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Common Bottlenose Dolphin, *Tursiops truncatus,* Seasonal Habitat Use and Associations with Habitat Characteristics in Roanoke Sound, North Carolina

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Understanding how habitat characteristics influence common bottlenose dolphin, *Tursiops truncatus*, distribution and behavior can be useful for conservation. The dolphin community in Roanoke Sound, North Carolina, primarily exhibits seasonal residency, and there is limited information on their habitat use. The objectives of this study were to increase habitat use knowledge and to determine the relationship between habitat characteristics and dolphin distribution using standardized photographic-identification data (2009-2017). A hot spot (Getis-Ord Gi*) analysis showed dolphins frequently use the southern region containing the mouth of the estuary for feeding and traveling. Habitat characteristics were modeled with zero-altered gamma (ZAG), generalized linear (GLM), and generalized additive (GAM) models to predict dolphin group density. Models showed that groups were more likely to be present in areas with greater benthic slope variation and shallow areas closer to land and that different habitat characteristics were associated with feeding, social, and travel activities. This study suggests that the Roanoke Sound provides a seasonal foraging area and travel corridor between the estuaries and coastal waters. This information contributes baseline knowledge of how habitat potentially influences dolphin distribution and behavior, which can be useful for management and conservation, especially in areas where both habitat changes and impacts need to be assessed.

Keywords: habitat utilization, hot spot (Getis-Ord Gi*), species distribution models, habitat-based density models, zero-inflated models, cetacean, standardized photographic-identification surveys

Understanding how and why common bottlenose dolphins, *Tursiops truncatus*,

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exhibit variation in their distribution and habitat use across study sites can be useful for management, conservation, and mitigating anthropogenic disturbance. Studies have found that dolphins aggregate in areas with high productivity, such as mouths of estuaries and deep, narrow channels (Acevedo, 1991; Ballance, 1992; Hanson & Defran, 1993; Harzen, 1998; Hastie, Wilson, & Thompson, 2003; Ingram & Rogan, 2002; Wilson, Thompson, & Hammond, 1997). Specific habitat characteristics, such as depth, benthic slope, distance to land, presence of submerged aquatic vegetation (hereafter called "SAV"), and environmental variables, including salinity and water temperature, have been associated with dolphin distribution and habitat use (Barco, Swingle, McLellan, Harris, & Pabst, 1999; Barros & Wells, 1998; Hastie et al., 2003; Hastie, Wilson, Wilson, Parsons & Thompson, 2004; Ingram & Rogan, 2002; Miller & Baltz, 2009; Shane, 1990; Wilson et al., 1997; Würsig & Würsig, 1979). An increasing number of studies are applying a variety of statistical models to examine and predict cetacean distribution using habitat characteristics to gain insight into how changes in habitat can impact a cetacean population (see Redfern et al., 2006, for review).

Dolphins exploit a wide variety of habitats including inshore, coastal, and oceanic waters. Photographic-identification studies have provided evidence that different habitats coincide with differences in dolphin distribution patterns, but more data are needed to determine the relationship between habitat and distribution across a range of habitats. Studies in inshore areas of the United States (US) Atlantic and Gulf of Mexico coasts have documented long-term, year-round residency of dolphins to a number of bay, sound, or estuary sites (Wells & Scott, 2018). However, dolphins may also exhibit seasonal residency or low site fidelity to these study areas (Balmer et al., 2008; Scott, Wells, & Irvine, 1990; Shane, 1990; Shane, Wells, & Würsig, 1986; Speakman, Lane, Schwacke, Fair, & Zolman, 2010; Zolman, 2002). As compared to the US Atlantic and Gulf coasts, multiple studies on the US Pacific coast have found that dolphins range over larger areas and exhibit low site fidelity to any specific location (Ballance, 1992; Defran, Weller, Kelly, & Espinosa, 1999). For example, in the eastern Gulf of Mexico, year-round resident dolphins in Sarasota Bay, Florida, have home ranges between approximately 11-146 km^2 with an average between 57-62 km^2 within the estimated 125 km^2 study area. Resident dolphins in this area feed primarily on fish associated with seagrass, which are prevalent within this shallow, protected inshore area (Barros & Wells, 1998; Wells, 2003; Wilkinson, 2014). By contrast, along the US Pacific coast, dolphins in the Southern California Bight have larger home ranges (range: 50-470 km), and their prey species are patchily distributed over an open coastline (Defran et al., 1999). These vast differences in distribution patterns may be influenced by habitat characteristics, environmental variables, and prey distribution (Ballance, 1992; Defran et al., 1999).

Along the US Atlantic coast, there is limited information on the distribution and habitat use of the Roanoke Sound, North Carolina, dolphin community. This community primarily utilizes the estuarine waters of North Carolina during warm months (Gorgone, Eguchi, Byrd, Altman, & Hohn, 2014; Hayes et al., 2018). Dolphins in Roanoke Sound and the neighboring inshore waters are considered to comprise the Northern North Carolina Estuarine System Stock based on a combination of photographic-identification data, telemetry data, and genetic data. This stock occupies inshore waters and coastal waters (≤1 km from land) from Beaufort, North Carolina, to Virginia Beach, Virginia, during warm months (July-August). During cold months, most dolphins move to nearshore coastal waters (<3 km from land) off the southern coast of North Carolina (Hayes et al., 2018). Dolphins have been observed to remain in inshore waters during the winter; however, these dolphins were distributed in the southernmost end of their stock range and close to coastal waters (Goodman, Braun-McNeill, Davenport, & Hohn, 2007). Photographic-identification data show that most dolphins exhibit low site fidelity to Roanoke Sound, but there are dolphins that exhibit moderate to high site fidelity, and at least 12 dolphins have been documented to return every year over a six-year period (Taylor, Fearnbach, & Adams, 2017). These results suggest there is a small, stable community in Roanoke Sound, and many dolphins are short-term visitors. Comparisons among photographic-identification catalogs show that at least 71 dolphins sighted in Roanoke Sound have been sighted in other study sites along the Maryland, Virginia, and North Carolina coasts (Urian, 2018, OBIS-SEAMAP), further supporting that many of these dolphins move between Roanoke Sound and other inshore and nearshore areas on the US Atlantic coast.

Habitat, environmental variables, and prey distribution likely influence the dolphins' seasonal distribution patterns in the northern Outer Banks. Seasonal changes in abundance have been correlated with changes in water temperature along the neighboring coast of Virginia. This observation suggests that dolphins may migrate to warmer waters during the winter to meet thermoregulation demands (Barco et al., 1999; Kenney, 1990). Additionally, dolphin prey species seasonally migrate to offshore Atlantic waters during winter to spawn and return to estuarine waters during the spring and summer (Gannon & Waples, 2004). McBride-Kebert et al. (2019) found that from late spring to early fall, Roanoke Sound dolphins frequently used the southern region of the sound containing the estuary mouth for feeding and traveling. This finding suggests that the dolphins may use Roanoke Sound as a seasonal foraging area and travel corridor between estuaries and Atlantic coastal waters. However, McBride-Kebert et al. (2019) did not examine the relationship between habitat characteristics and dolphin distribution, and more information is needed to determine why dolphins seasonally migrate to Roanoke Sound. Our objective was to expand on the study by McBride-Kebert et al. (2019) in order to increase our understanding of the interaction between dolphin distribution and habitat characteristics. Specifically, we (1) identified areas that were frequently used by dolphins, (2) determined which activities were observed most often in these frequently used areas, and (3) determined if habitat characteristics and environmental variables were associated with dolphin distribution and activity in Roanoke Sound, North Carolina.

Method

Survey Area

Roanoke Sound is located in the northern part of the Outer Banks of North Carolina, and it separates Roanoke Island from the Outer Banks barrier islands. This sound is a small part of the Albemarle Pamlico Estuary System, which is a drowned river valley, and it drains through Oregon Inlet out to the Atlantic Ocean (Giese, Wilder, & Parker, 1985). Roanoke Sound is an area of approximately 140 km^2.

Estimated average depth is 2.23 m (*SD* = 1.14 m) and the deepest estimated depth is 7.10 m. For this study, Roanoke Sound was divided into three regions: northern, central, and southern regions (Figure 1). The northern region is a more open area with a relatively small amount of variation in benthic slope and small patches of SAV. The central region is a narrow channel between Roanoke Island and the Outer Banks barrier islands, and it has small patches of SAV primarily on the shallow eastern side. The southern region contains the mouth of the estuary, Oregon Inlet, and is characterized by a large amount of slope variation and SAV. The division of the sound into regions serves to facilitate interpretation of results rather than represent distinct biological divisions in the survey area.

Data Collection

Standardized photographic-identification surveys were conducted from spring of 2009 through fall of 2017. There were originally two survey routes to cover the north-central and south-central regions on different days. North-central and south-central surveys were attempted at least once a month year-round, alternating route order each month. In the fall of 2011, these routes were joined into one full route that covered the entire survey area. A full survey was attempted at least once a month year-round. The full survey route was modified in 2014 to reduce the number of east to west cross-sections in the northern region. The survey vessel followed standardized navigational waypoints marked by GPS, and vessel tracklines were recorded by GPS since fall of 2011.

At least two researchers collected data and took photos of dolphins' dorsal fins for photographic-identification. Data recorded during dolphin sightings included GPS coordinates and times for start and end locations, estimated group size, number of calves, weather conditions, Beaufort sea state, sea surface temperature (hereafter "SST"), salinity, and activity. Dolphins within 10 m of each other engaging in similar activities were considered to be part of the same group (adapted from Smolker, Richards, Connor, & Pepper, 1992). Sightings ended when one of the following conditions were met: (1) The photographer obtained identification photos for each group member, (2) the group was not seen surfacing for nine minutes, or (3) the sighting lasted an hour, which is the maximum sighting time under the study permit. Any occurrence of an activity throughout the sighting was recorded (Table 1).

Table 1
Activity definitions (adapted from Urian & Wells, 1996; Waples, 1995)

Feed	Dolphin is observed with a fish in mouth
Probable Feed	Fish chase, multiple fast surfacings, tail-out dives/peduncle-out dives
Mill	Non-directional movement in which group members are headed in different directions and stay in the same area
Social	Active interactions with other individuals (rubbing, chasing, etc.)
Travel	Directional movement with regular surfacings

Identifying Frequently Used Areas

A hot spot analysis was conducted to identify areas frequently used by dolphins. A grid of 1 km × 1 km cells was created in ArcGIS 10.X geospatial software (Redlands, CA) to sample the survey area. This cell size was chosen because the average distance between the start and end coordinates of a sighting was approximately 0.98 km (*SD* = 0.76 km). The centroid of the start and end coordinates was used to represent group locations because it provides a general location of where the dolphins moved throughout the sighting as data were collected. All survey vessel tracklines from 2009 through 2017 were projected to WGS 1984 World Mercator spatial reference system, and tracklines were intersected with the grid to calculate survey kilometers within each grid cell. A survey trackline was recreated from navigational waypoints to represent north-central and south-central surveys from 2009 through 2011 which did not have vessel tracklines recorded by GPS. After reviewing effort logs to recreate survey tracklines, it was determined that north-central surveys from 2009 through 2011 did not consistently follow standardized navigational waypoints, and these surveys were excluded from analyses.

The number of dolphin groups were counted for each cell in the grid. Survey kilometers were also summed for each cell. The number of groups was divided by the survey kilometers within each cell to obtain group density (groups/km). The hot spot (Getis-Ord Gi*) statistic identified clusters of high (hot spot) and low (cold spot) group density values across the survey area in order to determine areas that were frequently used. This statistic compared an observed local sum of group density, which is the sum of a cell and its neighbors, to an expected local sum of group density. A *z*-score and *p*-value were calculated based on the ratio of observed local sum to expected local sum for each cell (ArcGIS Resource Center, 2012; Getis & Ord, 1992).

Initially, the average distance between neighboring groups was calculated in order to run the hot spot analysis (adapted from Smith et al., 2013). This distance was used as the minimum distance in the Incremental Spatial Autocorrelation (ISA) tool to detect peaks in spatial autocorrelation of group density. The first ISA peak was used as the distance threshold to detect hot spots. A spatial weights matrix file provided the analysis parameters to calculate the observed local sum for the hot spot (Getis-Ord Gi*) statistic. These parameters were to (1) use the first ISA peak as the distance threshold and (2) include at least eight neighboring cells to calculate the observed local sum (Getis & Ord, 1992). If eight neighboring cells were not within the distance threshold, then the distance threshold was extended to include a minimum of eight cells.

Multiple comparisons of the same cells were made during the hot spot analysis due to their inclusion for the observed local sum calculation. Thus, the introduction of Type I error (i.e., false hot spots) was possible (Ord & Getis, 1995). A Bonferroni correction, which divides the significance level by the number of comparisons, has been suggested to control for Type I error, but this correction can be too conservative for large sample sizes (Getis & Ord, 1992; Ord & Getis, 1995). The large sample size of this dataset (n = 140 cells) indicated a Bonferroni correction would be too conservative ($p < 0.00036$). Thus, the significance level of 0.001 was used to control for potential Type I error. Hereafter, hot spots have significance of $p < 0.001$. Additionally, the hot spot analysis can be sensitive to outliers, so five percent of the farthest groups were removed prior to analyses in order to eliminate outlier bias (Smith et al., 2013). Outlier groups were determined by calculating the distance between neighboring groups and removing groups with the largest neighbor distances.

Identifying Activities in Frequently Used Areas

In order to determine which activities were observed most often in frequently used areas, hot spot analyses were conducted for dolphin groups that were observed to feed, mill, socialize, or travel. Feed and probable feed activities were combined into a single hot spot analysis. Mill activity is hypothesized to be associated with feed, rest, and social activities (Shane et al., 1986). Since mill is associated with multiple activities, mill groups were analyzed separately in order to determine if this activity was more closely associated with other activities. Each activity was analyzed separately at the 1-km^2 resolution to maintain spatial parity with the frequently-used-areas analysis. If multiple activities were observed for a group, then that group was included in all relevant activity hot spot analyses.

Modeling Habitat Associations with Group Distribution and Activity

A species distribution model (SDM) was used to determine if habitat characteristics were associated with dolphin distribution and activity. Several habitat characteristics were tested in SDM models: average depth, minimum depth, maximum depth, average slope, slope standard deviation to represent slope variation, distance to land, and distance to SAV. A grid with 500 m × 500 m cells was created to sample the survey area. This resolution was used instead of the 1-km^2 resolution used for hot spot analyses because the 1-km^2 resolution was too coarse to represent variation in habitat characteristics. Dolphin group density (groups/km) and habitat characteristics were calculated for each cell. Depth data were extracted as point values from a digitized NOAA Raster Navigational Chart (available at NOAA Office of Coast Survey, 2014). These depth values were interpolated using the Topo to Raster tool to estimate depth for the entire survey area using a 100 m × 100 m cell size. The estimated depth data were masked by the land data so that land barriers would not interfere with depth calculations. Slope data were calculated based on the estimated depth using the Slope tool. The Zonal Statistics as Table tool was then used to calculate depth and slope for each 500-m^2 cell, and the statistical summary tables were joined with the grid containing group density. Distance to land (m) and distance to SAV (m) were calculated using the Near tool, which calculates the Euclidean distance between each cell and the closest land or SAV. The land data were obtained from NOAA Shoreline website (NOAA, 2016) and the SAV data were obtained from the North Carolina One Map Geospatial Portal (Albemarle-Pamlico National Estuary Partnership).

Three types of SDMs were tested to find the model that explained the most variation in dolphin distribution: generalized linear models (GLM), generalized additive models (GAM), and zero-altered gamma (ZAG) models. Dolphin group density was the dependent variable, and habitat characteristics were the predictor variables. A ZAG model, which is a type of zero-inflated model that fits both a presence-only GLM with a gamma distribution and a presence-absence GLM with a binomial distribution, was tested because the majority (82.89%) of group density values were zeros (Zuur & Ieno, 2016). Habitat characteristics were initially examined for collinearity to remove highly correlated variables ($r >$ 0.80) (MacLeod, 2013). Habitat characteristics and their interactions were evaluated for each model type through backward stepwise comparisons. These comparisons iteratively removed the least significant variable from the model and reevaluated model fit in order to avoid overfitting the model with too many variables. The model with the lowest Akaike information criterion (AIC) value was selected as the best fit model (Zuur & Ieno, 2016). Models with AIC value differences <2 were determined to have effectively the same fit (Burnham & Anderson, 1998). If the difference between the lowest AIC was <2 with other models, then the model with the highest explained variation (adjusted R^2) was selected as the best fit model. Predicted group density derived from the best fit model was compared visually with observed group density to assess model fit. A hot spot analysis was performed for both the observed group density and the model predicted group density in order to compare distribution results. These methods were repeated for each activity in order to determine the relationship between habitat characteristics and dolphin activity.

Determining Environmental Associations with Group Distribution

To determine if the number of dolphin groups was significantly different across salinity and SST ranges, a chi-square goodness of fit analysis was performed. Salinity was binned into the following parts per thousand (ppt) ranges: <10, 10-14.9, 15-19.9, 20-24.9, 25-29.9, and 30-35. SST was binned into the following Celsius (°C) ranges: <15, 15-17.9, 18-20.9, 21-23.9, 24-26.9, 27-29.9, and 30-32.9. Salinity and SST were recorded only during dolphin sightings; thus, nonnormal distributions of groups across salinity and SST ranges were expected since these data were not collected consistently across seasons or the survey area. To account for these nonnormal distributions, we calculated the average salinity and SST for each survey using its group sighting salinity and SST recordings. The proportion of surveys with an average salinity and SST within each range was then multiplied by the total number of groups to obtain the expected number of groups for each range. If the expected number of groups was <5, then the salinity or SST data were analyzed with an exact multinomial test in order to avoid violating assumptions of the chi-square goodness of fit statistic. The standardized residuals were examined to determine significant differences between ranges (Field, Miles, & Field, 2012).

Results

Data Collection

In total, 55 surveys were completed from 2009 through 2017 with 90.91% of surveys (*n* = 50 surveys) occurring from April through October each year due to poor weather conditions during the remainder of the year. In total, 138 groups were observed. Seven groups (5%) that had the largest neighbor distances were removed as potential outliers; thus, 131 groups were analyzed (Table 2; Figure 1).

Table 2
Number of surveys and groups by year and month throughout the study period

Year		2009	2010	2011	2012	2013	2014	2015	2016	2017	Total	
Surveys		4	2	7	11	6	7	7	5	6	55	
Groups		10	3	11	30	15	19	17	15	11	131	
Month	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec
Surveys	1	1	0	4	6	8	10	7	4	11	1	2
Groups	0	1	0	2	13	16	23	39	12	24	1	0

Frequently Used Areas

Dolphins were observed more often in the central and southern regions of Roanoke Sound and fewer groups were observed in the northern region. One hot spot was identified in the southern region near Oregon Inlet, indicating that this region is used more frequently than other regions by dolphins (Figure 1).

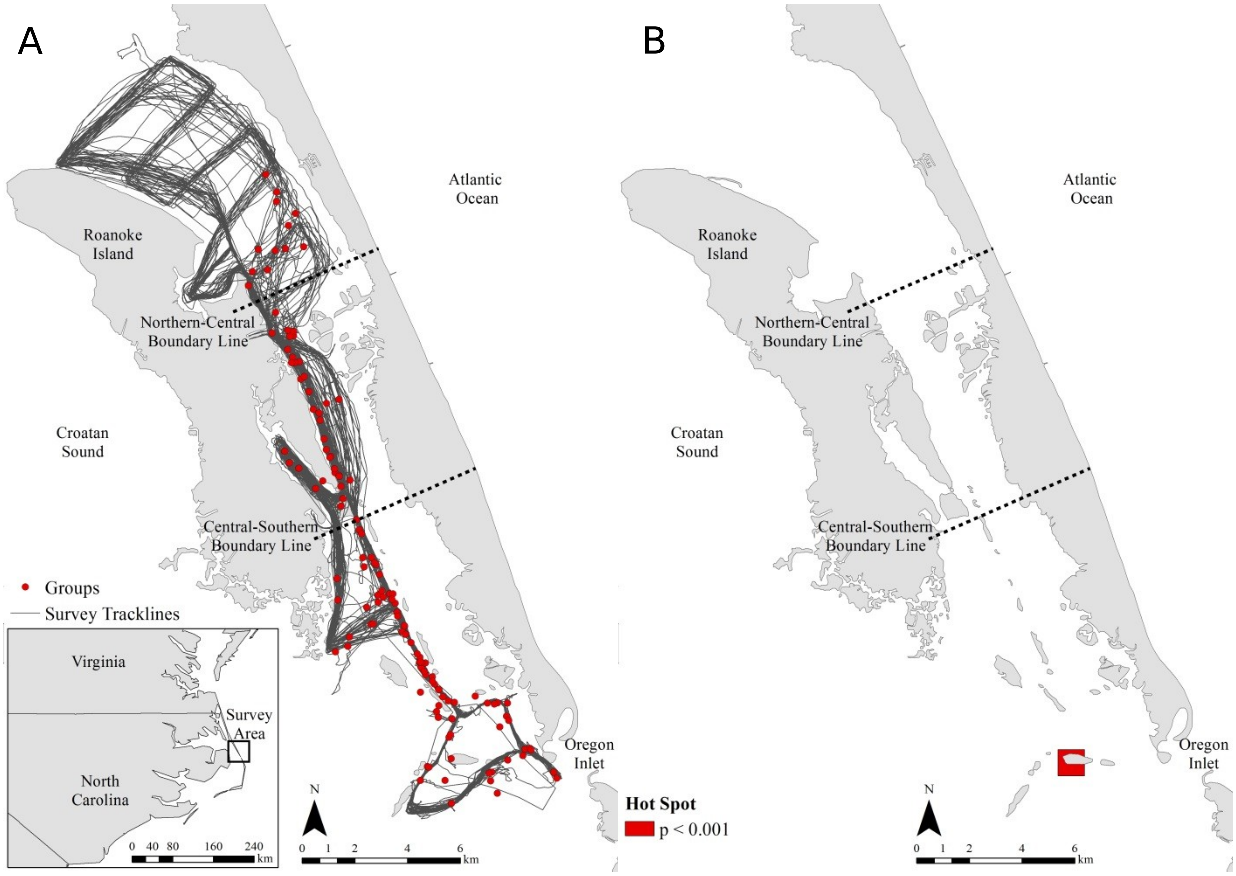

Figure 1. **(A) Groups and survey tracklines and (B) one hot spot for all groups in the southern region at 1-km² resolution.**

Activities in Frequently Used Areas

All activities were examined with hot spot analyses, except for mill because sample size was too small (*n* = 11 groups, 8.40%). Feeding was observed in 41.22% of groups (*n* = 54 groups). Most feed groups were observed throughout the central and southern regions. Three feed hot spots were detected in the southern region below Roanoke Island and near Oregon Inlet, suggesting that the southern region is frequently used for feeding (Figure 2).

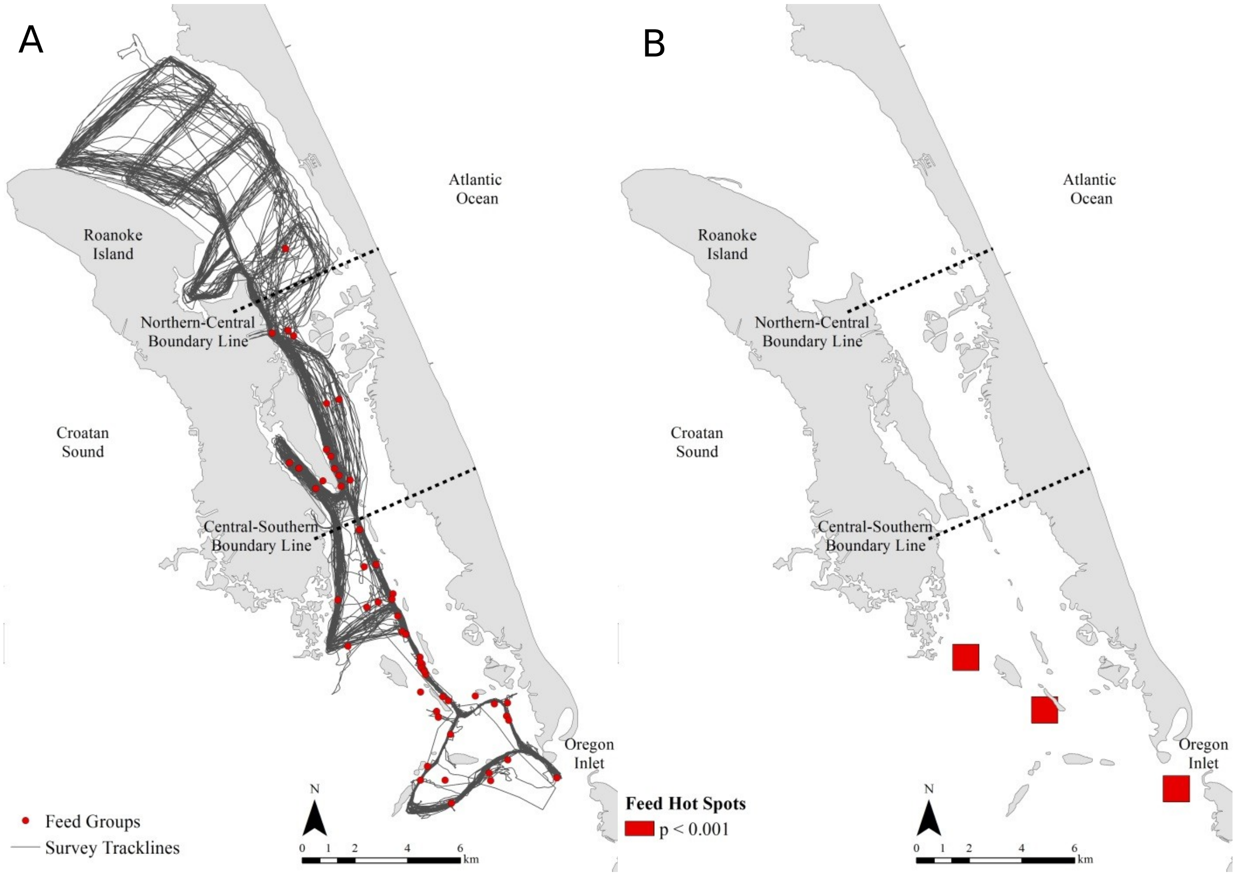

Figure 2. **(A) Feed groups and survey tracklines and (B) three feed hot spots in the southern region at 1-km^2 resolution.**

Social behavior was observed in 27.48% of groups (*n* = 36 groups). Social groups were distributed throughout all three regions. Three social hot spots were identified in areas close to shore. Two of these social hot spots were located in the northern region and one social hot spot was directly below Roanoke Island. These results indicate that both the northern and southern regions are frequently used areas for socializing (Figure 3).

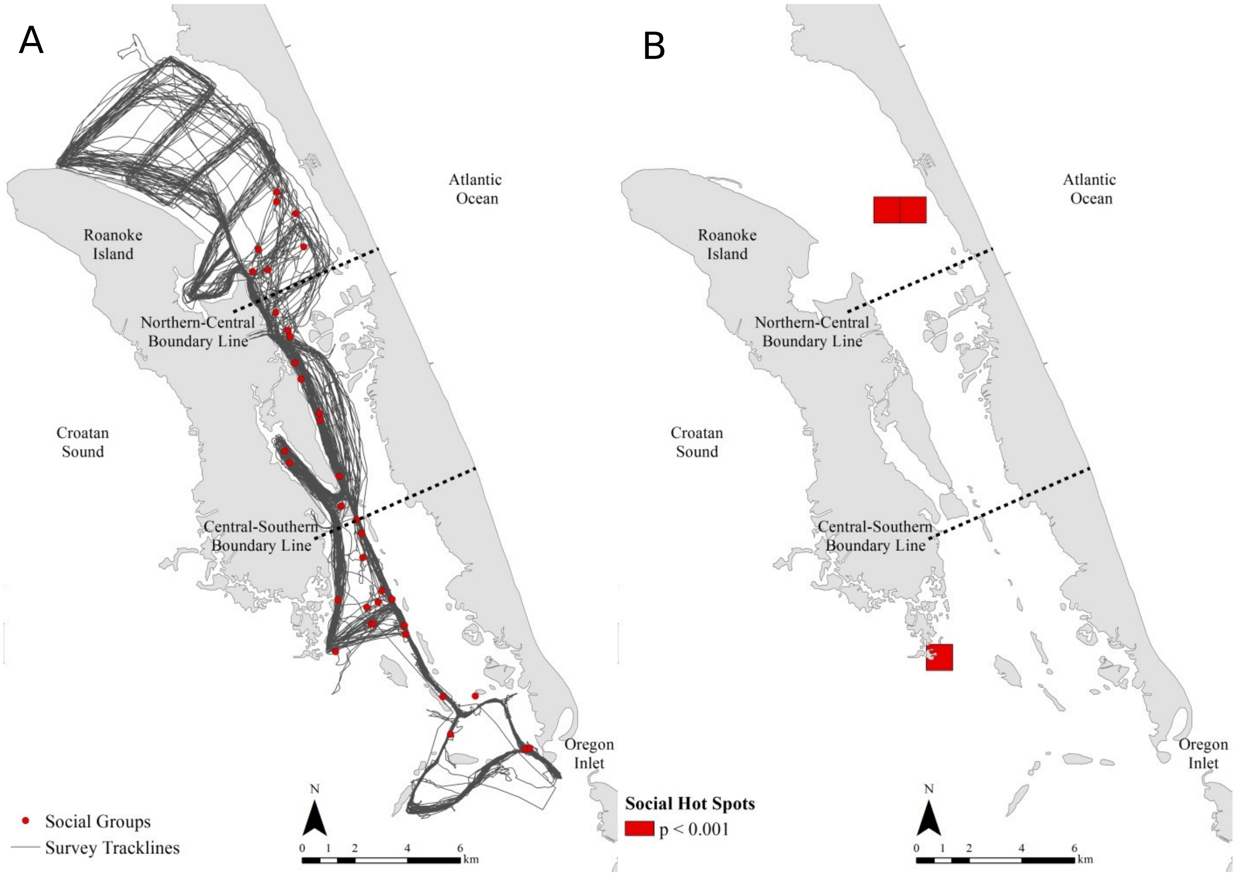

Figure 3. **(A) Social groups and survey tracklines and (B) three social hot spots in both the northern and southern regions at 1- km^2 resolution.**

Traveling was observed in 70.99% of groups (*n* = 93 groups). Most travel groups were observed in the central and southern regions. Only one travel hot spot was found in the southern region near Oregon Inlet suggesting the southern region is frequently used for traveling (Figure 4).

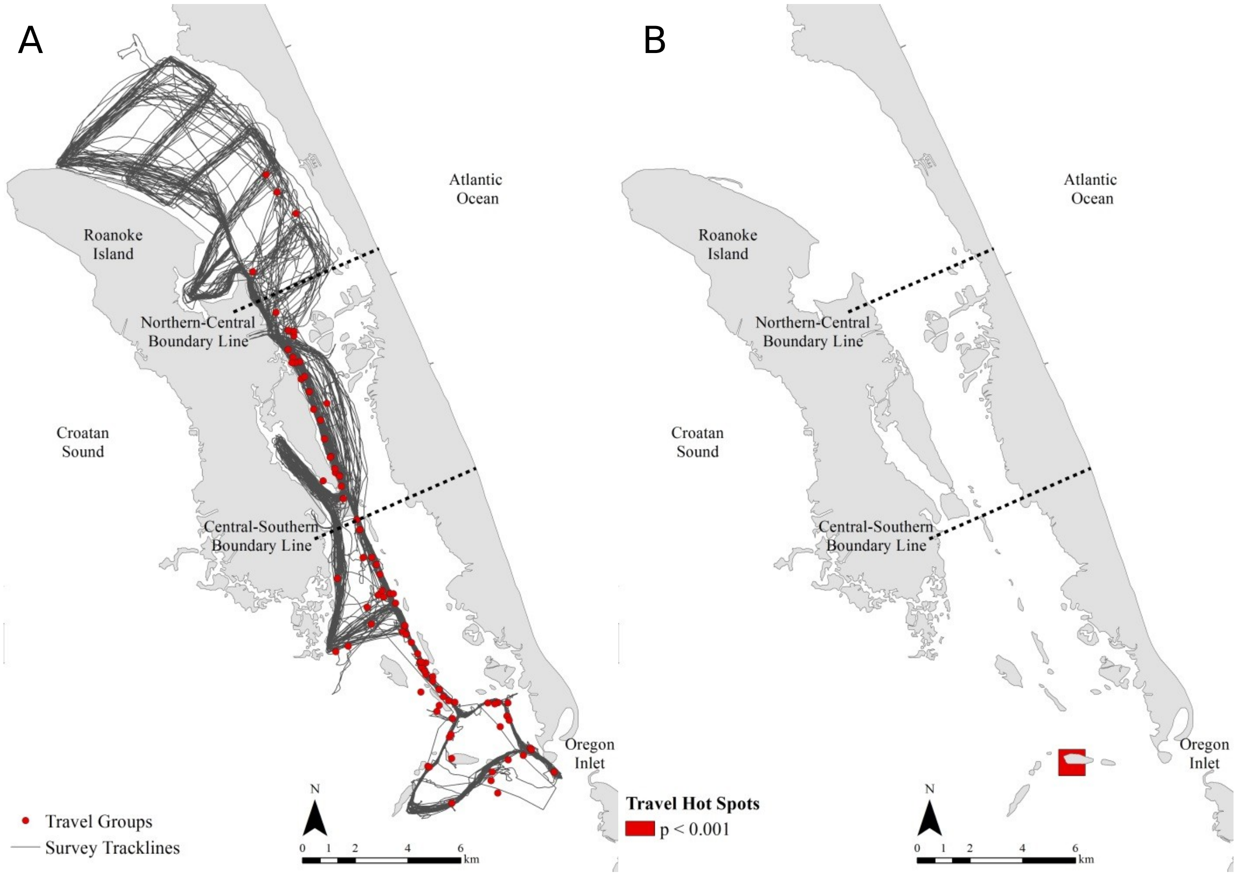

Figure 4. **(A) Travel groups and survey tracklines and (B) one travel hot spot in the southern region at 1-km² resolution.**

Associations between Habitat Characteristics, Group Distribution, and Activity

Exploratory analyses showed that minimum and maximum depths were highly correlated with average depth ($r > 0.80$); therefore, minimum and maximum depths were excluded from the models. Average slope and slope standard deviation were also highly correlated, so models containing either average slope or slope standard deviation were compared to determine which variable best explained the data. The species distribution models explained a small amount of variation (adjusted $R^2 < 10\%$) in group distribution; however, significant relationships between habitat characteristics and group distribution were detected. The ZAG model (AIC = 591.58; adjusted R^2 = 8.48%) performed substantially better than the GLM (AIC = -1068.68; adjusted R^2 = 2.08%) and GAM (AIC = -1073.60; adjusted R^2 = 1.89%). Consequently, only ZAG model results are reported (see supplemental material for comparison of GLM and GAM results). The ZAG model detected significant relationships between slope standard deviation and the interaction variable of average depth and distance to land with presence-absence group density. There were no significant relationships between habitat variables and presence-only group density. These results indicate that dolphins were more likely to be present in areas with greater variation in slope and shallow areas close to land. However, specific habitat characteristics were unable to accurately predict presence-only group density (Figure 5).

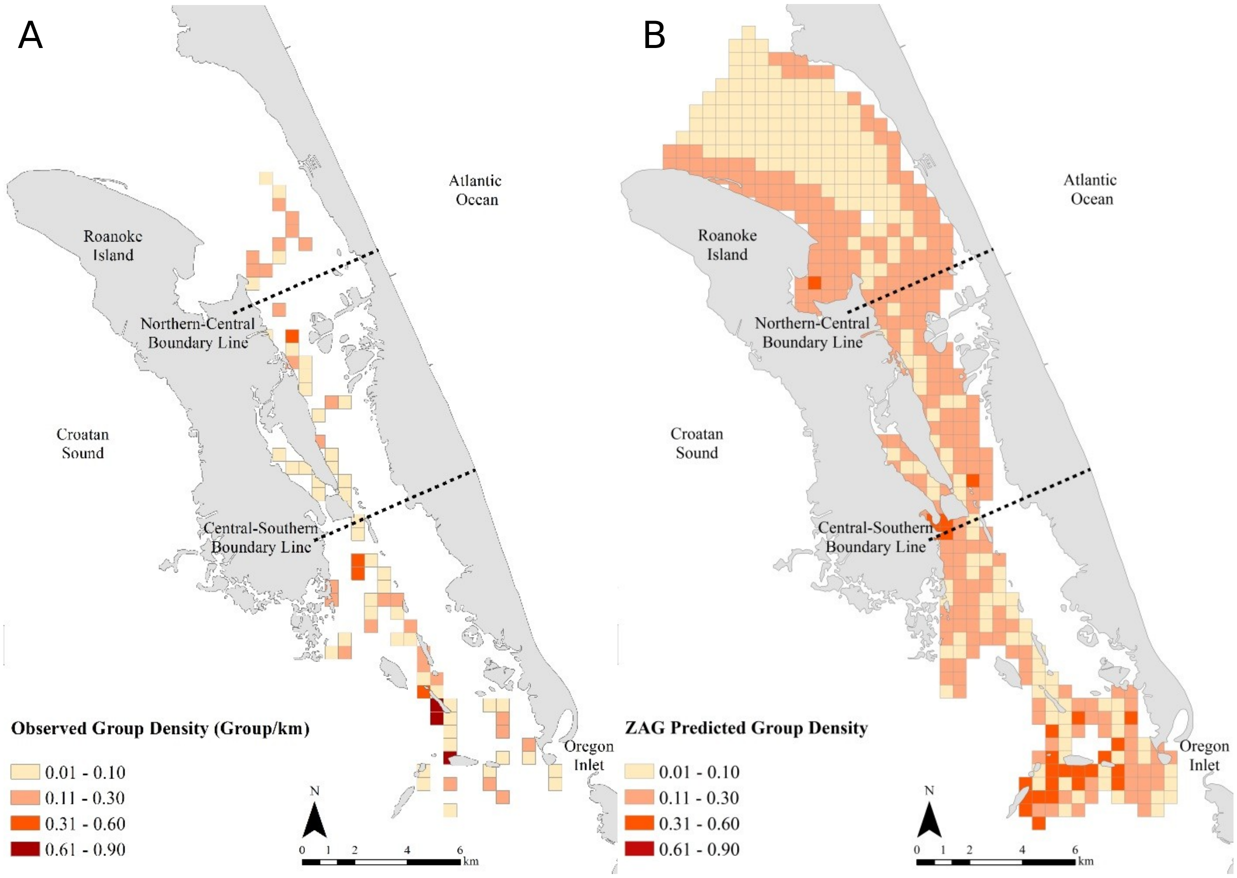

Figure 5. **(A) Observed group density (group/km) and (B) ZAG model predicted group density based on habitat characteristics at 500-m^2 resolution.**

Hot spot analyses of the observed group density and the ZAG predicted group density produced similar results, which showed that groups frequently used the southern region. Six hot spots were identified in the southern region and one hot spot was detected in the central region for observed group density. Three hot spots were identified in the southern region for ZAG predicted group density (Figure 6).

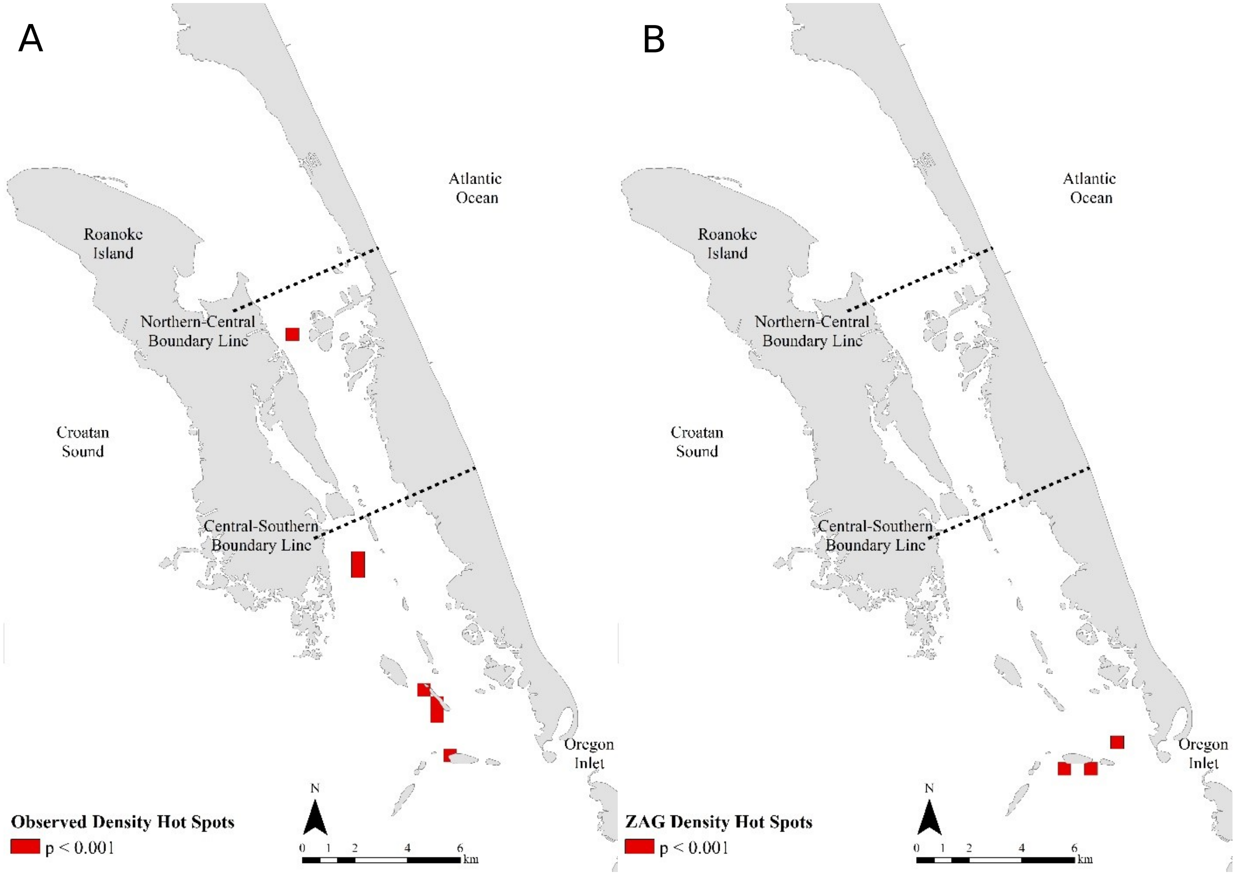

Figure 6. **Hot spots for (A) observed group density (group/km) and (B) ZAG model predicted group density at 500-m^2 cell resolution.**

Only a ZAG model was fitted to each activity because the GLM and GAM exhibited poor model fits. A ZAG model was not tested for mill groups due to small sample size. ZAG models containing either average slope or slope standard deviation were compared for each activity to determine the best fit model. The ZAG model using slope standard deviation performed slightly better in predicting feed group density than the ZAG model using average slope (AIC: 361.04 vs. 363.58, respectively). The variation explained by the feed ZAG model was 14.56%. Feed groups were more likely to be present in areas with greater slope variation and areas closer to land. There were no significant relationships between habitat variables and presence-only feed group density.

The ZAG model with slope standard deviation performed the same as the ZAG model with average slope to predict social group density (AIC: 298.11 vs 298.31, respectively). The variation explained by the social ZAG model was 9.86%, and the model only used distance to land and SAV to predict presence-absence social group density. All habitat variables were used to predict presence-only social group density. There were no significant relationships among habitat variables and presence-absence or presence-only social group density.

The travel ZAG model used slope standard deviation, distance to land, and distance to SAV to predict presence-absence travel group density. Average slope, depth, distance to land, and distance to SAV best explained presence-only travel group density. The variation explained by the travel ZAG model was 10.82% (AIC = 472.87). This model showed that travel groups were more likely to be present in areas with greater slope variation and areas closer to land; however, there were no significant relationships between habitat variables and presence-only travel group density.

Associations between Environmental Variables and Group Distribution

A total of 129 groups and 121 groups had associated salinity and SST measurements, respectively, to examine the number of groups observed across salinity and SST ranges. The average salinity was 17.67 ppt (*SD* = 6.44 ppt) and average SST was 25.60 °C (*SD* = 4.49 °C) for the study period. Salinity results showed that dolphins used areas with a wide range of salinity levels, and most groups were observed in salinity ranges between 10-19.9 ppt. The expected number of groups was <5 for salinity range 30-35 ppt, so these data were analyzed with an exact multinomial test using a chi-square distribution instead of a chi-square goodness of fit test (Table 3).

Table 3

Proportion of observed groups and expected groups represented by surveys for each salinity and SST range

Salinity (ppt)	<10	10-14.9	15-19.9	20-24.9	25-29.9	30-35	
Observed Groups	0.062	0.287	0.295	0.186	0.124	0.047	
Expected Groups	0.068	0.227	0.318	0.318	0.068	0.000	
SST (°C)	<15	15-17.9	18-20.9	21-23.9	24-26.9	27-29.9	30-32.9
Observed Groups	0.008	0.017	0.132	0.182	0.198	0.306	0.157
Expected Groups	0.023	0.047	0.140	0.209	0.233	0.302	0.047

Note. The proportion of surveys was multiplied by the total number of groups to obtain expected groups.

There was a significant difference between the number of observed groups and the expected proportion of groups for salinity based on an exact multinomial test using a chi-square distribution ($\chi^2 = 27910.27$, *df* = 5, $p < 0.01$). Based on post-hoc binomial comparisons between observed and expected proportions, there were fewer groups observed for salinity range 20-24.9 ppt ($p < 0.01$), and more groups were observed for salinity ranges 25-29.9 ppt ($p = 0.02$) and 30-35 ppt ($p < 0.01$) (Figure

7A). SST results showed that the majority of groups used areas with ≥18 °C. The chi-square goodness of fit test showed there was a significant difference between the observed and expected number of groups for SST ($\chi^2 = 36.40$, $df = 6$, $p < 0.01$). Based on standardized residuals, groups were observed more often in SST range 30-32.9 °C (standardized residual = 5.77) (Figure 7B).

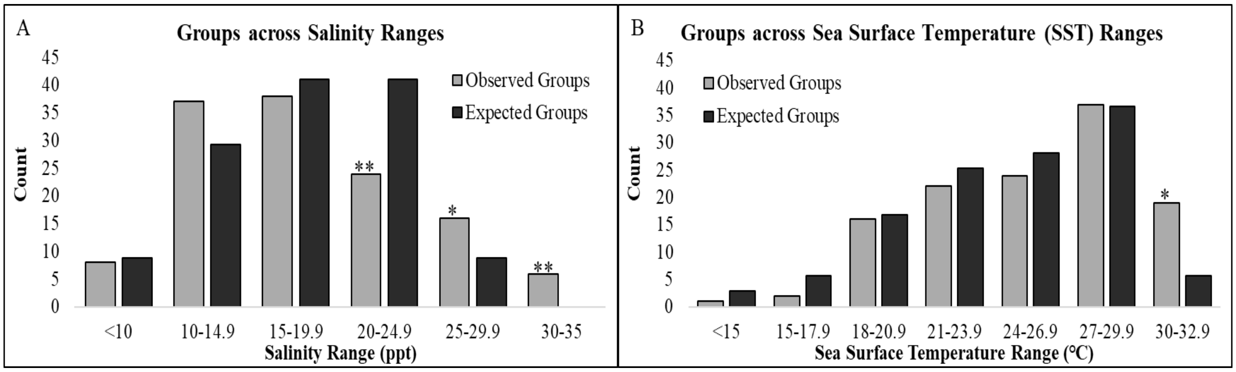

Figure 7. **The number of observed and expected groups for each (A) salinity and (B) sea surface temperature (SST) range.** Expected groups were calculated by multiplying the total number of groups by the proportion of surveys with an average salinity and SST within each range. Asterisks (*) and (**) represent significant differences at $p < 0.05$ and $p < 0.01$, respectively.

Discussion

Frequently Used Areas, Activity, and Inferences for Seasonal Habitat Use

Hot spot results showed that dolphins frequently used the southern region for feeding and traveling, which suggests that Roanoke Sound provides an important foraging area and travel corridor for dolphins. It is unlikely these results were influenced by spatial bias introduced from heterogeneous survey effort because we controlled for survey effort in our analyses. Most dolphins likely use Roanoke Sound seasonally during the warmest months (Goodman et al., 2007; Gorgone et al., 2014; Hayes et al., 2018). Seasonal fluctuations in our survey effort contributed to this observation; however, we observed more dolphins during warm months (May-October) compared to cold months (November-April) based on the ratios of groups per survey and dolphins per survey. This observation supports the hypothesis that many dolphins leave Roanoke Sound during cold months. The combination of these results indicates that Roanoke Sound provides a seasonal foraging area and travel corridor between estuaries and the Atlantic Ocean.

The seasonal use of Roanoke Sound as a foraging area coincides with the seasonal distribution of the dolphins' common prey species, such as Atlantic croaker (*Micropogonias undulatus*) and spot (*Leiostomus xanthurus*). These prey species use estuaries as nursery habitats from late fall (November) through summer during their larval and juvenile stages, and adults migrate to coastal waters during late fall to spawn (Gannon & Waples, 2004; Haven, 1959; Phillips, Huish, Kerby & Moran, 1989; Warlen & Burke, 1990). The overlap between dolphin and prey seasonal distribution patterns suggests that dolphins migrate to

Roanoke Sound primarily to forage from spring to fall (April-November). The dolphins may follow their prey into coastal waters in the winter when there is potentially not enough prey within the estuary to support the community. Cold water temperatures may also influence the seasonal distribution of the Roanoke Sound community. Very few groups were observed in waters <15 °C, even with accounting for a low number of surveys during winter. Adult dolphins can tolerate water temperatures between 5.5 and 10.6 °C depending on body mass, but calves and juveniles may not be able to tolerate these water temperatures for an extended amount of time (Yeates & Houser, 2008). The coldest SST in which dolphins were observed was 2.2 °C. This finding suggests that winter water temperatures likely drop below temperature tolerances for smaller individuals, and many dolphins may need to leave Roanoke Sound during winter to meet thermoregulation demands. Also, more dolphins were observed south of Roanoke Sound in southern Pamlico Sound during winter in waters ranging from 7.6 to 17 °C (Goodman et al., 2007), but these temperatures were slightly warmer than winter SSTs recorded in Roanoke Sound. Therefore, it is likely that a combination of less prey availability and cold water temperatures during the winter influence the seasonal distribution pattern of the Roanoke Sound community. Information on seasonal prey availability and more photographic-identification surveys during cold months are needed to examine the strength of the relationship between these variables and dolphin distribution.

Associations between Habitat and Group Distribution

The ZAG model explained a small amount of variation in group distribution, but it predicted a similar trend to the observed group distribution, in which higher group densities were predicted in the southern region. The ZAG model showed a few signs of poor fit by generally overestimating group densities in the northern region, where very few groups were observed, and group density estimates did not exceed 0.54 groups/km, which is lower than the maximum observed value (0.88 groups/km). However, hot spot results between observed group density and ZAG model predicted group density were consistent. These findings suggest that the ZAG model can be reliable for predicting general trends in dolphin distribution based on habitat characteristics, but it may be unreliable for predicting fine-scale changes in dolphin distribution due to the large amount of unexplained variance.

Dolphins were predicted to use both areas with greater slope variation and shallow areas close to land more frequently than other areas. These results describe the habitat characteristics of the southern region where higher group densities were observed. The southern region contains the mouth of the estuary, Oregon Inlet, which experiences constant tidal flows and occasional dredging that increases the slope variation in this region. There are also several islands located next to channels throughout the southern region, which likely contributes to variation in slope. The association between group density and shallow areas close to land may be explained by the higher group densities observed in the channels around these islands. Dolphins may potentially use these channels and shallow areas close to land for certain functions, such as a barrier in which to limit prey mobility. Higher dolphin density was observed in narrow, deep channels in Moray Firth, Scotland, which were hypothesized to act as bottlenecks for prey and potentially facilitate prey capture by providing a barrier against which to trap prey (Wilson et al., 1997). The combination of greater slope variation in the channels and shallow areas close to land probably creates an advantageous habitat that dolphins prefer to use for various activities, such as foraging.

Associations between Habitat and Activity

Feeding groups used the southern region frequently, which indicates that this area provides beneficial foraging habitat. Increased foraging activity in estuary mouths has been observed across multiple study sites (Acevedo, 1991; Ballance, 1992; Hanson & Defran, 1993; Harzen, 1998). The mixing of fresh water and sea water in the estuary mouth potentially stirs up nutrients, which may attract many prey species (Ballance, 1992). Additionally, the ZAG model showed that feeding groups were more likely to be present in areas with greater slope variation and areas closer to land. These results support the hypothesis that dolphins use areas with both steep slope and close proximity to land as a barrier to limit prey mobility so as to increase their foraging efficiency (Hastie et al., 2003; Hastie et al., 2004; Ingram & Rogan, 2002; Wilson et al., 1997). The combination of presumably high productivity and greater slope variation in the southern region likely provides favorable foraging habitat.

Social groups were most clustered in both the northern and southern regions in areas close to land that may be protected from boat traffic. The social group density model indicated that distribution was not influenced by a specific habitat characteristic. However, it is possible that these social hot spots are located in protected areas that have less boat traffic, considering that they are located far from the main boat channel in the middle of the sound. Encounters with boats have been observed to change dolphin behavior, including interrupting social behavior (Lusseau, 2003; Mattson, Thomas, & St. Aubin, 2005; Nowacek, Wells, & Solow, 2001). If these social hot spots have less boat traffic, then these areas may facilitate socialization due to fewer interruptions. It is likely that other factors, such as group size and group composition, also play a larger role influencing social group distribution. For example, group sizes were higher in social groups versus groups in which social activity was not observed, referred to as “nonsocial” groups (social group median = 12, nonsocial group median = 6, Mann-Whitney $U = 890.5$, $p < 0.01$). Sex and age were not known for all group members; thus, group composition could not be analyzed. However, the significant difference between sizes of social and nonsocial groups suggests that group size played a role in the occurrence of social behavior, and this may have affected the distribution of social groups. Additional variables, such as the amount of boat traffic, group size, and group composition, should be included in the social group density model to better determine how these variables are related to dolphin distribution and whether habitat characteristics may indirectly facilitate social interactions by offering protection from disturbance.

Dolphins frequently used the southern region for traveling, which suggests this area serves as a travel corridor through Oregon Inlet. The nearest inlets are approximately 97 km south (Hatteras Inlet) and 145 km north (Rudee Inlet) of Oregon Inlet. Access to Oregon Inlet is probably an important resource to the Roanoke Sound community during their seasonal movements. This information may be useful for conservation and population management efforts, especially when Oregon Inlet undergoes dredging and construction activities. For example, a new bridge has been under construction from March 2016 to February 2019 to replace the Herbert C. Bonner Bridge over Oregon Inlet, and demolition of the previous bridge is anticipated to last until late 2019 (NCDOT, 2018). Studies have shown that dolphin density decreased during bridge construction and that bridge construction can have effects on habitat use (Buckstaff, Wells, Gannon, & Nowacek, 2013; Weaver, 2015). It will be interesting to determine whether dolphins continue to use Oregon Inlet as a travel corridor during construction activities or change their habitat use patterns. Sample sizes are currently too small to examine habitat use before and during bridge construction, but this analysis can be revisited once bridge construction is complete.

Associations between Environmental Variables and Group Distribution

Dolphins used areas with a wide range of salinity levels, and most groups were observed in low to moderate salinity ranges (10-19.9 ppt). However, groups used areas with salinity ranges ≥25 ppt more often than expected. The majority of these groups were located in the southern region next to the estuary mouth, where salinity is typically higher. This result suggests that dolphins using areas with higher salinity is associated with their frequent use of the southern region. It is uncertain why dolphins used areas with 20-24.9 ppt less often. These groups were distributed throughout the sound, so it does not appear that there is a relationship with habitat characteristics. These groups were also observed across different months and years, so an obvious temporal trend does not appear to exist either. It is possible that this result may be explained by salinity fluctuations and their influence on prey distribution, which in turn influences dolphin distribution. Field experiments with Atlantic croaker and spot showed that these prey species can tolerate extreme fluctuations in salinity, but Atlantic croaker are more sensitive than spot to salinity fluctuations, and Atlantic croaker avoid areas with high salinity fluctuations (Moser & Gerry, 1989). The 20-24.9 ppt range may either be a large salinity fluctuation for some prey species or contain a transition salinity threshold that some prey species may avoid. More data on salinity fluctuations and prey availability across salinity ranges are needed to determine if this result represents a biologically meaningful trend or if it is a statistical artifact.

Most dolphin groups used areas with ≥18 °C SST, which is probably due to the seasonal migration of dolphins into the survey area from late spring to early fall. Dolphins used areas with SSTs between 30-32.9 °C more often than expected. These groups were distributed throughout the sound from June to August across multiple years and the majority of these groups were observed during August. It is likely these are the months with the hottest SSTs, and they coincide with peak dolphin abundance in Roanoke Sound. Monthly abundance estimates are needed to confirm this hypothesis, but the average number of groups per survey and the number of dolphins per survey is highest for August across years (approximately 5.3 groups/survey and 53 dolphins/survey). This finding suggests that more dolphins are present in Roanoke Sound during the warmest months. The opposite trend was observed in southern Pamlico Sound, south of Roanoke Sound, in which fewer dolphins were observed as SST increased (Goodman et al., 2007). It is possible that these conflicting results are explained by dolphins moving north of southern Pamlico

Sound into Roanoke Sound during warmer months, since Pamlico Sound is the most southern part of the Northern North Carolina Estuarine System Stock’s range.

Conclusions

This study demonstrates that the southern region is an important habitat for dolphins in Roanoke Sound, a community for which little is known, and that specific habitat characteristics and environmental variables are associated with dolphin distribution and activity in this area. The ZAG models explained rather little of the variation (8.48-14.56%) in dolphin distribution, which suggests that other factors likely influenced distribution and activity in this area, such as prey availability and distribution, reproduction, and anthropogenic disturbance. For example, the mating/calving season for dolphins in North Carolina is the spring and summer (Thayer et al., 2003), and reproductive demands, such as finding mates and providing protection to calves from predators and conspecifics, could also influence dolphin distribution in Roanoke Sound. Additionally, the study population was comprised of both dolphins that exhibit moderate to high site fidelity to Roanoke Sound and dolphins that are short-term visitors. It is possible that these short-term visitors used Roanoke Sound differently compared to dolphins that regularly inhabit the study area; therefore, associations between dolphin distribution and habitat characteristics may differ across site fidelity patterns. Dolphins are likely faced with tradeoffs between finding advantageous habitat for activities, meeting reproductive demands, and avoiding sources of disturbance; therefore, habitat interactions are only one piece of a complex puzzle. More data on these factors in addition to continued photographic-identification surveys are needed in order to build more comprehensive models that can potentially identify additional factors that influence dolphin distribution and habitat use.

This study provides baseline information about how dolphins interact with their habitat in Roanoke Sound. Such information can be useful in order to minimize negative impacts on dolphins from anthropogenic activity or in the case of habitat changes due to natural or anthropogenic disturbance. If such an event occurred, baseline knowledge gained from this study would allow for impacts to be accurately assessed for this community, which could lead to more informed population management decisions and effective conservation efforts. Moreover, information attained from this study may also be applicable to management and conservation of other populations. This study demonstrates that the combination of habitat use analyses and species distribution models can provide more comprehensive information to understand why dolphins exhibit variation in their distribution patterns and how specific habitat characteristics are associated with distribution and activity. Additionally, this study showed that a zero-inflated model may be more powerful than a GLM and GAM in detecting associations between habitat characteristics and dolphin distribution. These models should be considered as an option when comparing regression-based species distribution models, especially with datasets that contain a high proportion of zeros. The analyses from this study can be applied to other populations with sufficient habitat and environmental data and provide researchers with better insight into what variables are driving the distribution of dolphin communities and how habitat characteristics interact with important activities. Identifying these driving factors can be useful for predicting population trends and mitigating adverse population responses to climate change, human activities, and disturbance events.

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