Spatiotemporal Movements of Common Bottlenose Dolphins (*Tursiops truncatus truncatus*) in Northeast Florida, USA

Marilyn Mazzoil,[1] Quincy Gibson,[2] Wendy Noke Durden,[3] Rose Borkowski,[4]
George Biedenbach,[5] Zach McKenna,[6] Nadia Gordon,[7] Kristin Brightwell,[2]
Matthew Denny,[5] Elisabeth Howells,[1] Jennifer Jakush,[6] Lydia Moreland,[3]
Allison Perna,[7] Gerry Pinto,[4] and Marthajane Caldwell[8]

[1]*Harbor Branch Oceanographic Institute at Florida Atlantic University, 5600 U.S. 1 North, Ft. Pierce, FL 34946, USA*
[2]*University of North Florida, 1 UNF Drive, Jacksonville, FL 32224, USA*
[3]*Hubbs-SeaWorld Research Institute, 3830 South Highway A1A #4-181, Melbourne Beach, FL 32951, USA*
[4]*Jacksonville University, 2800 University Boulevard North, Jacksonville, FL 32211, USA*
[5]*Georgia Aquarium Conservation Field Station, 9509 Oceanshore Boulevard, St. Augustine, FL 32080, USA*
[6]*Saint Augustine Eco Tours, 1093 A1A Beach Boulevard, #430, St. Augustine, FL 32080, USA*
[7]*Florida Fish and Wildlife Conservation Commission, 370 Zoo Parkway, Jacksonville, FL 32218, USA*
[8]*Marine Mammal Behavioral Ecology Studies, Inc., Galleria Pozzo Rosso 4/1, 36100 Vicenza, VI, Italy*
E-mail: marthajanecaldwell@gmail.com
Current address for Marilyn Mazzoil and Elisabeth Howells:
Dolphin Census, Inc., 9611 U.S. Highway 1, Sebastian, FL 32958, USA
Current address for George Biedenbach: Geosan Services, LLC, 77 Farmsworth Drive, Palm Coast, FL 32137, USA

Abstract

Common bottlenose dolphins (*Tursiops truncatus truncatus*) (hereafter referred to as "dolphins") are distributed along the east coast of Florida in a longitudinal continuum within inland waterways and federally managed via assignment into stocks. Seven regional studies have identified local estuarine populations with resident and seasonally transient dolphins. However, study area boundaries limit understanding of distribution and movement patterns between these geographically separated regions. To reveal the bigger picture of spatiotemporal movements, a multi-organizational consortium conducted semiannual photo-identification surveys from the Florida–Georgia border to Titusville, Florida (331 km). The study area incorporated dolphins occurring in the Jacksonville Estuarine System (JES) stock in the north, the Mosquito Lagoon within the Indian River Lagoon Estuarine System (IRLES-ML) stock in the south, and the connecting 156-km inland waterway currently managed under the Western North Atlantic Northern Florida and Central Florida coastal stocks. The area was divided into segments, and simultaneous surveys were conducted from 2011 to 2016 during two primary sampling seasons within each year: five summers and five winters (primary period), with two to three surveys (secondary sessions) within each primary period separated by one-week intervals to allow mixing of the population.

A total of 6,896 dolphins, including 196 neonates, were observed, and 649 individuals were identified. Spatial autocorrelation analyses of 222 marked dolphins sighted in ≥ 5 primary surveys revealed that 78% exhibited significant regional and seasonal fidelity to one or more segments, which no single study could elucidate. Additionally, JES-North dolphins demonstrated strong regional site fidelity and were consistently sighted during both seasons, similar to studies in the 1990s, and continued to be partitioned from dolphins to the south. JES-South and IRLES-ML dolphin home ranges extended beyond previously known boundaries. Based on spatiotemporal movement patterns between the segments, recommendations are made to revise boundaries of the JES and IRLES stocks.

Key Words: common bottlenose dolphin, *Tursiops truncatus truncatus*, Northeast Florida, Jacksonville Estuarine System stock, Indian River Lagoon Estuarine System stock, St. Johns River, Mosquito Lagoon, site fidelity, movement patterns

Introduction

A cosmopolitan species, common bottlenose dolphins (*Tursiops truncatus truncatus*) (hereafter referred to as "dolphins") are distributed in a continuous spatial pattern along the east coast of the United States from New York to Florida. Despite limited geographic barriers to movement, recent

findings from photo-identification, aerial surveys, and genetic and telemetry research indicate that dolphins are partitioned along latitude and longitude in a complex population structure (National Oceanic and Atmospheric Administration [NOAA] Fisheries, 2017). Under the Marine Mammal Protection Act, NOAA Fisheries is tasked with identifying and assessing stocks of cetaceans in U.S. waters (a stock is recognized as a group of marine mammals of the same species in a common spatial arrangement that interbreed). Information on dolphin stock structure is necessary to assess the impacts of natural and anthropogenic stressors, and catastrophic events (e.g., large-scale mortality and oil spills), and to implement fisheries bycatch regulations to reduce incidental mortality and serious injury for individual stocks. Multiple dolphin stocks are considered to be present along the Atlantic seaboard; however, additional field sampling is required to adequately describe and refine individual ranging boundaries and geographic affinities for effective management strategies (NOAA Fisheries, 2017).

Along the east coast of Florida, recent evidence supports demographic separation between near-shore coastal dolphins and those residing within rivers and estuaries (Rosel et al., 2009; Mazzoil et al., 2011; Caldwell, 2016a, 2016b). In 2009, three inland stocks were designated by the NOAA Fisheries: (1) Jacksonville Estuarine System (JES), (2) Indian River Lagoon Estuarine System (IRLES), and (3) Biscayne Bay. Although considered a single stock, JES dolphins are divided into northern (JES-N, Segment 1 in Figure 1) and southern (JES-S, Segment 2 in Figure 1) areas based on habitat fidelity and social affiliation patterns, with the St. Johns River (SJR) demarcating the separation (NOAA Fisheries, 2009). The northern limit of the JES stock is the St. Marys River (Florida–Georgia border), while the southern limit extends 17 km south of the SJR in the Intracoastal Waterway (ICW) (NOAA Fisheries, 2009). The western boundary of the JES stock within the SJR is not stated in stock designations (NOAA Fisheries, 2009); however, a 1994-1997 study showed the presence of dolphins within 14 km of the SJR mouth (Caldwell, 2016a, 2016b). JES-N dolphins demonstrate year-round site fidelity and limited movement into the JES-S, while JES-S dolphins demonstrate oscillating, year-round abundance with lower numbers in winter when temperatures drop below 16°C (Gubbins et al., 2003; Caldwell, 2016a, 2016b).

In the IRLES, year-round, multi-decadal, multi-generational resident dolphins have been identified within six geographic and social communities (Odell & Asper, 1990; Mazzoil et al., 2005; Howells et al., 2009; Titcomb et al., 2015). Dolphins in the IRLES Mosquito Lagoon (IRLES-ML, Segment 6 in Figure 1) sub-basin demonstrate seasonal variability with increased abundance in winter (Durden et al., 2011, 2017), inverse to the JES-S population (Caldwell, 2016a, 2016b), suggesting seasonal movements may occur between these regions. As a result of expanded photo-identification survey efforts in 2011, dolphins identified in the IRLES-ML have been sighted in the JES-S and the inland waters between the JES and IRLES stocks (Nekolny et al., 2017).

Since no single, geographically constrained study has provided the longitudinal data required to delineate individual or seasonal movement patterns and establish affinities within, between, and across these adjacent stock regions, the Northeast Florida Dolphin Research Consortium coordinated research efforts to provide a contemporary account of dolphins utilizing the estuarine waters along the northeast coast of Florida (Florida–Georgia border to Titusville, Florida). Our objectives were to conduct systematic, synoptic surveys within seasons and across years using a robust design to explore spatiotemporal trends in movement and recommend stock affiliations based on these patterns. Once biologically relevant units are established, these units (stocks) will serve as the basis to estimate abundance, survival, detection, and state transition (movements) rates using a closed robust design multi-state model.

Methods

Sampling Effort
The survey area spans approximately one-third of the east coast of Florida in estuarine waters from Fernandina to Titusville. Comprised of numerous rivers (Nassau, Fort George, St. Johns, Guana, Tolomato, Matanzas, and Halifax) and the Mosquito Lagoon, the overall water body is narrow (0.1 to 1.0 km, with the exception of a portion of the ML, which has a maximum width of 4.4 km, and the upriver section of the SJR) and shallow (≤ 3.7 m, with the exception of the SJR). The study area encompassed a portion of the 500-km St. Johns River, which is bisected by the ICW 8 km from its mouth at the Atlantic Ocean and is characterized as a significantly used commercial waterway with a deep (13.3 m) shipping channel and fast-moving current. The ICW, which runs the length of the study area, is surrounded by a labyrinth of shallower waters, marsh grasses, and mangrove-lined corridors.

The 331-km study area was divided into six segments to allow vessel-based geographic coverage over a 1-d sampling period of the JES, IRLES-ML, and the connecting 156-km inland waterway currently managed under the Western North Atlantic Northern Florida (WNA-NFL) and Central
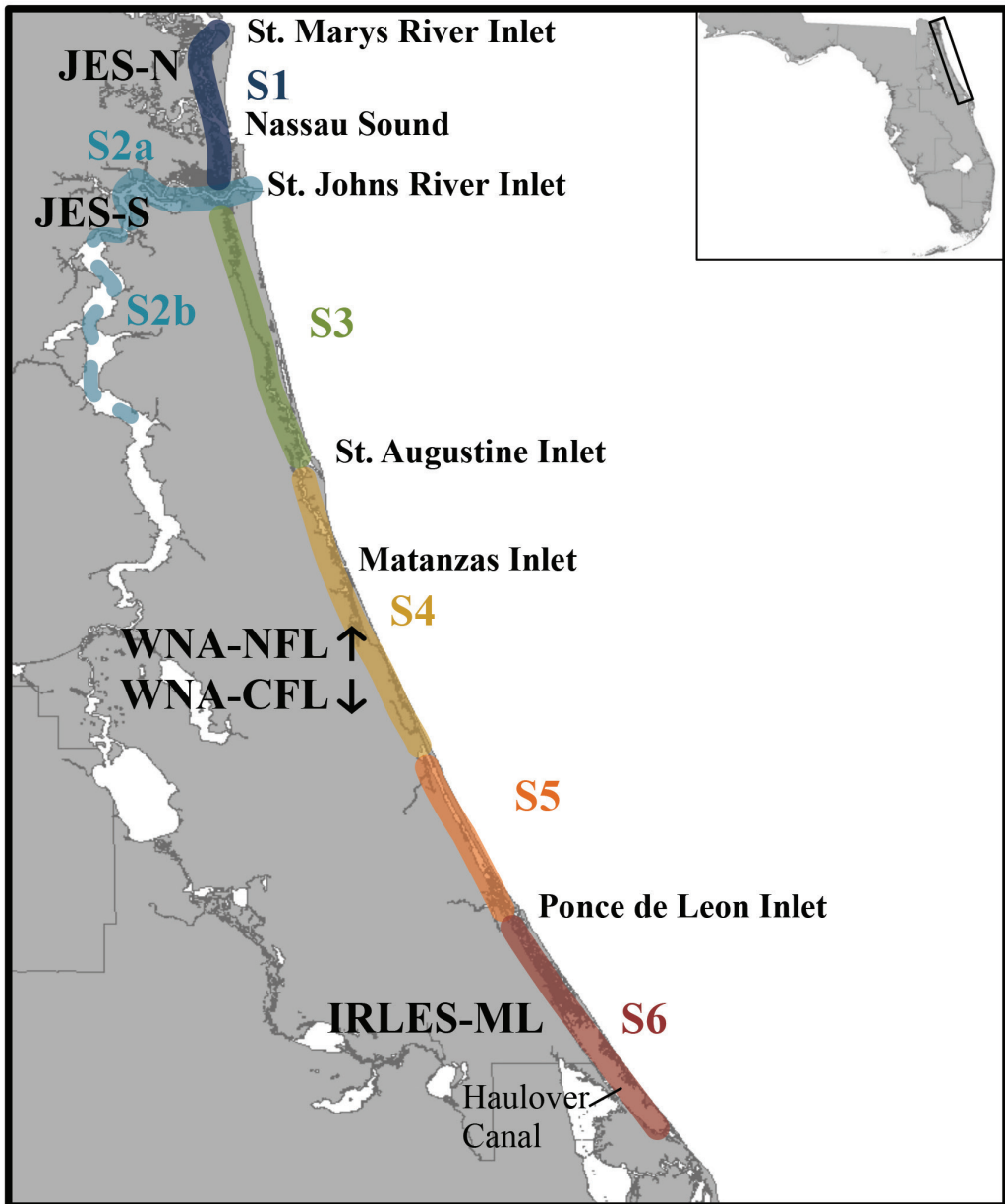
Figure 1. The survey area was partitioned into seven survey segments. Segments 1 and 3 terminated at the St. Johns River.

Florida (WNA-CFL) coastal stocks: Segment 1 (JES-N, 36 km), Segment 2a (JES-S, SJR mouth to Hart Bridge, 40 km), Segment 2b (JES-S, SJR Hart to Shands Bridges, 47 km), Segment 3 (JES-S, 17 km, and WNA-NFL, 40 km), Segment 4 (WNA-CFL, 56 km), Segment 5 (WNA-CFL, 43 km), and Segment 6 (IRLES-ML, 52 km) (Figure 1). Surveys were conducted from 2011 to 2016 during two primary sampling seasons within each year (wet/summer = July-August and dry/winter = January-March), with two to three surveys (secondary sessions) within each primary period; surveys were separated by 1-wk intervals to allow sufficient mixing of the population (Rosel et al., 2011). The survey route followed the main channel of the ICW or SJR as it provided shore-to-shore visibility; whereas in wider sections (3 to

5 km) of the lower SJR, the route was expanded to within 1 km from the east and west shores.

Sighting locations were plotted in *ArcMap*, Version 10.1 (Environmental Systems Research Institute [ESRI], 2011), and spatial autocorrelation (SAC) analysis using global Moran's I (Moran, 1950; Grigg et al., 2012; Miller, 2012) was used to evaluate whether sighting locations were clustered (the *p* value is statistically significant, and the z score is positive), dispersed (the *p* value is statistically significant, and the z score is negative), or random (the *p* value is not statistically significant) in distribution by segment or season (summer or winter) (Caldwell, 2016a). Sightings were categorized by the number of dolphins observed and by the number of neonates observed within each group. SAC of sightings with respect to location, number of dolphins per group, and season was also assessed. Calves were defined as < 75% of the length of an associated cow; whereas neonate determinations were based on size (< 50% in length) and newborn characteristics such as coloration, presence of fetal folds, or "popping" out of the water to breathe (Mann & Smuts, 1999; Mann et al., 2000; Whitehead & Mann, 2000); both were excluded in segmental and seasonal fidelity analyses due to non-random movement patterns due to dependency state.

Photo-Identification Analyses
Standardized photo-identification research protocols were followed for field work and photo analysis (Würsig & Würsig, 1977; Urian & Wells, 1996; Urian et al., 1999, 2015; Mazzoil et al., 2004; Rosel et al., 2011). In brief, the best prototype image of each dolphin was assigned a dorsal fin distinctiveness score (D score) based on the amount of information contained on the fin (D1-Major, D2-Moderate, D3-Minor, or D4-No distinctive features) and a photographic quality score (Q1-Excellent, Q2-Average, or Q3-Poor), based on a weighted system of criteria to reduce the chance of missing or making an incorrect identification (Urian et al., 1999, 2015). Each field team analyzed their respective data, assigned distinctiveness and quality scores, submitted the best prototype of each fin to the catalogue curator, and uploaded environmental and sighting data into a customized Microsoft *Access* database (due to technical difficulties resulting in a partial dataset, Segment 2b was excluded from photo analyses). Each team reviewed the master catalogue to identify potential mismatches and to verify assigned D scores; a majority vote was used in cases of D-score discrepancies. An assistant curator also verified all subsequent matches to the master catalogue. Data analyses were restricted to individuals with D1 to D2 distinctiveness and

Q1 to Q2 photo quality scores with the exception of "ranging limits" analyses wherein D3 fins were included to increase sample size as these analyses were not sensitive to analyst expertise (or bias) or photo quality scores (D3 fins are not always recognizable in Q2 photos).

Resighting Rate and Dolphins per Linear Kilometer
Dolphins per linear km was calculated by dividing the total number of D1 to D4 dolphins within a segment by the total linear km of each segment multiplied by the number of surveys conducted in that segment. The resighting rate was calculated for each segment by dividing the total number of sightings for D1 to D2 individuals by the total number of individually identified D1 to D2 dolphins seen in that segment. A discovery curve proxy was used to portray the number of dolphins and the rate at which they were identified as the number of previously identified individuals, new individuals, and total individuals in each segment per annual primary period.

Spatiotemporal Movement Patterns
Spatiotemporal patterns were analyzed using two analytical methods described in Caldwell (2016a) and briefly summarized herein. First, to examine whether dolphins were preferentially using any segment seasonally, D1 to D2 dolphins sighted in ≥ 5 primary periods were selected; multiple sightings within an annual primary period were only counted if the dolphin was observed in different segments. These criteria allowed for the possibility that a dolphin would be sighted across seasons within each year, which reduced possible bias introduced by individuals sighted repeatedly within a sampling session. A set of Bonferroni confidence intervals (CIs) were generated to examine whether individuals used each segment in proportion to the amount that segment was surveyed each season considering all segments simultaneously (Neu et al., 1974; Byers et al., 1984; White & Garrott, 1990). Separate analyses were performed for summer and for winter sightings. Henceforth, the terms *preference* and *avoidance* refer to whether a dolphin was sighted within a specific segment significantly more or less, respectively, than expected given the proportion of available segments, while the term *ambivalence* refers to dolphins that were not sighted more or less than expected. Second, dolphins were clustered based on segmental and seasonal fidelity patterns. Dolphin sighting patterns within each group were analyzed using SAC analysis. The SAC analysis allowed for examination of movement patterns based on GPS locations and, thus, was not influenced by the constraints of segment boundaries imposed by the study design and was able to facilitate the comparison

of spatiotemporal patterns from previous studies employing the same methods (Caldwell, 2016a, 2016b). Additionally, the percent of D1 to D2 dolphins exclusively photographed in each segment and pairwise comparisons of the percent of dolphins shared by pairs of segments was generated.

Ranging Limits

The southern boundary of the study area was the southern terminus of the ML, but movement into the Indian River proper (IRP; Indian, Banana, and St. Lucie Rivers) is possible through a 1.6-km-long × 0.07-km-wide manmade "Haulover Canal," constructed circa 1887 (Crawford, 2006), which connects the ML to the Indian River complex. Therefore, the southern ranging limits of all D1 to D3 dolphins sighted in the ML during the study were determined from supplementary data of historic sightings in the IRLES (1996 to 2015) using GIS coordinates of sighting locations plotted in *ArcMap*.

Dolphins were considered as "resident" to the ML water body if they spent > 50% of their time therein (Rosel et al., 2011).

Results

Sampling Effort

Twenty-seven surveys were conducted between August of 2011 and January of 2016, resulting in 13 summer and 14 winter secondary sessions (a minimum of two secondary sessions were in each primary period). A total of 6,896 dolphins were observed, including 196 neonates, with calves representing 20.0% of all dolphins observed. There was no significant difference in the total number of dolphins observed during summer and winter periods (F = 1.770, p = 0.145); however, more dolphins were observed during summer than winter in Segments 2a and 2b (F = 5.407, p = 0.001), and the opposite pattern was observed in Segment 6 (F =
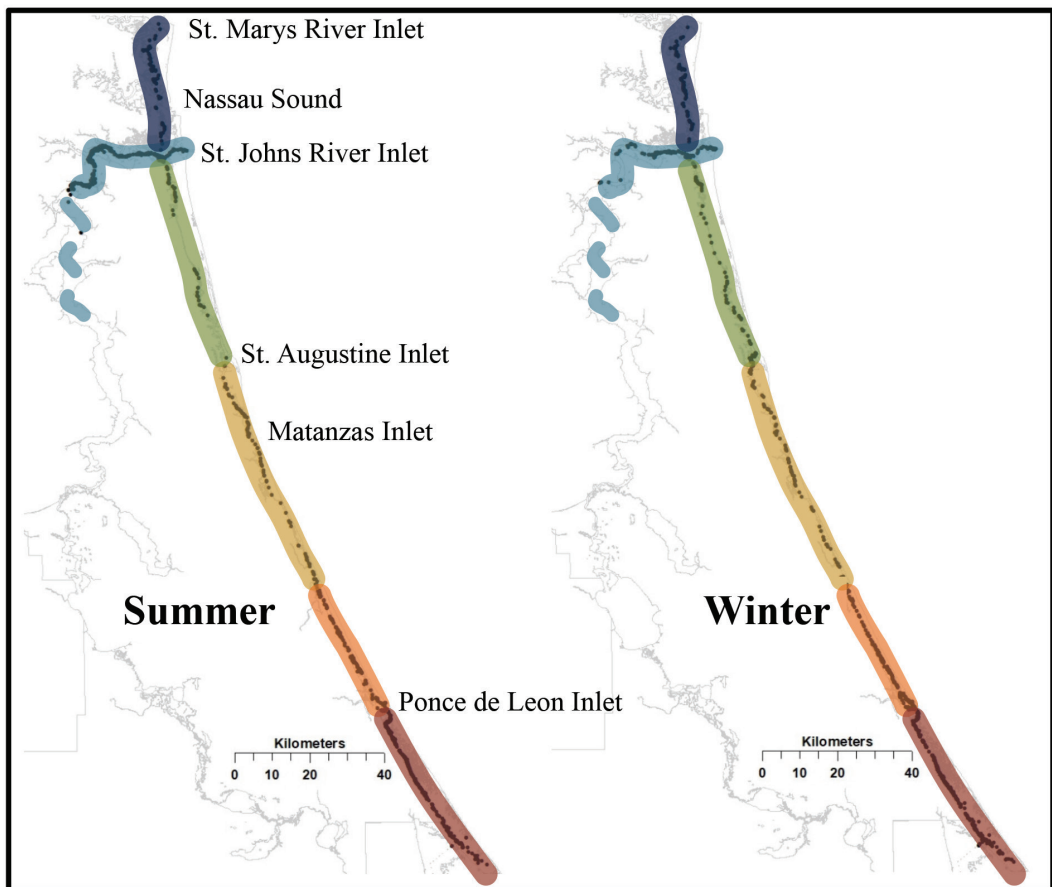
Figure 2. Distribution of common bottlenose dolphin (*Tursiops truncatus truncatus*) sightings during the five summer and five winter periods

3.154, p = 0.018). Overall, significantly more neo-nates were observed during summer than winter (F = 17.237, p = 0.000) and within Segments 2a and 2b (F = 11.276, p = 0.000), Segment 5 (F = 6.776, p = 0.000), and Segment 6 (F = 10.13, p = 0.000). In SAC analysis, sighting distribution was highly clustered within segment (Moran's I value = 0.576, z = 228.754, p = 0.000) and by season (Moran's I value = 0.084, z = 33.407, p = 0.000) (Figure 2). Clustering of dolphin sightings during the summer season was particularly visible in Segments 1, 3, and 4. Additionally, not only were few dolphins sighted within Segments 2a and 2b during the winter season, but the upstream distribution of these sightings was also truncated and clustered (Figure 2).

Photo-Identification Analyses
A total of 649 individual dolphins were identified: 442 (D1 or D2) and 207 (D3). Of the 442 distinctly marked dolphins, 54 (12%) were sighted only once (36 of the 54 dolphins were seen with other single sighted dolphins) and were distributed across segments (Segment 1 = 12; Segment 2a = 20; Segment 3 = 0; Segment 4 = 2; Segment 5 = 1; and Segment 6 = 18) and seasons (summer =

29; winter = 25). The average number of sightings per dolphin was 5.53 (SE = 0.17), and this number ranged from 1 to 22.

Resighting Rate and Linear Density
Segments 2a, 5, and 6 had the overall highest density of dolphins per linear km and the highest resight rates, respectively; inversely, Segments 3 and 4 had the lowest density and the lowest resight rates (Tables 1 & 2). The total number of newly identified and resighted dolphins varied by segment and season with, on average, more dolphins newly identified and resighted during winter in Segments 3 to 6 but during summer in Segment 2a (Table 3). Within Segment 1, there was little seasonal variation in the average number of dolphins newly identified; however, on average, more dolphins were resighted during winter sessions (Table 3). Unlike Segments 1, 2a, 5, and 6, the number of cumulative new dolphins continued to exceed the number of cumulative resighted dolphins in Segments 3 and 4 until after the third and fifth year of the study period, respectively (Figure 3).

Table 1. Total photo-identified common bottlenose dolphins (*Tursiops truncatus truncatus*) (D1 to D4, with no same day resights) per sighting per linear km by segment and season

| Segment number	Total linear km Summer	Total linear km Winter	Total dolphins Summer	Total dolphins Winter	Dolphins per linear km Summer	Dolphins per linear km Winter	Total dolphins per km
1	468	504	206	233	0.44	0.46	0.45
2a	520	560	1,256	524	2.42	0.94	1.65
2b*	611	658	278	41	0.50	0.10	0.30
3	741	798	197	278	0.27	0.35	0.31
4	728	784	191	318	0.26	0.41	0.34
5	559	602	353	586	0.63	0.97	0.81
6	676	728	924	1,215	1.37	1.67	1.52

*Based on field estimates

Table 2. Resighting rate per segment for D1 and D2 dolphins

Segment number	Total D1 to D2 sightings	Total D1 to D2 fins	Resight rate	Resighting rank
1	193	47	4.1	4
2a	1,062	200	5.3	1
3	246	111	2.2	6
4	183	64	2.9	5
5	440	89	4.9	3
6	1,052	202	5.2	2

Table 3. A comparison by segment of the average number of D1 and D2 dolphins newly identified and resighted during the five summer and five winter seasons from August 2011 through January 2016

Segment	New							Resight						
	1	2a	3	4	5	6	Total	1	2a	3	4	5	6	Total
Summer														
Mean	4.60	30.60	7.80	4.20	6.40	19.60	73.20	11.00	86.00	7.60	7.60	21.80	67.20	201.20
SD	2.07	17.67	5.07	3.56	7.73	25.72	51.30	6.12	64.58	5.13	5.73	11.97	33.59	110.93
Winter														
Mean	4.40	9.40	11.20	8.60	11.40	20.80	65.80	15.00	42.00	12.60	13.00	33.40	93.20	209.20
SD	2.51	12.05	10.99	6.99	8.47	27.12	57.28	2.65	12.06	6.54	8.72	7.99	39.96	64.66
Total														
Mean	4.50	20.00	9.50	6.40	8.90	20.20	69.50	13.00	64.00	10.10	10.30	27.60	80.20	205.20
SD	2.17	18.12	8.26	5.72	8.09	24.93	51.41	4.92	49.56	6.14	7.51	11.37	37.40	85.70
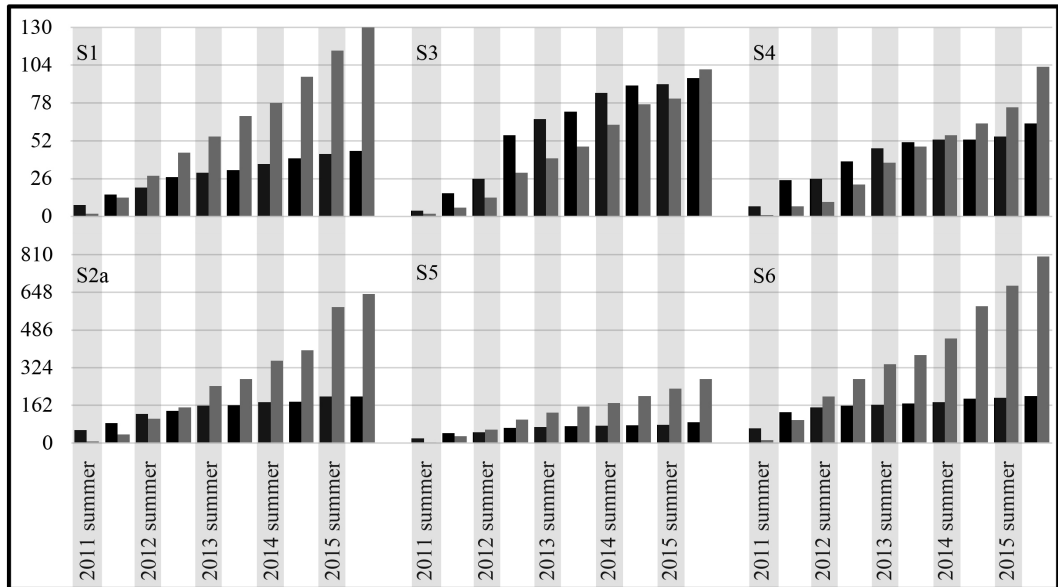
Figure 3. Number of cumulative new (black bars) vs cumulative resighted (grey bars) dolphins photographed between August 2011 and January 2016 analyzed for each segment independently. The light grey bars denote summer periods; the top and bottom rows are depicted by similar Y-axis scales.

Spatiotemporal Movement Patterns

A total of 222 dolphins were sighted in ≥ 5 primary periods, and while all of these dolphins exhibited significant avoidance for at least one segment, the majority (78% or 173 of 222) exhibited significant segmental and seasonal preference for at least one segment. The number of segments (not necessarily contiguous) in which individual dolphins were sighted varied seasonally. In the summer, 71% (157 of 222) of the dolphins were sighted in one segment, 22% (49 of 222) in two segments, and 7% (16 of 222) in three segments. In the winter, 46% (101 of 222) of the dolphins were sighted in one segment, 42% (94 of 222) in two segments, 11% (25 of 222) in three segments, and 1% (2 of 222) in four segments. Seasonally, 22% (48 of 222) of the dolphins were sighted an equal number of times in summer and winter,
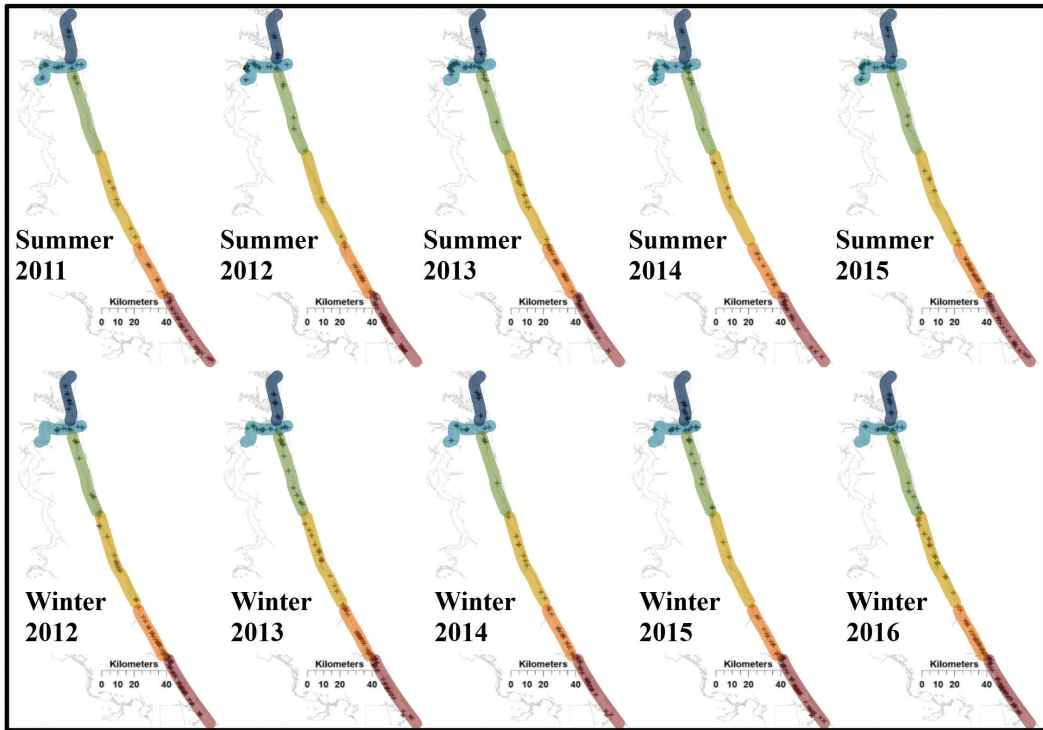
Figure 4. Plus signs represent the sighting locations for the 222 D1 and D2 dolphins sighted in more than five primary sessions during the summer and winter periods from 2011 to 2016. Segment 2b is not included.

Table 4. Preference summary by segment of the number of D1 and D2 dolphins sighted in five or more primary periods. "Preference" and "Avoidance" refer to whether a dolphin was sighted within a specific segment significantly ($p \leq 0.05$) more or less, respectively, than expected given the proportion of available segments. "Ambivalence" refers to dolphins sighted as expected within that segment.

Segment	# with segmental avoidance	# sighted within segment with preference	# with summer			# with winter		
			Preference	Ambivalence	Avoidance	Preference	Ambivalence	Avoidance
1	204 (92%)	18	12	4	206	16	2	204
2a	125 (56%)	77	75	21	126	31	42	149
3	145 (65%)	4	2	27	193	4	58	160
4	172 (77%)	2	2	24	196	3	37	182
5	150 (68%)	18	14	26	182	14	52	156
6	102 (46%)	72	74	22	126	64	47	111

while 34% (76 of 222) were seen more frequently in summer, and 44% (98 of 222) were seen more frequently in winter. SAC analyses of dolphin distribution for the study area, as a whole, revealed that sightings of individual dolphins were significantly clustered within segments (Moran's I value = 0.18, z score = 41.51, p = 0.00) and season (Moran's I value = 0.15, z score = 35.98, p = 0.00; Figure 4).

More dolphins avoided Segment 1 (92%) than any other segment (Tables 4 & 5). Of the 18 dolphins sighted within Segment 1, 12 were only

sighted within Segment 1 (Tables 5 & 6). SAC analysis of these 12 dolphins showed that individual dolphin sightings were randomly distributed within Segment 1 but were clustered within the segment seasonally (Group A in Table 7). Additionally, the sightings of the remaining six dolphins utilizing Segments 1, 2a, and 3 were significantly clustered within the segments, as well as clustered seasonally (Group a1 in Table 7). These clustered distributions and seasonal shifts in sighting distributions can be seen in Figure 4.

Of the remaining 204 dolphins, 6% (14 of 204) exclusively preferred Segment 2a, while 24% (49 of 204) exclusively preferred Segment 6 (Table 5; Groups B & F in Table 7). An additional 7% (15

of 204) preferred Segment 2a but were occasionally photographed in the northern section of Segment 3, and an additional 6% (13 of 204) also preferred Segment 6 but were occasionally photographed in the southern section of Segment 5. SAC analyses revealed that while these dolphins were randomly distributed within their respective segment(s), their sightings were significantly clustered seasonally (Tables 6 & 7; Figure 4) Additionally, Segment 2a dolphins shifted east toward the mouth of the SJR in winter. Two dolphins were exclusively sighted in Segment 2, one dolphin was exclusively sighted in Segment 3, and an additional two dolphins were exclusively sighted in Segment 5 (Table 5).

Table 5. Comparison of the percent and number of the 222 dolphins sighted in five or more primary periods that were exclusively photographed in each segment (on the diagonal) and the percent (above the diagonal) and number (below the diagonal) shared by each pair of segments.

% (*n*)	S1	S2a	S3	S4	S5	S6
S1	5.41 (12)	2.7	0.9	0	0	0
S2a	6	6.31 (14)	30.18	9.91	5.87	9.91
S3	2	67	0.90 (2)	9.91	6.76	6.76
S4	0	22	22	0.45 (1)	13.96	11.26
S5	0	13	15	31	0.90 (2)	23.87
S6	0	22	15	25	53	22.07 (49)

Table 6. Segmental and seasonal preference groups for dolphins sighted in five or more primary periods (S2 = S2a only). Dark bars within each color band represent significant preference, light bars represent ambivalence, and empty cells represent significant avoidance. * = one dolphin and ^ = two dolphins.
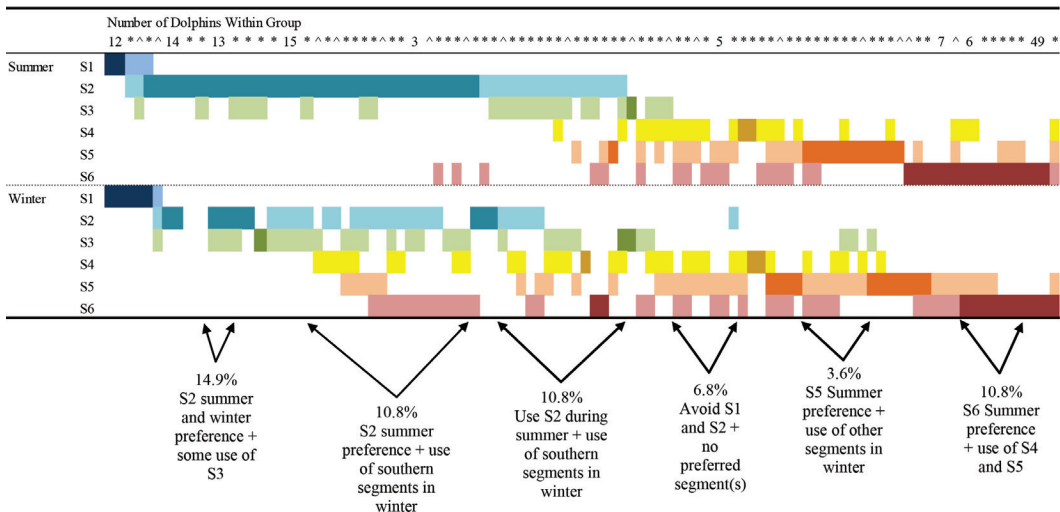
Table 7. The SAC analyses for groups (G) of individual dolphins within the similar segmental sighting patterns (S2 = S2a only). Capital letters indicate dolphins sighted only in one segment. All significantly positive Moran's I values indicate that dolphins were clustered in their spatial distribution. SAC analyses were not performed for groups with fewer than four dolphins. Dark bars within color band = significant preference, light bars = ambivalence, empty space = significant avoidance, and # = number of dolphins within that group. *p* values ≤ 0.05 are in bold.

S1 S2 S3 S4 S5 S6	#	G (%)	Moran's Index	Expected Index	Variance	z score	p value	Moran's Index	Expected Index	Variance	z score	p value
			Distribution within segment					Distribution within season				
	12	A (5.4)	0.07	-0.01	0.01	0.81	0.42	1.02	-0.01	0.01	10.35	**0.00**
	2	a1 (2.7)	0.47	-0.01	0.03	2.90	**0.00**	0.96	-0.01	0.03	5.81	**0.00**
	1	a1										
	1	a1										
	2	a1										
	14	B (6.3)	0.17	-0.01	0.02	1.31	0.19	0.79	-0.01	0.02	5.99	**0.00**
	33	b1 (14.8)	0.07	0.00	0.00	1.37	0.17	1.01	0.00	0.00	17.89	**0.00**
	1	b2 (6.3)	-0.08	-0.01	0.02	-0.51	0.61	0.91	-0.01	0.02	6.64	**0.00**
	1	b2										
	3	b2										
	2	b2										
	4	b2										
	1	b2										
	2	b2										
	4	b3 (1.8)	1.40	-0.03	0.25	2.87	**0.00**	0.75	-0.03	0.25	1.56	0.12
	1	b4 (0.4)										
	1	b5 (0.4)										
	4	b6 (1.8)	-0.97	-0.03	0.59	-1.21	0.22	1.44	-0.03	0.59	1.92	0.06
	1	b7 (0.4)										
	3	b8 (1.3)										
	2	b9 (0.9)										
	1	b10 (0.4)										
	8	b11 (3.6)	-0.30	-0.01	0.06	-1.19	0.23	1.04	-0.01	0.06	4.35	**0.00**
	1	b12 (0.4)										
	3	b13 (1.3)										
	2	C (0.9)										
	1	c1 (0.4)										
	1	c2 (0.4)										
	1	c3 (0.4)										
	4	c4 (1.8)	-1.07	-0.02	0.50	-1.49	0.14	0.94	-0.02	0.42	1.48	0.14
	1	D (0.4)										
	1	d1 (0.4)										
	1	d2 (0.4)										
	4	d3 (1.8)	0.30	-0.02	0.32	0.57	0.57	0.94	-0.02	0.33	1.67	0.09
	2	E (0.9)										
	7	e1 (3.1)	0.27	-0.01	0.02	1.93	**0.05**	0.95	-0.01	0.02	6.75	**0.00**
	4	e2 (1.8)	-0.49	-0.02	0.09	-1.58	0.12	0.95	-0.02	0.09	3.25	**0.00**
	1	e3 (2.5)	0.07	-0.01	0.09	0.30	0.77	1.03	-0.01	0.09	3.53	**0.00**
	3	e3										
	1	e3										
	8	e4 (3.6)	-0.13	-0.01	0.08	-0.42	0.67	0.98	-0.01	0.08	3.58	**0.00**
	19	f1 (8.5)	-0.03	-0.01	0.01	-0.17	0.87	1.01	-0.01	0.01	8.54	**0.00**
	5	f2 (2.2)	-0.01	-0.02	0.05	0.01	1.00	0.98	-0.02	0.05	4.46	**0.00**
	49	F (21.6)	-0.07	-0.01	0.02	-0.47	0.64	0.98	-0.01	0.02	7.66	**0.00**

In addition to the 14 dolphins that exclusively preferred Segment 2a, 44 dolphins (22%) preferred Segment 2a only during the summer and were sighted in southern segments during the winter (Table 6). In comparison, in addition to the 49 dolphins that exclusively preferred Segment 6, only 13 more dolphins (6%) preferred Segment 6 during the summer and were sighted within or in preferred segments to the north during the winter (Table 6). Although 22 dolphins were photographed in both Segments 2a and 6, more dolphins were shared between pairs of adjacent southern

segments than between a southern and a northern segment and vice versa (Table 5). Among the northern segments, Segments 2a and 3 shared the most dolphins, whereas Segments 5 and 6 shared the most dolphins among the southern segments. SAC analyses revealed that while these dolphins were randomly distributed within their respective segments, their sightings were significantly clustered seasonally (Table 7; Figure 4).

Sixteen dolphins (8%) preferred Segment 5 (Groups e1 to e3 in Table 7), and 24 dolphins (12%) preferred Segment 6 (Groups f1 and f2 in Table 7) but were also photographed in other segments. In all cases except one, SAC analyses revealed that while these dolphins were randomly distributed within their respective segments, their sightings were significantly clustered seasonally. The exception (Group e1 in Table 7) was a group of seven dolphins that exhibited significantly clustered sighting distribution as well as a clustered seasonal distribution (Tables 6 & 7; Figure 4). Finally, 24% (49 of 204) exhibited no segment preferences for which SAC analyses demonstrated variable segmental and seasonal patterns (Groups b3, b6, b11, c4, and d3 in Table 7).

Ranging Limits
Of the 275 D1 to D3 dolphins seen at least once in the ML (Segment 6), 62% (171 of 275) were not seen in another segment, and 38% (104 of 275) were sighted in one or more segments to the north. Of the 104 dolphins sighted north of Segment 6, 71% (74 of 104) were seen in the adjacent Segment 5. Historically, 82 dolphins (or 30% of the 275) were photographed outside of the confines of the study area in the IRP. A majority of these (74% or 61 of 82) had > 50% of their sightings within the ML, and the remaining non-resident ML dolphins aggregated within 4 km of the Haulover Canal.

Discussion

The current study revealed that similar spatiotemporal trends have persisted across decades within the JES-N (Segment 1) and JES-S (Segments 2a and 3). Dolphins utilizing Segment 1 continue to be spatially segregated from dolphins using Segments 2a and 3 and were not photographed in Segments 4 to 6. Further, dolphins in Segment 1 were randomly distributed relative to each other and demonstrate seasonal site fidelity with clustered sightings, similar to findings in the 1990s (Caldwell, 2016a, 2016b).

Dolphin sighting and distribution patterns in Segments 2a and 2b demonstrated seasonal oscillations, which were also similar to findings in the 1990s (Caldwell, 2016a, 2016b). However, the distribution patterns in Segments 2a and 2b (SJR) differed from previous distribution patterns seen in the 1990s when dolphins were infrequently seen in lower salinity waters more than 14 km from the SJR mouth (Caldwell, 2016a, 2016b). In the present study, sightings of SJR dolphins often occurred beyond 14 km and occasionally occurred as far as 54 km upriver. These sightings corroborate work ongoing since 2011 that shows repetitive dolphin use of mesohaline and oligohaline SJR areas through 57 km upriver (Borkowski, 2017) and sheds light on a 2010 dolphin Unusual Mortality Event (UME). The UME was co-associated with an algal bloom, fish kill, and dredging events in upriver areas of the SJR, and dolphin carcasses were retrieved from interior areas not previously recognized as dolphin habitat (NOAA Fisheries, 2017).

Further work is needed to understand if current dolphin utilization of upriver SJR habitat involves a range extension, a return to sporadically utilized habitat, and/or a relationship to dredging activities such as changes in water flow and salinity parameters. Other factors (i.e., competition, illness, habitat degradation, and shifts in prey distribution) may be driving exploratory expeditions or movement into less suitable habitat in the SJR (Brown et al., 2018). Extended exposure to low salinity can cause serious illness in dolphins (Carmichael et al., 2012; Ewing et al., 2017). Documentation of dolphins utilizing low salinity upriver areas of the SJR in the current study augments sparse information regarding a potentially vulnerable segment of the JES population.

The seasonal movement patterns observed during this study may reflect both female and male reproductive state and strategies; however, data on the sex of individual dolphins were unequally available in all segments and not considered. In cetacean species in general, female distribution typically reflects predation pressures and resource distribution, while males, unable to monopolize female groups, tend to associate for short periods of time with a given female and then move to find other receptive females (Schaeff, 2007). Male reproductive strategies differ between the SJR and IRLES dolphins, with more males in the SJR forming male pair bonds and second-order alliances (Karle, 2016; Ermak et al., 2017), which were observed to increase courtship and breeding opportunities (Connor et al., 1992). In Sarasota, Florida, male dolphin pairs have significantly larger overall ranging areas than unpaired males (Owen et al., 2002); and in Shark Bay, Australia, dolphin alliances vary systematically along a spatial axis with regard to alliance structure, consortship rates, and ranging behavior (Connor et al., 2017). In VHF radio tracking studies in the

IRLES, the summer linear ranging patterns of a juvenile male (focal followed at 7 and 10 y of age) increased; this may occur as male dolphins approach sexual maturity (Durden et al., 2019).

Female ranging patterns may also be altered during consortships with male alliances (Watson-Capps, 2005), and sequestered females may travel beyond normal ranging boundaries in the IRLES (B. Brunnick, pers. comm., 11 April 2018). However, two allied IRLES male dolphins that were extensively focal-followed were frequently seen in formation with a reproductive female. The triad primarily engaged in foraging (43%) vs travel (24%) behavior, differing from the mean activity budgets of the other tracked dolphins that mostly engaged in travel (53%) rather than foraging (17%), suggestive of a cooperative foraging strategy (Durden et al., 2019) or potential courtship ritual (Schaeff, 2007). Reproductive state has been shown to drive movement patterns of female dolphins within the IRLES as females decreased the size of their home ranges and core areas of use when with dependent calves (Gibson et al., 2013). Significantly more neonates also occur in summer in Segments 5 and 6, thus the breeding and calving season may influence movement patterns between these segments. In the IRLES, breeding occurs year-round with bimodal peaks in births and neonatal strandings in April and August (Urian et al., 1996; Stolen et al., 2007) after an 11- to 12-mo gestation period. An increase in Segments 2a and 2b (SJR) summer abundance coincides with significantly more neonate sightings, similar to earlier findings in which Caldwell (2016b) suggested the isolated, shallow, inland waters of Chicopit Bay served as a nursery area.

Seasonal resightings of SJR and ML dolphins show opposite seasonal patterns, with more cumulative resightings in summer in Segment 2a (SJR) and more in winter in Segment 6 (ML), supporting some movement between the areas. Segments 2a and 6 had the highest total number of dolphins identified and the most dolphins that were exclusive to, or preferred, each area, indicative of strong site fidelity to either the SJR or ML. Interestingly, Segment 5 had a similarly high resighting rate and high linear density, yet only two dolphins were exclusive to the area, indicative of a key mixing area. In contrast, Segments 3 and 4 had the lowest resighting rates and density, and fewer dolphins exclusive to each segment; newly discovered dolphins outnumbered cumulative resights for more sessions than any other segments, indicative that these areas may be primarily used as passage zones. Further long-term, year-round studies that evaluate monthly sighting rates, habitat use, and behavior will help to elucidate the importance of these mixing and passage zones.

The extent of the northern boundary is unknown for Segment 1 dolphins, but movement beyond the study area may account for their low resighting rate. Conversely, the southern boundary of Segment 1 dolphins continues to be demarcated by the SJR (Caldwell, 2016a, 2016b). The geographic segregation of Segment 1 from dolphins further south may be attributed to the deep, fast-moving waters of the SJR, serving as a barrier to movement. Movement by dolphins acclimated to shallow estuarine waters into deeper waters would require adaptations to the diverse habitats such as feeding specialization as seen in *Tursiops* spp. (Fertl, 1994; Barros & Wells, 1998; Mann et al., 2000). However, a small number of Segment 1 dolphins have been seen in the SJR, and SJR (Segment 2a) dolphins are frequently observed further south in the ICW, indicating that some dolphins are habituated to both types of habitat but demonstrate different spatial, temporal, and social preferences.

In previous studies, estimated dolphin home range sizes in the study area increased north to south from the SJR to the ML as data from more segments were added, reaching an asymptote when all segments were incorporated (Nekolny et al., 2017). The largest home range of any SJR dolphin covered 86% of the available geographic survey coverage within the confines of the combined study area, indicating a southern boundary could be established for SJR dolphins (Nekolny et al., 2017). Our current data corroborate this account of an established extreme southern border for SJR dolphins terminating in the ML as only two of 30 (7%) dolphins sighted in the SJR and ML were seen further south in the IRP.

Also in previous studies, the majority of dolphins seen in the ML exhibit strong site fidelity to the ML and were not seen further south in the IRP, with 71% (67 of 94) sighted exclusively in the water body from 2002 to 2005 (Mazzoil et al., 2008), 87% (100 of 115) from 2016 to 2017 (Durden et al., 2020), and 70% (193 of 275) in this study. In the current study, of the 30% (82 of 275) of dolphins seen outside the confines of the study area in the IRP, only 21 were considered non-resident ML dolphins. The mean geographic range of non-resident ML dolphins near the Haulover Canal in the ML is concordant with the social community of dolphins found in the southern ML and suggests decadal trends of limited interchange between ML and IRP dolphins. Dolphins near the Haulover Canal exhibit mixed ancestry, which is attributed to independent colonization of the ML and IRP prior to the connectivity of the water bodies via the Haulover Canal in the late 19th century (Richards et al., 2013). Interestingly, over a century later, geographic distribution and social

patterns indicate that, still, only a small proportion of dolphins seen in the southern ML (8% or 21 of 275) are non-residents.

In summary, our 5-y photo-identification findings support (1) decadal patterns of year-round residency and site fidelity in the JES-N, JES-S, and IRLES-ML; (2) some degree of seasonal movements between the JES and IRLES-ML; (3) the unassigned inland waterway between the JES and IRLES (Segments 3 and 4) are primarily passage zones that split the estuarine ranges of some JES and IRLES year-round residents, but Segment 3 appears to be more affiliated with the north and Segment 4 to the south; (4) Segment 5 encompasses only part of individual dolphin ranges and is more affiliated with the IRLES-ML population; and (5) IRLES-ML dolphins are more aligned with dolphins further to the north vs the IRP. These findings are further supported by genetic analyses indicating (1) JES-N dolphins are genetically differentiated from JES-S dolphins (Rosel et al., 2009), (2) JES dolphins could not be differentiated from IRLES-ML dolphins (Rodgers, 2013), and (3) IRLES-ML dolphins are differentiated from IRP dolphins (Richards et al., 2013). However, intraregional movements may not completely account for the inverse seasonal patterns between the JES-S and IRLES-ML. The change in JES-S winter distribution toward the SJR mouth may be in response to prey, conspecific shifts of transient dolphins away from the SJR mouth, or movements into the Atlantic Ocean. As well, ML dolphins have been seen in the nearshore coastal waters near Ponce de Leon Inlet (Durden et al., 2011) where low-level mixing between estuarine and coastal dolphins may occur as seen in the SJR (Caldwell, 2016a) and further south in the IRLES (Mazzoil et al., 2011). Future studies using photo-identification, stranding, and genetic analyses in the nearby coastal waters will help strengthen our understanding of the interplay of resident and transient dolphins and regional movement patterns along this expansive seaboard.

In conclusion, from a stock management perspective, based on the best available current knowledge, we recommend (1) separating the JES-N from the JES-S stocks with the SJR as the demarcation line, although the northern boundary of the JES-N is yet indeterminate; (2) recognizing a JES-S western boundary 57 km upriver in the SJR to Mandarin Point/Doctor's Inlet; (3) extending the JES-S southern boundary further south to St. Augustine Inlet (Segment 3, currently managed under the WNA-NFL stock); (4) extending the northern boundary of the IRLES-ML population to St. Augustine Inlet (currently managed under the WNA-CFL stock) or conservatively, to the northern Volusia County line, congruent with efforts to expand the management

boundaries of the IRL to integrate regional drainage basins and watersheds into a connected estuarine system with an ecosystem-based management program (Indian River Lagoon Council Board of Directors Resolution #2015-04); and (5) disconnecting the IRLES-ML dolphin population from the IRLES proper stock.

Literature Cited

Barros, N. B., & Wells, R. S. (1998). Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Journal of Mammalogy*, *79*(3), 1045-1059. https://doi.org/10.2307/1383114

Borkowski, R. (2017). Bottlenose dolphin inhabitance of the St. Johns River. In *River Report: State of the lower St. Johns River Basin, Florida* (pp. H1-H11). http://sjrr.domains.unf.edu

Brown, A., Foss, A., Miller, M., & Gibson, Q. (2018). Detection of cyanotoxins (microcystins/nodularins) in livers from estuarine and coastal bottlenose dolphins (*Tursiops truncatus*) from northeast Florida.

Harmful Algae, *76*, 22-34. https://doi.org/10.1016/j.hal.2018.04.011

Byers, C. R., Steinhorst, R. K., & Krausman, P. R. (1984). Clarification of a technique for analysis of utilization-availability data. *The Journal of Wildlife Management*, *48*(3), 1050-1053. https://doi.org/10.2307/3801467

Caldwell, M. (2016a). Historical evidence of *Tursiops truncatus* exhibiting habitat preference and seasonal fidelity in northeast Florida. *Aquatic Mammals*, *42*(1), 89-103. https://doi.org/10.1578/AM.42.1.2016.89

Caldwell, M. (2016b). Historical seasonal density and distribution patterns of *Tursiops truncatus* in northeast Florida. *Aquatic Mammals*, *42*(1), 74-88. https://doi.org/10.1578/AM.42.1.2016.74

Carmichael, R. H., Graham, W. M., Allen, A., Worthy, G., & Howden, S. (2012). Were multiple stressors a "Perfect Storm" for northern Gulf of Mexico bottlenose dolphins (*Tursiops truncatus*) in 2011? *PLOS ONE*, *7*(7). https://doi.org/10.1371/journal.pone.0041155

Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences of the United States of America*, *89*(3), 987-990. https://doi.org/10.1073/pnas.89.3.987

Connor, R. C., Cioffi, W. R., Randic, S., Allen, S. J., Watson-Capps, J., & Krützen, M. (2017). Male alliance behaviour and mating access varies with habitat in a dolphin social network. *Scientific Reports*, *7*, 46354. https://doi.org/10.1038/srep46354

Crawford, W. G., Jr. (2006). *Florida's big dig: The Atlantic Intracoastal Waterway from Jacksonville to Miami, 1881 to 1935*. Florida Historical Society Press.

Durden, W. N., Stolen, M. K., & Stolen, E. D. (2011). Abundance, distribution, and group composition of Indian River Lagoon bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals*, *37*(2), 175-186. https://doi.org/10.1578/AM.37.2.2011.175

Durden, W. N., Stolen, E. D., Jablonski, T. A., Puckett, S. A., & Stolen, M. K. (2017). Monitoring seasonal abundance of Indian River Lagoon bottlenose dolphins (*Tursiops truncatus*) using aerial surveys. *Aquatic Mammals*, *43*(1), 90-112. https://doi.org/10.1578/AM.43.1.2017.90

Durden, W. N., Stolen, E. D., Moreland, L., Howells, E., Jablonski, T., Sleeman, A., Denny, M., Biedenbach, G., & Mazzoil, M. (2020). *Robust design capture-recapture analysis of abundance and demographic parameters of Indian River Lagoon common bottlenose dolphins (*Tursiops truncatus*)*. https://doi.org/10.1101/2020.01.30.926683

Durden, W. N., O'Corry-Crowe, G., Shippee, S., Jablonski, T., Rodgers, S., Mazzoil, M., Howells, E., Hartel, E., Potgieter, B., Londono, C., Moreland, L., Townsend, F., McCulloch, S., & Bossart, G. (2019). Small-scale movement patterns, activity budgets, and association patterns of radio-tagged Indian River Lagoon bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals*, *45*(1), 66-87. https://doi.org/10.1578/AM.45.1.2019.66

Environmental Systems Research Institute (ESRI). (2011). *ArcMAP 10.1*. ESRI.

Ermak, J., Brightwell, K., & Gibson, Q. (2017). Multi-level dolphin alliances in northeastern Florida offer comparative insight into pressures shaping alliance formation. *Journal of Mammalogy*, *98*(4), 1096-1104. https://doi.org/10.1093/jmammal/gyx053

Ewing, R. Y., Mase-Guthrie, B., McFee, W., Townsend, F., Manire, C. A., Walsh, M., Borkowski, R., Bossart, G. D., & Schaefer, A. M. (2017). Evaluation of serum for pathophysiological effects of prolonged low salinity water exposure in displaced bottlenose dolphins (*Tursiops truncatus*). *Frontiers in Veterinary Science*, *4*, 80. https://doi.org/10.3389/fvets.2017.00080

Fertl, D. C. (1994). Occurrence patterns and behavior of bottlenose dolphins (*Tursiops truncatus*) in the Galveston Ship Channel. *Texas Journal of Science*, *46*, 299-317.

Gibson, Q. A., Howells, E. M., Lambert, J. D., Mazzoil, M., & Richmond, J. P. (2013). The ranging patterns of female bottlenose dolphins with respect to reproductive status: Testing the concept of nursery areas. *Journal of Experimental Marine Biology and Ecology*, *445*, 53-60. https://doi.org/10.1016/j.jembe.2013.03.020

Grigg, E. K., Allen, S. G., Craven-Green, D. E., Klimley, A. P., Markowitz, H., & Elliott-Fisk, D. L. (2012). Foraging distribution of Pacific harbor seals (*Phoca vitulina richardii*) in a highly impacted estuary. *Journal of Mammalogy*, *93*(1), 282-293. https://doi.org/10.1644/11-MAMM-A-128.1

Gubbins, C. M., Caldwell, M., Barco, S. G., Rittmaster, K., Bowles, N., & Thayer, V. G. (2003). Abundance and sighting patterns of bottlenose dolphins (*Tursiops truncatus*) at four northwest Atlantic coastal sites. *The Journal of Cetacean Research and Management*, *5*(2), 141-147.

Howells, E. M., Reif, J. S., Bechdel, S. E., Murdoch, M. E., Bossart, G. D., McCulloch, S. D., & Mazzoil, M. (2009). A novel case of non-offspring adoption in a free-ranging Atlantic bottlenose dolphin (*Tursiops truncatus*) inhabiting the Indian River Lagoon, Florida. *Aquatic Mammals*, *35*(1), 43-47. https://doi.org/10.1578/AM.35.1.2009.43

Karle, K. A. (2016). *Structure and function of male bottlenose dolphin alliances in northeast Florida* (Unpub. Master's thesis). University of North Florida, Jacksonville. https://digitalcommons.unf.edu/cgi/viewcontent.cgi?article=1675&context=etd

Mann, J., & Smuts, B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, *136*(5), 529-566. https://www.jstor.org/stable/4535627; https://doi.org/10.1163/156853999501469

Mann, J., Connor, R. C., Barre, L. M., & Heithaus, M. R. (2000). Female reproductive success in bottlenose dolphins (*Tursiops* sp.): Life history, habitat, provisioning, and group-size effects. *Behavioral Ecology*, *11*(2), 210-219. https://doi.org/10.1093/beheco/11.2.210

Mazzoil, M., McCulloch, S., & Defran, R. H. (2005). Observations of the site fidelity of bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon, Florida. *Florida Scientist*, *68*(4), 217-226. https://www.jstor.org/stable/24322274

Mazzoil, M., McCulloch, S. D., Defran, R. H., & Murdoch, M. E. (2004). Use of digital photography and analysis of dorsal fins for photo-identification of bottlenose dolphins. *Aquatic Mammals*, *30*(2), 209-219. https://doi.org/10.1578/AM.30.2.2004.209

Mazzoil, M., Murdoch, M. E., Reif, J. S., Bechdel, S., Howells, E., de Sieyes, M., Lawrence, C., Bossart, G. D., & McCulloch, S. D. (2011). Site fidelity and movement of bottlenose dolphins (*Tursiops truncatus*) on Florida's east coast: Atlantic Ocean and Indian River Lagoon estuary. *Florida Scientist*, *74*(1), 25-37. https://www.jstor.org/stable/24321785

Mazzoil, M., Reif, J. S., Youngbluth, M., Murdoch, M. E., Bechdel, S., Howells, E., McCulloch, S. D., Hansen, L. J., & Bossart, G. D. (2008). Home ranges of bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon, Florida: Environmental correlates and implications for management strategies. *EcoHealth*, *5*(3), 278-288. https://doi.org/10.1007/s10393-008-0194-9

Miller, J. A. (2012). Species distribution models: Spatial autocorrelation and non-stationarity. *Progress in Physical Geography*, *36*(5), 681-692. https://doi.org/10.1177/0309133312442522

Moran, P. A. (1950). Notes on continuous stochastic phenomena. *Biometrika*, *37*(1-2), 17-23. https://doi.org/10.2307/2332142

National Oceanic and Atmospheric Administration (NOAA) Fisheries. (2009). *U.S. Atlantic and Gulf of Mexico marine mammal stock assessments – 2009*. https://www.fisheries.noaa.gov/resource/document/us-atlantic-and-gulf-mexico-marine-mammal-stock-assessments-2009

NOAA Fisheries. (2017). *U.S. Atlantic and Gulf of Mexico marine mammal stock assessments – 2018*. https://www.fisheries.noaa.gov/resource/document/us-atlantic-and-gulf-mexico-marine-mammal-stock-assessments-2018

Nekolny, S. R., Denny, M., Biedenbach, G., Howells, E. M., Mazzoil, M., Durden, W. N., Moreland, L., Lambert, J. D., & Gibson, Q. A. (2017). Effects of study area size on home range estimates of common bottlenose dolphin (*Tursiops truncatus*). *Current Zoology*, *63*(6), 693-701. https://doi.org/10.1093/cz/zox049

Neu, C. W., Byers, C. R., & Peek, J. M. (1974). A technique for analysis of utilization-availability data. *The Journal of Wildlife Management*, *38*(3), 541-545. https://doi.org/10.2307/3800887

Odell, D. K., & Asper, E. D. (1990). Distribution and movements of freeze-branded bottlenose dolphins in the Indian and Banana Rivers, Florida. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 515-540). Academic Press. https://doi.org/10.1016/B978-0-12-440280-5.50034-2

Owen, E. C., Wells, R. S., & Hofmann, S. (2002). Ranging and association patterns of paired and unpaired adult male Atlantic bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies. *Canadian Journal of Zoology*, *80*(12), 2072-2089. https://doi.org/10.1139/z02-195

Richards, V. P., Greig, T. W., Fair, P. A., McCulloch, S. D., Politz, C., Natoli, A., Driscoll, C. A., Hoelzel, A. R., David, V., Bossart, G. D., & Lopez, J. V. (2013). Patterns of population structure for inshore bottlenose dolphins along the eastern United States. *Journal of Heredity*, *104*(6), 765-778. https://doi.org/10.1093/jhered/est070

Rodgers, S. E. (2013). *Population structure and dispersal of bottlenose dolphins (*Tursiops truncatus*) of the Indian River Lagoon estuary, Florida, and adjacent Atlantic Ocean waters* (Unpub. Master's thesis). Florida Atlantic University, Boca Raton.

Rosel, P. E., Hansen, L., & Hohn, A. A. (2009). Restricted dispersal in a continuously distributed marine species: Common bottlenose dolphins *Tursiops truncatus* in coastal waters of the western North Atlantic. *Molecular Ecology*, *18*, 5030-5045. https://doi.org/10.1111/j.1365-294X.2009.04413.x

Rosel, P. E., Mullin, K. D., Garrison, L., Schwacke, L. H., Adams, J., Balmer, B. C., Conn, P. B., Conroy, M. J., Eguchi, T., Gorgone, A. M., Hohn, A., Mazzoil, M., Schwarz, C., Sinclair, C., Speakman, T., Urian, K., Vollmer, N. L., Wade, P., Wells, R., & Zolman, E. (2011). *Photo-identification capture-mark recapture techniques for estimating abundance of bay, sound, and estuary populations of bottlenose dolphins along the U.S. east coast and Gulf of Mexico: A workshop report* (NOAA Technical Memorandum NMFS-SEFSC-621). National Oceanic and Atmospheric Administration. 30 pp.

Schaeff, C. M. (2007). Courtship and mating behavior. In B. G. M. Jamieson & D. Miller (Eds.), *Reproductive biology and phylogeny of Cetacea: Whales, dolphins and porpoises* (Vol. 7, pp. 349-370). Science Publishers. https://doi.org/10.1201/b11001-14

Stolen, M. K., Durden, W. N., & Odell, D. K. (2007). Historical synthesis of bottlenose dolphin (*Tursiops truncatus*) stranding data in the Indian River Lagoon system, Florida. *Florida Scientist*, *70*(1), 45-54.

Titcomb, E. M., O'Corry-Crowe, G., Hartel, E., & Mazzoil, M. S. (2015). Social communities and spatiotemporal dynamics of association patterns in estuarine bottlenose dolphins. *Marine Mammal Science*, *31*(4), 1314-1337. https://doi.org/10.1111/mms.12222

Urian, K. W., & Wells, R. S. (1996). *Bottlenose Dolphin Photo-Identification Workshop* (NOAA Technical Memorandum NMFS-SEFSC-393). National Oceanic and Atmospheric Administration.

Urian, K. W., Hohn, A. A., & Hansen, L. J. (1999). *Status of the photo-identification catalog of coastal bottlenose dolphins of the western North Atlantic* (NOAA Technical Memorandum NMFS-SEFSC-425). National Oceanic and Atmospheric Administration.

Urian, K. W., Duffield, D. A., Read, A. J., Wells, R. S., & Shell, E. D. (1996). Seasonality of reproduction in bottlenose dolphins, *Tursiops truncatus*. *Journal of Mammalogy*, *77*(2), 394-403. https://doi.org/10.2307/1382814

Urian, K., Gorgone, A., Read, A., Balmer, B., Wells, R. S., Berggren, P., Durban, J., Eguchi, T., Rayment, W., & Hammond, P. S. (2015). Recommendations for photo-

identification methods used in capture-recapture models with cetaceans. *Marine Mammal Science*, *31*(1), 298-321. https://doi.org/10.1111/mms.12141

Watson-Capps, J. (2005). *Female mating behavior in the context of sexual coercion and female ranging behavior of bottlenose dolphin (*Tursiops *sp.) in Shark Bay, Western Australia* (Doctoral dissertation). Georgetown University, Washington, DC. https://doi.org/10.1016/j.biocon.2005.03.001

White, G. C., & Garrott, R. A. (1990). *Analysis of wildlife radio-tracking data*. Academic Press.

Whitehead, H., & Mann, J. (2000). Female reproductive strategies of cetaceans. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 219-246). University of Chicago Press. 448 pp.

Würsig, B., & Würsig, M. (1977). The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). *Science*, *198*(4318), 755-756. https://doi.org/10.1126/science.198.4318.755