonal boat traffic on Hobe Sound was capable of doubling the effect of natural wind-generated wave energy. The increased turbidity caused by boat wakes in shallow water decreased the potential depth range of seagrasses in this region; seagrasses, predominantly *Halodule* and *Syringodium*, were only observed in waters less than 2 m in depth. Boat wakes, dredging, and some trawling activities are also capable of resuspending sediments which can directly smother seagrasses in other locations. Odum (1963) noted that dredging activities in Redfish Bay, Texas, caused localized smothering of *Thalassia* beds and increased turbidity, which caused a measured decrease in turtle grass chlorophyll content.

Boat traffic may also alter preferred habitat use by manatees. Manatees apparently avoid areas with heavy boat traffic, regardless of the location's habitat qualities. Kadal and Patton (1991) found that the southeast corner of Anna Maria Sound, an area distinguished by heavy manatee use, experienced a 58% decrease in manatee sightings shortly after an inactive marina was reopened in 1987.

Marine debris, mostly related to fishing activities, also poses both indirect and direct threats to manatees. Beck and Barros (1991) identified plastic bags, string, twine, rope, fish hooks, wire, paper, cellophane, synthetic sponges, rubber bands, and nylon stockings in the digestive tracts of dead manatees recovered from 1978 to 1986. These authors also noted that debris was present in the gastrointestinal tract of greater than 14% of all recovered manatee carcasses necropsied during this time period. Manatees presumably ingest human-discarded materials which have settled into submerged vegetation. Mortalities result from intestinal intussusception, acute peritonitis (caused mostly by punctures of the intestine), intestinal blockage and subsequent starvation, or massive infection. Manatees also are known to mouth crab pot lines (personal observation) and may occasionally directly ingest pieces of synthetic rope. Ingestion of such debris, especially if multiple types of plastics are consumed by an individual, may cause chronic or acute toxification of a manatee and may be responsible for far greater mortality than that identified by current pathological identifications (Beck and Barros, 1991).

Manatees also are at risk of entanglement in nets, ropes, and lines used by fishermen. Discarded or unattended fishing nets, lines and ropes, and monofilament fishing line have entrapped and subsequently killed 17 manatees in Florida and Puerto Rican waters from 1974 through 1991. These mortalities are broken down into different categories. Two manatee calves drowned in hoop nets in Putnam County, Florida, in 1979. Other types of nets, including trammel, cast, bait, and gill nets, have caused 7 manatee mortalities, including 2 in Puerto Rico. Lefebvre and coworkers (1989) also noted that gill and assorted fishery nets frequently entangle manatees in Caribbean countries, such

as Jamaica and Puerto Rico, and in most Central American countries. These authors reported that interviews with local fishermen indicated that unattended gill nets and beach seines are a major cause of manatee mortality in these countries. Four manatee deaths, mostly resulting from severe infections, are also attributed to entanglement in monofilament fishing line in Florida waters. Manatees become entangled, usually about the flippers and head, in long lengths of durable monofilament line discarded by careless fishermen. The thin line cuts into the animal's tissues, resulting in systemic infection. The manatee's propensity for "playing" with and chewing on crab trap lines has probably also resulted in the deaths of 4 manatees in Florida due to entanglement.

## RECOMMENDATIONS

Current estimates place the wintering manatee population in Florida at a minimum of 1,856 individuals (aerial synoptic survey data from FDNR for the winter of 1992). Protection of remaining habitat must be made a paramount regulatory issue if the manatee population is to recover in the United States. Educational programs that inform the public about the importance of submerged aquatic vegetation, effects of habitat destruction, and ways to avoid damage to these communities must be expanded to a statewide level. "Critical manatee habitat" (as defined by the U.S. Fish and Wildlife Service) in several natural warm-water refuges, including Crystal River, Homosassa Springs, and Blue Spring, is currently protected by federal and state programs. Boating speed zone restrictions are in place or are being implemented by the Florida Department of Environmental Protection for individually identified counties where manatee mortalities resulting from collisions with boats are greatest. Although gains have been made, more must be done to protect manatee habitat directly. The boating public in Florida must be further educated as to the adverse effects of their activities on manatee habitat, particularly with respect to the effects of marine debris and prop scarring. Information about these particular effects is available in certain regions of the state, but general documents should be developed and disseminated to all boaters using Florida waters. Future regulatory efforts must involve improving water quality for the maintenance and reestablishment of seagrasses and other aquatic vegetation and for limiting destruction of existing seagrasses by dredging, development, fishing, and boating activities. Seagrass mitigation, or the engineered replacement of seagrass habitat destroyed by human development activities, is not presently capable of consistently establishing seagrass communities that are functionally equivalent to those that have been destroyed. For this reason, seagrass mitigation should not be considered as an option to preservation of existing seagrass systems in Florida. Current mitigation techniques generally lead to the replacement of highly productive, dense, and biologically diverse established seagrass communities with those of limited productivity, sparse growth, and low diversity in areas where conditions are most often inadequate for the successful establishment of the intended community (Fonseca, 1989). This leads to a net loss in functional seagrass habitat or, at best, a tradeoff involving the exchange of an existing system with that of an ecologically dissimilar one (most often not even on a 1:1 spatial scale). This is especially true of areas where *Thalassia testudinum* has established its characteristic climax community. While mitigation is not an option over preservation, restoration techniques for areas once supporting seagrass growth should be further developed and encouraged in order to augment available habitat. Use of pesticides and herbicides in and around areas used by manatees must also be addressed in such regulatory efforts. Unless the habitat needs of the West Indian manatee are guaranteed, the Florida subpopulation will never be down-listed from its endangered status, and recovery of this species will not be possible.

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