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Distribution and Social Structure of an Estuarine Bottlenose Dolphin (Tursiops truncatus) Population in Northern South Carolina

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DISTRIBUTION AND SOCIAL STRUCTURE OF AN ESTUARINE BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) POPULATION IN NORTHERN SOUTH CAROLINA

by

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Submitted in Partial fulfillment of the

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For my mother, Linda, father, Ron, and sister, Elizabeth, who have always instilled a sense of confidence in me and constantly encourage me to reach my potential

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Abstract

Information regarding habitat preference of apex predators may pinpoint areas dense in resources such as prey species. Knowledge of how animals use their habitat can enable the classification and targeted management of important habitat features. This study was conducted to determine the distribution and social structure of an inshore population of bottlenose dolphins within the North Inlet-Winyah Bay estuary in northern South Carolina. Photo-identification surveys were conducted along defined transect routes. Home ranges of individual dolphins were calculated using the minimum convex polygon method and the fixed kernel density method using Geographic Information System (GIS) software. Mean group sizes and coefficients of association were compared between warm and cold seasons. Coefficients of association were calculated using the half weight index. Additionally, these same social parameters were compared between dolphins using only North Inlet, those using only Winyah Bay, and those using both systems. Surveys were performed during the warm months (221 hours of survey time from May through October) and during the cold season (52 hours of survey time from December through February). The 2011-2012 population estimate for the North Inlet-Wnyah Bay population was 84, and fewer dolphins were present in the North Inlet-Winyah Bay estuary during the cold months than during the warm months. The majority of the dolphins in this study used both North Inlet and Winyah Bay. However, three individuals were sighted only in North Inlet, and 38 individuals were sighted only in

Winyah Bay. Group sizes were larger in the warm season than the cold season. Dolphins that had at least 10 independent sightings associated non-randomly, and individuals in the population formed distinct communities with overlapping ranges. The mean coefficient of association was 0.24 for all dolphins with at least 10 sightings, and the associations were weaker than in most other studied populations. However, when determining mean coefficients of association within North Inlet transects (0.48) and Winyah Bay transects (0.34), the associations were similar those observed in other studies. The mean home range was 32.79 km^2. Home ranges were larger in the warm season than the cold season. While the kernel density method, compared to the Minimum Convex Polygon method, seems to more accurately estimate the home range of dolphins in open water systems, the small creeks in North Inlet coupled with the clipping feature in ArcGIS make the minimum convex polygon method just as accurate because dolphins had limited travel routes within the creeks.

Introduction

Estuarine habitats are decreasing in size and quality due to a suite of factors including climate change and coastal development (Van Dolah et al. 2008; Lotze et al. 2006). This habitat degradation can alter population sizes and ranging patterns of various species, affecting entire ecosystems. Knowledge of a population's distribution and social network can provide insight to the population's overall structure including its social organization.

To determine the distribution of a population, home ranges of the individuals are calculated. Burt (1943) described home range as the area encompassed by an animal during its normal activities. The most common method for calculating home ranges is the Minimum Convex Polygon method, which uses sighting positions as vertices to construct the smallest possible polygon to represent the animal's home range. With the minimum convex polygon method, the home range estimates are more accurate when a larger sampling area is covered and with a greater number of recaptures (Anderson 1982; Börger et al. 2006). Probability-based kernel methods can be used for estimating the extent to which animals occupy specific areas of the habitat (Worton 1989) by estimating the number of individuals in a particular area. These estimates are useful because they describe the overall distribution of the population and provide gradients to describe areas that are heavily used (Ingram and Rogan 2002; Rayment et al. 2009), thus enabling inferences to be made regarding the habitat preferences (Benhamou and Corélis 2010). The kernel density is estimated by using the utilization distribution, measured by different isopleths, which depicts how areas are used relative to each other (Sellas et al. 2005).

Several factors contribute to the total area an individual uses and how it partitions its time within its habitat. The availability of resources, population density, mate availability, body size (Gubbins 2002a), and predator avoidance (Yeates and Houser 2008) all dictate habitat preferences. The distribution of habitat sections most frequently used, called "core areas" (Oshima et al. 2010; Owen et al. 2002; Silva et al. 2008), of a population can often be used to indicate the abundance of resources required to support the population and how these resources are dispersed within the habitat (Ingram and Rogan 2002). Abundance and distribution of prey generally have the greatest influence on the size of home ranges of apex predators (Sandell 1989; Silva et al. 2008). Furthermore, top predator species commonly form small populations with larger home ranges because of intraspecies competition for prey items (Johnson et al. 2009). However, the cumulative effects of multiple factors determine the full extent of the home range (Yeates and Houser 2008). Estimates of population size and structure of an ecosystem's top predators help determine the top down control of an ecosystem (Heithaus et al. 2007).

Bottlenose dolphins (*Tursiops truncatus*) are top predators in marine environments. Thus, knowledge of their population structures and ranges could provide valuable insight into the environmental changes that affect entire ecosystems because marine mammals are sentinel species (Moore 2008). Bottlenose dolphins inhabit inshore waters (including estuaries), nearshore (or coastal) waters, and offshore waters; generally, offshore populations are larger than the nearshore and inshore populations (Zolman 2002). Populations are often separated according to different habitat features (Quérouil et al. 2007; Sellas et al. 2005), and the distinct characteristics of different estuaries could promote genetic differentiation and behavioral specialization among inshore dolphins (Sellas et al. 2005).

Rosel et al. (2009) suggested that highly structured, distinct inshore populations with limited gene flow to other populations could be the general state of bottlenose dolphin dispersal, especially for populations in bays and estuaries. Highly structured habitats, such as salt marshes and bays, often cause the inshore stocks to break up into small populations (Sellas et al. 2005). While offshore bottlenose dolphins often have large home ranges with little site fidelity and with seasonal migrations, nearshore and inshore dolphins usually have smaller home ranges, and inshore dolphins tend to remain in their specific bay or estuarine habitat (Gubbins 2002a; Zolman 2002; Krützen et al. 2004; Torres et al. 2005; Mancia et al. 2010). However, some inshore animals may expand or change their home ranges with changing seasons. Some inshore locations exhibit lower abundances during the cold months, as noted in the Doubtful Sound, New Zealand (Williams et al. 1993) and in the Stono River in Charleston, South Carolina (Zolman 2002).

Although many inshore bottlenose dolphins exhibit permanent or seasonal residency, these ranging patterns can only exist when an adequate abundance of prey species is available. Habitats with fewer or less dense food sources result in larger dolphin home ranges (Silva et al. 2008). The home ranges of small cetaceans are likely so dependent on food sources because these species have a high metabolic rate and limited room for energy storage (Silva et al. 2008; Rayment et al. 2009). Thus, the core areas of estuarine dolphins' habitat can reveal information about their prey species. Additionally, abundance estimates for these prey species can be used as an indicator of the habitat's carrying capacity for dolphins, providing further information for the development of new management procedures.

When dolphins are limited by prey availability, individuals in a localized population may become transient (Silva et al. 2008). However, the prey species present vary between inshore and nearshore habitats (Mead and Potter 1995; Torres et al. 2003), which may discourage estuarine dolphins from foraging in coastal waters. The inshore, nearshore, and offshore bottlenose dolphins are generally distinguished as ecotypes, and these distinct ecotypes differ based on morphologies, hemoglobin levels and erythrocyte counts (Duffield et al. 1983), genetic markers, and prey items found in stomachs (Klatsky et al. 2007; Torres et al. 2007). These differences have occurred as a result of divergent populations forming in the distinct inshore, nearshore, and offshore habitats, such that the characteristics of the dolphins in these populations are adapted to their particular habitats (Hoelzel 1998; Klatsky et al. 2007). However, in some locations, inshore dolphins have been reported to travel out of their estuarine habitats during either the cold season or the warm season (Maze 1997; Zolman 2002).

The seasonal changes in residency observed in some estuaries (Maze 1997; Zolman 2002) could complicate social networks. Several factors, such as mating strategies (Lusseau et al. 2003), common ranging patterns (Gubbins 2002b), and foraging habits (Lusseau et al. 2003), can affect the association patterns of bottlenose dolphins. An effective method to determine the level of association between two individuals is to construct an association index (Cairns and Schwager 1987). By analyzing the varying associations between each dyad, an understanding of the overall social structure for the population can be obtained. Many studies have reported non-random associations among individuals in bottlenose dolphin populations (Möller et al. 2001; Augusto et al. 2011).

Male dolphin groups tend to arise for mating purposes (Lusseau et al. 2003). Females that have strong associations are usually genetically related, but some non-related females associate to improve breeding (Wiszniewski et al. 2009b) or hunting (Lusseau et al. 2003) success. Generally, when males and females form associations, that behavior is reproductively driven, but mixed-sex groups also form for non-reproductive reasons (Lusseau et al. 2003). Furthermore, Gibson and Mann (2009) reported that, in several study areas, dolphins seem to form long-term (more than one year) alliances, in which dolphins are consistently sighted together for several years. Alliances are common to Shark Bay, Western Australia, in which non-kin male groups (Möller et al. 2001) ranging from two to four individuals associate most strongly with each other and actively pursue females as a team (Connor et al. 1992). In the Doubtful Sound, Lusseau et al. (2003) determined that the pairs with stronger associations than expected were between two males, and the pairs with weaker associations than expected were between individuals of the opposite sex. Similarly, in the coastal waters of the Bahamas, Rogers et al. (2004) found that while individuals of the same sex tended to form yearlong associations more often than members of the opposite sex, but very few associations were long term.

Most studies investigating the social structure of bottlenose dolphins study coastal (nearshore) populations (Rogers et al. 2004). Sellas et al. (2005) defined coastal populations as those using the water from the shore to 12 km seaward. Most coastal bottlenose dolphin populations exhibit a fission-fusion social structure, where groups of varying sizes are formed and reformed and members may join for a few days or even a few hours (Augusto et al. 2011; Gibson and Mann 2009; Krützen et al. 2003; Lusseau et al. 2003; Lusseau et al. 2006; Möller et al. 2001; Parsons et al. 2003; Quintana-Rizzo and Wells 2001; Urian et al. 2009; Wiszniewski et al. 2009b). Fission-fusion societies often develop from foraging patterns (Wiszniewski et al. 2009b), and associations can change depending on the season (Gubbins 2002b).

Different habitat types have also been found to assist in community formation (Wiszniewski et al. 2009b). While coastal dolphins associate for hours or days, estuarine dolphins associate with conspecifics with a greater degree of fidelity and for longer durations (Quinata-Rizzo and Wells 2001). The strength of social bonds depends upon the benefits of association. In some cases, resource allocation is enhanced with a strong social network, as older members of the population pass information about areas rich in prey to the younger individuals (Lusseau et al. 2003). The variability of prey distribution and abundance in estuarine systems can cause the social network of estuarine dolphins to be unique from other habitats (Quintana-Rizzo and Wells 2001).

Distinct communities are sometimes present within a population. As defined by Wells, (1986), a community refers to a group of dolphins inhabiting the same areas and interacting with others in that group to a greater degree than with the rest of the population. Gubbins (2002b) found separate communities present within a South Carolina estuarine population, and the dolphins in this population maintained a distinct community from the transients that entered the habitat However, contrary to her hypothesis, Gubbins (2002b) found no significant difference in associations between seasons.

In northern South Carolina, a small population of estuarine dolphins inhabits the waters of the North Inlet estuary and Winyah Bay (Young and Phillips 2002), and nearshore coastal migratory dolphin populations use the adjacent coastal waters of the Atlantic Ocean. The North Inlet-Winyah Bay National Estuarine Research Reserve (NIWB) is connected to the Atlantic Ocean; thus dolphins in this estuarine population have the potential to disperse beyond the NIWB system. Furthermore, in North Inlet, both nekton abundance and species richness significantly drop in November compared to the spring and summer months (Allen et al. 2007), which could lead to decreased dolphin abundances during the cooler months each year. Allen et al. (2007) reported the colder months in North Inlet to have a mean temperature of 16 °C and 22 °C respectively in 1997 and 1998. The estuarine dolphins may or may not be interbreeding with individuals in the coastal population. If no interbreeding is occurring, behavioral and genetic effects of small populations would be more prominent and easy to detect because the estuarine population is quite small. Additionally, dolphins inhabiting the NIWB system may be further distinguished by the proportion of time spent in the North Inlet marsh creeks versus the larger Winyah Bay system.

This study is part of a larger study to provide information about the distribution and population structure of bottlenose dolphins inhabiting North Inlet and Winyah Bay. Home range and abundance data have been published for Northwestern Atlantic estuarine bottlenose dolphin populations (Zolman 2002; Gubbins 2002a), but most studies that investigate population structure focus on coastal populations, and little information is available about population structure in estuarine habitats and between estuarine and coastal waters in the southeastern United States (Rosel 2009). The objectives of this study were to determine 1) the seasonal variation in abundance of dolphins inhabiting the NIWB, 2) the distribution of NIWB bottlenose dolphins via calculating home range estimates and kernel densities, 3) if non-random associations were present in the NIWB population, 4) communities were present, and 5) if association patterns differed between the warm season and the cold season. I hypothesized that 1) a greater number of dolphins would be present in the NIWB system during the warm season compared to the cold season, which would cause differences in association patterns, 2) certain dolphins would only use North Inlet while others would limit their ranges to Winyah Bay forming a distinct North Inlet community and a Winyah Bay community, 3) NIWB dolphins would have home ranges confined within the NIWB system, 4) dolphins would display preferences for North Inlet and Winyah Bay, including specific sections within the creek system and bay, and 5) non-random associations would be present leading to distinct communities.

Materials and Methods

Study Site

North Inlet and Winyah Bay are located in northern South Carolina. North Inlet, at 33.3° N and 79.2° W, is a tidally dominated, vertically well-mixed estuary (Dame et al. 1986) composed of meandering tidal creeks and salt marshes (Kjerfve et al. 1991) and covers about 32.2 km^2. Winyah Bay, connected to and just south of North Inlet and covering 62 km^2, is a partially-mixed estuary with freshwater input from the Pee Dee, Black, and Waccamaw rivers (Schwing and Kjerfve 1980). North Inlet connects to Winyah Bay via a small, shallow bay, called Mud Bay (fig. 1). North Inlet, located within a National Estuarine Research Reserve, is considered the more pristine of the two estuaries, as Winyah Bay has been affected by many anthropogenic activities, such as construction of dams, jetties, dikes, and golf courses, and receives pollutant input carried by rivers feeding into the Bay from upstream agricultural areas (Goñi et al. 2003), and also receives pollutants from nearby steel and pulp mills (Schwing and Kjerfve 1980).

Photo-Identification Surveys

Transect surveys were conducted and photo-identification was performed to determine spatial patterns and association behavior of bottlenose dolphins. Dolphins were identified by their unique markings on their dorsal fins, which can be easily captured in photographs (Ingram and Rogan 2002). Photo-identification can be used to distinguish almost all resident members of a population (Wells and Scott 1990) though the effectiveness of this technique is limited by distance from the subject and weather conditions (Berrow et al. 1996). The posterior edge of the dorsal fin is especially likely to show identifiable markings (Ingram and Rogan 2002). Extensive photo-identification surveys have been conducted in North Inlet since 1998, but limited effort has been expended in Winyah Bay (R. Young, pers. comm.).

Survey efforts were divided between the warm season (May 17 through October 25 when water temperatures ranged from 21.3 °C to 33.0 °C) and the cold season (December 9 through February 26, when water temperatures ranged from 8.7 ° C to 16.3 °C). Surveys were also divided into North Inlet days and Winyah Bay days. Surveys in North Inlet were conducted from either a 5.5 m or 4.9 m aluminum johnboat, which proceeded at a speed of 10-12 kts (18-22 km/hr). In Winyah Bay, surveys were conducted from a 6.1 m fiberglass outboard vessel, which traveled at a speed of 12-16 kts (22-30 km/hr). Surveys were conducted along pre-defined transect routes in each system (Fig. 1), which were occasionally modified as a result of the tidal stage and weather conditions. Not all areas of the habitat were included in the transect routes. In North Inlet, only the creeks that were wide and deep enough to pass through via boat at all tidal stages were included in the transect. Throughout my sampling periods, I performed photo-identification surveys during low, medium, and high tides. The NIWB system experiences two low and two high tides per day, and each tide (flood low, high, and medium, ebb low, high, and medium) lasted for 4 hours per day. Surveys were performed on waters of a Beaufort sea state of ≤ 3 to optimize potential for dolphin sightings. A minimum of two observers searched for dolphins for each transect. The survey boat traveled along the transect until dolphins were encountered.

Each sighting of a single or a group of dolphins was regarded as a sighting event. Upon discovery during surveys, dolphins were observed for several minutes before being approached for photo-identification. Sighting events commenced once the survey boat was within photo-identification range and concluded when multiple photographs of each fin were taken or, in a few cases, when dolphins were no longer seen. Minimum, maximum, and best estimates of total dolphins, calves, and young of year (defined as being approximately one half the length of the mother, dark gray in color (Quintana-Rizzo and Wells 2001), and sometimes exhibiting fetal folds) were recorded. For each sighting event, the starting and ending times and latitude and longitude coordinates using Global Positioning System (GPS) were recorded, and dorsal fin photographs were taken of each member of the group. Photographs in this study were taken with a Canon 20D digital SLR autofocus camera with a 100-400 mm zoom lens. The best photographs for each dolphin per event were rated on a scale of 1 to 3 for clarity, contrast, and angle of the fin, and only those with an overall rating of 2.0 or better were used for analyses.

Photographs of dorsal fins were used to identify individuals. In this study, the only individuals whose sex could be determined were 1) mothers with dependent calves (currently or in historical data from the past ten years (R. Young, pers. comm.)) and 2) adults never sighted with a calf in 10 years of historical data (considered to be males). Dolphins were categorized as adult, calf, and young of year based on size, historical sightings, and behavior. Calves were labeled as such by possessing a wave-like pattern on the trailing edge of their dorsal fin, being shorter than (between 50% and 75% the length of) the mother (Quintana-Rizzo and Wells 2001), and swimming no farther than 40 m from the mother. Individuals labeled as young of year (also referred to as neonate) were often darker in skin color than the mother, roughly half the length of the mother (Quintana-Rizzo and Wells 2001), exhibited fetal folds and a floppy dorsal fin, and remained in the echelon position (Gubbins et al. 1999). Tidal stage, air and water temperature, wind velocity, and salinity data were collected and recorded for each event, and these variables were later tested as predictors for dolphin abundance. After sufficient photographs were taken for each dolphin in the event, the survey resumed, returning to the transect route if necessary and continuing along the pre-defined path. Each transect concluded at the original starting point, and, time permitting, the procedure would repeat for another one or two transects before ending the survey day. A single transect took between 1.60 hours and 4.85 hours to complete, depending on the number sighting events and dolphins per event.

Groups are defined in various ways in the literature ranging from all dolphins within a 10 m radius to all dolphins within a 100 m radius within the restraints of visibility (reviewed by Gibson and Mann 2009). The geographic structure of salt marsh creeks restricts visibility for observers and limits dolphin dispersion within a group to relatively small areas. These physical constraints led me to define a group as multiple dolphins swimming together (moving in the same general direction and engaging in the same general behavior throughout the duration of the event), in which each individual was ≤ 40 m from at least one other individual in the group.

Some dependent calves were often sighted up to 40 m away from the mother. Additionally, events only consisting of a mother and its calf were not considered a group. In this study, the term, event, was used synonymously with group.

Analyses

Locations of each sighting and each individual dolphin were entered into a Geographic Information System (GIS) using ESRI ArcView version 9.3 (Redlands, CA, U.S.A.), and home range estimates were determined for each animal. Based on the plotted points for each animal, a total area was determined for the animal's home range using the Minimum Convex Polygon tool in the Animal Movement menu under Hawth's Tools for ArcGIS and fitted, using the clipping tool, to only include aquatic areas in the NIWB system. To determine which dolphins were appropriate to use for home range analyses, the number of sightings per individual were plotted against the home range sizes. Although the number of sightings per individual ranged from 1 to 25 during the warm season, only dolphins with at least 7 independent sightings were used for home range analyses because the point of inflection for the average home range sizes for each number of sightings per individual occurred at 7 sightings (fig. 2). To be included for cold season home range analyses, dolphins needed a minimum of 3 independent sightings. A minimum of 3 sightings was used because it is proportional to the 7 sightings used during the warm season relative to the number of transects completed in each season. The mean home range sizes for dolphins only sighted in North Inlet (North Inlet dolphins), only sighted in Winyah Bay (Winyah Bay dolphins), and sighted in both North Inlet and Winyah Bay (NIWB dolphins) were calculated for comparison between these three general groups.

In addition to using the minimum convex polygon method, the fixed kernel density method was also used to determine home ranges. The fixed kernel density method with smoothing parameters was used because it is both a precise and accurate protocol, based on probabilities, that provides detailed information on habitat usage within the overall home range and takes into account the complete utilization distribution of the habitat (Börger 2006; Urian et al. 2009). Fixed kernel densities were calculated using the Home Range Tools (HRT tools) extension for ArcGIS 9.3 (Rodgers et al. 2007). The least squares cross validation method was used to calculate the bandwidth, a function to best describe the pattern in the data, used for kernel density estimates. Additionally, the terrestrial areas of the habitat were removed from the kernel density output via the clipping technique in ArcGIS to obtain a more accurate understanding of habitat usage. Distributions are often shown using three different utilization distributions (95%, 50%, and 25%), which can also be referred to as isopleths. A 95% isopleth would indicate that 95% of the time, the animal is within the spatial boundary defined by the isopleth. The 95% isopleth was used to determine the overall distribution of the population, and the 50% isopleth and 25% isopleth were calculated to obtain estimates for core areas.

For analyses involving tidal data, sampling data were standardized to the sampling effort by determining the quotient of the total number of dolphins sighted at each tidal stage divided by total amount of survey time at that tidal stage for North Inlet and for Winyah Bay. The data were standardized because the area of and number of times through each defined section of the habitat were not equal. Thus, each estimate is in terms of the sampling effort. The tidal stage was recorded for the start of a sighting event, and if an event lasted through multiple tidal stages, only the tidal stage at the start of the event was used in this analysis.

Social analyses were conducted for the following: all dolphins with at least 3 independent sightings (sighted on at least three different days), all dolphins with at least 10 independent sightings, and mother/calf pairs. Because the minimum number of sightings per individual used for social structure analyses varies from 2-10 (reviewed by Rogers et al. 2004), a minimum of 3 sightings per individual on at least 3 different days was appropriate for this study because it allows for comparison with other studies. Coefficients of association were calculated to determine the degree of association between dolphins. Coefficients of association values range from 0 to 1, where a coefficient of association of 0 indicates that two animals are never seen together, and a coefficient of association of 1 denotes two animals are always observed together (Urian 2009; Cairns and Schwager 1987). Associations were determined via a matrix to represent all possible pairwise associations, and the number of associations for each pair, or dyad, was determined. Coefficients of association were calculated via the half-weight index (HWI), which is the most appropriate method for surveys that are more likely to encounter two animals in separate areas than in the same area (Cairns and Schwager 1987). In the case of bottlenose dolphins, the half-weight index is appropriate because dolphins that were present but not photographed in an event were assumed to not be in the group. The half-weight index is defined as:

$$HWI = \frac{x}{x + y_{ab} + 0.5(y_a + y_b)}$$

where x is the number of times both dolphin a and dolphin b were sighted together, y_a is the number of times dolphin a but not dolphin b was sighted, y_b is the number of times dolphin b but not dolphin a was sighted, and y_{ab} is the number of times where both dolphin a and dolphin b were sighted in different groups, which was always zero because there were no cases in which I saw two distinct dolphin groups simultaneously. Neighbor-joining (NJ) trees (Saitou and Nei 1987) were constructed using the online program T-Rex (Boc, Diallo, Alpha, and Makarenkov 2012) and the program SocProg v. 2.4 (Whitehead 2009) to show the relationships between individuals. The coefficients of association were used to determine distance measures for the dendrograms by subtracting the HWI value from 1 as in Möller et al. (2001). Half-weight index values and distance measurements were calculated using SocProg v. 2.4.

Statistical Methods

Shapiro-Wilk tests were used to determine if data were distributed normally. The Shapiro-Wilk test was used because it is appropriate for samples ranging from <50 to 2000, and my data fit this range. To describe the relationship between group (NIWB, North Inlet, or Winyah Bay), dolphin abundance, and season, a Fisher Exact Probability test was performed. The Fisher Exact Probability test was chosen because the data fit a 2×3 contingency table. Kruskal-Wallis and Mann-Whitney tests were used to determine if home range sizes varied between warm season and cold season, between North Inlet and Winyah bay, and between dolphins using North Inlet, Winyah Bay, or using both systems. To determine if associations were significantly different from random associations, a Monte Carlo permutation test was performed. The number of permutations was increased until the p-value stabilized. Statistical tests were performed in SPSS (v.20), VassarStats (©Richard Lowry 2001-2012), SocProg, and GraphPad Prism (v. 5.0a, GraphPad software, La Jolla, CA.)

Results

Seasonal and Cross-Estuary Abundances

A total of 126 transects were conducted during 58 opportunistic survey days. Survey effort is summarized in table 1. The mean duration for all sighting events was 20 minutes (range: 3-96 min.). In North Inlet, the mean duration for warm season events was 17 minutes (range: 3-64 min.) and for cold season events, 19 minutes (range: 5-42 min.). In Winyah Bay, the mean duration for warm season events was 25 minutes (range: 3-96 min.) and for cold season events, 22 minutes (range: 4-68 min.).

As an indicator of seasonal abundance, separate discovery curves were plotted for the warm season and cold season surveys. In the warm season, no new dolphins were sighted in North Inlet after the 15th survey day (fig. 3a). However, in Winyah Bay, the discovery curve never reached a plateau, though the slope of the curve decreased towards the end of the season (fig. 3a). During the cold season (Mid-December through February), the dolphin discovery curve commenced its plateau at day 9, but the warm season discovery curve increased throughout the first 16 survey days from Mid-May through early July (fig. 3b, table 2). The warm season discovery curve experienced a steep slope on day 10, which was the second day in Winyah Bay. On this day, data were recorded from two large events, in which 34% of all consistent Winyah Bay warm seasons users were sighted for the first time. Similarly, the cold season curve experiences a steep slope at day 4, which was the first Winyah Bay survey day in the cold season. After the first 16 days of surveys in the warm season, 62 unique dolphins had been sighted (273 total sightings), while during the cold season, 37 unique dolphins (78 total sightings) had been sighted after 16 surveys.

In the warm season, 103 distinct dolphins were sighted and identified in the NIWB system. Of these individuals, 82 dolphins were encountered ≥3 times on non-consecutive days. During the cold season, 37 dolphins were sighted in the NIWB system, 13 of which were seen ≥3 times on non-consecutive days. The resulting abundance estimate for the NIWB system was 84 individuals, which included 11 observed both during the warm and cold seasons, 71 observed only in the warm season, and 2 observed only in the cold season. The population structure was further broken down into North Inlet-only users, Winyah Bay-only users, and dolphins sighted in both North Inlet and Winyah Bay (NIWB group). During the warm season, 3 dolphins were only sighted in North Inlet, 38 dolphins were only seen in Winyah Bay, and 41 dolphins were observed in both North Inlet and Winyah

Bay (fig. 4). In the cold season, 8 dolphins were sighted in North Inlet exclusively, 1 dolphin was found only in Winyah Bay, and 4 dolphins were seen both in North Inlet and Winyah Bay (fig. 4).

The Fisher Exact Probability test, using all dolphins with ≥3 sightings, reveals a significant difference in location between the cold season and warm season ($P_{A\,B}$= $5.65*10^{-7}$, df=2, p<.05). The overall warm season abundance was greater than the cold season abundance, and during the warm season, the number of dolphins residing only in North Inlet was lower than the number of dolphins using only Winyah Bay and using both North Inlet and Winyah Bay. However, in the cold season, abundance was highest for the North Inlet-only group. As the dolphin abundance data was not normally distributed (Shapiro-Wilk test, p<0.001 for North Inlet and p=0.002 for Winyah Bay), non-parametric tests were used. For both North Inlet and Winyah Bay, the number of dolphins per event was greater in the warm season than in the cold season (Mann-Whitney test, U=1276, n=31, p<0.0001 and U=634.5, p<0.0001 respectively). There was no significant difference between the number of dolphins sighted per event in North Inlet and Winyah Bay during the cold season (Mann-Whitney test, n=31, U=360, p=0.15), but there was a significantly greater number of dolphins per event in Winyah Bay than in North Inlet during the warm season (Man-Whitney test, U= 2787, n=163, p<0.0001). Additionally, the percentage of survey days in which dolphins were seen was significantly higher in the warm season than in the cold season (Fisher's exact test, one-sided test, p=0.0010). During the warm season, new dolphins were identified up through

August. Although most of the dolphins were discovered in the warm season, two new dolphins were sighted during the cold season.

Abundance negatively depended on salinity through a range of 10 to 35 ppt (linear regression, $F_{1,150}$=3.94, p=0.049), as abundance had a small decrease with increasing salinity. Within seasons, dolphin abundance did not depend on temperature (linear regression, $F_{1,98}$=0.113, p=0.74 and $F_{1,28}$=1.54, p=0.29, warm season and cold season respectively). Tidal stage also did not have an effect on the abundance of dolphins (χ^2=0.184, df=11, p=1.0).

Home Range Estimates using Minimum Convex Polygon Method

Home range sizes in the NIWB, which were clipped to exclude land, were calculated to be larger in the warm season than in the cold season. The mean home range size within the NIWB system was 32.79 ± 13.02 km^2 for the warm season and 4.73 ± 3.51 for the cold season. As the number of sightings per dolphin increased, there was an increase in home range size up to 7 sightings per individual, at which point, the curve plateaued (linear regression, $F_{1,79}$=3.646, p=0.060, fig. 2). The warm season home range values for the North Inlet, Winyah Bay, and NIWB groups differed significantly (Kruskal-Wallis test, H=7.41, p=0.025). The warm season home range sizes for both the NIWB and Winyah Bay groups (35.68 ± 10.06 km^2 and 33.93 ± 12.71 km^2 respectively) were significantly greater than the warm season home range sizes for the North Inlet group (5.50 ± 0.04 k m^2) (Mann-Whitney test, U=0, n_1=22, n_2=3, p=0.0066 and U=3, n_1=15, n_2=3, p=0.022 respectively). However, the mean warm season home range sizes for NIWB and Winyah Bay groups were not significantly different (Mann-Whitney test, U= 166, n_1=22, n_2=15, p=0.78, fig. 5a). The cold season home range sizes for the North Inlet group were significantly smaller than the cold season home range sizes of NIWB users (Mann-Whitney test, U=0, n_1=3, n_2=7, p=0.028, fig. 5b), and there was only one individual using Winyah Bay during the cold season; thus the Mann-Whitney test could not be used to test for differences between the North Inlet group and the Winyah Bay group. The cold season sightings ranged from 3 to 6, with a mean of 4, sightings per individual, which could indicate that dolphins inhabited waters outside of the NIWB system because in the first 16 warm season survey days, dolphin sightings were significantly higher (mean number of sightings per individual was 6, range: 1-15, Mann-Whitney test, U=174.5, n=99, p<0.0001). Dolphins were never sighted in certain tidal creeks in North Inlet and certain regions of Winyah Bay during either season.

Habitat Usage using Kernel Density Estimates

The kernel density estimator revealed that bottlenose dolphins used most of the water in the NIWB system, as the sum of all of the 95% isopleth estimates from the population covers the entirety of the habitat (fig. 6). Kernel density plots are shown in figure 7. The mean 95% isopleth was 150.80 km^2; the mean 50% isopleth was 30.35 km^2; and the mean 25% isopleth was 16.48 km^2. The 95% isopleth for NIWB individuals did not differ significantly from the individuals only using Winyah Bay (Mann-Whitney test, U=132, n_1=22, n_2=15, p=0.31), and the 95% isopleth size for Winyah Bay users was not significantly different from North Inlet users (Mann-

Whitney test, U=12.5, n_1=15, n_2=3, p=0.089). Additionally, there was no significant difference for 50% isopleth or 25% isopleth between NIWB individuals and individuals only using Winyah Bay (Mann-Whitney test, U=139, n_1=22, n_2=15, p=0.43 and U=132, n_1=22, n_2=15, p=0.31 respectively), and 50% isopleth and 25% isopleth estimates between North Inlet users and Winyah Bay users were not significantly different (Mann-Whitney test, U=13.5, n_1=3, n_2=15, p=0.11 and U=15.5, n_1=3, n_2=15 p=0.16 respectively). However, the 95% isopleth, 50% isopleth and 25% isopleth for NIWB individuals were significantly greater than North Inlet users (Mann-Whitney test, U=14, n_1=22, n_2=3, $p<0.05$, U=14, n_1=22, n_2=3, p=0.036 and U=12, n_1=22, n_2=3, p=0.025 respectively). Heavy and moderately heavy use areas seemed to be more centrally located in North Inlet while the heavy and moderately heavy use areas were more patchily distributed in Winyah Bay (fig. 7b,c). Additionally, the three warm season individuals that were only sighted in North Inlet had the smallest home ranges of individuals sampled. Of the 26 dolphins sighted in both North Inlet and Winyah Bay, only three individuals had a preference of one area over the other, as the dolphins named, EVE, MAR, and KAI all had significantly more sightings in North Inlet than in Winyah Bay (table 3). These three individuals used North Inlet differently than the individuals that were only seen in North Inlet, as most of their core areas were in the southern regions while the sightings of individuals only seen in North Inlet were mostly limited to the northeast sections (fig. 7c,d). Additionally, the distribution of the individuals using both North Inlet and Winyah Bay but displaying a preference for North Inlet had a much smaller distribution in Winyah Bay, with all of their core areas in North Inlet, than the other individuals using both North Inlet and Winyah Bay (fig. 7a,f). However, the ranging patterns for these two groups had a greater overlap in both North Inlet and Winyah Bay, with many overlapping core areas, than they did in comparison to the distributions of the group only sighted in Winyah Bay and the group only sighted in North Inlet (fig. 7a,b,c,f).

The minimum convex polygon method and kernel density method estimated a similar mean home range size for the NIWB population (fig. 6, 8). The 95% isopleth size was significantly higher and 25% isopleth size was significantly lower than the minimum convex polygon-calculated sizes (Mann-Whitney test, U=495, n=41, p=0.0002, and U=261, n=41, p<0.0001 respectively). However, there was no significant difference between the calculated areas for the 50% isopleth and the home range size calculated using the minimum convex polygon method (Mann-Whitney test, U=573, n=41, p=0.069).

Social Groups

All association data failed Shapiro-Wilk tests for normality; thus, non-parametric tests were used for analyses. The dolphins in this study were observed in groups more often than alone. Ten percent of all events were either a single dolphin or mother-calf pair. Although solitary dolphins were observed in both systems, dolphins were observed alone more often in North Inlet (33 single-dolphin events or 36.3% of all North Inlet events) than in Winyah Bay (13 single-dolphin events or 17.6% of all Winyah Bay events). During the warm season, 11 different dolphins (totaling 32 events or 23.4% of all warm season events) were a single dolphin or mother-calf pair, and 5 different dolphins (totaling 14 events or 45.2% of all cold season events) were sighted alone or as a single mother-calf pair during the cold season. Of the 84 individuals sighted at least 3 times, 12 non-mothers were observed alone at least once. During the warm season, 9 non-mothers were sighted alone at least once (12.4% of all warm season events), but during the cold season, 3 non-mothers were observed as solitary at least once (12.9% of all cold season events). Similarly, 12.9% of all cold season events were single mother-calf pairs. During the warm season, 28.6% of all events were single mother-calf events. Three mother-calf pairs were observed without any other dolphins; 1 pair was observed alone in both seasons; 1 pair was only observed alone in the warm season; and 1 pair was only observed alone in the cold season. However, each of these pairs was observed in the NIWB system during both seasons.

Figure 10 shows the mean, 25th percentile and 75th percentile of group sizes for North Inlet and Winyah Bay in each season. Within the NIWB system, dolphin group sizes ranged from 1 to 42 dolphins in the warm season and 1 to 11 dolphins in the cold season. For the warm season, group sizes were significantly larger in Winyah Bay than in North Inlet (Mann-Whitney test, $U=1261$, $n=134$, $p<0.0001$). However, there was no significant difference in group sizes between North Inlet and Winyah Bay in the cold season (Mann-Whitney test, $U=423$, $n=31$, $p=0.20$).

Associations

To obtain a better understanding of the social organization present in the NIWB system, social coefficients of association were compared using all dolphins with at least 3 sightings and all dolphins with at least 10 sightings. Both of these groupings were analyzed because dolphins with fewer than 10 sightings could have been transients or seasonal residents, which could underestimate the overall associations, but these dolphins also contribute to the overall social network in the NIWB system. The Monte Carlo permutation test with 10,000 permutations revealed that overall associations between individuals sighted ≥3 independent times in the NIWB system were not significantly different from random ($p=1.0$), with 53 of the dyads being non-random. However, when limiting the data set to individuals sighted ≥10 independent times, the Monte Carlo permutation test with 42,000 permutations revealed that the associations were significantly different from random ($p=0.00003$). NIWB dolphins seemed to form loose associations with conspecifics (fig. 11), as the mean warm season coefficient of association value was 0.12 (including all individuals sighted ≥3 times) and 0.24 (including individuals sighted ≥10 times), and most of the coefficients of association fell within the 0.11-0.20 range (median of 0.08 for those sighted ≥3 times and 0.19 for those sighted ≥10 times, fig. 11a,b). However, the greatest association was 0.86, which was the calculated coefficient of association for 2 pairs. In one pair, the individuals were each sighted only 3 times, but in the other pair, the individuals were sighted 7 and 8 times. Mother-calf associations were not included in any of association analyses because all mother-calf pairs had a coefficient of association of 1.00. The mean coefficient of association value for individuals sighted 3 or more times was significantly different from the mean coefficient of association value for individuals sighted 10 or more times (Mann-Whitney test, $U=127100$, $n_1=2926$, $n_2=375$,

$p<0.0001$, fig. 11a,b). This finding is a likely result of the individuals that showed a higher fidelity to the NIWB system associating with one another more often than with those which only visited the system on occasion. The coefficient of association for the individuals only sighted in Winyah Bay (0.34) was not significantly different from those only sighted in North Inlet (0.48) (Mann-Whitney test, $U= 35.5$, $n_1=108$, $n_2=149$, $p=0.18$, fig. 11c,d). However, the associations observed on Winyah Bay transects, which included all individuals sighted in Winyah Bay were significantly stronger than the associations observed in North Inlet (Mann-Whitney test, $U=123500$, $n_1=442$, $n_2=624$, $p=0.0036$). Additionally, there was no significant difference for associations between the warm and cold seasons for dolphins with at least 3 sightings (Mann-Whitney test, $U=64740$, $n_1=2926$, $n_2=45$, $p=0.85$) or including warm season individuals with at least 10 sightings (Mann-Whitney test, $U=1525$, $n_1=375$, $n_2=45$, $p=0.44$).

Of the 8 mothers in this population, 3 (EVE, MAR, and WOB) associated most closely with another mother. There was no significant difference between coefficients of association for mothers and non-mothers (Mann-Whitney test, $U=186$, $n=84$, $p=0.15$). However, the mothers associated significantly more closely with other mothers than with other dolphins (Mann-Whitney test, $U=0$, $n=84$, $p=0.0009$). Additionally, group sizes including calves were significantly larger than groups absent of calves (Mann-Whitney test, $U=1125$, $n=163$, $p<0.0001$) (mother-calf pairs were counted as one dolphin).

Communities

Dolphins with observed home ranges limited to either Winyah Bay or North Inlet associated more closely with other individuals observed using only Winyah Bay or North Inlet respectively than with those observed using both systems. The coefficients of association for all dolphins sighted ≥10 times (calves not included) are summarized in table 5, and associations of individuals are depicted in the neighbor-joining dendrograms in figure 12. In the neighbor-joining dendrograms, each individual is represented by a three-letter code at the terminus of each branch. The individuals that associated more closely share a node. Individuals with similar home ranges and a greater degree of association with each other than with dolphins with dissimilar home ranges form social communities, which can be seen in the dendrogram in figure 12d, and kernel density plots for each community are shown in figure 13. The ranges of individuals in community 1 had a fairly patchy distribution (fig. 13a) consistent with the distribution of the individuals only using Winyah Bay shown in figure 7b. The individual that did not fit into any community (HOU) and is labeled as community 2 in figure 12d had a unique ranging pattern (fig. 13b). Even though this individual was sighted in Winyah Bay significantly more often than in North Inlet, it did not share any core areas with the other individuals sighted significantly more often in Winyah Bay. The members of community 3 had most of their core areas in the southern creeks of North Inlet (fig. 13c). The individuals that were only sighted in North Inlet (community 6, fig. 12d, 13f) formed the most distinct community, as most of their sightings were in the mouths of 2 northern creeks, and dolphins from other communities were rarely sighted in one of those creeks and never sighted in the other.

Discussion

This study expands knowledge of abundance and distribution of bottlenose dolphins residing in estuarine habitats of the southeastern United States. The home ranges of the NIWB dolphins would be expected to be smaller than those of most coastal dolphins because of the constraints of their estuarine habitat (Wiszniewski et al. 2009a). In this study, sampling was confined within the boundaries of the NIWB estuarine system. Thus, home ranges reported in this study should be regarded as known home ranges rather than complete home ranges. The dolphins observed in this study likely consist of a small core NIWB group of seasonal residents. Gubbins (2002b) noted that some coastal dolphins regularly venture into other South Carolina estuaries. However, seasonal transients are likely a minor supplement supplemented to the NIWB group of seasonal residents because only about 20% of all individuals sighted during the warm season were sighted fewer than 3 independent times. There are 3 possibilities to explain why the abundance of dolphins in the NIWB decreases during the cold months: 1) movement to the coast without significant coastal migration (remain just outside of the estuary), 2) movement to the coast with significant migration to another area up or down the coast, or 3) movement south along available estuarine corridors (via the Intracoastal Waterway and marsh creeks).

Dolphins with at least 10 independent sightings associated non-randomly with conspecifics, some weak associations have formed. While there is some overlapping of home ranges between the different communities, individuals in a community shared a common core area (fig. 13). Additionally, among the individuals that were sighted in the NIWB system during both the warm and cold seasons, most associations were maintained in both seasons, which is similar to Gubbins' (2002b) results from the Calibogue Sound and surrounding creeks. Because dolphin abundance in the NIWB system in the cold season was lower than in the warm season, and some individuals were only sighted during a few months throughout the year, group composition and size changed with the change in seasons. The smaller group sizes during the cold months likely reflect scarcity of prey items, as the NIWB system may not have enough food resources to support larger groups.

Group sizes in Winyah Bay were larger than in North Inlet, likely because Winyah Bay is a larger, less restricted habitat than the creek system in North Inlet. The group sizes observed in North Inlet and Winyah Bay are similar to those observed in coastal populations in the Bahamas (Rogers et al. 2004) and in the Gulf de Guayaquil, Ecuador (Félix 1997). In the Bahamas populations, evidence of shark bites were seen frequently, indicating predation pressures may have been high (Rogers et al. 2004), and potentially leading to larger group sizes for protection against sharks. However, in the current study, evidence of shark attacks was rarely observed, indicating that sizable groups probably formed for other reasons than protection from predation.

Dolphins were sighted at all tidal stages in both North Inlet and Winyah Bay. However, after standardizing the data to eliminate effects of transect survey time spent at each tidal stage, dolphin sightings appear to have occurred unequally at the various tidal stages (table 4, fig. 9). In 2002, Young and Phillips reported that dolphins in North Inlet were most often encountered during the lower tides, when dolphins were forced to leave the small, shallow creeks, which are impassible to boats at most tides. However, in the current study, ebb low and flood low were the rarest times for dolphin sightings. This inconsistency could be a manifestation of comparing the focal follow technique to the transect survey technique or differences in environmental conditions between the 2002 sampling period and the 2011 sampling period. Because most dolphins inhabiting North Inlet also inhabit Winyah Bay, these individuals may spend most of their time during low tide in Winyah Bay. This notion is supported by flood low and ebb low being the second and fourth most abundant tidal stages for dolphins to be sighted in Winyah Bay and flood low and ebb low being the stages with the fewest sightings in North Inlet. In Winyah Bay, sightings were low during flood high tide, which could be because dolphins were more difficult to sight, as deeper water presents opportunities for deeper, longer dives.

The abundance estimate of 84 individuals (82 warm season residents) inhabiting the NIWB system calculated in this study is small compared to most inshore and coastal populations (Wells 1991; Félix 1997; Quintana-Rizzo and Wells 2001; Owen et al. 2002; Zolman 2002; Silva et al. 2005; Sellas et al. 2005, but see Harzen 1998). Populations that contain fewer than 100 animals are at a high risk of extirpation; furthermore, a population size of 50 is unlikely to last longer than 50 years (Berger 1990; Cagnazzi 2011). Thus, the NIWB population could be at an elevated risk of extirpation if no interbreeding with other populations is occurring.

Furthermore, if the individuals sighted in this study swim in waters ranging beyond the NIWB system, a greater potential for interbreeding with coastal dolphins exists. To determine if the inshore dolphins in the NIWB system are interbreeding with the coastal dolphins in the adjacent Atlantic Ocean, molecular data are required. Molecular methods would provide additional data for genetic relatedness (Hoelzel 1992). Genetic relatedness data could provide further information regarding home ranges because if dolphins were found to be interbreeding with coastal dolphins, either coastal dolphins have ranges in the NIWB system or NIWB dolphins' ranges extend into coastal waters. Because transects did not include water past the boundaries of the NIWB system, the complete home ranges for individuals swimming beyond the NIWB system could not be calculated from survey methods.

The home range sizes calculated in this study were similar to those determined by Gubbins (2002a) for estuarine individuals sighted fewer than 15 times. Estimated home range sizes for the NIWB individuals were smaller than for the oceanic bottlenose dolphins studied by Silva et al. (2008). Home ranges in that study ranged from about 63 km^2 to about 725 km^2. The home range sizes observed in the current study are likely a result of a difference between open water and estuarine habitats. In an open water habitat, the polygon constructed via the minimum convex polygon method would include all areas within the polygon shape to connect the vertices. However, in the NIWB salt marsh habitat, the water areas are more limited. Additionally, using the minimum convex polygon method in a habitat with few travel routes compared to open water should allow for fewer variables in estimating where individuals swam because, unlike in open water, in many cases in the NIWB system, there is only one path to get from one point to another. Coastal dolphins could be using one distinct route to travel between several non-linear points, which would not be reflected in the polygon. With this potential variability between accuracy of minimum convex polygon measurements in open water versus salt marsh systems, comparing home range sizes between the two can be difficult.

Similar to Ingram and Rogan's (2002) findings in the Shannon estuary, various NIWB dolphins used different parts of the NIWB system. In the Shannon estuary, some dolphins used up to half of the estuary, while other dolphins were only found in a small section. In the NIWB system, some individuals were seen in nearly all creeks of North Inlet and throughout Winyah Bay, but a few individuals were only sighted in the northeast section of North Inlet or a few regions of Winyah Bay. Additionally, the individuals that were only sighted in North Inlet used the habitat differently than the individuals using both systems but preferred North Inlet. The individuals only sighted in North Inlet had a very small distribution and estimated core area of the habitat, but those favoring North Inlet seemed to use a larger area of the creek system and had a core area closer to Winyah Bay than the North Inlet only individuals (Fig. 7c,f).

Although the core areas of each community are segregated, many individuals from different communities have overlapping ranges. The association patterns observed between all dolphins with at least 3 sightings (fig. 12a) are quite similar to patterns observed when limiting the dataset to all dolphins with at least 10 sightings (fig. 12d). However, the dendrogram with individuals sighted 10 or more times shows a more distinct correlation of communities. Additionally, individuals with distributions only encompassing a small portion of either North Inlet or Winyah Bay associated more closely with other individuals with similar small ranges. Four of the 7 members of community 3 have been documented to use North Inlet and were often sighted together during focal follow surveys in North Inlet in 2002 (R. Young, pers. comm.), which is consistent to these dolphins belonging to the same community in 2011-2012. Another individual that was sighted consistently in 2002, KAI, was a member of community 4, which had a similar ranging pattern to community 3 (fig. 13c,d). The dolphins that were only sighted in Winyah Bay (community 1) did not share any core areas with the dolphins that used both North Inlet and Winyah Bay but were sighted more often in Winyah Bay (community 5) (fig. 13a,e). However, there was a slight overlap in core areas between community 5 and community 2 (fig. 13b,e), but the dolphins from community 5 were never sighted with the dolphins in community 2. Although these dolphins were never sighted together during surveys, they could be associating at a small scale because there is some overlap in core areas. The individuals with the smallest home ranges (community 6) were those that only used North Inlet (fig. 13f) and were often seen alone or with just one or two others. In some areas of North Inlet, these small groups or solitary dolphins may be more efficient than large groups at obtaining prey in narrow, shallow creeks.

NIWB dolphins observed in this study were sighted more often in a group than alone, but some events only contained one dolphin. Dolphins were likely observed alone or in small groups more often in North Inlet than in Winyah Bay because the prey are more evenly distributed in North Inlet. In Winyah Bay, dolphins likely congregate around areas rich in prey, thus increasing the likelihood of group formation. In both North Inlet and Winyah Bay, groups with calves tended to be larger than groups without calves, similar to what was reported by Rogers et al. (2004).

Mother-calf pairs occurred more often in groups than as solitary pairs, potentially indicating that there are benefits to associating with other mother-calf pairs. Swimming in larger groups may increase hunting efficiency of the mothers, and calves may develop better cognitively and socially when swimming in groups compared to only swimming with the mother. Mother dolphins in the NIWB system were always sighted in the same group as their calves, similar to the findings in the Gulf de Guayaquil (Félix 1997), but different from what was reported by Quintana-Rizzo and Wells (2001) and Rogers et al. (2004). North Inlet may provide better conditions for dependent calves because the three individuals (EVE, MAR, and KAI) that showed a significant preference towards North Inlet, despite also being found in Winyah Bay, were mothers with dependent calves. EVE, MAR, and KAI were the only moms among the individuals sighted in both North Inlet and Winyah Bay, which lends further evidence that North Inlet facilitated calf raising.

Quintana-Rizzo and Wells (2001) state that there is little variance in association patterns among different populations of bottlenose dolphins. However, the social structure of the NIWB inhabitants seems to be less of a tight-knit group than some other populations. Based on coefficients of association for dolphins sighted in North Inlet and/or Winyah Bay, individuals seem to form weaker bonds than those generally reported in other studied populations (Lusseau et al. 2003; Félix 1997; Augusto et al. 2011), but Quintana-Rizzo and Wells (2001) reported that most associations in the Cedar Keys had a coefficient of association between 0.01 and 0.40, which is similar to this study. When comparing association data using only dolphins sighted at least 10 times, the resulting non-random associations better captures the associations of dolphins showing a greater fidelity to NIWB system. The associations among the individuals using the system more often could provide greater benefits for these dolphins because they would have a greater knowledge of the system and would likely use it for all of their normal daily activities. Gubbins (2002b) observed this pattern of residents associating more closely with each other than with transients in a southern South Carolina estuary. Additionally, when breaking the dataset into associations observed on Winyah Bay transects only versus on North Inlet transects only, the observed mean coefficients of association were much closer to those determined in other studies (Lusseau et al. 2003; Félix 1997; Augusto et al. 2011). Thus, dolphins were preferentially associating with specific individuals with regard to distinct areas of the NIWB system (North Inlet versus Winyah Bay), which could indicate that there are two major distinct groups with overlapping distributions in the NIWB system. This behavior is also similar to that of the dolphins studied Gubbins (2002b), as there was a distinction between dolphins associating with conspecifics in the Calibogue Sound and with those in the creek system. However, the sound dolphins were never sighted associating with the creek dolphins, whereas in the NIWB system, there was some integration of dolphins between Winyah Bay and North Inlet.

The looser associations observed in the Winyah Bay compared to North Inlet could be a result of high competition for resources in this area, as Wiszniewski et al. (2009b) stated that the strength of bonds between individuals decreases with increased competition for resources. Furthermore, Wiszniewski et al. (2009b) continue to describe how associations within fission-fusion populations become stronger during times when resources are abundant. Thus, the greater mean group sizes and overall abundances for the warm season compared to cold season in the Winyah Bay are likely a result of the abundance of resources in the warm season and limited resources in the cold season. Quintana-Rizzo and Wells (2001) noted that association groups become altered with movement patterns, such as immigration to and emigration from the habitat. Thus, if only a few residents inhabit the NIWB system, overall associations for the population should be weaker. Augusto et al. (2011) suggested that smaller populations have a greater potential for higher mean coefficients of association. Because the mean associations for individuals observed using the NIWB system was low, it could indicate that either these individuals may not represent a closed population, or they comprise two major units, a North Inlet group and a Winyah Bay group, which could include individuals inhabiting coastal waters during the colder months of the year.

Cold season home ranges in the NIWB system were calculated to be smaller than warm season home ranges. In the warm season, 71% of the transect surveys contained at least one event. However, only 52% of the transect surveys contained at least one event during the cold season, and sightings were less frequent. Zolman (2002) explained that time lags between resightings can occur from dolphins traversing outside the study area. However, Zolman (2002) also acknowledged that time lags between resightings might also be a consequence of sampling methods, such as the survey boat never coming into contact with a dolphin even if it is swimming along the transect. While Young and Phillips (2002) reported sighting certain dolphins during all four seasons of the year, many dolphins sighted during 2011 and 2012 were only sighted during the warm season and could be using the NIWB system as a migration route. Some dolphins could be using the NIWB habitat as a route between the Atlantic Ocean and the Santee River, travelling through the Intracoastal Waterway, but if these individuals are travelling, they are likely interacting with NIWB dolphins because all dolphins were observed exhibiting feeding and social behaviors in groups.

The kernel density plot also shows a patchier distribution in the cold season, which is likely a result of fewer sightings in the NIWB system (fig. 7 d, e). However, the smaller number of events could indicate that dolphins are using only a few areas of the NIWB estuary and spending more time outside of the NIWB system to increase foraging success. In the cold season, dolphins were determined to have core areas near the inlet mouth in North Inlet and near an entrance to the Atlantic Intracoastal Waterway in Winyah Bay that were not present during the warm season (fig. 7 d, e), further suggesting that dolphins are using the coastal waters during the cold season. However, many of the core areas used in the warm season have remained in use during the cold season, which could indicate adequate resources, particularly prey items, in these areas. Torres et al. (2005) reported that coastal mid-Atlantic bottlenose dolphins had a wider distribution in the warm season and were more clustered in the cold season. This finding is consistent with the results of this study, as the number of dolphins sighted in the NIWB system was greater during the warm season than during the cold season and could be a result of coastal dolphins moving into the NIWB system. Range expansion from nearshore waters of coastal dolphins (as described by Torres et al. 2005) may have extended into the NIWB system during the warm season while their cold season distributions were confined to patches outside of the NIWB habitat. In this conceptual model, the presence of coastal dolphins in the NIWB system would cause the abundance and distribution in this habitat to be greater in the warm season than in the cold season. However, the warm season NIWB residents could, instead, be migrating south via corridors to different estuarine systems, which would also support the lower cold season NIWB abundances.

During the cold season, when production is lower (Lewitus et al. 1998), dolphins were often sighted in the mouth of North Inlet, which may be because dolphins used the coastal Atlantic Ocean area just outside of the estuary for foraging. Many salt marsh nekton populations move out of the inshore habitats into the oceanic waters to escape colder temperatures in the cold season (Rountree and Able 2007), as is the case in North Inlet (Allen et al. 2007), and the outflux of prey species is likely attracting the dolphins into the coastal oceanic waters. Similar to the NIWB system, in the nearby estuary of Cape Romain, SC, bottlenose dolphins were reported to have the lowest attendance during the winter months, and the dolphins were speculated to leave the estuary to follow prey into another area (Sloan 2006). Thus, the individuals that were only observed during the warm season in the NIWB are likely not moving to Cape Romain during the cold season but are traveling elsewhere.

Although some animals may be leaving the NIWB system, certain animals likely had home ranges fully contained within the NIWB system during the warm season because they were consistently sighted in the same general area. While the individuals named SWE, MAC, and LAN were never sighted during the cold season, these three dolphins were consistently sighted within a 5.5 km^2 area during the warm season. These dolphins were also among the most frequently sighted dolphins during the warm season surveys, which suggests that the calculated home ranges better reflect their true home ranges (Zolman 2002). LAN was sighted on 50% of all North Inlet warm season transect surveys. Thus, the estimates for home ranges within the NIWB system likely capture the core area or full home ranges for some individuals.

To increase the accuracy of the home range estimation for the warm season, sampling occurred until the dolphin discovery curve reached a plateau during the warm months for each system, to better account for all dolphins. However, the discovery curves for the cold season were constructed using only 16 days of sightings, and dolphins were only seen on 11 of these days. The discovery curve for Winyah Bay reached a plateau after 3 days, and the slope remained zero throughout the last 3 Winyah Bay sampling days. However, the North Inlet discovery curve reached a plateau after four days, but on the final North Inlet day, a new dolphin was sighted. It is possible that the discovery curve could have continued to increase with additional sampling days.

Increased sampling effort to include multiple years would provide further information pertaining to the association patterns of NIWB dolphins, as the observed associations in this study are only a sample of the overall associations occurring in the field. Because they are calculated as a proportion, the accuracy of associations is affected by the sample size (Lusseau et al. 2005). Thus, associations for individuals with a lower number of sightings could be imprecise. To examine how the association patterns might change with increased sampling, an association matrix was constructed using only individuals sighted ≥10 times (table 5). The significant difference between these mean coefficients of association for individuals sighted at least 3 times and individuals sighted at least 10 times indicates that a sample size of only 3 sightings per individual could be insufficient for determining all of the correct coefficients of association. However, it provides a greater view of the overall social network in the NIWB system and could be evidence that many of the dolphins using the NIWB system might not use the system for many resources and are not integrated into the social network of the other dolphins in this estuary.

Animals can only associate with each other if they have some degree of overlap in their ranges. Thus, separate mean coefficients of association were calculated for North Inlet users seen ≥10 times and for Winyah Bay users seen ≥10 times. With greater numbers and larger group sizes observed in Winyah Bay, Winyah Bay dolphins should be expected to find more associations than North Inlet dolphins, but not necessarily a greater coefficient of association with specific individuals. The NIWB population seems to share some characteristics of the social structure of the Moray Firth population studied by Lusseau et al. (2005). Lusseau et al. (2005) determined the Moray Firth population to be divided into two communities, which were separated according to geographic features. Although the communities may not be as distinct as the communities in the Moray Firth, the social structure of the NIWB population seems to be driven, at least in part, by differing core areas usage by different dolphins, leading to separate communities (fig. 13). Members of these communities share similar home ranges. Although the communities appear more distinct in the dendrogram in figure 12d, these communities cannot be as easily parsed out in the kernel density maps because members from each community disperse into areas used by at least one other community, causing the communities to be more fluid than those described by Gubbins (2002b) and Félix (1998).   While KAI, MAR, and EVE, used both North Inlet and Winyah Bay but preferred North Inlet, KAI was not found to associate closely with MAR and EVE. While MAR and EVE had a coefficient of association value of 0.63 and were members of the same community, KAI associated with MAR and EVE to a lower degree (0.17 with MAR and 0.18 with EVE) and was a member of a different community. Additionally, as these three dolphins shared common ranging patterns, it is possible that they associate more closely than observed during the surveys in this study.

Understanding the distribution and social network of apex predators provides information for top-down management of an ecosystem. Because the North Inlet-Winyah Bay estuary is an important area for bottlenose dolphins, information about their distribution can be used to manage the ecosystem and protect core habitat areas. Inshore populations of bottlenose dolphins are currently not recognized by the NOAA Marine Mammal Stock Assessments (2010), but a lack of such labels pose problems, as some northern South Carolina dolphins likely use both the estuarine waters of North Inlet and Winyah Bay, as well as the coastal Atlantic waters while others may be limited to inshore areas. Additionally, most social network studies focus on nearshore populations; however, information on the social organization of estuarine dolphin populations is much more sparse. Estuarine bottlenose dolphins in the North Inlet-Winyah Bay system associated more closely with conspecifics that shared similar home ranges, compared to dolphins in the North Inlet-Winyah Bay system with different ranging patterns. As observed in other inshore populations (Félix 1997; Gubbins 2002b), distinct communities were present among dolphins that used different core habitat areas within the North Inlet-Winyah Bay system. Seasonal changes also impacted associations between dolphins, as far fewer individuals were present during the cold season than there were during the warm season. Larger warm season abundances likely indicate either an estuarine migration out of North Inlet and Winyah Bay during the cold season or an influx of nearshore dolphins into this estuarine system, with only a small core estuarine population remaining in North Inlet and Winyah Bay through the cold season. This fluid interaction between inshore and nearshore dolphin populations indicates that dolphin social networks may extend beyond traditionally defined stocks. The core areas used by dolphins within the North Inlet-Winyah Bay system can provide a foundation for future studies, as well as management regulations, and the future inclusion of genetic data may help more specifically define inshore and nearshore stocks in this area. Additionally, this study provides baseline data, which can be used to determine any significant changes to the abundance or ranging patterns of dolphins in North Inlet and Winyah Bay in the future.

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Table 1. Summary of survey effort
Time spent on the water in transects, days, and hours

	Survey effort						
Season	North Inlet		Winyah Bay		Total		
	No. Transects	No. days	No. transects	No. days	No. transects	No. days	No. hours
Warm	52	21	41	21	93	42	221
Cold	19	9	14	7	33	16	52

Table 2. Monthly Summary of newly identified dolphins

Month	Survey effort (days)	No. new dolphins identified
May	6	30
June	8	28
July	13	22
August	10	19
September	2	3
October	3	1
December	1	1
January	9	1
February	6	0

Table 3. Preferences for dolphins using both North Inlet and Winyah Bay. *Preferences for North Inlet or Winyah Bay based on times sighted in North Inlet and in Winyah Bay. Significance was calculated via sign tests.*

Dolphin Code	Dolphin ID	Preference	North Inlet (NI)	Winyah Bay (WB)	Sign test p-value
JB001	KNO	--	11	9	0.4119
JB002	EVE	NI	20	4	0.0008
JB004	BEA	--	10	10	0.5881
JB005	SAT	--	2	6	0.1445
JB006	MAR	NI	20	7	0.0096
JB008	KAI	NI	16	4	0.0059
JB009	BER	--	14	10	0.2706
JB010	GAS	--	4	5	0.5000
JB011	HOU	--	4	7	0.2744
JB012	AST	--	1	5	0.1904
JB013	TOP	--	8	8	0.5982
JB015	TES	--	4	3	0.5000
JB020	DYN	--	4	5	0.5000
JB022	RYO	--	4	8	0.1938
JB024	DUS	--	6	2	0.1445
JB025	SAF	--	9	7	0.4018
JB026	BRN	--	11	5	0.1051
JB027	PUM	--	2	6	0.1445
JB029	KER	--	3	8	0.1133
JB052	COR	--	2	7	0.2266
JB057	HAB	--	2	8	0.0547
JB061	WAL	--	1	6	0.0625
JB071	MAT	--	1	6	0.0625
JB075	OHB	--	2	6	0.1445
JB087	BLO	--	1	6	0.0625

Table 4. Number of dolphins per tidal stage

The number of dolphins at each tidal stage were standardized by the survey time spent at each tidal stage.

Tidal Stage	No. of dolphins	Standardized total no. dolphins per tide	No. of North Inlet dolphins	No. of Winyah Bay dolphins	Standardized no. of North Inlet dolphins	Standardized no. of Winyah Bay dolphins
Ebb Low	82	1.39	26	56	1.00	2.84
Ebb Mid	183	1.49	64	119	1.71	1.83
Ebb High	212	2.65	97	115	3.11	2.71
Flood Low	52	1.29	24	28	1.28	2.31
Flood Mid	247	2.86	68	179	2.15	4.70
Flood High	77	1.00	36	41	1.55	1.00

Table 5. Association matrix of all dolphins with at least 10 independent sightings

BEA	1.00																											
BER	0.35	1.00																										
BRN	0.16	0.15	1.00																									
CAS	0.05	0.15	0.13	1.00																								
CHN	0.00	0.00	0.11	0.21	1.00																							
CHO	0.18	0.16	0.07	0.57	0.13	1.00																						
CHU	0.12	0.22	0.14	0.57	0.27	0.33	1.00																					
DRO	0.06	0.00	0.08	0.46	0.00	0.45	0.36	1.00																				
EVE	0.36	0.33	0.30	0.05	0.07	0.06	0.11	0.00	1.00																			
FAW	0.11	0.24	0.13	0.56	0.21	0.50	0.79	0.46	0.10	1.00																		
HAB	0.07	0.06	0.08	0.24	0.00	0.19	0.29	0.32	0.00	0.24	1.00																	
HOU	0.19	0.17	0.22	0.07	0.00	0.26	0.17	0.10	0.06	0.22	0.10	1.00																
KAI	0.15	0.31	0.22	0.17	0.00	0.13	0.13	0.20	0.18	0.11	0.07	0.13	1.00															
KER	0.25	0.17	0.15	0.15	0.00	0.17	0.17	0.10	0.00	0.22	0.30	0.18	0.06	1.00														
KNO	0.56	0.33	0.35	0.18	0.10	0.27	0.20	0.14	0.52	0.18	0.07	0.21	0.32	0.14	1.00													
LAN	0.13	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.05	0.04	0.05	0.09	1.00												
MAC	0.11	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.00	0.06	0.00	0.12	0.59	1.00											
MAR	0.29	0.23	0.37	0.00	0.00	0.10	0.05	0.00	0.63	0.05	0.00	0.11	0.17	0.00	0.53	0.08	0.10	1.00										
PAR	0.00	0.00	0.42	0.25	0.18	0.10	0.20	0.11	0.13	0.17	0.12	0.21	0.07	0.11	0.15	0.00	0.00	0.06	1.00									
RYO	0.19	0.00	0.15	0.30	0.00	0.26	0.17	0.29	0.00	0.15	0.60	0.09	0.06	0.45	0.07	0.05	0.00	0.00	0.11	1.00								
SAF	0.28	0.15	0.32	0.00	0.00	0.07	0.07	0.00	0.36	0.06	0.00	0.08	0.23	0.00	0.42	0.10	0.13	0.48	0.09	0.00	1.00							
SAT	0.21	0.13	0.09	0.17	0.00	0.21	0.21	0.24	0.06	0.17	0.13	0.11	0.07	0.11	0.16	0.00	0.00	0.12	0.00	0.11	0.18	1.00						
SWE	0.11	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.15	0.06	0.07	0.00	0.52	0.32	0.00	0.00	0.07	0.00	0.00	1.00					
TAG	0.12	0.26	0.07	0.48	0.00	0.40	0.64	0.35	0.05	0.69	0.18	0.25	0.12	0.33	0.19	0.00	0.00	0.05	0.10	0.17	0.07	0.20	0.00	1.00				
TOP	0.22	0.34	0.25	0.06	0.00	0.14	0.07	0.00	0.25	0.13	0.00	0.22	0.06	0.07	0.18	0.10	0.06	0.19	0.25	0.07	0.19	0.09	0.06	0.21	1.00			
TSU	0.24	0.16	0.00	0.36	0.00	0.08	0.50	0.27	0.00	0.36	0.29	0.17	0.13	0.00	0.13	0.00	0.00	0.00	0.00	0.09	0.07	0.21	0.00	0.40	0.07	1.00		
VAM	0.12	0.27	0.14	0.43	0.00	0.42	0.42	0.18	0.06	0.50	0.19	0.26	0.06	0.26	0.20	0.00	0.00	0.05	0.20	0.26	0.07	0.21	0.00	0.72	0.21	0.25	1.00	
YAN	0.13	0.11	0.15	0.69	0.31	0.55	0.64	0.50	0.12	0.54	0.21	0.19	0.20	0.10	0.29	0.00	0.00	0.05	0.22	0.19	0.08	0.24	0.00	0.43	0.15	0.27	0.27	1.00
	BEA	BER	BRN	CAS	CHN	CHO	CHU	DRO	EVE	FAW	HAB	HOU	KAI	KER	KNO	LAN	MAC	MAR	PAR	RYO	SAF	SAT	SWE	TAG	TOP	TSU	VAM	YAN

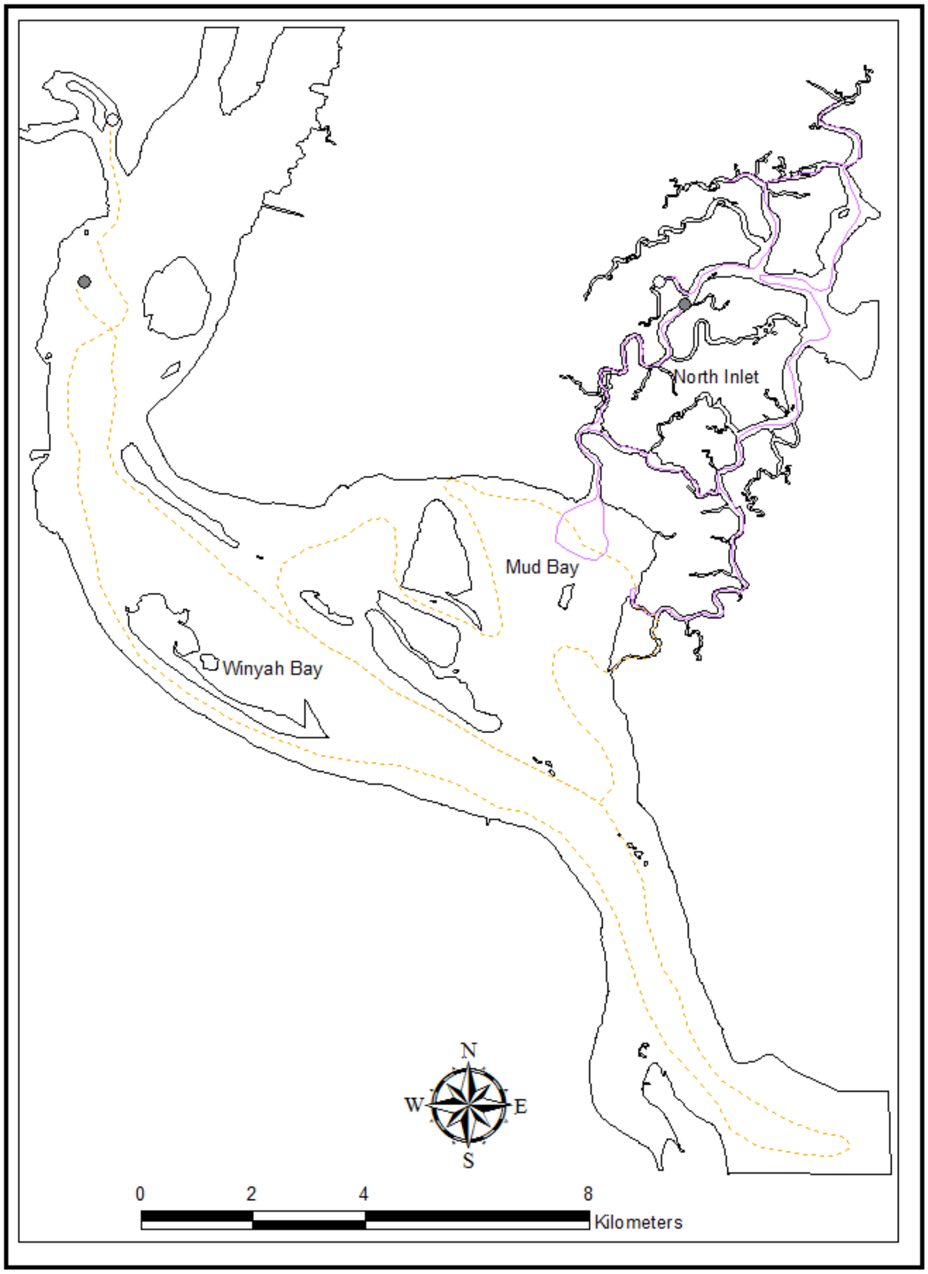


Figure 1. Map of transect surveys
Photo-identification transect surveys were conducted in the North Inlet-Winyah Bay National Estuarine Research Reserve in South Carolina. Transects were performed along the predefined routes for North Inlet (solid purple) and Winyah Bay (dashed yellow). Transects commenced at the white dots and were completed at the gray dots.

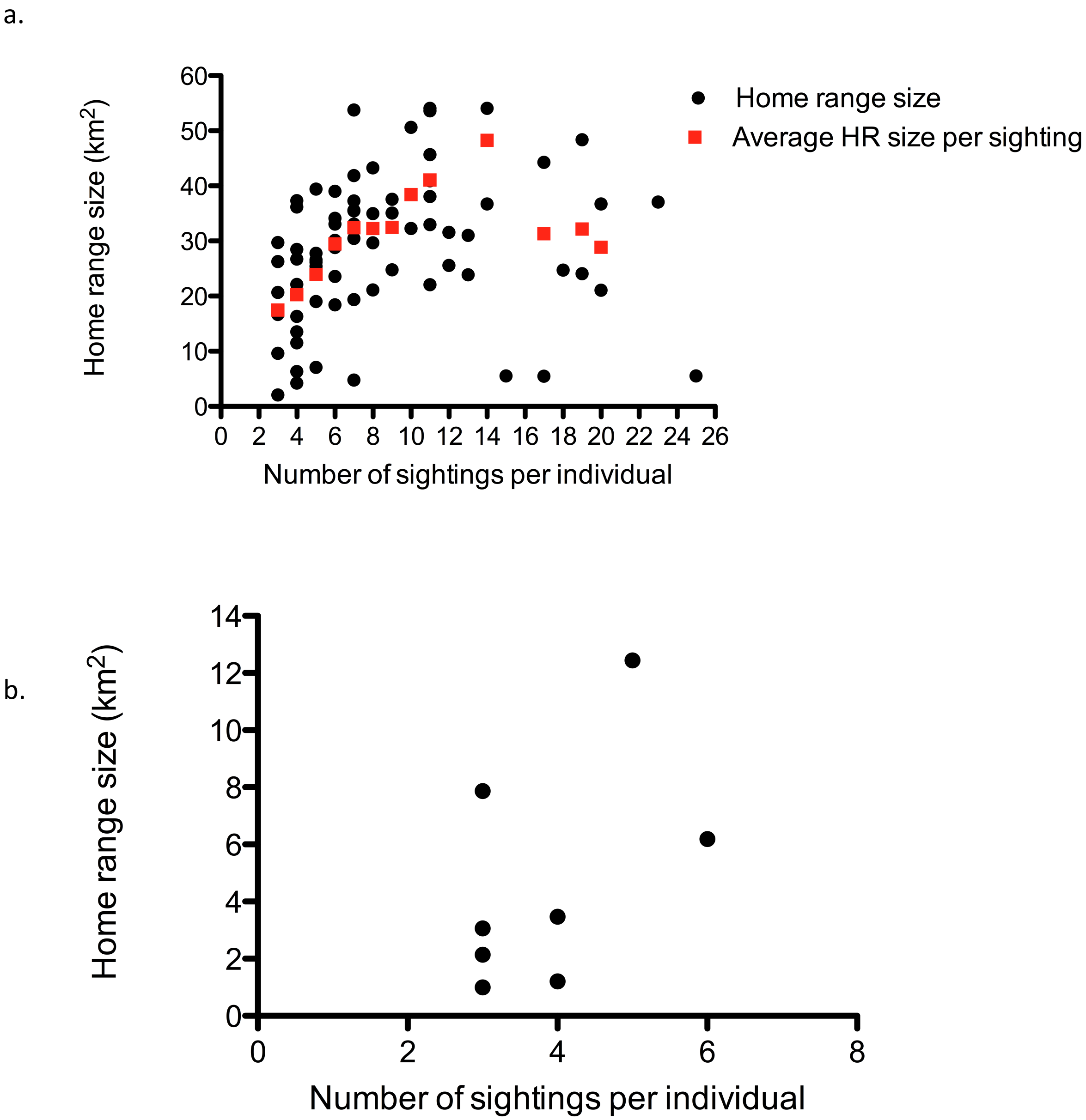


Figure 2. Home range sizes relative to number of sightings per individual
Home range sizes were calculated using the minimum convex polygon method. The home range sizes increased with the number of sightings per individual during both the warm (a) (May 2011-October 2012) and cold seasons (b) (December 2011-February 2012). However, these relationships were not significant. The red points in (a) represent the mean home range size for all dolphins with the specified number of sightings.

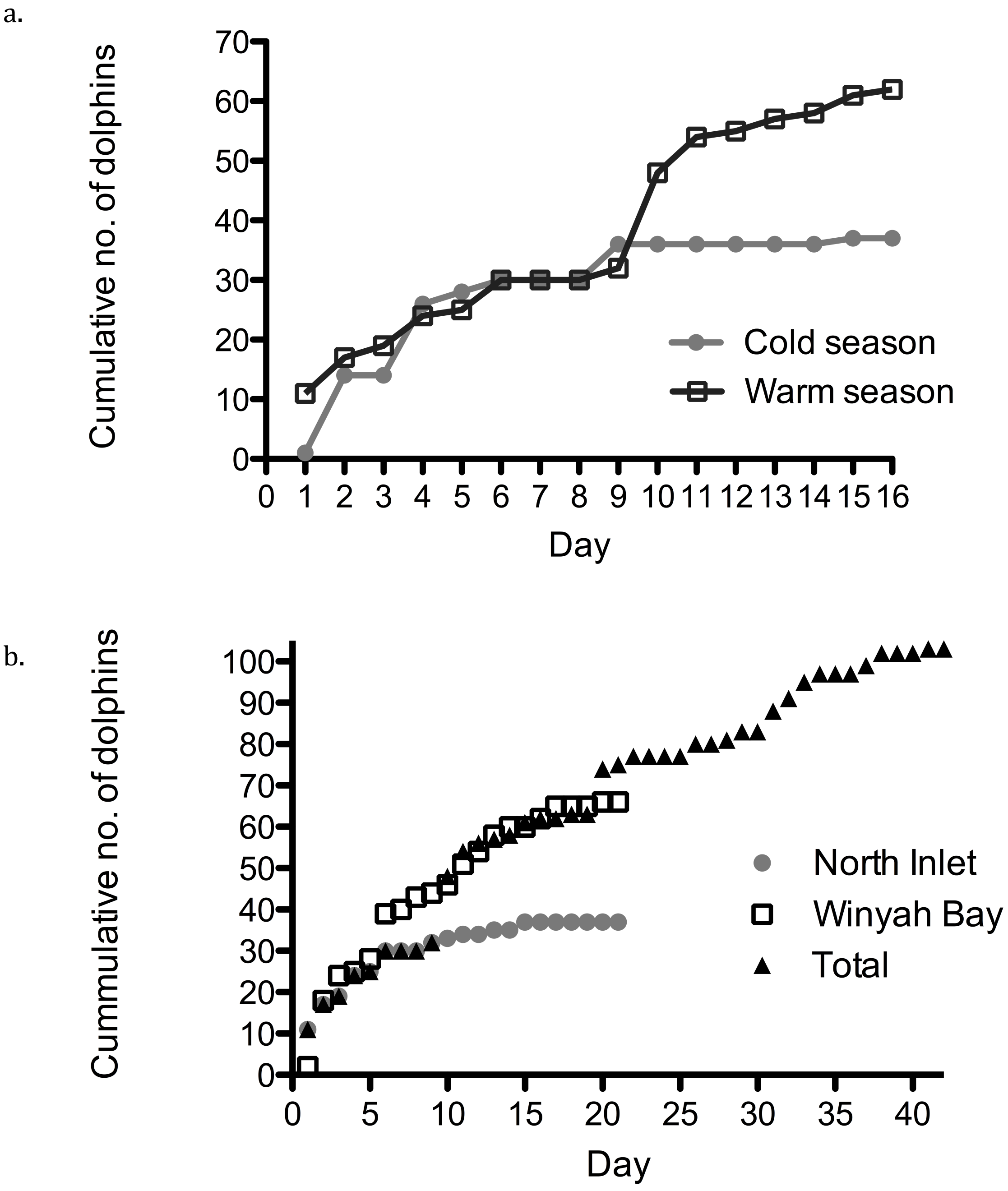


Figure 3. Dolphin Discovery Curve
The cumulative number of bottlenose dolphins observed during the first sixteen survey days of the warm (May 17, 2011-October 25, 2011, indicated by open squares) and cold (December 16, 2011-February 26, 2012, indicated by closed circles) seasons in the North Inlet-Winyah Bay habitat in South Carolina (a) and during the full warm season, which was separated into observations in North Inlet, observations in Winyah Bay, and total observations (b). The 9th warm season survey day was the 1st survey day in Winyah Bay. The warm season curve spikes at day 10 because most Winyah Bay dolphins were seen for the first time on this day.

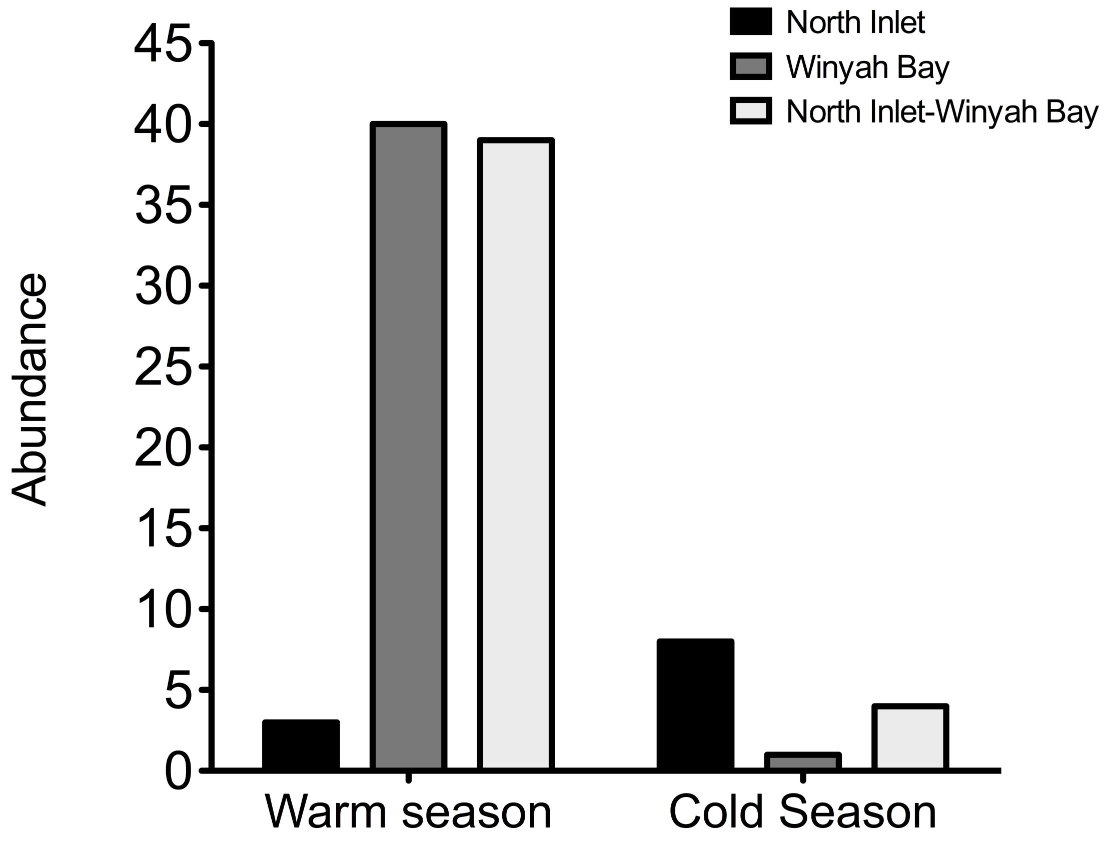


Figure 4. Seasonal Abundances
The number of bottlenose dolphins using North Inlet only Winyah Bay only, and both systems (North Inlet and Winyah Bay) for the warm (May 17, 2011-October 25, 2011) and cold (December 16, 2011-February 26,2012) seasons. Abundances for the Winyah Bay and North Inlet-Winyah Bay group were greater in warm season than in the cold season, but the abundance of North Inlet only users was higher in the cold season than in the warm season.

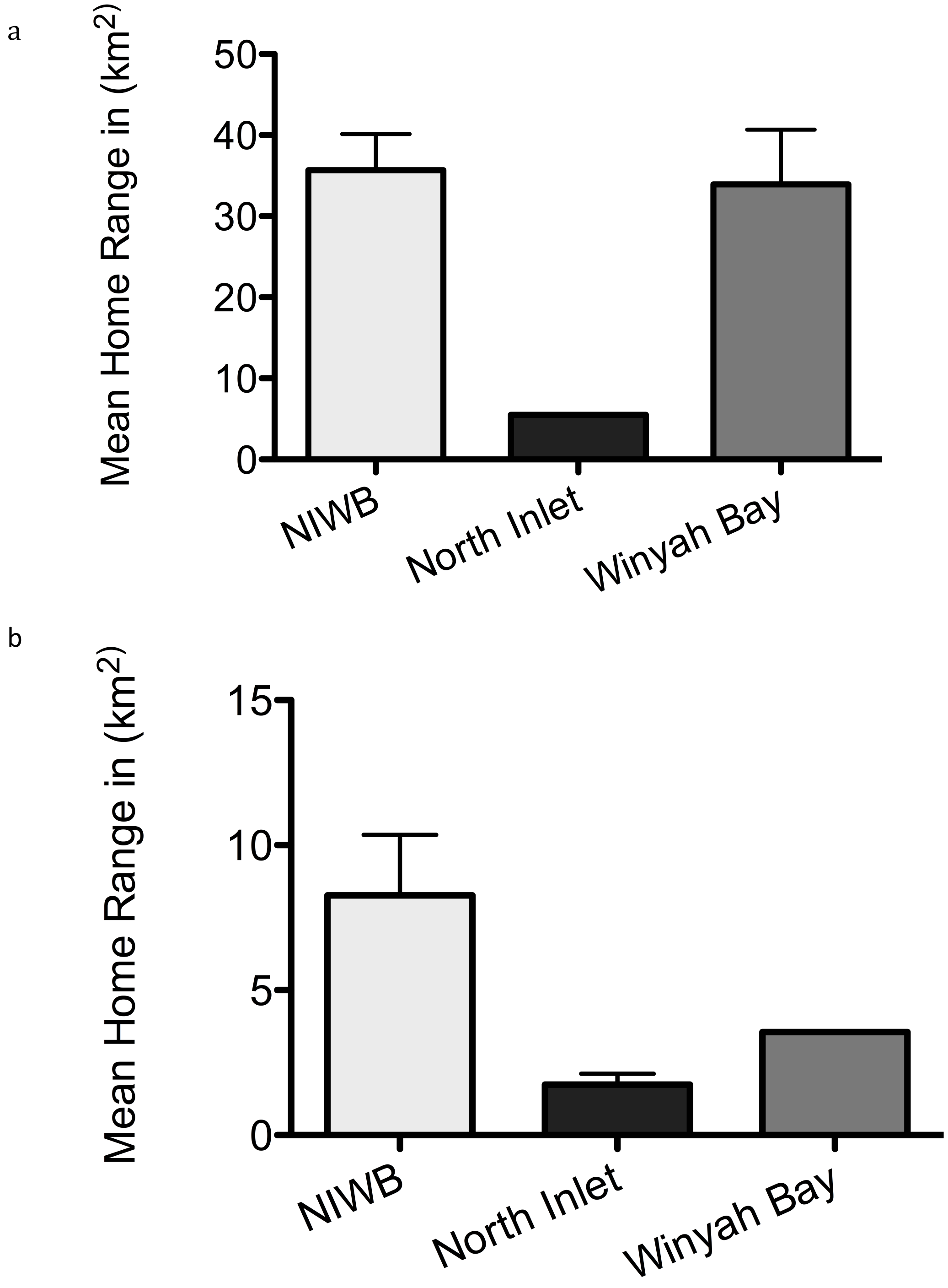


Figure 5. Mean home range size estimates

Home ranges for warm (May17, 2011-October 25,2011) (a) and cold (December 16, 2011-February 26,2012) (b) seasons were calculated via the minimum convex polygon method. The mean home range sizes appear to be larger during the warm season than the cold season but only include areas within the North Inlet-Winyah Bay estuary. In both the warm and cold seasons, the mean home range size of dolphins using both systems was greater than that of dolphins limited to Winyah Bay, which was greater than that of dolphins only swimming in North Inlet.

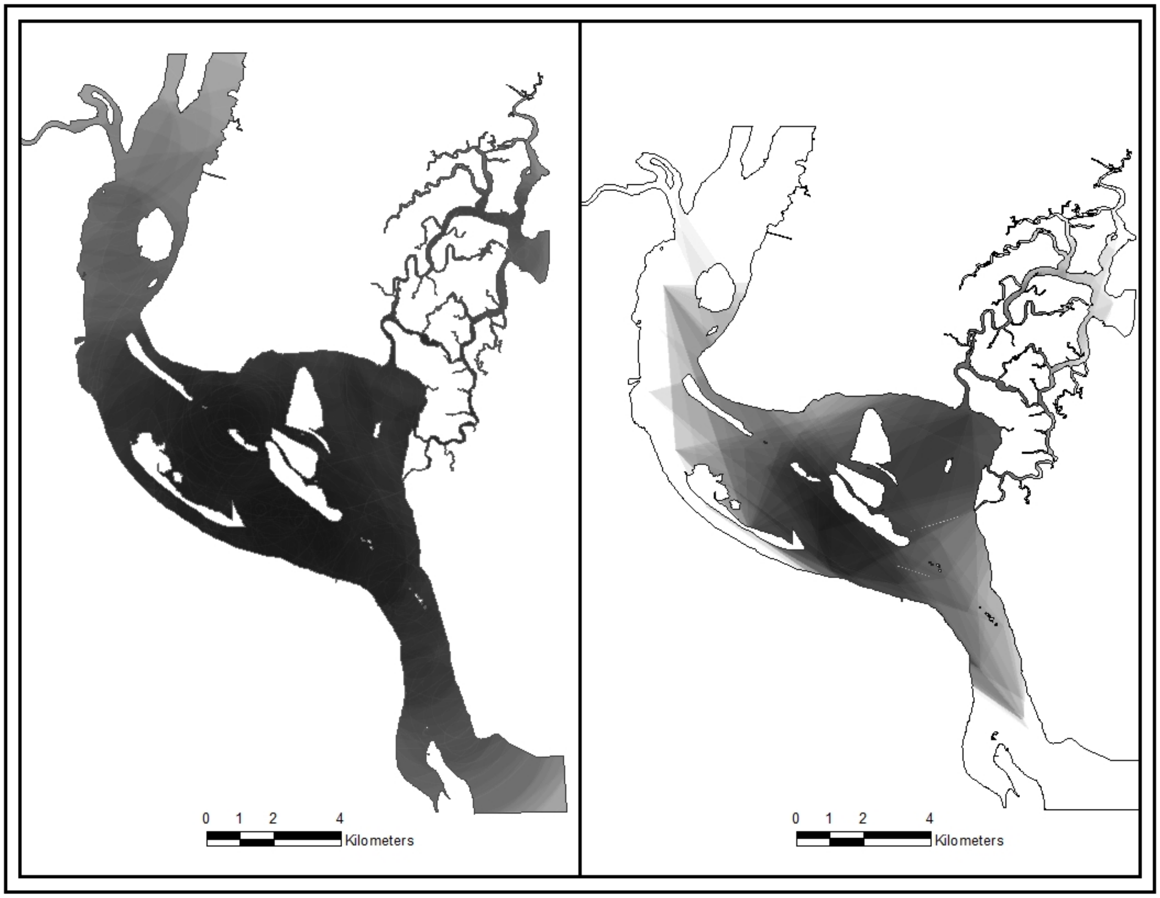
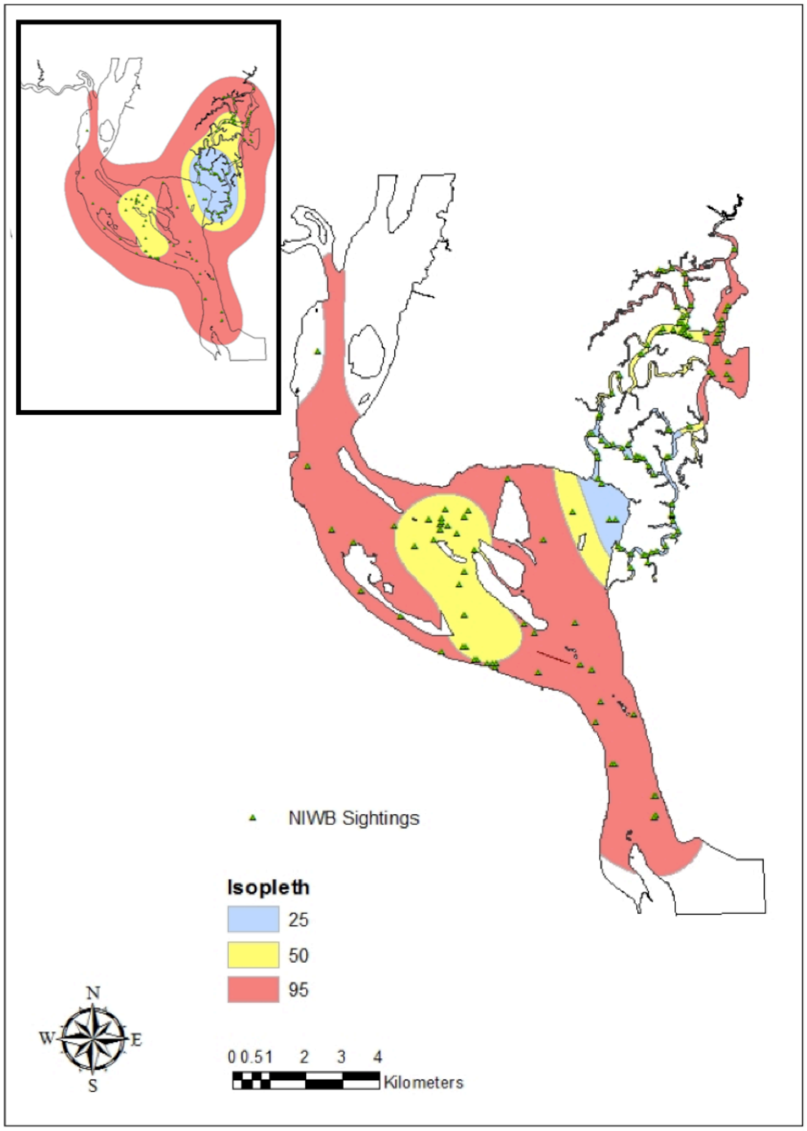
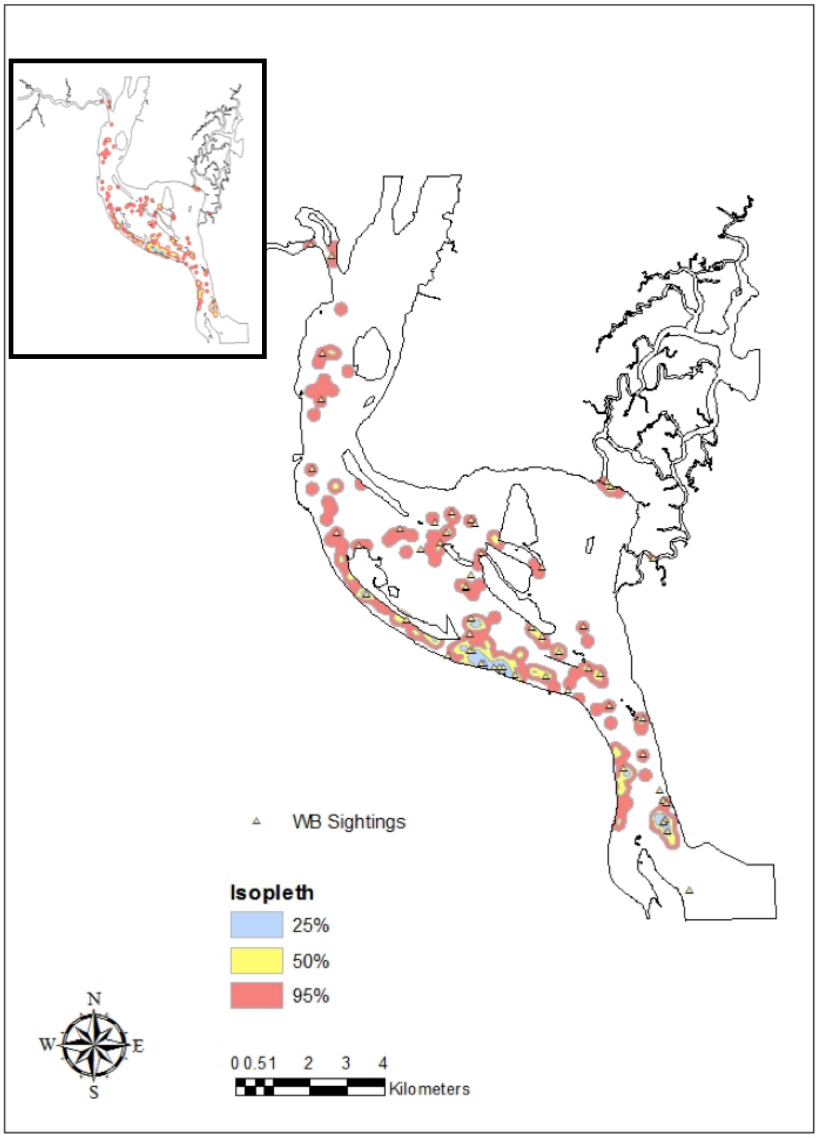


Figure 6. Kernel Density vs. Minimum Convex Polygon Method
The kernel density plots for each individual identified throughout the study are laid overlapping on the left, and the minimum convex polygons for each individual are laid overlapping on the right. Each density plot and polygon has 96% transparency to better see patterns of overlap.

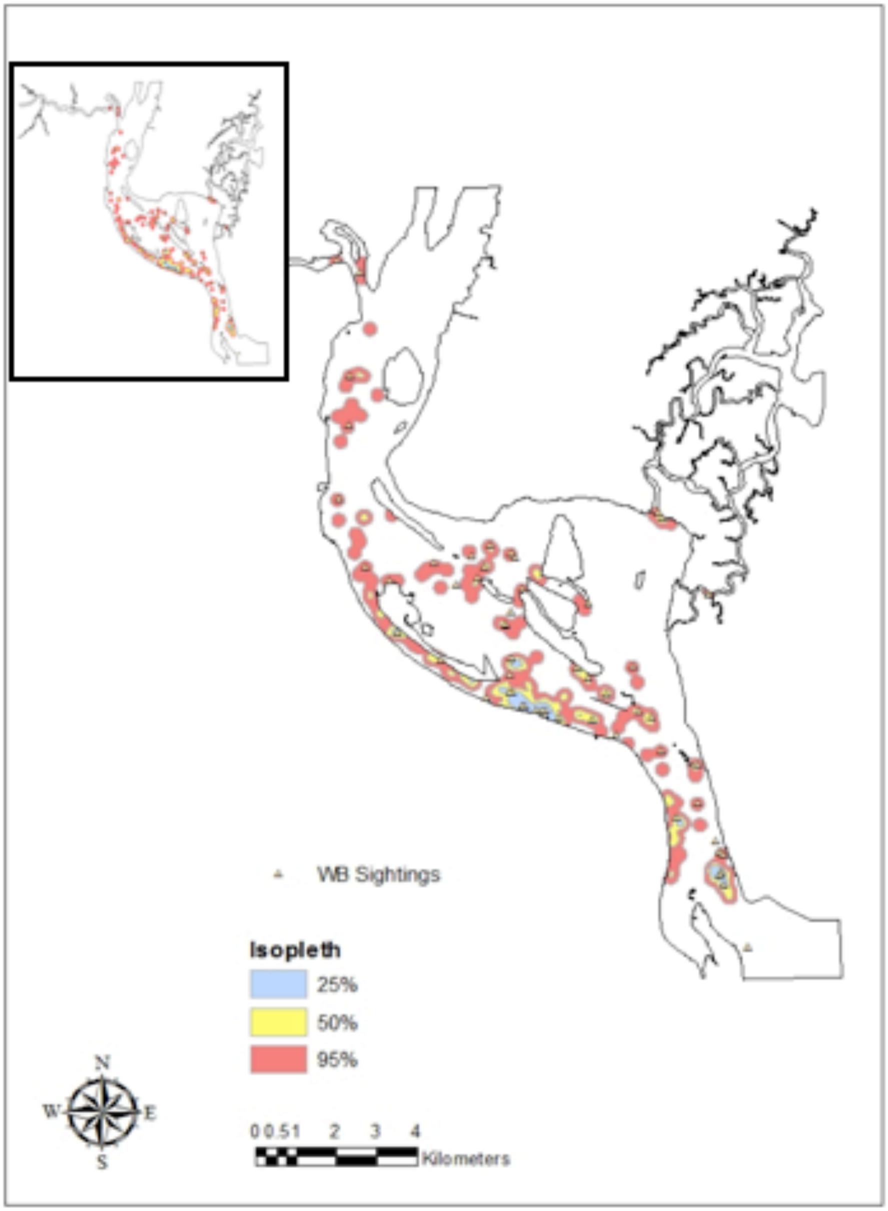
a.



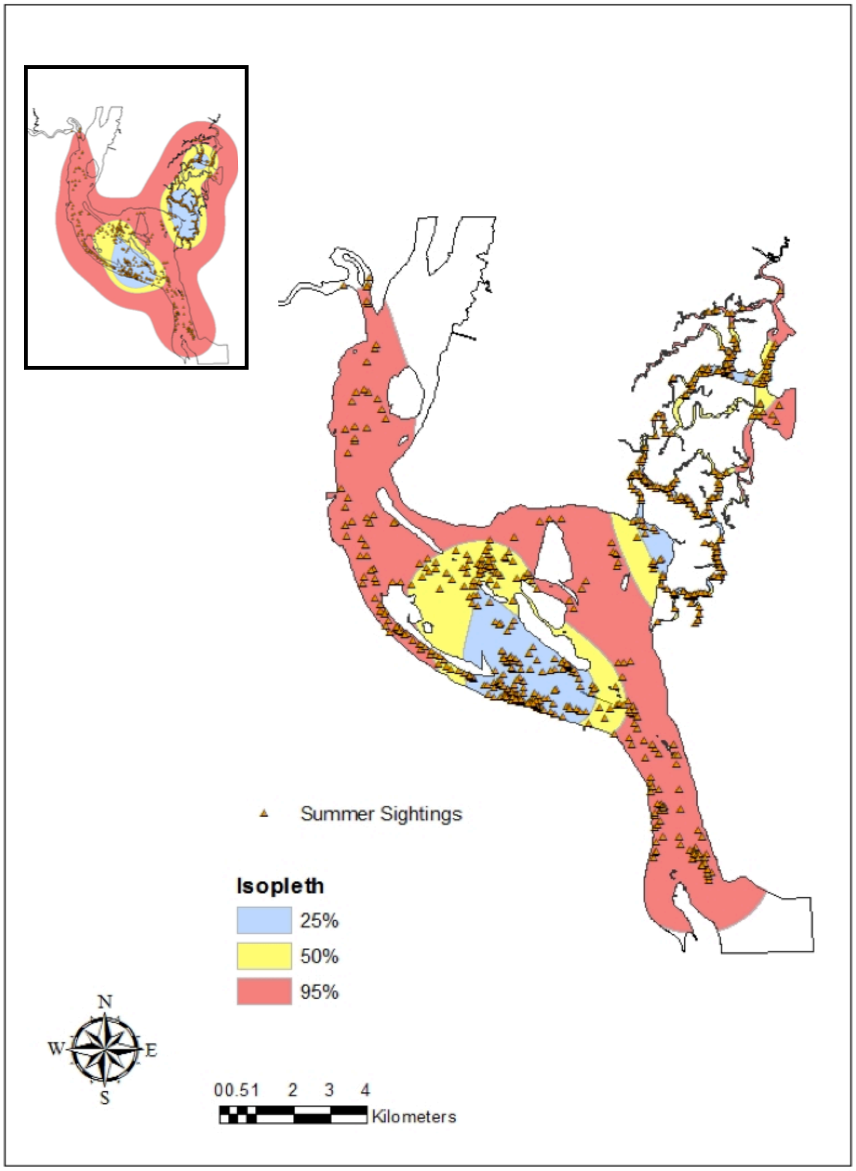
b



c

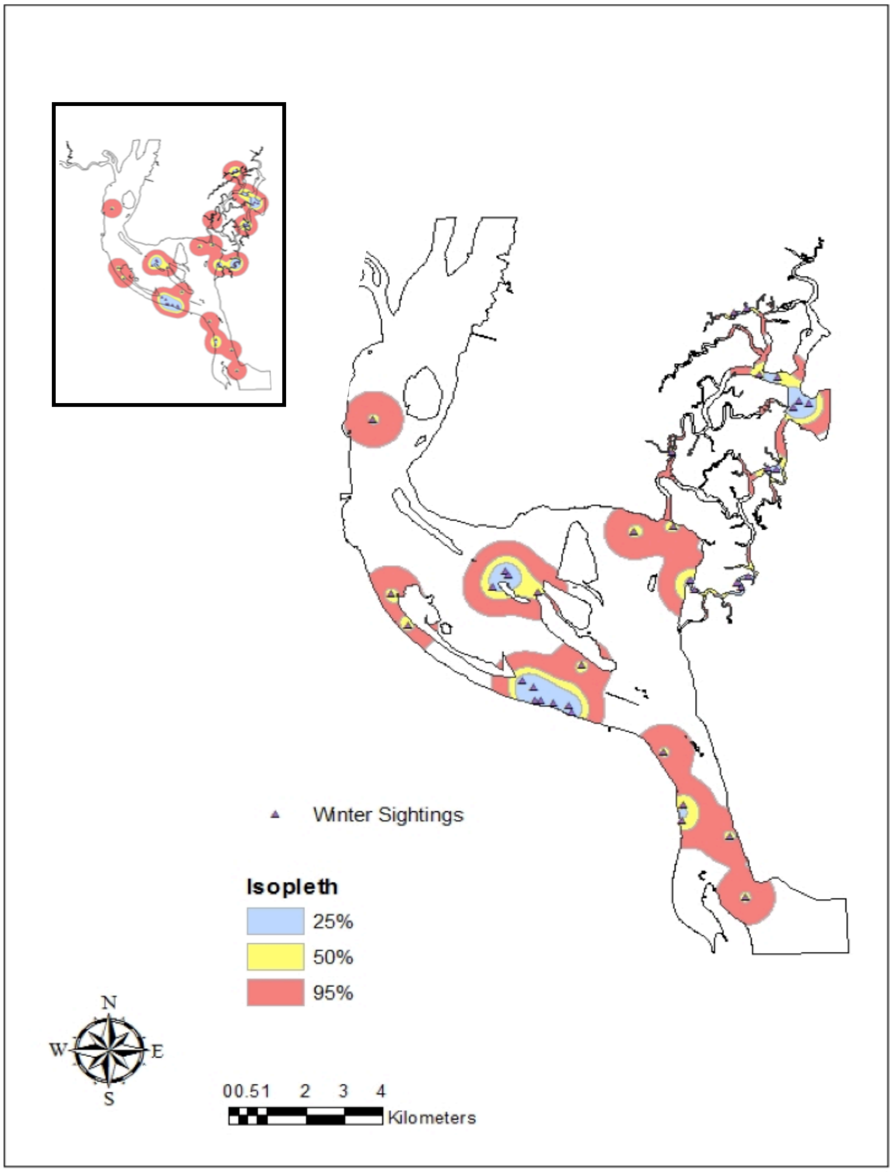


d



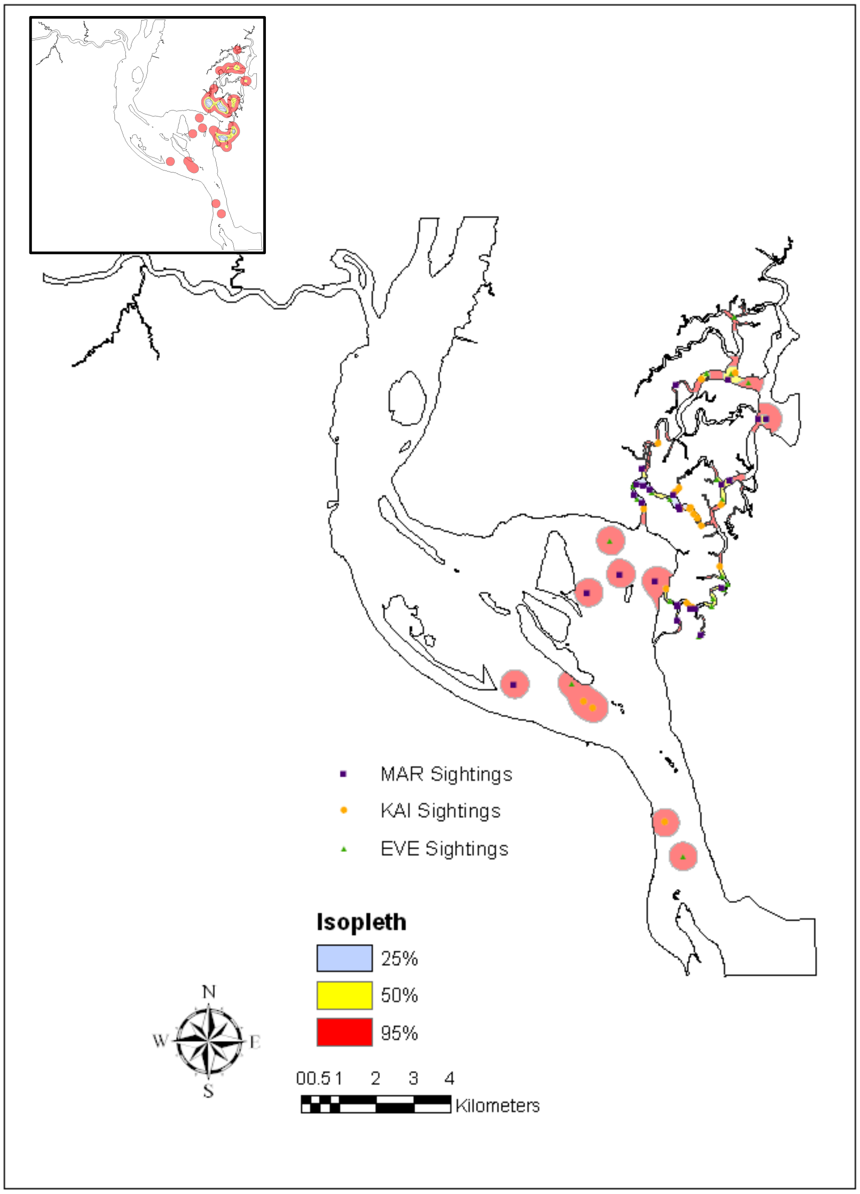
Summer Sightings
Isopleth
25%
50%
95%
N
W
E
S
00.51 2 3 4
Kilometers

e

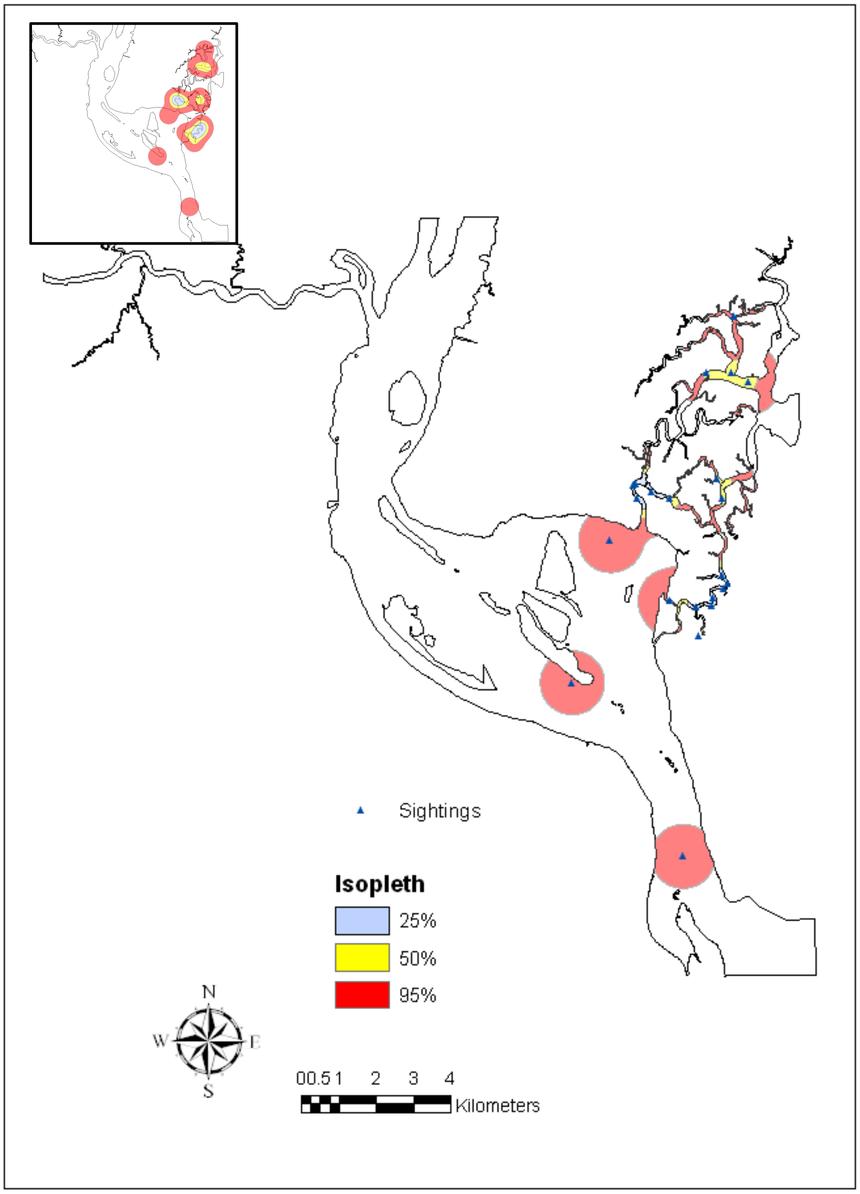


Winter Sightings
Isopleth
25%
50%
95%
N
W
E
S
0 0.5 1 2 3 4
Kilometers

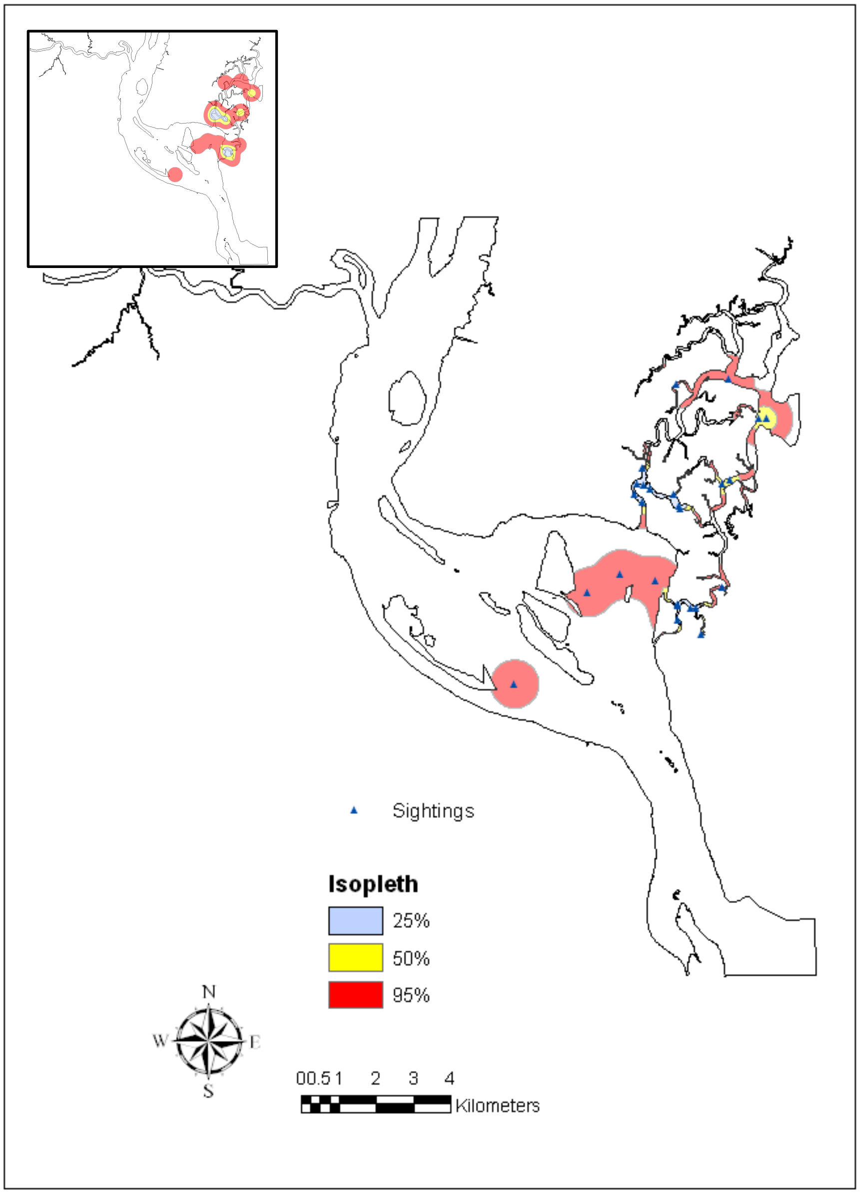
f


MAR Sightings
KAI Sightings
EVE Sightings
Isopleth
25%
50%
95%
N
E
S
W
0 0.5 1 2 3 4
Kilometers

g.



h.



i

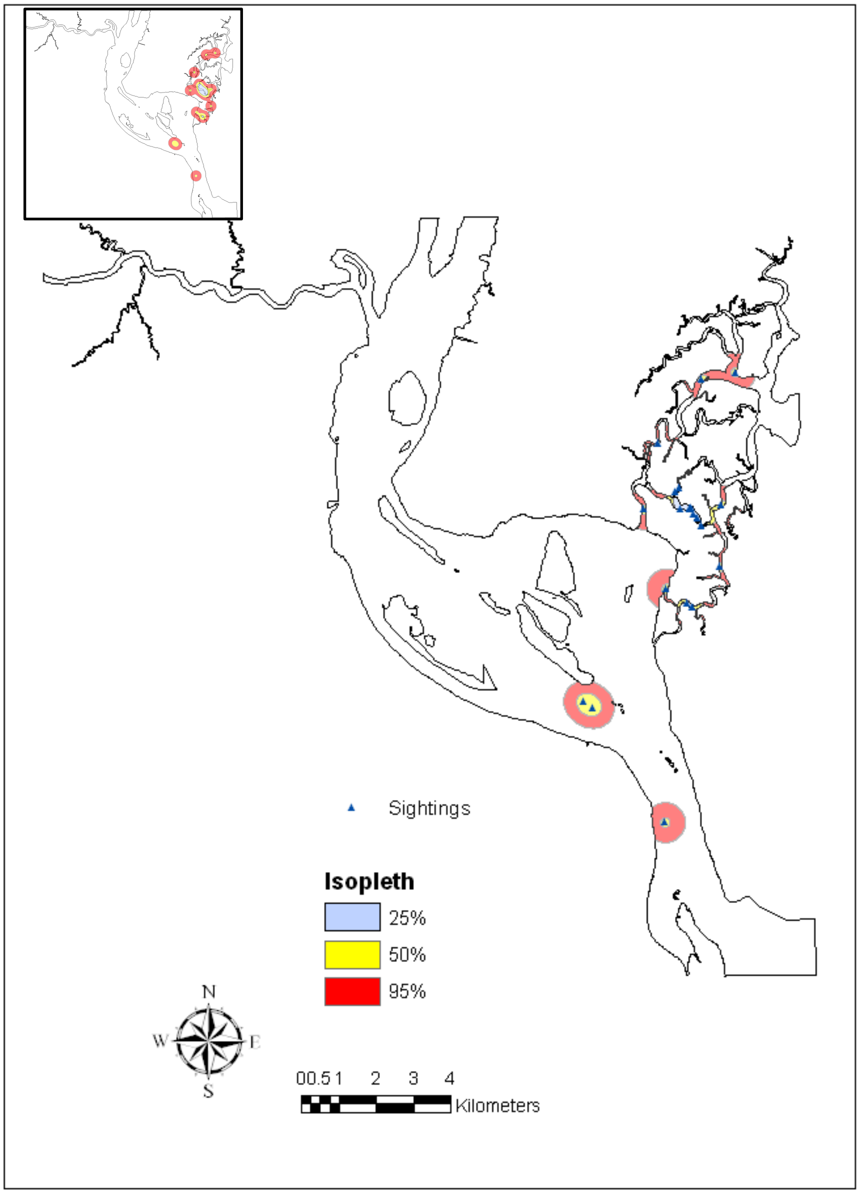


Figure 7. Kernel density map of the North Inlet-Winyah Bay estuary
95% utilization distributions (red) were determined to represent the overall range of the population. 50% (yellow) and 25% (blue) utilization distributions were calculated to determine the core areas within the range. Kernel densities for dolphins seen in both North Inlet and Winyah Bay (NIWB) are shown in (a), for dolphins only seen in Winyah Bay (WB) are shown in (b), and for dolphins only seen in North Inlet (NI) are shown in (c). Warm season distribution is shown in (d), and cold season distribution is shown in (e). Dolphins that were observed using both systems but preferred North Inlet are shown in (f), and each individual preferring North Inlet are shown in (g) (EVE), (h) (MAR), and (i) (KAI). Insets show the full kernel density output, and the large images have been clipped to only show kernel densities for water regions.

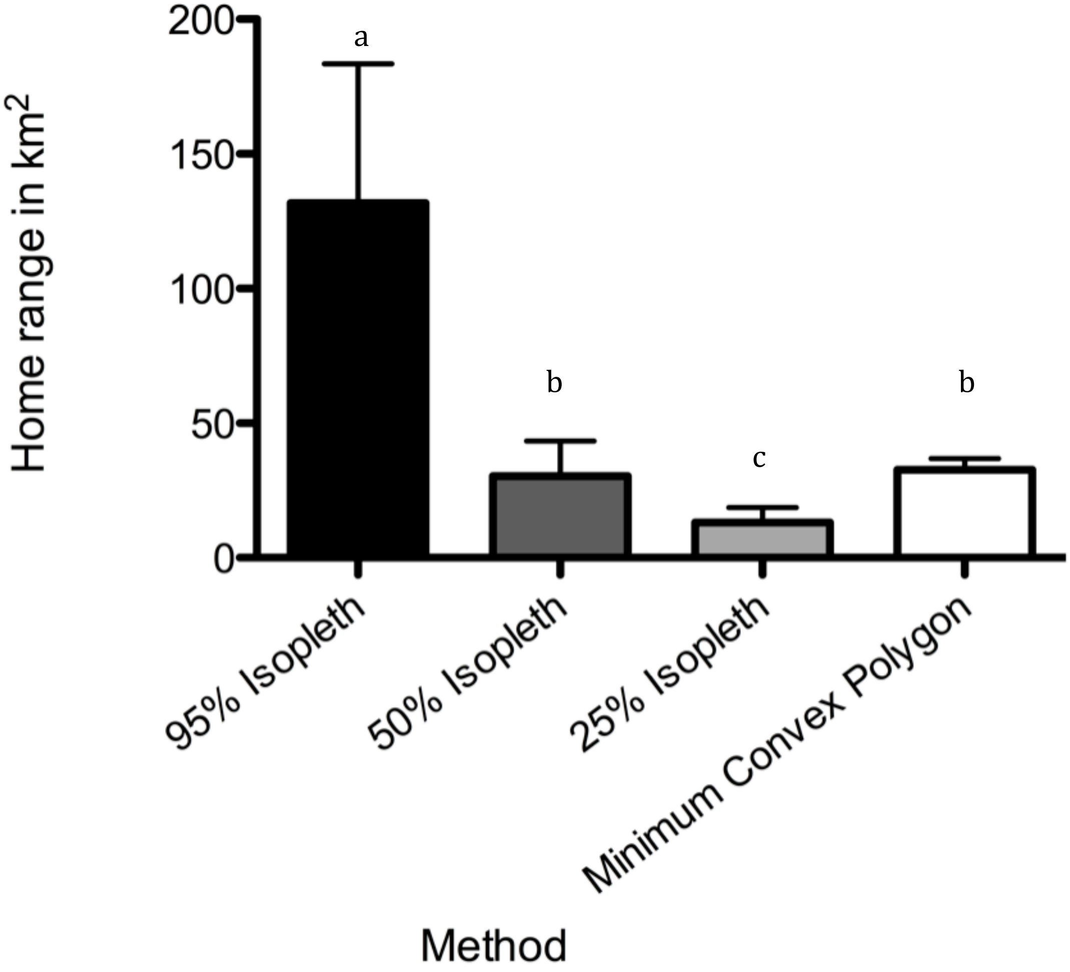


Figure 8. Home range sizes: kernel density vs. minimum convex polygon
The mean home range sizes calculated from three kernel density isopleths (95% isopleth, 50% isopleth, and 25% isopleth) and from the minimum convex polygon method. Mean home ranges were calculated using all identified dolphins with at least 7 sightings. The different letters denote significantly different groups.

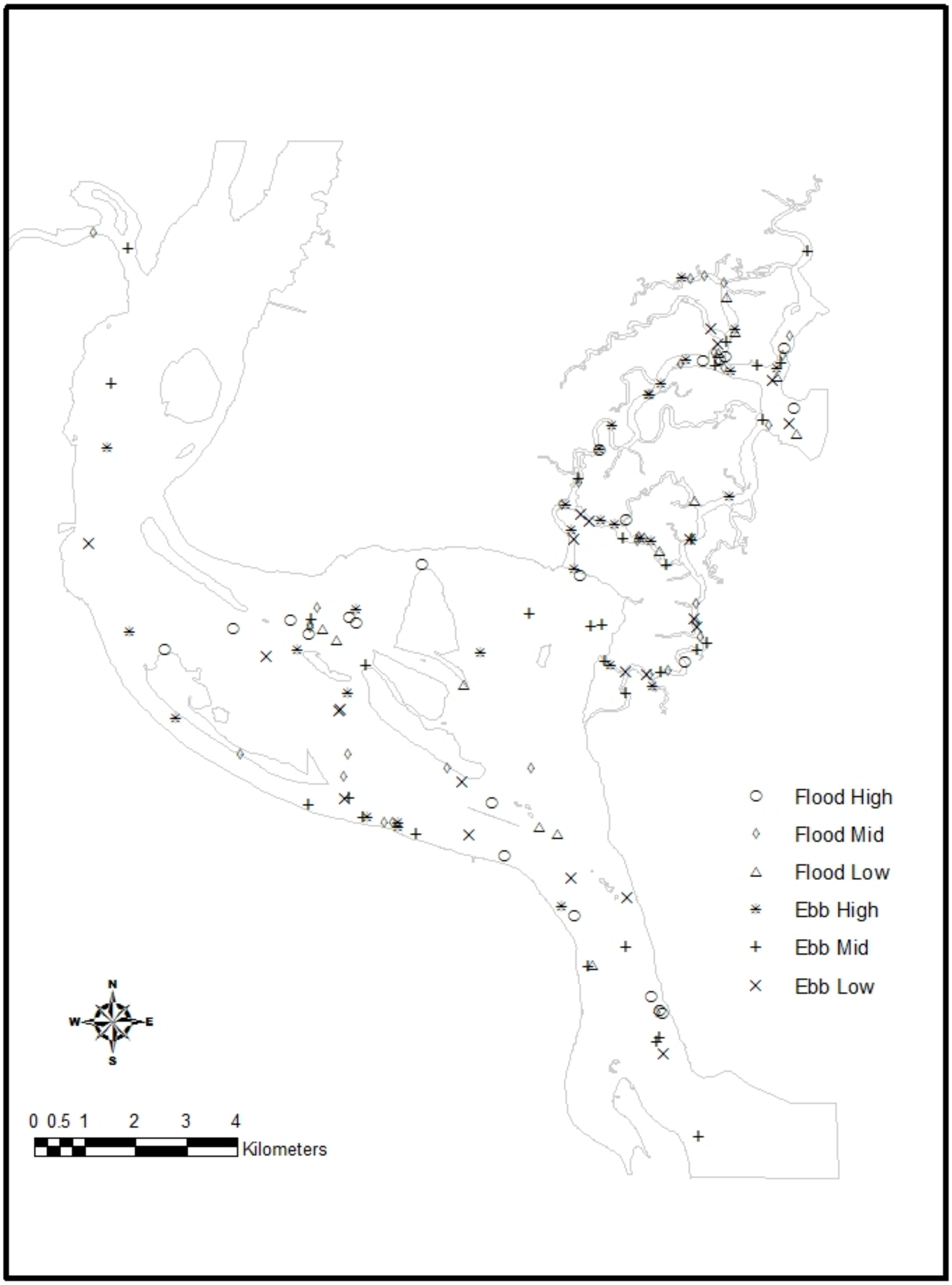


Figure 9. Distribution at various tidal stages

The distribution of bottlenose dolphin sighting events at different tidal stages in the North Inlet Winyah Bay habitat in South Carolina.

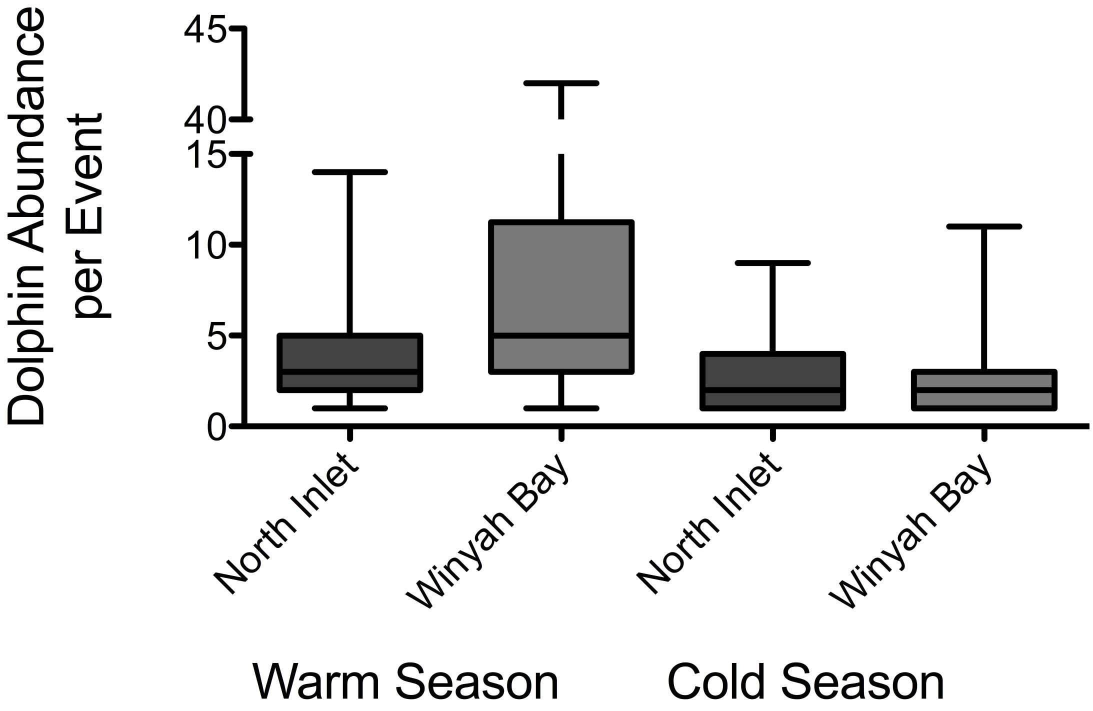


Figure 10. Bottlenose dolphin abundance per event box and whisker plot
The horizontal lines on each box represent the 25th percentile, mean, and 75th percentile for the number of dolphins per event, and the bars represent the range. During the warm season (May17, 2011-October 25, 2011), group sizes in Winyah Bay were greater than in North Inlet. However, in the cold season (December 16, 2011-February 26, 2012), larger groups formed in North Inlet.

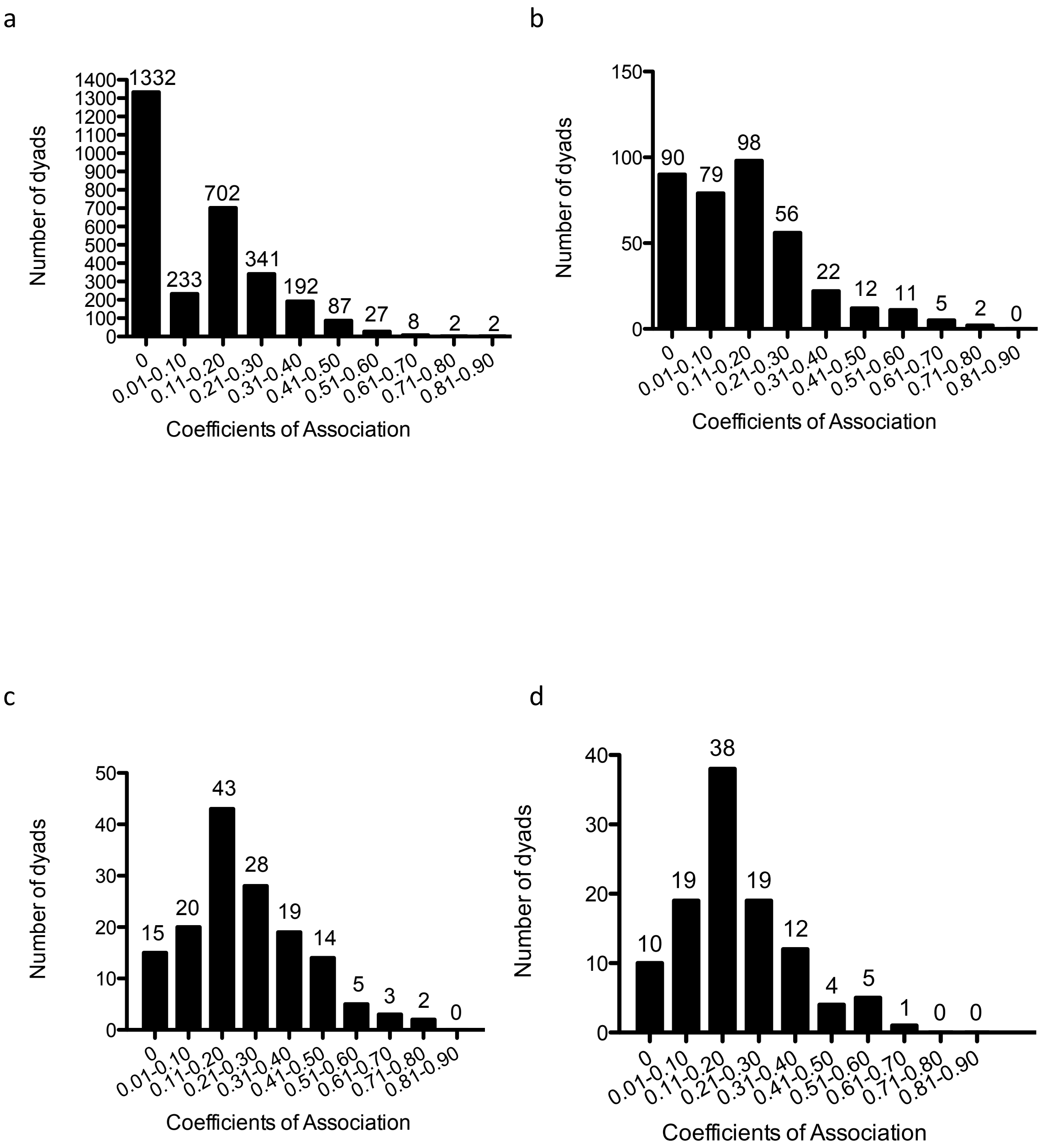
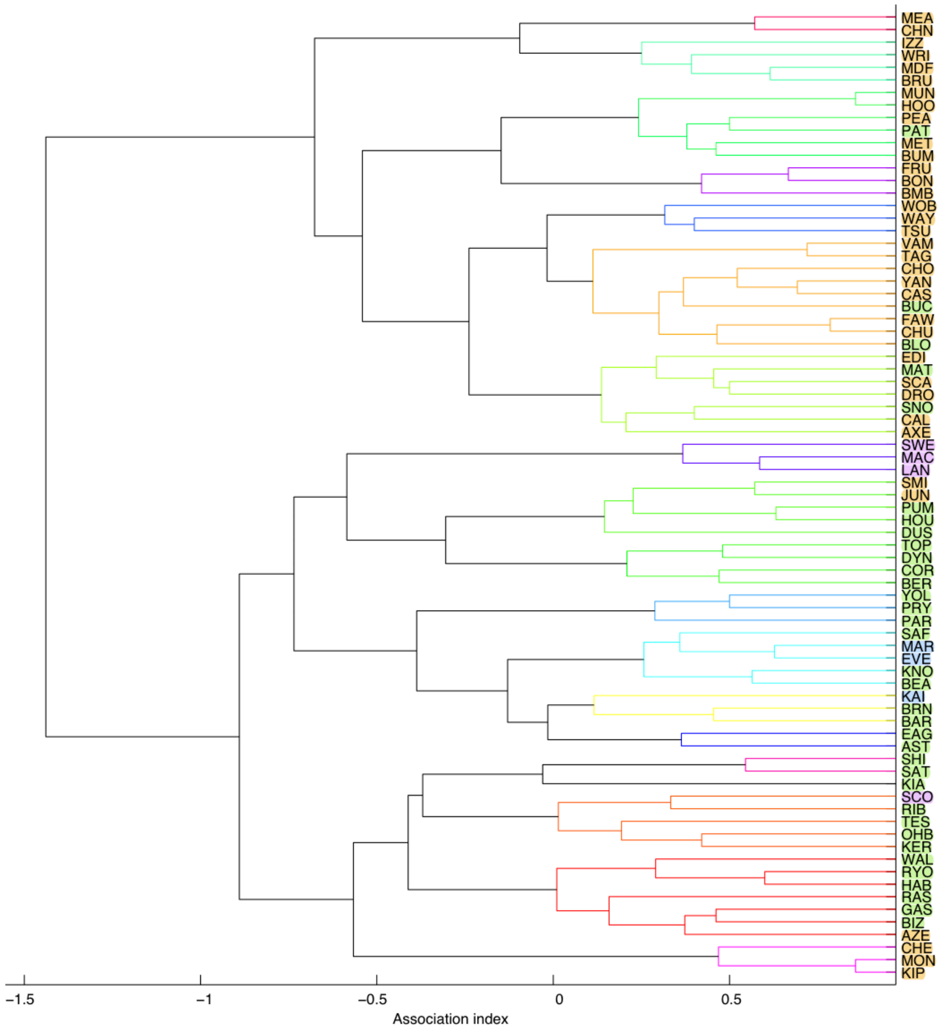


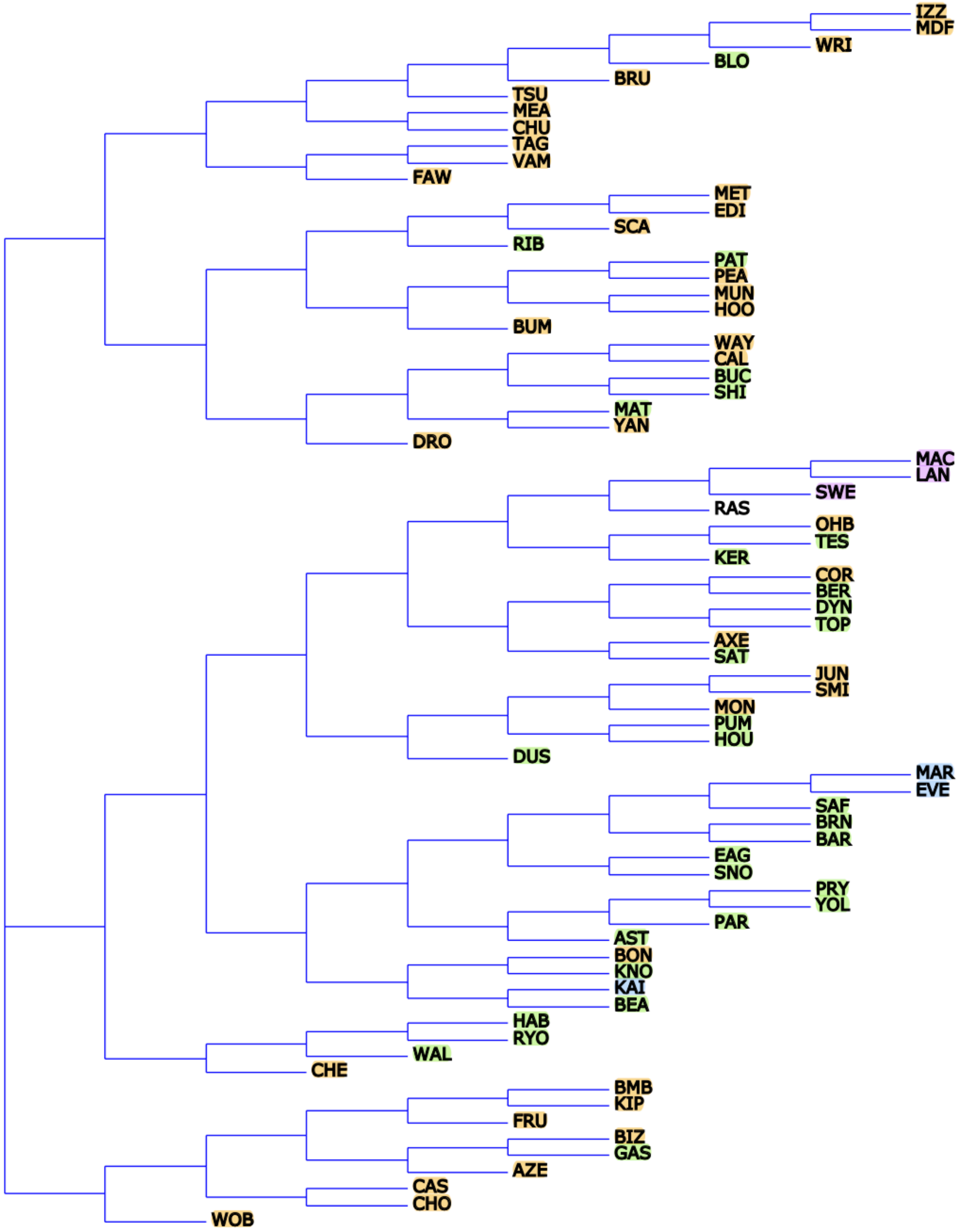
Figure 11. Coefficients of association distribution

The distribution of associations between all bottlenose dolphins sighted in the North Inlet-Winyah Bay system in South Carolina at least three times (random distribution) (a) and at least 10 times (non-random distribution) (b) were calculated using the half weight index. Associations, calculated using the half weight index, among individuals sighted at least 10 times in Winyah Bay are shown in (c), and the distribution of associations, calculated using the half weight index, among individuals sighted at least 10 times in North Inlet is shown in (d).

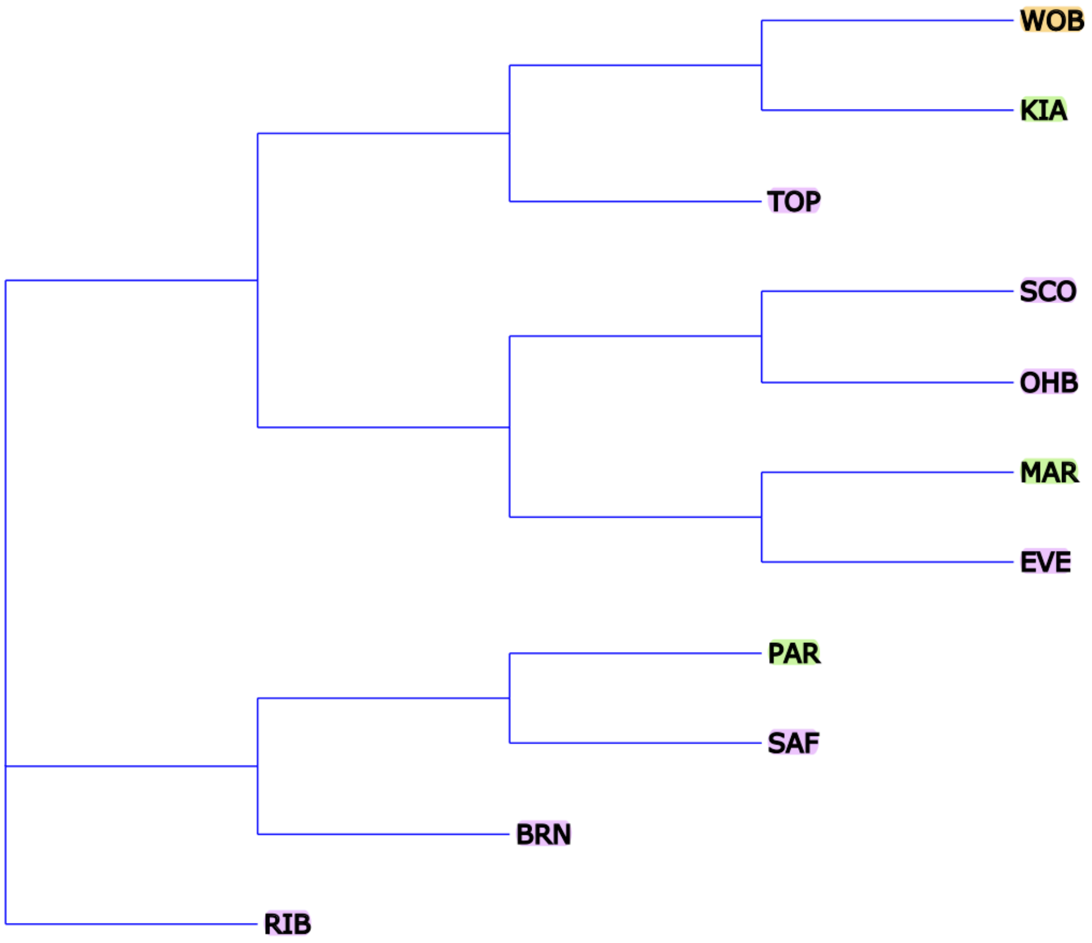
a


MEA
CHN
IZZ
WRI
MDF
BRU
MUN
HOO
PEA
PAT
MET
BUM
FRU
BON
BMB
WOB
WAY
TSU
VAM
TAG
CHO
YAN
CAS
BUC
FAW
CHU
BLO
EDI
MAT
SCA
DRO
SNO
CAL
AXE
SWE
MAC
LAN
SMI
JUN
PUM
HOU
DUS
TOP
DYN
COR
BER
YOL
PRY
PAR
SAF
MAR
EVE
KNO
BEA
KAI
BRN
BAR
EAG
AST
SHI
SAT
KIA
SCO
RIB
TES
OHB
KER
WAL
RYO
HAB
RAS
GAS
BIZ
AZE
CHE
MON
KIP
−1.5
−1
−0.5
0
0.5
Association index

b


IZZ
MDF
WRI
BLO
BRU
TSU
MEA
CHU
TAG
VAM
FAW
MET
EDI
SCA
RIB
PAT
PEA
MUN
HOO
BUM
WAY
CAL
BUC
SHI
MAT
YAN
DRO
MAC
LAN
SWE
RAS
OHB
TES
KER
COR
BER
DYN
TOP
AXE
SAT
JUN
SMI
MON
PUM
HOU
DUS
MAR
EVE
SAF
BRN
BAR
EAG
SNO
PRY
YOL
PAR
AST
BON
KNO
KAI
BEA
HAB
RYO
WAL
CHE
BMB
KIP
FRU
BIZ
GAS
AZE
CAS
CHO
WOB

c



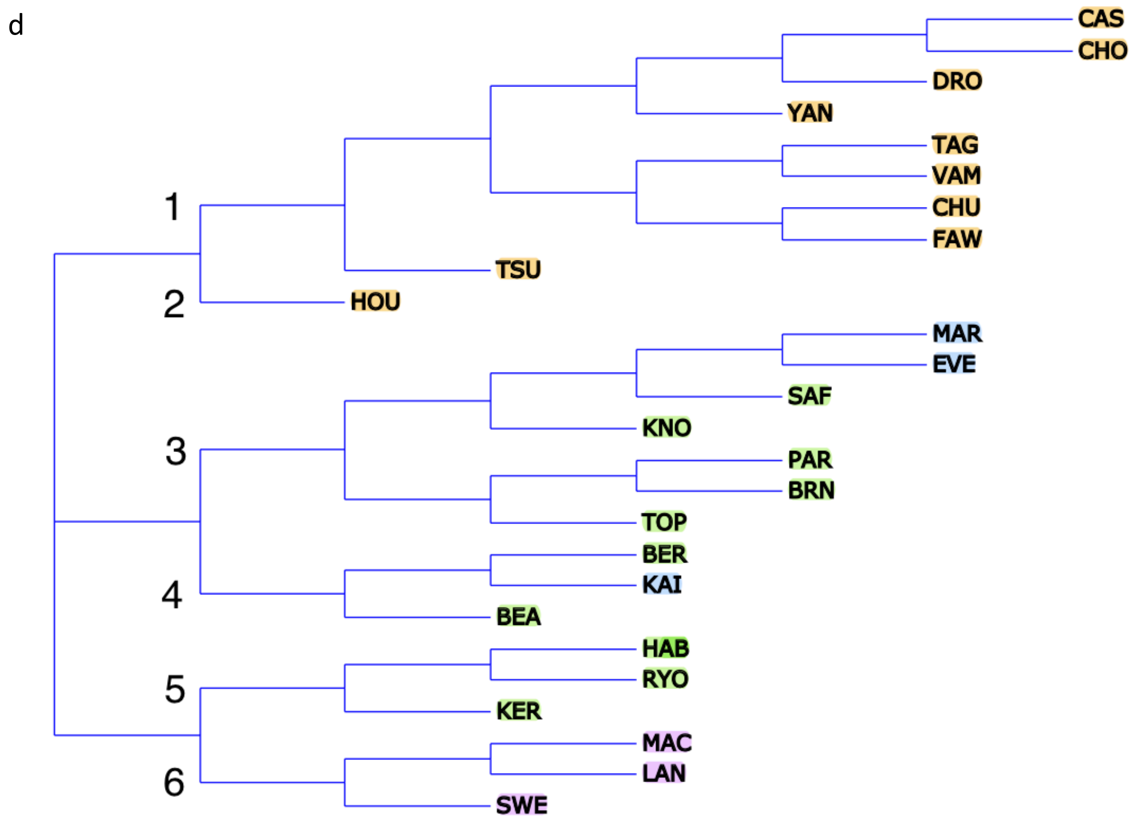
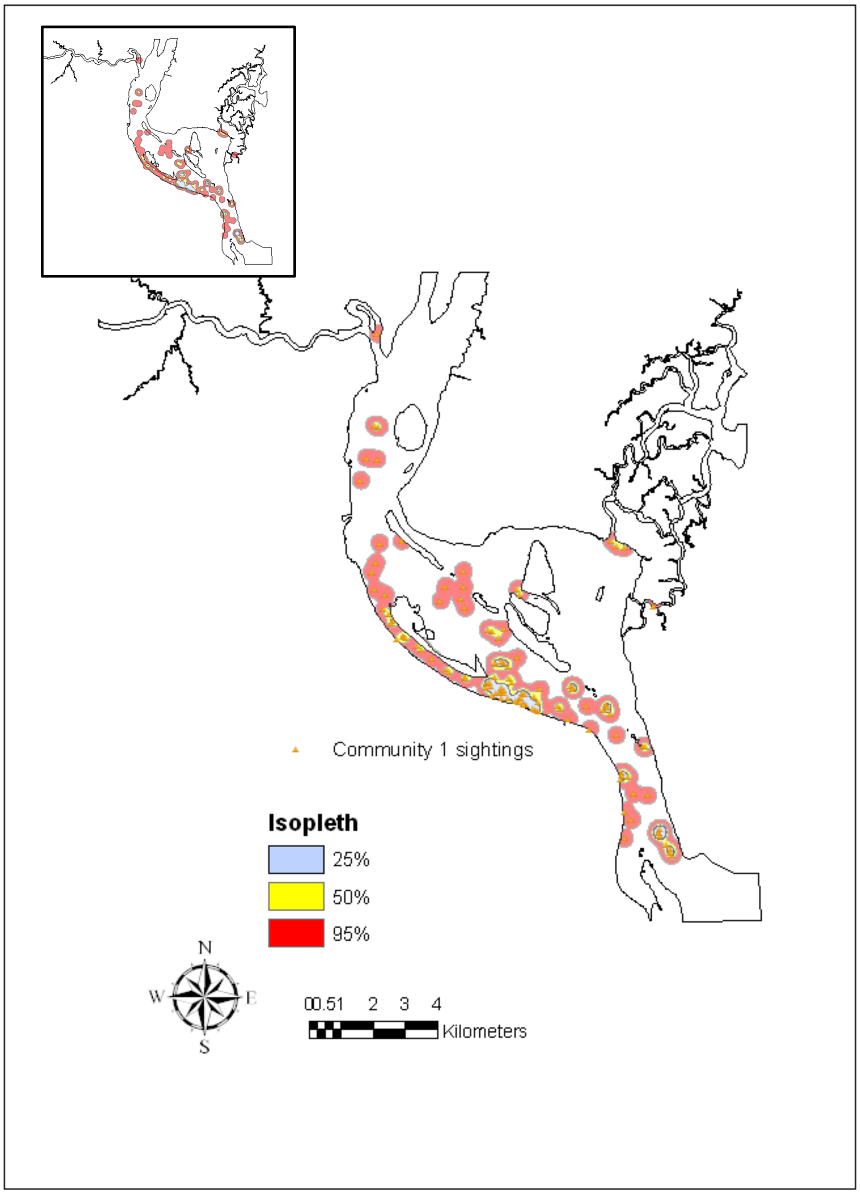
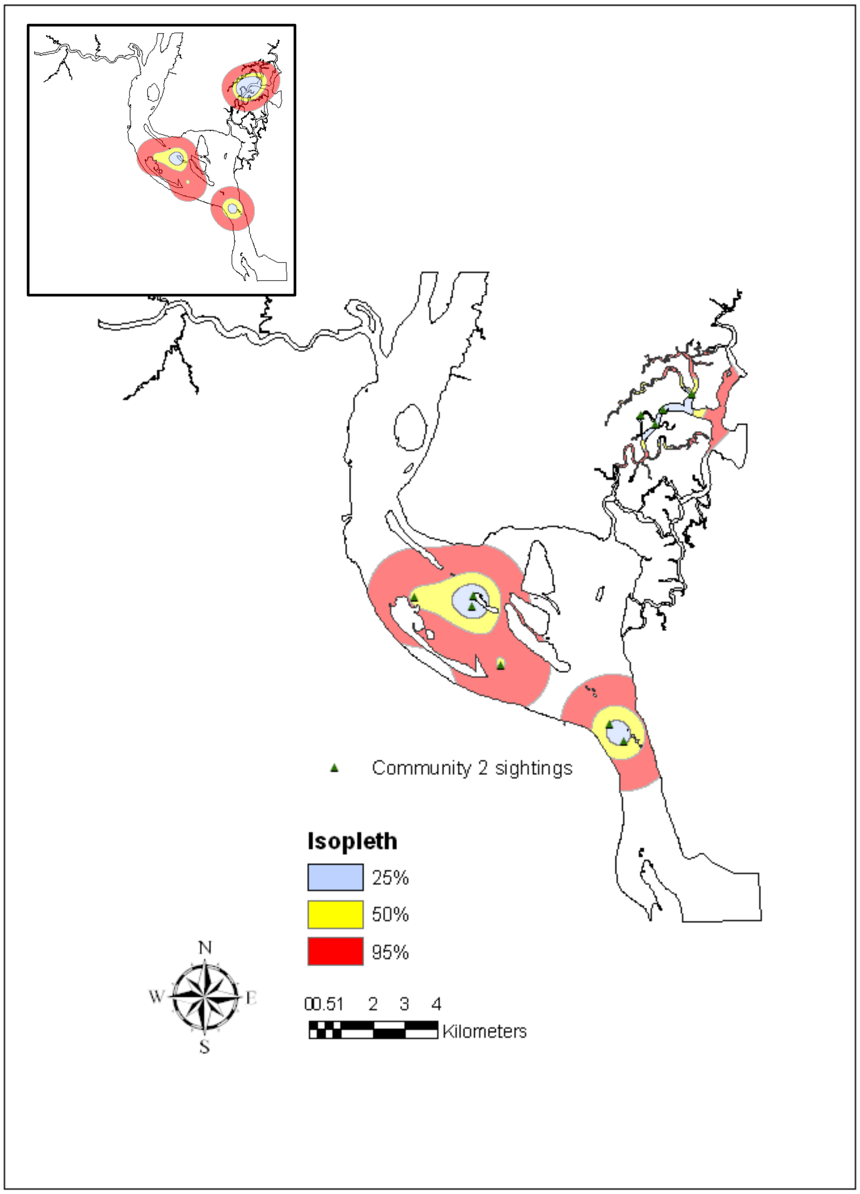


Figure 12. Dendrograms representing association relationships
Dendrograms(a), (b), and (c) represent associations between all adults sighted at least three independent times. Individuals sharing a single node are the most closely associated. Relationships remained quite consistent between warm (May 17, 2011-October 25, 2011) (b) and cold (December 16, 2011-February 26, 2012) (c) seasons. The relationships including both warm season and cold season data are shown in (a). Additionally, individuals sighted 10 or more times during either season are shown in (d). The names highlighted in purple were individuals only sighted in North Inlet. Orange highlighted names represent individuals only sighted in Winyah Bay. Green highlighted names are individuals that were seen in both North Inlet and Winyah Bay evenly. Blue names represent individuals that were seen in both North Inlet and Winyah Bay but preferred North Inlet. The numbers in (d) represent the 6 different communities present among dolphins in the NIWB system.

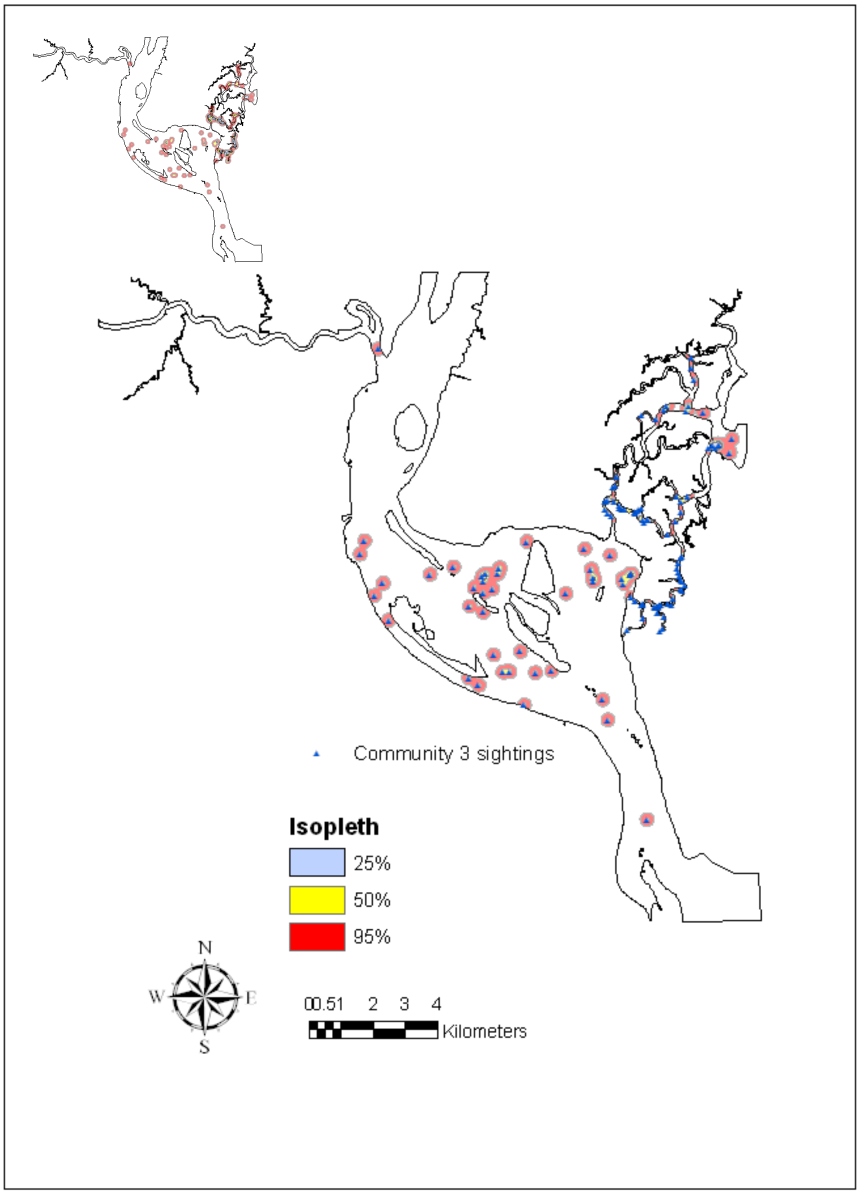
a.


Community 1 sightings
Isopleth
25%
50%
95%
N
W
E
S
00.51 2 3 4
Kilometers

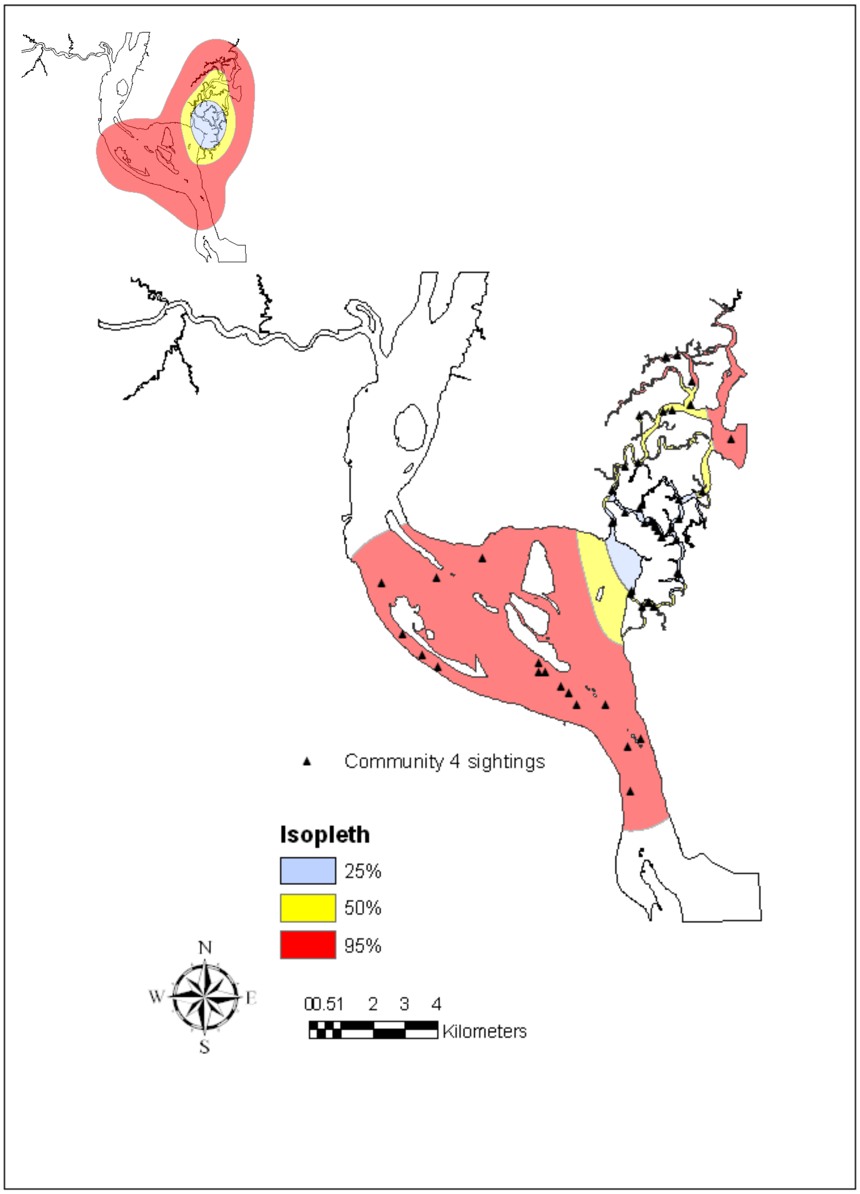
b.


Community 2 sightings
Isopleth
25%
50%
95%
N
W
E
S
0 0.5 1 2 3 4
Kilometers

c.

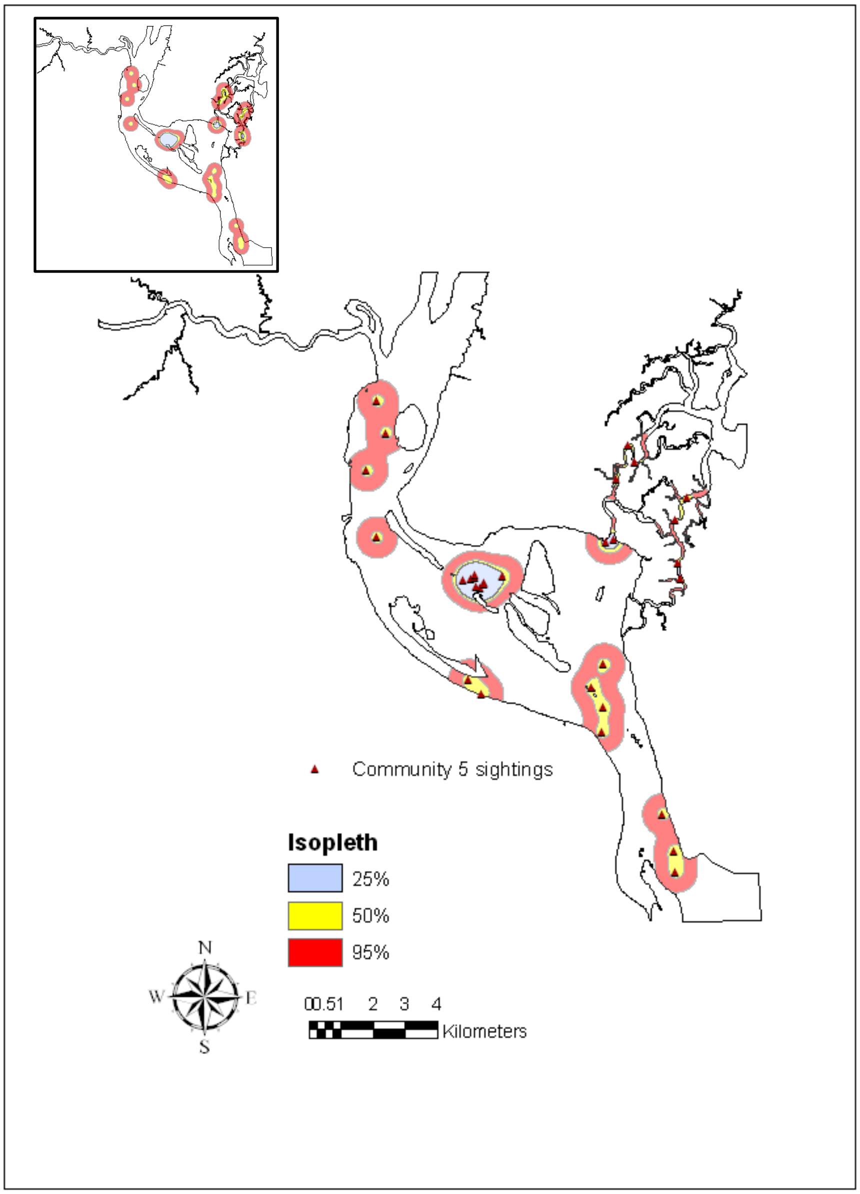

▲ Community 3 sightings
Isopleth
25%
50%
95%
N
W
E
S
00.51 2 3 4
Kilometers

d.



Community 4 sightings
Isopleth
25%
50%
95%
N
W
E
S
00.51 2 3 4
Kilometers

e.


Community 5 sightings
Isopleth
25%
50%
95%
N
W
E
S
00.51 2 3 4
Kilometers

f.

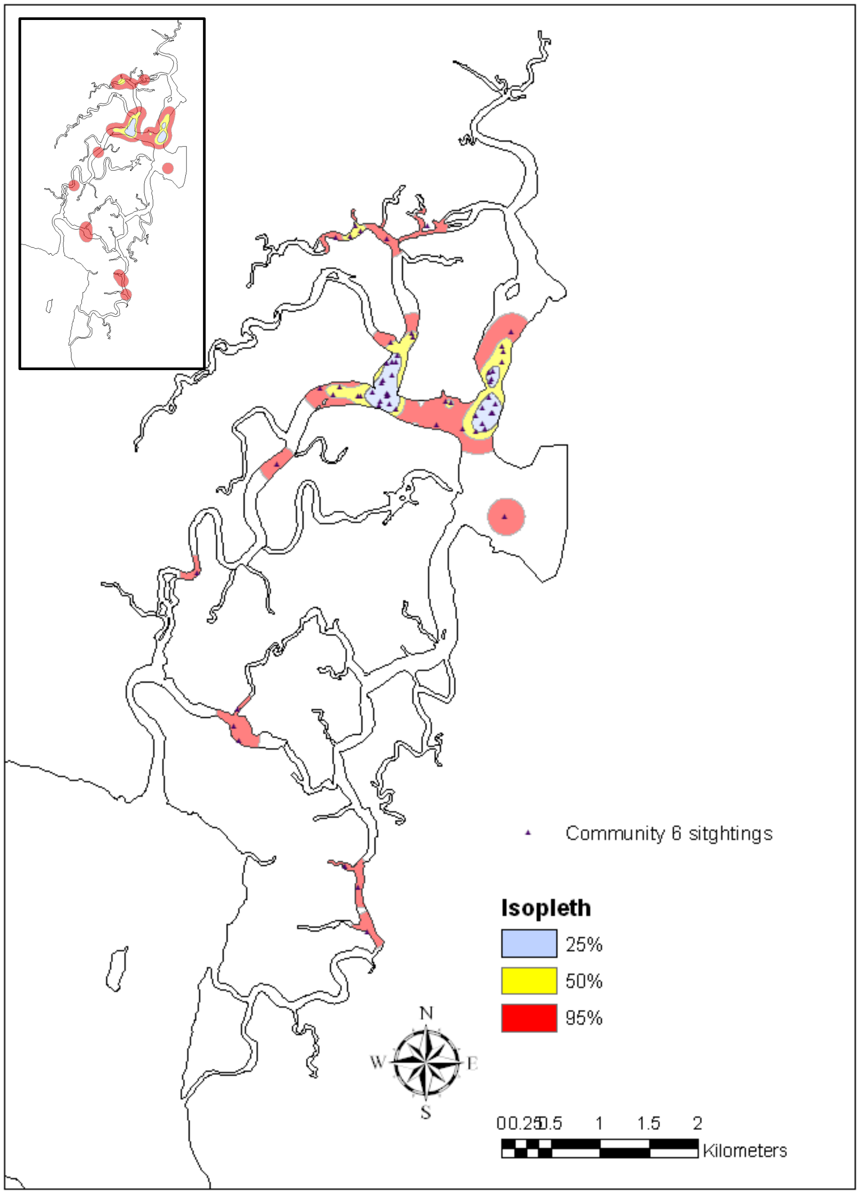


Figure 13. Kernel density map of North Inlet-Winyah Bay dolphin communities
Kernel densities were constructed for each of the 6 communities (a-f) represented in figure 12d.