

FACTORS RELATED TO SEASONAL MIGRATION AND DISTRIBUTION OF
BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) ALONG SOUTH CAROLINA
AND GEORGIA COASTS

by

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(Under the Direction of Steven Castleberry)

ABSTRACT

Little is known about factors related to bottlenose dolphin (*Tursiops truncatus*) seasonal migration and distribution along the southeastern Atlantic coast. Migratory dolphins often overlap with resident dolphins, making it difficult to obtain accurate abundance estimates. Habitat selection studies are lacking for southeastern dolphins, causing critical habitat to remain undefined. Therefore, it is important to understand environmental factors that may be related to migratory pulses and habitat selection to obtain accurate resident abundances and to identify important habitat. I used Robust Design and closed population capture-recapture models to estimate seasonal abundance and temporary emigration with water quality variables and Poisson point process models to determine if depth affected dolphin distribution. Results indicated a seasonal abundance and emigration pattern, with water temperature and salinity best explaining the seasonal patterns. Results also indicated depth had a significant effect on dolphin distribution for each season.

INDEX WORDS: Bottlenose dolphin, Migration, Seasonal abundance, Distribution

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DEDICATION

I would like to dedicate this thesis to my mother, Teresa, my father, Tommy, and my brother, Andrew. I am truly blessed to have parents that inspire me to follow my dreams. They are always there to celebrate the good times and to pick me up during the bad times. I would be lost without their everlasting love and support. I am also incredibly blessed to have an encouraging big brother, who provided me with endless advice throughout my academic career (and life). I owe all of my success to Mama, Daddy, and Andrew, the best of friends a girl could ever have.

I would also like to dedicate this thesis to my nannie, Virginia. Her passion for the ocean and sea life was passed down to me as a child. Though she is not here with us today, I feel a strong connection with her through this interest we shared. I know she is smiling in Heaven as she watches me chase my dreams.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Introduction

The bottlenose dolphin (*Tursiops truncatus*) is widely distributed in tropical to temperate seas worldwide. In the United States, the bottlenose dolphin ranges from central California to the Mexican border in the Pacific, throughout the Gulf of Mexico, and from the southern tip of Florida to Rhode Island in the Atlantic (Wilson et al. 1999, Reid 2006). Despite being the most commonly studied marine mammal, little is known about the population along the southeastern coast of the United States (Read et al. 2003, Waring et al. 2009, Speakman et al. 2010).

The southeastern bottlenose dolphin population is comprised of many stocks, such as estuarine system, coastal, and offshore (Waring et al. 2009, Conn et al. 2011). Estuarine stocks are geographically defined based the identification of resident dolphins from photo-identification studies (Waring et al. 2009, Conn et al. 2011). The relationships among stocks are unknown and likely overlap in range with neighboring stocks, making population estimates within stocks difficult to ascertain and therefore setting limitations on management (Zolman 2002, Read et al. 2003, Waring et al. 2009, Speakman et al. 2010, Conn et al. 2011, Bills and Keith 2012). The stocks of focus in this study are the Charleston Estuarine System Stock and an undefined stock between the

boarders of the Southern Georgia Estuarine System Stock and the Northern Georgia/Southern South Carolina Estuarine System Stock (Waring et al. 2009).

Bottlenose dolphins in southeastern estuaries are influenced by natural (e.g., diseases) and anthropogenic factors (e.g., agricultural runoff, crab pot entanglement, and direct interaction with humans), which may negatively impact overall population viability (Balmer et al. 2008, Waring et al. 2009, Conn et al. 2011, Balmer et al. 2013). The true impacts of these factors are unknown because of the lack of data (Waring et al. 2009, Waring et al. 2014).

Population size estimates for stocks in the Southeast are often unreliable because migratory, or non-resident, dolphins can enter the study area and artificially inflate the residential population size estimate (Waring et al. 2009). Habitat use studies are also lacking for southeastern dolphins, causing critical habitat to remain undefined. Therefore, it is important to determine what factors influence dolphin migration to better predict migration and obtain accurate stock assessments, as well as to describe habitat use to provide insight into critical habitat.

In this thesis, I present two studies that provide new information regarding movement and distribution patterns of bottlenose dolphins along South Carolina and Georgia coasts. In Chapter 2, I estimate abundance and temporary emigration for dolphins near Charleston Harbor, South Carolina and St. Catherine's Island, Georgia to determine if a correlation exists between dolphin migration and water quality variables. In Chapter 3, I identify and describe high-use areas for dolphins near St. Catherine's Island, Georgia. Chapter 4 presents a conclusion and summary of key findings for each chapter. My results will provide a better understanding of dolphin migration and habitat

use along the southeastern coast, allowing effective decision making for future population and habitat management.

Literature Review

Dolphin migration

Most cetacean species migrate north in the summer and south in the winter. However, the reasons for seasonal migration are better understood for mysticetes (i.e., baleen whales) than for odontocetes (i.e., toothed whales; Hoelzel 1994). Odontocete species have complex distributions, causing movement patterns difficult to understand (Hoelzel 1994, Bills and Keith 2012). Some stocks contain individuals that are resident in an area throughout the year, while others seasonally migrate through the area (Hoelzel 1994, Speakman et al. 2010, Bills and Keith 2012). A dolphin is considered a resident if it occurs in the area year-round, a seasonal resident if it occurs in the area in the same season in multiple years but not in consecutive seasons, and a transient if it only resides in the area for one season (Zolman 2002, Conn et al. 2011). Knowing when migratory dolphins (i.e., seasonal residents and transients) overlap with resident dolphins is important in estimating population size for the stock of interest because, if not accounted for, inclusion of transients will result in an overestimate in population size (Conn et al. 2011).

Migration patterns and factors that initiate movements in the Southeast are unknown (Bills and Keith 2012). Two migratory pulses, north in the spring and south in the fall, are believed to occur in the Southeast each year (Fertl 1994). However, transients were observed mostly in summer and fall in South Carolina estuaries during a

3-year photo-identification study, while the timing of transient entry into Georgia estuaries is unknown (Waring et al. 2009, Speakman et al. 2010).

Many environmental factors are believed to influence bottlenose dolphin seasonal migration patterns, such as water temperature and food availability (Shane 1980, Young and Phillips 2002, Torres et al. 2005). For example, as water temperature and prey abundance decrease in the north, dolphins will likely migrate south to warmer waters with higher prey availability (Torres et al. 2005, Speakman et al. 2010, Bills and Keith 2012). Examining environmental variables (e.g., water quality) that are possibly related to seasonal abundance increases and decreases is essential in better understanding when migration is likely to be observed in an area. This information will provide a basis for obtaining a more accurate estimate of resident abundance, allowing for effective management decisions regarding localized impacts on resident dolphins from natural and anthropogenic factors (Conn et al. 2011).

Dolphin habitat selection

Habitat selection is defined as the innate process in which an animal chooses a habitat (Johnson 1980). Habitats are often heterogeneous within coastal systems. Some areas may offer more food resources and protection from predators than other areas (Ballance 1992, Gubbins 2002). Many factors are believed to influence dolphin habitat selection, such as tidal state, depth, water temperature, turbidity, and prey availability (Shane 1980, Maze and Würsig 1999, Ingram and Rogan 2002, Bräger et al. 2003). Most dolphin species exhibit seasonal habitat selection changes, which is likely a direct effect

from the movement of prey along with indirect environmental factors (Bräger et al. 2003, Maze and Würsig 1999).

High-use areas can be calculated using many different methods (Redfern et al. 2006). Along the Charleston, South Carolina coast, Adams et al. (2006) found that visualization of long-term photo-identification data used in combination with a geographic information system (GIS) can be used to determine high-use areas by identifying the number of sightings observed within a defined area. An additional study in Charleston, South Carolina used point density tools in ArcGIS to locate high-use areas (i.e., number of sightings per km²) in which calves were encountered. The authors were able to locate high-density neonate areas, as well as conclude that habitat usage differs by season (i.e., spring neonate sightings were mainly within estuaries, while fall sightings were in more coastal areas; McFee et al. 2014). Off the Georgia coast, Balmer et al. (2013) used ArcGIS to classify stream order for estuarine rivers. Dolphin density was calculated for each stream order, and the results showed that dolphin densities differed among stream orders (Balmer et al. 2013). These studies were able to successfully identify high-use areas; however, the physical characteristics of these areas were not described.

Studies describing high-use areas using physical features and bathymetry are scarce for southeastern areas. Redfern et al. 2006 described many techniques to accomplish describing high-use areas using habitat variables. The most used technique is to plot sightings on maps of habitat variables (e.g., bathymetry, water temperature). Goodness-of-fit metrics can be used to evaluate whether sightings are evenly distributed

among habitat variables. Generalized linear models (GLM) can also be used to determine if presence or absence of sightings is related to habitat variables (Redfern et al. 2006).

A study in Moray Firth, Scotland used GLM to determine if there was a relationship between distribution and environmental factors (e.g., depth, sediment, and salinity; Bailey and Thompson 2009). Bailey and Thompson (2009) found that dolphin sightings were significantly related to distance from shore and slope. A study conducted near Sarasota, Florida found that habitat usage differed among seasons (i.e., in warmer months sightings occurred more in channels and bays inshore, rather than along the gulf shore sightings in winter), and dolphins showed a depth preference of < 3 m (Irvine et al. 1981). Similar studies have found that high-use areas were also correlated with bottom sediment (Ingram and Rogan 2002). These studies were able to identify and describe habitats of areas with high dolphin density, and therefore provided a better understanding of what areas might be critical to the dolphins' survival (Ballance 1992, Gubbins 2002).

Similar to GLM, point process modeling (PPM) is a technique used to describe covariate effects and spatial trends (Baddeley and Turner 2005), which may have applicability in providing insight into critical habitat for dolphins. PPM can be used to analyze patterns of randomly distributed points (e.g., dolphin sightings) and evaluate correlations between dolphin density and covariates (e.g., depth and sediment), which may influence dolphin distribution (Illian et al. 2008). Warton and Shepherd (2010) proposed using Poisson PPM (Cressie 1993, Diggle 2003), where the points are assumed independent. Poisson PPM can model the expected count, or intensity, of dolphin sightings per unit area for any location (Renner and Warton 2013). Regardless of the method used to identify and describe high-use areas, the implications are the same: to

provide insight into critical habitat, future habitat management, and impacts from anthropogenic sources (McFee et al. 2014).

Photo-identification

To gain knowledge about cetaceans, photo-identification has been used since the early 1970s to identify individuals using natural markings (Würsig and Jefferson 1990). For example, individual North Atlantic right whales are identified by their unique callosity patterns (Caswell et al. 1999), and individual Florida manatees are identified by their unique scar patterns (Beck and Reid 1995). In most dolphin species, individuals can be identified using the natural markings found on the dorsal fin (Würsig and Würsig 1977). These natural markings (i.e., notches and scars on fin) often last the lifetime of the individual, as dorsal fin tissue does not regenerate (Würsig and Würsig 1977).

Most cetacean photo-identification studies are conducted by boat; however, studies can take place on land or in air depending on the researcher's goals (Würsig and Würsig 1977, Torres et al. 2005). Photographs of dolphin dorsal fins are usually taken using a digital camera with a long-range lens (e.g., 75-300 mm or 100-400 mm). Ideally, a photograph of an individual fin is taken perpendicular to the camera, with background contrast to optimize visualization of distinct features (Speakman et al. 2010). Photographs are organized and matched to individuals using a database (e.g., FinBase; Adams et al. 2006). Sighting histories (i.e., mark-recapture data) can then be obtained for each individual (Würsig and Würsig 1977, Adams et al. 2006, Speakman et al. 2010). Using mark-recapture data analyses, photo-identification studies can provide estimates of population size, life history information, habitat utilization patterns, movement patterns,

and identification of resident and non-resident individuals (Würsig and Jefferson 1990, Zolman 2002, Adams et al. 2006, Speakman et al. 2010).

In Cedar Key, Florida, Caldwell (1955) was able to illustrate the first evidence of home range for an individual dolphin using photo-identification. The author's findings show that an individual dolphin's home range was possibly restricted to a channel in Cedar Key (Caldwell 1955). A photo-identification study near Charleston, South Carolina exported their sightings data stored within FinBase to program MARK (Cooch and White 2014, Speakman et al. 2010). Using both Lincoln-Peterson and Robust Design models, Speakman et al. (2010) estimated abundance and survival. The authors were able to determine that abundance was highest in the summer and lowest in the winter, and the annual survival rate was 0.951. They also found that emigration probabilities were highest between summer and fall seasons (Speakman et al. 2010). Zolman (2002) used photo-identification to better understand the resident dolphins of the Stono River estuary, South Carolina. The author was able to determine that 64% of identified dolphins were transients, 8% were seasonal residents, and 19% were residents (Zolman 2002).

Robust Design models

During a photo-identification study, dolphins are likely to immigrate and emigrate through the study area. This movement causes the population to violate closed model assumptions of mark-recapture analyses. Dolphins also exhibit seasonal movement patterns, violating the open model assumptions (Speakman et al. 2010, Conn et al. 2011). In situations where the population violates both open and closed model assumptions, Robust Design (RD) models can be used (Kendall et al. 1997). RD combines open and

closed models to allow for population gains and losses between sampling periods (i.e., temporary emigration; Kendall et al. 1997, Kendall 2014).

RD models require primary and secondary sampling periods. Primary periods are conducted with a sufficient amount of time (e.g., 2 months or a year) between them to allow population gains and losses to occur. Each primary period contains a number of secondary periods, which are conducted within a short time (e.g., days or a week) of each other. Therefore, the population is assumed closed between secondary periods, and the population is assumed open between primary periods (Kendall et al. 1997, Kendall 2014).

RD models can estimate the number of animals present in the study area (N), probability of capture (p), probability of recapture (c), probability of survival (S), probability of an animal temporarily emigrating during the current sampling period given that it was observable in the previous sampling period (γ''), and probability of an animal temporarily emigrating during the current sampling period given that it was unobservable in the previous sampling period (γ'). There are 2 different types of temporary emigration: random and Markovian (Kendall 2014). Random temporary emigration states that the probability of an individual temporarily emigrating between primary periods is independent of whether the individual was observable (γ'') or unobservable (γ') during the previous period (i.e., $\gamma'' = \gamma'$). Markovian temporary emigration states that the probability of an individual temporarily emigrating between primary periods is dependent on whether the individual was observable or unobservable during the previous period (i.e., $\gamma'' \neq \gamma'$; Kendall et al. 1997, Kendall 2014). Therefore, Markovian temporary emigration would be expected if dolphins in the area seasonally migrate.

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CHAPTER 2

FACTORS RELATED TO BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) SEASONAL MIGRATION ALONG SOUTH CAROLINA AND GEORGIA COASTS ¹

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Abstract

Little is known about factors related to bottlenose dolphin (*Tursiops truncatus*) seasonal migration along the southeastern Atlantic coast. Migratory dolphins often overlap with resident dolphins, making accurate abundance estimation difficult. Therefore, it is important to understand environmental factors related to seasonal abundance fluctuations and migratory pulses to obtain accurate resident abundances. Previously collected capture-mark-recapture data and water quality data from Charleston, South Carolina and St. Catherine's Island, Georgia were used to determine if water quality variables were related to seasonal changes in abundance and temporary emigration. Robust Design models were used to estimate seasonal abundance and temporary emigration probabilities for the Charleston Harbor population, whereas closed population capture-recapture models were used to estimate abundances for each season for the St. Catherine's population. Results for the Charleston Harbor population indicated a seasonal abundance and temporary emigration pattern, with low estimates in winter, increasing in spring, highest in summer, and decreasing in fall. Water temperature best explained the seasonal temporary emigration pattern. Results for the St. Catherine's population showed inconsistent seasonal abundance estimates, but salinity best explained the variation of abundance estimates. Predicting migratory pulses will allow for accurate abundance estimates, which will be important in future population monitoring and accurately assessing the impacts of natural and anthropogenic factors on resident dolphins.

Introduction

The bottlenose dolphin population along the Atlantic coast of the southeastern United States is comprised of geographically defined subpopulations, known as stocks, including estuarine, coastal, offshore ecotypes (Waring et al. 2009, Waring et al. 2014). Evidence suggests that estuarine stocks are genetically distinct from neighboring estuarine stocks, as well as distinct from coastal and offshore stocks (Waring et al. 2009). The relationships among stocks are unknown and likely consist of overlapping ranges with neighboring stocks, making accurate abundance estimates within stocks difficult to ascertain and therefore setting limitations on management (Zolman 2002, Read et al. 2003, Waring et al. 2009, Speakman et al. 2010, Bills and Keith 2012).

Bottlenose dolphins in southeastern estuaries are exposed to natural and anthropogenic factors. In South Carolina, McFee et al. (2006) found 44.4% of all strandings caused by human interaction were from crab pot rope entanglements. Contaminants from agricultural runoff can concentrate in blubber tissue, likely effecting population health and reproduction (Schwacke et al. 2002, Hansen et al. 2004, Balmer et al. 2011). Recreation and direct human contact (e.g., propellers and feeding dolphins) can also put dolphins at risk (Waring et al. 2009). The true impacts of these factors are unknown largely because of insufficient abundance data (Waring et al. 2009, Waring et al. 2014).

Despite being the most commonly studied marine mammal, little is known about bottlenose dolphin migration patterns along the southeastern Atlantic coast (Read et al. 2003, Waring et al. 2009, Speakman et al. 2010). Many odontocete (i.e., toothed whale) species have complex distributions, causing migration patterns difficult to understand

(Hoelzel 1994, Bills and Keith 2012). Estuarine bottlenose dolphin stocks contain individuals that are resident in an area throughout the year, while other stocks (e.g., coastal stocks) seasonally migrate through the same area (Hoelzel 1994, Waring et al. 2009, Speakman et al. 2010, Bills and Keith 2012). The lack of information regarding seasonal migration in the Southeast makes abundance estimates often unreliable because migratory dolphins artificially inflate resident abundance estimates (Waring et al. 2009, Conn et al. 2011). Therefore, it is important to examine possible environmental factors that could initiate migratory pulses and explain seasonal fluctuations in abundance estimates.

Although two migratory pulses, north in the spring and south in the fall, are thought to occur each year in the South Atlantic coast dolphin population (Fertl 1994), factors related to timing of migratory pulses are unknown (Bills and Keith 2012). Many environmental factors are believed to be related to dolphin seasonal migration patterns (Shane 1980, Hoelzel 1994, Maze and Würsig 1999, Young and Phillips 2002, Torres et al. 2005). For example, as water temperature and prey abundance decrease in the north, dolphins will likely migrate south to warmer waters with higher prey availability (Torres et al. 2005, Speakman et al. 2010, Bills and Keith 2012). However, prey availability data are difficult to obtain at a large scale, whereas environmental data are readily available, making environmental factors more practical for managers to evaluate and use as predictors of migration. Examining environmental variables (e.g., water quality) that are possibly related to migration and seasonal abundance fluctuations is essential in better understanding when a migratory pulse is likely to be observed in an area.

Photo-identification research using natural markings is a common method in cetacean research used to identify individuals and estimate population parameters (Würsig and Jefferson 1990). For example, individual North Atlantic right whales are identified by their unique callosity patterns (Caswell et al. 1999), and individual Florida manatees are identified by their unique scar patterns (Beck and Reid 1995). In most dolphin species, individuals can be identified using the natural markings found on the dorsal fin, which often last the lifetime of the individual (Würsig and Würsig 1977). Photo-identification databases contain sighting histories for each individual, which can be extracted as capture-mark-recapture (CMR) data (Würsig and Würsig 1977, Adams et al. 2006, Speakman et al. 2010). Using CMR data analyses, photo-identification studies can provide abundance and other population parameter estimates, as well as identification of resident and migratory (i.e., non-resident) individuals (Würsig and Jefferson 1990, Zolman et al. 2002, Adams et al. 2006, Speakman et al. 2010).

To better understand bottlenose dolphin migratory movement and seasonal abundance fluctuations along the southeastern Atlantic coast, I examined environmental factors potentially related to migration. My specific objective was to determine if changes in water quality variables (i.e., water temperature, salinity, pH, dissolved oxygen, and turbidity) were related to seasonal changes in abundance estimates and temporary emigration probabilities along the South Carolina and Georgia coasts. I examined water temperature, salinity, pH, dissolved oxygen, and turbidity in addition to water temperature in order to determine water quality variable explained seasonal changes. Changes in water quality variable values have the potential to affect dolphin movements by acting as a migration cue or influencing the movement of prey species

(Maze and Würsig 1999, Bills and Keith 2012). Of the water quality variables, previous studies have hypothesized that water temperature is related to dolphin movement (Torres et al. 2005, Speakman et al. 2010, Bills and Keith 2012); therefore, I hypothesized that water temperature would be related to increases and decreases in abundance estimates and temporary emigration probabilities. Knowledge of factors related to migration will provide a basis for obtaining a more accurate estimate of resident abundance, allowing for effective management decisions regarding natural and anthropogenic impacts on resident dolphins (Conn et al. 2011).

Methods

Study Area

Data for my study were collected along the South Carolina and Georgia coasts. The South Carolina study area included transects within five estuarine rivers (Stono, Folly, Ashley, Cooper, and Wando), transects in the upper and lower portions of Charleston Harbor, and a transect 1 km from shore stretching from Isle of Palms to Kiawah Island near Charleston, South Carolina (Figure 2.1; Speakman et al. 2010). The stock of focus in South Carolina was the Charleston Estuarine System Stock, which I will refer to as the “Charleston Harbor population” (Waring et al. 2009). The study area for Georgia included tidal waters and embayments around St. Catherine’s Island, Georgia (e.g., North and South Newport Rivers, Johnson Creek, Walburg Creek, Sapelo Sound, and St. Catherine’s Sound; Figure 2.2). The stock of focus in Georgia was an undefined stock between the Southern Georgia Estuarine System Stock and the Northern

Georgia/Southern South Carolina Estuarine System Stock, which I will refer to as the “St. Catherine’s population” (Waring et al. 2009).

Field Data Collection

The CMR data used in this study were collected by the National Oceanic and Atmospheric Administration office in Charleston, South Carolina (NOAA) and the Georgia Dolphin Ecology Program (GDEP). NOAA conducted boat-based photo-identification surveys from 2004-2006 as part of a long-term study to monitor bottlenose dolphin abundance and distribution near Charleston, South Carolina (Speakman et al. 2010). Seasonal surveys were conducted in winter (January), spring (April), summer (July), and fall (October), which produced 4 primary sampling periods per year (total primaries = 12), each with 2 secondary periods (total secondaries = 24). Secondary periods (3-5 days to sample all transects) were conducted within 3 weeks, and 3 months separated each primary period.

NOAA surveys were completed by 3-4 crew members aboard a 6 m center-console outboard-powered vessel. Survey speeds ranged from 28-30 km per hour until a dolphin was sighted. A Canon EOS-IDs digital camera with a 100-400 mm telephoto lens was used to photograph dorsal fins during a sighting. Information recorded at the time of the sighting included date, time, spatial coordinates, water depth, group size, composition of group (i.e., adults and calves), behavior (e.g., feeding, traveling, milling), and environmental conditions (e.g., sky and water conditions).

GDEP conducted boat-based photo-identification surveys from 2011-2013 as part of a long-term study to assess the ecology and behavior of bottlenose dolphins near St.

Catherine's Island, Georgia. Two-day surveys were conducted twice per month as weather permitted, resulting in 49 total surveys. Surveys were categorized by season (i.e., winter = December, January, February; spring = March, April, May; summer = June, July, August; fall = September, October, November).

GDEP surveys were performed by 2-4 crew members aboard a 5.8 m skiff with a 70 horsepower engine. Survey speed was 24 km per hour until a dolphin sighting occurred. A Nikon D90 DSLR with a 75-300 mm NIKKOR telephoto zoom lens was used to photograph dorsal fins. Data collected at the time of sighting include date, time of day, spatial coordinates, total number of animals, number of calves, behavior, and environmental conditions.

Photo Analysis

Images were organized by survey date and sighting event using Photoshop 7.0 (NOAA) or ACDSee Pro 7.0 (GDEP). Images were graded for quality and only the best left and/or right side of the dorsal fin in which distinct features could be clearly observed for each individual were retained to reduce fin-matching errors. Retained images were transferred to FinBase (Adams et al. 2006). Matching fins were entered under the same catalog identification number, and those without a match were assigned a new catalog identification number. At least 2 persons verified matches and new fins in the cataloging process to avoid introduction of observer bias. Fins with minimal or no markings were designated as 'unmarked.' Sighting histories of each 'marked' individual observed by NOAA and GDEP were contained within their respective photo catalogs, and CMR files were extracted for each dataset.

Water Quality Data

Water quality data were obtained for the Ashepoo, Combahee, and Edisto (ACE) Basin, South Carolina (approximately 62 km from the Charleston Harbor population) and Sapelo Island, Georgia (approximately 20 km from the St. Catherine's population) from the National Estuarine Research Reserve System Centralized Data Management Office (NERRS; NERRS 2014). Water quality variables used for analysis included water temperature, pH, dissolved oxygen, salinity, and turbidity. I extracted data from all water quality stations within the ACE Basin data for NOAA sampling dates and all stations within the Sapelo Island data for GDEP sampling dates. I calculated means for each water quality variable for each season. I standardized the values by subtracting values for each primary by the mean of the respective variable, and then divided by the standard deviation of the variable (i.e., mean = 0 and standard deviation = 1). I used a Pearson's correlation coefficient test to determine if any variables were correlated and evaluated whether to exclude variables with $r \geq |0.7|$.

Data Analysis

Abundance estimates for both the Charleston Harbor and St. Catherine's populations included only marked individuals. Adult dolphins typically have at least 1 distinctive dorsal marking (J. H. Schacke and A. R. Taylor, GDEP, personal observations), while calves and young individuals typically lack distinctive markings (Würsig and Jefferson 1990). Therefore, abundances were estimated for the marked adult individuals for each population, as calves and young dolphins were excluded by default because of their lack of markings.

To estimate abundance and temporary emigration for marked dolphins within the Charleston Harbor population, I used Robust Design (RD; Kendall 2014) models in program RMark (Laake 2013), which is an interface for program MARK (Cooch and White 2014) within program R (R Core Team 2013). I assumed *a priori* that survival probability was constant, as stranding records from the study area indicated there was no seasonal effect on the number of dolphin stranding events (Speakman et al. 2010). I also assumed that capture and recapture probabilities were equal. The Charleston Harbor population was subject to boat traffic and commercial and recreational fishing; therefore, the presence of a photo-identification boat should not have altered the ability to photograph an individual's fin. I estimated number of animals present in the study area (N), probability of an animal temporarily emigrating during the current sampling period given that it was observable in the previous sampling period (i.e., emigration, γ''), and probability of an animal temporarily emigrating during the current sampling period given that it was unobservable in the previous sampling period (i.e., immigration, γ' ; Kendall 2014).

I evaluated whether the Charleston Harbor population exhibited random or Markovian temporary emigration. In cases of random temporary emigration the probability of an individual temporarily emigrating between primary periods is independent of whether the individual was observable (γ'') or unobservable (γ') during the previous period (i.e., $\gamma'' = \gamma'$). With Markovian temporary emigration, the probability of an individual temporarily emigrating between primary periods is dependent on whether the individual was observable or unobservable during the previous period (i.e., $\gamma'' \neq \gamma'$; Kendall et al. 1997, Kendall 2014).

I first created a Markovian emigration model in which capture probability and temporary emigration remained constant across sampling periods. I then modeled temporary emigration containing a single uncorrelated water quality variable (salinity, turbidity, or water temperature), with constant capture probability. To determine if multivariate models were needed, I assessed each of the single-variable Markovian emigration models using Akaike's Information Criterion corrected for small sample size (AIC_C ; Burnham and Anderson 2002). I first obtained AIC_C values for the model with constant temporary emigration and the model with temporary emigration containing salinity. I added the model with temporary emigration containing turbidity to the AIC_C to evaluate whether AIC_C values for the model with constant temporary emigration or the model with temporary emigration containing salinity changed from previous AIC_C values. Finally, I added the model with temporary emigration containing water temperature and evaluated changes in AIC_C values for the previous models. If AIC_C values changed after a model was added, I added a respective multivariate model containing both variables. I created random emigration models using the same steps to create Markovian models. I assumed that if multivariate models were needed or not needed in Markovian emigration models they were also needed or not needed in random emigration models; therefore, I did not evaluate random emigration models with step-wise AIC_C .

I also created models with time-varying capture probability to account for capture variability among seasons (i.e., primary periods) or secondary periods. I created a set of Markovian and random temporary emigration models with capture probability varying by primary periods with constant temporary emigration, as well as models with temporary

emigration containing salinity, models with temporary emigration containing turbidity, and models with temporary emigration containing water temperature. I also created Markovian and random temporary emigration models with capture probability varying by secondary periods with constant temporary emigration, as well as models with temporary emigration containing salinity, models with temporary emigration containing turbidity, and models with temporary emigration containing water temperature. I evaluated all models using AIC_C to determine which model best explained the data.

I was unable to estimate abundance and temporary emigration for the St. Catherine's population using RD because 4 secondary surveys were not conducted due to weather. Therefore, I used closed population capture-recapture (closed-capture; Lukacs 2015) models using program RMark (Laake 2013) within program R (R Core Team 2013) to estimate abundance for marked dolphins within each season. I assumed *a priori* that the population was closed within each season and that capture and recapture probabilities were equal. Similar to the Charleston Harbor population, the St. Catherine's population was subject to boat traffic and commercial and recreational fishing so the presence of a photo-identification boat should not have altered the behavior of dolphins or the ability to photograph an individual's fin. I also assumed that capture probability was constant, as each season represented 1 primary period and there were no secondary periods.

I separated sighting history data into seasons and created a closed-capture model for each season with more than 2 surveys (winter 2011 and winter 2013 were excluded from analyses because only 1-2 surveys were conducted), resulting in 11 close-capture models, each with constant capture probabilities. After abundance estimates were

obtained, I examined the relationship of seasonal abundance with uncorrelated water quality variables using simple linear regression models using package stats (R Core Team 2014) within program R (R Core Team 2014). I created one linear regression model for each water quality variable with abundance estimates as the response variable. Statistical significance was accepted at $P \leq 0.05$. For comparison with abundance estimates, I calculated relative abundance as the number of dolphins per linear transect km (adjusted for effort) averaged for each season.

Results

The Charleston Harbor population contained 856 identified individual dolphins during the 3-year photo-identification study (Speakman et al. 2010), resulting in 694 individual marked dolphin capture histories after seasonal and photographic quality constraints were applied to the data. The St. Catherine's population contained 297 individual marked dolphins after photographic quality constraints during the 3-year photo-identification study.

For both the Charleston Harbor population and the St. Catherine's population, the Pearson's correlation coefficient test indicated that water temperature was negatively correlated with dissolved oxygen and pH ($r = -0.97$ and $r = -0.92$, respectively, for Charleston Harbor population; $r = -0.97$ and $r = -0.93$, respectively, for St. Catherine's population), and dissolved oxygen and pH were positively correlated ($r = 0.89$ for Charleston Harbor population and $r = 0.94$ for St. Catherine's population). To avoid collinearity, I excluded dissolved oxygen and pH from further analyses (Dormann et al. 2013), as water temperature influences the values of dissolved oxygen and pH (NOAA

2008). Therefore, water quality variables used in my modeling only included water temperature, salinity, and turbidity.

No multivariate models were created for the Charleston Harbor population, as AIC_C values did not change among Markovian temporary emigration models with constant capture probability (Table 2.1). The best model for the Charleston Harbor population was Markovian temporary emigration containing water temperature (Figures 2.3 and 2.4) and capture probability varying by primary period (Table 2.2). Abundance estimates followed a general seasonal trend of lowest in winter, increasing in spring, highest in summer, and decreasing in fall (Figure 2.3). The lowest abundance estimate occurred in winter 2004 ($N = 277 \pm 54$, 95% CI = 200-424), coinciding with the lowest water temperature value. Highest abundance estimates were in summer in 2004 ($N = 413 \pm 30$, 95% CI = 363-479) and 2005 ($N = 413 \pm 32$, 95% CI = 359-484) and in fall 2006 ($N = 529 \pm 27$, 95% CI = 483-592), with summer 2004 and 2005 coinciding with the highest water temperature values.

Temporary emigration probabilities for the Charleston Harbor population also followed a seasonal pattern, with lowest probabilities in the winter and highest in the summer (Figure 2.4). The lowest γ'' was in winter 2004 ($\gamma'' = 0.021 \pm 0.011$, 95% CI = 0.007-0.061), and the lowest γ' was in winter 2005 ($\gamma' = 0.739 \pm 0.072$, 95% CI = 0.576-0.864), coinciding with low water temperature values. The highest γ'' and γ' occurred in summer 2004 (0.255 ± 0.036 , 95% CI = 0.191-0.331; 0.908 ± 0.044 , 95% CI = 0.779-0.965, respectively), coinciding with the high water temperature values.

The St. Catherine's population abundance estimates varied from year to year (Figure 2.5). Abundance decreased from spring 2011 to fall 2011 and increased slightly

in winter 2011-2012, remaining steady through fall 2012. Abundance began to increase in winter 2012-2013 and continued to increase through summer 2013, decreasing in fall 2013. Linear regression results indicated that salinity was significantly related to abundance ($F_{1,9} = 9$, $p = 0.01$, $r^2 = 0.44$; Figure 2.6). The lowest abundance estimate was found in fall 2011 ($N = 20 \pm 11$, 95% CI = 12-64), which corresponds to the highest salinity value. Although summer had low abundance estimates in years 2011 ($N = 52 \pm 7$, 95% CI = 44-73) and 2012 ($N = 34 \pm 9$, 95% CI = 25-62), the highest abundance estimate occurred in summer 2013 ($N = 266 \pm 35$, 95% CI = 212-352). Excluding 2012, relative abundance estimates followed the same general pattern as abundances from closed-capture models (Figure 2.5).

Discussion

Abundance estimates for the Charleston Harbor population showed a consistent seasonal trend. Low abundance estimates occurred in winter, increasing in the spring, reaching high estimates in the summer, and decreasing in the fall (excluding fall 2006). This seasonal trend indicates that the Charleston Harbor population abundance is not constant throughout the year. Abundance variability has also been documented in Florida (Weigle 1990, Balmer et al. 2008), North Carolina (Torres et al. 2005), South Carolina (Zolman 2002), and Texas (Shane 1980, Fertl 1994). Consistent low estimates in winter support the idea that the Charleston Harbor population contains resident dolphins (i.e., dolphins residing in the area year-round) that remain in the area through all environmental conditions (Fertl 1994, Zolman 2002, Speakman et al. 2010).

The Charleston Harbor population abundance estimates also suggest the presence of seasonal resident dolphins (i.e., dolphins occurring in the area in the same season for multiple years, but not consecutive seasons). Seasonal residents likely move into the area during warmer seasons and emigrate before winter, resulting in an increase in abundance estimates from spring to summer (Zolman 2002, Speakman et al. 2006, Speakman et al. 2010). Therefore, the abundance estimates for the Charleston Harbor population likely included dolphins that resided in the study area, as well as dolphins that moved within the study area and eventually emigrated. Evidence of seasonal residents was also noted in South Carolina (Zolman 2002) and in Texas (Fertl 1994). Zolman (2002) proposed that seasonal residents present in a South Carolina estuary could be migratory dolphins, as seasonal residents only occur within the study area during certain seasons. The seasonal abundance trend for the Charleston Harbor population and evidence of seasonal residents support the possibility of migratory dolphins entering the area in spring and leaving in fall.

Temporary emigration probabilities for the Charleston Harbor population followed the same seasonal pattern as abundance estimates. The best fitting RD model was Markovian temporary emigration (i.e., the probability of encountering a dolphin during the current sampling period did depend on its presence in the previous sampling period), meaning there was a seasonal emigration pattern (Balmer et al. 2008, Speakman et al. 2010, Smith et al. 2013, Kendall 2014). The RD model also indicated that more dolphins immigrated than emigrated, as γ' were consistently higher than γ'' (Kendall 2014). In Australia, Smith et al. (2013) found that Indo-Pacific bottlenose dolphins (*T. aduncus*) also exhibit Markovian temporary emigration rather than random, with γ'

higher than γ '. The seasonal pattern of temporary emigration probabilities, coinciding with seasonal abundance estimates, provides evidence that migratory dolphins are likely overlapping with the Charleston Harbor population during spring, summer, and possibly fall.

Model results indicate that water temperature is related to the Charleston Harbor population temporary emigration probabilities. Water temperature has previously been proposed as a migration cue (Kenney 1990, Mead and Potter 1990, Bräger et al. 1994, Barco et al. 1999, Zolman 2002, Torres et al. 2005), but water temperature could be correlated with other factors. For example, water temperature could influence prey availability (Hoelzel 1994, Young and Phillips 2002, Torres et al. 2005, Speakman et al. 2010, Bills and Keith 2012) and other environmental factors (e.g., dissolved oxygen, pH, and salinity; NOAA 2008). Temporary emigration probability trends could indicate dolphins immigrate to the Charleston Harbor because of increased prey, which are likely being influenced by water temperature. Increased prey availability also usually leads to increased commercial fishing efforts. Shrimp trawling increases within the Charleston Harbor in summer, which could attract migratory dolphins to the area to feed on discarded bycatch (Speakman et al. 2010). Therefore, while water temperature is related to temporary emigration for the Charleston Harbor population, other factors could be indirectly related as well.

My study is the first to estimate abundance and relate abundance to water quality for the St. Catherine's population. Abundance estimates from closed-capture models varied considerably from year to year. Although abundance results do not have a consistent yearly trend as the Charleston Harbor population, results confirm that seasonal

abundance variability (Shane 1980, Weigle 1990, Fertl 1994, Zolman 2002, Torres et al. 2005, Balmer et al. 2008) exists for the St. Catherine's population. The data also suggest that the St. Catherine's population contains residents, as there are some individuals that remain in the area through all seasons (Figure 2.5; Fertl 1994, Zolman 2002, Speakman et al. 2010). Similar to the Charleston Harbor population, increases in abundance estimates for the St. Catherine's population provide evidence that abundance estimates likely included dolphins that resided within the study area, as well as dolphins that moved within the study area and eventually emigrated.

The water quality variable that best explained variation in abundance estimates for the St. Catherine's population was salinity. Low salinity levels are likely to occur in spring when rainfall increases the freshwater flow, and high salinity levels likely occur in the summer when evaporation increases (Young and Phillips 2002, NOAA 2008). Higher abundance estimates occurred at unusually low salinity levels in spring 2013 through fall 2013 (Figure 2.6), which indicates that migration is likely to occur at low salinity values. These results add salinity as a possible factor related to dolphin migration. The validity of salinity as a migration cue has not been evaluated in previous studies. However, possible dolphin prey, such as blue crab (*Callinectes sapidus*), menhaden (*Brevoortia tyrannus*), and spot (*Leiostomus xanthurus*), are influenced by salinity (Rogers and Van Den Avyle 1983, Tankersley et al. 1998, Young and Phillips 2002). For example, female blue crabs, when inseminated, emigrate from low-salinity level areas within estuaries to high-salinity areas at mouths of estuaries to spawn (Tankersley et al. 1998). An increased amount of blue crabs near mouths of estuaries could attract migratory dolphins to the area. The dolphins are following their prey, which

are being influenced by salinity; therefore, salinity could be indirectly related to seasonal fluctuations of the St. Catherine's population abundance estimates.

It is important to note that my results indicated water temperature and salinity were related, not necessarily driving factors, to seasonal abundance fluctuations and seasonal temporary emigration probabilities related to migration. Other vertebrate species, such as birds (Helm et al. 2009, Price et al. 2010) and fish (Capossela et al. 2013, Zydlewski et al. 2014), rely on photoperiod as a migration cue. In fish species, photoperiod can determine a range of dates in which a migration can occur, but other environmental factors (e.g., water temperature) act as releasing factors (Baggerman 1960). Zolman (2002) found a relationship between dolphin density and photoperiod in a South Carolina estuary. Therefore, it is likely that photoperiod is a primary dolphin migration cue, while water temperature and salinity are secondary migration cues for the Charleston Harbor and St. Catherine's populations, respectively.

I examined relative abundance for comparison to closed-capture abundance estimates for the St. Catherine's population to evaluate the reliability of relative abundance, as calculating relative abundance is a common method used to quantify dolphin abundance. Abundance estimates from closed-capture models and calculated relative abundances for the St. Catherine's population followed the same general trend (excluding 2012; Figure 2.5). Deviations of relative abundance from the trend of modeled abundance estimates are likely due to overestimates or underestimates of relative abundance, as it is calculated using counts from the field that could include counts of the same individuals more than once or could also exclude individuals. While relative abundances and indices can be useful to identify overall seasonal trends,

population parameter models using CMR data should be used when possible to obtain accurate abundance estimates.

Both datasets showed evidence of transients (i.e., dolphins only sighted once throughout the study period; Conn et al. 2011) in the study area during spring, summer, and fall seasons. It is important to note that single-sighted dolphins classified as transients might be residents, who by chance were only seen once (Zolman 2002, Conn et al. 2011), and should be considered as “possible transients.” For the Charleston Harbor population, 32% of individuals observed were possible transients. The number of possible transient encounters was low in winter, increasing the spring and summer, and decreasing in fall (excluding fall 2006; Figure 2.7). Speakman et al. (2010) observed an unusually high number of possible transients in fall 2006, resulting in an upward bias in abundance estimates (Zolman 2002; Figures 2.3 and 2.7). Zolman (2002) proposed that transients encountered in a South Carolina estuary could be migratory dolphins, as they are only encountered within the study area once. Therefore, the presence of possible transients, along with increased abundance estimates and temporary emigration probability trends, further supports the idea that migratory dolphins overlap with the Charleston Harbor population in spring through fall. Charleston Harbor population abundance estimates could have been biased by the presence of possible transients by increasing abundance estimates and decreasing capture probability. The RD model assumption that the population is closed to immigration and emigration during all secondary sampling periods (Kendall 2014) could have been violated. Although secondary periods were conducted within 3-5 days, it is possible that transients utilized the area and emigrated during secondary periods. In addition, RD models can only

estimate temporary emigration (Kendall 2014) and cannot differentiate between temporary emigration, death, and permanent emigration, which would cause a bias in the survival estimate (Speakman et al. 2010). The best fitting RD model for the Charleston Harbor population indicated that survival probability was 0.99 ± 0.00004 (95% CI = 0-1). This survival probability is unrealistic and likely a result of RD models not being able to differentiate death and emigration.

The St. Catherine's population showed a similar observation of possible transients pattern with 56% of individuals only sighted once. The high percentage of possible transients in the area could be due, in part, to sampling effort. For example, missed surveys due to weather could have resulted in missed resighting opportunities, thus increasing the number of possible transients. The number of possible transient encounters was consistently low in winter seasons. In 2011, possible transient encounters were high in spring and decreased through fall; in 2012, possible transient encounters were low in spring and increased through fall (Figure 2.8). The seasons with the highest number of possible transients corresponds to higher abundance estimates, indicating that the presence of transients does inflate abundance estimates. Similar to the Charleston Harbor population, the seasonal pattern of possible transients overlapping with the St. Catherine's population, along with the increased abundance estimates, supports a migration pattern in spring through fall (Zolman 2002, Speakman et al. 2010, Bills and Keith 2012). Abundance for the St. Catherine's population could also have been biased because of possible transient presence. The closed-capture model assumption that the population is closed (Lukacs 2015) was likely violated. Although seasonal surveys were conducted within relatively short time intervals (i.e., 3 months), it is possible that

transients could have utilized the area and emigrated within these intervals. The assumption that all animals have the same likelihood to be captured (Lukacs 2015) could have also been violated. A transient dolphin would have a lower capture probability than a resident dolphin, as transients are only sighted once. In addition, seasonal residents who emigrate would also have a lower capture probability than residents because seasonal residents are only present in the area during certain seasons. However, it is likely that resident dolphin individuals have an equal capture probability, as they occur in the area year-round.

My study is one of the first to attempt to find environmental variables that are related to migratory movements. From my results, I infer that migration is likely to occur from spring to fall through both populations based on seasonal abundance estimates, seasonal temporary emigration trends for the Charleston Harbor population, and evidence of seasonal residents and possible transients (i.e., possible migrants). For example, estimates for the Charleston Harbor population showed that increases in abundance occurred when immigration probability (γ') was high, which correlated with water temperature. High abundance estimates, which correlated with salinity, for the St. Catherine's population occurred when encounters of possible transients were high.

Management Implications

The goal of this study was to determine if changes in water quality variables were related to seasonal changes in abundance and temporary emigration estimates along the South Carolina and Georgia coasts. Water temperature best explained variation in temporary emigration probabilities for the Charleston Harbor population, and salinity

best explained variation in abundance estimates for the St. Catherine's population. Knowing that water temperature and salinity are related to seasonal abundance fluctuations and temporary emigration probabilities for these 2 southeastern dolphin populations is an important step to understanding factors related to dolphin migration. Managers could monitor environmental data, such as water temperature and salinity, to predict when a migration is likely to occur and monitor the health and abundance of resident dolphins as migratory dolphins move through the area, as well as warn trawlers of increased possibility of dolphin by-catch. Predicting migratory pulses can also lead to more accurate abundance estimates, which will be important in future population monitoring to accurately assess the impacts of natural and anthropogenic factors on resident dolphins.

Future studies regarding factors related to migration should use a sampling design that will allow for RD analyses. Temporary emigration probabilities from RD models will allow evaluation of migration patterns through the study area. If possible, studies should also collect primary sources for environmental data (e.g., water temperature, salinity) and, if possible, prey abundance and diversity to have a better representation of conditions at the time of sightings. Future studies should also incorporate models that will estimate other important population parameters, such as recruitment. Using RD models from long-term photo-identification studies and primary environmental data could lead to accurate abilities to predict when a migratory pulse is likely to occur.

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Table 2.1. Results from steps used to determine if multivariate water quality models were needed to estimate temporary emigration probabilities for the Charleston Harbor population, South Carolina, 2004-2006. AIC_C values did not change after each water quality variable model was added; therefore, no multivariate models were used.

	Model	K	AIC_C	ΔAIC_C	w_i	Deviance
Step 1:	S(.) $\gamma''(\text{sal}) \neq \gamma'(\text{sal})$ p(.) = c(.) N(s)	18	-9649.639	0	0.995	3315.232
	S(.) $\gamma''(.) \neq \gamma'(.)$ p(.) = c(.) N(s)	16	-9639.167	10.472	0.005	3329.755
Step 2:	S(.) $\gamma''(\text{turb}) \neq \gamma'(\text{turb})$ p(.) = c(.) N(s)	18	-9656.565	0	0.969	3308.306
	S(.) $\gamma''(\text{sal}) \neq \gamma'(\text{sal})$ p(.) = c(.) N(s)	18	-9649.639	6.926	0.995	3315.232
	S(.) $\gamma''(.) \neq \gamma'(.)$ p(.) = c(.) N(s)	16	-9639.167	17.398	0.005	3329.755
Step 3:	S(.) $\gamma''(\text{temp}) \neq \gamma'(\text{temp})$ p(.) = c(.) N(s)	18	-9670.953	0	0.999	3293.918
	S(.) $\gamma''(\text{turb}) \neq \gamma'(\text{turb})$ p(.) = c(.) N(s)	18	-9656.565	14.388	0.001	3308.306
	S(.) $\gamma''(\text{sal}) \neq \gamma'(\text{sal})$ p(.) = c(.) N(s)	18	-9649.639	21.314	0	3315.232
	S(.) $\gamma''(.) \neq \gamma'(.)$ p(.) = c(.) N(s)	16	-9639.167	31.786	0	3329.755

Table 2.2. Random ($\gamma'' = \gamma'$) and Markovian ($\gamma'' \neq \gamma'$) temporary emigration model selection results, including number of parameters (K), AIC_C values, ΔAIC_C values, model weights (w_i), and deviances, used to estimate abundance and temporary emigration probability for the Charleston Harbor population, South Carolina, 2004-2006. Parameters were modeled constant (.), by primary period (s), by secondary period (t), by water temperature (temp), by salinity (sal), and by turbidity (turb).

Model	K	AIC_C	ΔAIC_C	w_i	Deviance
S(.) $\gamma''(\text{temp}) \neq \gamma'(\text{temp})$ p(s) = c(s) N(s)	29	-9701.484	0.000	0.999	3241.007
S(.) $\gamma''(\text{turb}) \neq \gamma'(\text{turb})$ p(s) = c(s) N(s)	29	-9686.605	14.879	0.001	3255.886
S(.) $\gamma''(\text{sal}) \neq \gamma'(\text{sal})$ p(s) = c(s) N(s)	29	-9686.187	15.298	0	3256.305
S(.) $\gamma''(.) \neq \gamma'(.)$ p(s) = c(s) N(s)	27	-9681.743	19.741	0	3264.830
S(.) $\gamma''(\text{temp}) \neq \gamma'(\text{temp})$ p(t) = c(t) N(s)	19	-9676.834	24.650	0	3286.010
S(.) $\gamma''(\text{temp}) \neq \gamma'(\text{temp})$ p(.) = c(.) N(s)	18	-9670.953	30.531	0	3293.918
S(.) $\gamma''(\text{turb}) \neq \gamma'(\text{turb})$ p(t) = c(t) N(s)	19	-9664.428	37.056	0	3298.416
S(.) $\gamma''(\text{turb}) \neq \gamma'(\text{turb})$ p(.) = c(.) N(s)	18	-9656.565	44.919	0	3308.306
S(.) $\gamma''(\text{sal}) \neq \gamma'(\text{sal})$ p(t) = c(t) N(s)	19	-9655.665	45.819	0	3307.179
S(.) $\gamma''(\text{sal}) \neq \gamma'(\text{sal})$ p(.) = c(.) N(s)	18	-9649.639	51.845	0	3315.232
S(.) $\gamma''(.) \neq \gamma'(.)$ p(t) = c(t) N(s)	17	-9645.161	56.323	0	3321.736
S(.) $\gamma''(\text{turb}) = \gamma'(\text{turb})$ p(s) = c(s) N(s)	27	-9643.536	57.978	0	3303.037
S(.) $\gamma''(.) \neq \gamma'(.)$ p(.) = c(.) N(s)	16	-9639.167	62.317	0	3329.755
S(.) $\gamma''(\text{sal}) = \gamma'(\text{sal})$ p(s) = c(s) N(s)	27	-9635.965	65.519	0	3310.608
S(.) $\gamma''(.) = \gamma'(.)$ p(s) = c(s) N(s)	26	-9632.358	69.126	0	3316.255
S(.) $\gamma''(\text{temp}) = \gamma'(\text{temp})$ p(s) = c(s) N(s)	27	-9630.353	71.131	0	3316.221
S(.) $\gamma''(\text{turb}) = \gamma'(\text{turb})$ p(t) = c(t) N(s)	17	-9597.219	104.265	0	3369.678
S(.) $\gamma''(\text{turb}) = \gamma'(\text{turb})$ p(.) = c(.) N(s)	16	-9591.212	110.272	0	3377.710
S(.) $\gamma''(\text{sal}) = \gamma'(\text{sal})$ p(t) = c(t) N(s)	17	-9583.275	118.209	0	3383.622
S(.) $\gamma''(.) = \gamma'(.)$ p(t) = c(t) N(s)	16	-9580.193	121.292	0	3388.729
S(.) $\gamma''(\text{temp}) = \gamma'(\text{temp})$ p(t) = c(t) N(s)	17	-9578.546	122.939	0	3388.352
S(.) $\gamma''(\text{sal}) = \gamma'(\text{sal})$ p(.) = c(.) N(s)	16	-977.275	124.209	0	3391.646
S(.) $\gamma''(.) = \gamma'(.)$ p(.) = c(.) N(s)	15	-9574.191	127.293	0	3396.753
S(.) $\gamma''(\text{temp}) = \gamma'(\text{temp})$ p(.) = c(.) N(s)	16	-9572.546	128.938	0	3396.376

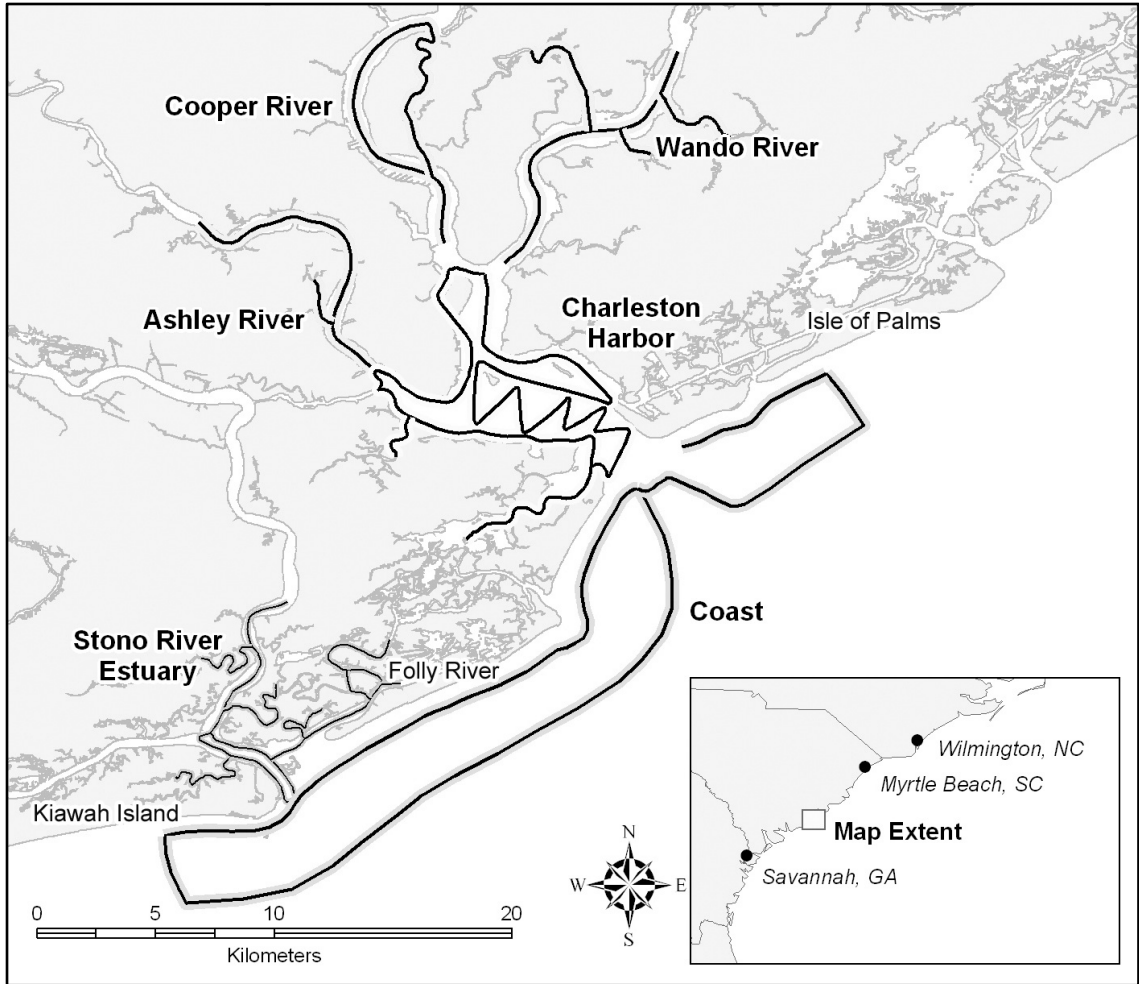


Figure 2.1. Survey transects (black lines) conducted by the National Oceanic and Atmospheric Administration at Charleston, South Carolina to obtain bottlenose dolphin photo-identification data near Charleston, South Carolina, 2004-2006 (Speakman et al. 2010).

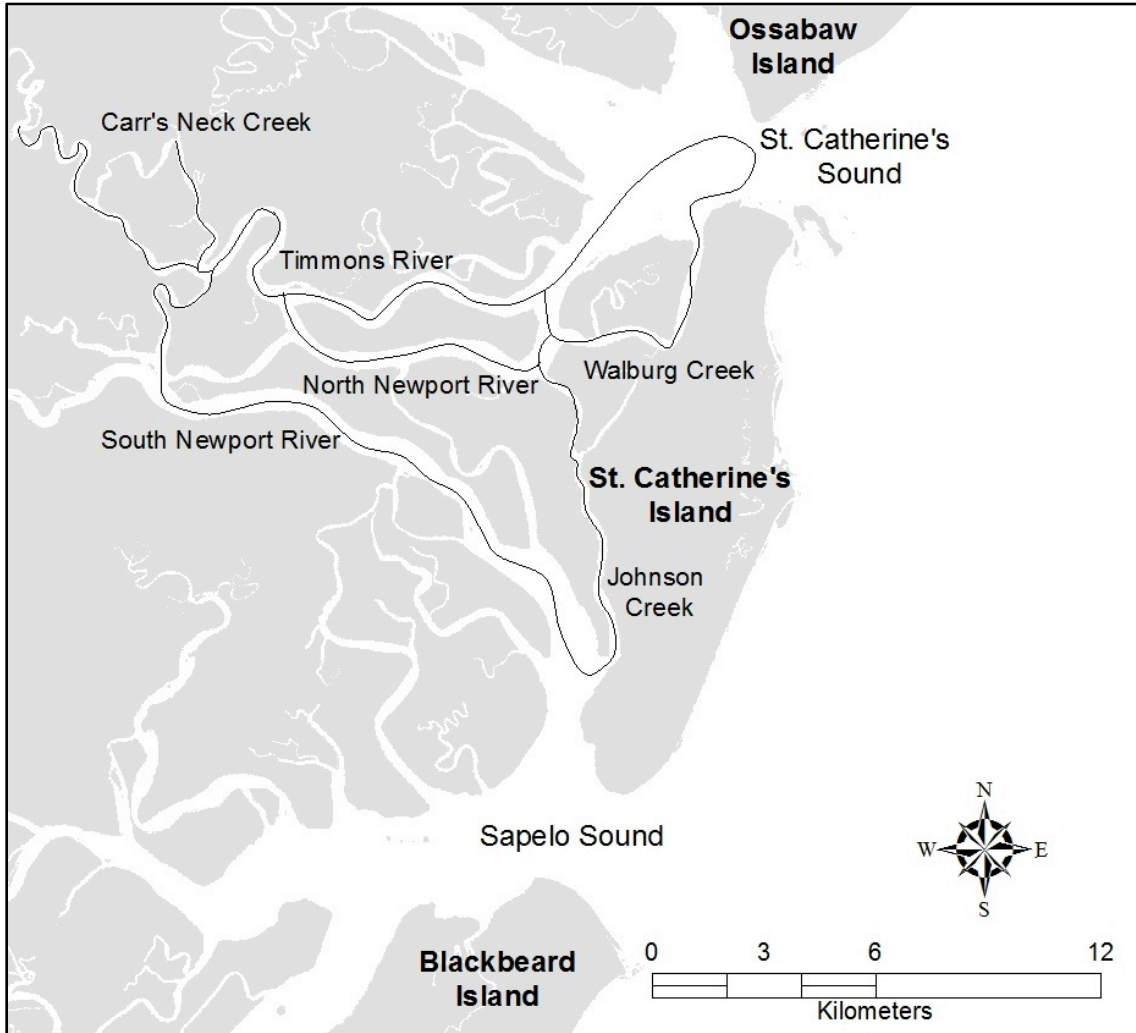


Figure 2.2. Survey transects (black lines) conducted by the Georgia Dolphin Ecology Program to obtain bottlenose dolphin photo-identification data near St. Catherine's Island, Georgia, 2011-2013.

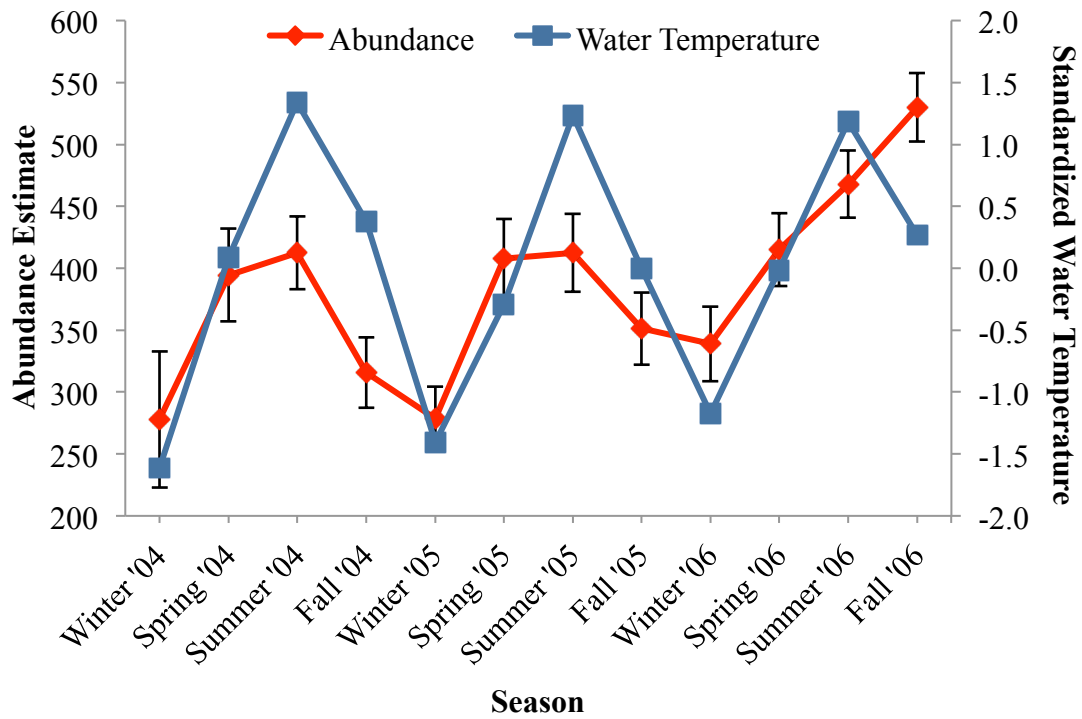


Figure 2.3. Seasonal bottlenose dolphin abundance estimates with standard errors and water temperature near Charleston Harbor population, South Carolina, 2004-2006.

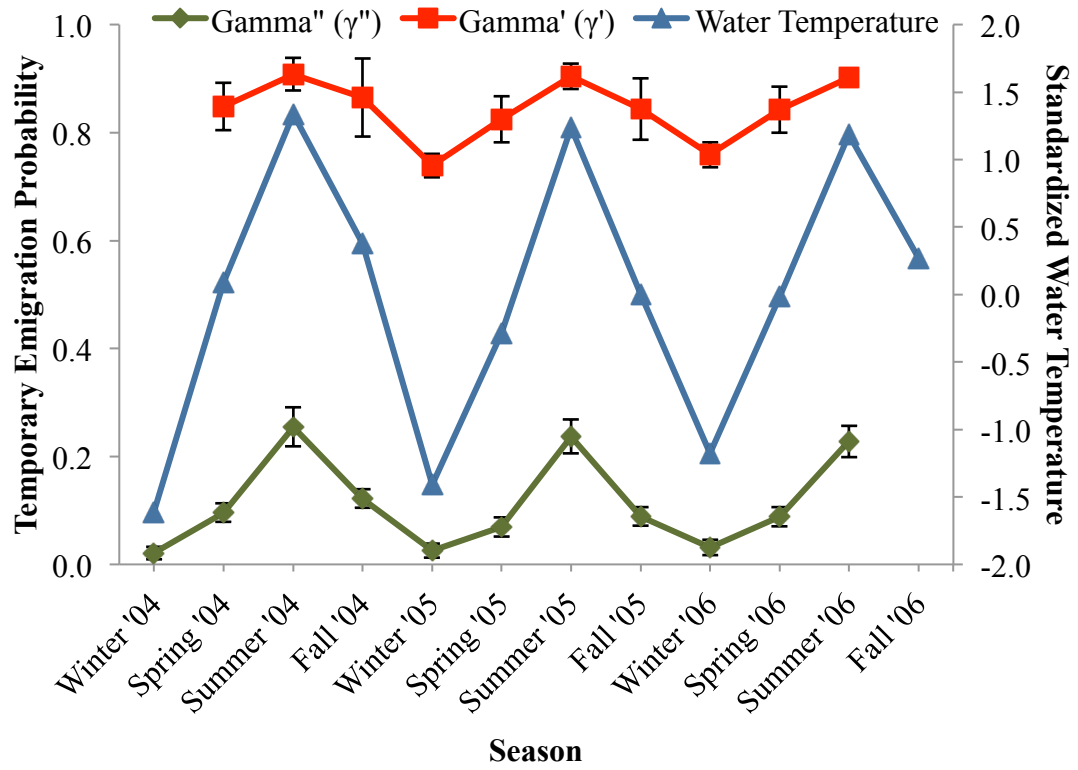


Figure 2.4. Seasonal bottlenose dolphin temporary emigration probabilities with standard errors and water temperature for the Charleston Harbor population, South Carolina, 2004-2006.

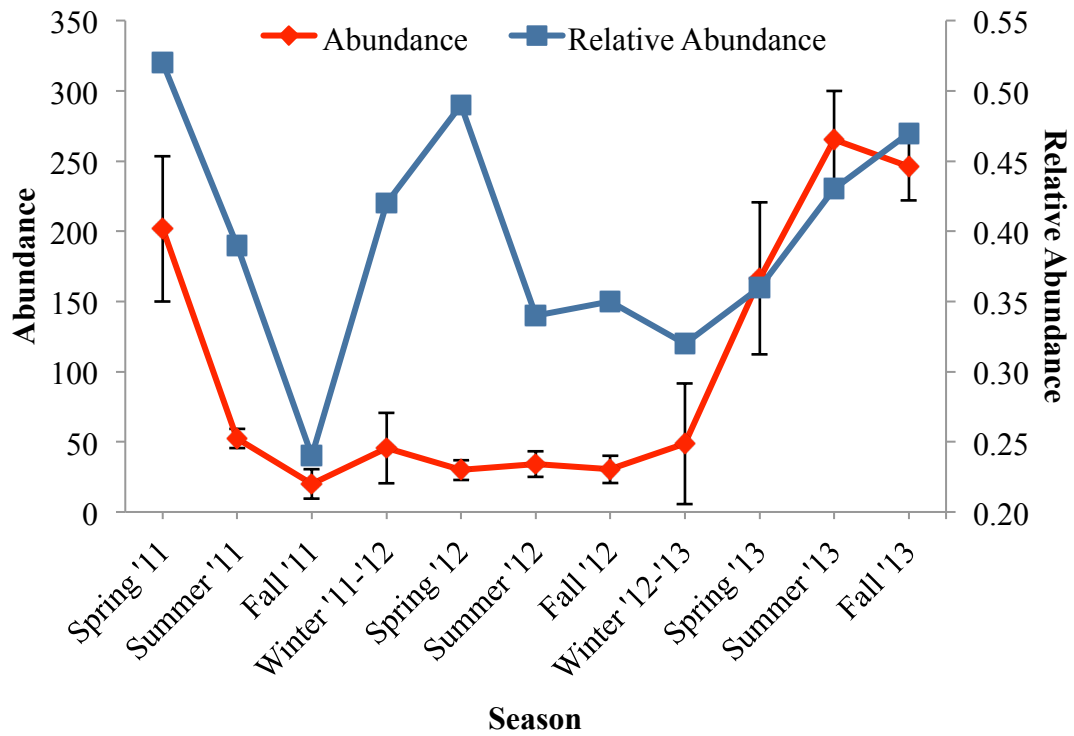


Figure 2.5. Seasonal bottlenose dolphin abundance estimates with standard errors and relative abundance (number of dolphins/transect km adjusted for effort) for the St. Catherine's population, Georgia, 2011-2013.

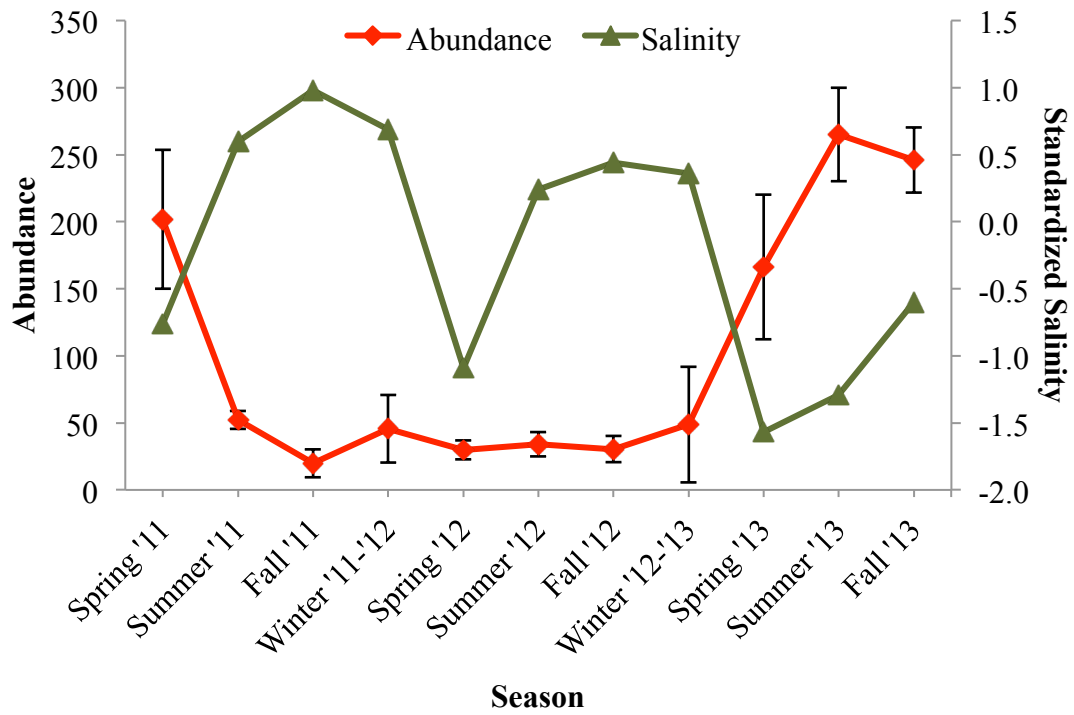


Figure 2.6. Seasonal bottlenose dolphin abundance estimates with standard errors and salinity for the St. Catherine's population, Georgia, 2011-2013.

CHAPTER 3

SEASONAL DISTRIBUTION OF BOTTLENOSE DOLPHINS (*TURSIOPS*
TRUNCATUS) NEAR ST. CATHERINE'S ISLAND, GEORGIA ²

² Taylor, A. R., J. H. Schacke, S. B. Castleberry, and R. B. Chandler. To be submitted to *Southeastern Naturalist*.

Abstract

Little is known about factors related bottlenose dolphin (*Tursiops truncatus*) habitat selection along the Georgia coast. Because of the lack of habitat selection studies, important habitat for species survival remains undefined. In addition, dolphin habitats are affected by many anthropogenic sources, which may negatively impact overall population viability. Therefore, it is important to identify and describe high-use areas to provide insight into critical habitat. Previously collected dolphin sightings data and depth data from St. Catherine's Island, Georgia were used to determine if depth affects seasonal dolphin distribution for the St. Catherine's population using Poisson point process models. Results indicated depth had a significant effect on dolphin sighting distribution for each season. These results will be a useful tool in providing insight into critical habitats and mitigating coastal development, recreation, and fisheries near potential critical habitats.

Introduction

Bottlenose dolphins are distributed from tropical to temperate seas worldwide. Despite being the most commonly studied marine mammal, little is known about habitat selection along the Georgia coast (Read et al. 2003, Waring et al. 2009, Speakman et al. 2010). Bottlenose dolphins in southeastern estuaries are influenced by natural (e.g., diseases) and anthropogenic factors (e.g., coastal development), which may negatively impact overall population viability (Waring et al. 2009, Conn et al. 2011, Balmer et al. 2013). The true impacts of these factors are unknown because of the lack of abundance and habitat selection data (Waring et al. 2009, Waring et al. 2014). Habitat selection

studies are lacking for southeastern dolphins, causing critical habitat areas to remain undefined; therefore, it is important to identify and describe high-use areas to provide insight into critical habitat.

Habitats within coastal systems are heterogeneous, with some areas offering more food resources and protection from predators than other areas (Ballance et al. 1992, Gubbins 2002). Many factors are believed to influence dolphin habitat use, such as tidal state, depth, prey availability, and water temperature (Shane 1980, Maze and Würsig 1999, Ingram and Rogan 2002, Bräger et al. 2003). Most dolphin species exhibit seasonal changes in habitat use, which is likely a direct effect from prey movement and indirect effect from environmental factors (Bräger et al. 2003, Maze and Würsig 1999).

Identification of high-use areas, areas in which the species is found at high densities (e.g., hotspots), can provide insight into characteristics of habitat that are essential for species survival (Redfern et al. 2006). In South Carolina, Adams et al. (2006) found that long-term photo-identification data used in combination with a geographic information system (GIS) was useful in determining high-use areas by identifying the number of sightings observed within a defined area. Another study in South Carolina used density tools in ArcGIS to locate high-use areas (i.e., number of sightings per km²) in which neonates were encountered (McFee et al. 2014). The authors were able to identify high-density neonate areas, as well as conclude that habitat usage differs by season (i.e., spring neonate sightings were mainly within estuaries, while fall sightings were in coastal areas). Off the Georgia coast, Balmer et al. (2013) calculated dolphin density for each stream order and found that dolphin densities differed among

stream orders. These studies successfully identified high-use areas, but the physical characteristics of these areas were not described.

Redfern et al. (2006) described many techniques for defining high-use areas using habitat variables. For example, topobathymetric data can provide insight into characteristics of related to dolphin habitat selection. Coastal Relief Models (CRM) contain both bathymetric and topographic data, which could be used as a proxy for elevation or depth (National Oceanic and Atmospheric Administration National Geophysical Data Center (NGDC) 1999). Depth may influence dolphin habitat selection indirectly by influencing the distribution of prey (Wells et al. 1980 and Irvine et al. 1981). A study in Moray Firth, Scotland found that depth did not have a significant relationship with dolphin distribution (Bailey and Thompson 2009). However, Irvine et al. (1981) found that dolphin habitat use near Sarasota, Florida differed among seasons (i.e., in warmer months sightings occurred more in channels and bays inshore, rather than along the gulf shore sightings in winter), and dolphins showed a depth selection of < 3 m. These studies were able to identify and describe habitats of areas with high dolphin density using depth, and therefore provided a better understanding of what areas might be critical to the dolphins' survival (Ballance 1992, Gubbins 2002).

Point process modeling (PPM) is a technique used to describe covariate effects and spatial trends (Baddeley and Turner 2005) and may have applicability in defining important areas for dolphins. PPM can be used to analyze patterns of randomly distributed points (e.g., dolphin sightings) and evaluate correlations between dolphin density and covariates (e.g., depth), which may influence dolphin distribution (Illian et al. 2008). Inhomogeneous locations of sightings likely reflect influences of covariates

(Illian et al. 2008). Warton and Shepherd (2010) proposed using inhomogeneous Poisson PPM (Cressie 1993, Diggle 2003) for presence-only data (i.e., set of point locations where only presences were recorded), where the points are assumed independent (Renner and Warton 2013). Poisson PPM can model the expected count, or intensity, of dolphin sightings per unit area for any location (Renner and Warton 2013). Regardless of the method used to identify and describe high-use areas, the implications are the same: to provide insight into critical habitat, future habitat management, and impacts from anthropogenic sources (McFee et al. 2014).

To better understand bottlenose dolphin habitat selection along the Georgia coast, I examined CRM data as a proxy for depth and identified high-use areas using Poisson PPM. My specific objectives were to determine if dolphin distribution was significantly affected by depth and if high-use areas differed by season for dolphins near St. Catherine's Island, Georgia. Previous studies have found significant relationships among dolphin distribution and depth (Irvine et al. 1981, Ballance 1992, Ingram and Rogan 2002, Bräger et al. 2003) and that habitat selection differs by season (Irvine et al. 1981, McFee et al. 2014). Therefore, I hypothesized that high-use areas were influenced by depth and that high-use areas would differ by season for the St. Catherine's population.

Methods

Study Area

This study involved previously conducted photo-identification surveys along the Georgia coast. The study area included tidal waters and embayments around St. Catherine's Island, Georgia (e.g., North and South Newport Rivers, Johnson Creek,

Walburg Creek, Sapelo Sound, and St. Catherine's Sound; Figure 3.1). The stock of focus was an undefined stock between the Southern Georgia Estuarine System Stock and the Northern Georgia/Southern South Carolina Estuarine System Stock, which I will refer to as the "St. Catherine's population" (Waring et al. 2009).

Field Data Collection

The sighting data used in this study were collected by the Georgia Dolphin Ecology Program (GDEP) from boat-based photo-identification surveys from 2011-2013 as part of a long-term study to assess the ecology and behavior of bottlenose dolphins near St. Catherine's Island, Georgia. Two-day surveys were conducted twice per month as weather permitted. Surveys were categorized by season (i.e., winter = December, January, February; spring = March, April, May; summer = June, July, August; fall = September, October, November).

GDEP surveys were performed by 2-4 crew members aboard a 5.8 m skiff with a 70 horsepower engine. Survey speed was 24 km per hour until a dolphin sighting occurred. A Nikon D90 DSLR with a 75-300 mm NIKKOR telephoto zoom lens was used to photograph dorsal fins. Data collected at the time of sighting included date, time of day, spatial coordinates, total number of animals, number of calves, behavior, and environmental conditions.

Habitat Data

I used the Southeast Atlantic United States CRM to obtain topographic and bathymetric data for the St. Catherine's Island area (NGDC 1999). Topographic and

bathymetric data sources for the CRM include: NGDC's National Ocean Service hydrographic surveys, multibeam and trackline bathymetry, United States Geological Survey, and digital elevation models (NGDC 1999). The vertical accuracy of the CRM is at best 1 m. The differences between various vertical datums (e.g., Mean Sea Level, Mean Lower Low Water, Mean High Water, and North American Vertical Datum of 1988) are less than 1 m, meaning these datums can be used interchangeably (Barry Eakins, NGDC, personal communication). Because the vertical datums relate to depth and some are used to create navigational charts (e.g., Mean Lower Low Water; National Oceanic and Atmospheric Administration Office of Coast Survey 2015), I used the CRM as a proxy for depth.

Using ArcGIS 10.2.2 (ESRI 2014), I imported the CRM ASCII file of the study area as a raster layer and defined the layer's coordinate systems. I also imported coordinate data from a spreadsheet to create a shapefile of all sighting event locations. I set the extent of the raster layer to the same extent as the sighting locations layer. Finally, I exported the raster file to an ASCII file to be used for analyses within program R (R Core Team 2014).

Data Analysis

I used Poisson point process models (PPM) in package spatstat (Baddeley and Turner 2005) within program R (R Core Team 2014) to determine if high-use areas differed by season and depth. To prepare the data for point process model analysis, I transformed the point data from each season from comma-separated values spreadsheet files (.csv) to point pattern objects using package spatstat. I created a raster object from

the CRM ASCII grid with package Raster (Hijmans 2015) and transformed the raster into an image object using package geostatsp (Brown 2015). I excluded land habitat from the CRM (i.e., values > -1 were excluded) and plotted the CRM image object and the point pattern object for each season to ensure that the data lined up correctly. Using package spatstat, I created a PPM for each season, with the point pattern object as the pattern term, the CRM image object as the trend and covariate term, and Poisson process as the interaction term. I used the plot and predict functions to visualize a density (sighting events/km²) surface map for each season.

Results

A total of 717 dolphin sighting events occurred from 2011-2013 for the St. Catherine's population. Of these sightings, 114 occurred during winter, 196 occurred during spring, 241 occurred in summer, and 166 occurred in fall (Figure 3.2).

Depth had a significant effect on dolphin distribution in winter, spring, summer, and fall (Table 3.1). The model for each season indicated significance of depth on sighting events, as the confidence intervals around the estimated coefficients did not include zero. During winter, the highest predicted density was 1.14 (95% CI = 0.80-1.50) events/km² and occurred at a depth of -8.3 m (Figures 3.3 and 3.4). The highest predicted density for spring was 2.05 (95% CI = 1.56-2.66) events/km² and occurred at -9.5 m (Figures 3.3 and 3.4). For summer, the highest predicted density was 1.85 (95% CI = 1.50-2.21) events/km², occurring at -6.2 m (Figures 3.3 and 3.4). The highest predicted density for fall was 1.31 (95% CI = 0.96-1.71) events/km², occurring at -8.4 m (Figures 3.3 and 3.4).

Discussion

Results indicated that the number of dolphin sighting events was significantly related to depth; generally, sighting events decreased as depth increased. Similar studies have also found that dolphins show a depth preference (Irvine et al. 1981, Ballance 1992, Ingram and Rogan 2002, Bräger et al. 2003, Torres et al. 2005, Bailey and Thompson 2009). An aerial-conducted study along the United States mid-Atlantic coast also found that dolphin sightings occurred more in shallow waters, and sightings decreased as depth increased (Torres et al. 2005). In Florida, Irvine et al. (1981) found that dolphins prefer shallow waters (< 3 m). Dolphin sightings in Scotland were also significantly related to shallow areas, as more dolphins were observed near shore where the slopes were less steep (Bailey and Thompson 2009). Similar studies have proposed that depth selection is most likely influenced by prey distribution (Irvine et al. 1981, Ingram and Rogan 2002). Dolphins are likely to select areas with high prey concentration and habitats that will aid in foraging activities (Ballance 1992, Ingram and Rogan 2002). Therefore, high-use areas for the St. Catherine's population may reflect depths at which it is easiest to forage.

The St. Catherine's population also showed a seasonal shift in habitat selection. Dolphins used shallow areas throughout estuarine rivers in summer, while using deep areas in sounds and mouths of estuarine rivers in spring. Seasonal shifts in dolphin habitat selection have been previously documented in Georgia (Balmer et al. 2013), Florida (Waples 1995), Texas (Maze and Würsig 1999), and in New Zealand for Hector dolphins (*Cephalorhynchus hectori*; Bräger et al. 2003). Shifts in habitat selection for the St. Catherine's population could be related to prey (Irvine et al. 1981, Ballance 1992, Maze and Würsig 1999, Ingram and Rogan 2002, Balmer et al. 2013), reproductive

opportunities (Gubbins 2002, McFee et al. 2014), or presence of migratory dolphins (Balmer et al. 2013).

Seasonal shifts in prey distribution are likely a direct cause in dolphin habitat selection (Irvine et al. 1981, Ballance 1992, Ingram and Rogan 2002, Balmer et al. 2013). Possible dolphin prey, such as blue crab (*Callinectes sapidus*), menhaden (*Brevoortia tyrannus*), and spot (*Leiostomus xanthurus*), have seasonal movements (Rogers and Van Den Avyle 1983, Tankersley et al. 1998, Young and Phillips 2002). For example, blue crab mating season occurs from spring to fall. When female crabs become inseminated, they emigrate from estuarine rivers to mouths of estuaries and sounds to spawn (i.e., deeper areas; Tankersley et al. 1998). Dolphins following prey, such as blue crabs, to deeper areas in spring could explain the result of the St. Catherine's population selecting deep waters in spring. Therefore, prey movement is a likely cause of the St. Catherine's population exhibiting seasonal habitat selection.

Seasonal shift in dolphin habitat selection might also be influenced by reproductive opportunities. Dolphins generally have a seasonal mating season (Robeck et al. 1994), beginning in spring and ending in fall (Thayer et al. 2003, McFee et al. 2006). In South Carolina, McFee et al. (2013) found that spring sightings of neonates occurred within estuarine rivers, while fall sightings were coastal and within the Charleston Harbor. Dolphin mothers with neonates might be selecting habitats that offer safety from predators or habitats with high prey availability (Mann et al. 2000). Therefore, the St. Catherine's population could be selecting deep waters with high prey availability for mothers and young in spring, while selecting shallow waters in summer for protecting young from predators.

Presence of transients (i.e., possible migratory dolphins only seen once throughout the study period) and seasonal residents (i.e., dolphins occurring in the area in the same season for multiple years, but not consecutive season) could have artificially influenced the seasonal shift in habitat selection (Zolman 2002, Speakman et al. 2010). While transient entry near St. Catherine's Island is not yet well understood (Chapter 2), migration is believed to begin in spring and end in fall (Fertl 1994, Zolman 2002, Torres et al. 2005), which causes increases in dolphin abundance within a study area (Shane 1980, Weigle 1990, Fertl 1994, Torres et al. 2005, Zolman 2002, Balmer et al. 2008). Migratory dolphins entering the study area could be the cause of higher density estimates in spring and summer in comparison to winter and fall (Balmer et al. 2013). Migratory dolphins are also likely the cause of higher predicted densities occurring in the sounds and mouths of estuarine rivers in spring, as migratory dolphins use the habitat differently than residents (i.e., dolphins occurring in the area year-round; Zolman 2002, Balmer et al. 2013). Balmer et al. (2013) found that during peaks in abundance estimates off the Georgia coast, dolphins with low site-fidelity (i.e., migratory dolphins) were found in larger tributaries, while dolphins with high site-fidelity (i.e., residents) were sighted with high densities across all tributaries. Therefore, habitat selection shifting towards sounds and mouths of estuarine rivers in spring, as well as higher predicted densities occurring in spring and summer, indicate that migratory dolphins likely overlap with the St. Catherine's population in spring and summer.

Management Implications

The goal of this study was to determine characteristics of high-use areas and if high-use areas differed by season for the St. Catherine's dolphin population. The distribution of the St. Catherine's population was correlated with depth and showed a seasonal shift in habitat selection. Knowing environmental variables that influence dolphin distribution is important for gaining insight into critical habitat. Wildlife managers could use this information to moderate coastal development that might negatively impact important habitat that the dolphins need for survival, as well as evaluate the impacts on population viability from coastal development.

Future studies should evaluate the influences of other environmental data (e.g., sea surface temperature, bathymetric variables, and distribution and abundance of prey if possible) on dolphin distribution using PPMs. In addition, it would be useful to determine what habitats residents, seasonal residents, and transients use and if the habitats differ among the 3 groups. This distinction would allow identification of critical areas for resident dolphins, as well as determine if migratory dolphins use the same habitats, and therefore interact, with resident dolphins. Determining if migratory dolphins interact with resident dolphins is important in monitoring the health of resident dolphins as migratory dolphins move through the area. Using PPMs will be a useful tool in providing insight into critical habitats and mitigating coastal development, recreation, and fisheries near critical habitats.

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Table 3.1. Results of Poisson point process model, including coefficient estimates (Estimate), standard errors (S.E.), 95% confidence intervals (CI95.lo and CI95.hi), Z significance test results, and Z values, used to determine if depth (crm2) and quadratic depth terms (I(crm2^2)) had a significant effect on distribution of bottlenose dolphin sighting events (Intercept) for each season near St. Catherine’s Island, Georgia, 2011-2013.

Season	Coefficients	Estimate	S.E.	CI95.lo	CI95.hi	Ztest	Zval
Winter	(Intercept)	-2.311	0.317	-2.933	-1.689	***	-7.286
	crm2	-0.589	0.121	-0.826	-0.353	***	-4.880
	I(crm2^2)	-0.036	0.010	-0.055	-0.016	***	-3.578
Spring	(Intercept)	-1.673	0.236	-2.134	-1.211	***	-7.102
	crm2	-0.501	0.087	-0.672	-0.330	***	-5.753
	I(crm2^2)	-0.026	0.007	-0.040	-0.013	***	-3.810
Summer	(Intercept)	-1.323	0.217	-1.749	-0.897	***	-6.086
	crm2	-0.631	0.097	-0.820	-0.441	***	-6.520
	I(crm2^2)	-0.051	0.009	-0.070	-0.033	***	-5.475
Fall	(Intercept)	-1.321	0.231	-1.772	-0.869	***	-5.728
	crm2	-0.377	0.095	-0.563	-0.191	***	-3.977
	I(crm2^2)	-0.022	0.008	-0.038	-0.007	**	-2.782

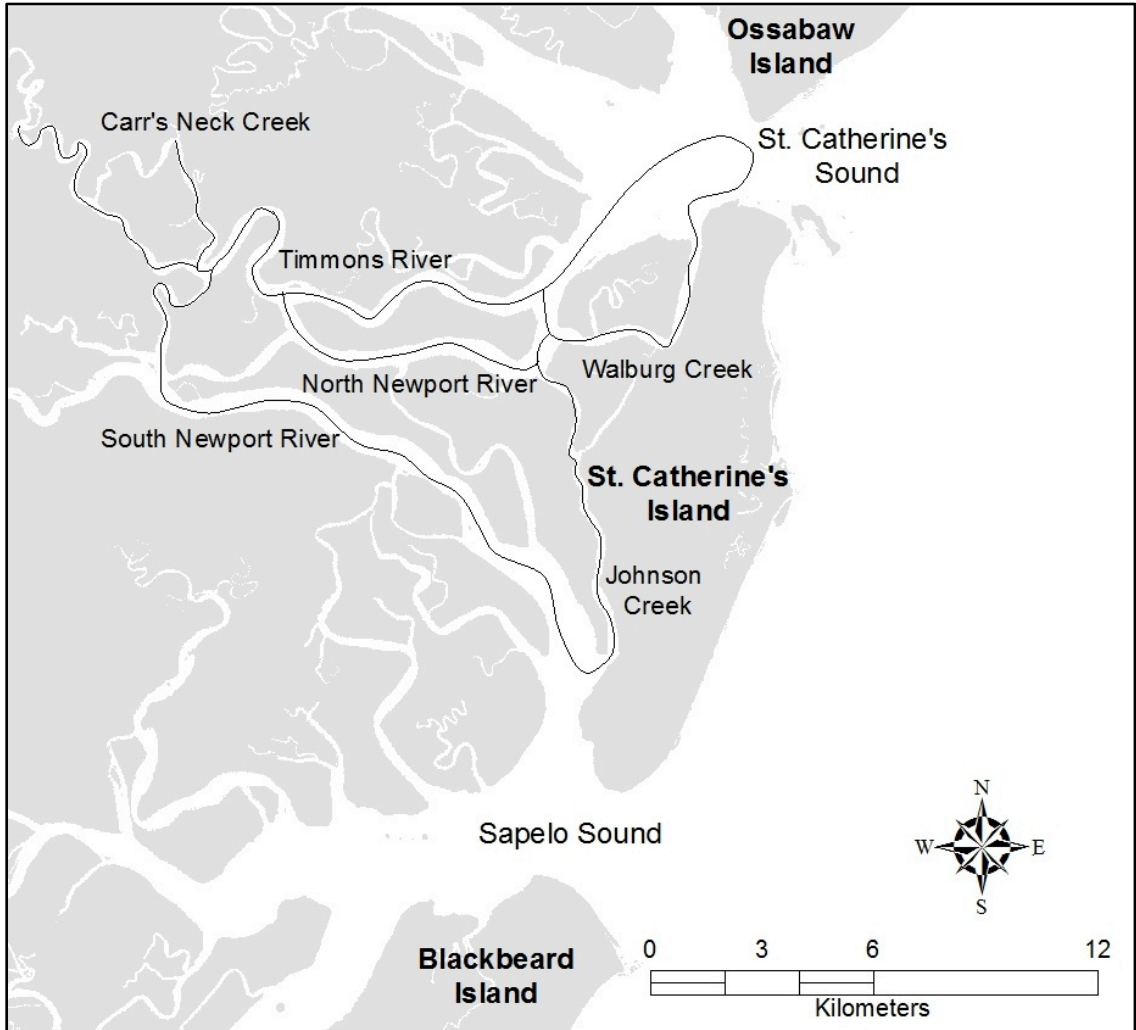


Figure 3.1. Survey transects (black lines) conducted by the Georgia Dolphin Ecology Program to obtain bottlenose dolphin photo-identification and sighting locations data near St. Catherine's Island, Georgia, 2011-2013.

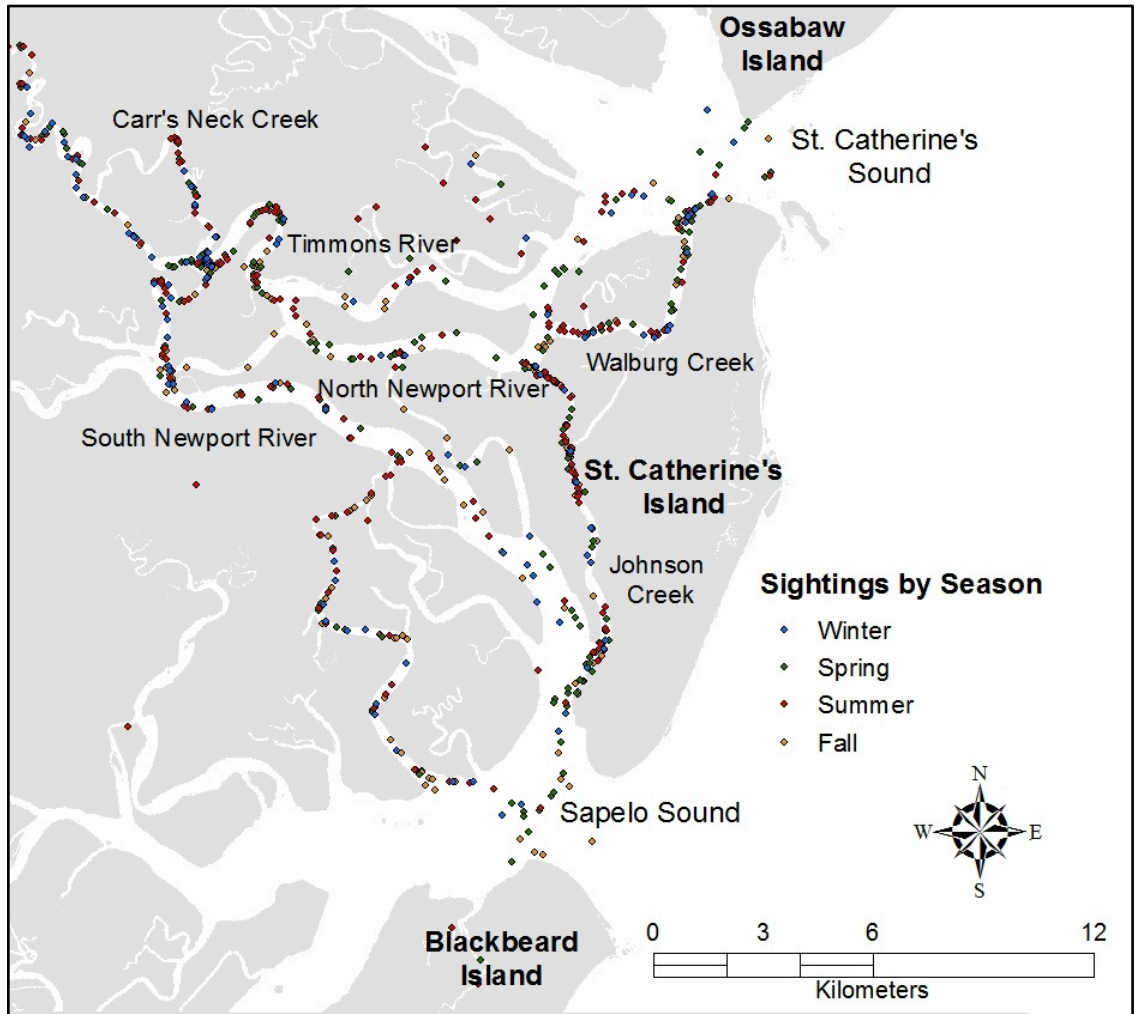


Figure 3.2. Sighting events of bottlenose dolphins during winter, spring, summer, and fall seasons near St. Catherine's Island, Georgia, 2011-2013.

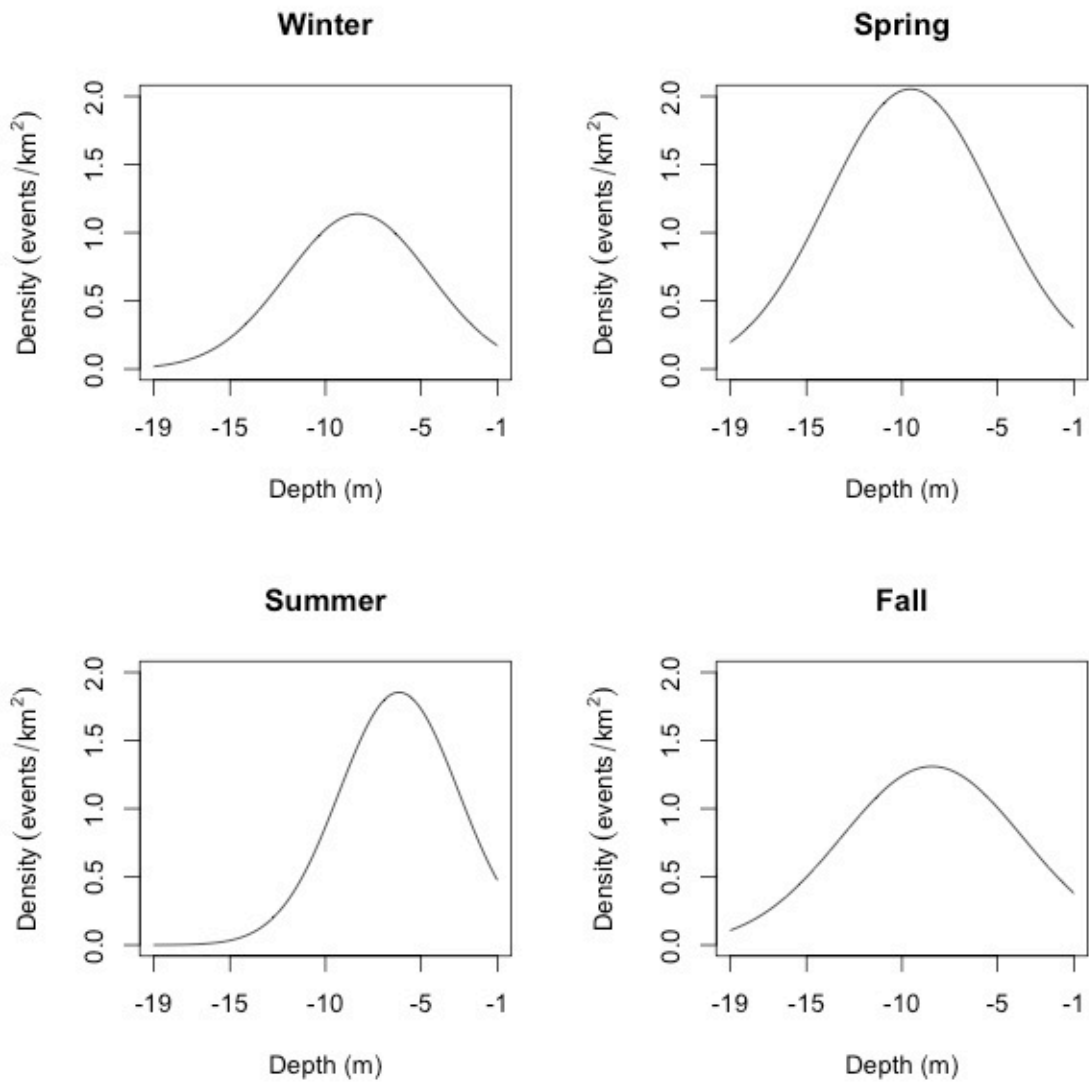


Figure 3.3. Predicted bottlenose dolphin density (sighting events/km²) at each depth (m) for winter, spring, summer, and fall seasons near St. Catherine’s Island, Georgia, 2011-2013.

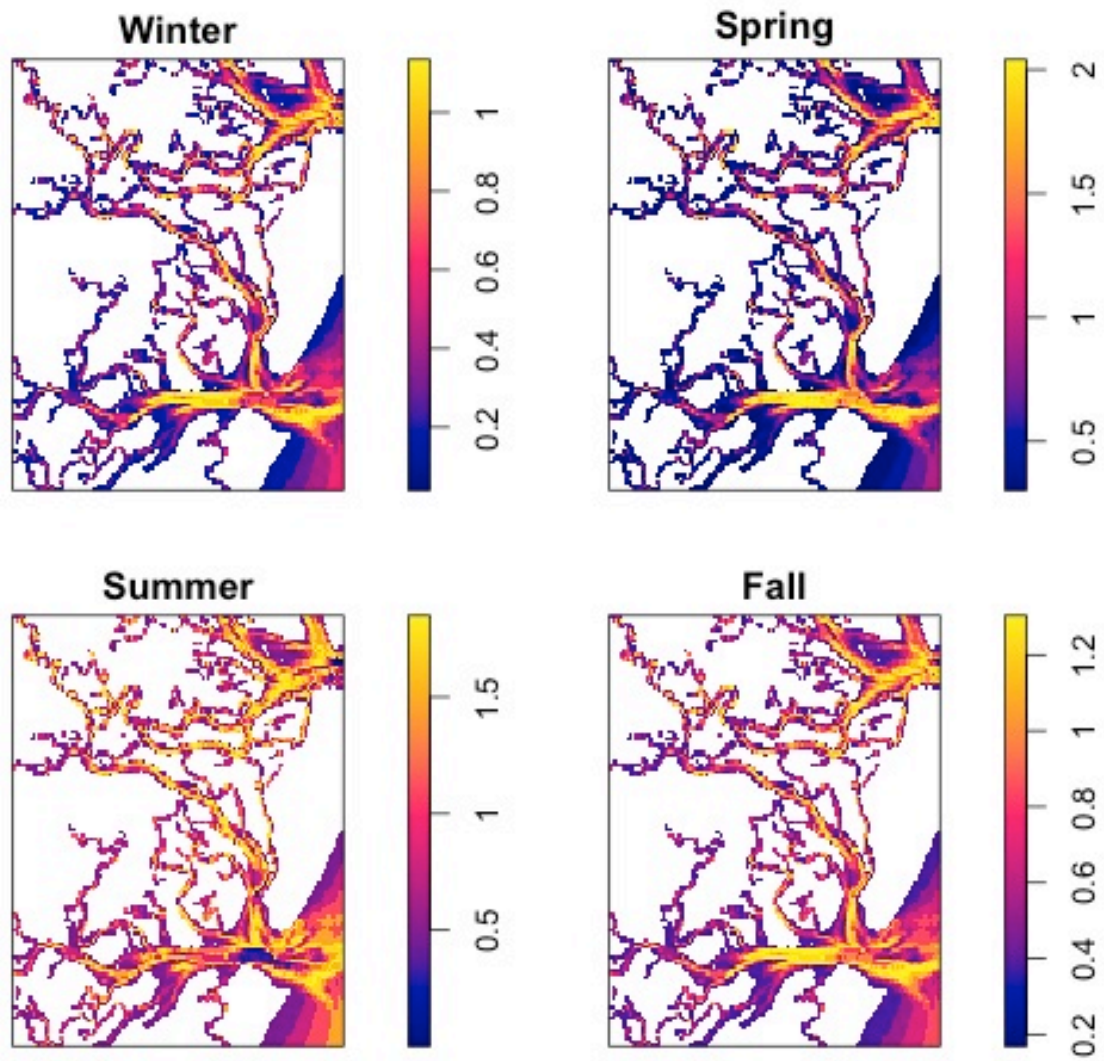


Figure 3.4. Predicted bottlenose dolphin density (sighting events/km²) for winter, spring, summer, and fall seasons near St. Catherine's Island, Georgia, 2011-2013.

CHAPTER 4

CONCLUSIONS AND KEY FINDINGS

Migration patterns and habitat selection information for bottlenose dolphins of the southeastern Atlantic coast is needed for future resident population monitoring and habitat management. Bottlenose dolphins in southeastern estuaries are exposed to natural and anthropogenic factors, and the impacts of these factors are unknown largely because of insufficient abundance and habitat selection data (Waring et al. 2009, Waring et al. 2014). The purpose of this study was to identify factors related to bottlenose dolphin seasonal migration along the South Carolina and Georgia coasts and to describe high-use areas near St. Catherine's Island, Georgia.

Migratory dolphins often overlap with resident dolphins, making accurate abundance estimates difficult to achieve (Zolman 2002, Read et al. 2003, Waring et al. 2009, Speakman et al. 2010, Conn et al. 2011, Bills and Keith 2012). Knowledge of environmental factors that may be related to seasonal abundance fluctuations and migratory pulses is needed to obtain accurate resident abundances. My specific objective was to determine if changes in water quality variables (i.e., water temperature, salinity, pH, dissolved oxygen, and turbidity) were related to seasonal changes in abundance estimates and temporary emigration probabilities along the South Carolina and Georgia coasts. I estimated seasonal abundance and temporary emigration using Robust Design models (Kendall 2014) with and without water quality variables for dolphins observed

near Charleston Harbor, South Carolina. I also estimated seasonal abundance using closed population capture-recapture models (Lukacs 2015) for dolphins observed near St. Catherine's Island, Georgia and used simple linear regression models to determine which variable was most significant in explaining the abundance estimates.

My results indicated that the Charleston Harbor population exhibited a seasonal trend in abundance and temporary emigration with low estimates in winter, increasing in spring, high estimates in summer, and decreasing in fall. This abundance and temporary emigration trend supports the notion of resident (i.e., those that remain in the study area year-round) and seasonal resident (i.e., those that are seen in the same season for multiple years, but not consecutive seasons) dolphins present in the area (Fertl 1994, Zolman 2002, Speakman et al. 2010). The results also indicated that Charleston Harbor dolphins exhibited Markovian temporary emigration (i.e., the probability of encountering a dolphin during the current sampling period depended on its presence or absence in the previous sampling period), and water temperature best explained the trend in temporary emigration probabilities (Torres et al. 2005, Balmer et al. 2008, Speakman et al. 2010, Smith et al. 2013, Kendall 2014). Seasonal abundance estimates and temporary emigration probabilities indicate that migratory dolphins (i.e., seasonal residents and transients) overlap with the Charleston Harbor dolphins in spring through fall, and the movement of migratory dolphins is related to water temperature.

Seasonal abundance estimates for St. Catherine's dolphins varied from year to year, but confirmed a seasonal variation in abundance estimates (Fertl 1994, Zolman 2002, Speakman et al. 2010). The water quality variable that best explained variation in abundance estimates was salinity. The validity of salinity as a migration cue has not been

evaluated in previous studies. However, possible dolphin prey, such as blue crab (*Callinectes sapidus*), menhaden (*Brevoortia tyrannus*), and spot (*Leiostomus xanthurus*), are influenced by salinity (Rogers and Van Den Avyle 1983, Tankersley et al. 1998, Young and Phillips 2002). Salinity could be indirectly related to seasonal fluctuations of dolphin abundance estimates and temporary emigration probabilities, as they are following their prey being influenced by salinity. Seasonal abundance estimates indicate the presence of residents and seasonal residents, supporting the idea that migratory dolphins likely overlap with the St. Catherine's population in spring, summer, and fall seasons.

Both datasets showed evidence of possible transients in the study area during spring, summer, and fall seasons. The presence of possible transients, along with abundance estimates and temporary emigration, further support the finding that migratory dolphins are overlapping with resident dolphins. Possible transient dolphins could have violated key assumptions and biased estimates for Robust Design (RD) and closed-population capture-recapture models. Therefore, transient dolphins need to be accounted for when estimating resident abundance.

Identification of high-use areas can provide insight into characteristics of habitats that are essential for species survival (Redfern et al. 2006). Poisson point process models (PPM) can be used to analyze patterns of dolphin sightings and evaluate correlations between dolphin density and habitat covariates (Baddeley and Turner 2005) to model the expected count of dolphin sightings per unit area (Renner and Warton 2013). To better understand bottlenose dolphin habitat selection along the Georgia coast, my specific objectives were to determine if high-use areas are significantly affected by depth based

on the distribution of dolphin sightings and to determine if high-use areas differed by season for dolphins near St. Catherine's Island, Georgia

My results indicated that depth had a significant effect on dolphin distribution in winter, spring, summer, and fall. Similar studies have also found that dolphins show a depth preference (Irvine et al. 1981, Ballance 1992, Ingram and Rogan 2002, Bräger et al. 2003, Bailey and Thompson 2009). The St. Catherine's population also showed a seasonal shift in habitat selection (Waples 1995, Maze and Würsig 1999, Bräger et al. 2003, Balmer et al. 2013), which could have been caused by prey distribution (Irvine et al. 1981, Ballance 1992, Ingram and Rogan 2002, Balmer et al. 2013), reproductive opportunities (Gubbins 2002, McFee et al. 2006, McFee et al. 2014), or presence of migratory dolphins (Balmer et al. 2013).

Future studies regarding factors related to migration should use a sampling design that will allow for RD analyses. Temporary emigration probabilities from RD models will allow evaluation of migration patterns through the study area. Using RD models from long-term photo-identification studies and primary environmental data could lead to the ability to predict when a migratory pulse is likely to occur. Predicting migratory pulses could lead to accurate abundance estimates, which is important for future population monitoring and accurately assessing the impacts of natural and anthropogenic factors on resident dolphins. Future studies should also consider incorporating models (e.g., Jolly-Seber; Schwarz and Arnason 2015) that will estimate other demographic parameters, such as recruitment. Calves and young dolphins were excluded from analyses by default because of their lack of markings, but should be considered in future population parameter modeling to obtain accurate resident abundance estimates.

Future habitat selection studies should evaluate the influences of other environmental data (e.g., sea surface temperature, bathymetric variables, and distribution and abundance of prey if possible) on dolphin distribution using PPM. In addition, it would be useful to determine what habitats residents, seasonal residents, and transients use and if the habitats differ among the 3 groups. This distinction would allow identification of critical areas for resident dolphins, as well as determine if migratory dolphins use the same habitats, and therefore interact, with resident dolphins. Determining if migratory dolphins interact with resident dolphins is important in monitoring the health of resident dolphins as migratory dolphins move through the area. Using PPMs will be a useful tool in providing insight into critical habitats and mitigating coastal development, recreation, and fisheries near critical habitats.

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Appendix

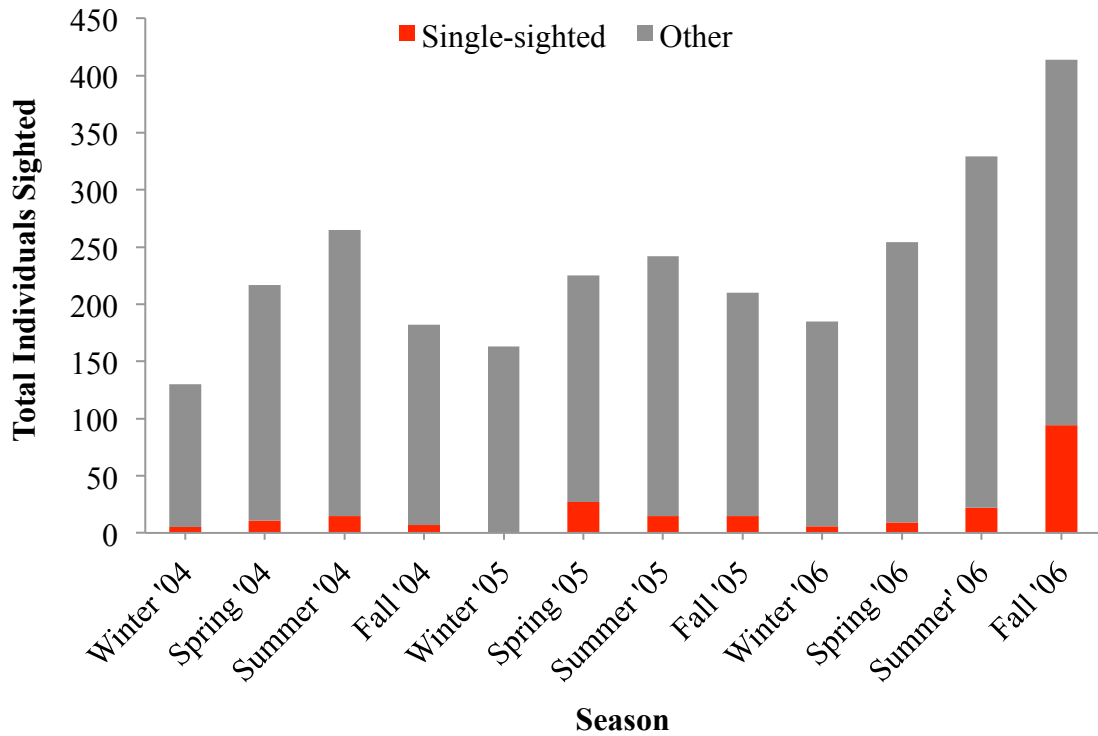


Figure 2.7. Total number of bottlenose dolphin sightings in each season categorized as single-sighted individuals (i.e., possible transients) and other individuals (i.e., seasonal residents or residents) for the Charleston Harbor population, South Carolina, 2004-2006.

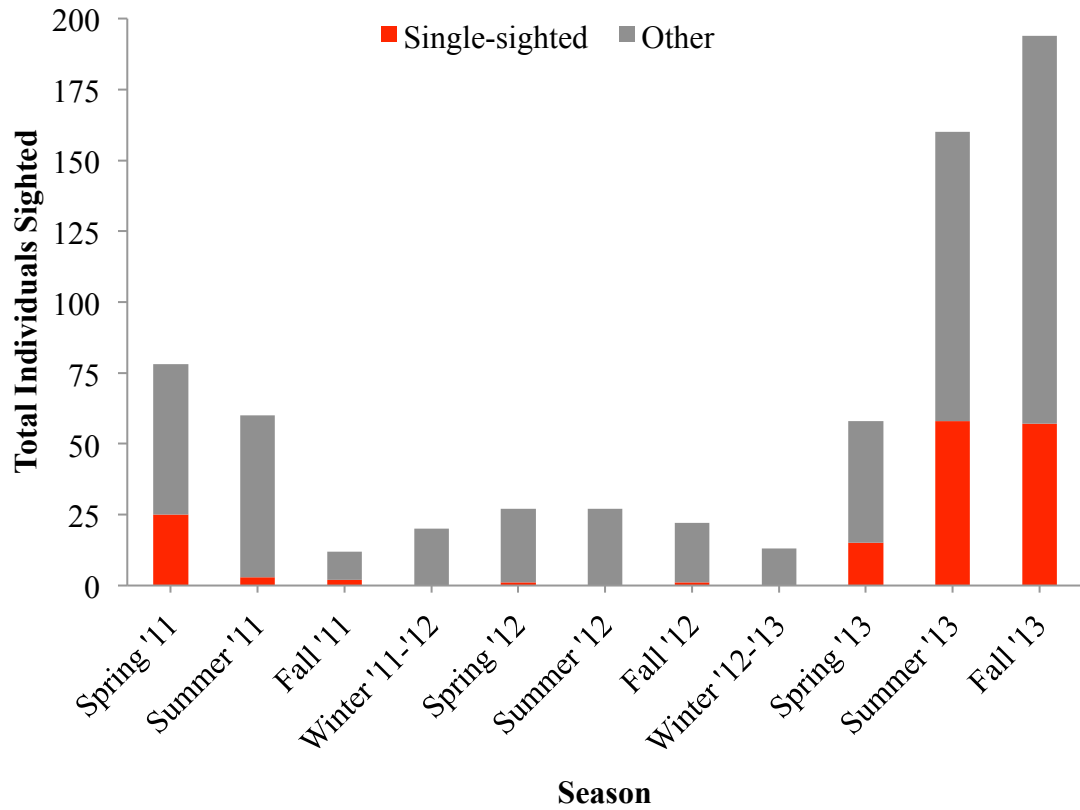


Figure 2.8. Total number of bottlenose dolphin sightings in each season categorized as single-sighted individuals (i.e., possible transients) and other individuals (i.e., seasonal residents or residents) for the St. Catherine's population, Georgia, 2011-2013.