Aquatic Mammals 2016, *42*(1), 89-103, DOI 10.1578/AM.42.1.2016.89

Historical Evidence of *Tursiops truncatus* Exhibiting Habitat Preference and Seasonal Fidelity in Northeast Florida

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Abstract

Degradation of coastal and estuarine habitats is probably inevitable when more people move to coastal regions. To determine potential effects of habitat degradation on a species, the extent of exposure due to habitat fidelity and any characteristics that make the habitat preferable need to be identified. Common bottlenose dolphin (*Tursiops truncatus*) density and distribution in northeastern Florida were seasonally heterogeneous in 1994 through 1997. Regional and seasonal fidelity patterns and habitat variable preferences (e.g., salt marsh, residential density, etc.) of individual dolphins were examined to determine if this heterogeneity was due to significant preferences. Thirty-six bottlenose dolphins were sighted more than expected (preferred) in estuarine waters north (ICN) of the St. Johns River (SJR), whereas 87 dolphins preferred estuarine waters south (ICS) of the SJR. Of dolphins with an ICN preference, 78% exhibited no preference for water season. In contrast, 93% of dolphins with an ICS preference exhibited cold season avoidance. Dolphins exhibited specific preference and avoidance patterns for specific habitat variables. Although undeveloped habitats comprised the majority of total area available within the ICN (94%) and ICS/SJR (54%) regions, less than 25 and 7%, respectively, of the dolphins preferred these ICN and ICS/SJR habitats. Regional, seasonal, and habitat variable preferences, such as those identified in this study, result in different levels to which highly mobile bottlenose dolphins may be affected by changes in habitat suitability. Lack of measurable fidelity observed for bottlenose dolphins sighted in alongshore coastal waters suggests reduced susceptibility of this community to anthropogenic habitat changes in northeastern Florida. In contrast, the highly philopatric nature of dolphins in the ICN increases their vulnerability to habitat changes and degradation. Seasonal use of the SJR and ICS regions of northeastern Florida, on the other hand, may mitigate the impact of habitat changes and degradation experienced by dolphins preferring these regions.

Key Words: habitat preference, seasonal fidelity, common bottlenose dolphin, *Tursiops truncatus*, northeast Florida

Introduction

As the human population along the eastern seaboard of the United States continues to increase, marine habitat degradation will most likely escalate. Habitat degradation can occur from indirect (e.g., eutrophication and toxicity from increased runoff of fertilizers, sewage, pesticides, and industrial chemicals) and direct (e.g., marine construction and demolition, and channel dredging) causes. Marine life also can be affected by habitat changes such as changes in behavior or health directly due to recreational and commercial fishing activities (Bejder et al., 2006; Ansmann et al., 2012b; Byrd et al., 2014), exposure to toxins (Pulster & Maruya, 2008; Yogui & Sericano, 2009), or habitat degradation that affects prey species and thereby indirectly impacts predator species.

The extent to which a highly mobile species such as the common bottlenose dolphin (*Tursiops truncatus*) is affected by habitat change may be related to the amount of time it spends in the habitat. Philopatry and small range sizes have been observed for many alongshore and estuarine dolphin communities (Gubbins, 2002a; Mazzoil et al., 2005; Kent et al., 2008; Merriman et al., 2009; Frère et al., 2010; Caldwell, 2016). Evidence suggests philopatric resident dolphins are more vulnerable to anthropogenic changes within their habitat than nonresident or transient dolphins. For example, dolphins utilizing the Turtle/Brunswick River estuary of Georgia (TBRE) are exposed to organochlorine pollutants (POPs) such as polychlorinated biphenyls (PCBs), organochlorine pesticides (OCPs), and toxaphene (chlorinated monoterpenes). These POPs and other toxins enter the estuary via runoff from several Superfund sites, other hazardous waste sites, and former chloralkali and toxaphene manufacturing facilities (Pulster & Maruya, 2008; Pulster et al., 2009; Ross et al., 2011). Mean total

PCBs and toxaphene were significantly higher in dolphins sampled in the TBRE than in dolphins stranded near Savannah, Georgia, 80 to 100 km to the north (Pulster & Maruya, 2008). The mean total POP for the TBRE animals was well above (Pulster et al., 2009) published total PCB thresholds at which immunosuppression and/or reproductive anomalies are thought to occur (Kannan et al., 2000). Additionally, dolphins sampled in the TBRE have Aroclor 1268 (a specific PCB manufactured in Brunswick) signatures closely resembling those in local preferred fish prey species but distinct from those observed in dolphins sampled in Savannah, Georgia, as well as in other southeastern U.S. estuaries (Pulster & Maruya, 2008). The similarity of PCB signatures in dolphin blubber and local prey species supports the hypothesis that when dolphins exhibit fidelity to a specific estuary, they can be impacted by the health of the estuary (Pulster & Maruya, 2008).

From 1994 through 1997, bottlenose dolphins exhibited heterogeneous and seasonal patterns in density within northeastern Florida (Figure 1; Caldwell, 2016). These findings raised the question as to whether the observed density and distribution patterns were the result of habitat and seasonal fidelity of individual dolphins or a byproduct of random movements of dolphins in and out of the area. Habitat fidelity (or *preference*) describes the extent to which an individual, by selecting one habitat over others, spends more time in that habitat than would be predicted based on the availability of each habitat (Neu et al., 1974; Byers et al., 1984; White & Garrott, 1990). Similarly, seasonal fidelity would indicate that an individual utilizes an area more often during specific seasons. Dolphins exhibiting regional and/or seasonal fidelity would more likely be impacted by habitat changes than would transient dolphins.

As with most coastal regions, the human population in the northeastern Florida counties of Nassau and Duval is continuing to grow. Census data from 1990 to 2009 showed that the population of Duval County increased 28% from 672,971 to 858,291. Nassau County experienced a greater rise in population size, increasing 65% from 43,941 to 72,349 in the same time period (Florida Office, 2014). Consequently, regional land use within these two northeast Florida counties has changed (St. Johns River Water Management District [SJRWMD], 2014). Comparison of land-use patterns in 1995 to those in 2009 show an increase in residential and commercial land use and a subsequent decline in forests and wetlands encompassing the northern and southern estuaries as well as increased development of beach front and barrier island areas (Figure 2). Additionally, the U.S. Army Corps of Engineers (USACE) Jacksonville District (2012, 2014a, 2014b; JAXPORT, 2014) will be deepening the St. Johns River and changing the flow of the river at its intersection with the Intracoastal Waterway (ICW). The potential for marine habitat degradation will most likely escalate within northeastern Florida and, thus, will have the potential to affect residential dolphin habitat fidelity and behavioral patterns.

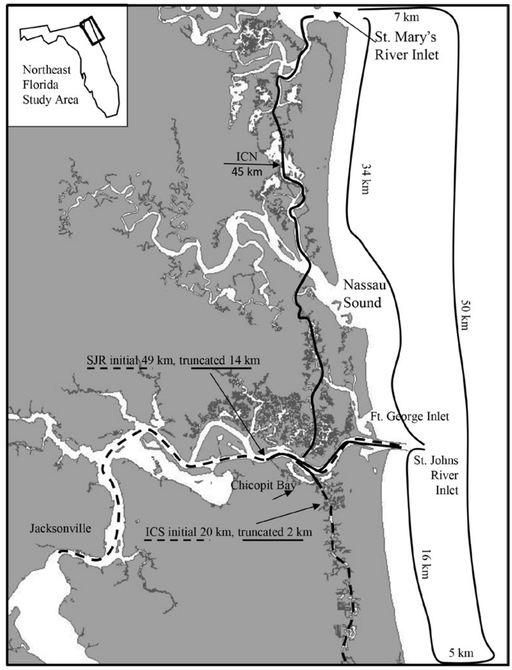

Figure 1. The location landmarks, transect route, and lengths for each region within the northeast Florida study area; survey transects of the ICS and SJR regions were truncated in length after 1995 due to a lack of sightings.

Bottlenose dolphins originally sighted during the 1994-1997 study have been opportunistically re-sighted since 2010 in the same areas in which they were originally identified (Caldwell et al., 2011; M. Mazzoil, pers. comm., 10 March 2014; R. Borkowski, pers. comm., 11 March 2014). Given the fact that these areas have been impacted by anthropogenic changes in land use (Figure 2) and are about to be impacted by marine construction projects (USACE, 2012, 2014a, 2014b; JAXPORT, 2014), knowledge of individual dolphin regional and seasonal preferences, and the variables (e.g., salt marsh, agriculture, and residential/commercial building density) that make a habitat preferable, is necessary for understanding the potential effects of habitat change and degradation. Thus, there were three objectives. The first two objectives were to determine the regional and seasonal fidelity patterns of individual dolphins

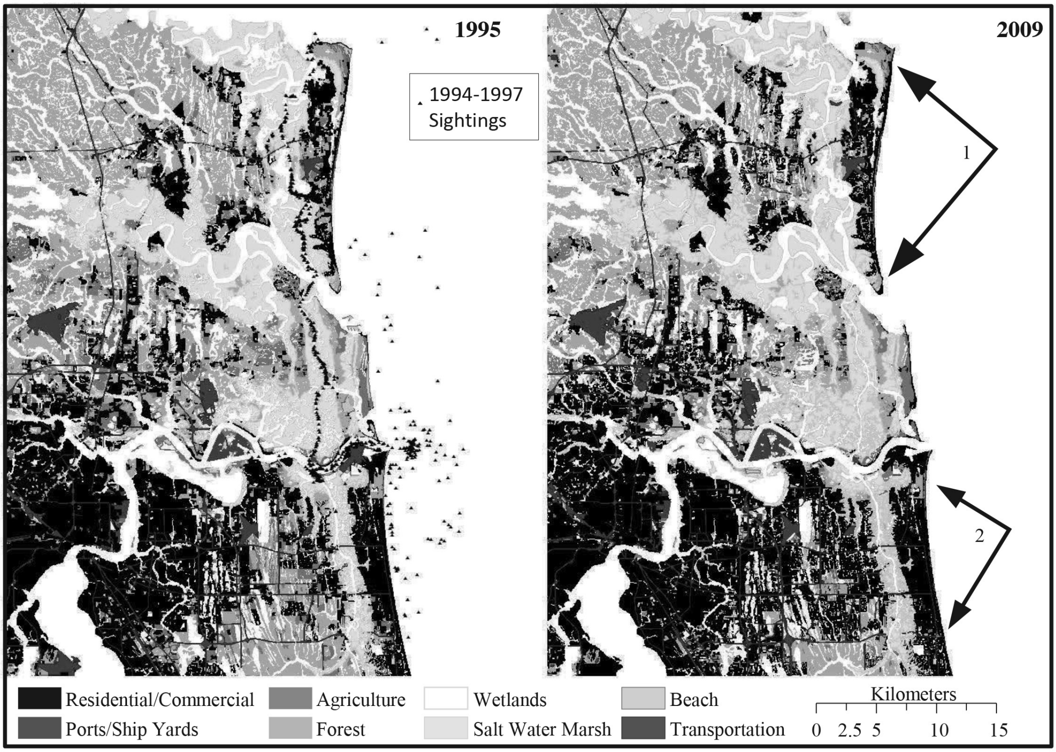

Figure 2. Comparison of habitat distribution for 1995 and 2009. The 2009 map shows an increase in residential/commercial land use in the northern barrier island region as well as in the northern (1) and southern (2) estuaries.

using the coastal and estuarine waters of northeastern Florida from 1994 through 1997. The third objective was to identify habitat variables that constitute preferred dolphin habitat during the 1994-1997 study.

Methods

Study Area

The northeast Florida study area (Figure 1) was selected for several reasons: the estuarine system is connected to the coastal waters by four inlets, including one that is underdeveloped (Nassau Sound) and one that is a major shipping channel (the St. Johns River; Figure 1); the area encompasses estuarine waters surrounded by heterogeneous areas ranging in levels of human impact and development (Figure 2); and dolphin distribution and density were documented to be heterogeneous and seasonal in portions of the study area (Caldwell, 2016). 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 = the 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

Individual bottlenose dolphins were identified using standard photo-identification analysis and survey techniques described by Würsig & Jefferson (1990). Once 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, was recorded. Biweekly photo-identification surveys were conducted along transects from December 1994 through December 1997 (Figure 1; Caldwell, 2016). Both the ICS and SJR transects were truncated (20 km to 2 km and 38 km to 9 km, respectively) after 1995 due to a dearth of sightings.

Region Fidelity Analyses

To examine whether bottlenose dolphins were preferentially using the COAST region or the estuarine regions (ICN, ICS, and/or SJR), individually identified dolphins re-sighted eight or more times were selected. This criterion allowed for the possibility that a dolphin would be sighted twice within each region and also reduced possible bias introduced by individuals sighted on a few occasions within a short time period (i.e., within 2 mo). A set of confidence intervals (CI) were generated to examine whether a dolphin used each region in proportion to the amount that region was surveyed considering all regions simultaneously (Neu et al., 1974; Byers et al., 1984; White & Garrott, 1990). In this test, the proportion of regional habitat availability was determined by totaling the number of km surveyed in a region and dividing it by the overall total number of km surveyed to obtain the relative proportion of each region potentially available to the dolphins (COAST = 0.26, ICN = 0.56, ICS = 0.05, and SJR = 0.13). To obtain the expected use for each region, the total number of a dolphin's sightings was multiplied by the relative proportion each region was surveyed. The Bonferroni correction factor with k = 4 for the number of regions in the study area was used to reduce the possibility of Type I error. Bonferroni confidence intervals were generated using the following formula:

$$\bar{p}_i - z_{\left(\frac{\alpha}{2k}\right)} \sqrt{\frac{\bar{p}_i(1-\bar{p}_i)}{n}} \leq p_i \geq \bar{p}_i + z_{\left(\frac{\alpha}{2k}\right)} \sqrt{\frac{\bar{p}_i(1-\bar{p}_i)}{n}}$$

In this formula, p_i was the proportion of sightings in region i, n was the total number of sightings for an individual, and $z_{\alpha/2k}$ was the standard normal variant associated with the upper and lower probability area of α/k where α = 0.05 (Byers et al., 1984). If the range of the upper and lower Bonferroni corrected CI, which represents the expected proportion of usage for each region, excluded the actual proportion of available region, then the actual usage and the expected usage of the region were significantly different (Byers et al., 1984). Henceforth, the terms *prefer* and *avoid* simply refer to whether a dolphin was sighted within a specific region significantly more or less, respectively, than expected given the proportion of available region. The term *ambivalent* will be used when dolphins were not sighted more or less than expected.

Seasonal Fidelity Analysis

A previous study has shown that water temperature influences dolphin density within the Mid Atlantic Bight (Gubbins et al., 2003). Therefore, the seasonal definition used in this analysis was based on water temperature (cold and warm). The cold season was defined as the time period when water temperature was equal to or less than 16° C, while the warm season encompassed water temperatures greater than 16° C. This division resulted in six survey periods (three cold and three warm), starting with the cold season of 1994-1995 and ending with the warm season of 1997 (Caldwell, 2016).

To examine whether dolphins exhibited year-round or seasonal fidelity, only bottlenose dolphins sighted six or more times were selected for analysis. This criterion allowed for the possibility that a dolphin would be sighted at least once within each of the six survey periods and, thus, three times in each water season. As above, the confidence intervals were used to examine the relationship of season utilization to season availability. In this analysis, however, no correction factor was needed since only two seasons were being compared (Neu et al., 1974; Byers et al., 1984; White & Garrott, 1990). If the range of the upper and lower CI, which represent the expected proportion of usage for each season, excluded the actual proportion of the available season, then the actual usage and the expected usage of the season were significantly different (Byers et al., 1984). In this test, the proportion of surveys conducted for each period was used as the proportion of season available (cold = 0.18; warm = 0.82).

Fidelity to Specific Habitat Variables Analyses

Habitat variables were obtained from four sources (Southeast Area Monitoring and Assessment Program, 1998; Florida Department of Environmental Protection, 2000; Flamm et al., 2002; SJRWMD, 2014). The amount and type of habitat data available varied for the coastal and estuarine habitats. Data for the distance to the nearest road and/or boat ramps were available for all regions. Bottom composition variables (e.g., hard or "live" bottom, possible hard bottom, no evidence of hard bottom, or artificial reef) were only available for the COAST region. No other estuarine habitat data were available. However, there was a wealth of terrestrial land-use data available for the area directly surrounding the waters surveyed. Estuarine and coastal habitat degradation can result from terrestrial land use—for example, eutrophication and toxicity from increased runoff of fertilizers, sewage, pesticides, and industrial chemicals are associated with agriculture and industrial land use (Pulster & Maruya, 2008; Yogui & Sericano, 2009). Additionally, marine construction and demolition, and the channel dredging associated with residential, industrial, and transportation land use can also affect the adjoining marine habitat and affect dolphin behavior (Buckstaff et al., 2013; Pirotta et al., 2013; Weaver, 2015). Consequently, land-use data were used as potential indicators of estuarine habitat type.

Two methods were used to identify habitat variables associated with dolphin sighting location, density, and habitat variable preference. The analyses were performed independent of region unless significant regional preferences were found. First, Spearman rank correlation analyses were used to determine whether dolphin density was correlated with the distance to the nearest bottom composition for the COAST region and the distance to the nearest road and/or boat ramp for all regions. To generate the data for these analyses, *ArcView 3.2* (Environmental Systems Research Institute [ESRI], 1995) and the *Animal Movement Analysis Extension to ArcView* (Hooge & Eichenlaub, 1997) were used to calculate the shortest distance from each habitat variable to each sighting location. Second, the Bonferroni confidence interval method described previously was used to examine whether dolphins exhibited significant preference or avoidance for specific terrestrial habitat variables (Neu et al., 1974; Byers et al., 1984; White & Garrott, 1990). Habitat variable availability was determined by adding a 1 km buffer to all dolphin sighting locations and then extracting the area, in km^2, of each habitat variable encompassed by the buffers. Preference and/or avoidance for a specific habitat variable was analyzed by calculating the Bonferroni confidence intervals for the proportion of dolphins photographed within 1 km of each habitat variable. If the range of the upper and lower Bonferroni intervals, which represent the expected proportion of usage for each habitat variable, excluded the actual proportion of available habitat, then the actual usage and the expected usage of the habitat variable were significantly different (Byers et al., 1984).

Table 1. Summary of sighting rates within northeastern Florida by region. Regional sighting rates are reported only for bottlenose dolphins sighted eight or more times and with significant regional fidelity. The terms *preference* and *avoidance* are used when dolphins were sighted within a specific region significantly more or less, respectively, than expected given the proportion of available region. *Ambivalence* is used when bottlenose dolphins were sighted within a region as expected given the proportion of available region.

	COAST	ICN	ICS	SJR	ICS/SJR combined	Northeast Florida
Sighting rates for each region						
# dolphins identified	685	106	155	198	230	904
Mean # of sightings	1.62	9.03	9.93	3.66	9.84	4.79
Standard error	0.04	1.12	0.71	0.25	0.74	0.28
Standard deviation	1.09	11.57	8.81	3.54	11.29	8.33
Maximum # of sightings	7	47	36	15	51	53
Total # of sightings	1,109	957	1,539	725	2,264	4,330
Sighting rates for dolphins with significant regional fidelity						
# dolphins with preference	2	36	87	18	12	
Mean # of sightings	7.00	22.11	15.98	10.44	25.50	
Standard error	0.00	0.44	0.78	0.56	2.95	
Standard deviation	0.00	11.11	7.26	2.36	10.22	
Maximum # of sightings	7	47	36	15	51	
# dolphins with avoidance	120	94	36	33		
# dolphins sighted	38	12	0	0		
Mean # of sightings	1.74	1.33				
Standard error	0.15	0.14				
Standard deviation	0.92	0.49				
Maximum # of sightings	4	2				
# ambivalent dolphins	13	3	10	82		
Mean # of sightings	3.15	10.33	2.10	4.85		
Standard error	0.62	3.33	0.59	0.37		
Standard deviation	2.23	5.77	1.85	3.31		
Maximum # of sightings	7	17	6	13		

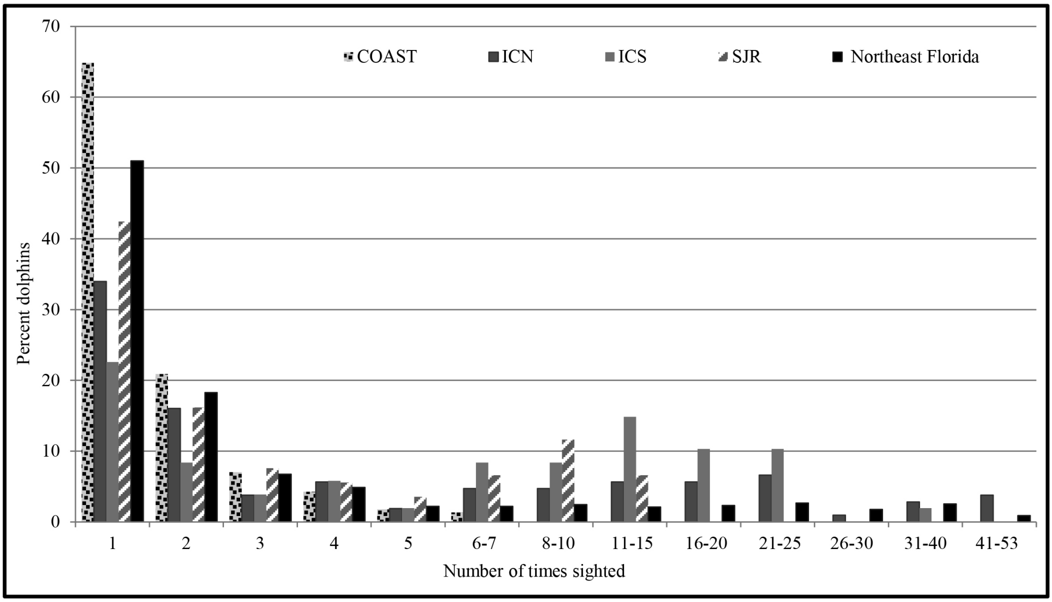

Figure 3. Percent of dolphins photographed 1 to 53 times within each region of the northeast Florida study area

Results

During 198 surveys, 7,345 dolphins in 751 groups were encountered, and 904 individually recognized dolphins were photographed between one and 53 times ($\bar{x}$ = 4.79, SD ± 0.28) from December 1994 through December 1997. The number of individual dolphins identified and the mean number re-sightings per dolphin varied by region (Table 1). Although more dolphins were identified in the COAST and SJR regions than in the ICN and ICS regions, the mean number of sightings for individual dolphins was greater in the ICS and ICN regions (Table 1). Fewer dolphins were re-sighted within the COAST (35%) compared to the SJR (58%), ICN (66%), and ICS (77%) regions. Additionally, more dolphins were sighted over 10 times in the ICN and ICS regions than in the COAST and SJR regions (Figure 3). The cumulative new and resight curves (Figure 4) show that more new dolphins were identified and fewer dolphins were re-sighted within the COAST region (total new = 637; total resights = 391) as compared to the ICN (total new = 92; total resights = 762), SJR (total new = 76; total resights = 600), and ICS (total new = 104; total resights = 1,404) regions. Also, while the cumulative number of new dolphins identified within the ICN, SJR, and ICS regions continued to rise at a steady rate, the cumulative number of re-sighted dolphins in the SJR and ICS regions increased steadily, primarily

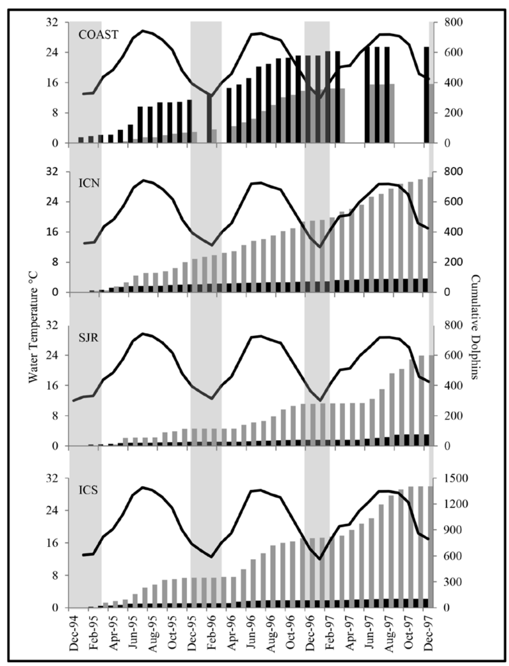

Figure 4. Regional comparison by monthly totals of cumulative new (black bars) and cumulative re-sighted dolphins (dark grey bars) overlaid on water temperature; the light grey shaded regions represent cold water survey months.

during warm water surveys with few dolphins resighted during cold water surveys (Figure 4).

Region Fidelity Analyses

Bonferroni confidence intervals were calculated for 133 bottlenose dolphins photographed eight or more times. Sighting rates for dolphins with significant regional fidelity varied with region and fidelity type (Table 1). More dolphins preferred the ICS region ($n = 87$) than the ICN ($n = 36$), SJR ($n = 18$), or COAST ($n = 12$) regions. Conversely, more dolphins avoided the ICN ($n = 94$) and the COAST ($n = 120$) regions than the ICS ($n = 36$) or SJR ($n = 33$) regions. None of the dolphins with significant avoidance of the ICS and SJR regions were sighted within those regions whereas 33 and 13% of the dolphins that avoided the COAST and ICN regions, respectively, were sighted at least once in those regions. The average number of times dolphins were sighted within a region for which they exhibited avoidance was less than two (COAST = 1.69, SD = 0.86, range = 1 to 4; ICN = 1.25, SD = 0.45, range = 1-2).

Of the 36 bottlenose dolphins that preferred the ICN, 72% avoided the other three regions (Table 2). No dolphins were ever photographed in a region for which they exhibited avoidance. Ten (28%) exhibited ambivalence to other regions (Table 2). Two dolphins were photographed once each in the ICS and SJR regions; one was photographed twice in the ICS region; and seven were sighted once in the COAST region. The 36 bottlenose dolphins with ICN preference form what will be henceforth named the Northern community.

Of the 87 bottlenose dolphins that preferred the ICS region, only two avoided the SJR region and all but one avoided the ICN region. The 85 bottlenose dolphins that had ICS preference coupled with SJR preference ($n = 9$) or ambivalence ($n = 73$) and ICN avoidance ($n = 85$) form what will be henceforth named the Southern community (Table 2). The sighting rate for Southern community dolphins within a habitat for which they exhibited ambivalence was higher than that seen for Northern community members (SJR: $n = 73$, $\bar{x} = 5.33$, SD = 3.20, range = 1 to 13; COAST: $n = 4$, $\bar{x} = 3.25$, SD = 1.71, range = 1 to 5). Unlike Northern community members, some Southern community dolphins were photographed in an avoided habitat, 12 in the ICN region ($\bar{x} = 1.33$, SD = 0.49, range = 1 to 2), and 39 in the COAST region ($\bar{x} = 1.74$, SD = 0.92, range = 1 to 4).

Twelve bottlenose dolphins could not be assigned to a community based on their preference patterns (Table 2). Only two dolphins preferred the COAST region. Both were sighted seven

Table 2. Summary of the individual preference and/or avoidance tests for each habitat. *Prefer* and *Avoid* refer to whether a bottlenose dolphin was sighted within a specific region significantly ($p \leq 0.05$) more or less, respectively, than expected given the proportion of available region. *Ambivalent* refers to dolphins sighted as expected within that region.

# dolphins	ICN	ICS	SJR	COAST
Northern community (n = *36)*				
26 (72%)	Prefer	Avoid	Avoid	Avoid
4 (11%)	Prefer	Avoid	Ambivalent	Avoid
3 (8%)	Prefer	Ambivalent	Avoid	Avoid
2 (6%)	Prefer	Ambivalent	Ambivalent	Avoid
1 (3%)	Prefer	Avoid	Avoid	Ambivalent
Southern community (n = *85)*				
69 (81%)	Avoid (*9)	Prefer	Ambivalent	Avoid (*30)
4 (5%)	Avoid	Prefer	Ambivalent	Ambivalent
12 (14%)	Avoid (*3)	Prefer	Prefer	Avoid (*8)
Not assigned (n = *12)*				
3 (25%)	Avoid	Avoid	Prefer	Ambivalent
3 (25%)	Avoid	Ambivalent	Prefer	Ambivalent
2 (17%)	Avoid	Avoid	Ambivalent	Prefer
1 (8%)	Avoid	Prefer	Avoid	Avoid
1 (8%)	Ambivalent	Prefer	Avoid	Avoid
1 (8%)	Ambivalent	Ambivalent	Avoid	Avoid
1 (8%)	Ambivalent	Ambivalent	Ambivalent	Avoid

(**n*) = # of bottlenose dolphins sighted at least once within an avoided region times in the COAST region, avoided the ICN and ICS regions, and were ambivalent to the SJR region (Table 2). Although both of these dolphins exhibited warm water preference, one avoided cold water, while the other was ambivalent to cold water (Table 3). Of the six bottlenose dolphins that exhibited SJR preference and ICN avoidance, three were ambivalent to the COAST region and avoided the ICS region, while the other three were ambivalent to both the COAST and ICS regions. Two bottlenose dolphins preferred the ICS and avoided the SJR and COAST regions but differed in their preferences for the ICN region. Finally, two bottlenose dolphins avoided the COAST region and were ambivalent to the ICN and ICS regions but differed in their preferences for the SJR region (Table 2).

Seasonal Fidelity Analysis

Bonferroni confidence intervals were calculated for the 153 bottlenose dolphins photographed six or more times (Table 3). Of these dolphins, 110 (72%) avoided cold water and preferred warm water; one preferred cold water and was ambivalent to warm; and the remaining 42 (27%) were ambivalent to both warm and cold water. The Northern and Southern community dolphins varied in their seasonal preferences. Specifically, 93% ($n = 79$) of the Southern community dolphins preferred warm water and avoided cold compared to only 19% ($n = 7$) of the Northern community dolphins (Table 3). Conversely, more Northern community dolphins were ambivalent to water season than were Southern community dolphins (78 vs 7%).

Fidelity to Specific Habitat Variables Analyses

There was no significant correlation between dolphin density in the COAST region and bottom type (e.g., hard or "live" bottom, possible hard bottom, no evidence of hard bottom, or artificial reef). Additionally, there was no significant correlation between dolphin density in any region and distance to the nearest road or boat ramp. Only 30 (8%) of the 391 coastal sightings were within 1 km of the land and, thus, the consequent habitat variable data were not representative of coastal sightings as a whole, which prevented analysis of terrestrial habitat variable preference/avoidance for dolphins using the COAST region.

Because bottlenose dolphins exhibited specific regional and seasonal preference/avoidance patterns within the study area (Tables 2 & 3), Bonferroni confidence intervals were calculated to examine seasonal differences in habitat variable utilization to habitat variable availability within the ICN and within the ICS/SJR regions independently. The proportion available for each terrestrial habitat category varied between the ICN and the combined ICS/SJR regions (Figure 5). Within the ICN region, 94% of the available habitat was undeveloped and, thus, potentially less disturbed by human activities (84% salt marsh, 9% forest, 0.55% wetlands, and 0.61% beaches vs 5% residential/commercial, 0.33% agriculture, 0.55% transportation, and 0.08% ports/shipyards; Figure 5). More bottlenose

Table 3. Summary of the individual preference and/or avoidance tests for each water season. *Prefer* and *Avoid* refer to whether a bottlenose dolphin was sighted during a water season significantly ($p \leq 0.05$) more or less, respectively, than expected given the proportion of each season surveyed. *Ambivalent* refers to dolphins sighted as expected within that season.

# dolphins	Cold water	Warm water
*Northern community (*n*=36)*		
7 (19%)	Avoid (*5)	Prefer
1 (3%)	Prefer	Ambivalent
28 (78%)	Ambivalent	Ambivalent
*Southern community (*n*=85)*		
79 (93%)	Avoid (*27)	Prefer
6 (7%)	Ambivalent	Ambivalent
*Dolphins sighted ≥ 8 that were not assigned (*n*=12)*		
8 (67%)	Avoid	Prefer
4 (33%)	Ambivalent	Ambivalent
Additional 20 dolphins included in seasonal fidelity analysis		
16 (80%)	Avoid	Prefer
4 (20%)	Ambivalent	Ambivalent

(*n) = # of dolphins sighted at least once within an avoided region.

dolphins were sighted within undeveloped ICN habitats during cold (86%) and warm (83%) surveys than in developed habitats. Although salt marsh and upland coniferous hardwood forest comprised over 92% of the ICN available habitat, they were avoided during both seasons. In contrast, regardless of season, bottlenose dolphins preferred undeveloped and developed habitats that comprised about 3% of the total available area (Table 4). When sighted in developed ICN habitats, bottlenose dolphins avoided the airport on Amelia Island and were ambivalent to swimming beaches, major roads and highways, and port facilities during both seasons. Preferences for the remaining ICN habitats varied with season (Table 4).

Only 54% of the available ICS/SJR habitat was undeveloped (40% salt marsh, 5% forest, 2% wetlands, and 7% beach vs 18% residential/commercial, 5% agriculture, 18% transportation, and 5% ports/shipyards; Figure 5). More dolphins were sighted within undeveloped ICS/SJR habitats during cold (72%) and warm (68%) surveys than in developed habitats (Table 5). Although salt marsh and sand comprised over 47% of the ICS/SJR available habitat, over 40% of the sighted bottlenose dolphins exhibited cold ambivalence and warm avoidance to these predominantly undeveloped habitats. In contrast, regardless of

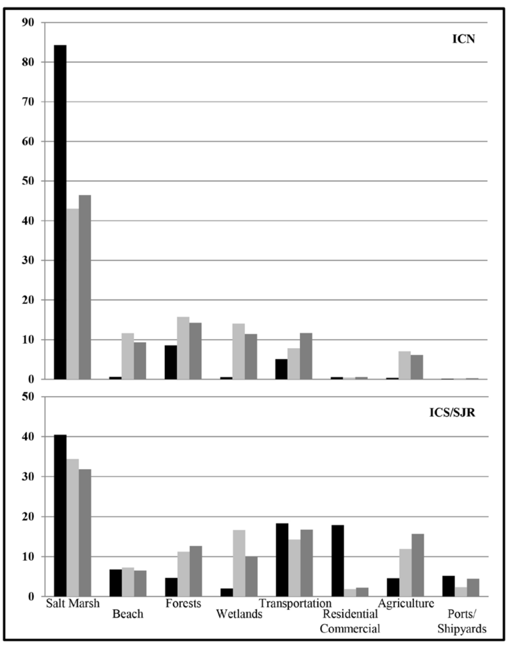

Figure 5. Percent of expected sightings (black bars) compared to the proportion of observed cold (light grey bars) and warm (dark grey bars) water sightings within 1 km of each habitat category for the ICN and the ICS/SJR regions.

season, over 23% preferred undeveloped ICS/SJR habitats that comprised just over 6% of the total available area (Table 5). Additionally, over 15% of the bottlenose dolphins preferred developed habitat, regardless of season, that comprised less than 5% of the total ICS/SJR habitat available. Port facilities, ship building and repair, airports, military complexes, other light industrial areas, sand and gravel pits, major roads and highways, medium density residential areas (2 to 5 dwelling units/acre), and swimming beaches were avoided during both seasons. As within the ICN region, preferences for the remaining ICS/SJR habitats varied with season (Table 5).

Discussion

The regional and seasonal preference/avoidance patterns of individual bottlenose dolphins presented in this article distinguish two distinct intracoastal communities within the northeast Florida study area, although regional and seasonal patterns for bottlenose dolphins using the COAST region could not be determined. Dolphins used the COAST region year-round as is typical of coastal dolphin populations (Hanson, 1990; Defran & Weller, 1999; Defran et al., 1999; Bearzi et al., 2009; Merriman et al., 2009; Hwang et al., 2014), but only two dolphins preferred the COAST. Furthermore, while those two preferred warm water, only one was sighted in cold water. The paucity of re-sighted dolphins in the COAST region suggests that the range of the Coastal community extended an undetermined distance beyond the borders of the northeast Florida study area and that dolphins using the COAST region were highly mobile. As stated previously, this was not an unexpected finding as other studies have documented short-term, repeated habitat fidelity and long-range movements for coastal dolphins (Defran & Weller, 1999; Defran et al., 1999; Gubbins et al., 2003; Bearzi et al., 2009; Hwang et al., 2014).

Anthropogenic factors, such as the shrimping industry, may influence coastal dolphin movements and, consequently, their regional, seasonal, and habitat variable preferences, which might affect encounter rates with potential associates (Corkeron et al., 1990; Svane, 2005; Gonzalvo et al., 2008; Ansmann et al., 2012a). Substantially reduced trawling in Moreton Bay, Australia, resulted in the blending of two previously separate communities (Ansmann et al., 2012a). Specifically, former "trawler" and "nontrawler" dolphins were integrated into the entire social network and associated with each other after the reduction of shrimping. The shrimping industry is prevalent in coastal waters off the eastern seaboard

Table 4. Summary of preference and/or avoidance patterns for each habitat variable by water season for bottlenose dolphins using the ICN region. *Prefer* and *Avoid* are significant at $p \leq 0.05$; *Ambivalent* = not significant.

% total area available	% dolphins observed cold/warm	ICN habitat type (% habitat available)
Prefer cold and prefer warm		
1.52	24.82/20.01	Beaches (non-swim) (0.06), sand (0.56), pine flatwoods (0.33), wetland forested mixed (0.03), freshwater marshes (0.005), mixed scrub-shrub wetland (0.05), non-vegetated wetland (0.44), shrub & brushland (0.05)
1.64*	10.52/10.83	< 2 dwelling units/acre (1.2), commercial & services (0.1), marinas & fish camps (0.06), field crops (0.01), mixed rangeland (0.24), lakes (0.01), reservoirs less than 10 acres (0.01), woodland pastures (0.01)
Avoid cold and prefer warm		
0.07*	0/0.69	Cemeteries (0.07)
Avoid cold and avoid warm		
92.21	60.25/62.33	Salt marshes (82.47), upland coniferous/hardwood (7.94)
0.45*	0.13/0.18	Airports (0.45)
Avoid cold and ambivalent warm		
1.45*	0.37/1.44	> 5 dwelling units/acre (0.93), pulp & paper mills (0.51), water supply plants (0.003), facilities under construction (0.007), open land (0.002)
Ambivalent cold and prefer warm		
0.01	0.15/0.52	Bays & estuaries (0.004), wet prairies (0.01), emergent aquatic vegetation (0.0002)
2.01*	2.65/4.33	2 to 5 dwelling units/acre (1.76), golf courses (0.2), parks & zoos (0.03)
Ambivalent cold and ambivalent warm		
0.25*	0.28/0.23	Swimming beach (0.23), major roads & highways (0.08), port facilities (0.08)
Prefer cold and avoid warm		
0.07*	0.45/0.03	Institutional (0.003), governmental (0.005), railroads (0.003), ornamentals (0.003)

* = developed habitats

from North Carolina to Florida. Therefore, there is potential for bottlenose dolphins to access concentrated food sources and move along large stretches of coastline by following trawling shrimp boats. Shrimp boats trawling parallel to the coast and traveling either north or south were sighted during 36% of the 128 sightings within the COAST region. Dolphins were always sighted and photographed behind trawling shrimp boats when the boats were in the study area. Furthermore, three of the dolphins sighted behind trawling shrimp boats offshore of the COAST region were also photographed behind shrimp boats trawling off Hilton Head and/or Myrtle Beach, South Carolina (C. Gubbins & R. Young, pers. comm., 20 March 2000; K. Urian, pers. comm., 29 June 2004). These data, coupled with the dearth of resightings, support the hypothesis that bottlenose dolphins using the COAST region of the northeast Florida study area were utilizing a larger range than encompassed by the area surveyed.

Bottlenose dolphins that utilize an extensive coastal range are not only more likely to encounter a higher number of possible social affiliates, but also are less likely to be exposed to the continuous effects of localized habitat change and degradation. By utilizing multiple estuary outflows and large stretches of coastline, these dolphins may minimize their exposure to point source pollutants and toxins such as those identified in the TBRE of Georgia (Pulster & Maruya, 2008). Comparative analysis of contaminate levels found in coastal dolphins, residential estuarine dolphins, and localized prey species would help elucidate whether coastal dolphins benefit from feeding in multiple locations and are thereby less likely to be impacted by localized habitat change and degradation.

Unlike the bottlenose dolphins using the COAST region, many dolphins using the estuarine waters of the northeast Florida study area exhibited distinct regional, seasonal, and habitat preference patterns. Examination of individual

Table 5. Summary of preference and/or avoidance patterns for each habitat variable by water season for bottlenose dolphins using the ICS/SJR regions. *Prefer* and *Avoid* are significant at $p \leq 0.05$; *Ambivalent* = not significant.

% total area available	% dolphins observed cold/warm	ICS/SJR habitat type (% habitat available)
Prefer cold and prefer warm		
6.34	27.54/23.98	Pine flatwoods (0.44), upland mixed coniferous/hardwood (4.23), shrub & brushland (0.52), bays & estuaries (0.06), wetland coniferous forests (0.01), wetland forested mixed (0.06), emergent aquatic vegetation (0.03), mixed scrub-shrub wetland (0.44)
4.91*	16.54/15.25	< 2 dwelling units/acre (0.18), commercial & services (0.79), marinas & fish camps (0.1), mixed rangeland (3.84)
Avoid cold and prefer warm		
0.03	0.00/0.17	Freshwater marshes (0.01), wet prairies (0.02)
0.91*	0.09/3.40	Reservoirs less than 10 acres (0.02), other heavy industrial areas (0.01), recreational areas (0.33), parks & zoos (0.01), sewage treatment (0.08), open land (0.22), herbaceous range (0.25)
Avoid cold and avoid warm		
38.55*	7.73/11.55	2 to 5 dwelling units/acre (7.24), other light industrial areas (0.02), sand & gravel pits (0.13), military (3.33), swimming beach (4.83), airports (12.91), major roads & highways (4.91), port facilities (5.15), ship building & repair (0.03)
Avoid cold and ambivalent warm		
0.01	0.00/0.003	Coniferous pine (0.01)
0.01*	0.00/0.01	Cemeteries (0.001), governmental (0.005), inactive land with street pattern but no structures (0.002), auto parking facilities (0.01), communications (0.001)
Ambivalent cold and prefer warm		
0.03	0.14/0.72	Beaches (non-swim) (0.03)
0.42*	0.19/1.07	Oil & gas storage (0.38), institutional (0.05)
Ambivalent cold and avoid warm		
47.25	44.74/42.84	Salt marshes (40.49), sand (6.76)
0.7*	0.81/0.51	> 5 dwelling units/acre
Ambivalent cold and ambivalent warm		
0.06	0.09/0.04	
Prefer cold and avoid warm		
0.77*	2.13/0.43	Reservoirs – pits, retention ponds, dams (0.77)

* = developed habitats

regional and seasonal preference patterns identified two distinct dolphin communities (Northern and Southern) using the estuarine waters of this study area. The Northern community is comprised of 36 bottlenose dolphins that were sighted significantly more than expected within the ICN region of the study area; most (72%) avoided the other three regions, and 22% avoided two regions. No Northern community dolphins were sighted in an avoided region. Seventy-eight percent of the Northern community dolphins were ambivalent to changes in water temperature. These data support that the lack of variation in dolphin density with season reported in the ICN region (Caldwell, 2016) is a result of the movements of a small, resident community of dolphins. This finding is not surprising as other estuarine study areas also have been identified to support small, year-round residential communities of bottlenose dolphins (Ballance, 1990; Scott et al., 1990; Shane et al., 1990; Wells, 1991; Gubbins, 2002b; Gubbins et al., 2003; McHugh et al., 2011; Wilson et al., 2012; Caldwell, 2016).

The pattern of a year-round, small, resident population does not hold true for the estuarine waters south of the ICW and SJR intersection. The 85 bottlenose dolphins comprising the Southern community exhibited ICS preference coupled with SJR preference or ambivalence. All Southern community dolphins avoided the ICN region, and all but four avoided the COAST region. Unlike the Northern community dolphins, many Southern community dolphins were sighted within an avoided region. Also, unlike the Northern community dolphins, 93% of Southern community dolphin exhibited cold water avoidance coupled with warm water preference. These data suggest that the bottlenose dolphins that make up the Southern community are primarily using the ICS and SJR regions of the study area during the warm season. These data also suggest that the high dolphin density observed during the warm season reported in the ICS/SJR regions (Caldwell, 2016) is a result of movements of a large community of dolphins repeatedly using the area primarily during the warm season and not a seasonal influx of new dolphins.

Fidelity to Specific Habitat Variable

The different distribution and density patterns identified (Caldwell, 2016) and the regional and seasonal fidelity patterns observed within the ICN, ICS, and SJR regions may be artifacts of habitat distribution and preferences in this region. Preference for specific habitat variables for coastal dolphins could not be determined since there was no significant correlation between dolphin density and each bottom type variable. As most sightings (92%) within the COAST region occurred more than 1 km from the shore, the effect of land habitat variables on dolphin density were not examined since the consequent habitat variable data was not representative of coastal sightings as a whole. Unexamined factors, such as chlorophyll, may play an indirect role in regional fidelity of coastal dolphins by affecting the availability of prey species. Chlorophyll concentration was shown to be the most important variable associated with the distribution and abundance of common dolphins (*Delphinus delphis*) (Spyrakos et al., 2011; Moura et al., 2012) and Franciscana dolphins (*Pontoporia blainvillei*) (Mendez et al., 2010). Analysis of the relationship between chlorophyll concentration and the regional and seasonal preferences of dolphins within the COAST region may be informative for understanding dolphin movements within this region.

Bottlenose dolphins showed specific habitat preference/avoidance patterns within the ICN and ICS/SJR regions during the 1994-1997 study. The majority of dolphin sightings for both the ICN and ICS/SJR regions occurred in undeveloped habitats. However, land-use patterns within the area have changed as the influx of people into northeastern Florida have caused increases in tracks of residential and industrial land use and coinciding decreases in forested and non-forested uplands. The increase in development in northeastern Florida may be problematic since all dolphins avoided airports, and Southern community dolphins avoided medium and high density residential areas (> 2 houses per acre), commercial areas, shipyards, and port facilities during the 1994-1997 study. On the other hand, the decrease in undeveloped salt marsh habitat may not be an issue for bottlenose dolphins in northeastern Florida because they primarily avoid this habitat. Further studies are needed to determine the current habitat preferences of dolphins in this study area as well as to determine what specific aspects of the habitat dolphins prefer and avoid. A particular line of interest is whether dolphins are avoiding the waters near airports and other developed habitats because of noise pollution, water pollution, and/or increased human contact.

When compared to the ICN region, it is probable that dolphin density was not resource-limited in ICS and SJR regions for two reasons. First, since the St. Johns River is deep and fast moving, with an average tidal flux of 3 m, the prey distribution within the SJR region is unlikely to be similar to the ICN region. At changing tidal periods, there is also a strong tidal boundary zone between the ICS and the SJR regions. This boundary may concentrate fish in a limited space. Feeding bottlenose dolphins and recreational fishermen were frequently observed together during surveys in this tidal boundary. Second, all bottlenose dolphins (except one) sighted in the ICS and/or SJR regions were also sighted in at least one other region. Thus, it was probable that they were feeding in multiple areas. Again, additional data on the change in group size with behavior state and region and the distribution of preferred prey species are required in order to determine why mean dolphin group size was higher in the ICS and SJR regions than in the ICN region or in other estuarine study areas (Caldwell, 2016).

Implications

The regional, seasonal, and habitat variable preferences, such as those identified in this study, result in different levels to which highly mobile bottlenose dolphins are affected by changes in habitat suitability. As discussed above, the lack of measurable fidelity observed for bottlenose dolphins sighted in the COAST region suggest that they will be the least susceptible to anthropogenic habitat changes within the northeast Florida study area. In direct contrast, the highly philopatric nature of the Northern community to a limited year-round range increases their vulnerability to anthropogenic habitat changes and degradation. Surveys of the ICN region resumed in 2010 to assess the Northern community's current range patterns and to monitor the community's responses to anthropogenic habitat changes and degradation.

On the other hand, the seasonal use of the SJR and ICS regions of the study area by the Southern community may mitigate the impact of anthropogenic habitat changes and degradation experienced by these bottlenose dolphins. Although, members of the Southern community population range over a large stretch of the eastern Florida coast, they do spend extended periods of time within the ICS and SJR regions. Moreover, it has been hypothesized that they use the ICS region as a nursery area (Caldwell, 2016); thus, increased habitat degradation has the potential to adversely impact the Southern community. Consequently, it is highly recommended that the current importance of the ICS and SJR regions to the Southern community be determined and monitored as the USACE Jacksonville District (2012, 2014a, 2014b) implements the projects that will deepen the St. Johns River and change the confluence of the SJR and ICS regions in the area known as Mile Point.

Acknowledgments

This research was conducted under National Oceanic and Atmospheric Administration Permit (Marine Mammal Research Permit Number 738) and represents a portion of the author's dissertation research. The author thanks the NOAA, National Marine Fisheries Service (NMFS), Southeast Fisheries Science Center (SEFSC); the University of Miami, Coral Gables, Florida; and Marilyn Mazzoil of Harbor Branch Oceanographic Institute at Florida Atlantic University (HBOI-FAU Contribution No. 1981) for financial and technical support. Laurance Macke of HBOI-FAU and Jane Nangle provided editorial comments.

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