THE USE OF A ROBUST DESIGN TO DETECT CHANGE IN MANATEE USE OF A WARM-WATER REFUGE

By

AMY LYNN TEAGUE

A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2011

To Will, Katie, Thomas, Finn, and Clay

ACKNOWLEDGMENTS

I would like to thank my committee: Dr. Jim Nichols, Dr. Cathy Langtimm, and Dr Franklin Percival, whose enormous amount of wisdom, patience, and understanding kept me moving forward. I feel incredibly lucky to have had the opportunity to work with them. I would like to thank The U.S. Geological Survey who graciously allowed me the opportunity to work on this project. Sirenia Project veterans, Cathy Beck, Susan Butler, Bob Bonde, Jim Reid, Gaia Meigs-Friend, and Howard Kochman, provided me with opportunities and advice that furthered my knowledge of manatee ecology and have helped me grow to become a better biologist. Cathy Beck and Susan Butler supported me through this whole process, keeping me sane by listening to thoughts, not allowing me to quite and reminding me that it will be worth it in the end. I would like to thank Wayne Hartley who spent over 3 decades collecting the data used for my study. Kristin Monkhorst, Kathy Sohar, Bonnie Bowman, Megan Murphy, Kim Snyder, Adam Reinhardt, and Robert Coe were essential support staff throughout the project. Lastly, I could not have done this without my family's love and emotional support.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science

THE USE OF A ROBUST DESIGN TO DETECT CHANGE IN MANATEE USE OF A WARM-WATER REFUGE

By

Amy Lynn Teague

December 2011

Chair: James D. Nichols
Major: Interdisciplinary Ecology

Physiological constraints of the Florida manatee (*Trichechus manatus latirostris*), require them to have access to winter warm-water refugia when water temperatures fall below 20-21˚C (Powell and Waldron 1981). Natural springs and industrial power plant effluents are the primary warm-water refuges, and changes in power plant operations are leading to temporary or permanent disruptions in warm-water availability. Manatees may need to rely more on natural refugia, leading to an increase in current over-wintering populations at such areas. During periods of extreme cold, manatees would not be expected to leave winter refuges and risk exposure to life threatening cold water. Therefore, deviations from historic within-winter movement patterns during cold spells could indicate that carrying capacities are being approached at natural refugia. It is important that managers have the ability to detect such deviations in order to engage in such actions as warm-water habitat protection and enhancement.

The multistate open robust design framework has provided an opportunity to use capture-recapture data to compare historic to present patterns of within-winter season use by manatees of Blue Spring, a primary warm-water refuge on the Atlantic coast of

Florida. The results of this study did not provide evidence that the over-wintering manatee population at Blue Spring is showing indications of approaching carrying capacity. However, despite model uncertainty that often occurred with the this modeling framework, estimates associated with top ranking models were able to characterize predicted, as well and unexpected, within-winter manatee movement patterns relating to temperature. The multistate open robust design, using proper covariates influencing manatee use of warm-water refugia, has the capability to be a useful monitoring tool for winter aggregation sites when investigating manatee use and habitat change.

CHAPTER 1
INTRODUCTION

Manatees and Warm Water

The Florida manatee (*Trichechus manatus latirostris*), an endangered subspecies of the West Indian Manatee, is a semi-tropical marine mammal that inhabits rivers and coastal areas of the southeastern United States and the Gulf of Mexico (Moore 1951, Lefebvre 2001). Manatees have a low metabolic rate and high heat conductance (Irvine 1983), and exposure to cold water temperatures (<20˚C) for extended periods may cause chronic symptoms such as weakened immune systems (Bossart et al. 2002), as well as death (O'Shea et al. 1985). These physiological constraints require them to have access to warm-water refuge when winter water temperatures drop below approximately 20-21˚C (Powell and Waldron 1981, Shane 1984, Deutsch et al. 2003). The primary refuges are natural springs, which maintain an average 23°C year round, and warm-water outflows of industrial power plants. Manatees exhibit a high degree of yearly winter site fidelity to primary aggregation sites (Reid et al. 1991, Deutsch et al. 2003) that is most likely due to traditional patterns learned as young from adults (Bengtson 1981, Reid et al. 1991). When ambient river water temperatures start to decline, manatees begin to arrive at warm-water aggregation sites; departures are associated with increasing ambient water temperatures and possibly photo period (Deutsch et al. 2003). Within-season manatee movements into and out of a refuge are balanced between the need to stay warm and the need to leave a refuge to forage.

Fine scale manatee movements at warm-water refuges have thus far been studied primarily using telemetry and have been restricted to a small number of individuals for a limited time period, due to cost and logistical constraints. Recent development of multistate capture-recapture models offers the potential to answer questions about manatee movement using data from long term monitoring of individually scarred manatees at aggregation sites throughout Florida. Capture-recapture models have already been used to estimate demographic parameters, such as survival and reproduction rates (O'Shea and Hartley 1995, Langtimm et al. 2004). With the availability of over 20 years of capture-recapture data at many aggregation sites, this approach could be used to examine changes in habitat use with changing environmental conditions.

Information on how manatees use warm-water refuges is important to managing this critical resource. Many of the industrial plants that manatees rely on are slated for closure and some will repower, causing a long-term disruption in warm-water availability. This disruption may force manatees to seek alternate refuge, leading to an increase in numbers of individuals using natural springs. In addition, increasing anthropogenic demands on spring discharge flow may effectively reduce warm-water availability for manatees at natural sites (Harrington et al. 2008, Rouhani et al. 2007). Loss of warm-water habitat was identified as a large threat, second to boat mortality, to the recovery of the species (Runge et al. 2007). Maintaining and enhancing warm-water habitat for the Florida manatee is a primary objective for state and local agencies. The need to set minimum spring flows was identified as an action to preserve critical manatee habitat.

Minimum flow levels (MFLs) have been established for many of Florida's springs and rivers, to prevent ecological degradation due to an increase in demand on water withdrawal for human use. The Saint Johns River Water Management District (SJRWD) established MFLs at Blue Spring, a primary manatee winter refuge. The flow regime was developed to allow for a temporary increase in water withdrawal from the aquifer until alternate sources of water can be identified. The recommended flow rates were calculated primarily to maintain adequate winter warm-water refuge for a projected increasing manatee population using the spring run (Figure 1-1) and allowed for a 15% reduction in the current long-term mean flow beginning in 2009. Unless the over-wintering manatee population increases at a faster rate than projected, minimum flows will be increased incrementally over 15 years until they return to current mean levels.

Carrying Capacity

Theory pertaining to large mammal population dynamics argues that variation in patterns of vital rates will emerge as environmental and population density changes occur, particularly when populations are reaching carrying capacity (Fowler 1981a, 1981b). Gaillard et al. (1998) reviewed multiple studies on the effects of population density on vital rates in large herbivorous mammal populations and found evidence that density dependence occurs in many of them.

The MFL analysis (Rouhani et al. 2007) for Blue Spring, based on an untested model of manatee carrying capacity, suggests that the spring run is able to support the current increase in the over-wintering population. However, there is concern that the population may be approaching a carrying capacity sooner than originally expected and that Blue Spring may not be able to support the projected increasing population. If manatees are approaching carrying capacity, it may be evident in changes of temporary or permanent movements. Winter season cold spells (ambient river temperatures < 20-21˚C) may vary from one season to the next and may last for short or long periods of time. During mild winters when cold spells may last for shorter time periods, temporary movements out of the run would be expected to be higher if individuals are only using the run for short periods of time, leaving to forage in the river. During winters where cold spells last for extended time periods, individuals would be expected to remain in the run to thermoregulate, and temporary movement out of the run would be expected to be low. Permanent movements out of the run would imply that manatees have moved to alternate warm-water refugia or that mortality has occurred. A population nearing carrying capacity may experience different patterns of temporary movements, and permanent movements might increase. Reduced spring flow, high river stage, and cold river temperatures have been attributed to the presence of a visible cold water wedge in the spring run. A wedge extending far enough up the spring run may reduce the area usable by manatees (Rouhani et al. 2007). A reduction in useable area, due to an increased population, in addition to the presence of a cold water wedge, may further influence temporary and permanent movements.

Multistate Models and Movement

The ability to use capture-recapture models to estimate parameters and test hypotheses about sources of variation associated with movement of wildlife populations is well documented (Hestbeck et al. 1991, Nichols and Kendall 1995, Spendelow et al. 1995, Duriez et al. 2009). Capture-recapture models allow for two types of populations; ”open”, where birth, death, immigration, and emigration may occur between sampling periods and “closed”, where no demographic processes may occur between sampling periods. An assumption central to open capture-recapture models is that all emigration from the study area is permanent. Temporary emigration is assumed to be random as to not bias estimates (Pollock et al. 1990, Kendall et al. 1997, Williams et al. 2002). However, situations can occur where neither assumption may hold true, such as with sea turtles monitored at nesting beaches. Females may skip a nesting season and stay out to feed, returning the following year to nest, therefore being temporarily unavailable for capture. Kendall and Bjorkland (2001) developed an open robust design to specifically address this issue where temporary movements (emigration) out of the study area were non-random. Departures from the nesting site may be either permanent or temporary if females return to nest. The model of Kendall and Bjorkland (2001) allows for the direct estimation of temporary emigration and annual survival probabilities in the presence of within-season permanent emigration and Markovian temporary emigration. Similarly, manatee movement into and out of a refuge within a winter season can be permanent (e.g., moved to alternate refugia) or temporary (leave the refuge to forage), therefore allowing for the estimation of manatee temporary or permanent movements.

Additionally, Fujiwara and Caswell (2002), Kendall and Nichols (2002) and Schaub et al. (2004) presented multistate models for open populations where being a temporary emigrant means that an individual has transitioned (moved) from an observable (O) state at some time *t*, to an unobservable (U) state at time *t* +1, with probability denoted by parameter ψ_t^{OU}. Parameters associates with this type of model are estimated using information from 2 temporal scales (e.g., weekly primary periods and daily secondary periods). Parameters include: between primary period survival (*S*, its compliment is indicative of permanent emigration in the absence of alternate sampling, White et al. 2006), first entry into a study area (β) during a secondary sampling period, the probability of remaining in a study area (φ) during the secondary sampling period, and detection probability (*p)* during each secondary period. The transition parameter, ψ , is estimated using information from both temporal scales. Daily or weekly records of the presence or absence of individual manatees at a refuge allow for the application of multistate models to estimate similar use parameters in this framework. An individual manatee may be considered in an observable state if in a refuge and available for detection. An individual away from a refuge may be considered unobservable. Parameters, including weekly state transition probabilities indicative of temporary and permanent movement (Table 1-1) can be further modeled as a function of time and of temporal or individual covariates (Breininger et al. 2010).

Objectives and Hypotheses

Understanding how manatees use warm-water and what factors affect use is important for developing management strategies. Capture-recapture models that have the ability to estimate parameters that support current knowledge of how manatees use winter refugia could be an important management tool. As the population of manatees using Blue Spring increases over time and as availability of the established warm-water refuge is altered, the ability to estimate parameters regarding movement may be important in determining if changes in behavior are occurring. Changes in behavior may indicate the approach of the population to carrying capacity, thus apprising managers of the need to protect and enhance current and alternate refugia.

The objectives of this study were to apply capture-recapture models to manatee detection history data in order to 1) test hypotheses regarding manatee winter use at a winter aggregation site as a function of winter temperatures and cold water wedge; and 2) determine if there is evidence that the current over-wintering manatee population using Blue Spring is approaching a carrying capacity.

For this study, I examined the influence of temperature and wedge (potentially reducing useable area) on manatee movement into (for thermoregulation) and out of (for the need to forage) Blue Spring run. In addition, I compared historic to present manatee winter use patterns to address whether the influence of environmental variables on winter use has changed. As the population using the spring increases, deviations from historic use patterns may indicate that the population is approaching carrying capacity. I addressed questions regarding winter use by evaluating hypotheses using model selection. These hypotheses involved sources of variation in my model parameters (ψ, β, and φ).

Question 1: How does temperature affect manatee use of the spring?

I hypothesized movement into and out of the run was dependent on ambient river temperature, and permanent emigration was not expected to have occurred (Table 1-2, Model a). When temperatures decrease and cold stress becomes more likely, individuals were expected to have a greater probability of moving into the run from one week to the next. As temperatures increase and manatees leave to forage, movements out of the run were expected to increase. Daily temperature decreases were expected to lead to higher probabilities of entering the run for the first time and remaining in the run within a week. Manatee movement between the St. Johns River and the Atlantic coast region, during both winter and warmer seasons, is limited (Reid et al. 1991, Deutsch et al. 2003). Therefore, it was not expected that permanent emigration will occur when river temperatures are severe (<20-21˚C).

Question 2: How does manatee movement change under differing patterns of cold temperatures?

I hypothesized that during winter seasons experiencing patterns of recurrent severe temperatures (<20-21˚C), individuals were expected to have a higher probability of being present in the run and remaining in the run (table 1-2, Model b). During winter seasons experiencing patterns of less recurrent severe temperatures, as manatees spend more time foraging, individuals were expected to move into and out of the run more frequently and remain away for longer periods of time; therefore, leading to greater temporal variation in movement, first entry, and probability of remaining in the spring run (Table 1-2, Model c).

Question 3: Are there deviations in movement parameters from historic to present that could indicate manatee use of the refuge is changing?

As the overwintering manatee population approaches carrying capacity, greater numbers of individuals using the run to thermoregulate may create less useable area; a cold water wedge encroaching far enough into the run may further reduce useable area, therefore forcing manatees to seek alternate refugia. I hypothesized that given similar severe temperature patterns, as the population is approaching carrying capacity, it was expected that individuals were less likely to move into and remain in the run. As alternate warm-water refuges are sought, permanent emigration was more likely (Table 1-2, Model d). A wedge encroaching farther into the run, as the population is approaching carrying capacity, might further reduce the probability of moving into and remaining in the run (Table 1-2, Model e).

Table 1-1. Definition of parameters associated with the multistate open robust design.

Parameter	Definition
p_{st}	The probability that an individual alive and available for detection is detected during secondary sampling period s of primary period *t, s* = day 1, 2, 3; *t* = week 1,2 3,….*k*.
β_{st}	The probability an individual enters the study area between secondary sampling period *s* and *s*+1 of primary period *t*, given that the individual is present at some time during primary period *t*. The probability of already being present in study area is 1- β_{st} , *s* = day 1,2 ,3; *t* = week 1,2 3,….*k*.
φ_{st}	The probability an individual present in the run in secondary period *s* of primary period *t*, remains in the run to be present in secondary period *s*+1...*k*, *s* = day 1,2 ,3; *t* = week 1,2 3,…*k*.
S_t	Probability that an individual alive and available for detection in primary period *t* survives and is still in the run in primary period *t*+1, *t* = week 1, 2 3…*k*-1.
ψ_t^{OU}	The probability that an individual in the observable (O; i.e., in the run) state in time *t* moves to an unobservable (U; i.e., out of the run) state in time *t*+1, *t*= week 1, 2, 3,…*k*. The probability of remaining in the observable state from week *t* to *t*+1 is 1- $\psi_t^{OU} = \psi_t^{OO}$.
ψ_t^{UU}	The probability that an individual in an unobservable state in time *t* , given that it was in an observable state at some time prior to *t*, remains in an unobservable state in time *t*+1, *t*= week 1,2,3,…*k*. The probability of moving from an unobservable state at time *t to* an observable state at time *t*+1 is 1-$\psi_t^{UU} = \psi_t^{UO}$.

Table 1-2. Predicted relationships of model parameters with environmental covariates under prior hypotheses about variation in winter manatee movement at Blue Spring, St. Johns River, Florida.

Hypothesis	Model	Predicted Outcome
(1) Movement is a function of ambient river temperature.	(a) S (.) ψ (temp), β (temp), φ (temp)	(a) ψ_t^{UO} And ψ_t^{OO}, β_{st}, and φ_{st} are expected to have a negative relationship with temperature, as manatees move in to run to thermoregulate. ψ_t^{UU} and ψ_t^{OU} are expected to have a positive relationship with temperatures as manatees leave to forage. S_t is expected to be high as permanent emigration is unlikely.
(2) Movement is a function of magnitude of cold (extreme versus moderate).	(b) S (.) ψ (temp), β (temp), φ (temp)	(b) During seasons with patterns of frequent severe river temperature, to avoid prolonged exposure to cold, φ_{st} and ψ_t^{OO} are expected to remain high (ψ_t^{UU} low). β_{st} is expected *to* remain low (close to 0), when temperatures remain severe within a week due to individuals already being present in the run (1-β_{st}).
	(c) S (.) ψ (temp), β (temp), φ (temp)	(c) During seasons with patterns of less frequent severe river temperature, as manatees have more opportunities to forage and less need to thermoregulate, greater variations, in ψ_t, β_{st}, and φ_{st} are expected.

Table 2-1. Continued.

	(d) S (.) ψ (temp), β (temp), φ (temp)	(d) During seasons later in the study, where the over-wintering population is larger driving manatees to alternate refugia, with patterns of more frequent severe river temperature, ψ_t^{UO} and ψ_t^{OO} are expected to be lower. ψ_t^{UU}, ψ_t^{OU}, and S_t are expected to be higher.
	e) S (.) ψ (wedge), φ (wedge	(e) During seasons with patterns of more frequent severe river temperature later in the study, ψ_t^{OU} and ψ_t^{UU} are expected to be positively associated with wedge and φ_{st} is expected to be negatively associated with wedge, due to reduced useable area and undesirable habitat.

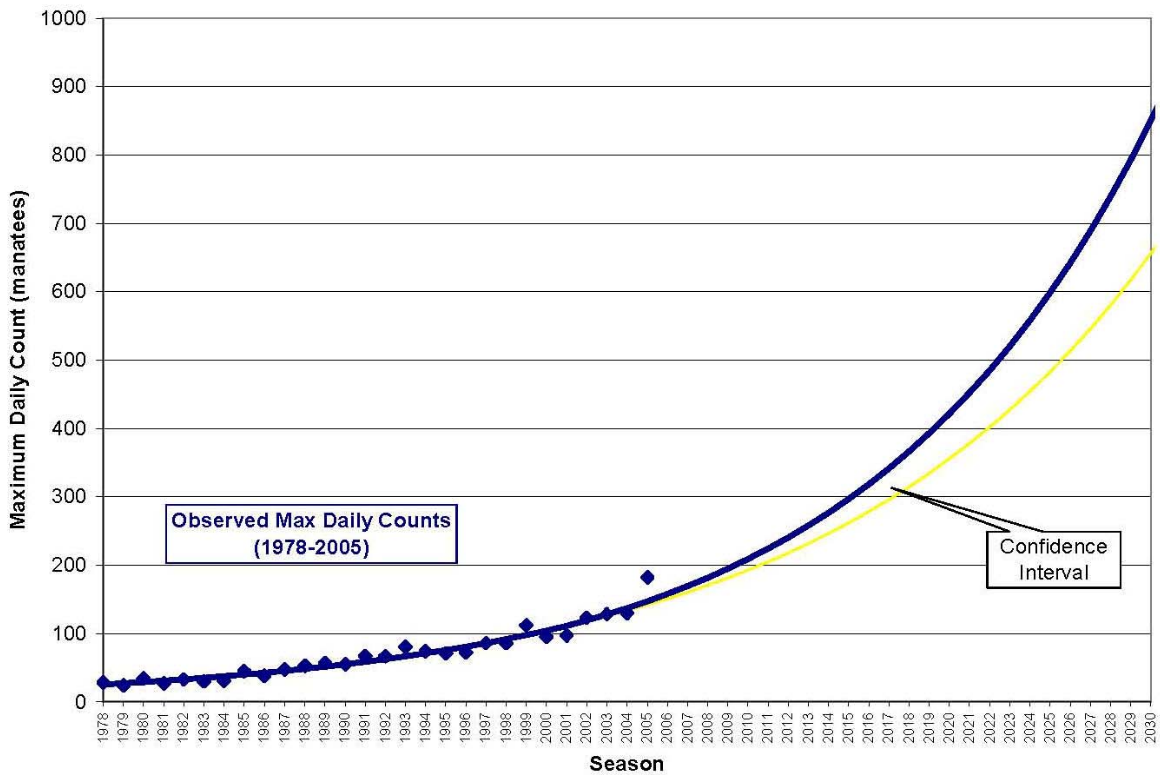

Figure 1-1. The projected increase in the manatee population using Blue Spring run, St. John's River, FL, as a winter refuge (Rouhani et al. 2007).

CHAPTER 2
METHODS

Study Area

Blue Spring is a first magnitude spring (spring flow > 100 cubic feet per second (cfs) located in Volusia County, Florida, off the St. Johns River. The spring discharge flows at a long term mean of 157 cfs (Rouhani et al. 2007) and remains a constant 23˚C (Rosenau et al. 1977). Blue Spring run is the primary manatee winter aggregation site in the St. Johns River (Beeler and O'Shea 1988). The spring run flows approximately 712 m until it converges with St. Johns River and is located within Blue Spring State Park (BSSP). The park is open for public use year-round, however, during the winter, when there are manatees present in the spring run, members of the public are not allowed to enter the water. Observational, telemetry, and photo-identification studies of the manatee population at BSSP date back to the late 1970's (Hartman 1979, Bengtson 1981, Powell and Waldron 1984). Following winter cold spells, when the water temperature of the St. Johns River drops below that of the spring, manatees begin to move into the spring run (Bengtson 1981, Powell and Waldron 1981). If the ambient river temperature is severe (<16˚C), individuals will remain in the run as long as temperatures remain severe (Wayne Hartley, personal communication). During less severe cold river temperatures (>16 ˚C) individuals have been observed to leave the run during the warmer part of the day to feed (Bengtson 1981, Powell and Waldron 1981). While most manatees exhibit high winter season return rates (Powell and Waldron 1981, Langtimm et al. 2004), some individuals, known as transients, will leave the run early in the winter season in route to alternate refugia. Transient individuals will not return for the remainder of the season. The primary manatee aggregation areas tend to be in the lower 225 m (up to Zone 8) of the run (Powell and Waldron 1981, Smith et al. 2000) where the dark water wedge occurs most frequently (Figure 2-1) (Rouhani et al. 2007). Frequency and extent of the wedge are increased by low discharge, high river stage, and cold river temperatures (Sucsy et al. 1998, Rouhani et al. 2007, Saint Johns River Water Management District, unpublished report).

Manatee Photo-identification System

The Manatee Individual Photo-identification System (MIPS) is a long-term sightings database which identifies individuals based on unique features, primarily healed scars caused by boat strikes. MIPS began development in the 1980's and has facilitated the study of manatee population ecology, providing information about site fidelity, dispersal, (Reid et al. 1991) and reproductive traits (O'Shea and Hartley 1995). Additionally, MIPS has enabled the application of capture-recapture statistical analyses to make inference on population dynamics including survival (Langtimm et al. 1998, 2004) and reproduction (Kendall et al. 2004). The MIPS catalog consists primarily of photographs of unique features of individual manatees. To meet assumptions associated with capture-recapture data analysis, strict criteria are employed when cataloging a recognizable individual (Beck and Reid 1995). At Blue Spring, the clarity of the water and low numbers of over-wintering individuals relative to other aggregation sites, has allowed 1 investigator to visually identify manatees on a daily and yearly basis with minimal error. However, MIPS criteria are still used when cataloging recognizable individuals using photographs taken by BSSP, USGS, and field staff of other agencies. Photo-identification and telemetry data have demonstrated long distance movements between the St. Johns River and the Atlantic coast of Florida, (Langtimm et al. 1998, Deutsch et al. 2003, Sirenia Project unpublished data) therefore, strict criteria are needed to ensure correct identification.

Data Collection

I used visual sightings of individually identifiably manatees collected during the winter seasons of 1985 through 2006 for this study. The winter season typically starts around November when air temperatures and associated ambient river temperatures begin to decline and ends mid to late March when water temperatures begin to increase and remain warm. However, to focus on the winter resident population at Blue Spring and avoid transient individuals moving on to other sites, I restricted the yearly sampling periods to mid-December through February (e.g., December 2000 through Feb 2001 = the 2000-2001 season). The following information was recorded: total daily manatee counts, individual identification numbers, daily river temperature, daily run temperature, manatee aggregation areas, and cold water intrusion length (Figure 2-1).

Data Analysis

The multistate open robust design (MSORD) uses information from 2 temporal scales to estimate parameters. For my study, each winter season consisted of 7 to 12 weekly primary periods. Individual detection histories were constructed, using daily visual attendance data recorded by Blue Spring staff, during 2 to 3 daily secondary periods within each week. Detection histories consisted of a series of 1’s and 0’s, 0 if an individual was not observed on a day and 1 if an individual was observed. To avoid violations of important assumptions associated with robust design capture-recapture models (Pollock et al. 1990, Kendall et al. 1997, Williams et al. 2002), data were censored in the following manner: To avoid misidentification violations, only visual records of individuals that had been photographed before and met the criteria to be entered into MIPS were used. First capture of an individual was dependent on the sighting date an individual was completely documented in MIPS (Beck and Reid 1995). Only sightings from adult manatees (>5 years old) were used, as juveniles and cows with calves may use the run differently during the winter. Adult males and non-reproductive females were pooled because of small sample sizes.

The MSORD model allows for the estimation of 5 kinds of parameters (Table 1-1) that correspond to 2 temporal scales. Daily capture probabilities (*p*) correspond to the secondary sampling periods, and entry and exit probabilities (β and φ) correspond to the intervals between them. Permanent emigration (defined as the compliment of the survival parameter, *S*) corresponds to the periods between weekly primary periods. Temporary emigration between weekly primary periods is estimated using the information from both temporal scales. An individual manatee is characterized as in the observable state (O) if in the spring run during a daily sampling period and the unobservable (U) state if outside the run. Movement for this study is quantified as state transitions between U and O over the time interval week *t* to *t*+1. When an individual permanently leaves the study area, in the absence of monitoring additional warm-water sites, permanent emigration is confounded with mortality; therefore, estimated survival (*S*) from 1 week to the next is apparent survival. Manatees are not expected to leave the run and be exposed to life threatening water temperatures. Therefore, it is likely that little mortality would occur between weeks so apparent survival can be used to estimate the compliment of permanent emigration.

An environmental covariate that may be an important influences on ψ_t , φ_{st} , and β_{st} is ambient river temperature (temp). Potential Influences on ψ_t and φ_{st} , also include the cold water intrusion length (wedge).

Using Program MARK (White and Burnham 1999) and following the step down approach recommended by Lebreton et al. (1992), for each season I started by modeling individual parameters in the following order, starting with p_{st}, φ_{st} , β_{st} , S_t, and ψ_t . I focused on 1 parameter at a time, retaining the top model(s) for each group of parameters that had already been investigated and the most general parameterization possible for those not yet investigated. The most parsimonious models for each group of parameters were chosen using Akaike's Information Criterion adjusted for small sample size, AICc (Burnham and Anderson 2002), and associated model weights. Models with a Δ AICc of < 2 were considered to have similar support from the data. Where there was support for multiple models with similar weights, I used model averaging to obtain the best estimates. The parameters pertaining to the interval between the weekly primary sampling periods, ψ_t^{OU} , ψ_t^{UO} (transitions to and from outside the study area), and *S* were modeled as time varying (*t*), constant (.), and with no movement (ψ_t^{OU} and ψ_t^{UO} = 0, ψ_t^{UU} and ψ_t^{OO} = 1). Parameters associated with the secondary sampling periods (p_{st}, β_{st} , and φ_{st}) were modeled as fully time specific (*t*), as constant across all sampling periods (..) and constant within primary periods but time specific across primary periods (*t*.). To investigate hypotheses involving covariates, I modeled ψ_t as a function of the average weekly river temperature (˚C) and highest zone in which the wedge was recorded in the run at week *t*+1. β_{st} and φ_{st} were modeled as a function of the actual covariate values obtained on each day. I included a wedge effect and explored both additive (temp+wedge) and interactive effects (temp*wedge) of covariates on ψ_t and φ_{st} as well as additive effect of time (*t*) and covariate (e.g., *t*+temp) on ψ_t .

The time periods representing seasons were chosen to correspond to the coldest weeks of the winter season, as noted above. For many seasons, average weekly temperatures did not reach above 20°C, the temperature at which individuals begin to seek out warm-water refuge, and never reached above 22°C. Park staff reported that individuals were observed to not leave the run at or below 16°C. Upon inspection of average weekly temperatures for each winter season, two within-season temperature patterns occurred with regard to the 16˚C threshold. Severe winters were characterized by average weekly temperatures that remained at or below 16˚C for at least half of the primary sampling periods (weeks) within the winter season. Moderate winters were characterized by average weekly temperatures that dropped below 16˚C, at most, for 2 weeks of the season. Therefore I used 16˚C as a critical threshold to examine the parameters estimated under the most parsimonious models for general patterns in movement. To detect deviations from historic to present use of the run, and hence to test carrying capacity hypotheses, I compared parameter estimates between early seasons of the data set, representing low numbers of individuals using the run and later seasons representing high numbers.

Based on knowledge of how manatees use warm-water refuges, non-random temporary emigration (Kendall et al. 1997) is expected to occur. Program U-CARE (Choquet et al. 2005) is a stand-alone program that tests model fit. Subtest 2.Ct of this program tests for trap dependence (Pradel 1993) and can be used to test for non-random temporary emigration (Schaub et al. 2004). Lack of fit for this test component provides evidence that non-random temporary emigration is occurring. To test the expectation of non-random temporary emigration, I ran a GOF test (Ucare) on 6 randomly chosen seasons of the data set, using the most general model with time dependence on all parameters.

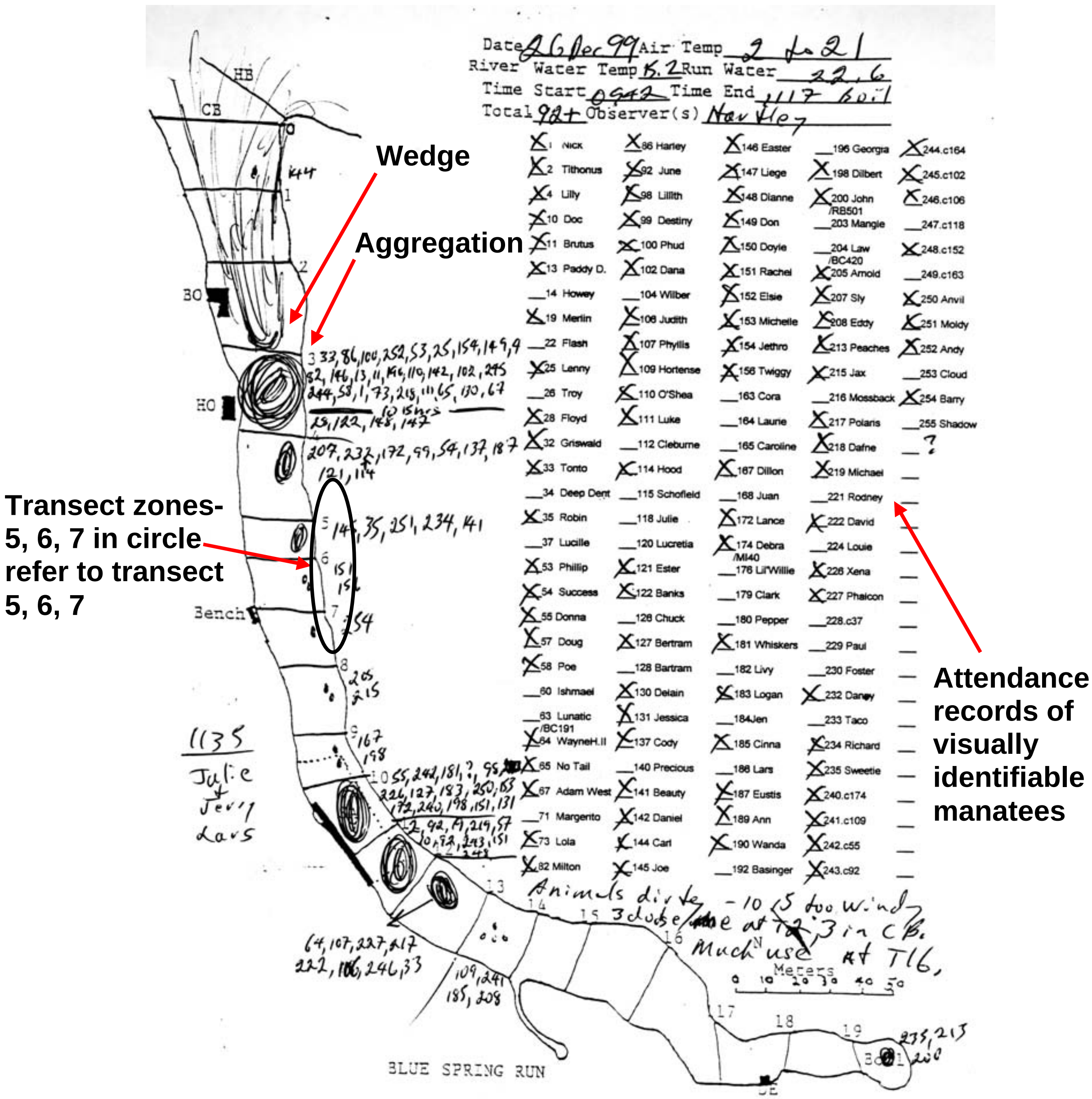

Figure 2-1. Manatee data sheet and map of Blue Spring run, St. Johns River, FL. Daily recognizable individual attendance records are on right. The map on the left shows manatee aggregations (dark circles), zones (numbered sections), cold water wedge length (Wayne Hartley, BSSP).

CHAPTER 3
RESULTS

Of the 21 year data set, 12 seasons fell under severe cold conditions and 9 fell under moderate cold condition. Early and later seasons were represented in both cold characterizations. Detection probabilities were relatively high. The average seasonal estimated detection probabilities across the entire study ranged between 0.59 and 0.94.

The most parsimonious models for probability of first entering the run at some point after the first sampling occasion within each week (β_{st}) was time dependent for 15 of the 21 seasons. The top model was constant $\hat{\beta}_{st}$ for 5 seasons and temperature effect for 1 season. Model selection did not indicate temperature improved the models for most seasons; however patterns relating to temperature were apparent when I examined the estimates. When daily temperatures within a week remained below 16˚C, manatees were more likely to be present in the run at the first secondary sampling day and new individuals were less likely to enter later in the week ($\hat{\beta}_{st}$ were rarely above 0.20). It was more likely individuals would enter the run for the first time later in the week ($\hat{\beta}_{st}$ ranged 0.30 and 0.91) when daily temperatures started off warmer (>16˚C) within a week or as temperatures declined. These apparent relationships suggest that different temperature covariates could be used to explore alternative models of entry probabilities. Deviations from historic patterns were not evident when I compared earlier seasons to later seasons.

The most parsimonious models for the probability of remaining in the run each week ($\hat{\varphi}_{st}$) were time-dependent for most seasons. While model selection did not provide evidence that the temperature covariate improved the models, patterns relating to temperature were apparent when I examined the estimates. Colder weeks when temperatures remained at or below 16˚C were generally associated with estimates between 0.80 and 1 over the entire study. Daily temperatures that remained below 16˚C, coupled with a decrease in $\hat{\varphi}_{st}$ below 0.80, typically occurred following a temperature increase from one day to the next within a week. The estimates suggest that when temperatures remained severe, individuals were more likely to remain in the run for the entire week; however, following multiple days of critical temperatures, they were more likely to move out, presumably to forage as park staff has observed. When daily temperatures were above 16˚C, estimates of $\hat{\varphi}_{st}$ were more variable. More often, $\hat{\varphi}_{st}$ was <0.60 during warmer weeks, however $\hat{\varphi}_{st}$ of >0.60 to 1 occurred during warmer weeks at the beginning of moderate seasons. Results suggest that individuals were less willing to leave the run to forage within a week at the beginning of the winter season despite less severe temperatures. However towards the end of the season, as perhaps the threat of prolonged cold exposure diminished, the lower estimates suggest individuals were more likely to leave. As with the modeling of entry probabilities, these a posteriori hypotheses could be incorporated into models via development of different temperature covariates. Deviations from historic patterns were not evident when I compared earlier seasons to later seasons.

The most parsimonious model for the probability of remaining in the area of the run between weeks over the entire season (S_t) was constant. $\hat{S}_t$ was high for all seasons (range 0.92 to 1), therefore, permanent emigration (1-S_t) within a year was relatively low. There was no indication of differences between cold and moderate seasons or between early and late seasons when population numbers differed.

Movement Probabilities In and Out of the Run

The goodness of fit test under subtest 2.Ct was significant for all 6 seasons (sum of χ2 = 439.64, sum of df = 142), indicating lack of fit and the presence of non-random temporary movement (emigration) in and out of the run.

Temperature, Wedge, and Movement

The most parsimonious models for most winter seasons, over the entire study, were models that included temperature or wedge (or both) affects on the weekly movement parameters. Model selection resulted in support for my hypotheses on the positive main effect of temperature on $\hat{\psi}_t^{OU}$ and $\hat{\psi}_t^{UU}$ (negative main effect on $\hat{\psi}_t^{OO}$ and $\hat{\psi}_t^{UO}$) (Table 1-2, Prediction a) during some years of the study. Model selection did support a negative relationship between wedge and $\hat{\psi}_t^{UU}$ during 2 seasons categorized as severe, however only 1 season was later in the study (1999-2000). Therefore, showing minimal support, based on model selection, for my carrying capacity (Table 1-2, Prediction e). During severe winter seasons, later in the study, there was lack of evidence that presence of a wedge increased the probability of manatees remaining out of the run. The most parsimonious models for most seasons of the study included interactive and additive effects (often resulting in equal support for both type of effects) of temperature and wedge on movement. Inference was unclear from these results; therefore, I performed a post-hoc correlation analysis and identified a negative correlation between temperature and wedge in all but 2 seasons (Tables 3-1 and 3-2). Across all seasons of the data set, often the negative correlation between temperature and wedge was strong. As a result, interpretation of covariate model results is more difficult. It may be wise in the future to consider a set of models with only one of these covariates to improve model selection and inference.

Movement during severe and moderate winters

The top ranking models for the estimated probability of movement out of the run ($\hat{\psi}_t^{OU}$) across all severe winter seasons, included a temperature, and/or wedge effect, on $\hat{\psi}_t^{OU}$ for 8 seasons, a constant $\hat{\psi}_t^{OU}$ in 2 seasons, and full time variation only in 2 seasons (Table 3-1). A positive main effect of temperature was only supported during 2 severe winter seasons. Averaged weekly $\hat{\psi}_t^{OU}$ suggested that manatees were less likely to move out of the run ($\hat{\psi}_t^{OU}$ <0.31) and more likely to remain in the run ($\hat{\psi}_t^{OU}$ > 0.69) during severe winters (Figure 3-1A), as expected (Table 1-2, Prediction b). In contrast, the top ranking models for the estimated probability of remaining out of the run during severe seasons included a temperature, and/or wedge, effect during 10 seasons, 1 resulted in constant $\hat{\psi}_t^{UU}$, and 1 season resulted in equal support for constant $\hat{\psi}_t^{UU}$ and interactive model (Table 3-1). Average weekly estimates of remaining out of the run during severe winters did not remain low as expected (Table 1-2, Prediction b). During several seasons average $\hat{\psi}_t^{UU}$ was >0.71 (Figure 3-1B), suggesting there was variability in use during severe seasons where remaining out of the run would exposé manatees to life threatening temperatures.

During moderate seasons, the top ranking models for movement out of the run ($\hat{\psi}_t^{OU}$) included a temperature and/or wedge effect during 5 seasons, time variation only during 3 seasons, and 1 season resulted in constant $\hat{\psi}_t^{OU}$ (Table 3-1). There was minimal support for the expected positive main effect of temperature (Table 2-1, Prediction a).

The averaged weekly estimates for each moderate season (Figure 3-2A) were low. Averaged estimates did not suggest variability in movement out of the run, as expected (Table 2-1, Prediction c) during moderate seasons when manatees have more opportunities to leave the run to forage. However, averaging weekly estimates may not reflect variably if the range of the actual (not averaged) weekly estimates is large (e.g., the 1998-1999 winter season, $\hat{\psi}_t^{OU}$ ranged from 0 (95%CI=0 to 0.44) to 0.84 (95%CI=0.71 to 0.92).

The top ranking models for remaining out of run during moderate seasons resulted in temperature and/or wedge effects (Table 3-1), and did not support a positive relationship between temperature and $\hat{\psi}_t^{UU}$ as expected (Table 1-2, model c). The average weekly estimates were not as variable as expected and estimates suggested that manatees were less likely to remain out of the run when temperatures were not as life threatening. However, similar to $\hat{\psi}_t^{OU}$, averaged weekly estimates may not reflect variability if the range of the actual weekly estimates is large.

Averaged estimates varied greatly between earlier and later seasons of my study. Thus there was no evidence, based on my hypotheses, that there were deviations from historic to present movement patterns (Table 1-2, Prediction d).

A posteriori examination of temperature and movement

I examined weekly movement's parameter estimates, *a posteriori*, as a result of the difficulty in making inference based on model selection with regard to temperature. While model selection did not always result in a clear relationship between temperature and movement, including it often improved the model. Interestingly, when weekly estimates were plotted with temperature, patterns emerged, specific to the 16˚C critically cold threshold reported by Blue Spring Staff that were often concurrent with my hypotheses. These patterns were relatively consistent throughout the study, given similar winter season conditions. For example, model selection resulted in an interactive effect of temperature and wedge on $\hat{\psi}_t^{OU}$ as the top ranking model during the 1986-1987 severe winter season (Figure 3-3A) and a time variation only model during the 1994-1995 season (Figure 3-3B). In contrast, model selection resulted in a positive main effect between temperature and wedge (based on AIC_c weights) during the 2004-2005 severe winter season (Figure 3-2B). All 3 patterns suggest that when river temperatures remained at or below 16˚C between weeks, manatees were less likely to move out of the spring run (Table 1-2, Prediction b).

In another example, model selection resulted in a negative main effect between wedge and remaining outside the run ($\hat{\psi}_t^{UU}$) during the 1999-2000 severe winter season (Figure 3-4A). Estimates plotted with temperature indicate that higher wedge values result in lower $\hat{\psi}_t^{UU}$. However, the plot additionally suggests a positive relationship between temperatures and $\hat{\psi}_t^{UU}$, as expected, where at temperatures below 16˚C between weeks, manatees were less likely to be outside the run. Contrary to my hypotheses, during the 1986-1987 severe winter season (Figure 3-4B), it was more likely that manatees remained out of the run when temperatures remained below 16˚C between weeks. Model selection for this year included equal support for multiple types of effects (e.g., constant, interactive) making it difficult to infer results.

Lastly, model selection resulted in equal support for additive effects of both time and temperature, in addition to time and wedge, on movement out of the run ($\hat{\psi}_t^{OU}$)

during the 1988-1989 (Figure 3-5A) moderate winter season. However, plots of the weekly estimates suggested a large amount of variation in $\hat{\psi}_t^{OU}$, as expected, during moderate seasons that was not captured when examining the averaged weekly estimates for the season. The resulting plots of weekly $\hat{\psi}_t^{UU}$ estimates for the 1992-1993 moderate season (Figure 3-5B) resulted in a negative main effect of wedge on $\hat{\psi}_t^{UU}$. Plots of estimates suggested that at higher wedge lengths, $\hat{\psi}_t^{UU}$ is lower, however the variation appears to be minimal. Additionally, contrary to what was expected, manatees were more likely to remain in the run despite warmer temperatures. This is opposed to the 1998-1999 moderate season (Figure 3-5C), where model selection resulted in a positive main effect of temperature on $\hat{\psi}_t^{UU}$ as expected. When weekly river temperatures remained below 16˚C, manatees were less likely to remain outside the run. As temperature increased to above 16˚C, manatees were more likely to remain out of the run. Additionally, the average weekly $\hat{\psi}_t^{UU}$ for this season was 0.44 (95%CI=0.17 to 0.71). Inference based on the average estimates did not show the within season variation, however, inference based on plots of estimates obtained from model selection provided support for both effect and variation hypotheses (Table 2-1, Models a and c).

Table 3-1. Model selection results for the top ranking models (<2ΔAICc) and the associated correlation coefficient [a] for temperature (temp) and wedge, for movement parameters that included a covariate effect during severe [b] winter seasons at Blue Spring, St. Johns River, FL.

Season	Model	ψ^{OU} (c)	ψ^{UU} (c)	AICc	ΔAICc	AICc weights	Correlation coefficient
1985-1986	1	t	temp*wedge	880.54	0	0.33	-0.25
	2	temp	temp*wedge	880.72	0.17	0.30	
	3	temp+wedge	temp*wedge	881.44	0.89	0.21	
	4	temp*wedge	temp*wedge	882.29	1.74	0.14	
1986-1987	1	temp*wedge	.	1305.72	0	0.32	-0.74
	2	temp*wedge	temp*wedge	1305.89	0.17	0.30	
	3	temp*wedge	temp	1306.34	0.61	0.24	
	4	temp*wedge	temp+wedge	1307.58	1.85	0.12	
1987-1988	1	temp+wedge	.	1221.51	0	0.26	-0.84
	2	temp+wedge	temp*wedge	1222.03	0.52	0.20	
	3	temp*wedge	.	1222.05	0.54	0.20	
	4	temp*wedge	temp*wedge	1222.26	0.75	0.18	
1993-1994	1	.	wedge	1166.06	0	0.58	0.29
	2	temp+wedge	wedge	1166.79	0.72	0.41	
1994-1995	1	t	temp*wedge	2097.06	0	1	-0.37
1995-1996	1	t+temp	t+temp	1725.69	0	0.50	-0.76
	2	t+wedge	t+wedge	1725.69	0.00	0.49	
1999-2000	1	t	wedge	1811.53	0	1	-0.85

Table 3-1. Continued

Season	Model	ψ^{OU} (c)	ψ^{UU} (c)	AICc	ΔAICc	AICc weights	Correlation coefficient
2000-2001	1	temp*wedge	.	1703.97	0	0.26	-0.52
	2	temp+wedge	.	1704.39	0.42	0.21	
	3	.	.	1704.42	0.45	0.20	
	4	wedge	wedge	1705.71	1.74	0.10	
	5	.	.	1705.77	1.79	0.10	
	6		temp	1705.77	1.80	0.10	
2002-2003	1	temp*wedge	temp	2431.11	0	1	-0.93
2003-2004	1	.	temp	2034.40	0	0.21	-0.18
	2	.	.	2034.47	0.07	0.20	
	3	.	temp*wedge	2034.88	0.48	0.16	
	4	wedge	temp	2035.62	1.21	0.11	
	5	.	temp+wedge	2035.85	1.45	0.10	
	6	.	.	2036.36	1.96	0.08	
2004-2005	1	temp	temp+wedge	1488.89	0	0.35	-0.40
	2	temp+wedge	temp+wedge	1489.86	0.96	0.21	
	3	temp	.	1490.52	1.62	0.15	
	4	temp*wedge	.	1490.80	1.91	0.13	
	5	temp+wedge	.	1490.82	1.92	0.13	
2005-2006	1	t+temp	t+temp	1572.44	0	1	-0.57
	2	t+wedge	t+wedge	1572.44	0.00	0.99	

[a] The correlation coefficient associated with temperature and wedge. Values close to -1 indicate a strong negative correlation.
[b] Severe cold seasons correspond to winter seasons where >50% of weekly primary periods at or below the 16˚C critical threshold.
[c] ψ^{OU} represents the probability of moving out of the spring run and ψ^{UU} represents the probability of remaining out of the spring run between week *t* and *t*+1.
"*" refers to interactive model, "+" refers to additive model, "." Refers to constant model, and "t" refers to time varying model.

Table 3-2. Model selection results for the top ranking models (<2 ΔAICc) and the associated correlation coefficient [a] for temperature (temp) and wedge, for movement parameters that included a covariate effect during moderate [b] winter seasons at Blue Spring, St. Johns River, FL.

Season	Model	ψ^{OU} (c)	ψ^{UU} (c)	AICc	ΔAICc	AICc weights	Correlation coefficient
1988-1989	1	t+temp	t+temp	944.25	0	0.50	-0.93
	2	t+wedge	t+wedge	944.25	0	0.50	
1989-1990	1	t	temp+wedge.	1020.73	0	1	-0.91
1990-1991	1	temp	temp	977.33	0	1	-0.53
19911992	1	wedge	.	1302.05	0	0.41	-0.92
	2	temp	.	1303.24	1.18	0.22	
	3	.	.	1303.47	1.41	0.20	
	4	temp+wedge	.	1304.01	1.95	0.15	
1996-1997	1	.	temp*wedge	1642.61	0	0.61	-0.90
	2	.	temp	1643.55	0.94	0.38	
1997-1998	1	temp+wedge	wedge	1864.15	0	0.31	0.88
	2	temp+wedge	temp	1864.35	0.20	0.28	
	3	wedge	t	1865.69	1.54	0.14	
	4	temp+wedge	t	1866.06	1.91	0.12	
	5	wedge	wedge	1866.09	1.94	0.12	
1998-1999	1	t	temp	1437.35	0	0.42	-0.90
	2	t	temp*wedge	1438.11	0.75	0.29	
	3	t	temp+wedge	1438.14	0.78	0.28	

Table 3-2. Continued

Season	Model	ψ^{OU}	ψ^{UU}	AICc	ΔAICc	AICc weights	Correlation coefficient
2000-2001	1	t	temp	1513.69	0	0.52	-0.52
	2	t	.	1514.93	1.23	0.28	
	3	t	temp+wedge	1515.63	1.93	0.19	

[a] The correlation coefficient associated with temperature and wedge. Values close to -1 indicate a strong negative correlation.
[b] Moderate cold seasons correspond to winter seasons where <2 weekly primary periods at or below the 16˚C critical threshold..
[c] ψ^{OU} represents the probability of moving out of the spring run and ψ^{UU} represents the probability of remaining out of the spring run between week *t* and *t*+1.
"*" refers to interactive model, "+" refers to additive model, "." refers to constant model, and "t" refers to time varying model.

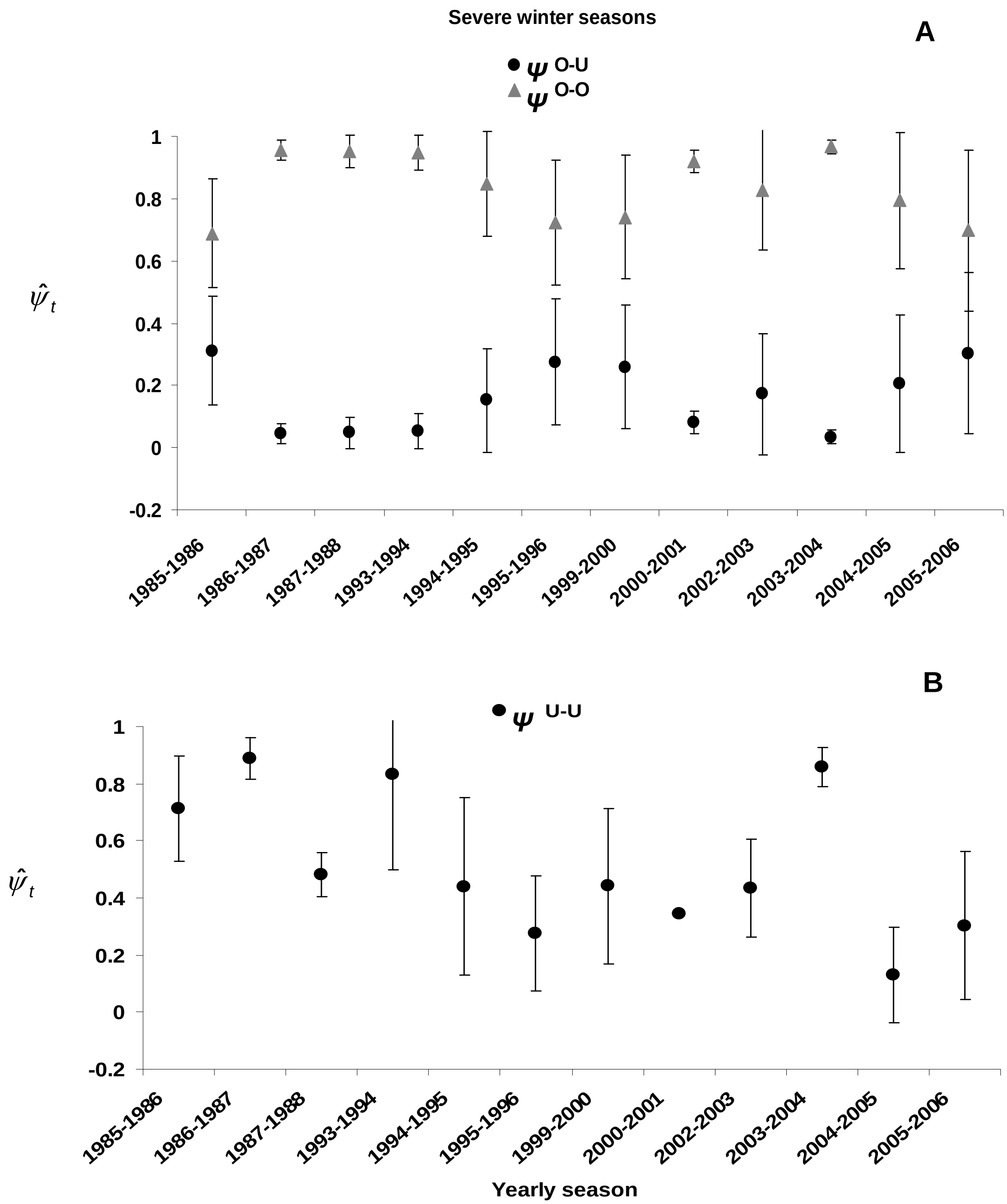

Figure 3-1. The average weekly estimated probability of manatee A) movements out of the spring run ($\hat{\psi}_t^{OU}$) and remaining in the run ($\hat{\psi}_t^{OO}$), and B) remaining out of the spring run ($\hat{\psi}_t^{UU}$) during severe cold winters at Blue Spring, St. Johns River Florida. Error bars are the 95%CI.

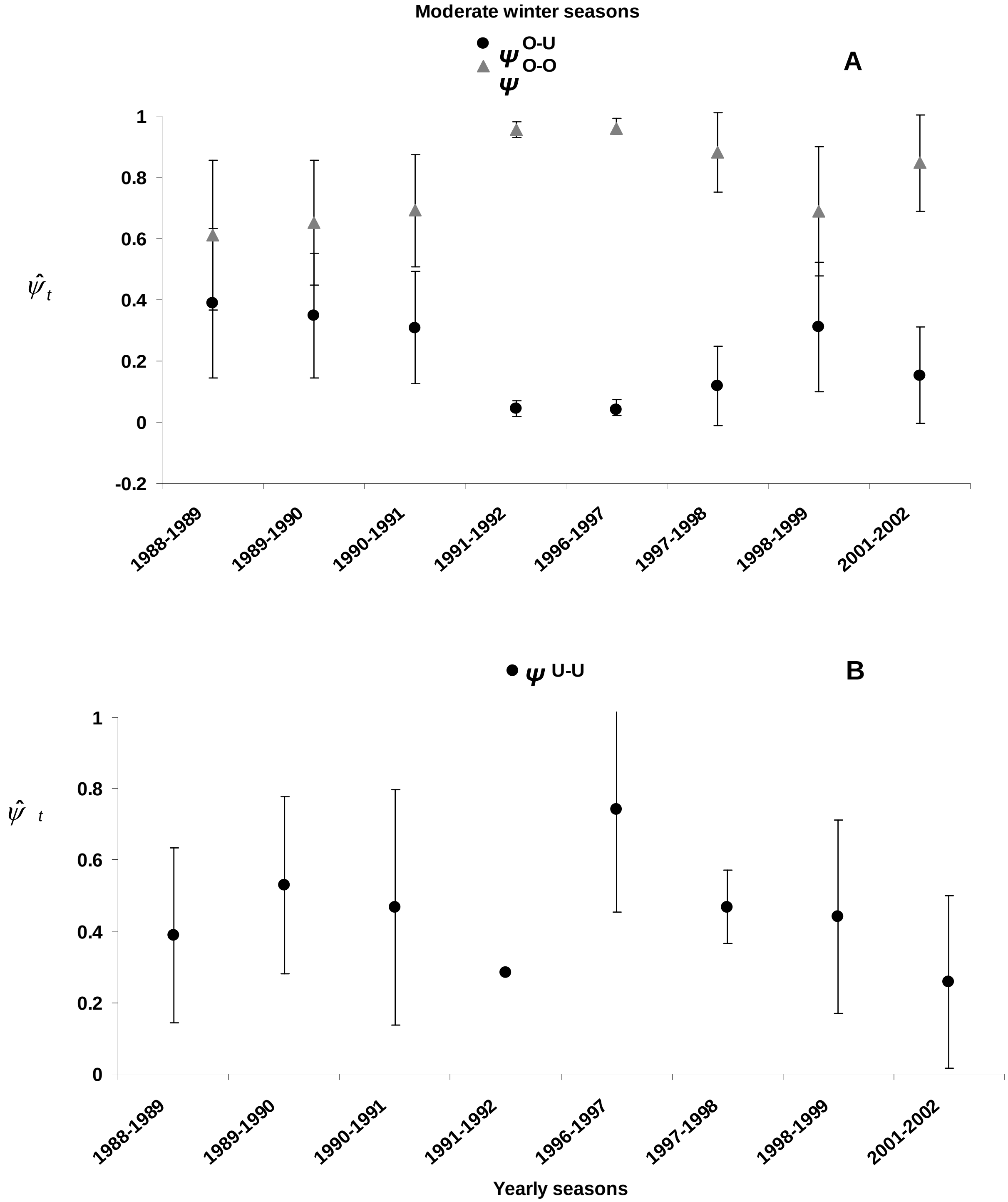

Figure 3-2. The average weekly estimated probability of manatee A) movements out of the spring run ($\hat{\psi}_t^{OU}$), remaining in the run ($\hat{\psi}_t^{OO}$), and B) remaining out of the spring run ($\hat{\psi}_t^{UU}$) during moderate cold winters at Blue Spring, St. Johns River Florida. Error bars are the 95%CI.

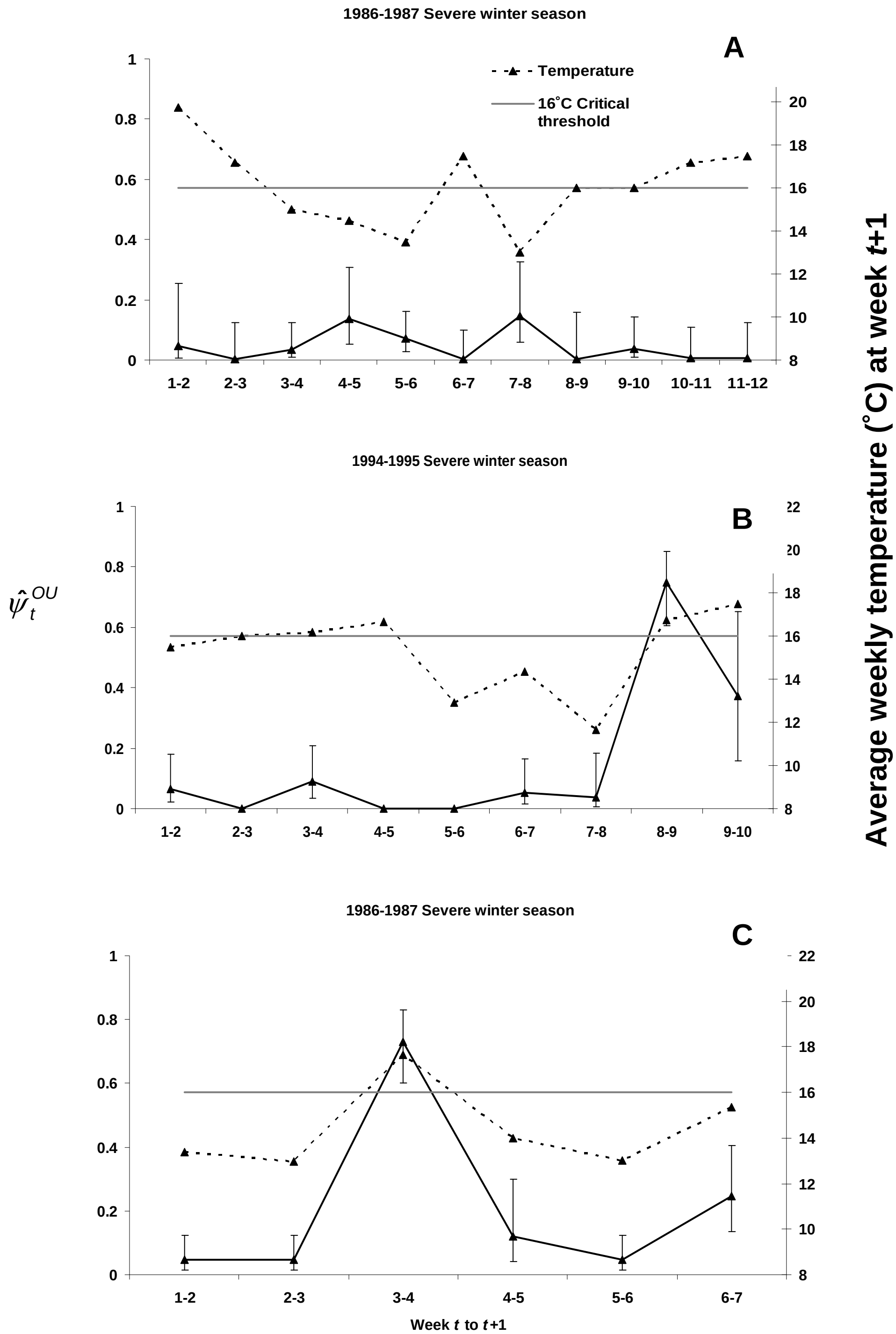

Figure 3-3. The probability of moving out of ($\hat{\psi}_t^{OU}$) Blue Spring run, St. Johns River, FL, during 2 severe winter seasons. Model selection resulted in A) an interactive effect of temperature and wedge on ($\hat{\psi}_t^{OU}$) during the 1986-1987 season, B) a time variation only ($\hat{\psi}_t^{OU}$) model during the 1994-1995 season, and C)

positive main effect of temperature on ($\hat{\psi}_t^{OU}$) during the 2004-2005 season. Inference based on model selection was difficult to interpret during the 1986-1987 and 1994-1995 seasons. Time frame on x axis is movement between week *t* to *t*+1 (i.e., “1-2” represents movement from in the run during week 1 to outside the run during week 2). Movements from *t* to *t*+1 were modeled as a function of average river temperature at week *t*+1 (secondary y axis). Error bars are the 95%CI.

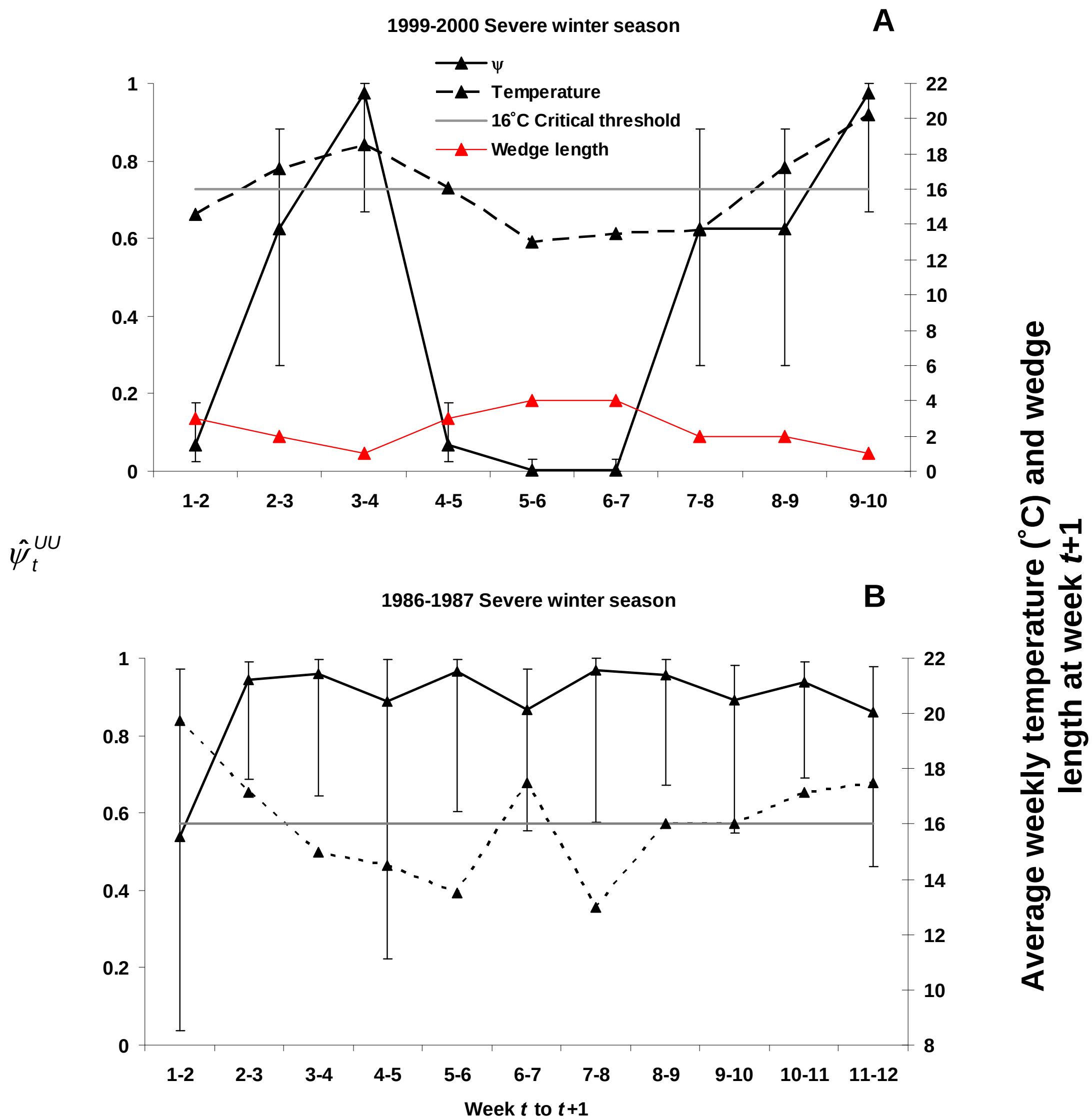

Figure 3-4. The probability of moving out of ($\hat{\psi}_t^{UU}$) Blue Spring run, St. Johns River, FL, during 2 severe winter seasons. Model selection resulted in A) a negative main effect between wedge and ($\hat{\psi}_t^{UU}$) during the 1999-2000 season and B) equal support for multiple types of effects (e.g., constant and interactive) during the 1986-1987. Inference based on model selection was difficult to interpret during these seasons. Time frame on x axis is movement between week *t* to *t*+1 (i.e., “1-2” represents movement from in the run during week 1 to outside the run during week 2). Movements from *t* to *t*+1 were modeled as a function of average river temperature and wedge at week *t*+1 (secondary y axis). Error bars are the 95%CI.

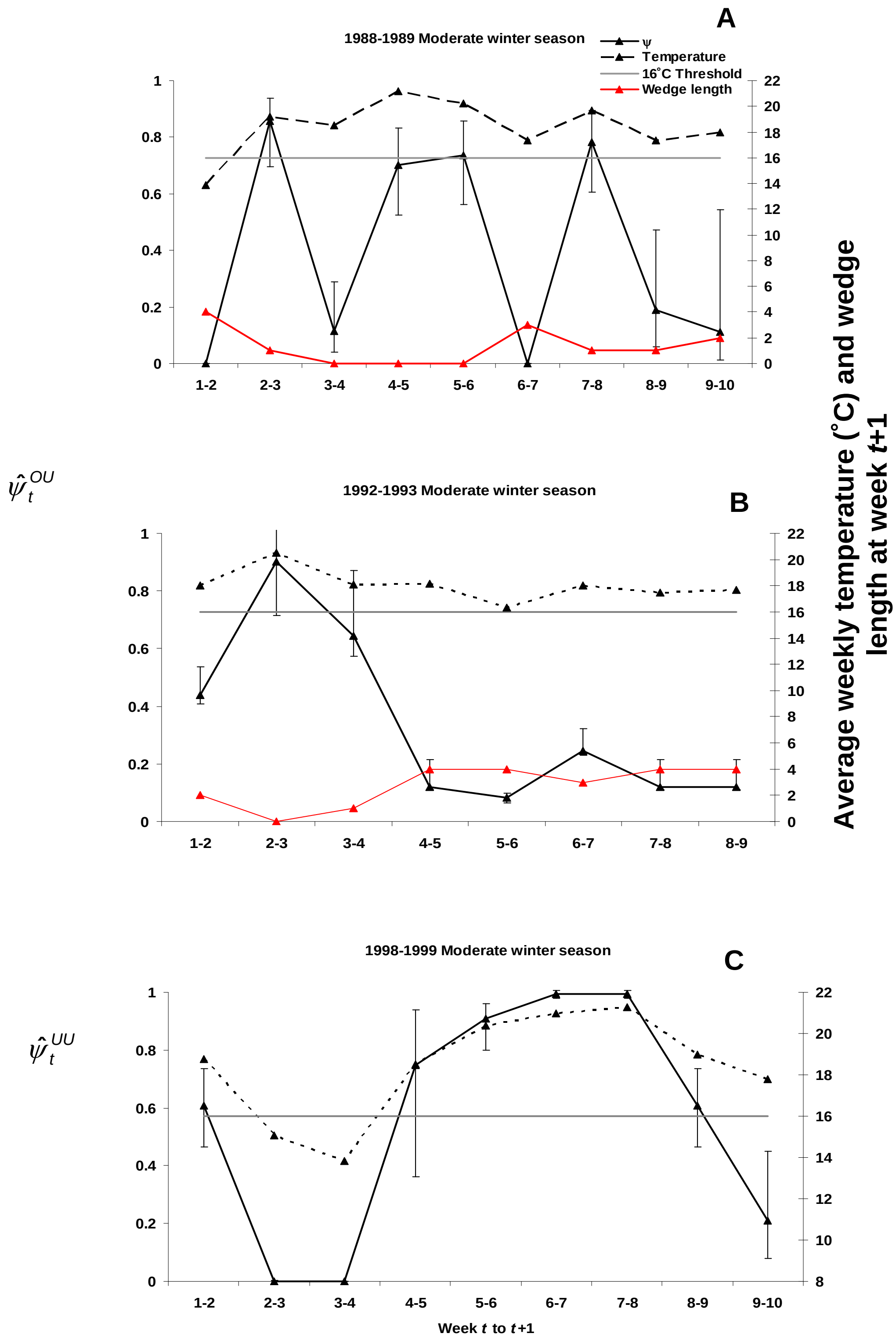

Figure 3-5. The probability of moving out of ($\hat{\psi}_t^{OU}$) and remaining out of ($\hat{\psi}_t^{UU}$) Blue Spring run, St. Johns River, FL, during 3 moderate winter seasons. Model selection resulted in A) an additive effect of time and temperature and an

additive effect of temperature and wedge on ($\hat{\psi}_t^{UU}$)during the 1988-1989 season, B) a negative main effect of wedge on ($\hat{\psi}_t^{UU}$) during the 1992-1993 season, and C) a positive main effect of temperature on ($\hat{\psi}_t^{UU}$) during the 1998-1999 season**.** . Inference based on model selection was difficult to interpret during these seasons. Time frame on x axis is movement between week *t* to *t*+1 (i.e., “1-2” represents movement from in the run during week 1 to outside the run during week 2). Movement from *t* to *t*+1 was modeled as a function of average river temperature and wedge at week *t*+1 (secondary y axis). Error bars are the 95%CI.

CHAPTER 4
DISCUSSION

Temperature and Movement

The results of this study identified temperature as a factor in manatee use of the spring run at Blue Spring. While model selection often resulted in unclear or difficult to interpret models based on *a prior* hypotheses, temperature was included in top ranking models for many of the winter seasons of my study. The weekly movement parameter estimates obtained through model selection and the examples of the *a posteriori* plots of the estimates, provided additional support that temperature is an important factor to consider when modeling movement at Blue Spring. Plots of daily estimates indicated that daily river temperatures predicted when manatees first entered the spring run (β_{st}) as well as length of stay (φ_{st}) within a weekly period. Generally, once manatees entered the spring run, they were likely to remain on a daily basis as long as temperatures remained below 16˚ C when exposure to cold temperatures would be life-threatening. Results indicated that manatees made short daily movements, most likely to foraging sites in the vicinity of Blue Spring run, to forage when temperatures were under 16˚C. Bengtson (1981) reported this behavior where radio-tagged manatees left the run to feed at sites closer to Blue Spring when river temperatures were colder. When weekly temperatures remained severe (<16˚C) movements out of the spring run (ψ_t^{OU}) were almost always lower as hypothesized (Figures 3-3A and 3-3B). Movements out of the run were more likely to increase as temperatures warmed up (Figures 3-3B, 3-3C, and 3-5A). Bengtson (1981) observed a similar behavior when river temperatures were milder, radio-tagged mentees traveled to foraging sites further from the run.

Model selection also indicated that the presence of a wedge interacting with temperature was an important factor influencing both when manatees move out of the run as well as when they remained out (ψ_t^{UU}). However, the correlation between temperature and wedge made it difficult to identify the nature of the effect. The negative correlation I found between temperature and wedge is explained by the hydraulic conditions that create the wedge. Cold water is more dense and heavier than warm water. The greater the difference in temperature between two water bodies, the greater the difference in density. Rouhani et al. (2007) modeled the hydraulics of the wedge at Blue Spring. Increased density differences between the river and spring water (colder river temperatures) lengthened the intrusion of the wedge, along with higher river stage and lower discharge.

Wedge effects alone were rarely supported from model selection. However, it was frequently important as an additive or interactive effect with temperature and the two types of effects were often equally supported. The uncertainty concerning the type of effect (additive or interactive) and relationship to weekly movement parameters was most likely due to the high degree of correlation between lower temperature and presence of wedge.

Although model selection identified temperature as a factor influencing ψ_t^{OU} and ψ_t^{UU}, the direction of the effect and the magnitude was often difficult to interpret. On *a posteriori* examination of plots of the best estimates, I found recurring patterns of movement that accounted for the lack of consistency in the direction of the effect. The most common pattern indicated that weekly movement out of the spring did not occur when river temperatures remained below 16˚C (Figure 3-3). This occurred in both severe and moderate winters. While estimates were often low, a slight increase or decrease in ψ_t^{OU} corresponding to a temperature change, such as during the 1886-1987 season (Figure 3-3A), may influence model selection. These patterns of remaining in the run were the most common pattern reported by park staff based on daily counts. Similar patterns, based on telemetry, have been reported at other warm-water refugia. In the Northwest region of Florida, radio tagged manatees remain in warm-water refugia when temperatures are below 16˚C and movements out are rare (Sirenia Project, unpublished data). Stith et al. (2011) never located tagged manatees in waters <15˚C during a 6 year study in the Ten Thousand Islands and Everglades region of Florida. Movements out of the run during severe seasons only occurred during warmer weeks (Figures 3-3B and 3-3C), most likely to forage at nearby feeding sites. Bengtson (1981) observed the same patterns at Blue Spring during his telemetry study.

My capture-recapture study showed a similar pattern with probabilities of remaining out of the run. Higher estimates of ψ_t^{UU} were associated with temperatures >16 ˚C (Figures 3-4B and 3-5C). However counter to what I had hypothesized, ψ_t^{UU} was often higher during severe winters (Figure 3-4A). Several factors could account for this pattern. First, it could be the result of limited foraging opportunities if a winter season has started early. I chose the coldest portion of the winter season for my study, however, the timing of the start of the winter seasons can vary from year to year. If severe cold in November limited foraging, by mid-December hunger may be the critical factor and manatees may be more likely to remain out to feed despite life threatening temperatures. During the extreme cold and manatee mortality event in 2009-2010, 2 manatees died of acute cold stress and were recovered with vegetation in their esophagus (Barlas et al. 2010). Additionally, during the same cold event, The Florida Fish and Wildlife Research Institute monitored abundance at power plant effluents in Brevard County. They estimated a decline in abundance during the extended cold and concluded that they left to find food (Barlas et al. 2010).

Alternatively, it is possible that once a manatee has moved out of the run, if severe cold temperatures occur and feeding is not an issue, the best strategy may be to use alternate warm-water sites. Manatees that use Blue Spring have been photo-documented using alternate springs of lesser quality in the St. Johns River as well as winter refugia on the Atlantic coast (Sirenia Project unpublished data).

Movement patterns examined *a posteriori* during moderate seasons of my study provided evidence that movement into and out of the run is variable, as there is less of a need to thermoregulate and more opportunities to forage. However, there were moderate seasons where manatees were more likely to remain in the run for most of the season (Figure 3-5B), suggesting that there might be a comfort zone as park staff suggested, where at temperatures above 16˚C, manatees remain in the run for comfort more than the need to keep warm.

There was considerable variation in use patterns across all season of the data set. It is well documented that manatee use of winter refugia is associated with ambient water temperature and that there is a high degree of individual variation in use. While tagged manatees exhibit high fidelity to warm-water sites, within winter season variation occurs with regard to timing of arrival, departure and length of stay (Deutsch et al. 2003). It is not surprising that this study identified yearly variation in use patterns as well.

The movement patterns I identified over the entire study also suggest that there is individual variation in manatee use of Blue Spring that often can be complex. The movement patterns I found with regard to movement into and out of the spring run during severe winters were similar to those reported during the 2009-2010 unusually cold winter. Manatees in Brevard County responded to severe water temperatures in 3 ways. They remained at the current warm-water site, moved to another nearby warm-water site, or moved out of the area completely (Barlas et al. 2010).

Carrying Capacity

Results from this study did not support my hypothesis that the population is approaching carrying capacity. I expected that if the population was nearing carrying capacity and useable area was reduced, movement patterns would change. However there was no evidence that deviations from historic patterns had occurred. During severe cold spells, I have observed manatees densely packed into warm-water sites at Blue Spring and power plant effluents. Therefore it is not surprising that my analysis showed the current population at Blue Spring has not been influenced by reduced area relating to large numbers of manatees or wedge. Nevertheless, the population is growing at a faster than expected rate and patterns of use most likely will change over the next decade as the manatee population continues to increase and warm-water availability at the spring is altered by human use and changing climatic conditions.

Recently, photo-identification and telemetry data have documented an increase in both the numbers and length of stay of overwintering manatees at natural refugia where winter use has historically been limited, most likely due to high human use. Many of the recognizable individuals have switched winter site fidelity from well known primary natural refugia to alternate natural refugia (Sirenia Project, unpublished data). The pattern resulting from my study, where manatees were more likely to remain away from the run during severe winters may be a way to detect a population approaching carrying capacity if the pattern is a regular occurrence in the future.

Sources of Uncertainty

The confounding effects of temperature and wedge are an example of the complexity of the system that often led to model uncertainty with regard to selection of the top models. For example, while temperature was a considerable factor influencing movement, model results did not always yield statistically significant or clear relationships. I modeled covariates on a linear-logistic scale with time dependence to obtain the best estimates and explain sources of variation on movement parameters; however, modeling covariates using other models (e.g., quadratic models on the logit scale) may be more appropriate to explain the variation. Modeling movement as a function of covariate values between sampling periods or degree of change between weeks, in addition to incorporating other factors (e.g., spring flow and river stage), might facilitate further understanding of system complexity. Expanding the time frame of the yearly sampling periods to incorporate conditions before the winter seasons begins may further explain the variation in patterns identified in the analysis.

Small sample size may lead to model selection that does not always represent the best approximating models (Burnham et al. 1995). While sample size for this study was large compared to telemetry studies, sample size (especially in earlier seasons of the study) may have led to model uncertainty. However capture probabilities were high due the clarity of the water and the low numbers of manatees to monitor at the site, making the estimation procedures more robust. Despite the uncertainty, the MSORD approach worked well, providing estimates that reflected relative consistency in patterns of use over 21 seasons.

CHAPTER 5
CONCLUSION AND MANAGEMENT IMPLICATIONS

As specific habitat features change over time, it is increasingly important to relate these changes to demographic rates in wildlife populations (Breininger et al. 2010). This is especially important for habitat specialist such as the Florida manatee where loss of warm-water could curtail recovery efforts. The need to understand how manatees respond to changing environmental conditions as well as to develop monitoring tools to accomplish this are important objectives relating to the recovery of the species (United States Fish and Wildlife Service 2001).

This study was the first analysis to apply a multistate open robust design to explore fine-scale within season manatee use and movement patterns of a winter refuge over time. Movement behavior of wildlife species in response to habitat change, paralleled with localized population density change, has been a complicated process to understand (Patterson et al. 2008). Recent studies have used long-term data sets to explore historic demographic patterns as a means to detect change in species response to changing climates and density dependence (Barbraud and Weimerskirch 2003, Jacobson et al. 2004, Rotella et al. 2009). This study attempted to incorporate specific factors that are of known (temperature) and unknown (wedge) importance to manatee habitat use and suitability. Despite the complexity of environmental variation (such as the importance of spring flow and river stage), as well as individual variation in behavior that may be occurring, this type of design characterized how the Florida manatee use this warm-water refuge based on decades of research. Additionally, unexpected patterns were revealed that may be useful when further testing hypotheses related to manatee use of refugia.

This study encompassed long-term sighting data through the 2005-2006 winter seasons. More recent winter seasons have experienced an even greater increase in the population using Blue Spring and even successively colder river temperatures, both in degree and duration. With the loss of artificial habitat manatees are going to have to rely on existing natural warm-water sites. If overcrowding becomes an issue, manatees will be forced to seek out alternate habitat that may be of lesser quality. As increasing stress may be put on the Blue Spring population and deviations from current patterns are potentially detected, detecting change in historic use patterns may emphasize the need to re-evaluate MFLs as well as highlight the need to monitor, enhance and protect additional natural refugia in the St. Johns River.

As the next step in advancing this research to address management issues, I would like to identify a subset of seasons from my study to further refine the models. The *a posteriori* examination of the estimate plots from this study has led to additional hypotheses regarding sources of variation in manatee movement. Using additional or alternative covariates as well as different time scales may provide additional information about the key factors producing observed effects. Furthermore, I would like to incorporate data from the most recent severe winters as the Blue Spring population has increased. Analyzing recent severe cold winters, such as the 2009-2010 season in which unusual mortality occurred (Barlas et al. 2010), may reveal additional insights, particularly regarding the question of behavioral changes as the population nears carrying capacity. Lastly, I would like to design a study to jointly model capture-recapture and telemetry data. Capture-recapture data increases sample size and provides information on a population level, while telemetry data provides information more on an individual level. Combining the 2 allows for improved estimation of movement parameters such as emigration (Nichols and Kaiser 1999).

The application of multistate open robust design models to manatee capture-recapture data has the potential to address issues, similar to what has been presented for this study, occurring at additional warm-water sites. Blue Spring is the only winter refuge that has documentation of almost daily winter attendance of recognizable manatees. Further studies involving a similar design applied to long term data on a broader scale, yearly primary periods as opposed to weekly, has the capability to provide important information when addressing habitat use relating to changing environmental conditions over time. Additionally, this type of design may be useful for more targeted studies when to addressing questions such as manatee response to pre and post habitat alterations.

LIST OF REFERENCES

Barbraud, C., and H. Weimerskirch. 2003. Climate and density shape populations of a marine top predator. Proceedings of the Royal Society 270:2111-2116.

Barlas, M. E., C. J. Deutsch, M. de Wit, and L. I. Ward-Geiger. 2011. Florida manatee cold-related unusual mortality event, January-April 2010 final report. Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute. Saint Petersburg, Florida, USA.

Beeler, I. E., and T. J. O'Shea. 1988. Distribution and mortality of the West Indian (*Trichechus manatus*) manatee in the southeastern United States: A compilation and review of recent information. Volume 1: The Atlantic coast. National Ecology Research Center, Springfield, VA, USA.

Beck, C.A., and J. P. Reid. 1995. An automated photo-identification catalog for studies of the life history of the Florida manatee. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Gainesville, FL, USA.

Bengtson, J. L. 1981. Ecology of manatees (*Trichechus manatus*) in the St. Johns River. Dissertation, University of Minnesota, Minneapolis, MN, USA.

Bossart, G. D., R. A. Mesiner, S. A. Rommel, S. Ghim, and A. B. Jenson. 2002. Pathological features of the Florida manatee cold stress syndrome. Aquatic Mammals 29:9-17.

Breininger, D. R., J. D. Nichols, B. W. Duncan, E. D. Stolen, G. M. Carter, D. K. Hunt, and J. H. Drese. 2010. Multistate modeling of habitat dynamics: factors affecting Florida scrub transition probabilities. Ecology 91:3354-3364.

Burnham, K. P., G. C. White, and D. R. Anderson. 1995 Model selection strategy in the analysis of capture-recapture data. Biometrics 52:888-898.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: A practical information –theoretic approach, second edition. Springer-Verlag. New York, New York, USA.

Choquet, R. A., A. M. Reboulet, and L. D. Lebreton, O. Gimenez, and R. Pradel. 2005. U-CARE 2.2 users manual. Centre d'EcologieFonctionnelle et Evolutive, Montpellier, France. <http://www.cefe.cnrs.fr/images/stories/DPTEEvolution/biostatistiques/Chercheurs/remi_choquet/Choquet-USER%20MANUAL%20U-CARE%202.2.pdf>. Accessed 10 Oct 2011.

Deutsch, C. J., J. P. Reid, R. K. Bonde, D. E. Easton, H. I. Kochman, and T. J. O'Shea. 2003. Seasonal movements, migratory behavior, and site fidelity of West Indian manatees along the Atlantic Coast of the United States. Wildlife Monographs 151:1-77.

Duriez, O., S. A. Saether, B. J. Ens, R. Choquet, R. Pradel, R. H. D., Lambeck, and M. Klaassen. 2009. Estimating survival and movements using both live and dead recoveries: a case study of Oystercatcher confronted with habitat change. Journal of Applied Ecology 46:144-153.

Fowler, C. W. 1981a. Density dependence as related to life history strategy. Ecology 62:602-610.

Fowler, C. W. 1981b. Comparative population dynamics in large mammal populations. Pages 437-455 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. John Wiley and Sons, New York, New York, USA.

Fujiwara, M., and H. Caswell. 2002. A general approach to temporary emigration in mark-recapture analysis. Ecology 83:3266-3275.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of Large herbivores: variable recruitment with constant adult survival, Trends in Ecology and Evolution 13:58-63.

Harrington, D., Maddox, G. and R. Hicks. 2008. Florida springs initiative monitoring network report 2008. Florida Department of Environmental Protection, Tallahassee, FL, USA.

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

Hestbeck, J. B., J. D. Nichols, and R.A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology 72(2):523-533.

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

Jacobson, A. R., A. Provenzale, A. von Hardenberh, B. Bassano, and M. Festa-Bianchet. 2004. Climate forcing and density dependence in a mountain ungulate population. Ecology 85:1598-1610,

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563-578.

Kendall, W. L., and R. Bjorkland. 2001. Using open robust design models to estimate temporary emigration from capture-recapture data. Biometrics 57:1113-1122.

Kendall, W. L., and J. D. Nichols. 2002. Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. Ecology 83:3276-3284.

Kendall, W. L., C. A. Langtimm, C. A. Beck, and M. C. Runge. 2004. Capture-recapture analysis for estimating manatee reproductive rates. Marine Mammal Science 20:424-437.

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

Langtimm, C. A., C. A. Beck, H. H. Edwards, K. J. Fick-Childs, B. B. Ackerman, S. L. Barton, and W. C. Hartley. 2004. Survival estimates for Florida manatees from the photo-identification of individuals. Marine Mammal Science 20:438-463.

Lebreton, J.-D., K.P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypothesis using marked animals – a unified approach with case studies. Ecological Monographs 62:67-118.

Lefebvre, L. W., M. Marmontel, J. P. Reid, G.P. Rathbun, and D. P. Domning. 2001. Status and biogeography of the West Indian manatee. Second edition. CRC Press, Boca Raton, FL, USA.

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

Nichols, J. D., and W. L. Kendall. 1995. The use of multi-state capture-recapture models to address questions in evolutionary ecology. Journal of Applied Statistics 22:835-846.

Nichols, J. D., and A. Kaiser. 1999. Quantitave studies of bird movement: a methodological review. Bird Study 46:S289-S298.

O'Shea, T. J., C. A. Beck, R. K. Bonde, H. I. Kochman, D. K. Odell. 1985. An analysis of manatee mortality patterns in Florida, 1976-1981. The Journal of Wildlife Management. 49:1-11.

O'Shea, T. J., and W. C. Hartley. 1995. Reproduction and early age survival of Manatees at Blue Spring, upper St. Johns River, Florida. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service. Information and Technology Report 1:157-170.

Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. State-space models of individual animal movement. Trends in Ecology & Evolution. 22:87-94.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:1-97.

Powell, J. A., and J. C. Waldron. 1981. The manatee population in Blue Spring, Volusia County, Florida. Pages 14-51 *in* R. L. Brownell and K. Ralls, editors. The West Indian Manatee in Florida. Proceedings of 1978 Florida Department of Natural Resources workshop, 27-29 March 1978, Orlando, Florida, USA.

Pradel, R. 1993. Flexibility in survival analysis from recapture data: handling trap-dependence. Pages 29-37 *in* J. D. Lebreton and P. M. North, editors. Marked individuals in the study of bird populations. Birkhaüser, Basel.

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

Rotella, J. J., W. A. Link, J. D. Nichols, G.I. Hadley, R. A. Garrott, and K. M. Proffitt. 2009. An evaluation of density-dependent and density-independent influences On population growth rate in Weddell seals. Ecology 90:975-984.

Rouhani, S., P. Suscy, G. Hall, W. Osburn, and M. Wild. 2007. Analysis of Blue Spring discharge data to determine a minimum flow regime. St. Johns Water Management District, Palatka, FL, USA.

Rousenau, J. C., G. L. Faulkner, C. W. Hendry, and R. W. Hull. 1977. Springs of Florida. US Geological Survey Bulletin 31:1-461.

Runge, M. C., C. A. Saunders-Reed, C. A. Langtimm, and C. J. Fonnesbeck. 2007. A quantitative threats analysis for the Florida manatee (*Trichechus manatus latirostris*). U. S. Geological Survey Open File Report 2007-1086. <http://www.pwrc.usgs.gov/resshow/manatee/>. Accessed 05 May 2008.

Schaub, M., O. Gimenez, B. R. Schmidt, and R. Pradel. 2004. Estimating survival and temporary emigration in the multistate capture-recapture framework. Ecology 85:2107-2113.

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

Smith K., J. B. Miller, and R. Harris. 2000. Manatee use of the Blue Spring run, Blue Spring State Park, Volusia County, Florida. Blue Spring Minimum Flow Interagency Working Group, Palatka, FL, USA.

Spendelow, J. A., J. D. Nichols, C. T. Nesbit, H. Hays, and G. D. Cormons. 1995. Estimating annual survival and movement rates of adults within a metapopulation of roseate terns. Ecology 76:2415-2428.

Suscy P., R. Hupalo, and B Freeman. 1998. Minimum flow determination for Blue Spring, Volusia County: The relationship between ground water discharge and winter refuge for manatees. Unpublished report, Department of Water Resources, St. Johns River Water Management District, Palatka, FL, USA.

United States Fish and Wildlife Service. 2001. Florida manatee (Trichechus manatus latirostris) recovery plan, third revision. Atlanta, G.A., USA.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal Populations. Academic Press, San Diego, California, USA.

White, G. C., K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46:120-138.

White, G. W., W. L. Kendall, and R. J. Barker. 2006. Multistate survival models and their extensions in program MARK. Journal of Wildlife Management 70:1521-1529.

BIOGRAPHICAL SKETCH

Amy Teague was born in Boston, Massachusetts in 1975. Amy earned her AS in Zoo Animal Technology in 1998 and a BS in wildlife ecology in 2007. Amy entered graduate program at The School of Natural Resources and Environment during the summer of 2007. Amy began working for U.S. Geological Survey in 1998 and has been studying manatee population ecology for 13 years. Amy has worked with the Manatee Photo-identification System as a database manager assistant and spends the winter field season traveling around the state of Florida photographing manatees at warm-water aggregation sites.