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The Influence of Habitat Features on Selection and Use of a Winter Refuge by Manatees (*Trichechus manatus latirostris*) in Charlotte Harbor, Florida

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The Influence of Habitat Features on Selection and Use of a Winter Refuge by Manatees

(*Trichechus manatus latirostris*) in Charlotte Harbor, Florida

by

Sheri L. Barton

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
Department of Biology
College of Arts and Sciences
University of South Florida

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ABSTRACT

Investigating alternate winter refuges for Florida manatees is increasingly important as sustained warm-water discharges from industrial and some natural sites becomes more uncertain. This study examined habitat features of possible importance to manatees by comparing a winter refuge in Charlotte Harbor, FL (the Matlacha Isles canal system) to two nearby, seemingly similar sites that are not frequented by manatees during winter. Water temperature, salinity, boat traffic, canal depth, and tidal flushing were assessed at these sites. Additionally, this study examined when and how manatees use the Matlacha Isles refuge by documenting movements, habitat use, and behaviors of manatees during the winters of 1999/2000 through 2001/2002. Water temperatures had a profound influence on manatee selection of Matlacha Isles over the two comparison canal systems. Matlacha Isles did not experience the sudden drops in water temperature following cold fronts, extreme low temperatures, or long periods of temperatures below manatees' reported thermal tolerance of 18-20°C that were recorded in Matlacha Pass (ambient) and the two comparison canal systems. Heat retention within Matlacha Isles may be associated with greater water depth and lower tidal flushing. Salinity and boat traffic did not seem to influence site selection by manatees. During moderately cold weather, manatees occupying Matlacha Isles forage at night in nearby Matlacha Pass and return early in the morning to Matlacha Isles, where they primarily rest all day. Neither tidal state nor boat traffic levels affected manatee travel patterns into or out of Matlacha Isles. Manatees may passively thermoregulate in the warmer waters of Matlacha Isles during the day (when they are inactive) and sustain their body temperatures at night through the

heat generated during traveling to feeding sites and during ingestion (chewing) and digestion. During extreme or prolonged cold weather, Matlacha Isles provides inadequate warmth for manatees; during such times, most of them travel to a power plant on the Orange River, approximately 50 kilometers away. Findings from this study may inform resource managers as they consider attributes manatees find desirable or necessary in winter. Such information will help managers create new or enhance existing winter refuges to protect manatees.

INTRODUCTION

The Florida manatee (*Trichechus manatus latirostris*), a subspecies of the West Indian manatee, occupies the coastal, estuarine, and riverine habitats of the southeastern United States (Domning and Hayek 1986). Outside of winter, Florida manatees may be found as far west as Louisiana and as far north as Virginia, with occasional wanderers outside this range (Reynolds and Odell 1991; Reynolds and Powell 2002). Their winter range, however, is much more restricted because of physiological traits that limit their thermal tolerance (Irvine 1983, O'Shea 1988).

Manatees have a metabolic rate 17-22 % of that expected for an animal their size, a high rate of thermal conductance, and a limited capacity for thermogenesis (Irvine 1983). These traits allow manatees to subsist on a low-energy food source of aquatic and semiaquatic vegetation, while also causing them to be vulnerable to cold. Water temperatures of 15-20°C prompt physiological and behavioral changes in manatees, such as an increase in metabolic rate and migrations to warmer water (Irvine 1983). When exposed to water temperatures of 18-20°C for several days, captive manatees feed erratically, and feeding may cease altogether at temperatures below 15-18°C (Campbell and Irvine 1981). Examinations of carcasses suggest that extended periods of exposure to cold can cause manatees to die slowly as they stop feeding, use fat reserves, and eventually starve (Burgelt et al. 1984; O'Shea et al. 1985; Bossart et al. 2002). Short-term exposure to extreme cold can result in death from hypothermia (O'Shea et al. 1985), although Hartman (1979) observed manatees entering water as cold as 13.5°C. Manatees appear to be unable to survive for long periods of time in water temperatures lower than 16°C; however, lethal temperatures and exposure periods have not been well documented (Ackerman et al. 1995). Young manatees appear to have a higher vulnerability than adults to cold temperatures, perhaps because of excessive amounts of heat loss during cold weather, caused by such physical characteristics as their surface area:volume ratios

and lower amounts of insulation, and inadequate experience with seeking warm water (O'Shea et al. 1985).

To survive periods of cold weather, manatees need to seek refuge in areas with warm water. Generally, when water temperatures fall below 20°C, many manatees migrate to warm-water refuges (Hartman 1979; O'Shea 1988; Lefebvre et al. 1989; Laist and Reynolds 2005a and b). Moore (1951) suggested that the historical winter range of Florida manatees existed within the southern regions of Florida and at natural warm-water springs, with the northernmost boundaries being the Sebastian River on the east coast and Charlotte Harbor on the west coast. Recent development of coastal habitats, including the introduction of industrial warm-water effluents and obstruction of access to some springs, has helped to alter and expand the winter range of Florida manatees. Whereas most of the winter refuges remain within central and southern Florida (U.S. Fish and Wildlife Service 2001), at least 60% of all Florida manatees now rely on 10 major power plant effluents and 15% rely on 4 major warm-water springs to survive periods of cold weather (Laist and Reynolds 2005a and b). Some currently used springs (at Crystal and Homosassa Rivers and Blue Spring) lie well north of the boundary of the historical winter range suggested by Moore (1951), and Laist and Reynolds (2005a and b) suggest that springs in the northern and central parts of Florida could become important warm-water refuges in the future, if access to them is restored for manatees.

One of the major threats facing manatees is the potential loss of warm-water refuges (U.S. Fish and Wildlife Service 2001). Effluents from power plants can be unreliable as they may cease temporarily because of routine maintenance and equipment failure. When these temporary cessations have occurred in the past, some manatees remained at or near the site, as if they were waiting for the effluent flow to resume (Reynolds and Wilcox 1986; Packard et al. 1989; Reynolds 2000). A more serious situation would be the complete shutdown of a plant, particularly older power plants that are due to be retired or are no longer economically productive.

Some of the natural springs providing warm-water refuges for manatees may also become unreliable (U.S. Fish and Wildlife Service 2001). The depletion of the aquifer, caused by increased human demands for water and occasional periods of drought, has

lowered some important spring flow rates and resulted in less warm-water output (Vergara 1994; Sucusy et al. 1998). If flows continue to decrease, these springs may be insufficient at warming the surrounding water to the level at which manatees can survive during intensely cold periods. Manatees relying on sites impacted by these alterations may succumb to cold stress if they are unable to find a suitable alternative site.

Whereas most of the winter refuges for manatees, consisting of natural warm springs or industrial discharges, have been well documented, many lesser known alternate sites also exist and require further investigation (U.S. Fish and Wildlife Service 2001). Many of the alternate sites are not influenced by industrial discharges and consist of dredged boat basins and canal systems, apparently capable of retaining water temperatures above those in adjacent waterways (Laist and Reynolds 2005b). Possible explanations for the heat retention at these sites include ground-water seeps or springs and/or the structure and configuration of certain boat basins or canal systems that may be able to maintain warmer water temperatures through limited tidal flushing and solar heating of the water held within them (U.S. Fish and Wildlife Service 2001).

The current Florida Manatee Recovery Plan (U.S. Fish and Wildlife Service 2001) has identified the “protection, enhancement, and investigation” of non-industrial warm-water refuges as Objective 3.2.3; and the role that winter refuges play in the survival of the species is considered extremely important for managers and researchers to understand. The Florida Manatee Recovery Plan advocates using data collected on attributes of non-industrial warm-water refuges that are attractive to manatees to develop a series of additional sites for manatees as a safeguard in the event that warm water at a power plant or spring ceases to exist (U.S. Fish and Wildlife Service 2001).

Several habitat features have been identified as being important to Florida manatees. Access to warm water is perhaps most influential in determining their distribution, particularly during the winter (Hartman 1979; Irvine 1983; O’Shea 1988; Lefebvre et al. 1989). Other key habitat features are abundant seagrasses or other food source, access to freshwater, and absence of human disturbance (Hartman 1979; Reynolds 1999; U.S. Fish and Wildlife Service 2001).

Manatees are herbivorous, feeding primarily on submerged, floating, and emergent plants, and incidentally on items such as tunicates and epiphytic organisms growing on the plants (Hartman 1979; Packard 1981). Because of the relatively low quality of this food source, manatees need to spend a considerable amount of time foraging to fulfill their energy requirements. Studies by Bengtson (1983) and Etheridge et al. (1985) estimate that manatees may spend approximately 5 hours per day during the winter consuming between 4 and 9% of their body weight. As hindgut digesters, the bulk of their digestion takes place in an enlarged large intestine (hindgut) where microbes break down the cellulose in the plant material. This microbial activity is thought to generate enough heat to help regulate the body temperature of well-fed manatees during the winter (Rommel et al. 2003).

Florida manatees are euryhaline; however manatees frequently seek sources of freshwater (Hartman 1979; Belitsky and Belitsky 1980; Powell et al. 1981; Powell and Rathbun 1984; U.S. Fish and Wildlife Service 2001). Scientists have even used this to their advantage by “baiting” manatees with freshwater hoses to specific sites for capture and tagging as part of telemetry studies (Reid et al. 1995; Deutsch et al. 2003). Manatees may not necessarily need to drink freshwater, however, as the structure of the manatee kidney suggests manatees are able to excrete excess salt by producing concentrated urine (Hill and Reynolds 1989). Manatees also possess renal and endocrine mechanisms that would allow them to maintain sodium balance and avoid dehydration (Ortiz et al. 1998). These mechanisms, however, may be unable to prevent dehydration during extended periods without freshwater (Ortiz et al. 1998). It has also been shown that manatees exposed to saltwater for extended periods have reduced body mass from the oxidation of fat, suggesting that manatees are able to produce the water they need by oxidizing fat stores (Ortiz et al. 1999). Manatees may favor habitats where osmotic stress is minimal and freshwater is accessible, because it may be more metabolically advantageous (O’Shea and Kochman 1990). Regardless of the reason, it is apparent that manatees are attracted to sources of freshwater.

Human waterborne activities, such as boating and swimming can have adverse effects on manatees, both indirectly and directly. Manatee habitat is affected by the scarring of

seagrass beds, increased turbidity, and noise pollution caused by over 980,000 boats registered in the state of Florida (Sargent et al. 1995; Florida Fish and Wildlife Conservation Commission 2005a) that share these areas with manatees. Collisions with watercraft constitute the single largest identified cause of mortality of manatees in Florida (Florida Fish and Wildlife Conservation Commission 2005b); and those manatees that survive these collisions bear scars and mutilations from their injuries. The disturbance and harassment by boats, as well as other human waterborne activities, such as swimming and scuba diving, affect manatee distribution, habitat use, energetics, and behavior (Buckingham et al. 1999; Reynolds and Powell 2002; King and Heinen 2004; Nowacek et al. 2004).

Objectives

There were two main objectives of this study. The first objective was to collect data on physical and chemical features of a non-industrial winter refuge and compare them to those of nearby sites that are not frequented by manatees during the winter. This first objective provides information on habitat characteristics that manatees may find attractive in a winter refuge and may also help to determine why manatees use some seemingly similar sites over others. The second objective was to investigate whether environmental factors, such as time of day, tidal height, and water temperature influence site use and behavioral patterns of manatees. This second objective further suggests why manatees use certain sites during the winter, while also giving insight into when and how these sites are used.

METHODS

Study Area

The Matlacha Isles canal system is a winter refuge for manatees in southwestern Florida. Located in western Cape Coral, Lee County, approximately 26.64° north latitude and 82.05° west longitude (Figure 1), the Matlacha Isles canal system is an approximately 5-km² series of brackish canals through a residential neighborhood. Although dredged in the 1970s as part of the northern Cape Coral canal system, Matlacha Isles remains separated from the remainder of this larger system by a small dam and boatlift, and it is the only section that has open water access. Aerial surveys have documented manatees using Matlacha Isles year-round and especially during the winter (Florida Department of Environmental Protection 1998; Mote Marine Laboratory unpublished data). Photographic identification studies have further shown that manatees consistently use Matlacha Isles throughout the winter and spring, a high proportion of individuals return annually, and many of these individuals travel the approximately 50 kilometers between this site and the Florida Power & Light Company power plant in Ft. Myers throughout the winter (Koelsch and Barton 1999).

The study area centered on the Matlacha Isles canal system and encompassed Matlacha Pass, from its northernmost boundary to the power lines south of Little Pine Island (Figure 1). Matlacha Pass is a 65-km² body of water in the lower Charlotte Harbor estuary, between Pine Island and the city of Cape Coral. It contains abundant sea grass beds, and consists of numerous small bays, mangrove islands, backwater areas and shallows. The Matlacha Isles canal system is accessed by a dredged channel, which runs along the northeastern side of the Matlacha Bridge and causeway and continues east, through a small shallow bay (Site 3), located between Matlacha Pass and Matlacha Isles (Figure 2a). The canal system begins in the southeastern corner of this bay as a single 1.5 m deep and 8-10 m wide entrance/exit canal. The entrance/exit canal then branches into

multiple finger canals, with a “lake” (Site 2) at the easternmost end. Manatees can usually be found in three of the dead-end canals (Sites 1, 2, and 6) from late fall through early spring. Two other dead-end canals (Sites 4 and 5) appear to be very similar in structure to Site 6; however they have very limited use by manatees. Sites 7a-c, 8, and 9 lead to other canals and are used primarily by manatees as travel corridors.

Two nearby canal systems were included in the study area and used for comparison with the entire Matlacha Isles canal system because they are generally similar in configuration but have little to no manatee use. The canals located at the northeastern end of the northern Pine Island canal system (Figure 2b) are physically the most similar to those of Matlacha Isles. A small shallow “bay” is located to the north of the entrance to the canals. The canals are branched, forming multiple finger canals, with similar shorelines to those in Matlacha Isles. The canals in West Island are located directly across Matlacha Pass from Matlacha Isles (Figure 2a). The canals on West Island that were used for comparison are less similar to those in Matlacha Isles. The West Island canals open directly into Matlacha Pass, are much shorter and have less branching than those in Matlacha Isles, and also have shorelines that are almost entirely sea-walled. All three canal systems are just a short distance from dense sea grass beds: the Matlacha Isles and northern Pine Island canal systems are both less than 1.5 km from the nearest dense sea grass bed and the West Island canal system is approximately 0.75 km away.

Data Collection

Habitat Characterization

Data on habitat features were collected during three field seasons (winter – early spring 1999/2000 – 2001/2002). These features included bottom water temperatures, surface and bottom salinity, amount of boat traffic, tidal flushing, and bathymetry. Additionally, presence/absence of ground-water seeps was investigated within the Matlacha Isles canal system to determine if there was a source of warm-water input and/or a source of freshwater. Availability of aquatic vegetation was also investigated within the Matlacha Isles canal system to determine whether submerged aquatic

vegetation (SAV) was available for manatees to consume within the canal system (which would eliminate manatees' need to leave the site to forage).

Temperature loggers measuring bottom water temperatures were placed throughout the study area. Water temperature loggers were used to compare: 1) Matlacha Isles to ambient (Matlacha Pass), 2) Matlacha Isles to the West Island and northern Pine Island canal systems, and 3) specific sites within Matlacha Isles (sites that have frequent vs. infrequent/no use by manatees). A total of 11 loggers was used within Matlacha Pass, Matlacha Isles, and comparison canal systems in northern Pine Island and West Island. Water temperature loggers within canal systems were attached to the ends of residential docks. Water temperature loggers within Matlacha Pass were attached to channel markers in three different sections of the pass: northern (marker 71), middle (marker 56), and southern (marker 30). All temperatures were collected at 40-minute intervals using Optic StowAway[®] Temp data loggers (Onset Computer Corporation; accuracy = $\pm 0.2^{\circ}\text{C}$). The water temperature loggers were housed in casings made of PVC with multiple holes, which allowed ample water flow to reach the loggers, while protecting them from biofouling. Each logger and casing was cleaned and data from each logger were downloaded approximately once per month.

To measure salinity in the three canal systems, sampling stations within Matlacha Isles, northern Pine Island, and West Island were established. Surface and bottom salinity and temperature were collected between October and April 1999/2000 – 2001/2002 at each sampling station using a YSI[®] 30 handheld SCT meter with a 7.6 m cord (accuracy = ± 0.8 ppt for salinity and $\pm 0.1^{\circ}\text{C}$ for temperature). Ancillary data collected at each station included time, air temperature, surface and bottom water temperature, and depth (m).

Boat traffic surveys were conducted to measure the amount of human disturbance in four sections of the study area: 1) the entrance of Matlacha Isles, 2) West Island canal system, 3) northern Pine Island canal system, and 4) Matlacha Pass. The surveys were

conducted for approximately 10-hour periods to assess daytime boat use and for 24-hour periods to assess both day and nighttime boat use during winter and spring 2002. Each time a motorboat was observed, the time of day was recorded along with the boat's origin (i.e., first observed location), destination (i.e., last observed location), and relative speed (i.e., plane, plow, slow, idle).

Differences in water temperature and salinity between bodies of water can be partially explained by the amount of tidal exchange or flushing the bodies of water experience. The amount of tidal exchange or flushing in each of the three canal systems was examined to determine whether the Matlacha Isles canal system has lower tidal exchange or flushing than the canals in West Island and northern Pine Island. The estimated total volume that does not change during a given tidal cycle was calculated for each of these canal systems using a simple tidal prism model (Dyer 1973):

$$\text{volume not exchanged} = \text{total canal system volume} - \text{tidal prism}$$

Canal system volumes were estimated by multiplying the mean canal depth by the estimated surface area of each canal. Mean depths were obtained by measuring depths at three points (2 edge and 1 center) along 3-5 cross-sections of each individual canal, correcting for tide, and calculating the average for each canal system. Depths were measured using a standard lead line. Canal surface areas were estimated from digital maps with ArcView GIS software (version 3.3). The tidal prism is the domain volume between high and low tide, and was estimated by multiplying the tidal range (from predicted tide charts) by the surface area of each of the canal systems (Dyer 1973; Monsen et al. 2002).

To detect evidence of ground-water seeps, transects measuring surface and bottom salinity and water temperature were conducted within the Matlacha Isles canal system March 2000. Transects were performed in a zigzag pattern using a YSI[®] 30 (YSI, Incorporated) handheld SCT (salinity, conductivity, temperature) meter with a 7.6 m

cord. Because manatees are attracted to warm-water (during the winter) and freshwater, it is reasonable to assume that if warm- and/or freshwater seeps exist within the canal system, manatees would be concentrated near those areas. Therefore, transects were only conducted within the three canals where manatees are regularly observed (sites 1, 2, and 6).

Transect surveys of submerged aquatic vegetation were conducted in the Matlacha Isles canal system and the small bay outside in August 2000. These surveys were conducted during the summer to allow any seagrasses or other vegetation that may have been grazed and/or uprooted by foraging manatees to grow. Snorkelers inspected the canal bottoms and seawalls. In areas known to have resident alligators, however, transects were conducted using a long handled rake to “feel” along the bottom and limit the amount of time snorkelers were in the water.

Temporal Use of Matlacha Isles

Photographic identification studies in Matlacha Isles have provided information on site fidelity and movement and travel patterns of manatees that use this site (Koelsch and Barton 1999). In addition to a seasonal pattern of manatee presence within the Matlacha Isles canal system, preliminary observations suggested that they also have a distinctive pattern of daily use of Matlacha Isles, as individuals were documented traveling into and out of the canal system during certain times of the day. To examine the conditions under which manatees use Matlacha Isles, observations of manatees were documented at the entrance of the Matlacha Isles canal system. Observations were conducted from a balcony and/or dock at the entrance to the canal system. These observations were carried out in 24-hour periods, generally beginning around 0900 hours. Data were collected each time a manatee passed the entrance and/or at half-hour intervals. These data included: time of day, tidal height, tidal direction, sighting conditions (how well manatees could be spotted), weather, wind speed and direction, number of manatees sighted, and their travel direction (into or out of the canal system). Tidal height was measured as the distance to

the surface of the water from a fixed point on the survey dock. Most surveys were conducted for 2-3 consecutive days.

During most of the sampling periods, manatees could be easily spotted as they traveled into or out of the canal system. Fortunately, a sandy shoal was just outside the mouth of the canal system and the entrance canal was narrow, shallow, and had a sandy bottom. These features enabled observers to see to the bottom so that the manatees could be counted even when they were not breaking the surface of the water. At higher tides and lower light levels, manatees were not as easily observed or counted; under these conditions, manatees had to be closer to or break the surface of the water in order to be detected; or more subtle cues were used, such as manatee “footprints” (smooth swirls on the surface of the water caused by the swimming action of the manatee’s tail) or the sound of breathing. At night, a dual shop-light on a 3-ft stand was used to provide enough light to see the cues listed above.

Capture and Tagging

Tagging of manatees was used in this study to provide a means of facilitating visual contact of individuals during behavioral sampling. The tagging technique used in this study involved capturing and temporarily restraining individual manatees while the tagging assemblies were fitted. Specific manatees that were known to return annually to the study area during the winter were targeted for capture and tagging. The number of manatees often present in the canals during the winter, however, made it difficult to capture only targeted individuals.

One area within Matlacha Isles (Figure 2) has a few sloping sandy shorelines, allowing captured manatees to be pulled onto the banks. The method used to capture manatees at this site involved a 122-m long, 9-m deep net with 10-cm mesh that was stretched across the mouth of Site 1, which is known to have high manatee use during the winter. The net was positioned so that one end was kept on the net boat at one side of the canal, while the other was stationary at the bank where the captured manatees were hauled. Positioning the net in this manner formed an open pocket across the canal into which the manatees swam as they tried to enter this canal. When one or more manatees

approached the net, the net boat circled to the opposite bank, enclosing the manatee(s) in the net. The net was then used to secure the manatees and pull them onto the bank. If more manatees were netted at one time than available personnel could safely handle, some of the individuals were released immediately or soon after capture.

Individuals recognized as target animals were fitted with a standard manatee peduncle belt, tether of appropriate strength, and either a single very high frequency (VHF) radio-transmitter or platform transmitter terminal (PTT) with VHF and ultrasonic transmitters, as described by Reid et al. (1995) and Deutsch et al. (2003). Each tag was uniquely colored in order to distinguish individuals and aid obtaining visual locations. Because of the method of capture that was used, target manatees were captured infrequently; therefore it was not uncommon for a previously unknown manatee to receive a tag. Once data collection and/or tagging procedures were completed, the manatees were moved back into the water and released. A total of 14 manatees was tagged during the study (2000: 3 females, 2 males; 2001: 4 females, 1 male; 2002: 2 females, 1 male). Tags were removed or lost from the manatees by the summer of the year each manatee was tagged.

Behavioral Observations of Tagged Manatees

Focal animal observations were conducted on tagged individuals during 24-hour sampling periods to determine how manatees that use Matlacha Isles distribute their time among different activities throughout the day and examine the affect of temperature on behavioral patterns. Prior to the onset of each sampling period, the focal manatee was chosen randomly among the tagged individuals present within the study area. The focal manatee was chosen randomly because of the small sample size and uneven ratios of males and females, age classes, and reproductive status of the tagged individuals. Instantaneous sampling methods (Altmann 1974) were used to collect data on the focal individual's activity at four-minute intervals (following Koelsch 1997). A watch with a countdown timer was used to mark the four-minute sample points. If the focal manatee's activity could not be determined within one minute of the sample point, no behavioral data were collected for that point. Additionally, if the focal manatee's activity appeared

to be altered by observer's presence, no behavioral data were collected during those intervals and responses were noted in comments. Focal manatee observations were conducted from 6-7 meter outboard motorboats with observation towers. Boats were anchored or docked nearby, drifting, or maneuvered with electric trolling motors to minimize disturbance of the manatees.

The data collected at each sample point included: time of day, activity, confidence level, location, habitat type, and sighting conditions. "Confidence level" was a measure of the observer's certainty of the manatee's activity at the sample point. The range was from 1 to 4, with 1 being the highest level of confidence and 4 being the lowest. The activities (from Hartman 1979; Urian and Wells 1996; and Koelsch 1997) that were recorded include:

- Rest - encompassed both surface resting/basking and bottom resting
 - Surface rest – floating motionless at or near the surface of the water without changing location
 - Bottom rest – submerged for extended periods of time, coming to the surface in the same general area only to breathe, then submerging again
- Travel - directed movement within or among sites
- Mill - non-directed movement within a site
- Feed - evidence of feeding was used to determine this, i.e. grass in mouth, chewing; focal manatee within a sea grass bed, surrounded by cropped sea grass blades and/or sediment cloud
- Possible Feed -used when the focal manatee was in a sea grass bed, either remaining in the same spot or movement was very slight, and conditions made it difficult to confirm feeding. This activity category was designated frequently at night. Clues that were used to determine this include: feeding confirmed at least once while the focal manatee was at the same location, but conditions made it difficult to confirm feeding throughout the time the manatee was in that spot; cropped sea grass blades floating downwind of focal manatee; and/or focal manatee in subgroup in which other manatees were confirmed to be feeding, but conditions made it difficult to confirm focal manatee's behavior. Chewing sounds recorded by a hydrophone were also used to help assign this behavioral category during the first year of the study.

Socialize - tactile or active (grabbing, rolling, splashing, etc.) interaction with at least one other manatee

Play - tactile or active (grabbing, mouthing, pushing, etc.) interaction with an inanimate object

Habitat type was based on definitions used by Koelsch (1997) and included the following: seagrass bed (GB), dredged basin (DB, >50% altered shoreline), dredged channel (DC, <50% altered shoreline), shoal/sand bar (SB, unvegetated, <1.5 m deep), open bay (>1.5 m deep), and grass bed/shoal-sandbar [GB/SB; used in areas <1.5 m deep when bottom composition (vegetated vs. unvegetated) could not be determined or in areas where seagrass cover was very sparse].

Data Analysis

Habitat Characterization

Descriptive statistics are reported for bottom water temperature, surface and bottom salinity, boat traffic, depth, and seep detection transects. Only bottom water temperatures in December, January, and February of each winter were used to calculate descriptive statistics comparing the three canal systems and Matlacha Pass, because the coldest periods primarily occurred during these months. Surface and bottom salinity were infrequently sampled in all three canal systems on the same day, therefore descriptive statistics were calculated once for all data points and a second time using only those data that were collected on days that all three canal systems were sampled. The boat traffic data collected from 0700 to 1800 hours during the 24-hour surveys were combined with those from the daytime only surveys in the analyses of daytime boat traffic. Tidal flushing estimates are presented as the total volume of each canal system that is not exchanged with a given tidal cycle. Findings of aquatic vegetation transects within the Matlacha Isles canal system are reported as species present at each specific location.

Temporal Use of Matlacha Isles

Data on time of day, tide height, and water temperature were each compared to counts of manatees traveling into and out of the Matlacha Isles canal system to determine

if these environmental factors influence site use. A relationship between manatees traveling into and out of the Matlacha Isles canal system and time of day was tested using circular statistics. Time of day is a special type of interval scale, a circular scale, meaning it has equal intervals (hours), an arbitrarily assigned zero point (midnight), and no true designation of high or low values. Hours of day were converted to angular directions (a , in degrees) using the following formula (Zar 1999):

$$a = \frac{(360^\circ)(X)}{24}$$

where X is the unit of time (hour). Rayleigh's test of circular uniformity (Zar 1999) was applied separately to the counts of manatees traveling in each hour and to those traveling out each hour to test whether either is randomly distributed around the clock. The Watson-Williams test (Zar 1999) was employed to determine if the circular distribution (mean time of day) of counts of manatees entering was different from those leaving the Matlacha Isles canal system.

To determine if manatees choose certain tidal heights when traveling into or out of the Matlacha Isles canal system, data collected on manatees traveling in and out of Matlacha Isles at each tide height measurement were analyzed. Counts of manatees were continuous, whereas tide heights were recorded only at half-hour intervals when no manatees were observed; therefore data were condensed into half-hour intervals for each sampling period (counts of manatees were summed to give half-hour totals). Data on tidal heights were then grouped into two categories, heights recorded when manatees were observed and those when no manatees were observed. Both categories of tidal heights were then each condensed into 7 groups of 12.7-cm (i.e., 5-inch) increments. A chi-square contingency table was used to test whether observations of manatees traveling into/out of Matlacha Isles were independent of tidal height.

A correlation analysis was used to determine if counts of manatees are correlated with water temperature. Bottom water temperature data from the three sites in Matlacha Pass were averaged and used to calculate average water temperatures for the 24-, 72-, and 120-hour periods preceding each sampling date. The one-, three-, and five-day period lengths were chosen arbitrarily. Total counts of manatees traveling into and out of

Matlacha Isles during each sampling date could not be summed because of lack of independence (i.e., a manatee counted traveling in may also be counted traveling out later in the day or visa versa), therefore only daily counts of manatees traveling into Matlacha Isles were used in the analyses. Also, some of the sampling periods were conducted consecutively. To prevent violating the assumption of independent samples, only the first 24-hour sampling period of multi-day surveys were used in the analysis.

Behavioral Observations of Tagged Manatees

Behavioral data were used to determine manatees' diel distribution of time spent among activities as well as whether water temperature influenced the percentage of time manatees spent in each activity per day. All analyses of behavioral data included only those activities recorded with a confidence level of 1 or 2 (the 2 highest levels of confidence). Only five of the seven activity categories recorded in the field were used in the analyses. Socialize and play were excluded from the analyses because of inadequate sample sizes. The remaining activities were condensed into four categories: 1) Rest, 2) Feed, 3) Mill, and 4) Travel. Feed and possible feed were combined into one activity category, "feed", for the analyses.

To determine daily activity budgets of manatees using Matlacha Isles, total frequencies of each activity per hour were calculated for each sampling period, combined, and then graphed. Percentages of each of the four behavior categories were calculated for each sampling period and then averaged for each behavior. The number of hours spent in each behavior was calculated by multiplying the number of intervals for each behavior by four (since behaviors were recorded at four-minute intervals) and then dividing by 60.

To examine the influence of change in water temperature on activity, temperature differences were calculated by subtracting the average water temperature in Matlacha Pass during the 24- or 72-hour period preceding the behavioral sampling from the daily average water temperature in Matlacha Pass on the day of the behavioral sampling. Percentages of behaviors when water temperature was colder the day of sampling than the previous 24- or 72-hours were compared to those when water temperature was

warmer. Percentages of each activity category were calculated using the total number of intervals with confidence levels of 1 or 2 for each of the sampling periods. T-tests for independent samples were used on behaviors that were normally distributed with equal variances. Mann-Whitney rank sum tests for independent samples were used on those that were not normally distributed and/or lacked equal variance.

RESULTS

Habitat Characterization

Water Temperature

Ambient (i.e., Matlacha Pass) water temperatures within the study area dropped to a daily minimum of 18°C or less 108 days, or 40% of the days, over the three winters of the study (Figure 3). The comparison canal systems only experienced slightly fewer days than ambient when daily minimum water temperatures were below 18°C, with 100 days in West Island and 92 days in northern Pine Island. The shallow bay outside the mouth of Matlacha Isles (MI site 3) had similar daily minimum temperatures to the two comparison canal systems. The Matlacha Isles canal system, however, experienced less extreme cold temperatures, with 34 of the total days over the three winters having daily minimum water temperatures less than 18°C. The entire Matlacha Isles canal system did not experience daily minimum water temperatures less than 15°C.

The examination of daily minimum temperatures showed the low temperature on a given day, but did not give an indication of the duration of that temperature (i.e., if there was just one reading that cold or if it was most of the day); therefore daily mean temperatures were also calculated for each site. Cold fronts that maintained ambient daily mean water temperatures below 20°C occurred 9 times during the three winters and lasted between 4 and 32 days ($\bar{X} = 18.3 \text{ days} \pm 11.65 \text{ SD}$). Cold fronts that maintained ambient daily mean water temperatures below 18°C occurred 14 times during the three winters and lasted between 2 and 28 days ($\bar{X} = 6.9 \text{ days} \pm 6.91 \text{ SD}$).

Matlacha Pass (used in this study as ambient) had a total of 99 days over the three winters when daily mean water temperatures were less than 18°C, and 96 days when at least one of its sites had daily mean temperatures less than 18°C (Figure 4). West Island and northern Pine Island had 79 and 73 days, respectively, of daily mean water

temperatures less than 18°C, whereas Matlacha Isles only experienced 17 days over the three winters when the entire canal system averaged less than 18°C. More than 62% of the daily mean water temperatures within Matlacha Isles were greater than or equal to 20°C and approximately 90% were greater than 18°C. Individual canals within the Matlacha Isles canal system had similar numbers of days when daily mean water temperatures were 18°C or below, with site 6 having only slightly fewer than the rest.

On days when the daily mean water temperature in Matlacha Pass (ambient) was less than 18°C, water temperature in the entire Matlacha Isles canal system averaged greater than 2°C warmer than those in northern Pine Island and West Island (Table 1). Water temperatures in Matlacha Isles also averaged more than 3°C warmer than Matlacha Pass during these colder days.

The differences between daily mean temperatures in all three canal systems and ambient were calculated in order to assess each canal system's insulating ability. Temperatures in northern Pine Island and West Island were generally similar to ambient, with 83% and 87%, respectively, of their daily mean temperatures within 1°C of ambient (Figure 5). Northern Pine Island never had daily mean temperatures more than 1.6°C warmer than ambient and West Island never had daily mean temperatures more than 2.4°C warmer than ambient. The small bay outside the mouth of Matlacha Isles (MI site 3) demonstrated a similar pattern to northern Pine Island and West Island, although it had a few more days of the warmer temperatures.

Within the Matlacha Isles canal system, daily mean water temperatures remained warmer than ambient following cold fronts, when ambient water temperatures dropped suddenly (Figure 5). Specific canals within Matlacha Isles varied slightly in their differences from ambient temperatures. Site 1 maintained daily mean water temperatures at least 2°C warmer than ambient 40% of the total days over the three winters and ranged up to 6°C warmer than ambient. Site 2 experienced 43.6% of the total days with daily mean water temperatures at least 2°C warmer than ambient, however the majority of these days were 2-3°C warmer, with the largest difference being 4.8°C. Sites 4, 5, and 6 experienced 48.7%, 59.5%, and 61.8%, respectively, of the total days with daily mean water temperatures at least 2°C warmer than ambient and ranged up to 5.6°C (sites 4 and

5) and 5.8 °C (site 6) warmer. Temperature differences of 3 °C or more were typically when ambient daily mean water temperatures were less than 18 °C and as low as 11.7 °C. There were 33 days over the three winters when daily mean temperatures in site 1 were up to 0.8 °C colder than ambient, however these days were during periods when ambient temperatures were increasing and already above 20 °C.

Overall, the Matlacha Isles canal system was able to maintain warmer, more stable water temperatures than the two comparison canal systems. Unlike ambient, northern Pine Island, and West Island, Matlacha Isles did not experience the sudden drops in water temperature following cold fronts, extreme low temperatures, or long periods of temperatures less than 18 °C. Daily mean water temperatures within Matlacha Isles ranged up to 6 °C warmer than ambient and were warmer than 18 °C over 90% of the days of the three winters of the study. Water temperatures in northern Pine Island and West Island, however, were generally similar to ambient, dropping suddenly with passing cold fronts and most temperatures within 1 °C of ambient.

Salinity

Salinity was sampled a total of 21 days in the Matlacha Isles canal system, 15 days in the northern Pine Island canal system, and 16 days in the West Island canal system. The Matlacha Isles canal system exhibited slightly lower salinity than the canal systems in northern Pine Island and West Island. Northern Pine Island had the highest salinity readings, ranging from 15 to 31.8 ppt, for both surface and bottom (Figure 6). Surface salinity in Matlacha Isles averaged 8.7 and 6.0 ppt lower than northern Pine Island and West Island, respectively, and bottom salinity averaged 6.7 and 4.3 ppt lower than northern Pine Island and West Island, respectively. Seventy-five percent of the surface salinities recorded in Matlacha Isles were below 19 ppt and 75% of its bottom salinities were below 21.5 ppt. In northern Pine Island, however, 75% of its surface and bottom salinities were greater than 19 ppt. Surface and bottom salinities in West Island were greater than 20 and 21 ppt, respectively, for 75% of the samples.

There were 8 days during the combined three winters that all three canal systems were sampled on the same day. The data from these days were used to further compare

salinity among the canal systems (Figure 7). Overall, these censored data followed the same patterns as the complete dataset, with descriptive statistics generally remaining within 1 ppt. A few notable exceptions occurred within Matlacha Isles and West Island. The minimum bottom salinity in Matlacha Isles was nearly 6 ppt higher than that of the complete dataset. The minimum surface and bottom salinities in West Island were 8.9 and 8.5 ppt, respectively, higher than those of the complete dataset.

Salinity readings recorded at the six salinity sampling stations within the Matlacha Isles canal system were compared to each other to assess salinity within Matlacha Isles (Figure 8). Salinity at each of the sampling stations was generally similar, with all stations having average salinities within 1 to 3 ppt of each other. Station 3 had the highest mean bottom salinity and station 2 had the highest mean surface salinity. All stations had higher bottom salinities than surface salinities, ranging from a mean difference of 0.6 ppt at station 6 (MI site 2) to 4.5 ppt at station 3 (MI site 1). Station 3 was almost always stratified, whereas station 6 was almost never stratified. Surface and bottom salinities in station 4 were nearly equal for most of the samples, with only 3 exceptions. Stations 1, 2, and 5, varied in their levels of stratification.

Overall, Matlacha Isles had slightly lower salinity readings than the two comparison canal systems; however, salinities in all three canal systems remained within brackish to estuarine levels. Additionally, Matlacha Isles showed some stratification in certain areas, whereas northern Pine Island and West Island had little to no stratification.

Boat Traffic

Of the three canal systems, northern Pine Island had the highest mean number of boats traveling through it per day (Table 2). West Island had the fewest boats each day and counts in Matlacha Isles were intermediate. Few to no boats were observed in any of the locations between 0000 and 0500 hours (Figure 10). Boating activity in all locations generally began just prior to dawn, peaked in Matlacha Pass around 1400 hours, and then rapidly declined around sunset. Northern Pine Island was the only canal system that had boats in use between 2100 and 0600 hours. During the day, northern Pine Island had peaks in counts of boats in the morning and afternoon, whereas Matlacha Isles, West

Island, and Matlacha Pass appeared to slowly increase in the number of boats throughout the day and decrease at the end of the day (Figures 9 and 10). All of the boats that leave Matlacha Isles and West Island travel into Matlacha Pass. Boats that leave northern Pine Island travel into Bokeelia, Charlotte Harbor, Pine Island Sound, or Matlacha Pass.

Manatees encountered boats as they were entering and leaving Matlacha Isles. These encounters were observed repeatedly during the 24-hour surveys from the entrance to Matlacha Isles, as well as during focal observations. The entrance/exit canal is approximately 1.5 m deep at high tide and 8-10 m wide for 40-50 m. A boat ramp is located about 30 m inside the entrance/exit canal. Manatees entering the canal system when boats were exiting were observed turning around after starting to enter and traveling to the far side of either an oyster bar or shoal beyond the channel, where they remained until the boat(s) passed during 12 different occurrences affecting 34 individual manatees. One of the tagged manatees was observed waiting outside Matlacha Isles for over two hours one morning while boats continued to pass by. Manatees entering the canal system when boats were also entering increased their swimming speed or turned away from the entrance canal at the last minute and “waited” for the boat(s) to pass during 2 different occasions affecting 5 individual manatees. The responses of manatees exiting the canal when boats were either entering or leaving, however, were not observed because the opposite end of the canal was beyond view.

Canal Depths

The Matlacha Isles canal system averages over 0.3 meters deeper than northern Pine Island and West Island (Table 3). The shallowest areas in all three canal systems tended to be at the edges/shorelines and terminal ends of canals, whereas the deepest areas tended to be along the center of canals. The West Island canal system had the most uniform depths, with the greatest difference being 0.5 meters. The entire West Island canal system and 91% of the northern Pine Island canal system were less than 2.0 m in depth.

The Matlacha Isles canal system had the greatest variation in depths of the three canal systems; however the average depth in each of its canals was still greater than those

of northern Pine Island and West Island. Although the mean depth in Matlacha Isles was only 0.3 m deeper than the other two systems, 46% of Matlacha Isles was 2 m or greater in depth. Site 1 of Matlacha Isles was the deepest canal in the system and depths along the center of this canal ranged from 2.3 to 5.1 m. The mean depths of the other four canals were within 0.3 m of each other. Site 2 was the most uniform of the “high use” and “little/no use” canals in Matlacha Isles. Sites 4 and 5 (“little/no use” canals) had the least uniformity in depth.

Tidal Flushing

The total volume that is not exchanged during a tidal cycle was calculated for each of the three canal systems. Matlacha Isles had the lowest estimated tidal flushing, as the volume of water that remains within the canal system is 4 times greater than that remaining in northern Pine Island and nearly 14 times greater than that remaining in West Island with a given tidal cycle (Figure 11).

Ground-water Seeps and Submerged Aquatic Vegetation

No notable differences in salinity or temperature readings were detected within any of the three canals in Matlacha Isles that are regularly used by manatees. All four variables that were measured (i.e., surface salinity, bottom salinity, surface temperature, and bottom temperature) remained fairly uniform within each site (Table 3). Any differences greater than 2 ppt or °C generally occurred at opposite ends of the canals. No bottom salinity readings less than 20 ppt were recorded in any of the canals during the transects.

No submerged aquatic vegetation was found within the Matlacha Isles canal system. The alga *Cladophora* and very sparse patches of sea grass, *Halodule wrightii*, were found in the small bay just outside the mouth of Matlacha Isles (MI site 3).

Temporal Use of Matlacha Isles

A total of twenty-two 24-hour surveys of manatees traveling into and out of the Matlacha Isles canal system was conducted during January through March of 2000 and

January through February of 2001 and 2002. Manatees followed a distinctive daily pattern of traveling into and out of Matlacha Isles that was significantly different from being uniformly dispersed around the clock. Counts of manatees traveling into Matlacha Isles were concentrated in the morning hours of the day (Rayleigh's $z = 651.95$, $N = 1321$, $p < 0.001$), with the majority of them entering the canal system between 0600 and 1000 hours (Figure 12). Counts of manatees traveling out of Matlacha Isles were concentrated in the late afternoon/evening hours of the day (Rayleigh's $z = 738.12$, $N = 1336$, $p < 0.001$), with the majority leaving between 1600 and 1900 hours. Mean times were also calculated for both counts of manatees traveling in and those traveling out. The mean time of day that manatees were entering Matlacha Isles (0725 hours) differed significantly from the mean time of day that manatees were leaving Matlacha Isles (1750 hours; Watson-Williams $F = 6437.73$, $df = 1$, $df2 = 2655$, $p < 0.00001$).

Manatees did not choose certain tidal heights when traveling into or out of the Matlacha Isles canal system. Tidal heights, ranging from 25 cm (the highest tide) to 114 cm (the lowest tide) below a reference point on the survey dock, were recorded a total of 1,056 half-hour intervals during the 22 sampling periods. The proportions of half-hour intervals with and without manatees observed did not vary significantly with tidal height ($\chi^2 = 6.14$, $df = 6$, $p = 0.41$).

Additionally, frequencies of available tidal heights were graphed against tidal heights when manatees were entering (Figure 13A) and leaving (Figure 13B) Matlacha Isles. A range of heights, which included high and low tides, was observed in both periods of high manatee movement. The frequencies of the tidal heights that were available versus those when manatees were observed are nearly identical for both periods and show that manatees used all tidal heights when traveling both into and out of Matlacha Isles.

Scatter plots of counts of manatees traveling into Matlacha Isles against average water temperatures during the 24-, 72-, and 120-hours prior to sampling revealed a difference in the relationship between counts and water temperatures when temperatures

were below and above 18°C (Figure 14). When water temperatures were below 18°C, counts were extremely low, with little variation. When water temperatures were above 18°C, counts were higher, with much more variation. The data points above 18°C also appear to have a negative correlation with 24-, 72-, and 120-hour average water temperatures. Results of simple linear regressions (Table 5) run on the data points above 18°C showed that there was a significant relationship between manatee counts and 72- and 120-hour water temperature ($p = 0.016$ and 0.007 , respectively).

Behavioral Observations of Tagged Manatees

Behavioral data were collected over a total of 7,268 intervals during 27 focal observations of 10 individual manatees (Table 6). Seven of these individuals were sampled more than once. A total of 6,327 intervals had behavioral data recorded with the two highest levels of confidence (1 and 2), which were used in the analyses. Eighty-one percent of the sampling periods were 24-hours in duration, and only 2 of the sampling periods were less than 20 hours in duration. Three additional sampling periods were initiated, but were not used because of their short durations (each was less than 8 hours in length).

When behaviors were examined over all sampling periods, manatees spent most of their time resting and feeding, both in terms of percentage of total number of observations recorded and number of hours (Table 7). Resting was the primary activity within Matlacha Isles (76.3% of recorded behaviors within Matlacha Isles). Observations of rest were highest between 0600 and 1800 hours (Figure 15a), whereas those of feeding were highest from 1900 to 1200 hours, with only a slight decrease between 1300 and 1800 hours (Figure 15b). Observations of milling peaked during the afternoon hours (Figure 15c) and frequencies of observed traveling were highest between 1600 and 1800 hours (Figure 15d).

During 11 of the sampling periods, the focal manatees demonstrated the distinctive diel pattern of using Matlacha Isles during the day, traveling into Matlacha Pass during the late afternoon/early evening, and then returning to Matlacha Isles in the morning. The average time that the focal manatees entered Matlacha Isles was 0814 hours and the

average time they left was 1709 hours, which corresponded with the peak travel periods demonstrated in Figure 12. Histograms of each behavior per hour during these 11 sampling periods further demonstrated the diel pattern (Figure 16). Manatees primarily rested during the day (Figure 16a) and feeding occurred primarily during the night and early morning hours (Figure 16b). Of the habitats recorded between 2000 and 0600, 65-100% were grass beds. Little to no feeding was recorded between noon and 1800 hours. Daily average water temperatures in Matlacha Pass during these sampling periods were between 18.3 and 24.6°C (mean = 20.7°C).

During four of the sampling periods (1-2, 4, and 29), the focal manatees never left Matlacha Isles. They primarily rested (mean = 84% of observed behaviors), milled or traveled within the canal system during these sampling periods. Daily average water temperatures in Matlacha Pass during these four sampling periods were between 15.5 and 17.7°C.

During eight of the sampling periods (9-11, 14, 16, 23-25), the focal manatees were in Matlacha Pass the entire time. Histograms of each behavior per hour revealed that a diel behavioral pattern also existed during these 8 sampling periods (Figure 17). Focal manatees primarily fed (mean = 49% of observed behaviors) throughout these sampling periods, with an increase in feeding frequency between 0100 and 1200 hours (Figure 17b). The majority of resting occurred during the day and dropped off after 2100 hours (Figure 17a). Daily average water temperatures in Matlacha Pass during these eight sampling periods were >20°C (five of these were >23°C) and had remained >20°C for an average of 9 days prior.

Percentages of the sampling periods that each manatee engaged in each of four behavior categories were also used to examine whether change in water temperature influenced activity patterns. Average daily water temperatures in Matlacha Pass during the behavioral sampling periods ranged from 15.5 to 24.9°C. The focal manatees spent a significantly higher percentage of time resting when water temperatures were colder during the sampling period than the previous 24- (Mann-Whitney rank sum test, $p = 0.0328$; Table 9) and 72-hours (t-test, $p = 0.0017$; Table 8). Except for a single outlying

data point (Figure 18a), manatees rested between 21 and 95% of the sampling period when water temperatures were colder during the survey than the previous 24-hours. Additionally, manatees rested 25.7 – 95% of the sampling period when water temperatures were colder during the survey than the previous 72-hours (Figure 19a). Conversely, manatees spent a significantly higher percentage of time feeding when water temperatures were warmer during the sampling period than the previous 24- or 72-hours (t-tests, $p = 0.0300$ and 0.0148 , respectively; Table 8). When water temperatures were warmer during the sampling period than the previous 24- or 72-hours, manatees spent 13.6 – 73.5% and 23.9 – 73.5%, respectively, of their time feeding [except for 1 outlying data point in the 24-hour comparison (Figure 18b) and 2 outlying data points in the 72-hour comparison (Figure 19b)]. Manatees also spent more time milling when water temperatures were warmer during the sampling period than the 24- and 72-hours prior (t-tests, $p = 0.0099$ and 0.0001 , respectively; Table 8). The percentages of time manatees spent traveling did not vary significantly between relatively warmer and colder days (Tables 8 and 9).

DISCUSSION

The Florida Manatee Recovery Plan (U.S. Fish and Wildlife Service 2001) advocates the collection of data on the attributes of non-industrial warm-water refuges in order to better understand why these sites are attractive to manatees, as well as what role they may play in the survival of the species if warm water at nearby refuges is no longer available. This study addressed the need for data on these winter refuges by providing (1) information on several habitat features that appear to be important to Florida manatees, which suggest why manatees use some, but not other, seemingly similar sites during the winter, (2) insight into when and how certain winter refuges are used by manatees, and (3) criteria for managers to use when selecting and potentially altering/enhancing additional alternative winter refuges, in the event that the creation of such sites becomes necessary.

Why Do Manatees Use Matlacha Isles Rather Than Other Seemingly Similar Sites During The Winter?

Organisms exhibit preferential use of habitats that contain features necessary for survival, such as access to food and shelter, whether the shelter is from predators, environmental conditions, or both (aquatic invertebrates: Gallien 1985; Moran 1985; Williams and Morrill 1985; amphibians and reptiles: Downes and Shine 1998; Schlesinger and Shine 1994; Lecis and Norris 2003; birds: Holmes and Robinson 1981; Martin 1995; Yanes et al. 1996; Sachot et al. 2003; Gavashelishvili 2004; and mammals: Craighead et al. 1973; Collins et al. 1978; Cowlshaw 1997; Milner and Harris 1999; Alvarez-Cardenas et al. 2001; Lyons et al. 2003; Marin et al. 2003; Tweheyo et al. 2004). Habitat features that are frequently noted as being important to manatees include access to warm water in winter, availability of seagrasses or other vegetation on which to forage, freshwater to drink, and absence of human disturbance (Hartman 1979; Irvine 1983;

O'Shea 1988; Lefebvre et al. 1989; Reynolds 1999; U.S. Fish and Wildlife Service 2001). When these habitat features were examined at a winter refuge (the Matlacha Isles canal system) and compared to those of two similar appearing, but rarely used sites nearby, results indicated that water temperature had the most influence on site selection. No submerged aquatic vegetation was found within Matlacha Isles and all three sites are a short distance from dense sea grass beds (each is less than 1.5 km away); therefore access to foraging sites did not play a role in site selection in this study. Although slight differences in salinity did occur between Matlacha Isles, northern Pine Island, and West Island, these differences were not great and therefore did not show any obvious influence on site selection. Human disturbance (measured as levels of boat traffic) also differed only slightly between the three canal systems, with Matlacha Isles having fewer boats than the northern Pine Island canal system but more than the West Island canal system. Thus, it appears that human disturbance did not influence manatees' selection of Matlacha Isles over the two comparison canal systems.

Environmental temperature is a substantial determinant of the distribution of organisms because of its effect on biological processes and the imprecise thermoregulatory capabilities of most organisms. Although endotherms are able to regulate their body temperature through metabolic heat production, insulation, and vascular adjustments, each species functions best within certain environmental temperature ranges (Campbell and Reece 2002). Manatees possess physiological traits (low basal metabolism, low-energy food source, high rate of thermal conductance, and limited capacity for thermogenesis) that limit their thermal tolerance and cause them to be vulnerable to cold (Irvine 1983). Extended exposure to temperatures below 15-20°C causes "manatee cold stress syndrome", a complex multifactorial disease process that involves a compromise to metabolic, nutritional, and immunologic homeostasis, and culminates in secondary opportunistic and idiopathic diseases which can be lethal (Burgelt et al. 1984; O'Shea et al. 1985; Bossart et al. 2002).

Ambient water temperatures within the study area ranged from 10.0°C to 26.8°C during the three winters of the study (December – February 1999-2002). Ambient daily average water temperatures dropped below 18°C a total of 99 days, with some of these

periods lasting up to 28 days. It is therefore critical that manatees in this region find warm water during cold periods in order to survive (Campbell and Irvine 1981; Irvine 1983; Bossart et al. 2002).

The Matlacha Isles canal system was able to maintain warmer water temperatures than nearby monitored locations during cold periods, with differences of 2-6°C warmer than ambient (i.e., Matlacha Pass), and the lowest temperature within the site only dropping to 14.7°C. Approximately 90% of the days during the 3 winters of the study had daily average water temperatures greater than 18°C within Matlacha Isles. Extended periods of extreme cold did, however, drop water temperatures within Matlacha Isles below 18°C during 4 periods, which lasted between 2 and 7 days. Thus, Matlacha Isles has warmer, more stable water temperatures than ambient and maintains temperatures within or above manatees' thermal threshold of 18-20°C (Irvine 1983) throughout most of the winter. During extended periods of extreme cold, however, the canal system appears unable to maintain sufficient warmth and drops below manatees' thermal tolerance. Matlacha Isles is therefore an inadequate refuge during the coldest periods.

Water temperatures in the comparison canal systems in northern Pine Island and West Island, however, were very similar to each other, did not maintain warmer water temperatures following cold fronts, and generally remained within 1°C of ambient. The canal systems in northern Pine Island and West Island, therefore, do not provide adequate thermal shelter from even moderately cold ambient temperatures.

Results suggest that the difference in water temperatures between Matlacha Isles and the comparison canal systems may be a result of the deeper canals and lower tidal flushing in Matlacha Isles. Ground-water seeps, however, were not found and therefore do not contribute to the warmer temperatures within Matlacha Isles. Nearly half of the Matlacha Isles canal system is deeper than the deepest areas of either comparison canal system. Deeper canals have smaller surface area:volume ratios, which limit the effect of decreases in air temperature on water temperature. Additionally, the decreased tidal flushing within Matlacha Isles allows a much greater volume of water to remain within

the canal system and not be mixed with colder ambient water. As stated above, however, these features are not able to retain sufficient warmth during extended periods of extreme cold.

The model used in this study to estimate tidal flushing only estimated the volume of water that could potentially be exchanged with the receiving water body (i.e., Matlacha Pass) during a given tidal cycle in an idealized circumstance (Monsen et al. 2002; Sanford et al. 1992). It did not, however, give any information about age (the amount of time water remains within each canal system; Zimmerman 1988), residence time (the amount of time it takes to effectively flush each canal system), or the return flow factor (the fraction of water leaving during ebb that returns during flood; Monsen et al. 2002; Sanford et al. 1992). These factors are often difficult to measure (Monsen et al. 2002; Sanford et al. 1992) and require the use of tracer dyes. A hydrologic study of this kind, however, was beyond the scope of the current study.

Water temperatures alone seem unable to explain fully the differential distribution of manatees within the Matlacha Isles canal system itself, as individual canals within Matlacha Isles experienced very similar water temperatures to each other. Manatees use Sites 1 and 2 consistently and in high numbers. Site 6 is also used regularly by manatees, but not by as many. Water temperatures in Site 1 were much more stable than those of the other canals within Matlacha Isles, likely a result of the greater water depths in this site. When ambient water temperatures dropped suddenly and dramatically, temperatures in Site 1 remained warm and took much longer to decrease (1-4 days longer) than the other canals in Matlacha Isles, which average 2.8-3.1 m shallower than the deepest areas of Site 1. Conversely, when ambient water temperatures, as well as those in the rest of Matlacha Isles, increased quickly following cold fronts, temperature increases in Site 1 generally lagged by 1-2 days. Water temperatures in the other two canals used regularly by manatees (Sites 2 and 6), however, increased and decreased at similar rates to the canals that are not used by manatees (Sites 4 and 5).

Although Florida manatees can tolerate a wide range of salinities (Ortiz et al. 1998), they are attracted to sources of freshwater (Hartman 1979; Belitsky and Belitsky 1980; Powell et al. 1981; Powell and Rathbun 1984; U.S. Fish and Wildlife Service 2001). No

fresh ground-water seeps or any other freshwater sources were detected within the Matlacha Isles canal system that might serve as any obvious attractant of manatees to this site. Differences in salinity and levels of stratification among sampling stations within the Matlacha Isles canal system may be explained by their proximities to potential freshwater/nearly freshwater sources, water depths, and exposure to wind energy. For example, two of the sampling stations are located near breaks in the spreader canal system (part of the north Cape Coral canal system to the north of Matlacha Isles). These two breaks provide potential sources of freshwater/nearly freshwater; however no manatees were observed congregated at these sites, and average salinities remained within 1-3 ppt of the rest of Matlacha Isles.

Overall, Matlacha Isles had the lowest salinity readings among the three canal systems; however the differences between Matlacha Isles and the comparison canal systems were not great, all readings were within brackish to estuarine levels, with mean differences less than 9 ppt, and ranging in difference between 1 and 18 ppt for surface salinity and -4 and 11 ppt for bottom salinity. It seems unlikely, therefore, that salinity had a strong influence, if any, on manatee selection of Matlacha Isles over the other two canal systems during the winter.

Human disturbance is another important factor potentially affecting manatees' habitat selection. This study sampled human disturbance by recording numbers of motorboats observed at each location. Boat traffic in Matlacha Isles was lower than in Matlacha Pass and northern Pine Island; however boat traffic in West Island was less than that in Matlacha Isles. Mean counts of boats per day did not differ greatly between the three canal systems, so it seems unlikely that levels of boat traffic had any influence on manatee selection of Matlacha Isles over the other two canal systems during the winter.

This study, however, only examined levels of human disturbance at the entrance of the canal systems, not within the canal systems themselves. Buckingham et al. (1999) and King and Heinen (2004) found that manatees near the springs of the Crystal and Homosassa Rivers increased their use of sanctuaries that are off-limits to boats and swimmers as the number of boaters and swimmers in the vicinity increased. Future habitat studies of non-industrial warm-water refuges should address human disturbance

within refuges to assess whether manatees endure encounters in order to gain access to a site, but may be forced to use suboptimal regions of the site in order to avoid disturbance once they are inside. This may be an important conservation concern because studies have indicated that use of suboptimal habitat can affect reproductive rates, predation intensity, growth rates, and even survival of species (Sullivan 1979; Adolf and Porter 1993; Muller et al. 1997; Loeb 1999; Krijgsveld et al. 2003).

The extent to which species respond behaviorally to a disturbance, however, may depend on their perception of the severity of the threat (Frid and Dill 2002; Cassini et al. 2004) and the costs of the response (West et al. 2002; Stillman and Goss-Custard 2002; Beale and Monaghan 2004). The use of behavioral responsiveness as an index of disturbance effects may be inappropriate, because animals might make state-dependent decisions about responding to disturbances (Gill et al. 2001; Beale and Monaghan 2004). Two studies that examined costs of behavioral responses in shorebirds showed that the level of response depends on the state of the individual as well as the state of the current habitat, regardless of the level of disturbance (Stillman and Goss-Custard 2002; Beale and Monaghan 2004). Birds in good condition and/or in a richer habitat responded more to human disturbance than birds in poorer condition and/or habitat, presumably because the better condition/richer habitat individuals had more response options open to them and less to lose fitness-wise by responding. In contrast, individuals in poorer condition and/or habitat may be more constrained by their current requirements, which may force them to endure certain levels of disturbance in order to survive (Gill et al. 2001; Beale and Monaghan 2004). If this is true for Florida manatees (for which constraints include the need for warm-water and adequate forage during the winter, and limited sites that provide one or both of these), individuals may tolerate some human disturbance at a winter refuge if that site provides the warm water and access to foraging sites that are necessary for their survival.

When and How is Matlacha Isles Used By Manatees?

Manatees exhibited a distinctive daily pattern in their use of Matlacha Isles during the winter. Manatees entered the canal system during the morning (primarily between 0600 and 1000 hours), where they rested throughout the day, and left during the late afternoon/evening (primarily between 1600 and 1900 hours) to travel to Matlacha Pass to feed. Bengtson (1981) observed a similar diel pattern at Blue Spring Run, off the St. Johns River, FL.

Daily patterns of site use in manatees have been attributed to tidal cycles at some locations either because individuals cannot cross a shallow barrier to enter/exit a site at lower tidal levels or specific feeding areas are only accessible during higher tidal levels (Hartman 1979; Zoodsma 1991). Tides, however, did not explain daily site use patterns at Matlacha Isles. Although some of the lowest tidal heights did occur during the morning and some of the highest occurred during the afternoon/evening hours, both high and low tides took place during the two peak periods when manatees traveled into and out of Matlacha Isles, and analyses showed that there was no tidal range that was used disproportionately to its availability. Manatees were even observed fighting strong outgoing tidal currents at the mouth of the canal system and pulling themselves across the shoal at the mouth of the canal system during extreme low tides in order to enter in the morning and leave in the afternoon/evening.

Another possible explanation for the diel pattern of site use is avoidance of the high levels of boat traffic in Matlacha Pass during the day. The two peak periods when manatees enter and leave the Matlacha Isles canal system do not correspond to peak periods of boat use, but boat counts are still much higher during daylight than non-daylight hours. Manatees entering and leaving Matlacha Isles encountered boats during the periods they traveled to and from Matlacha Isles, and many were observed waiting for boats to pass or quickly swimming out of the way. It appears, therefore, that although human disturbance (boat traffic) may have some effect on manatee behavior and habitat use, it is not sufficient to deter them from using Matlacha Isles. As stated above, the

physiological constraints of needing warm water and access to forage may outweigh the perceived costs of enduring certain levels of disturbance (Gill et al. 2001; Beale and Monaghan 2004).

If, however, avoiding boat traffic played a strong role in determining the temporal use of this winter refuge, it seems plausible that manatees would wait until dusk or later to leave Matlacha Isles and return prior to or at dusk. Traveling during these time periods would allow them to travel and feed at night with few to no encounters with boats as opposed to frequently crossing paths with them.

Bengtson (1981) suggested that manatees exhibit this diel pattern in their use of certain warm-water refuges to take advantage of daily fluctuations in ambient water temperatures (i.e., travel to feeding areas when ambient water temperatures are warmest). Ambient water temperatures during this study peaked late in the day; however water temperatures quickly dropped after sunset and were already increasing before most manatees returned to Matlacha Isles. It seems more likely that they would travel to feeding sites before water temperatures had peaked and return to Matlacha Isles prior to the coldest period of the day if they were indeed taking advantage of the warmest water temperatures in order to feed. Measurements of manatee body temperatures at different water temperatures suggest that manatees can temporarily maintain core temperature during movements from warm-water refuges into colder adjacent waters (Irvine 1983). Manatees have been observed leaving winter refuges to feed in areas where ambient temperatures are $\leq 16^{\circ}\text{C}$ (Hartman 1979; Powell and Waldron 1981; Shane 1981). Irvine (1983) suggested that these foraging trips into cold water might be possible if they can later digest in warmer water.

Animals can obtain heat from their environment and help regulate their body temperature behaviorally by adjusting habitat selection, body posture, and timing of activity. Some species may rest during the day in warmer sites, allowing them to maintain a higher body temperature at minimal cost, and forage at night, generating heat through muscular activity and digestion. Pregnant female solitary bats (*Myotis evotis*) forage at night, therefore roost site selection is based on daytime temperature, even if the site cools rapidly at night (Chruszcz and Barclay 2002). When they return to the roosts at

dawn they are warmed passively as the roosts warm during the day, thus reducing energetic costs. Trumpeter swans and many other species of waterfowl also feed at night (Jorde and Owen 1988). Squires and Anderson (1997) suggested that because swans wintering in the greater Yellowstone area do not appear to have factors that might force nighttime feeding (such as human disturbance, predator avoidance, or hunting), they may forage at night to conserve energy. If waterfowl are able to generate heat during nocturnal foraging bouts through muscular activity and digestion and use solar radiation to help thermoregulate while they rest during the day, the total thermoregulatory costs would be reduced (Jorde et al. 1984; Squires and Anderson 1997). If manatees also thermoregulate in this manner, then it may explain the diel pattern observed at Matlacha Isles.

Manatees may have been taking advantage of the warmth within Matlacha Isles during the day in order to passively thermoregulate during periods of inactivity. Manatees within Matlacha Isles typically bottom rested during the morning (when bottom temperatures were warmer than those at the surface) and surface rested or even basked with their backs out of the water during mid-day to late afternoon. By traveling to Matlacha Pass at night to feed (even though water temperatures may have been cooler) manatees may sustain body temperatures somewhat through the heat generated during muscular activity and digestion. Conversely, the thermoregulatory cost of resting within Matlacha Isles at night (when temperatures are cooler) would be much higher as the manatees would have to expend much more energy in order to thermoregulate in the cooler water while inactive. This activity pattern may continue to a lesser extent as water temperatures continue to warm above 20°C (as shown by the decrease in the number of manatees entering and exiting Matlacha Isles and the 8 sampling periods when the focal manatees remained outside of Matlacha Isles). As temperatures increase further, the diel activity pattern may be abandoned, as Bengtson (1981) found that Blue Spring manatees no longer exhibited a strong diel cycle outside of the winter season.

Water temperature also influenced the number of manatees that traveled into and out of Matlacha Isles among days. A clear distinction existed in the relationship between the number of manatees traveling into Matlacha Isles and ambient water temperature above

and below 18°C. Few to no manatees were observed when water temperatures were below 18°C and there was an inverse relationship between manatee counts and water temperature above 18°C. The mean ambient temperature of the three-day period prior to sampling appears to be the best predictor of the number of manatees that enter the canal system. As ambient temperatures continued to increase above their thermal threshold, the number of manatees observed decreased, likely due to a higher proportion remaining in the grass beds feeding when they were not as thermally dependent on the refuge. This change in site use with warmer water temperatures was also confirmed by the behavioral data, as individuals that were observed during 8 sampling periods when water temperatures were >20°C remained within Matlacha Pass (primarily feeding) and overall, manatees spent a significantly higher percentage of time feeding when ambient water temperatures were warmer.

Conservation and Management Implications

Water temperature appears to be the primary attractant of manatees to the Matlacha Isles canal system during the winter. Although the Matlacha Isles canal system has no direct thermal input, it maintained water temperatures within or above manatees' thermal threshold of 18-20°C (Irvine 1983) approximately 90% of the three winters of the study, making it an adequate winter refuge for most of the winter. Because of its inability to maintain water temperatures high enough during prolonged periods of extremely cold weather to provide sufficient warmth for manatees, however, Matlacha Isles is not a reliable winter refuge. During these times, most of the manatees leave Matlacha Isles and travel the approximately 50 km to the Florida Power & Light plant on the Orange River (Koelsch and Barton 1999). Between these extremely cold days however, Matlacha Isles provides a warm-water refuge that is close to abundant sea grass beds, as opposed to the limited forage at and near the power plant effluent.

Findings from this study may allow resource managers and conservationists to develop a more informed approach to creating sanctuaries or refuges. Sites that provide access to warm water and adequate forage should be the most important habitat features to provide. Additionally, little to no disturbance (especially human) would be ideal, even

though manatees at Matlacha Isles appear to tolerate certain levels in order to have access to the warmer water and proximity to sea grass beds. If the creation of new winter refuges becomes necessary, similar sites to Matlacha Isles may need to be modified and/or enhanced with environmentally sensitive, non-industry-dependent methods of maintaining temperature or heating water during extended periods of extreme cold. These sites should also be deep with limited tidal flushing to retain the warm water.

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Table 1. Descriptive statistics for daily mean water temperature in the three canal systems and Matlacha Pass for days when water temperature in Matlacha Pass was 18°C (N=99 days).

Location	Mean	SD	Min	Max	Range
Matlacha Isles	18.9°C	1.22	16.0	21.7	5.7
West Island	16.6°C	1.59	12.6	19.2	6.6
northern Pine Island	16.8°C	1.53	13.0	19.8	6.8
Matlacha Pass	15.8°C	1.65	11.7	18.0	6.3

Table 2. Descriptive statistics for counts of boats per day in the three canal systems and Matlacha Pass. Only daytime hours (0700-1800 hours) were used in the calculations.

Location	Mean	SD	Min	Max	Range
Matlacha Isles	125.5	88.43	46	206	160
West Island	78.8	46.20	32	126	94
northern Pine Island	178.0	74.78	86	257	171
Matlacha Pass	415.8	237.93	195	649	454

Table 3. Descriptive statistics of depth (m) measurements in the three canal systems. Data for specific canals within Matlacha Isles are also included.

Location	Mean	SD	Min	Max	Range
Matlacha Isles	1.9	0.7	0.6	5.1	4.6
northern Pine Island	1.6	0.4	0.5	2.6	2.1
West Island	1.6	0.2	1.3	1.8	0.5
MI site 1	2.8	1.1	1.1	5.1	4.0
MI site 2	2.0	0.2	1.5	2.5	1.0
MI site 4	2.2	0.5	1.3	2.9	1.6
MI site 5	2.0	0.6	1.1	2.7	1.6
MI site 6	2.3	0.3	2.0	2.8	0.9

Table 4. Descriptive statistics for seep detection transects in the Matlacha Isles canal system.

	MI site 1		MI site 2		MI site 6	
Salinity (ppt)	Surface	Bottom	Surface	Bottom	Surface	Bottom
average	22.6	26.7	22.7	22.8	20.5	22.0
SD	1.0	1.3	0.1	0.4	0.8	0.7
min	21.1	22.1	22.6	20.0	19.7	20.7
max	25.2	28.1	22.9	23.6	24.0	23.0
range	4.1	6.0	0.3	3.6	4.3	2.3
N	60	60	59	59	29	29
Temperature (°C)	Surface	Bottom	Surface	Bottom	Surface	Bottom
average	24.1	24.9	25.5	25.2	26.2	26.2
SD	0.7	0.4	0.4	0.4	0.4	0.4
min	22.6	23.6	24.7	24.7	25.6	25.4
max	25.5	25.7	26.4	25.8	27.5	26.8
range	2.9	2.1	1.7	1.1	1.9	1.4
N	60	60	59	59	29	29

Table 5. Results of linear regressions correlating counts of manatees traveling into the Matlacha Isles canal system with average water temperature during the 24-, 72-, and 120-hour periods prior to sampling.

	Period	N	R ²	p
Average water temperature	24-hours	12	0.304	0.063
	72-hours	12	0.453	0.016
	120-hours	12	0.534	0.007

Table 6. Sampling effort for behavioral observations of tagged manatees.

	2000	2001	2002	Total
Number of individuals	3	4	3	10
Number of sampling periods	11	7	9	27
Mean length of sampling period (minutes)	1337.8	1426.1	1418.2	1387.5
Number of intervals:	--	--	--	--
All intervals	2115	2280	2873	7268
Confidence 1 or 2 only	1941	1845	2541	6327

Table 7. Summary of behaviors recorded and descriptive statistics for behavioral observations. Sampling periods 18, 19, and 21 were not included in any of the analyses because each was less than 8 hours in duration.

Sampling Period	Number of intervals					Percent				Number of Hours			
	Total	Feed	Mill	Rest	Travel	Feed	Mill	Rest	Travel	Feed	Mill	Rest	Travel
1	300	0	23	261	16	0.0	7.7	87.0	5.3	0.0	1.5	17.4	1.1
2	240	0	9	228	3	0.0	3.8	95.0	1.3	0.0	0.6	15.2	0.2
3	103	14	13	57	19	13.6	12.6	55.3	18.4	0.9	0.9	3.8	1.3
4	112	10	23	61	18	8.9	20.5	54.5	16.1	0.7	1.5	4.1	1.2
5	137	52	37	41	7	38.0	27.0	29.9	5.1	3.5	2.5	2.7	0.5
6	148	50	29	45	24	33.8	19.6	30.4	16.2	3.3	1.9	3.0	1.6
7	160	35	28	55	42	21.9	17.5	34.4	26.3	2.3	1.9	3.7	2.8
8	233	68	25	124	16	29.2	10.7	53.2	6.9	4.5	1.7	8.3	1.1
9	113	34	12	52	15	30.1	10.6	46.0	13.3	2.3	0.8	3.5	1.0
10	213	64	26	108	15	30.0	12.2	50.7	7.0	4.3	1.7	7.2	1.0
11	182	71	39	58	14	39.0	21.4	31.9	7.7	4.7	2.6	3.9	0.9
12	283	92	67	93	31	32.5	23.7	32.9	11.0	6.1	4.5	6.2	2.1
13	254	76	41	84	53	29.9	16.1	33.1	20.9	5.1	2.7	5.6	3.5
14	219	91	49	46	33	41.6	22.4	21.0	15.1	6.1	3.3	3.1	2.2
15	311	156	27	60	68	50.2	8.7	19.3	21.9	10.4	1.8	4.0	4.5
16	199	126	36	0	37	63.3	18.1	0.0	18.6	8.4	2.4	0.0	2.5
17	286	0	53	152	81	0.0	18.5	53.1	28.3	0.0	3.5	10.1	5.4
20	293	70	71	88	64	23.9	24.2	30.0	21.8	4.7	4.7	5.9	4.3
22	292	137	37	75	43	46.9	12.7	25.7	14.7	9.1	2.5	5.0	2.9
23	342	230	100	0	12	67.3	29.2	0.0	3.5	15.3	6.7	0.0	0.8
24	162	119	37	0	6	73.5	22.8	0.0	3.7	7.9	2.5	0.0	0.4
25	263	150	52	16	45	57.0	19.8	6.1	17.1	10.0	3.5	1.1	3.0
26	358	6	28	315	9	1.7	7.8	88.0	2.5	0.4	1.9	21.0	0.6
27	254	76	22	124	32	29.9	8.7	48.8	12.6	5.1	1.5	8.3	2.1
28	324	108	33	139	44	33.3	10.2	42.9	13.6	7.2	2.2	9.3	2.9
29	343	0	49	285	9	0.0	14.3	83.1	2.6	0.0	3.3	19.0	0.6
30	203	50	21	110	22	24.6	10.3	54.2	10.8	3.3	1.4	7.3	1.5
Average						30.4	16.0	41.0	12.7	4.7	2.4	6.6	1.9
SD						20.9	6.7	26.3	7.6	3.8	1.3	5.7	1.4
Min						0.0	3.8	0.0	1.3	0.0	0.6	0.0	0.2
Max						73.5	29.2	95.0	28.3	15.3	6.7	21.0	5.4
Range						73.5	25.5	95.0	27.1	15.3	6.1	21.0	5.2

Table 8. Results of T-tests comparing percentages of each behavior when water temperatures were warmer versus colder the day of sampling than the previous 24- or 72-hours.

Period	Behavior	critical t	df	p value
24-hours prior	Feed	-2.30	25	0.0300
	Travel	-1.32	25	0.1988
	Mill	-2.79	25	0.0099
72-hours prior	Feed	-2.62	25	0.0148
	Rest	3.51	25	0.0017
	Travel	-0.83	25	0.4168
	Mill	-4.61	25	0.0001

Table 9. Results of Mann-Whitney rank sum tests comparing percentages of each behavior when water temperatures were colder versus warmer the day of the sampling than the previous 24- or 72-hours.

Period	Behavior	Group	Median	25%	75%	p value
24-hours prior	Rest	colder	80.6	33.00	85.70	0.0328
		warmer	30.8	25.00	41.10	

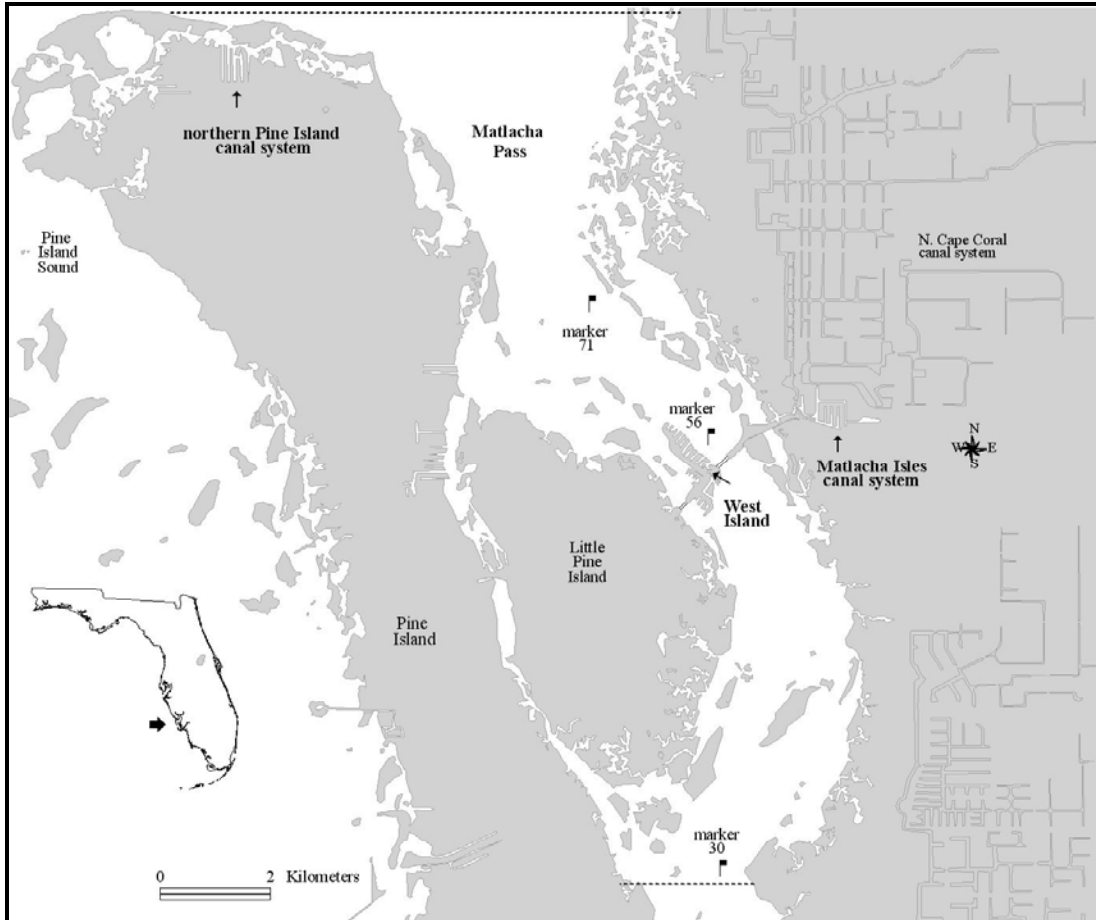


Figure 1. Map of the study area, which includes Matlacha Pass from the northernmost tip of Pine Island to the power lines just south of channel marker 30. Dotted lines indicate the boundaries of the study area.

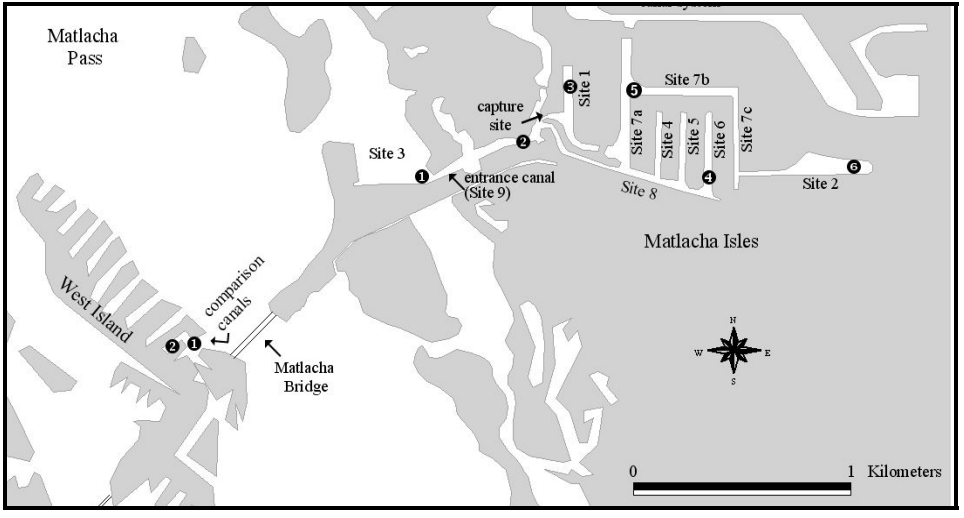


Figure 2a. The Matlacha Isles and West Island canal systems, including canal identifications within Matlacha Isles and locations of salinity stations (numbered circles) within both canal systems.

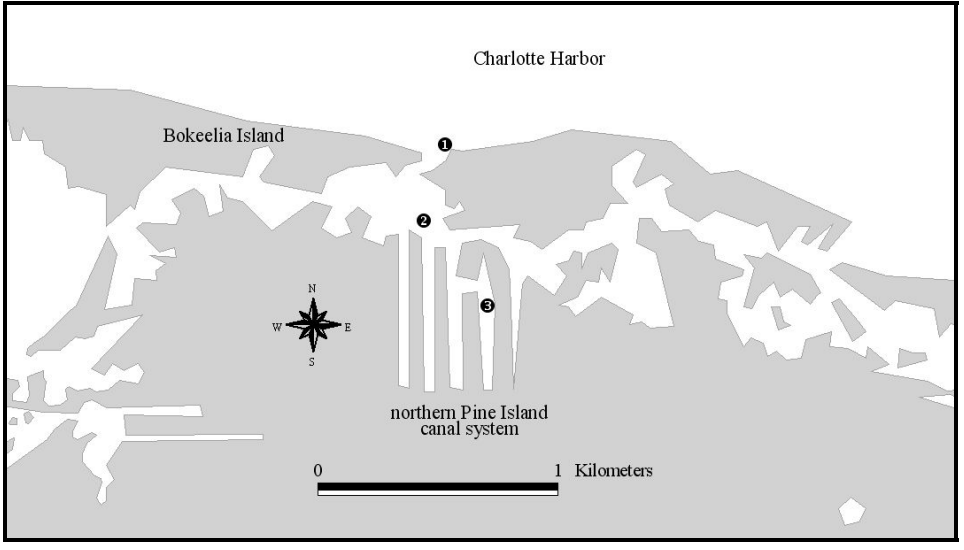


Figure 2b. The northern Pine Island canal system, including locations of salinity stations (numbered circles).

Figure 2. Maps of the three canal systems used in the study.

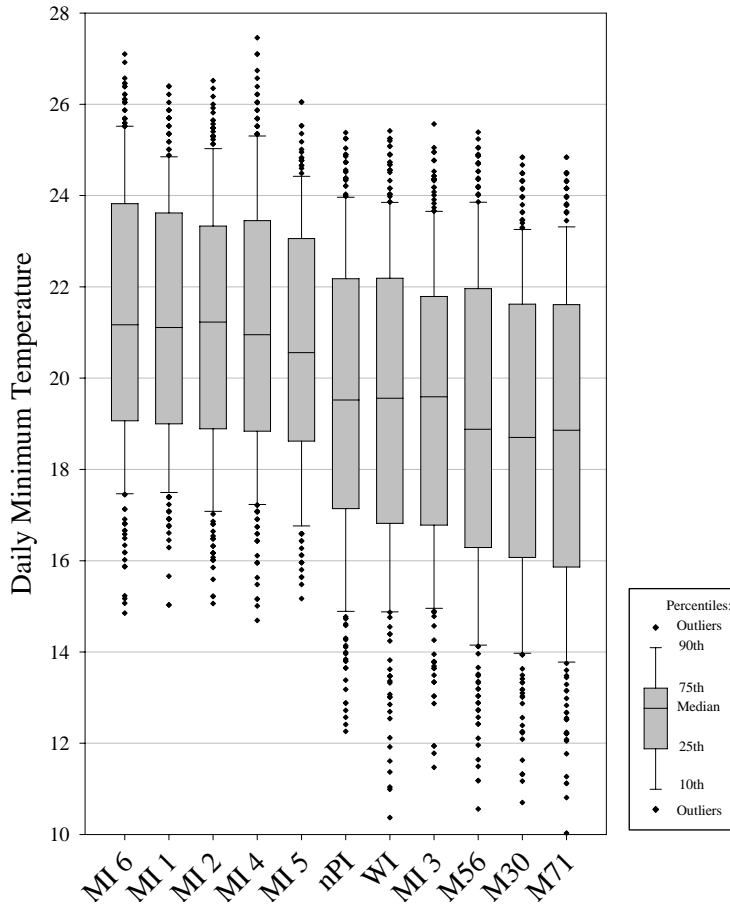


Figure 3. Daily minimum bottom water temperatures at each sampling site. Data are for December through February for all three years of the study. Sites are arranged graphically in rank descending order of the mean of their daily minimum temperature. Canal system names have been abbreviated as “MI” for Matlacha Isles, “nPI” for northern Pine Island, and “WI” for West Island. The three sampling sites in Matlacha Pass are labeled as “M30” (channel marker 30), “M56” (marker 56), and “M71” (marker 71).

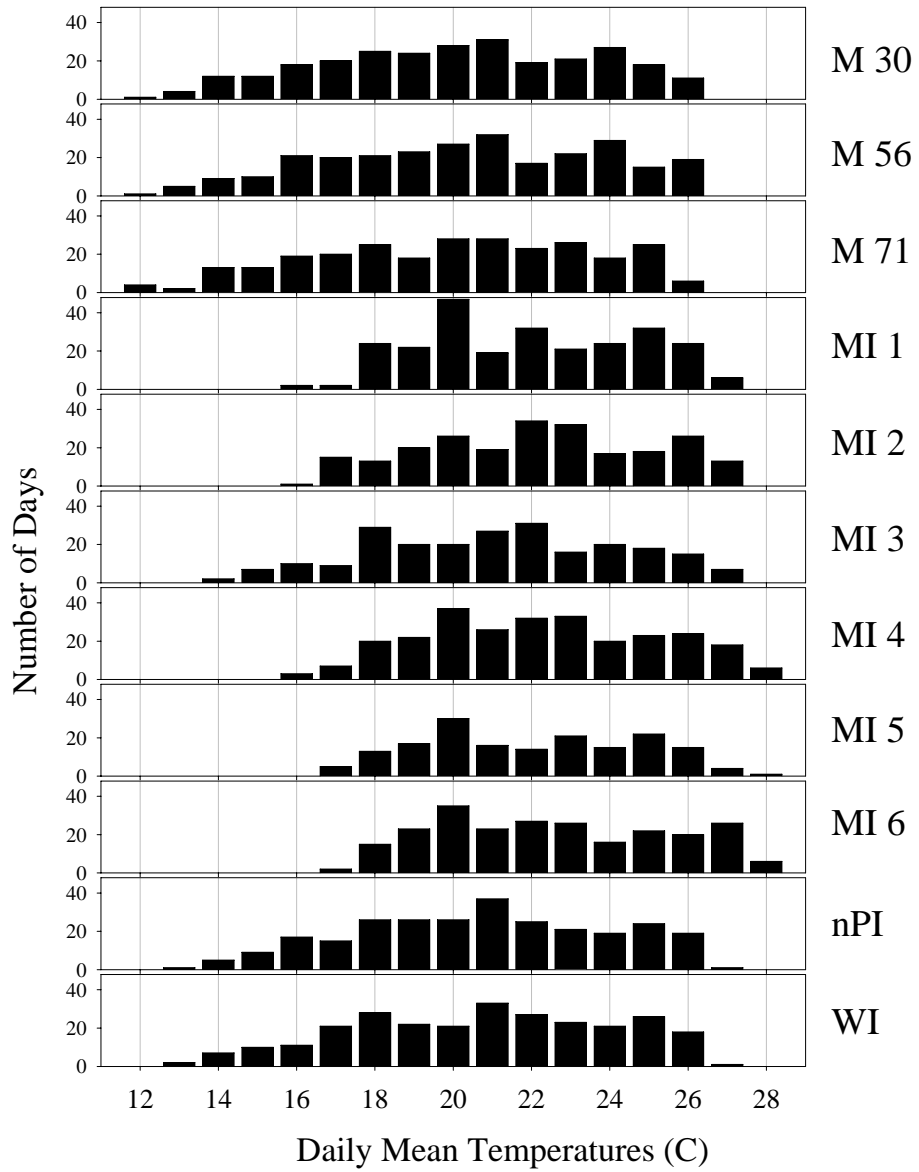


Figure 4. Frequencies of daily mean bottom water temperatures at each sampling site during the three winters.

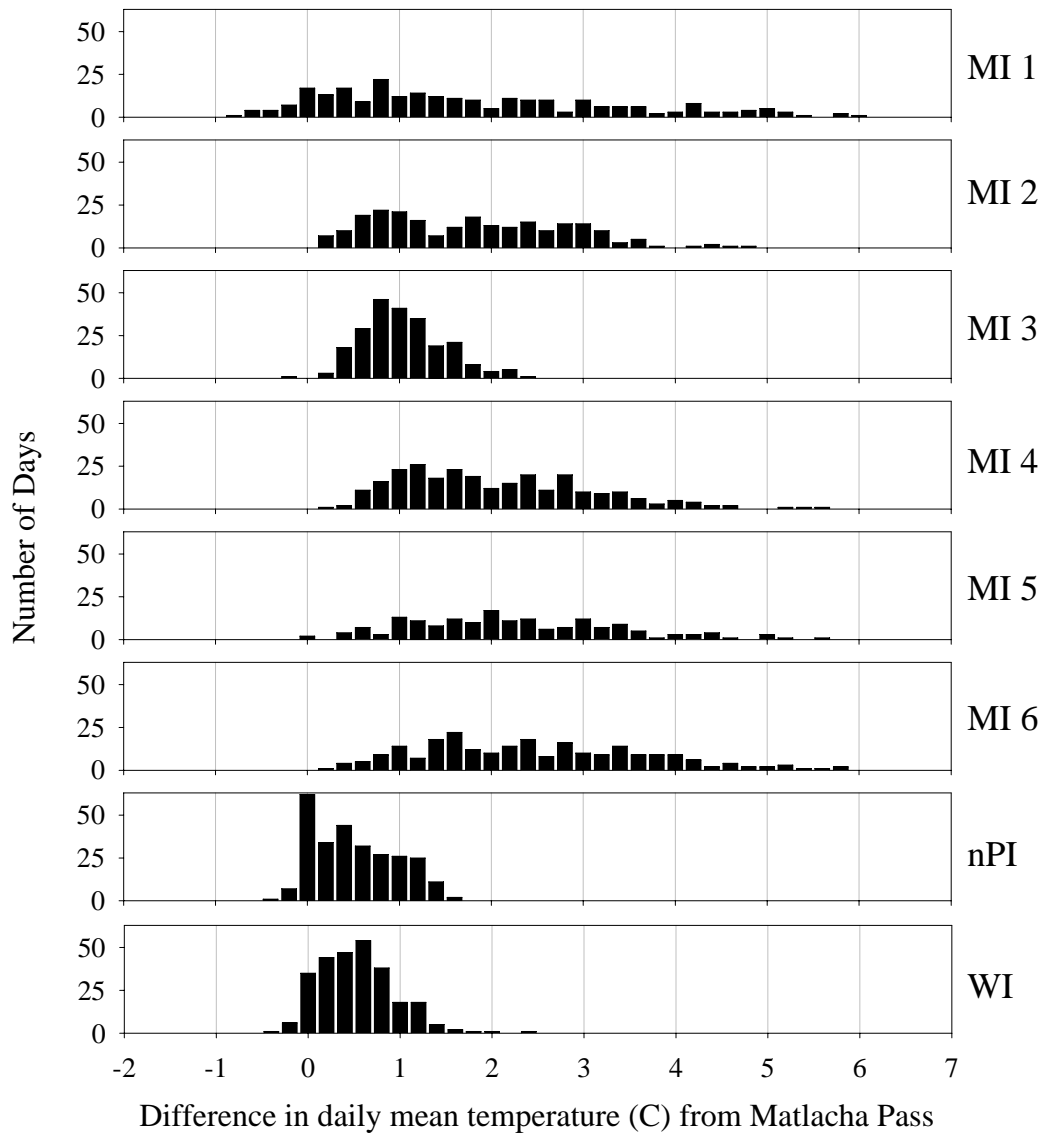


Figure 5. Histogram showing the differences in daily mean bottom water temperature between each sampling site and Matlacha Pass (ambient).

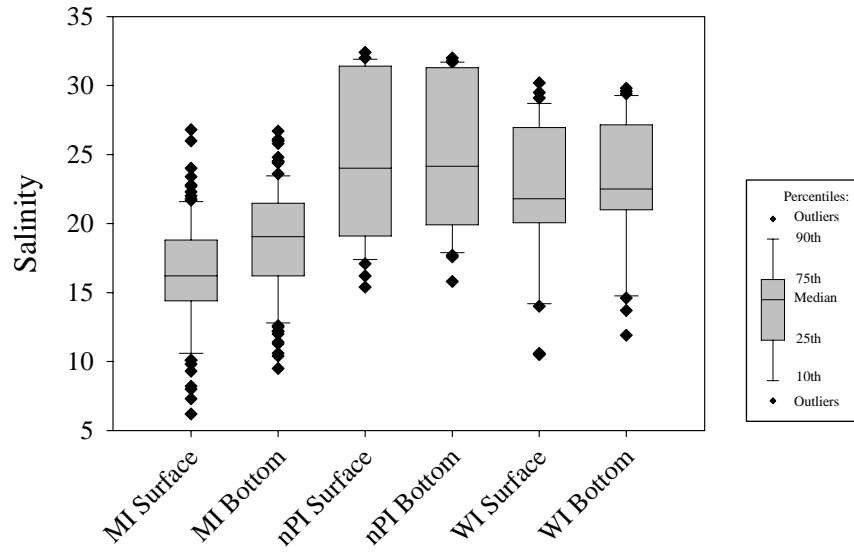


Figure 6. Surface and bottom salinities in Matlacha Isles, northern Pine Island, and West Island.

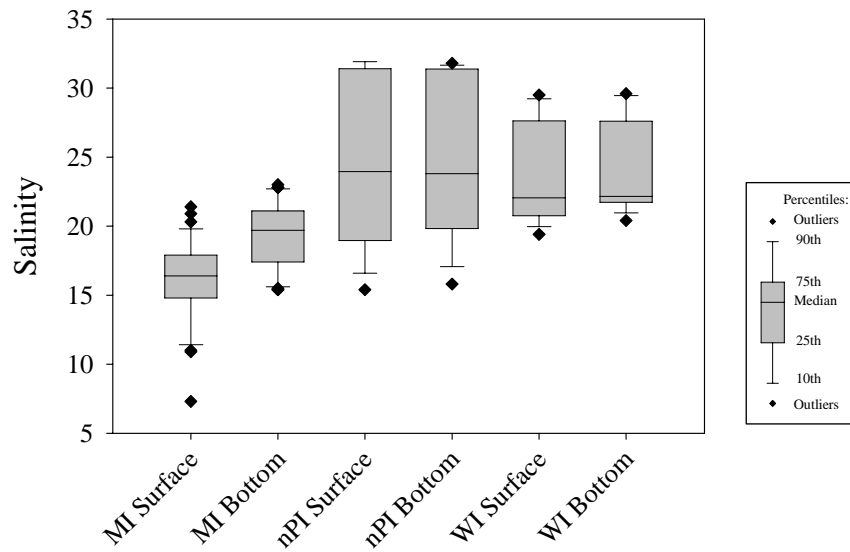


Figure 7. Surface and bottom salinities in Matlacha Isles, northern Pine Island, and West Island when all sites were sampled on the same day.

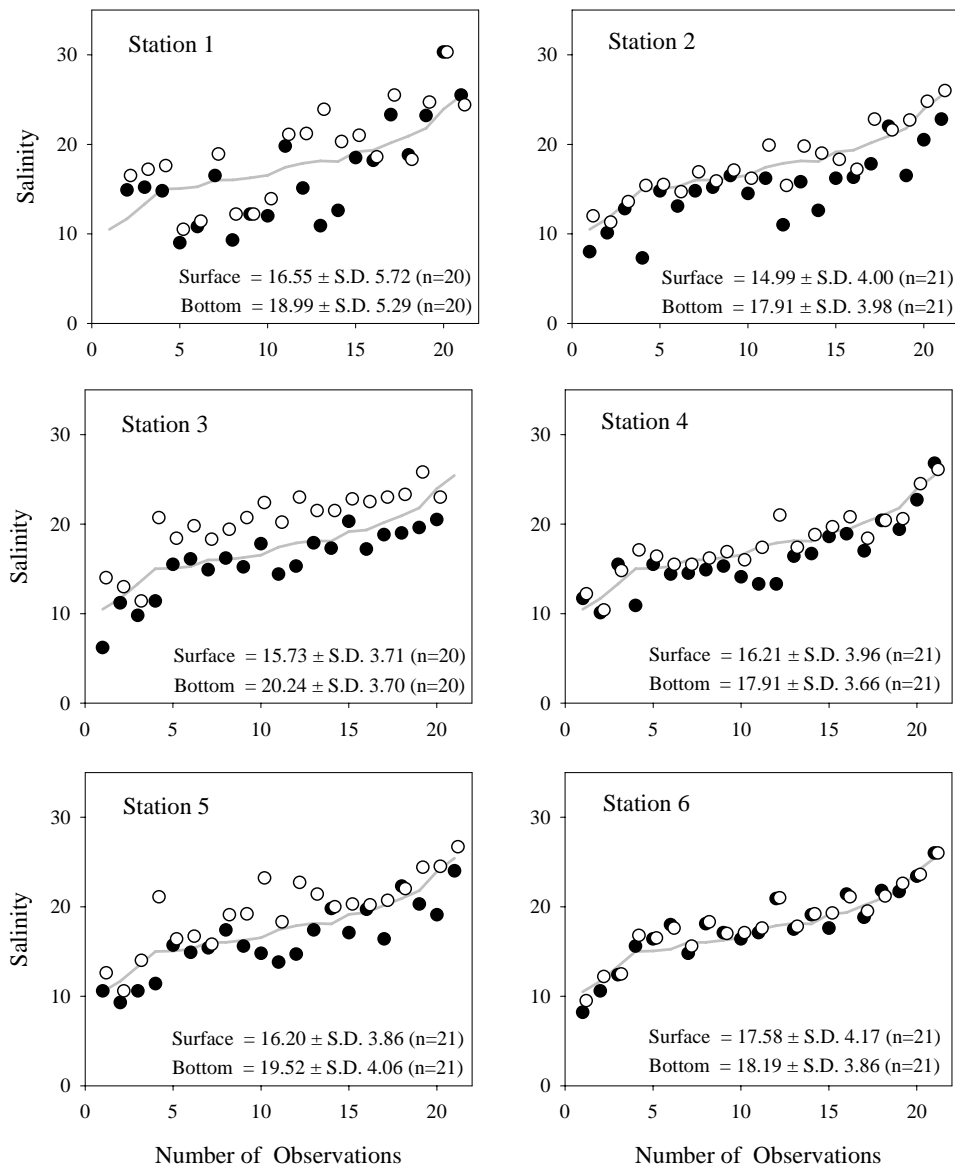


Figure 8. Surface and bottom salinities at each sampling station within the Matlacha Isles canal system. Black circles represent surface salinity readings and white circles represent bottom salinity readings. Data are graphed in rank order of salinity. The gray line represents the average of all Matlacha Isles surface and bottom salinities. Mean ppt \pm SD and sample size for each sampling station are reported on each graph. The surface and bottom data plots are slightly staggered so that both can be seen when they are similar or equal.

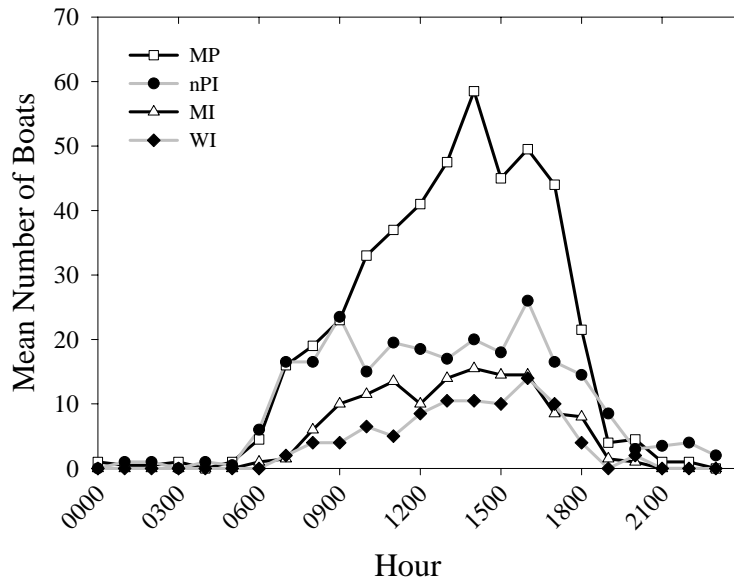


Figure 9. Mean number of boats observed per hour at each location during 24-hour surveys (N=2 days).

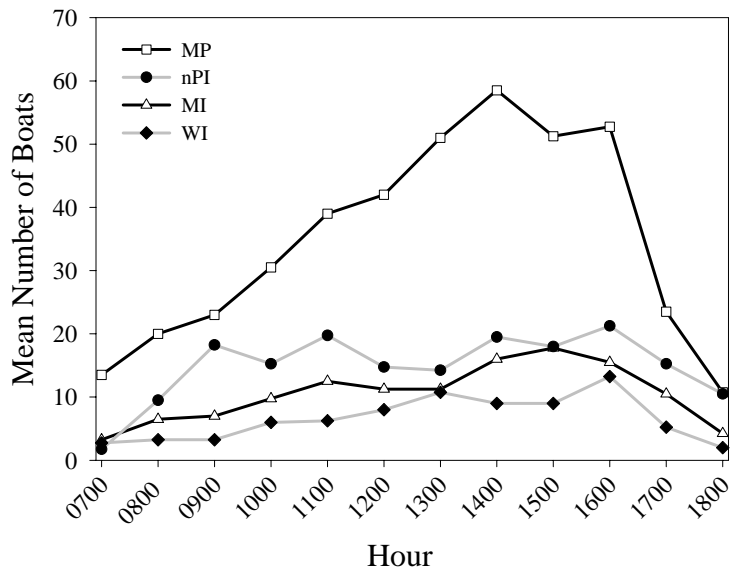


Figure 10. Mean number of boats observed per hour at each location during daytime surveys (N=4 days).

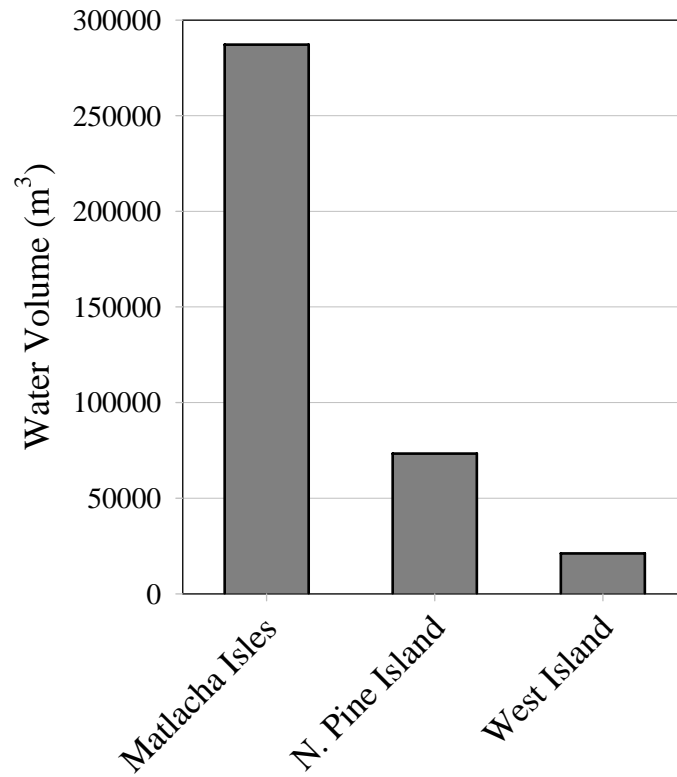


Figure 11. Estimated volume of water (m³) remaining within each canal system during a tidal cycle.

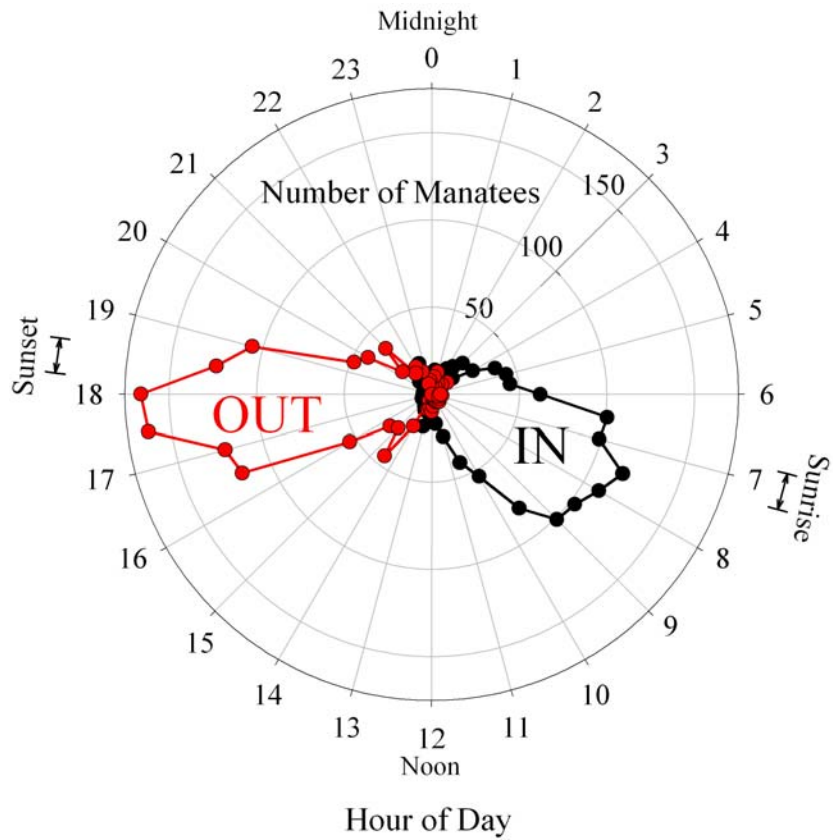


Figure 12. Total number of manatees observed traveling into and out of the Matlacha Isles canal system each hour, plotted on a circular scale. Counts were pooled from all sampling periods. The ranges of times of sunrise and sunset during the three winters are also noted on the graph.

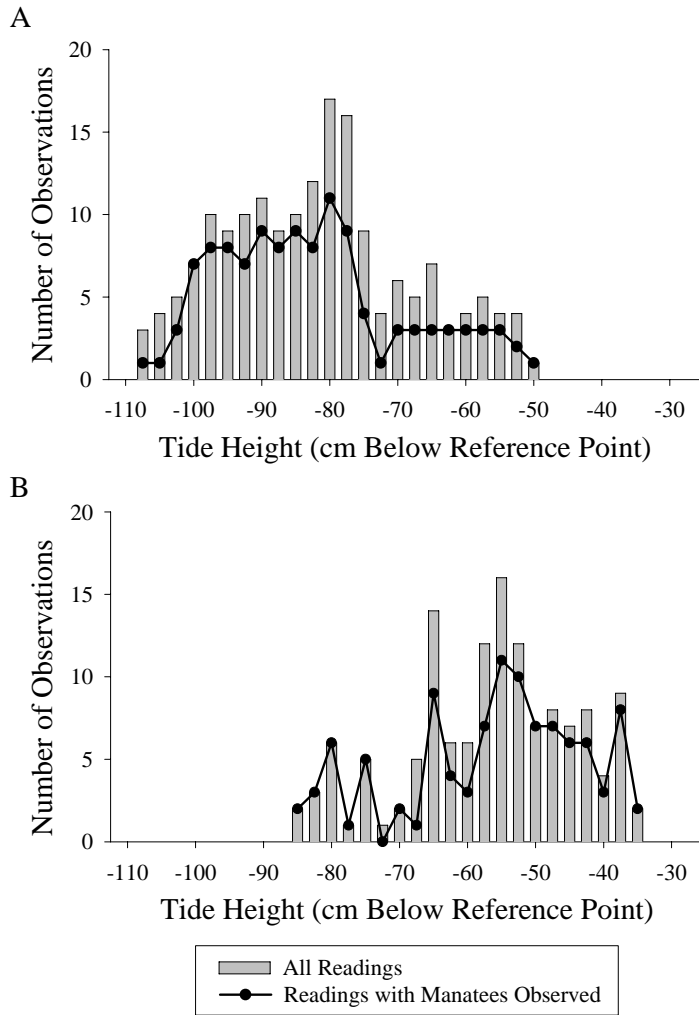


Figure 13. Frequencies of tide readings at different heights recorded at the entrance of the Matlacha Isles canal system during 24-hour sampling periods. The half-hour intervals that had the highest counts of manatees during the morning (A) and afternoon/evening (B) are represented on the graphs.

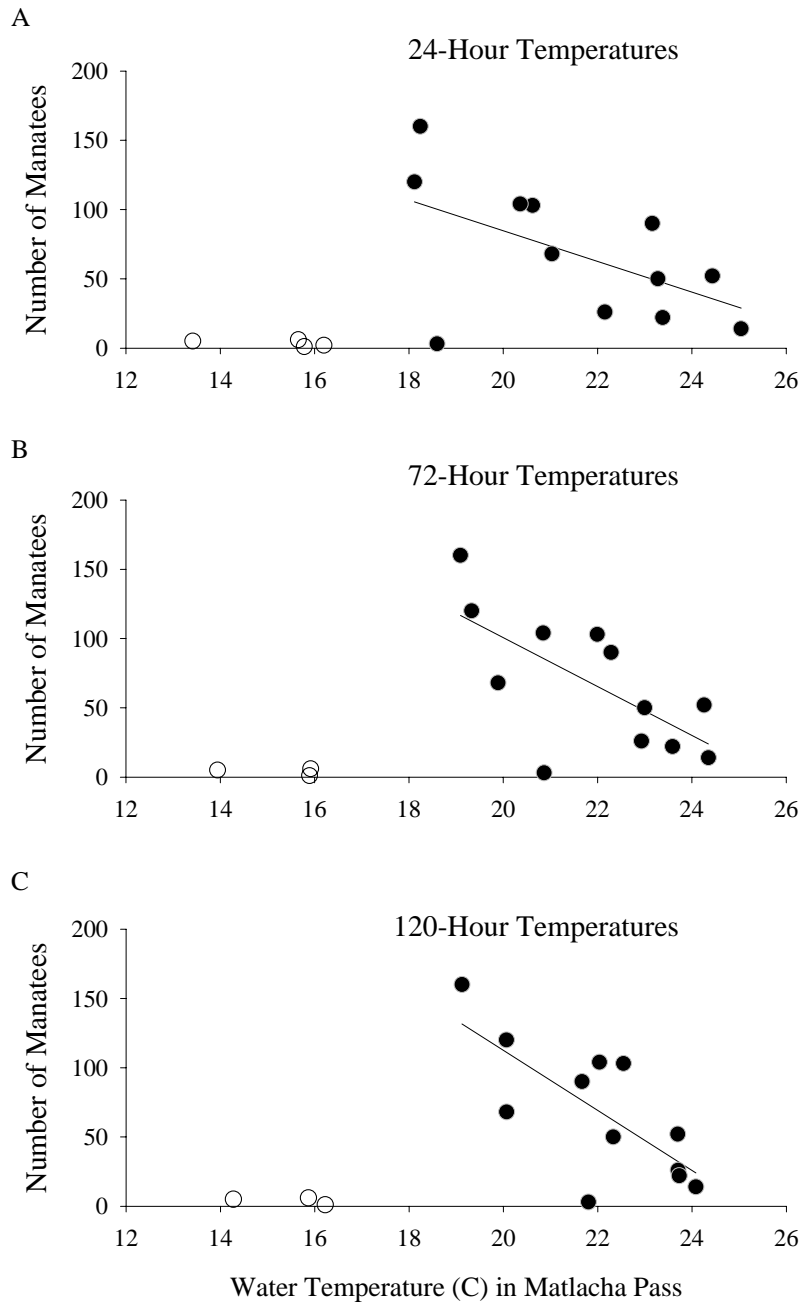


Figure 14. Number of manatees observed traveling into Matlacha Isles versus average water temperature in Matlacha Pass 24-, 72-, and 120-hours prior to each sampling period. Regression lines are also plotted. Data points when the average water temperature was $<18^{\circ}\text{C}$ are not shaded to differentiate them from data points that were used in the regression analyses.

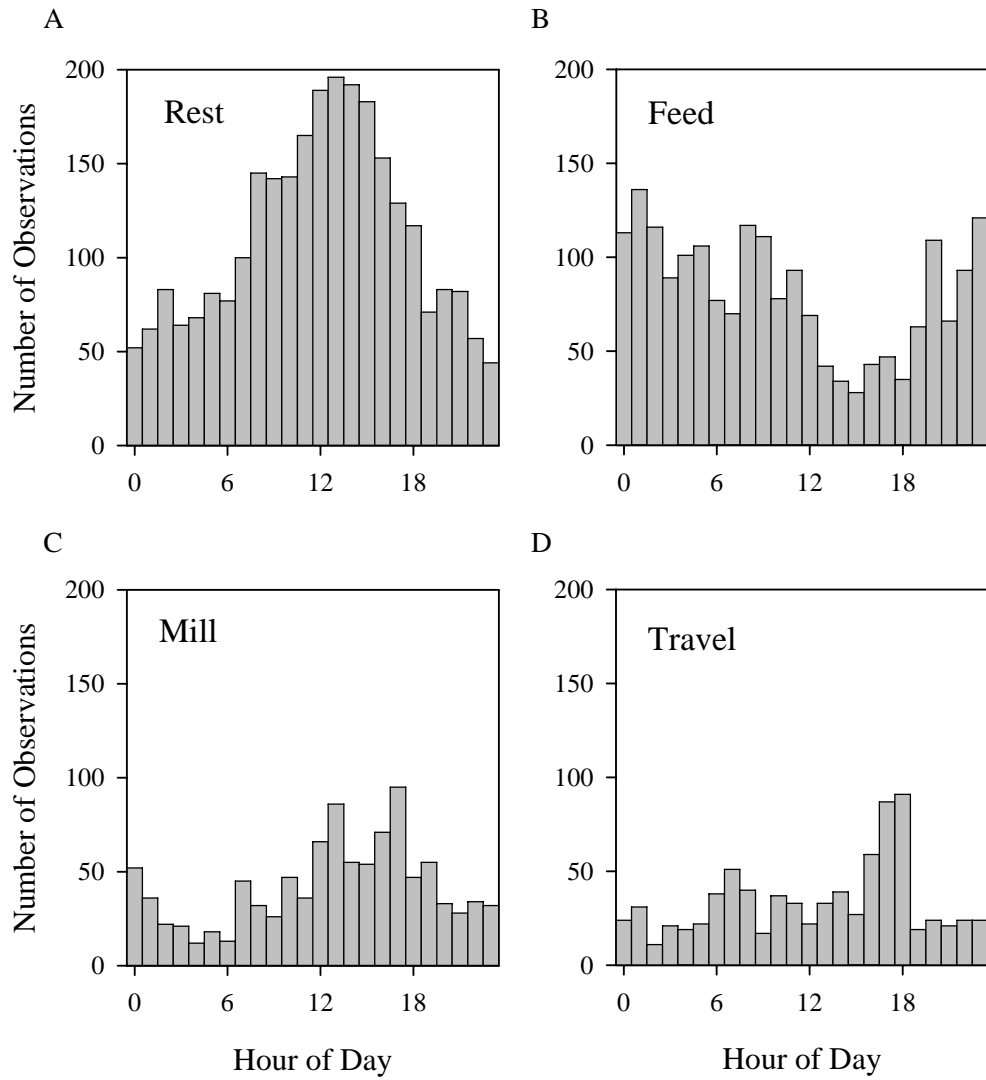


Figure 15. Total frequencies of each activity observed over all sampling periods.

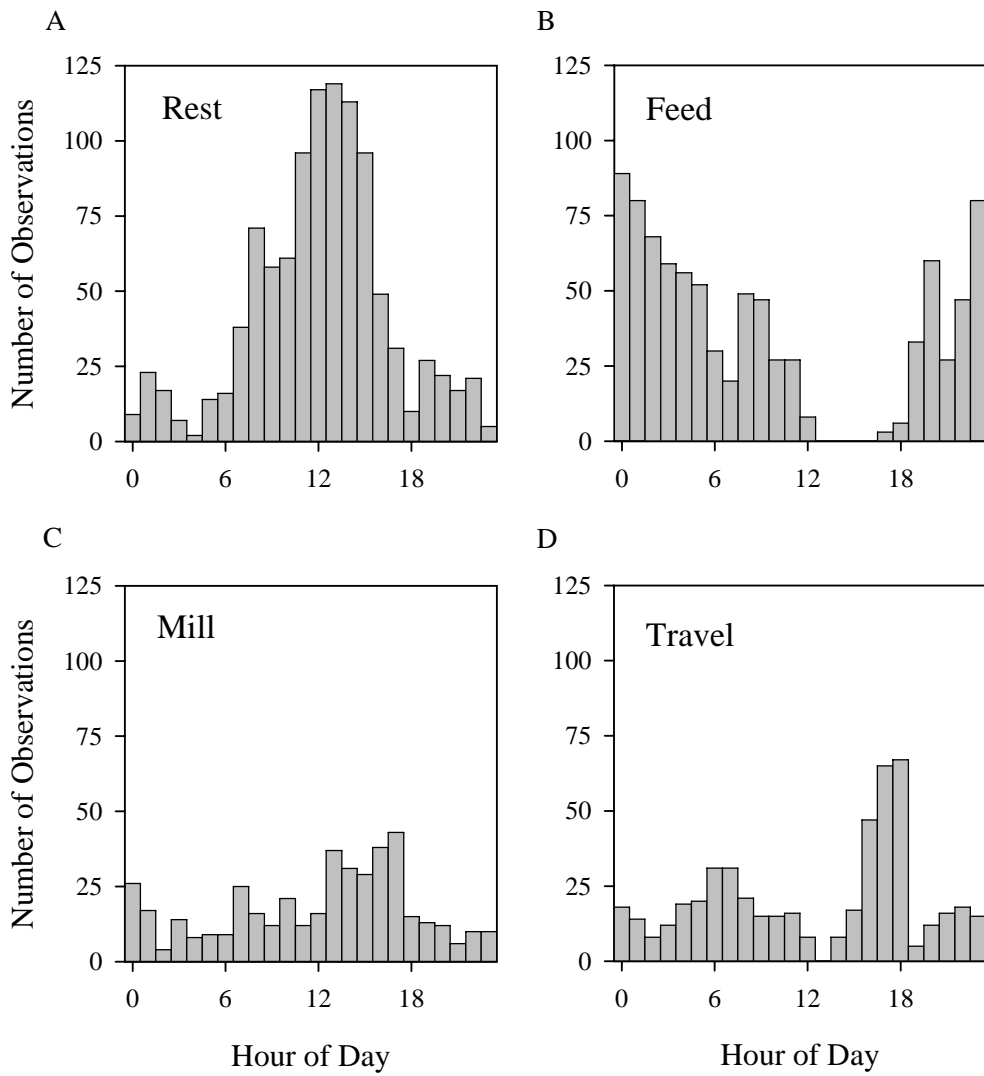


Figure 16. Total frequencies of each activity observed during the 11 sampling periods that focal manatees used Matlacha Isles during the day and Matlacha Pass at night.

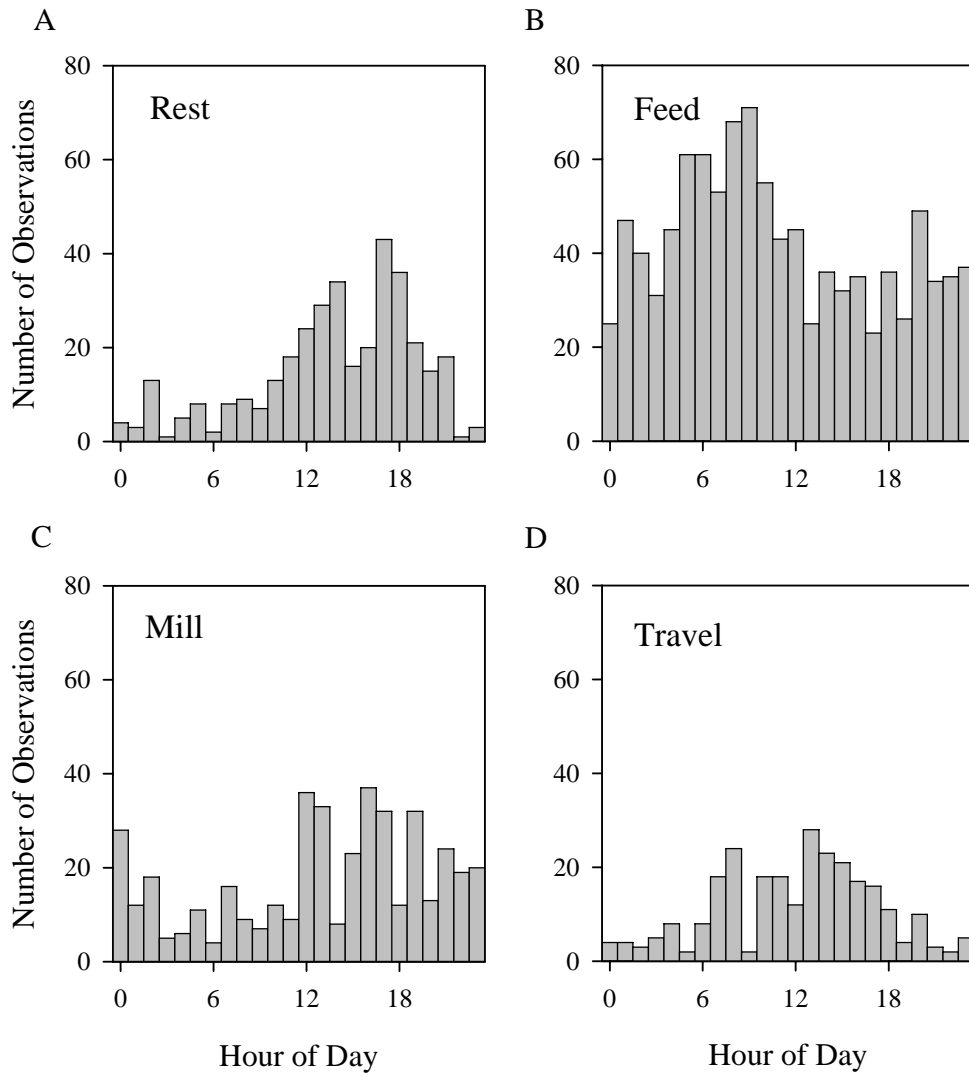


Figure 17. Total frequencies of each activity observed during the 8 sampling periods that focal manatees remained in Matlacha Pass.

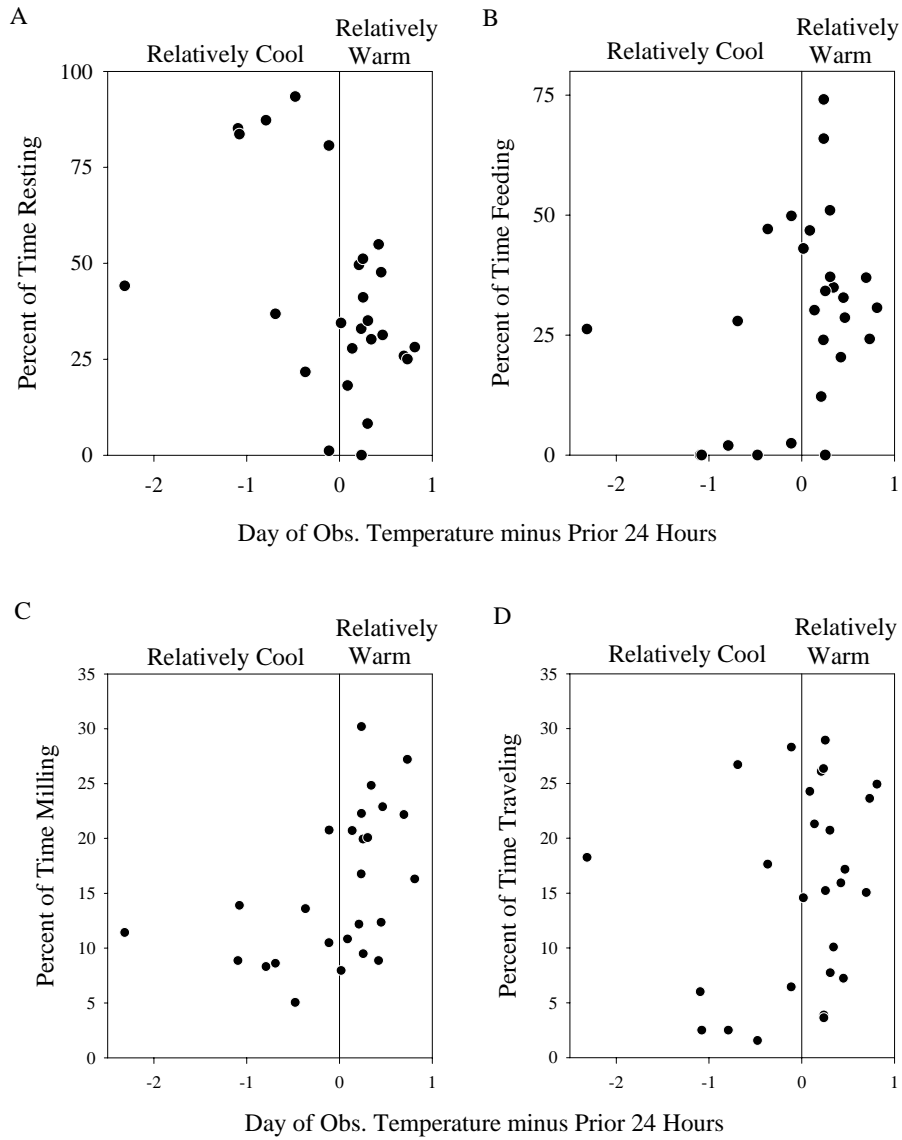


Figure 18. Percentages of time manatees were engaged in the observed behaviors versus the difference between the temperature on the day of the sampling and the prior 24-hour period.

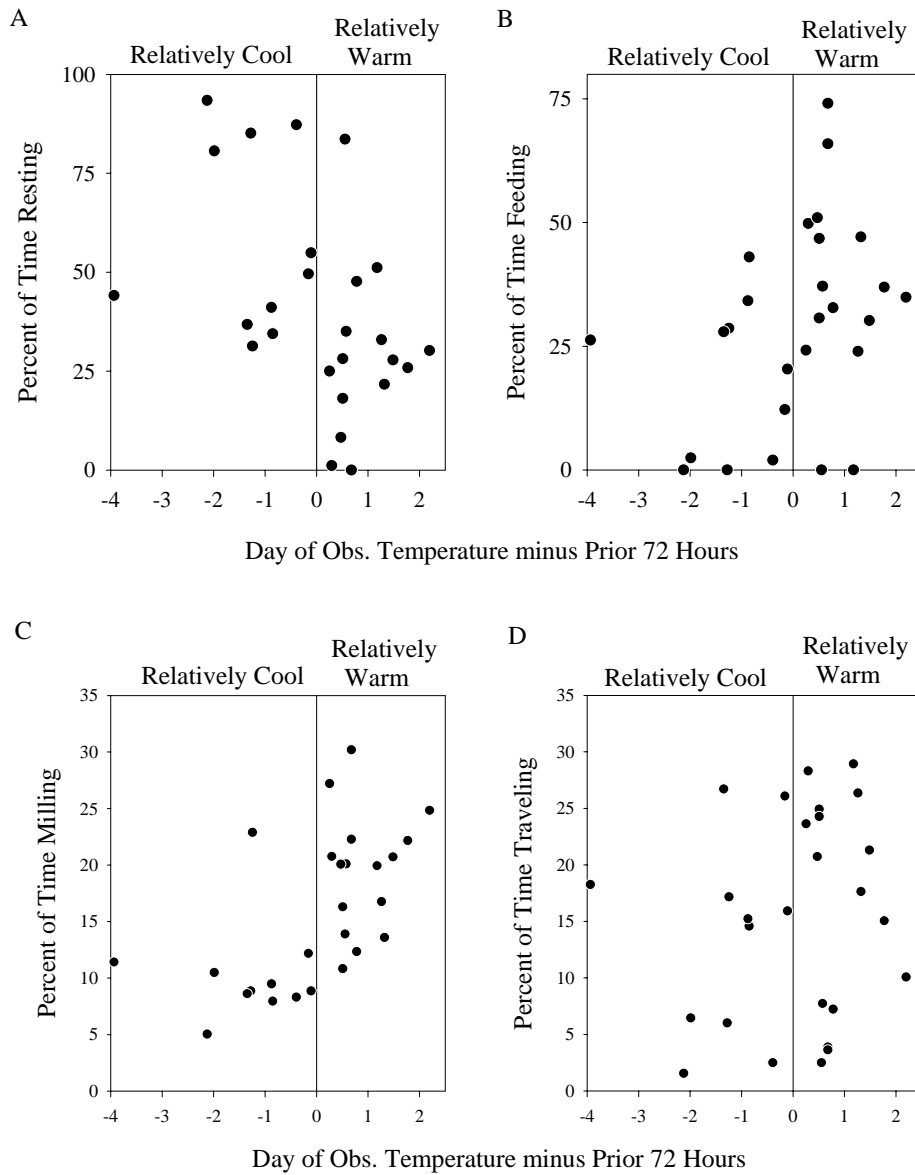


Figure 19. Percentages of time manatees were engaged in the observed behaviors versus the difference between the temperature on the day of the sampling and the prior 72-hour period.