Historical Seasonal Density and Distribution Patterns of *Tursiops truncatus* in Northeast Florida

Marthajane Caldwell

Marine Mammal Behavioral Ecology Studies, Inc., 8429 Cresthill Avenue, Savannah, GA 31406, USA E-mail: marthajane_c@yahoo.com

Abstract

The potential impact of scheduled channel changes in the St. Johns River, Florida, upon Tursiops truncatus communities within the area underscores the need for access to unpublished historic datasets. Thus, this article reports seasonal density and distribution patterns observed from December 1994 through December 1997 in the alongshore and estuarine waters of northeastern Florida. Frequency of social interactions and number of possible affiliates are influenced by abundance and distribution patterns of a species within a given area; thus, dolphin density as measured by both dolphins per km² and dolphins per group was analyzed. Dolphin density was highly variable and significantly correlated with water temperature in the COAST region as well as the St. Johns River (SJR) study region and intracoastal waters south (ICS) of the SJR, but not in intracoastal waters north (ICN) of the SJR. Although sightings were randomly distributed with respect to water temperature in three regions, they were significantly clustered within the ICN. Neonate density (number per km²) in the ICS was over four times greater than in the exposed COAST region, more than five times greater than in the estuarine SJR region, and 17 times greater than in the ICN region. The number of neonates per group in the ICS was significantly higher than that in the exposed habitat of the COAST as well as in the estuarine SJR and ICN regions, which suggests that in 1994 through 1997, dolphins used the isolated, shallow, small inland Chicopit Bay of the ICS region as a nursery area. Since significant changes in the bathymetry and tidal flow patterns in these regions are scheduled, current dolphin density and distribution patterns are needed to determine if the seasonal density and distribution patterns identified in 1994 through 1997 are still relevant.

Key Words: seasonal density, distribution, bottlenose dolphin, *Tursiops truncatus*, northeastern Florida

Introduction

Description of bottlenose dolphin (Tursiops truncatus) abundance and distribution patterns within an area is a key component to understanding the social structure within communities because abundance and distribution affect the frequency of social interactions and the number of possible affiliates (Smolker et al., 1992), as well as the amount and variation of cultural information available to group members from groups leaders (Lewis et al., 2011, 2013). Social structure is the result of specific strategies adopted by individuals to meet the three basic requirements of life: (1) obtaining food, (2) avoiding predators, and (3) finding mates (Jarman, 1974; Crook et al., 1976; van Schaik & van Hooff, 1983; Sterck et al., 1997; Gygax, 2002). Eisenberg et al. (1972) observed that different populations of the same species living in a variety of different habitats exhibit an equally wide range of social structures and that this intraspecific variation in social structures is partially due to habitat differences in resource distribution and predation pressure.

Bottlenose dolphins are found throughout the world's temperate and tropical oceans in two distinct habitat types: (1) unobstructed habitats (open coastal shoreline, pelagic waters, and open ocean) and (2) structurally complex habitats (enclosed bays, estuaries, and tidal marshes) (Leatherwood & Reeves, 1983). The terms *coastal* and *inshore* are often used to refer to unobstructed and structurally complex habitats, respectively. Dolphins in coastal habitats (1) may exhibit philopatry to a study area but seldom exhibit year-round residency, (2) range over large sections of coastal habitat, (3) are found in large groups, and (4) form few definable social units other than mother-calf pairs (Würsig & Würsig, 1979; Ballance, 1990; Hansen, 1990; Kenney et al., 1990; Würsig & Harris, 1990; Würsig et al., 1991; Barco et al., 1999; Defran & Weller, 1999; Defran et al., 1999). In contrast, dolphins using inshore habitats (1) exhibit philopatry and year-round residency, (2) use small ranges, (3) are found in small

groups, and (4) form strong associations with specific individuals resulting in several different types of social structural units (Wells et al., 1980, 1987; Irvine et al., 1981; Odell et al., 1990; Shane, 1990; Wells, 1991; Gubbins, 2002).

Behavioral and photo-identification data obtained from December 1994 through December 1997 identified three behaviorally differentiated bottlenose dolphin communities-Coastal, Northern, and Southern-utilizing the coastal and intracoastal waters of northeastern Florida. These parapatric communities differed in habitat fidelity and social affiliation patterns; however, only two of the three communities exhibited the characteristics predicted for the habitats they utilized (Caldwell, 2001, 2016). Individual dolphins of the Coastal community showed little regional fidelity as was typical of other previously described coastal populations (Hanson, 1990; Barco et al., 1999; Defran & Weller, 1999; Bearzi et al., 2009; Merriman et al., 2009; Hwang et al., 2014; Defran et al., 2015). Although the Northern and Southern communities both inhabited the intracoastal waters of northeast Florida (Caldwell, 2001, 2016), only the Northern community exhibited the typical year-round residency to a localized range pattern seen in other estuarine communities (Ballance, 1990; Scott et al., 1990; Shane, 1990; Wells, 1991; Gubbins, 2002; Gubbins et al., 2003; McHugh et al., 2011; Wilson et al., 2012).

This article reports the seasonal density and distribution patterns observed within the ranges of these three communities from December 1994 through December 1997. Although these data are over 18 y old, it is important to move these data from the grey literature to make the findings more accessible. The following is the rationale behind this statement:

- This work represents the first concerted effort to collect behavioral and photo-identification data within northeastern Florida.
- Genetic data suggest further population subdivision within the northeastern Florida samples (Caldwell, 2001; Rosel et al., 2009).
- In 2010, an Unusual Mortality Event (UME) was declared within the St. Johns River (SJR). Dead dolphins were found 40 to 80 km upstream of the St. Johns Inlet in locations considered "out of habitat." Managing agencies were interested in finding historical records of dolphins within this area.
- Opportunistic photo-identification surveys conducted in late 2010 and 2011 re-sighted dolphins originally identified within their 1994-1997 ranges and identified a range extension for the Southern community (Caldwell et al., 2011).

- A consortium of researchers have been collecting biannual mark/recapture data along the northeastern Florida coast from 2011 to the present and have consistently re-sighted many of the dolphins originally identified in 1994 through 1997.
- A second UME was declared in this area during the summer of 2013.
- Plans are underway to significantly change the bathymetry and tidal flow patterns of the St. Johns River and the region where the intracoastal waterway (ICW) intersects the SJR and Mile Point (U.S. Army Core of Engineers [USACE] Jacksonville District, 2012, 2014a, 2014b; Jacksonville Port Authority [JAXPORT], 2014).

During the 1994-1997 study, the Southern community utilized the area known as Mile Point and Chicopit Bay as their 50% minimum convex polygon kernel contour (Caldwell, 2001). Moreover, opportunistic surveys conducted during 2010-2011 re-sighted 1994-1997 individuals within their established community's range. Specifically, Southern community dolphins were only re-sighted within the intracoastal waters south (ICS) of the SJR and in the SJR regions, and Northern community members were only sighted within the intracoastal waters north (ICN) of the SJR region. Thus, the 2010-2011 data suggest that the Southern community is still using the ICS and SJR regions, and the Northern community is still occupying the ICN region (Caldwell et al., 2011). Plans are underway to significantly change the bathymetry and tidal flow patterns in the region where the ICW intersects the SJR. Currently, the USACE Jacksonville District (2012, 2014a, 2014b) has two scheduled projects: (1) deepening the St. Johns River from the current depth of 13.3 m to a maximum depth of 16.6 m, and (2) changing the confluence of the St. Johns River with the ICW in the Mile Point area.

The Southern community is the one most likely to be impacted by the Mile Point channel changes. Interpreting the potential impact of the channel changes within the SJR region upon its dolphin communities underscores the need for access to previously unpublished historic datasets. To that end, this article reports the seasonal density and distribution patterns observed from December 1994 through December 1997 in the alongshore and estuarine waters of northeastern Florida. Additionally, the seasonal density and distribution patterns of neonates within this region are also described. The choice to examine neonate rather than calf density was made because the standard for defining a dolphin as a neonate in the field is straightforward (Wells et al., 1999). Since bottlenose dolphin communities exhibit fission-fusion

group dynamics (Wells et al., 1999), understanding dolphin density within a region is critical as density influences the frequency and number of possible interactions. Thus, dolphin density was determined in two ways: (1) as dolphins per km² surveyed and (2) as dolphins per group. Both measures are important for understanding the impact of dolphin density on group fission-fusion dynamics since the number of dolphins per km² determines the frequency of encountering a dolphin not of the current group, while the number of dolphins within a group determines the number of possible associates. Although neonates do not move independently of their mothers, description of neonate density and distribution patterns are important for identifying potential nursery areas and for understanding the habitat utilization of a community. Taking this historic dataset out of grey literature will facilitate comparisons of the 1994-1997 density and distribution patterns to current and future data. Furthermore, these data will establish a baseline that can be used to help assess potential impacts of the channel improvement projects and the most recent UMEs.

Methods

Study Area

The northeast Florida study area encompassed the coastal and intracoastal waters of Nassau and Duval Counties, Florida, from St. Mary's River to Jacksonville Beach to 4.8 km offshore and encompassed an extensive estuarine habitat connected to a homogeneous coastal habitat by four rivers. The northeast Florida study area was divided into four regions: (1) COAST = coastal waters up to 4.8 km offshore from the Florida–Georgia border to 50 km south, (2) SJR = the St. Johns River from the mouth to 49 km upstream, (3) ICS = 20 km of the ICW south of the St. Johns River, and (4) ICN = the 45 km of the ICW north of the St. Johns River (Figure 1).

Data Collection

The survey transect for each habitat is given in Figure 1. Using standard photo-identification analysis and survey techniques (Würsig & Jefferson, 1990), biweekly photo-identification surveys were conducted from December 1994 through December 1997. Once bottlenose dolphins were sighted, the research vessel stopped approximately 20 to 40 m from the dolphins. From this vantage point, the time, latitude and longitude, sea/weather state, water temperature, and dolphin behavior state, as well as the number of adults and neonates present, were recorded. Because the standard for defining a dolphin as a neonate in the field is straightforward (Wells et al., 1999), neonate rather than calf density was determined. An individual is considered a neonate based on three traditional criteria: (1) physical



Figure 1. The location landmarks, transect route, and lengths for each region within the northeast Florida study area; survey transects of the ICS and SJR regions were truncated in length after 1995 due to a lack of sightings.

appearance, including body size (roughly estimated to be < 1.2 m) relative to other group members, dark coloration, and apparent fetal folds; (2) physical ability, including immature and stereotyped swimming style and an awkward, head-up respiratory pattern; and (3) surface association, including constant affiliation with a particular or several large individuals judged to be adults (Wells et al., 1999).

Dolphin Density

A previous study has shown that water temperature influences dolphin density within the Mid Atlantic Bight (Gubbins et al., 2003). Therefore, a Spearman rank correlation was used first to test for a significant effect of water temperature on dolphin density for each habitat. If a temperature effect was found for any of the four habitats, then an effect of habitat on dolphin density was tested for each season. The seasonal definition used in this analysis was based on water temperature. The cold water season was defined as the time period when water temperature was equal to or less than 16° C, while the warm water season was when water temperature was greater than 16° C (Caldwell, 2001; Gubbins et al., 2003). Using SPSS 21.0 and the analyses described below, dolphin density was examined in two ways: (1) as

the total number of dolphins per km² surveyed and (2) as total number of dolphins per group.

The number of dolphins observed per km² surveyed for each transect in each habitat was not normally distributed, so a Kruskal-Wallis One-Way Nonparametric ANOVA (Zar, 1999) was used to test for an effect of habitat on dolphin density (as measured by dolphins per km²). The independent variable was habitat (COAST = coastal habitat; estuarine = ICN, ICS, and SJR habitats), and the dependent variable was dolphin density (dolphins per km²). If a significant difference was found among the four habitats, pairwise Mann-Whitney U tests (n = 6) were performed to look for differences in dolphin density between each pair of habitats. The Bonferroni correction factor was used to correct for multiple comparisons (Zar, 1999). Any comparison with a p value less than or equal to 0.008 was significant.

The value for dolphins per group was calculated as the number of dolphins observed in each sighting. In this analysis, dolphins were considered within the same group if they were within a 100-m radius of each other following the method of Wells (1986). All bottlenose dolphins observed during a single sighting were within 100 m of each other on 82 and 100% of the occasions dolphins were observed in coastal and estuarine waters, respectively. Group size data were not normally distributed, so a Kruskal-Wallis One-Way Nonparametric ANOVA (Zar, 1999) was used to test for an effect of habitat on density (as measured by group size). The independent variable was habitat, and the dependent variable was group size (dolphins per group). If a significant difference was found among the four habitats, then pairwise Mann-Whitney U tests (as described above) were performed to look for differences in dolphin group size between each pair of habitats.

Neonate Density

Neonate distribution is dependent upon that of their mothers. Analysis of neonate density was conducted as described above for dolphin density. However, neonate density was only examined for the warm water season since neonates were only observed during two cold water surveys of the COAST region.

Dolphin Distribution

Dolphin sighting locations were plotted in *ArcMap* 10.1 (Environmental Systems Research Institute [ESRI], Redlands, CA, USA), and spatial autocorrelation (SAC) analysis was used to evaluate whether the relationships between sighting locations and other factors were clustered, dispersed, or random. Sightings were categorized by number of dolphins observed and by number of neonates observed within each group. SAC of sightings with respect to location, number per group, temperature, and depth was assessed in the geographic information system using global Moran's *I-Value* (Moran, 1950; Grigg et al., 2012; Miller, 2012). SAC of sightings containing neonates was also assessed with respect to location, number per group, and depth. Other anthropogenic or environmental factors were not considered since other studies found no correlation between dolphin distribution and any factor other than temperature (Caldwell, 2001; Gubbins et al., 2003).

Results

Dolphin Density

A total of 15,582 linear km (transect width = 500 m or less depending on the width of the waterway) were surveyed during 198 d from December 1994 through December 1997. The number of transects conducted in each area is given in Table 1. Dolphin density was highly variable from day to day in all four regions (Figure 2). The variability of the number of dolphins observed per km² surveyed was significantly correlated with water temperature in the COAST, ICS, and SJR regions (rho = 0.29, n = 64, p = 0.02; rho = 0.48, n = 145, p < 0.001; and rho = 0.36, n = 191, p < 0.001, respectively) but not in the ICN (rho = 0.05, n = 142, p = 0.59). Based on these data, two Kruskal-Wallis One-Way



Figure 2. The number of dolphins observed per km² surveyed in each habitat; shaded regions represent cold water surveys. Note that the scale varies with region.

Nonparametric ANOVAs were performed, one for each season, in order to test for an effect of region on dolphin density independent of season.

There was a significant effect of region on dolphins observed per km² for both the cold (H = 22.36, $df = 3, p \le 0.001$) and warm (H = 50.91, $df = 3, p \le 0.001$) water seasons. During the cold water season, significantly more dolphins were observed per km² surveyed in the COAST, SJR, and ICS regions vs the ICN region (Table 2). However, there were no significant differences in the number of dolphins observed per km² surveyed in the COAST and SJR regions, the COAST and ICS regions, and in the ICS and SJR regions during

the cold water season (Figure 3). During the warm water season, the number of dolphins observed per km² was significantly different for each region comparison (Table 2). Dolphin density as measured by dolphins per km² surveyed was greatest in the ICS, then in the COAST, followed by the SJR, with the least in the ICN (Figure 3).

There was also a significant effect of region on the number of dolphins observed per group sighted for both seasons (cold: H = 13.11, df = 3, p= 0.004; warm: H = 173, df = 3, $p \le 0.001$). During both cold and warm seasons, the number of dolphins observed per group sighted was significantly different in the COAST region compared to both

Table 1. Survey effort by region and season from December 1994 through December 1997; cold water season consisted of days when water temperature was at or below 16° C.

| Region and survey period | # transects surveyed | Km traversed | No. of groups observed | No. dolphins observed | Neonates observed |
|--------------------------|----------------------|--------------|---------------------------|--------------------------|----------------------|
| COAST | | | | | |
| Cold water 1994-1995 | 4 | 179 | 18 | 142 | 0 |
| Warm water 1995 | 22 | 698 | 43 | 777 | 7 |
| Cold water 1995-1996 | 2 | 122 | 9 | 88 | 1 |
| Warm water 1996 | 25 | 737 | 74 | 1440 | 27 |
| Cold water 1996-1997 | 3 | 89 | 9 | 107 | 1 |
| Warm water 1997 | 8 | 163 | 8 | 224 | 2 |
| 1994-1997 total | 64 | 1,988 | 161 | 2.778 | 38 |
| ICN | | - , | | _, | |
| Cold water 1994-1995 | 14 | 666 | 21 | 114 | 0 |
| Warm water 1995 | 42 | 2711 | 87 | 452 | 10 |
| Cold water 1995-1996 | 10 | 535 | 23 | 116 | 0 |
| Warm water 1996 | 35 | 2330 | 94 | 440 | 22 |
| Cold water 1996-1997 | 7 | 519 | 19 | 52 | 0 |
| Warm water 1997 | 35 | 2836 | 134 | 484 | 12 |
| Cold water 1997 | 2 | 145 | 2 | 14 | 0 |
| 1994-1997 total | 145 | 9,742 | 380 | 1.672 | 44 |
| SIR | | , | | , | |
| Cold water 1994-1995 | 18 | 243 | 10 | 34 | 0 |
| Warm water 1995 | 53 | 733 | 25 | 242 | 2 |
| Cold water 1995-1996 | 10 | 144 | 1 | 2 | 0 |
| Warm water 1996 | 53 | 780 | 44 | 314 | 4 |
| Cold water 1996-1997 | 9 | 172 | 2 | 6 | 0 |
| Warm water 1997 | 48 | 831 | 41 | 588 | 4 |
| Cold water 1997 | 2 | 37 | 0 | 0 | 0 |
| 1994-1997 total | 193 | 2,940 | 123 | 1,186 | 10 |
| ICS | | | | | |
| Cold water 1994-1995 | 8 | 170 | 6 | 41 | 0 |
| Warm water 1995 | 41 | 230 | 28 | 439 | 13 |
| Cold water 1995-1996 | 11 | 58 | 1 | 7 | 0 |
| Warm water 1996 | 41 | 219 | 24 | 569 | 34 |
| Cold water 1996-1997 | 7 | 56 | 2 | 8 | 0 |
| Warm water 1997 | 37 | 169 | 27 | 646 | 22 |
| Cold water 1997 | 2 | 10 | 0 | 0 | 0 |
| 1994-1997 total | 147 | 912 | 88 | 1.710 | 69 |
| Grand total | 549 | 15,582 | 752 | 7,346 | 161 |

| Cold season Warm season | COAST | ICN | SJR | ICS |
|----------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|
| COAST | 2.22 (± 4.46) 3.76 (± 5.00) | p = 0.001 | <i>p</i> = 0.11 | <i>p</i> = 0.54 |
| ICN | p = 0.000 | 0.21 (± 0.16) 0.20 (± 0.15) | p = 0.000 | p = 0.000 |
| SJR | p = 0.000 | p = 0.000 | 0.40 (± 0.40) 0.99 (± 0.99) | p = 0.39 |
| ICS | p = 0.001 | <i>p</i> = 0.000 | <i>p</i> = 0.000 | 0.97 (± 1.40) 6.14 (± 5.46) |

Table 2. The values on the diagonal represent the average number of dolphins observed per km² surveyed (\pm SD) during cold and warm water surveys (upper and lower values, respectively). Values given above and below the diagonal represent the *p* values for comparisons between habitats by cold and warm water surveys, respectively.

Table 3. The values on the diagonal represent the average number of dolphins observed per group (\pm SD) during cold and warm water surveys (upper and lower values, respectively). Values given above and below the diagonal represent the *p* values for comparisons between habitats by cold water and warm water surveys, respectively.

| Cold season Warm season | COAST | ICN | SJR | ICS |
|----------------------------|----------------------------------|--------------------------------|----------------------------------|----------------------------------|
| COAST | 9.36 (± 9.20) 19.93 (± 25.32) | p = 0.001 | <i>p</i> = 0.004 | <i>p</i> = 0.22 |
| ICN | p = 0.000 | 4.58 (± 3.41) 4.39 (± 3.42) | <i>p</i> = 0.31 | <i>p</i> = 0.51 |
| SJR | p = 0.001 | p = 0.000 | 3.42 (± 2.57) 10.49 (± 14.93) | p = 0.28 |
| ICS | p = 0.09 | p = 0.000 | <i>p</i> = 0.000 | 6.22 (± 5.72) 20.69 (± 14.89) |

the ICN and the SJR regions; however, there was no difference in group size between the COAST and ICS regions for either season (Table 3). The number of dolphins observed per group was not significantly different between the ICN and the SJR, the ICN and the ICS, nor the SJR and the ICS regions during the cold water season (Table 3; Figure 3). Although there was no difference between group size in the ICS and COAST regions during both water seasons, as with the number of dolphins observed per km² in the ICS region during the warm water season, more bottlenose dolphins were observed per group within the ICS region than in the ICN and SJR regions (Figure 3).

Neonate Density

Density, as measured by the number of neonates observed per km² surveyed, was highly variable from day to day in all four regions (Figure 4). Based on the fact that only two neonates were sighted during two cold water surveys (Table 1), only the statistical comparisons of warm season data were conducted. During the warm water season, significantly more neonates were observed per km² and per group observed in the ICS vs the COAST, SJR, and ICN regions (Table 4). However, there were no significant differences in the number of neonates observed per km² surveyed or per group observed in the COAST vs the ICN or SJR regions (Figure 4).

Dolphin Distribution

Since the 751 sighting locations were significantly clustered (Moran's *I-Value* = 0.013, p = 0.000) within the northeast Florida study area, the SAC of sightings with respect to location, water temperature, and depth were analyzed independently for each region. Region analysis found that sighting locations were randomly distributed within the COAST, ICN, and ICS regions but were significantly dispersed (spread out) within the SJR region (Table 5; Figures 6-9). Although sightings were randomly distributed with respect to water temperature in the COAST (Figure 6), SJR (Figure 8), and ICS (Figure 9) regions, they were significantly clustered within the ICN (Table 5; Figure 7). Additionally, sighting locations were significantly clustered with respect to water depth in the COAST and ICN regions but not the SJR and ICS regions (Table 5). Dolphin density, as measured by number of dolphins within a group, was significantly clustered within the northeast Florida study area as a whole; however, regional SAC analysis only found a significant clustering of dolphins within the ICN region (Table 5).

SAC analysis of sighting locations for only those groups containing neonates revealed that neonate sightings were only significantly clustered within the ICN region (Figure 7). Neonate sighting locations were randomly distributed with respect to depth in each region (Table 5). A SAC analysis of neonate sighting location with respect to water temperature was not conducted since only two neonates were sighted during winter surveys in the COAST region. Although neonate density was clustered within the study area, when all sighting locations were considered (Moran's *I-Value* = 0.010174, p = 0.000), density was randomly distributed within each of the four regions (Table 5; Figures 6-9).

Discussion

Dolphin density as measured by dolphins per km and dolphins per group was significantly variable within the northeast Florida study area. As expected, dolphin density, regardless of measure,



Figure 3. The boxplots for dolphins per km² and per group in each region; shaded areas represent cold water surveys.



Figure 4. The number of neonates observed per km² surveyed in each habitat; shaded regions represent cold water surveys. Note that the scale varies with region.



Figure 5. The boxplots for neonates per km² and per group for each region; shaded areas represent cold water surveys.

Table 4. The upper values on the diagonal represent the average number of neonates observed per km² surveyed (\pm SD) during warm water, while the values above the diagonal represent the *p* values for these comparisons. The lower values on the diagonal represent the average number of neonates observed per group (\pm SD) during warm water, while the values given below the diagonal represent the *p* values for these comparisons.

| Per km ² Per group | COAST | ICN | SJR | ICS |
|----------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|
| COAST | 0.12 (± 0.16) 0.27 (± 0.81) | <i>p</i> = 0.01 | <i>p</i> = 0.045 | p = 0.000 |
| ICN | <i>p</i> = 0.06 | 0.03 (± 0.02) 0.14 (± 0.46) | <i>p</i> = 0.000 | p = 0.000 |
| SJR | <i>p</i> = 0.07 | p = 0.000 | 0.09 (± 0.04) 0.12 (± 0.42) | <i>p</i> = 0.000 |
| ICS | <i>p</i> = 0.000 | <i>p</i> = 0.000 | <i>p</i> = 0.000 | 0.53 (± 0.30) 0.86 (± 1.27) |

Table 5. Spatial autocorrelation (SAC) of sightings with respect to location, number per group, temperature, and depth

| | Moran's I-Value | p value | Pattern |
|---|-----------------|---------|-----------|
| Dolphin distribution by sighting location | | | |
| Northeast Florida Study Area | 0.01 | 0.00 | Clustered |
| COAST | 0.00 | 0.27 | Random |
| ICN | 0.02 | 0.14 | Random |
| SJR | -0.01 | 0.00 | Dispersed |
| ICS | -0.01 | 0.91 | Random |
| Sighting location distribution by water temperature | | | |
| COAST | 0.00 | 0.52 | Random |
| ICN | 0.03 | 0.04 | Clustered |
| SJR | -0.01 | 0.85 | Random |
| ICS | -0.01 | 0.15 | Random |
| Sighting location distribution by depth | | | |
| COAST | 0.11 | 0.00 | Clustered |
| ICN | 0.15 | 0.00 | Clustered |
| SJR | -0.01 | 0.11 | Random |
| ICS | -0.01 | 0.13 | Random |
| Dolphin per group by location | | | |
| Northeast Florida Study Area | 0.06 | 0.00 | Clustered |
| COAST | -0.01 | 0.75 | Random |
| ICN | 0.04 | 0.02 | Clustered |
| SJR | -0.01 | 0.27 | Random |
| ICS | -0.01 | 0.14 | Random |
| Distribution by sighting location for sightings only we | ith neonates | | |
| COAST | -0.04 | 0.94 | Random |
| ICN | 0.07 | 0.02 | Clustered |
| SJR | -0.65 | 0.23 | Random |
| ICS | -0.02 | 0.89 | Random |
| Neonate sighting location distribution by depth | | | |
| COAST | -0.05 | 0.50 | Random |
| ICN | -0.07 | 0.35 | Random |
| SJR | -0.36 | 0.55 | Random |
| ICS | -0.15 | 0.18 | Random |
| Neonate per group by location | | | |
| COAST | -0.05 | 0.74 | Random |
| ICN | -0.06 | 0.45 | Random |
| SJR | 0.13 | 0.35 | Random |
| ICS | -0.15 | 0.18 | Random |



Figure 6. Distribution depicted as number of dolphins per group for each cold (a) and warm (b) water sighting within the COAST region; distribution of neonates depicted as number per group for cold (c) and warm (d) water sightings.



Figure 7. Distribution depicted as number of dolphins per group for each cold (a) and warm (b) water sighting within the ICN; distribution of neonates depicted as number per group for warm (c) water sightings.



Figure 8. Dolphin distribution depicted as number of dolphins per group for each cold (a) and warm (b) water sighting within the SJR; distribution of neonates depicted as number per group for warm (c) water sightings.

was, with a few exceptions (see discussion below), greater in the exposed area of the COAST region than in the estuarine region. The large group sizes and large number of dolphins observed per km² within the COAST region, coupled with the fact that sightings were randomly distributed with respect to temperature, location, and number of dolphins per group, resulted in numerous opportunities for multiple associations among dolphins. These data are congruent with the transient nature of regional fidelity and social affiliations reported within the COAST region (Caldwell, 2001, 2016).

COAST region group sizes ($\bar{x} = 9.36 \pm 9.2$ SD cold, $\bar{x} = 19.93 \pm 25.32$ SD warm) were comparable to those found in Southern California ($\bar{x} = 18.9 \pm 18.4$ SD [Defran & Weller, 1999]); Santa Monica Bay, California ($\bar{x} = 10.1 \pm 7.6$ SD [Bearzi, 2005]); and Azores, Portugal ($\bar{x} = 21.3 \pm 1.6$ SE [Silva et al., 2008]). It is possible that the similarities in mean dolphin group size among these studies are due to similarities in the distribution and abundance of prey resources and predation pressures. However, additional data are needed to test this hypothesis.

As expected, both measures of dolphin density were greater in the exposed area of the COAST



Figure 9. Distribution depicted as number of dolphins per group for each cold (a) and warm (b) water sighting within the ICS; enlargement of Chicopit Bay and the Mile Point reconstruction area (black oval) with sightings depicted as number of neonates per group (c).

region than in the estuarine region of the ICN region for both cold and warm surveys, as well as for the SJR region during warm surveys. Still, the COAST-to-SJR difference was only significant when measured as number of dolphins per group during cold surveys. Unlike the COAST and SJR regions, the number of dolphins per km² and dolphins per group in the ICN did not vary significantly with season. Mean group sizes in the inshore ICN region ($\bar{x} = 4.58 \pm 3.41$ SD cold, $\bar{x} = 4.39 \pm 3.42$ SD warm) were intermediate to reported means in inshore regions that used the same definition of group (Sanibel, Florida, $\overline{x} = 5.5 \pm 4.2$ SD [Shane, 2004]; Indian River Lagoon, Florida, $\overline{x} = 4.1 \pm 3.4$ SD [Kent et al., 2008]; and Lower Florida Keys, $\overline{x} = 4.4 \pm 3.3$ SD [Lewis et al., 2011]). Additionally, ICN sightings were significantly clustered with respect to temperature, location, and number of dolphins per group. The nonrandom distribution, coupled with low dolphin density as measured by number of dolphins per km² ($\overline{x} = 0.21 \pm 0.16$ SD cold, $\overline{x} = 0.20 \pm 0.15$ SD warm) and dolphins per group observed in the ICN, may be an artifact of resource distribution in this region. It has been hypothesized that dolphins using inshore regions are feeding on prey species that are distributed

as individual prey items or on small predictable patches of prey (Wells et al., 1999). Thus, the clustered distribution of ICN sightings may be a result of prey distribution since previous analysis found no correlation between other regional variables and dolphin sightings (Caldwell, 2001, 2016). However, additional data on the change in group size with behavior state (e.g., feeding vs nonfeeding) and the distribution of preferred prey species is required in order to examine this hypothesis.

Unexpectedly, there were significantly more dolphins sighted per km² within the estuarine ICS region than in the COAST region during the warm season. Additionally, none of the other three dolphin density comparisons were found to be significantly different between the ICS and COAST regions. Another unexpected finding was that dolphin density was significantly greater in the estuarine SJR and ICS regions than it was in the estuarine ICN region for all comparisons except for the number of dolphins per group in the SJR vs ICN during the cold water season. Furthermore, dolphin group sizes reported for the ICS ($\bar{x} = 6.22$) \pm 5.72 SD cold, $\bar{x} = 20.69 \pm 14.89$ SD warm) and SJR ($\bar{x} = 3.42 \pm 2.57$ SD cold, $\bar{x} = 10.49 \pm$ 14.93 SD warm) were up to six times greater than those in other inshore regions (Sanibel, Florida, $\overline{x} = 5.5 \pm 4.2$ SD [Shane, 2004]; Indian River Lagoon, Florida, $\overline{x} = 4.1 \pm 3.4$ SD [Kent et al., 2008]; and Lower Florida Keys, $\overline{x} = 4.4 \pm 3.3$ SD [Lewis et al., 2011]).

Although bottlenose dolphin sighting locations were significantly dispersed within the SJR but randomly distributed within the ICS, they were randomly distributed with respect to temperature, depth, and number of dolphins per group for both the SJR and ICS regions. Interestingly, dolphin groups were often followed from the SJR into the ICS or from the ICS into the SJR and then to the mouth of the St. Johns River. On all occasions, these groups maintained their cohesive nature while traveling from region to region. Additionally, for all sightings within ICS, all bottlenose dolphins were observed within 100 m of another dolphin and, thus, constituted only one group. Region preference (Caldwell, 2016) and home range analysis (Caldwell, 2001) found that bottlenose dolphins preferentially using the ICS region, with Chicopit Bay identified as their 50% kernel contour, also used the SJR region but tended to avoid the ICN. The high dolphin density found in the SJR and ICS regions, coupled with high levels of sight fidelity (Caldwell, 2016), provide bottlenose dolphins utilizing these regions ample opportunity to associate and form strong, repeatedly reinforced social bonds. Ninety-four percent of the ICS/SJR dolphins associated with at least 90% of the possible affiliates within their range (Caldwell, 2016). In contrast, in the less dense ICN region, only 39% percent of the ICN dolphins associated with at least 90% of the possible affiliates within their range (Caldwell, 2016).

Higher dolphin density within the ICS region (Figure 9) and at the ICS/SJR intersection (Figures 8 & 9) as opposed to the ICN may be associated with the bathymetry and hydrology of the regions, prey distribution patterns, and the regional preferences of dolphins using these areas (Caldwell, 2016). It is probable that dolphin density is not resourcelimited in the ICS and SJR regions. Because of the influence of the southern confluence of the ICW with the St. Johns River, the current in the upper 2 to 7 m of the water column exhibits a significant cross-channel flow (Bourgerie, 1999). This boundary may concentrate fish in a limited space, a supposition supported by the fact that feeding dolphins and recreational fishermen were often observed congregating in this tidal boundary. Furthermore, dolphin density was also concentrated at the mouth of the St. Johns River-another area associated with tidal boundaries and concentrated prey. Since prey distribution is not likely to be uniform within the northeast Florida study area, it is not surprising that dolphin distribution was also variable. Still, additional data on the change in group size and group membership with behavior state and sighting location, coupled with the distribution of preferred prey species, is required in order to determine why mean dolphin group size and number of dolphins observed per km² was higher in the ICS and SJR regions than in the ICN region or in other inshore study areas.

Because of high maternal dependence, neonate density and distribution is predicated by that of maternal density and distribution. If one reason mothers with neonates are grouping together is to reduce predation pressure, then neonate density would be expected to be greater in exposed coastal habitats rather than protected estuarine habitats based on the assumptions of predation pressure in each habitat (Gowans et al., 2008). Surprisingly, neonate density in the estuarine ICS was more than four times greater than in the exposed COAST region, more than five times greater than in the estuarine SJR region, and 17 times greater than in the ICN region. Moreover, the number of neonates per km² in the ICS region was also twice that found in the exposed habitat of Virginia Beach (Barco et al., 1999).

As in many species, female dolphins tend to associate with females in the same reproductive condition rather than with nonreproductive females (Jarman, 1974; Goodall, 1986; Grinnell & McComb, 1994; Wells et al., 1999). This tendency can result in high neonate density when density is measured as the number of individuals per group. Not surprisingly, neonate density, when measured as number per group, followed the trends discussed above for dolphin density and was significantly greater in the ICS region than in any other region in the estuarine habitat. However, surprisingly, the number of neonates per group in the ICS region was three times greater than that number in the exposed habitat of the COAST region. Interestingly, the number of neonates per group was also significantly lower in the SJR than in the ICN region. Quick passage through the SJR, a region not likely conducive to nursing due to swift tidal currents, would have reduced the possibility of encountering mothers and neonates during a survey; while conversely, if mothers with neonates lingered in the shallower, more calm, ICS, they would have been more likely to be encountered. Focal follows of groups with neonates would elucidate if this difference might be due to the fact that mothers move quickly through the SJR but linger in the ICS.

If all aspects of a habitat are randomly distributed, then neonate distribution could also be expected to be random. However, if resources favorable to mothers with nursing neonates are clustered or dispersed, then one would expect neonate distribution to also be clustered or dispersed. Neonate distribution was found to be random within the northeast Florida study area with respect to sighting location for all regions except the ICN where sightings with neonates were significantly clustered. This was not surprising for two reasons: (1) dolphin sightings within the ICN were clustered by temperature, depth, and location; and (2) sightings of neonates within the ICN were SAC clustered in the same areas identified as the 50% kernel contour for Northern community dolphins using this region (Caldwell, 2001). The fact that the ICS neonate sightings were not clustered can be explained by the fact that dolphin sightings within the ICS were randomly SAC and that the entire area of Chicopit Bay was identified as the 50% kernel contour for Southern community dolphins using the ICS and SJR regions (Caldwell, 2001).

Southern community members exhibited seasonal fidelity for the ICS and SJR regions (Caldwell, 2016) and utilized the ICS region as their 50% minimum convex polygon kernel contour (Caldwell, 2001). The significantly high neonate densities within the ICS and SJR regions, coupled with the region preference, region fidelity, and home range data (Caldwell, 2001, 2016), lead to the hypothesis that in 1994 through 1997, dolphins used the isolated, shallow, small inland Chicopit Bay of the ICS region as a nursery area. Use of estuarine habitats as possible nursery areas has been proposed for dolphins in Sarasota

Bay, Florida (Scott et al., 1990); Virginia Beach, Virginia (Barco et al., 1999); and Beaufort, North Carolina (Wang et al., 1994). Mothers with neonates primarily utilized the ICS region during the calving peak and warm water season then progressed out of the sheltered ICS region as the water temperature fell below 16° C. When neonates were sighted within the SJR region, they were sighted within groups traveling either to or away from the ICS region.

Use of the ICS region as a nursery area is supported by two conditions. The first condition is that 12 of the 30 potential prey species are known to spawn in this estuarine habitat during warm water months (Perlmulter, 1961; McErlean et al., 1973; Wilson, 1991). Additionally, at changing tidal periods, a strong tidal boundary zone between the ICS and SJR regions may concentrate fish in a limited space. Thus, the ICS region may provide abundant and concentrated prey resources to mothers with neonates. Abundant and concentrated resources may decrease the amount of time mothers need to spend foraging and, consequently, increase the time they have to nurse their calves.

A second condition favoring the ICS region as a nursery area is that it is a shallow bay with areas that are protected from wind-generated waves and extreme tidal flow by dredge spoil islands and the rock jetty between the St. Johns River and the entrance to the ICS region. Shallow water habitats also may provide protection from potential predators by reducing the avenues of attack (Scott et al., 1990; Wells et al., 1999; Mann et al., 2001). Reproductive success was predicted by water depth for dolphins using Shark Bay in Australia (Mann et al., 2001), with those in shallower water exhibiting higher reproductive success than those in deeper water. Additionally, protection from currents and waves may reduce the energy expenditure needed to fight these elements and thereby allow more resources to be allocated to growth rather than to swimming.

Despite the advantages offered as a dolphin nursery, the ICS and Mile Point area is being restructured by the Mile Point project (USACE, 2012, 2014a, 2014b; JAXPORT, 2014). The plans call for removing the current rock jetty, redirecting water flow, and dredging a channel behind the current dredge spoil islands on the southwest side of the bay. Although increased water flow into the south ICW is predicted to rejuvenate the tidal estuaries south of Chicopit Bay, the impacts on the Southern dolphin community are unknown. Marine construction, demolition, and dredging have been documented to affect dolphin density and distribution (Buckstaff et al., 2013; Pirotta et al., 2013; Weaver, 2015). Additionally, Weaver (2015) documented that female, but not male, sightings significantly decreased during construction and speculated that sex differences in environmental monitoring and vigilance associated with maternal behavior may have been responsible for the decline in female sightings.

In order to assess the impact of the Mile Point project, it is crucial to determine if the Chicopit Bay and Mile Point areas are as important to bottlenose dolphins today as they were in 1994 through 1997. While opportunistic photo-identification surveys conducted during 2010-2011 (Caldwell et al., 2011) re-sighted dolphins originally sighted during the 1994-1997 study in their 95 and 50% kernel contour (Caldwell, 2001), suggesting that these regions are still important, Southern community dolphins also were sighted in areas beyond their 1994-1997 identified range. Furthermore, opportunistic aerial- (G. Pinto, pers. comm., 27 January 2015) and dock-based sightings (R. Borkowski, pers. comm., 25 May 2015) also suggest that bottlenose dolphins are using other areas of the SJR not identified as preferred habitat in the 1994-1997 study.

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