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Small-Scale Movement Patterns, Activity Budgets, and Association Patterns of Radio-Tagged Indian River Lagoon Bottlenose Dolphins (*Tursiops truncatus*)

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Abstract

Information on movement patterns and habitat selection for critical activities are fundamental to understanding and managing animal populations. While bottlenose dolphins (*Tursiops truncatus*) inhabiting the Indian River Lagoon (IRL), Florida, are known to exhibit long-term residency, data regarding short-term movement and association patterns, habitat use, and activity budgets are limited. These parameters and the percentage of time dolphins occurred within a predetermined survey strip were evaluated utilizing VHF radio-telemetry. A total of nine IRL dolphins (eight males and one female) were captured and fitted with radio transmitters (summers of 2007 and 2010). Focal follows utilized instantaneous scan samples and standardized behavioral categories. Conspecifics were identified, and the half-weight index was utilized to evaluate association patterns. Radio tags remained adhered for 15 to 97 days (mean: 45.8 ± 25.3 days), and the tag attachment site influenced attachment longevity. The linear distances traversed by tagged dolphins ranged between 13.4 to 39.4 km (mean: 28.1 ± 9.49 km). While shallow water (< 1 m) habitats were frequently utilized (42.8% observations), dolphins selected deeper waters based on availability. Activity budgets differed between individuals and age-classes and were associated with water depth. Foraging and play behavior were observed significantly more in the shallowest water (≤ 1 m). Dolphins exhibited a high number of low-level associations (mean: 25.0 ± 14.58; range: 8 to 43 marked individuals), while one male individual exhibited a high-level male association (coefficient of association [COA] = 0.88) and a moderately high-level female association (COA = 0.67). This study represents the most extensive radio-tracking effort for IRL dolphins; it established radio-telemetry as a useful method to evaluate seasonal ranging patterns and provided important baseline data on short-term association patterns, activity budgets, and habitat use. Future studies that incorporate remote tracking capabilities, increased time and sample sizes, and nocturnal behavior are warranted to expand our understanding of movement patterns and habitat utilization.

Key Words: Indian River Lagoon, movement patterns, radio-telemetry, activity budgets, habitat selection, bottlenose dolphin, *Tursiops truncatus*

Introduction

Understanding animal movements and how they relate to the dynamics of a population is essential to management and conservation efforts. Bottlenose dolphin (*Tursiops truncatus*) distribution, ranging patterns, and habitat use are likely associated with several factors, including social dynamics, water temperature, and productivity, as well as oceanographic parameters that may alter prey distribution (Kenney, 1990; Shane, 1990; Wells et al., 1990; Quinn & Brodeur, 1991; Hedrick & Duffield, 1991; Barco et al., 1999;

Bristow & Rees, 2001). Changes in habitat and the distribution of prey species may alter how dolphins utilize resources and may consequently modify movement patterns. In addition, human activities have the potential to impact dolphin distribution (Jefferson, 2000). Bottlenose dolphin behavior is influenced by vessel traffic (Lusseau, 2003; Mattson et al., 2005; Pirotta et al., 2015; Marley et al., 2017), and dolphins may actively avoid high boat traffic areas (Lusseau, 2004). Likewise, fishery interactions may influence dolphin behavior and movement patterns (Noke & Odell, 2002; Durden, 2005; Powell & Wells, 2011) and pose a serious mortality risk for estuarine bottlenose dolphins (Wells et al., 1998, 2008; Noke & Odell, 2002; Durden, 2005; Stolen et al., 2013). The use of radio-telemetry allows researchers to address questions regarding movement patterns and habitat utilization since individual animals can be consistently monitored over time. The bottlenose dolphin population inhabiting the Indian River Lagoon (IRL) along the east coast of Florida has been routinely monitored via photo-identification surveys (Mazzoil et al., 2005, 2008b). These surveys were designed to determine large-scale ranging patterns and community structure (Mazzoil et al., 2008b; Titcomb et al., 2015), and provide only an intermittent evaluation of movement patterns over a broad temporal scale; while radio-telemetry can provide a substantial amount of data over a short time period. Photo-identification survey data may also be limited when assessing movement patterns as survey designs are typically correlated to search effort rather than individual movement patterns. For example, 95% of historical photo-identification sighting data in the IRL were contained within a 1.25-km-wide observation window on either side of the survey track line (Intracoastal Waterway) which provided visual access to varied bathymetry and aided navigation (M. Mazzoil, unpub. data); however, the width of the lagoon extends up to 9.3 km, and numerous spoil islands and a convoluted coastline create many areas where dolphins are unavailable for detection. Comparisons between short-term telemetry and an established "observation window" from long-term data collected during routine photo-identification surveys present an opportunity to examine the potential impact of search effort differences when evaluating ranging patterns and habitat use and to explore the use of telemetry data to supplement long-term studies.

The degree to which movement patterns of one individual are influenced by another is an important consideration when examining ranging patterns. Bottlenose dolphins, like some other social mammal species (e.g., chimpanzees [*Pan troglodytes*], Wrangham, 1986; and spider monkeys [*Ateles paniscus*], McFarland, 1986), exhibit a fission–fusion social organization where some associations may change frequently in composition and size over small spatial and temporal scales, while other associations may remain stable over many years (Würsig & Würsig, 1977; Wells et al., 1987; Wells, 1991; Connor et al., 1992a; Smolker et al., 1992; Titcomb et al., 2015). Bottlenose dolphin social organization (i.e., the number of affiliates and degree of affiliation) may be influenced by ecological factors, including the nature of the habitat (closed vs open), movement patterns of affiliates, variation in predation risk, reproductive state, and distribution and availability of prey (Wells et al., 1987; Wells, 1991; Smolker et al., 1992; Wilson, 1995; Connor, 2000; Fury et al., 2013; Gazda et al., 2015; Connor et al., 2017). In some estuarine systems, male bottlenose dolphins have been found to form stable long-term associations (Wells et al., 1987; Wells, 1991). In contrast, these associations can be absent in open-sea embayments (Wilson, 1995). Patterns and complexity of bottlenose dolphin alliance formation vary and may be correlated with population density and degree of sexual dimorphism. In a high-density population with little sexual dimorphism (females only slightly smaller), males have been found to associate in alliances since partnerships may be required to monopolize receptive females (Connor et al., 1992a, 2011; Connor, 2000). In contrast, alliances are not evident in low-density populations where males are substantially larger than females and can utilize solitary reproductive strategies (Wilson, 1995) or in areas where males associate in large, stable, mixed sex-groups (Lusseau et al., 2003). Understanding association patterns is essential as they may also influence community structure, disease transmission, reproductive success, and gene flow, as well as the cultural transmission of behaviors, including depredation and other anthropogenic interactions (Wells, 2003; Whitehead et al., 2004; Cunningham-Smith et al., 2006; Mann et al., 2012; O'Corry-Crowe et al., 2018).

Likewise, behavioral activity budgets can provide valuable data on how animals interact with their environment and conspecifics (Hanson & Defran, 1993; Bearzi & Notarbartolo di Sciara, 1999; Neumann, 2001; Chilvers et al., 2003; Constantine et al., 2004; Lusseau, 2006; McHugh et al., 2011; Miketa et al., 2017). Large-scale ecosystem changes can influence the portion of time dolphins spend engaging in different activities (Powell & Wells, 2011). In small estuarine populations which may be frequently impacted by a variety of human interactions (e.g., fishing activities, boating, and ecotourism), activity budgets can be utilized to assess the impact of these activities

(Chilvers et al., 2003; Lusseau, 2006; Stockin et al., 2008; Powell & Wells, 2011). Behavioral budgets, therefore, serve as critical background information and allow managers to evaluate how a population may be impacted by changes in prey, habitat, social structure, anthropogenic activities, or environmental parameters. Furthermore, behavioral budgets may be helpful in determining the ontogeny of behaviors (Mann et al., 2008; Cartwright & Sullivan, 2009). Currently, there is a need for background information on behavioral budgets for IRL dolphins as scant data are available (Noke & Odell, 2002; Durden, 2005).

Dolphins residing in the IRL estuary along the east coast of Florida are known to exhibit site fidelity (Odell & Asper, 1990; Mazzoil et al., 2005); however, little detailed data are available on this population's individual habitat utilization, movement patterns, activity budgets, and short-term association patterns. This population faces numerous threats that warrant an improved understanding of these types of behavior. IRL dolphins may be directly (e.g., boat strikes and fishing gear entanglement) and indirectly (e.g., introduction of marine contaminants) impacted by human activities (Noke & Odell, 2002; Durden, 2005; Durden et al., 2007; Stolen et al., 2007, 2013; Bechdel et al., 2009; Fair et al., 2010). Interactions with fishing gear (e.g., entanglement and/or gear ingestion) are the cause of mortality in 4.9% of stranded IRL dolphins (Stolen et al., 2013). High-risk behaviors such as depredation and begging have also been documented (Noke & Odell, 2002; Durden, 2005) and likely contribute to harmful fishery interactions and mortality in IRL dolphins. Furthermore, as a long-lived top-level predator, IRL dolphins are exposed to and accumulate persistent pollutants (Durden et al., 2007; Titcomb et al., 2017) that may increase their susceptibility to disease (Fair & Becker, 2000). Dolphins inhabiting the IRL are known to exhibit skin disease (Caldwell et al., 1975; Bossart et al., 2003; Reif et al., 2006; Murdoch et al., 2008; Durden et al., 2009) and are described as an immune-compromised population (Bossart et al., 2003). This population has undergone three documented Unusual Mortality Events (UMEs) of unknown origin (2001, 2008, and 2013), as well as a fourth UME (Mid Atlantic Unusual Mortality Event, 2013-2015; tentative cause is morbillivirus), which impacted dolphins in the northern portion of the lagoon. Understanding the impacts of past and future UMEs may hinge on our understanding of habitat utilization, ranging patterns, behavioral budgets, and association patterns of these animals. The IRL dolphin estuarine stock is considered a strategic stock since the number of human-induced injuries and mortalities likely exceeds the potential biological removal (National Oceanic and Atmospheric Administration [NOAA] Fisheries, 2013). All of these factors highlight the need for an improved understanding of the ecology of these animals. The objectives of this study were (1) to use radio-telemetry to investigate the influence of tag placement on tag attachment duration; (2) to study the proportion of time that tracking locations were beyond the photo-identification survey observation window; and (3) to increase our knowledge of site fidelity, association patterns, activity budgets, ranging patterns, and habitat utilization in IRL dolphins.

Methods

Study Area

The Indian River Lagoon is a shallow estuarine system located along the east coast of central Florida that consists of three interconnected bodies of water: (1) the Indian River, (2) Banana River, and (3) Mosquito Lagoon. The lagoon spans an approximate linear distance of 250 km, from Ponce de Leon Inlet to Jupiter Inlet (U.S. Environmental Protection Agency [EPA], 1996; Figure 1). The lagoon is open to the Atlantic Ocean at five inlets, and the width of the system varies from less than 0.93 to 9.30 km at the northern end of the estuary (Leatherwood, 1979). Although much of the estuary is shallow (< 1 m at high tide), depths of greater than 5 m can be found in the dredged basins and channels of the Intracoastal Waterway (ICW) (Gilmore, 1977). The IRL is a diverse estuary with more than 400 fish species (Mulligan & Snelson, 1983; Tremain & Adams, 1995). At least six distinct communities of bottlenose dolphins have been described inhabiting the IRL estuary (Titcomb et al., 2015). The current study focused on the north-central, south-central, and southern Indian River (289 km^2; maximum width: 3.7 km) which encompassed three communities of dolphins, two of which are known to have a large degree of overlap (Woodward-Clyde Consultants, 1994; Titcomb et al., 2015; Figure 1).

Radio-Tag Attachment

During dolphin health and environmental risk assessments (HERA) conducted within the IRL, dolphins were temporarily captured and restrained by standardized methods (Fair et al., 2006). To ensure the animals were representative of the resident population, individual "marked" dolphins (D1 and D2; Urian et al., 1999), a few animals with sighting histories ranging from 2 to 12 y (mean: 8.0 ± 2.92 SD), were selected during two summer health assessments (2007 and 2010) and were fitted with radio transmitters. A VHF radio transmitter (Custom2 [2007] or MM 120 [2010] backmount transmitter; Advanced Telemetry

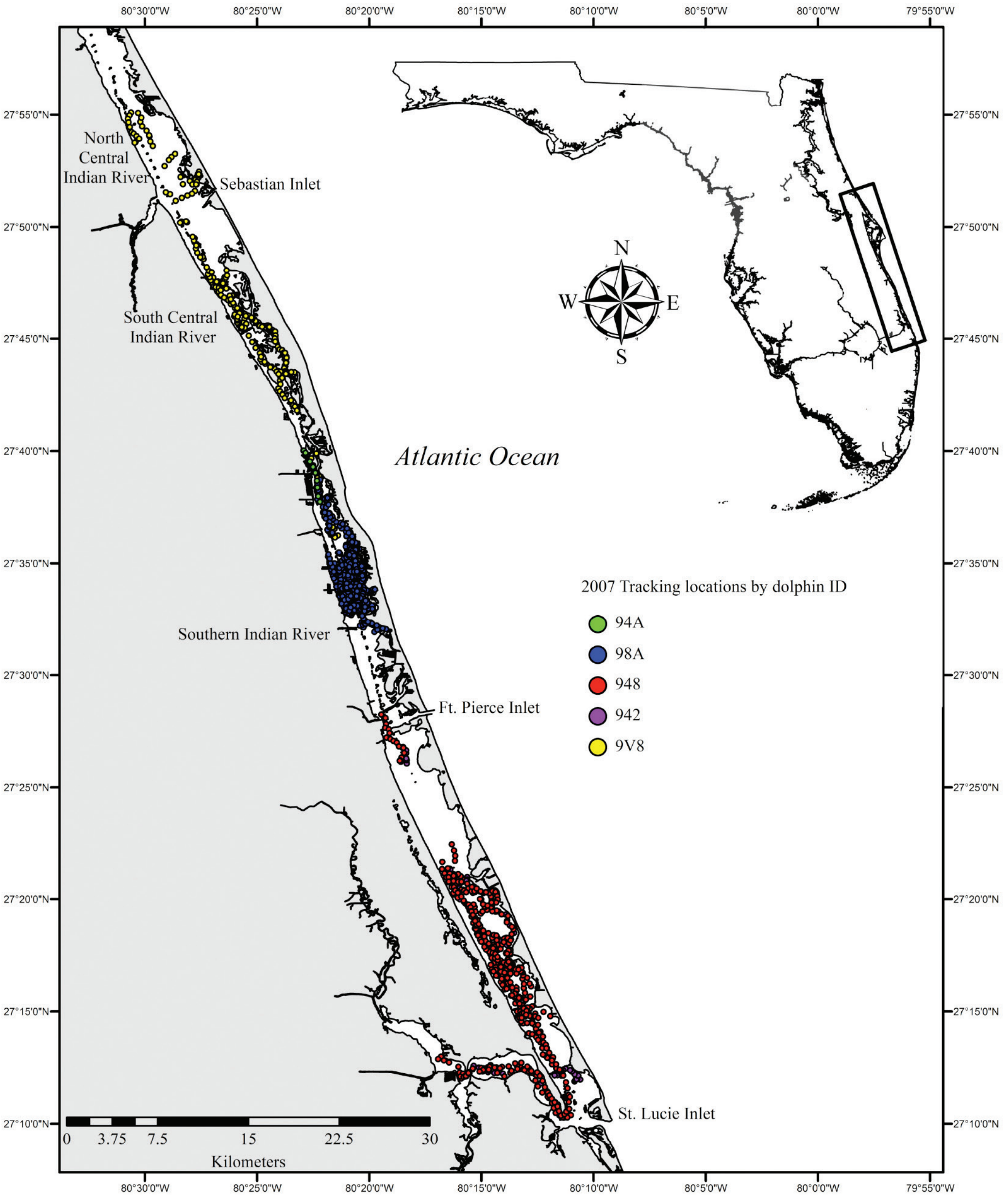

Figure 1. The study area which encompassed the north central, south central, and southern portions of the Indian River where tagged bottlenose dolphins (*Tursiops truncatus*) were resighted, and the Indian River Lagoon (IRL) in its entirety (inset within the rectangle) which was searched by aircraft to locate tagged animals. Five-minute scan sample location points are mapped for each tracked individual in 2007 ($n = 5$).

Systems, Inc., Isanti, MN, USA) was attached to each animal via a thermoplastic sleeve (bullet tag; Trac Pac, Ft. Walton Beach, FL, USA) that encapsulated a radio transmitter. Transmitters broadcasted in the frequency range of 166.000 to 166.999 MHz, at a pulse rate of 100/min, and with a maximum lifespan of 67 to 87 d.

Each transmitter was attached to the trailing edge of either the upper, middle, or lower third of the dorsal fin (Figure 2). Prior to tag attachment, the attachment site on the dorsal fin was prepared by cleansing it with ethanol and a betadine scrub, followed by the administration of a local anesthetic (lidocaine 2% with epinephrine). A small hole was then pierced 23 to 42 mm from the trailing edge of the fin using a sterile 5-mm biopsy punch (variations due to individual dorsal fin morphology and small discrepancies in the thermoplastic sleeve). A sterilized delrin pin (0.64 cm) was then passed through the piercing and fastened to the bullet sleeve with non-stainless steel nuts and stainless steel washers.

Dolphin total length (cm) was measured as straight-line length from the tip of the rostrum to the fluke notch (Norris, 1961), and sex was also determined. Age was determined following extraction of a single tooth under local anesthesia using an injection of 3% mepivacaine (Ridgway et al., 1975). Age estimation was determined by counting growth layer groups (GLGs) in teeth (Myrick et al., 1983; Hohn et al., 1989), or the minimum age was estimated based on photo-identification survey data (i.e., the date the individual was first sighted and then subsequently resighted throughout its life). Adults and juveniles were classified as follows: juvenile female (1.5 to 7 y old), juvenile male (1.5 to 10 y old), adult female (≥ 8 y old), and adult male (≥ 11 y old).

Radio-Tracking and Transmitter Performance

Minimum tag transmission was calculated based on the number of days from tag attachment until the last day of signal transmission. Likewise, minimum tag attachment was calculated as the number of days from tag attachment until the last day when the animal was seen with an attached transmitter. The relationship between tag placement on the dorsal fin (e.g., upper, middle, or lower third) and minimum tag attachment time was evaluated via linear regression using *Microsoft Excel 2013*.

Radio-tracking was conducted from a vessel or Cessna 172 aircraft with the objective to visually locate and focal follow each animal several times per week. Field efforts were suspended during inclement weather (e.g., thunderstorms and/or strong winds), although opportunistic land-based tracking by vehicle was implemented to ascertain tag transmission between field efforts. Efforts to radio-track individuals ceased when no signal was detected after an extensive search (e.g., vessel search within and beyond the animal's ranging area and a lagoon wide search by aircraft), the animal

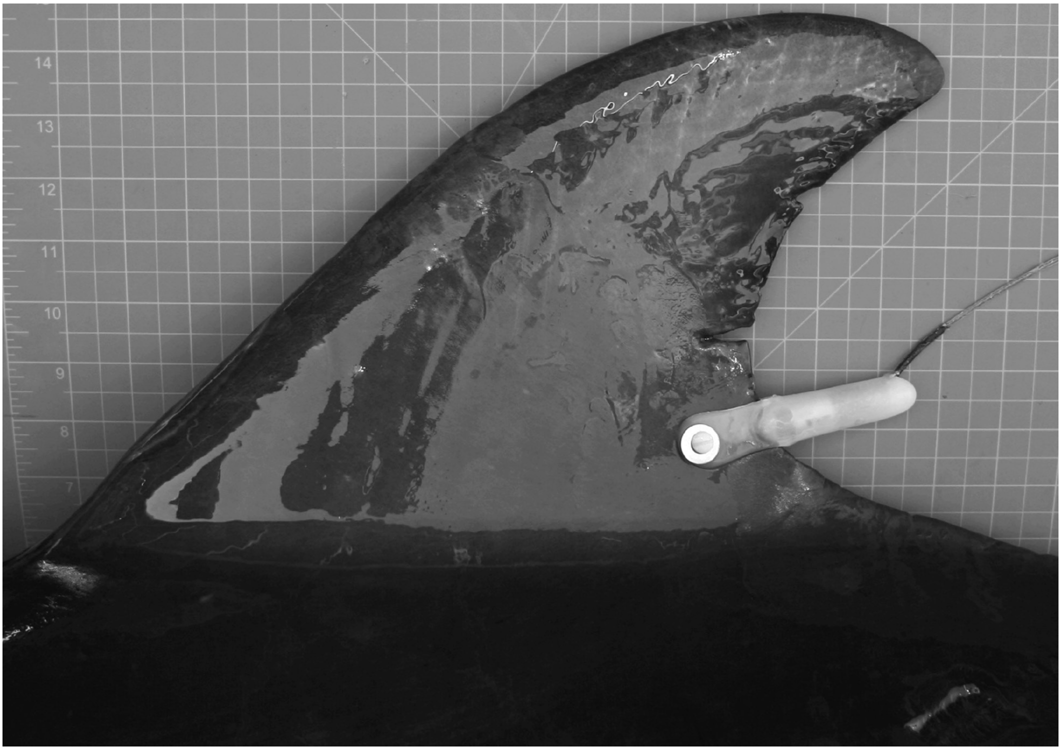

Figure 2. A radio transmitter attached to the trailing edge of the lower third of the dorsal fin of 98A; the deep notch just above the tag is the result of the migration of the first radio transmitter.

was sighted without its tag, or the animal was sighted with a tag that was no longer transmitting.

Aerial survey flights were utilized to expedite locating the tagged animal, to relay generalized location to boat-based teams, and to determine tag failure via expansive area coverage (~250 linear km). Aerial surveys were conducted from a fixed wing Cessna 172 at altitudes ranging from 152 to 457 m and a ground speed of 167 km/h. Due to aircraft regulations (Federal Aviation Administration [FAA]) regarding aircraft modification, aerial tracking used modified methods developed by Mech (1983) with antennas placed within the plane rather than affixed to aircraft struts. Two handheld VHF receivers, with attached four-element yagi antennas, were monitored by two observers seated in the front right and back left seats, and signal transmission information was relayed to a data recorder seated in the back right seat. Once a signal was detected, an attempt to localize the signal was made by orienting the aircraft at multiple angles. When possible, the tagged individual was visually located, and the latitude/longitude, habitat, and behavior were recorded. When it was not efficient to visually locate the individual, the loudest signal strength was localized, and an approximate location was recorded for the animal based on the coordinates of the aircraft.

Vessel tracking was conducted from small, shallow draft vessels (4.8 to 6.7 m in length). The observation crew searched the general geographic area where the target animal was previously sighted. When multiple platforms were utilized, search patterns for target animals were coordinated between the vessels or between the vessel and aircraft. Four element yagi antennas were mounted on vessels on aluminum poles (~3 m high), and radio transmissions were monitored on unidirectional VHF receivers or via an automatic direction finder unit (Advanced Telemetry Systems). When radio signals were detected, the crew focused in on the direction of the sound to localize the animal and bring the observer into visual distance. Once visually located, the observers began systematic data collection. A Garmin Global Positioning System (GPS map 76 CSx) unit was used to collect continuous detailed information about the search route and animal movements, and environmental conditions were collected every 2 h.

Focal Follows

Focal follows conducted during boat-based surveys allowed for direct observation of the tagged animal. Behavioral data were collected systematically for a subset of tagged animals (*n* = 6). Each individual behavioral focal follow spanned approximately 1 to 5 h and was conducted from an approximate distance of 10 to 50 m. During focal follows, the behavior of the tagged animal was documented using standardized behavior categories (Urian & Wells, 1996; Table 1) and instantaneous scan sampling with *ad libitum* notes (Altmann, 1974; Mann, 1999). To calculate activity budgets, the following behavioral states were evaluated: mill, forage (probable feed and feed combined), travel, play, and social. Instantaneous scan samples were collected at 5-min intervals and recorded: behavior, location (latitude and longitude), water depth, group size, group composition, and cohesion (Mattson et al., 2005). Activity

Table 1. Behavioral categories (Urian & Wells, 1996) recorded during Indian River Lagoon (IRL) bottlenose dolphin focal follows. The behaviors "probable feed" and "feed" were combined into the category "forage."

Behavioral state	Description
Mill	Non-directional movement, often occurs in conjunction with other activities
Feed	When a dolphin is observed with a fish in its mouth
Probable feed	When there are indications of feeding but feeding cannot be confirmed (e.g., active milling by a dolphin with marine birds diving in area)
Travel	Directed movement, including zig-zag movement
Play	Interactions with objects other than dolphins (e.g., throwing a stingray repeatedly)
Resting	Slow, quiescent activity in the absence of other identifiable activities
Leap, tailslap, and chuff	Aerial or acrobatic behaviors
Social	All active interactions with other dolphins, including contact, chasing, following, sexual interactions, etc.
With boat	Includes all cases where the dolphins are interacting with a boat, including bowriding, stern wake riding, making figure-eights ahead of the boat, etc.
Other	To accommodate dolphins' behavioral flexibility

budgets were calculated as the number of observations in each behavioral state divided by the total number of observations (scan samples) and were reported as percent of occurrence. Since it was necessary to keep the focal animal in sight at all times, group size was defined as dolphins within 100 m of the focal animal that were associated and engaging in similar behavior (Irvine et al., 1981). Data were recorded for the focal individual at the first surfacing during each time point. Care was taken to ensure that location and depth data (e.g., GPS waypoints and depth) were taken in close proximity to where the dolphin was observed at each time period. If the individual could not be located within the 5-min interval, no data/observations were recorded for that interval. During focal follows, photographs of the tagged dolphin (i.e., dorsal fin, body, and unusual behaviors) were taken with Nikon and Canon DSLR cameras with telephoto lenses to document the progression of radio-tag attachments. Attempts were made to photograph all conspecifics in the group to identify marked associates via distinct dorsal fin features. Photo-identification protocols closely followed those outlined in the *Sarasota Dolphin Research Program Field Techniques Photo-Identification Handbook* (SDRP, 2006). Subsequent photo-identification, fin matching, and sorting were performed by standardized methods (Mazzoil et al., 2004), and association patterns and group composition were further evaluated.

To examine the degree of association among dolphins, the half-weight index (HWI) coefficient of association (COA) (Cairns & Schwager, 1987; Ginsberg & Young, 1992), which is most robust to biases, was calculated. This association index results in values ranging from 0 to 1, where zero indicates that the two individuals were never seen together and one indicates that the two individuals were always seen together. The unit of measurement used to calculate the association index consisted of each 5-min time point in which the focal animal was observed with an identified associate. Indices were grouped into five association categories: (1) low (0.01 to 0.20), (2) moderate–low (0.21 to 0.40), (3) moderate (0.41 to 0.60), (4) moderate–high (0.61 to 0.80), and (5) high (0.81 to 1.00) (Quintana-Rizzo & Wells, 2001). Indices were calculated for tagged animals with a minimum of ten independent sightings/behavioral focal follows conducted on ten separate days (n = 4; juvenile included twice during separate years). Association indices were calculated for identifiable associates (marked D1 and D2; Urian et al., 1999) that were observed with the tagged dolphins.

Ranging Patterns

Data on dolphin distribution patterns collected via radio-tracking present fewer biases than those collected during boat-based photo-identification surveys since the locational data are determined by the individual animal (rather than search effort) and, therefore, may represent individual habitat use more accurately. Likewise, searches in this study were unbiased as the receiver range spanned the width of the study area, while the search strategy spanned the length. Home range has historically been defined as the area traversed by an individual during normal activities (e.g., foraging, mating, and caring for young) and is intended to describe time periods that encompass a large proportion of an individual's life (Burt, 1943). While the use of radio-telemetry facilitates the collection of detailed movement patterns, these data are temporally close and may produce a biased home range estimate. Similarly, home range calculation is known to be sensitive to sample size (i.e., the number of sightings for each individual), and home range size has been shown to increase with an increased sample size (Mares et al., 1980; Anderson, 1982). The minimum suggested sample size to ensure home range accuracy has been reviewed by several authors resulting in a range of 20 to 80 sightings (Mares et al., 1980; Arthur & Schwartz, 1999; Seaman et al., 1999). Due to the potential bias of temporally close data and small sample sizes (number of resighting days), conventional home range analyses were not conducted.

In circumstances where dolphins traverse a narrow strip of water, linear ranges may be more meaningful than an area measurement (Balmer et al., 2008). The linear range of each radio-tagged dolphin was defined as the maximum distance traveled along the main axis of the lagoon between its farthest northwest and southeast tracking locations (linear distance). Linear range was calculated for tagged animals with greater than five sighting days. Geographical data were imported into *Arc GIS*, Version 10.1, and plotted onto maps of the IRL to determine these calculations. To evaluate potential biases of photo-identification survey design in estimating ranging patterns, the survey path and associated observation window was calculated as a strip 1.25 km in width on either side of the ICW. Locational data from each 5-min point, for each individual, was mapped, and the percentage of points contained within the survey strip was evaluated by selecting the points located within the polygon (Clementini) in *Arc GIS*, Version 10.1 (Clementini et al., 1993).

To evaluate habitat selection and correlations between behavioral activities and habitat types, the study area was divided into four depth categories: (1) shallow water (≤ 1 m), (2) shallow to

Table 2. Summary of bottlenose dolphin radio-tracking efforts during summer 2007 and 2010 in the IRL, Florida. Animal ages in bold type are estimated based on sighting history (other ages estimated by a single tooth sectioning for six individuals; growth layer groups [GLGs]). Ranging patterns, attachment site along the trailing edge (TE) of the dorsal fin, tag longevity, and reason for tag failure are summarized. Linear range not applicable (NA) for 94A (only one sighting day). 98A* indicates the animal's second tagging event.

ID	Sex	Length (cm)	Age	Tagging date	# d resighted	Last signal	# d with regular signal	Last seen with tag	Linear ranging distance (km)	TE site	TE inset (mm)	Tag type	Min. # d attached	Reason for tag failure
9V8	M	283	17	20/6/07	9	25/7/07	36	25/7/07	35.7	Middle	25	Custom 2	36	Migration
948	M	248	12	22/6/07	10	2/8/07	42	2/8/07	33.7	Middle	25	Custom 2	42	Migration
942	M	243	14	22/6/07	7	23/7/07	32	23/7/07	32.3	Upper	25	Custom 2	32	Migration
94A	M	282	>**14**	27/6/07	1	10/7/07	15	27/6/07	NA (4.4)	Upper	23	Custom 2	15	Dislodged/attachment failure
98A	M	222	7	28/6/07	37	20/9/07	85	10/10/07	13.4	Lower	23	Custom 2	97	Battery reached expectancy, then migration
9A7	F	251	**14***	21/6/10	8	13/7/10	22	13/7/10	20.5	Lower	35	MM120	22	Dislodged/attachment failure
98D	M	269	23	21/6/10	10	30/7/10	39	30/7/10	17.8	Lower	42	MM120	40	Dislodged/attachment failure
98E	M	286	18	24/6/10	16	20/8/10	57	27/8/10	39.4	Lower	38	MM120	65	Battery reached expectancy, then attachment failure
98A*	M	235	10	23/6/10	17	24/8/10	62	24/8/10	32.1	Lower	35	MM120	63	Assume battery reached expectancy, then migration
				Mean ± SD	12.8 ± 10.24		43.3 ± 21.60		28.1 ± 9.49		30.1 ± 7.33		45.8 ± 25.34	

mid-depth (> 1 to 2 m), (3) mid-depth (> 2 to 3 m), and (4) deep water (> 3 m). GIS contour maps of the four depth categories were created using sounding data obtained from the St. Johns River Water Management District (bathymetric survey collected by Coastal Planning and Engineering [1997]) and South Florida Water Management District (1998) using the program *QGIS* (QGIS Development Team, 2016). Bathymetry in the study area was largely shallow water (84%), followed by shallow to mid-depth (13%), deep water (2%), and mid-depth (1%). The frequency of dolphin occurrence in each depth category was calculated as the number of locations within each depth bin, which was further compared to the percentage of each habitat type (depth category) available in the study area. The relationship between the water depth and behavioral activity was evaluated utilizing water depth measurements taken at each scan sample and the corresponding behavioral state using Chi-square analyses. Chi-square analysis was also used to investigate the relationship between habitat (depth category) availability and selection (observations in each depth category). Chi-square analyses were conducted in *Microsoft Excel 2013* and *Graph Pad*.

Results

Field Effort and Tag Longevity

A total of nine bottlenose dolphins were selected and fitted with radio tags (June 2007 and 2010). One individual (94A) was radio-tagged because the animal was exhibiting signs of stress upon examination, and post-release tracking was paramount to monitoring the animal's health. Eight males and one female were tagged (one animal, 98A, was tagged during both years). All animals were adult except for one juvenile, 98A (Table 2). Animal age and total length ranged from 7 to 23 y and 222 to 286 cm (Table 2). Two animals were caught and tagged together (942 and 948; Table 2). Tags were tested prior to deployment and were found to have a maximum range of approximately 4 km at sea level. During aerial surveys, tag transmission could be heard at a distance of > 6 km. Radio-tracking efforts were conducted between 20 June 2007 to 10 October 2007 and 21 June 2010 to 27 August 2010. A total of 447 h (n = 59 boat surveys; n = 4 flights) in 2007 and 192 h (n = 38 boat surveys; n = 4 flights) in 2010 were spent searching for or conducting focal follows of radio-tagged animals.

A total of 202 h were spent conducting focal follows of tagged animals (2007: 136 h; 2010: 66 h). Tags were applied to the upper (n = 2), middle (n = 2), or lower (n = 5) third of the dorsal fin (Table 2). While tag attachment duration varied by tag placement location, a positive but statistically non-significant relationship ($r = 0.585$, $p = 0.0981$, n = 9) was observed between tag duration and attachment site, with the longest durations for tags attached in the lower third of the dorsal fin (Table 2). Tags remained adhered for 15 to 97 d (mean: 45.8 ± 25.3 d) (Table 2). The maximum number of days with a regular signal was 85 d (Table 2). Six of the transmitters were positively determined to have dislodged based on subsequent sightings during the study period (three via tissue migration and three via attachment failure resulting from delrin pin shearing or nut loss; Table 2). Two transmitters ceased operating during the study period due to the battery reaching its life expectancy, and the remaining tag was assumed to have battery failure since the tag was firmly attached at last transmission, and a few months later it was confirmed to have migrated out (Table 2).

Ranging Patterns

The tagged dolphins were resighted in a narrow portion (range: ~0.40 to 3.7 km wide) of the IRL (Figures 1 & 3). One dolphin was resighted on only one occasion with the transmitter attached (94A), while the other eight dolphins were relocated on seven to 37 different days (mean: 12.8 ± 10.24 SD; Table 2). Linear ranges (excluding 94A) were 13.4 to 39.4 km (mean: 28.1 ± 9.49), with the juvenile dolphin (98A) having the shortest linear range (Table 2; Figure 4). The linear range for this dolphin increased substantially from 13.4 km in 2007 to 32.1 km in 2010. The majority of tracking locations for all dolphins (mean: 87.83 ± 8.52%; range: 66.43 to 100%) were found within the 2.5 km photo-identification survey observation window. 98D spent the greatest percentage of time (33.57%) outside the observation window (Figure 5).

Activity Budgets and Habitat Use

A total of 1,390 scan samples were conducted during 122 h of observations (Table 3), with activity budgets varying between animals (Table 3). On average, focal animals spent the majority of the time traveling (53%), followed by milling (27%), foraging (17%), and socializing (2.3%). The percentage of time spent traveling for each animal ranged from 39 to 80%. Only social interactions and play activity states varied by age class with the juvenile animal spending more time socializing and playing with foreign objects (mangrove propagules and seagrass) than adult animals (Table 3).

Habitat-use patterns varied among individual dolphins. The proportion of time each dolphin was observed in each water depth category ranged from 7.48 to 56.59% of observations in shallow water, 33.33 to 60.75% of observations in shallow to mid-depth water, 0.14 to 14.95% of observation in mid-depth water, and 0 to 16.82% of observations in deep water. Tagged dolphins predominantly utilized shallow to mid-depth water (> 1 to 2 m; mean: 43.6 ± 10.52%) and shallow water (≤ 1 m; mean: 42.8 ± 17.28%), followed by mid-depth (> 2 to 3 m; mean: 7.33 ± 5.24%) habitats, with the fewest observations occurring in deep water (> 3 m; mean: 6.3 ± 6.91%; Figure 6). Shallow habitat (≤ 1 m), however, was predominant in this region of the IRL (84% of available habitat), and tagged dolphins tended to select deeper water habitats (all categories:

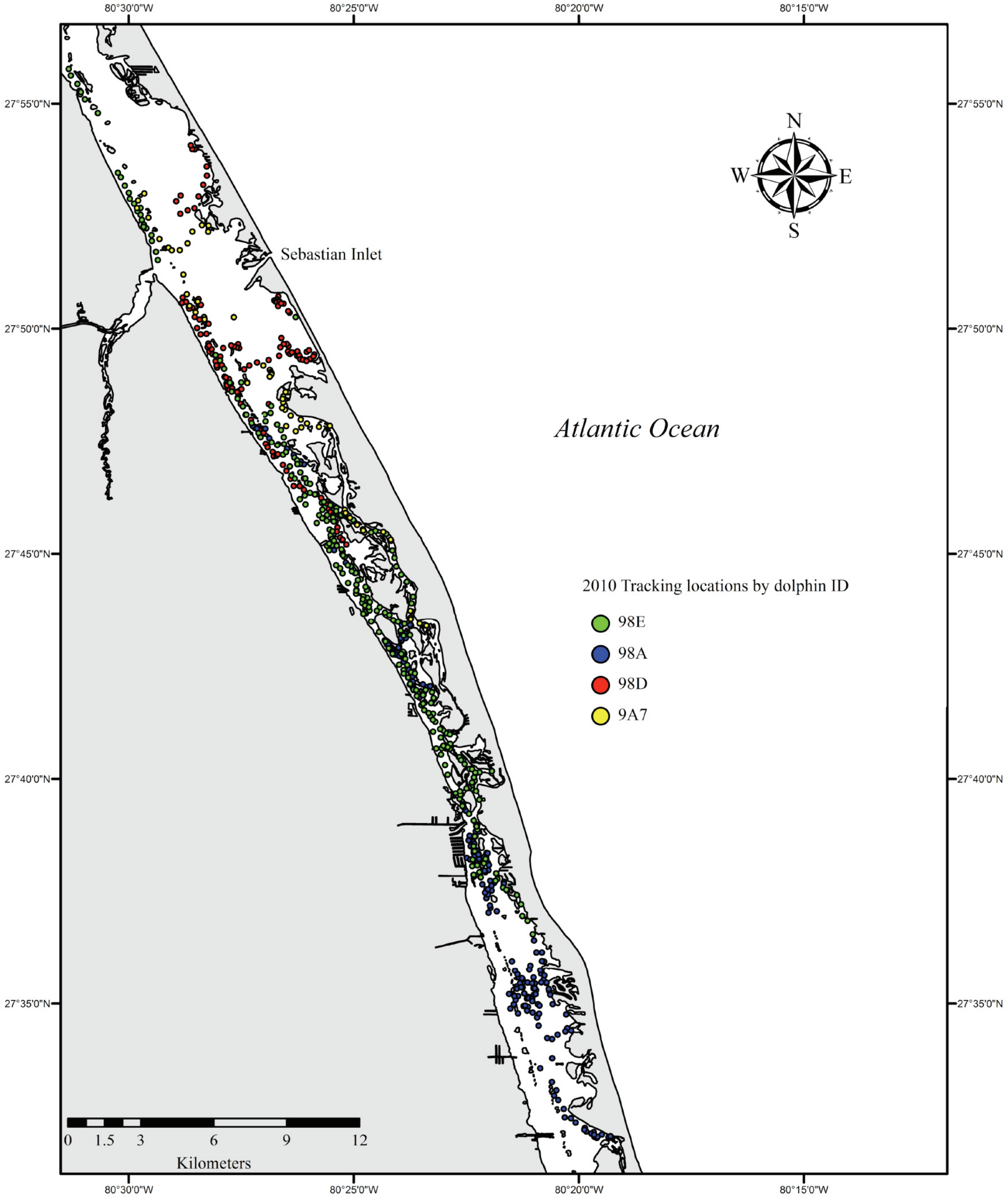

Figure 3. The study area in 2010 which encompassed the north central, south central, and southern portions of the Indian River; map indicates 5-min behavioral scan sample location points mapped for each tracked bottlenose dolphin (*n* = 4).

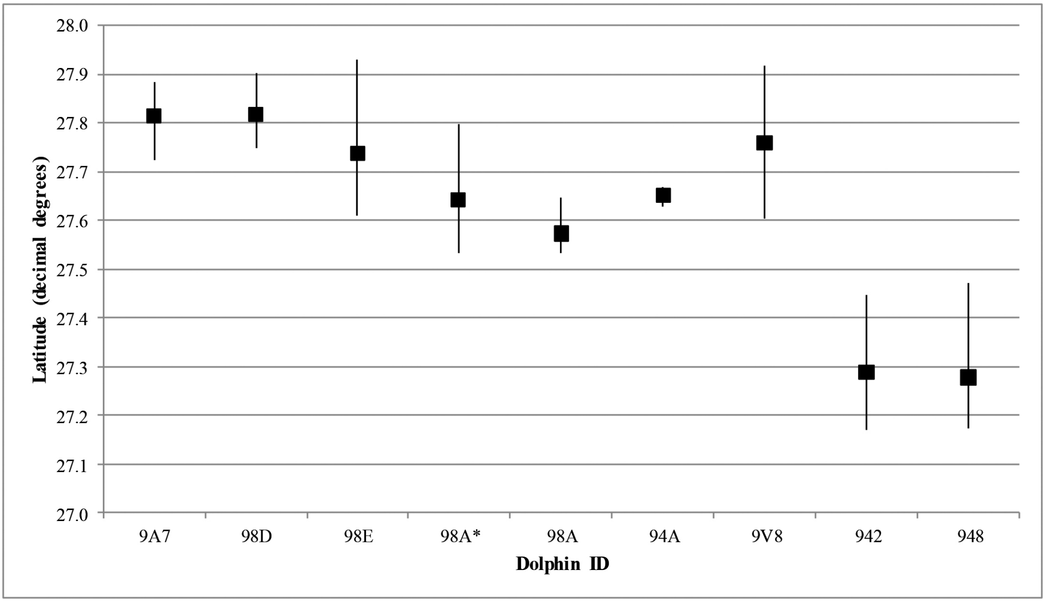

Figure 4. Linear range (latitude-decimal degrees) of tagged bottlenose dolphins ($n = 9$) from data obtained from summer telemetry locations in the IRL. Lines indicate the northern- and southernmost latitude, and the marker (square) indicates the mean latitude. 98A* indicates the animal's second tagging event in 2010.

> 1 m) more frequently than would be expected based on habitat availability ($\chi^2 = 3{,}426$, $df = 3$, $p < 0.0001$; Figure 6).

Significantly more foraging ($\chi^2 = 33.23$, $df = 3$, $p < 0.0001$) and playing ($\chi^2 = 10.74$, $df = 3$, $p = 0.0132$) were observed when dolphins were in shallow water (≤ 1 m) compared to their occurrence at other depth categories (Figure 6). Dolphins were found to engage in milling behavior significantly more when in shallow–mid-depth water (> 1 to 2 m) ($\chi^2 = 28.11$, $df = 3$, $p < 0.0001$) and were found traveling significantly more in deep water (> 3 m) ($\chi^2 = 29.86$, $df = 3$, $p < 0.0001$; Figure 6). Social behavior did not occur significantly more at any of the four depth categories ($\chi^2 = 6.33$, $df = 3$, $p < 0.0964$).

Association Patterns

Focal dolphins were found in group sizes that ranged from one to 12 animals, with mean group size ranging from 1.5 to 3.3 animals (Table 4). The percentage of time a dolphin was observed alone ranged from 3.9 to 71.6% (mean: 45.8 ± 26.97%). The percentage of time a dolphin was observed alone was greatest for the juvenile animal (98A) that was documented alone 72% of the time in 2007, decreasing to 36% in 2010 (Table 4). Each focal dolphin was found to associate with a mean of 25.0 ± 14.58 SD identifiable (marked) associates during the tracking period. The number of marked affiliates ranged from eight to 43 per individual, and the individual with the fewest affiliates was 98D. 98D, an adult male, was rarely seen alone (4% observations), however, and exhibited high affiliation (COA = 0.88) with an adult male ("PERW") and a moderate–high affiliation with a 14-y-old adult female ("DIDO"; COA = 0.67). These three individuals were found in a group together during 51% of all observation periods. The other focal animals exhibited mostly low to low–moderate level associations (COA: 0.0 to 0.34).

Discussion

This study provides important insights on the ranging and short-term association patterns, habitat use, and activity budgets of estuarine bottlenose dolphins during the summer season. More specifically, it provides important baseline data on the behavioral ecology of the dolphin population in the Indian River Lagoon, Florida, that are critical to their effective management. The study also provides practical insights into study design, including the utility of the combined use of aircraft and vessel-based tracking, tag attachment and longevity, and the calibration of track lines utilized for photo-identification surveys that cover only part of a population's range.

In the current study, on average, tags remained adhered for a minimum of 46 d, and the minimum transmission duration was 43 d, a finding similar to Balmer et al. (2008, 2011b) that estimated an average minimum transmission period of 35 to 71 d. Maximum tag attachment documented during this study was 97 d. Tag attachment days for this animal (98A) well exceeded the other individuals. As others have found, tag placement appeared to play a critical role in tag migration and endurance (i.e., longest duration for tags attached to the lower third of the dorsal fin) and should be considered when applying radio transmitters with similar attachment gear to estuarine dolphins (Shippee et al., 2008; Balmer et al., 2011a, 2013). A portion of tags dislodged (33%) prematurely as a result

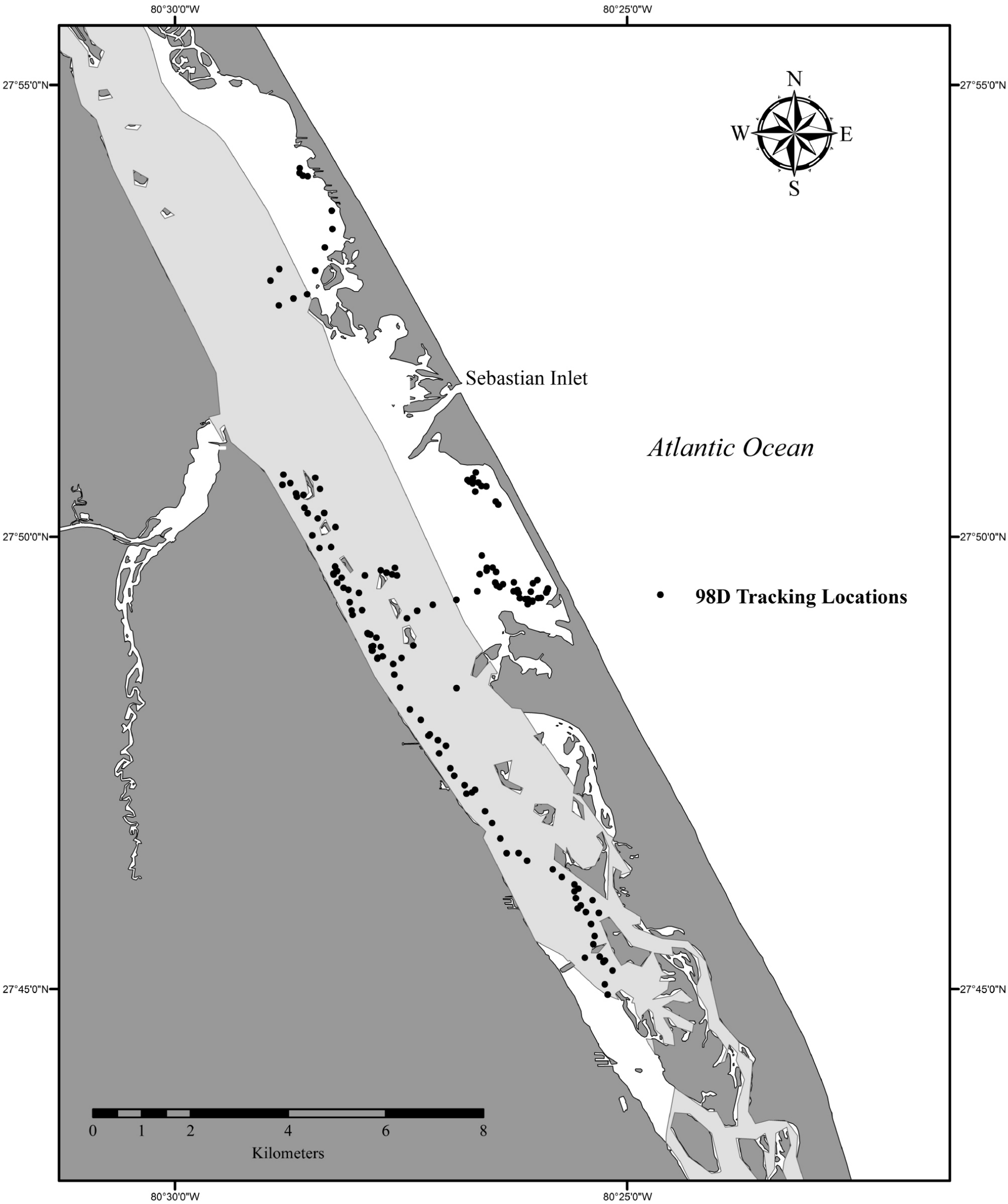

Figure 5. The observation window (2.5 km wide, light grey shading) obtained from the inclusion of 95% of historical photo-identification survey dolphin sightings, mapped concurrently with 5-min scan sample locations (black dots) from dolphin 98D, which utilized portions of the lagoon beyond the observation window during 33.57% of observations.

Table 3. Summary of IRL bottlenose dolphin focal follow data. Activity budgets are reported as percent of time engaged in each behavior per tagged animal. The number of observations (# observ.) indicates the number of 5-min behavioral scan samples. Age in bold type was estimated based on sighting history (other ages estimated from tooth sectioning; GLGs). 98A* indicates the animal's second tagging event.

ID	Sex	Age	Total length (cm)	# d resighted	Focal follow (min)	# observ.	Mill (%)	Forage (%)	Travel (%)	Play (%)	Social (%)
9V8	M	17	283	9	526	110	38	6	56	0	0
98A	M	7	222	37	2,862	697	36	17	39	2	6
9A7	F	**14**	251	8	397	48	21	19	60	0	0
98D	M	23	269	10	721	144	28	32	39	0	1
98E	M	18	286	16	1,586	219	11	6	80	0	2
98A*	M	10	235	17	1,256	172	28	20	45	2	5
		Total			7,348	1,390					
	Mean ± SD			12.8 ± 10.24	1,224.7 ± 920.8	231.7 ± 235.15	27.0 ± 10.0	16.7 ± 9.8	53.2 ± 15.8	0.7 ± 1.0	2.3 ± 2.6

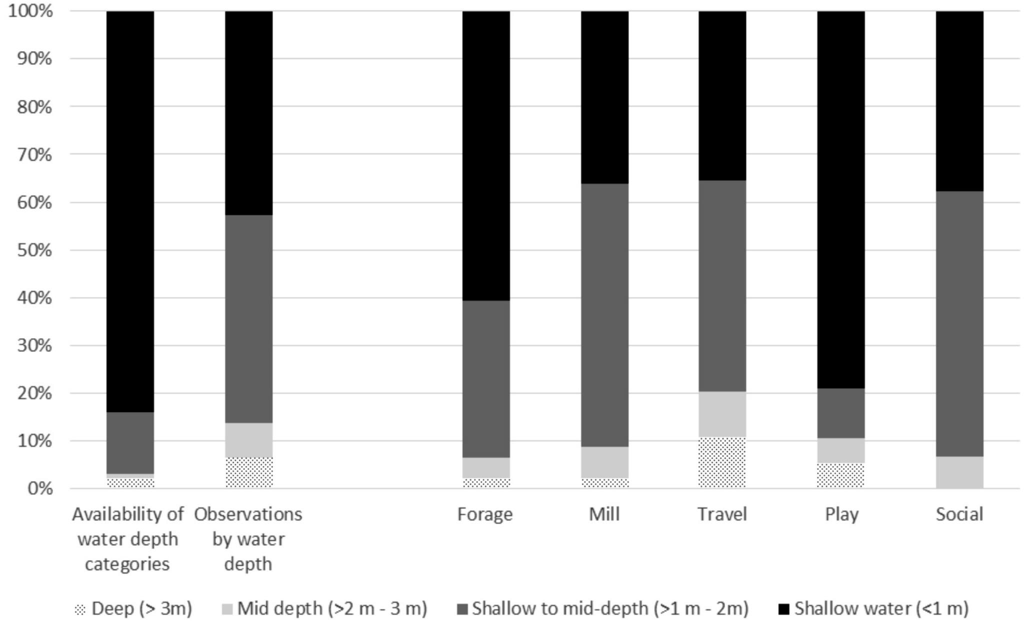

Figure 6. The percent of time tagged IRL dolphins occurred in each water depth category and the percent of time spent engaging in each behavioral state by water depth (m); availability of each water depth category vs observations is illustrated in the two bars along the left side of the chart.

of attachment failure (e.g., delrin pin shearing or nut loss). Tag loss via attachment failure causes less tissue damage, leaving only a small hole. Contrary to this, pin migration migrates through the dorsal fin from the attachment site to the trailing edge of the dorsal fin. Premature dislodging such as this is not ideal and can result in a less than desired amount of data being collected, especially when dislodging occurs substantially before the expected battery life. Ultimately, tag loss by migration or dislodgment resulted in the dorsal fin presenting either a well-healed hole or a

Table 4. Summary of group size and composition for each tagged bottlenose dolphin. Number of observations reflects the number of scan samples for each individual. Association patterns and conspecifics were not examined (NE) in two animals with less than ten observation days. 98A* represents the animal's second tagging event in 2010.

	9V8	98A	98A*	98D	98E	9A7
Number of observations	110	697	252	154	290	56
Group size range	1 to 8	1 to 9	1 to 12	1 to 6	1 to 11	1 to 6
Mean group size	2.6 ± 2.33	1.5 ± 1.08	2.8 ± 2.07	3.1 ± 2.23	3.3 ± 2.14	1.8 ± 2.28
# observations alone	72	499	91	6	87	38
% time alone	65.45	71.59	36.11	3.9	30	67.86
# of marked conspecifics	NE	28	21	8	43	NE

well-healed notch. Improvements in tag design, in comparison to prior designs (Norman et al., 2004), and the small tag size results in both minimal drag and damage to the dorsal fin (Balmer et al., 2013), and no behavioral response to the tag was noted during this study. Continued efforts to optimize dislodging rates, expand transmitter battery life, and facilitate the temporal correspondence of these factors will aid future research efforts.

The use of aerial surveys was found to be an efficient means to determine the geographic location for multiple animals within a short time period. Furthermore, these surveys provided an opportunity to discern between suspected long-distance movements vs battery failure or tag migration/shedding. While the initial intent was to follow the protocol by Mech (1983), the use of hand-held antennas orientated along a vertical access allowed the signal to be received over a sufficient range, provided efficient triangulation, and, in most cases, led to the visual sighting of the tagged animal. These methods may provide an efficient, lower cost, non-invasive (not "modifying" the aircraft) option for radiotelemetry studies conducted in shallow waters. Likewise, opportunistic land-based tracking from vehicles traveling along linear estuaries such as the IRL also provide an alternative means to confirm tag transmission when aerial and vessel efforts are not feasible (e.g., inclement weather).

Tagged dolphins were found to utilize discrete habitats over short temporal periods that are not readily available for observation from the survey strip. Likewise, dolphins utilized discrete areas over short temporal periods, and data indicated that temporal changes in seasonal ranging patterns may occur as dolphins mature. For example, the juvenile dolphin (98A) tagged in 2007 and 2010 exhibited a substantial increase in summer linear range over that 3-y period. The considerable change in this animal's summer ranging pattern corresponded with an increase in the percentage of time it spent traveling as well as the time it spent with other animals. Bottlenose dolphins reach reproductive maturity between 9 and 14 y (Sergeant et al., 1973; Wells & Scott, 1999), and the change in ranging patterns coincided with this animal approaching reproductive maturity (10 y). Results, therefore, provide uniquely detailed insight into the ontogeny of ranging and association patterns. Additional research is needed to further evaluate seasonal changes in habitat use.

The study revealed individual differences in the proportion of time dolphins engaged in various activities. The juvenile dolphin, for example, was found to engage in "play" substantially more than the adult animals. These findings are similar to Greene et al. (2011), who found that juvenile dolphins engage in play more frequently than other age classes. Furthermore, activity budgets for this animal changed over time, with an increase in the amount of time spent traveling and a decrease in milling behavior as the animal approached reproductive maturity. While not a specifically targeted behavior in this study, dolphin 98E was observed 0.46% of the time interacting with crab pots in a manner consistent with crab pot depredation (Noke & Odell, 2002), a behavior which can lead to injury and entanglement (Noke & Odell, 2002; Durden, 2005). Examination of mean activity budgets indicated dolphins spent the majority of time traveling (53%), followed by milling (27%), foraging (17%), socializing (2.3%), and playing (0.7%). These values are remarkably similar to eight estuarine dolphins (seven males and one female) in Sarasota Bay (Florida's Gulf coast), which were also found to spend the majority of time traveling (59%), followed by milling (19%), foraging (20%), and socializing (2%) (Powell & Wells, 2011), and comparable to activity budget analyses for eight suction-cup (Trac Pac) tagged dolphins that spent 48% of time traveling (Shippee, 2014), suggesting that estuarine dolphins may spend a considerable amount of time and energy traveling between foraging sites.

While there appears to be some evidence of the selection-avoidance of habitat types of differing depths, with the shallowest depth category (< 1 m) being utilized in significantly lower proportions relative to its abundance (84%) and the converse for the other depth categories, data should be interpreted with caution as it is not clear how much of the shallowest habitat is truly available to dolphins. Travel was the predominant activity state observed in the deepest water, suggesting that the ICW may provide a more energy-efficient travel route for IRL dolphins. Furthermore, IRL summer water temperatures can reach 36°C (Gilmore, 1977) and may yield thermoregulatory stress in IRL dolphins as hypothesized in other estuarine dolphin populations (Wells et al., 2004); therefore, deeper waters may be slightly cooler and more advantageous in maintaining thermoregulation. Likewise, deeper waters may better facilitate vessel strike avoidance, whereas very shallow waters (< 1 m) provide fewer options in regard to avoidance (i.e., diving below the vessel is not feasible). IRL dolphins spent an average of 6% of their time in the waters > 3 m (i.e., the dredged canal). While these deeper waters may provide space to avoid boats, exposure to vessel traffic is increased in these areas, and dolphins may be exposed to up to 40 vessels/h (W. Durden, unpub. data). Further research is needed to investigate the impacts that vessels have on IRL dolphin behavior and fitness.

Perhaps more striking is just how much time some IRL dolphins spend in very shallow water in summer. Tagged dolphins were found to vary in the use of different habitat types with the percentage of time utilizing the shallowest water (< 1 m), for example, varying from 7.48 to 56.59% between individuals. Furthermore, dolphins utilized different depth categories for different behaviors with foraging occurring primarily in shallow water (≤ 1 m). Foraging in shallow water may provide some advantage in terms of prey availability and/or foraging success rate. The most important prey species for IRL dolphins were found to be associated with vegetated habitats (Barros, 1993) and, therefore, likely inhabit this depth category. Similarly, other studies have observed bottlenose dolphins using shallow bathymetry to assist with prey search, chase, and capture, including strand feeding and beach hunting where dolphins intentionally beach themselves to capture fish chased onto shore (Rigley, 1983; Silber & Fertl, 1995; Sargeant et al., 2005). Therefore, it is possible that IRL dolphins may increase foraging success by hunting in the shallowest water category (< 1 m).

Aggregative behavior may be influenced by many factors, including the physical environment, ecological pressures, prey distribution/availability, habitat preference, predation risk, and life history traits (Wilson, 1995; Connor, 2000; Gibson & Mann, 2008). Bottlenose dolphins are known to form fission–fusion societies (Wells et al., 1987; Connor, 2000), so it is not surprising that low-level association patterns were common for the focal animals examined in this study. A recent study using long-term photo-identification sighting histories found that some IRL dolphins displayed highly interconnected networks of associated individuals, while others formed networks comprised of loosely affiliated individuals with more ephemeral associations (Titcomb et al., 2015). Survey-based studies of association patterns, however, do not reveal the duration and nature of short-term associations but, rather, provide snapshots of associations over a broad temporal scale. Individual focal follows, on the other hand, can provide detailed information on how these short-term associations may be correlated with behavioral states and habitat utilization. The current study found focal animals exhibited low to moderate associations (short-term) with numerous conspecifics (up to 43 marked dolphins during 26 h of observation) but were also observed spending a substantial amount of time alone. This finding added a new dimension to the sociality of IRL dolphins which is not readily apparent from sighting data and may be influenced by the deceased detectability of single animals. The relatively low occurrence of obvious social behavior (although less demonstrative behavior, including social vocalizations, may be involved) suggests that associations are not primarily driven by social purposes. Further quantification of conspecific encounters (e.g., rate, duration, and group size) via continuous observation and elucidation of their function could assist in the development of models that incorporate dolphin social behavior and association patterns in the assessment of gene flow, information transfer, and disease transmission.

Adult male bottlenose dolphins have been known to form male–male alliances that may remain stable for several years (Owen et al., 2002). In Sarasota Bay, Florida, male dolphins have been documented forming alliances at an average age of 11 y, with the youngest alliance forming at 7 y of age (Owen et al., 2002). Among the Sarasota dolphin population, the majority of adult males (57%) are paired in a male alliance (COA ≥ 0.5; Owen et al., 2002). During the current study, three adult males (17 to 23 y of age) were extensively focal followed, and conspecific associations were examined for these individuals. Only one of these adult male focal animals (98D) was paired. IRL dolphins inhabit a closed estuarine system (open only at five inlets) and exhibit little sexual dimorphism, with males reaching a slightly larger asymptotic length (256 cm) than females (246 cm) (Stolen et al., 2002). Comparisons with other studies of male alliances suggest that IRL males (little sexual dimorphism and inhabiting a closed estuary) would form higher-level associations with males (i.e., male–male alliances) (Wells et al., 1987; Wells, 1991; Connor et al., 1992a, 2011; Connor, 2000). While the percentage of paired males (33%) in our study is less than reported in the Sarasota Bay population, the low sample size and short temporal period should be considered when examining these results. Future research is needed to evaluate association patterns in these animals.

The adult male (98D) from this study that was found to form a high-level association was older (23 y) and was predominantly seen with a known adult male dolphin (PERW, 23 y). 98D was found to associate with fewer conspecifics than the other individuals in this study. These findings mirror the findings of other studies in which males that are in established alliances are observed in smaller group sizes, while males in a more fluid social network exhibit larger group sizes (Wiszniewski et al., 2012). Interestingly, 98D also demonstrated a moderately high-level association (0.68) with a known adult female dolphin (DIDO, ≥ 14 y), and the three animals (98D, PERW, and DIDO) were frequently seen together. Male trio-alliances and super-alliances containing multiple males have been described in other communities (Connor et al., 1992b, 2011); however, male alliances that form high-level associations with a single female have typically been described in concert with a consortship (Connor et al., 1992b). A consortship is formed when male dolphins in an alliance aggressively sequester or control the movement of a female (herding), an event that can last from minutes to weeks (Connor et al., 1996). Male–female associations have been described as being dependent on the female's reproductive state and are mainly linked to the goal of reproduction (Connor, 2000). While this is a plausible explanation for the trio, there was only a single event of social behavior that was observed for the trio, and the event involved an unmarked fourth individual. The primary behavior observed for the trio was foraging (43%) followed by milling (32%), traveling (24%), and socializing (1%), suggesting that the group may associate as part of a foraging rather than reproductive strategy. In the majority of estuarine or bay-dwelling dolphin communities that have been extensively studied, female dolphins exhibit large variability in association patterns, with some females forming alliances with related and unrelated females, and others having few or no high-level associations (Duffield & Wells, 1991; Smolker et al., 1992; Mann et al., 2000). Conversely, resident bottlenose dolphins inhabiting the deep waters of Doubtful Sound, New Zealand, have been documented forming long-lasting male–female alliances (Lusseau et al., 2003). Further research is needed to determine if these mixed-sex alliances form to further enhance prey acquisition in the IRL as has been speculated in other dolphin communities (Lusseau et al., 2003).

In recent years, the IRL has been subjected to multiple UMEs, including birds and marine mammal species (e.g., dolphins and manatees) and has undergone significant ecological disturbances yielding a catastrophic loss of nearly 50% of seagrass habitat in 2011 (St. Johns Water Management District, 2013). This study provides baseline data on the ranging patterns, activity budgets, associative behavior, and habitat utilization of an important long-lived, top-level predator in the IRL which is critical to assessing species impacts and ecological changes following large-scale environmental shifts. Dolphins were found to have comparably small linear ranges compared to tagged dolphins from similar embayed/estuarine populations (e.g., mean linear range: 40 to 59 km, St. Joseph Bay, Florida; Balmer et al., 2008) but did not differ considerably from longer-term photo-identification data that estimated a mean linear range of 22 to 54 km for IRL dolphins (Mazzoil et al., 2008b). This suggests that IRL dolphins exhibit substantial site fidelity in ranging patterns and habitat utilization throughout their lives. Given recent environmental changes in the IRL, fixed habitat utilization is concerning as animals inhabiting areas undergoing significant ecological pressures (e.g., fish kills, seagrass loss, and phytoplankton blooms) will need to adapt and or modify ranging patterns or inevitably suffer from decreased fitness. For example, two dolphins from the current study (942 and 948) exhibited ranging patterns that extended into the St. Lucie River, a low salinity area that is subject to poor water quality and recently experienced a large, toxic cyanobacterial bloom (Kramer et al., 2018), illustrating the wide array of ecological pressures that IRL dolphins may encounter. Furthermore, the finding that shallow water habitats are extensively used by IRL dolphins, particularly for foraging, indicates that these habitats are likely critical to dolphin health and fitness, and suggests that ecosystem changes (i.e., seagrass loss, fish kills, etc.) in these habitats may significantly impact IRL dolphins.

Despite the narrow width of the study area where dolphins were tracked (maximum width: 3.7 km), individual dolphins still spent a small to moderate amount of time beyond the 2.5-km-wide photo-identification survey observation window. Even considering that portions of the lagoon are extremely shallow and, therefore, may not be available to dolphins, the proportion of time dolphins spend beyond this window would likely be significantly increased in wider portions of the lagoon (up to 9.3 km) where the majority of the habitat is beyond the observation window. Future survey efforts should incorporate measures to correct for animals that may not be available for observation and should consider IRL dolphin ranging patterns and habitat utilization findings from this study when designing ecological, behavioral, health, and population assessment studies for IRL dolphins.

While photo-identification surveys provide needed data on abundance, distribution, survival, and association patterns in coastal and estuarine dolphin populations (Quintana-Rizzo & Wells, 2001; Owen et al., 2002; Read et al., 2003; Mazzoil et al., 2008b; McDonald et al., 2017; Mullin et al., 2017; Titcomb et al., 2017), these data typically provide snapshots of associations over a broad temporal scale. Focal follows in the current study revealed how dynamic the fission–fusion aspect of dolphin societies can be over short temporal periods, with tagged dolphins having brief associations with a large number of marked (and many other unmarked) individuals. These short-term close associations with numerous individuals may facilitate not only information transfer but also disease transmission. These types of data, in concert with social network analysis of longer-term association patterns from photo-identification surveys (Titcomb et al., 2015, 2017), could be used to model risk and the spread of disease, especially epidemic diseases.

While others have reported on the use of radio-tracking for post-release monitoring of two IRL dolphins (Mazzoil et al., 2008a), this study represents the most extensive radio-tracking efforts for IRL dolphins. Currently, the use of radio/satellite telemetry and photo-identification are the only efficient logistical methods available to monitor short-term movement patterns of individual dolphins within the IRL. Photo-identification programs are enormously labor intensive and require many years of data collection to accumulate large enough sample sizes to evaluate ranging patterns. Radio-telemetry studies can provide a wealth of data over a short temporal period; however, telemetry studies are also labor intensive and in cases of tag failure, may result in relatively small amounts of data. Therefore, efforts should be made to enhance tag reliability and longevity to fulfill the objectives of future studies. Likewise, additional studies that utilize satellite telemetry may yield larger quantities of data across the entire 24-h daily cycle that would facilitate comparisons of nocturnal and diurnal behavior. While some satellite tags may facilitate remote data collection and focal follow observations, receiver range is typically reduced from that of VHF telemetry capacity. The utility of radio-telemetry to facilitate close proximity observation and tracking, and to enable valuable data collection on individual habitat use, behavior, and interactions with conspecifics is unparalleled.

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Literature Cited

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3-4), 227-267. https://doi.org/10.1163/156853974X00534

Anderson, D. J. (1982). The home range: A new non-parametric estimation technique. *Ecology*, *63*(1), 103-112. https://doi.org/10.2307/1937036

Arthur, S. M., & Schwartz, C. C. (1999). Effects of sample size on accuracy and precision of brown bear home range models. *Ursus*, *11*, 139-148.

Balmer, B. C., Schwacke, L. H., Wells, R. S., George, R. C., Houget, J., Kucklick, J. R., . . . Pabst, D. A. (2011a). Relationship between persistent organic pollutants (POPs) and ranging patterns in common bottlenose dolphins (*Tursiops truncatus*) from coastal Georgia USA. *Science of the Total Environment*, *409*(11), 2094-2101. https://doi.org/10.1016/j.scitotenv.2011.01.052

Balmer, B. C., Wells, R. S., Howle, L. E., Barleycorn, A. A., McLellan, W. A., Pabst, D. A., . . . Zolman, E. S. (2013). Advances in cetacean telemetry: A review of single-pin transmitter attachment techniques on small cetaceans and development of a new satellite-linked transmitter design. *Marine Mammal Science*, *30*(2), 656-673. https://doi.org/10.1111/mms.12072

Balmer, B. C., Wells, R. S., Nowacek, S. M., Nowacek, D. P., Schwacke, L. H., McLellan, W. A., . . . Pabst, D. A. (2008). Seasonal abundance and distribution patterns of common bottlenose dolphins (*Tursiops truncatus*) near St. Joseph Bay, Florida, USA. *Journal of Cetacean Research and Management*, *10*(2), 157-167.

Balmer, B. C., Wells, R. S., Schwacke, L. H., Rowles, T. K., Hunter, C., Zolman, E. S., . . . Pabst, D. A. (2011b). Evaluation of a single-pin, satellite-linked transmitter deployed on bottlenose dolphins (*Tursiops truncatus*) along the coast of Georgia, USA. *Aquatic Mammals*, *37*(2), 187-192. https://doi.org/10.1578/AM.37.2.2011.187

Barco, S., Swingle, W. M., McLellan, W. A., Harris, R. N., & Pabst, D. A. (1999). Local abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia Beach, Virginia. *Marine Mammal Science*, *15*(2), 394-408. https://doi.org/10.1111/j.1748-7692.1999.tb00809.x

Barros, N. B. (1993). *Feeding ecology and foraging strategies of bottlenose dolphins on the central east coast of Florida* (Unpublished Doctoral dissertation). University of Miami, Coral Gables.

Bearzi, G., Politi, E., & Notarbartolo di Sciara, G. (1999). Diurnal behavior of free-ranging bottlenose dolphins in the Kvarnerić (Northern Adriatic Sea). *Marine Mammal Science*, *15*(4), 1065-1097. https://doi.org/10.1111/j.1748-7692.1999.tb00878.x

Bechdel, S. E., Mazzoil, M. S., Murdoch, M. E., Howells, E. M., Reif, J. S., McCulloch, S. D., . . . Bossart, G. D. (2009). Prevalence and impact of motorized vessels on bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon, Florida. *Aquatic Mammals*, *35*(3), 367-377. https://doi.org/10.1578/AM.35.3.2009.367

Bossart, G. D., Meisner, R., Varela, R., Mazzoil, M., McCulloch, S., Kilpatrick, D., . . . Defran, R. H. (2003). Pathologic findings in stranded Atlantic bottlenose dolphin (*Tursiops truncatus*) from the Indian River Lagoon. *Florida Scientist*, *66*, 226-238.

Bristow, T., & Rees, E. I. S. (2001). Site fidelity and behaviour of bottlenose dolphins (*Tursiops truncatus*) in Cardigan Bay, Wales. *Aquatic Mammals*, *27*(1), 1-10.

Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, *24*(3), 346-352. https://doi.org/10.2307/1374834

Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, *35*(5), 1454-1469. https://doi.org/10.1016/S0003-3472(87)80018-0

Caldwell, D. K., Caldwell, M. C., Woodard, J. C., Ajello, L., Kaplan, W., & McClure, H. M. (1975). Lobomycosis as a disease of the Atlantic bottle-nosed dolphin (*Tursiops truncatus* Montagu, 1821). *American Journal of Tropical Medicine and Hygiene*, *24*(1), 105-114. https://doi.org/10.4269/ajtmh.1975.24.105

Cartwright, R., & Sullivan, M. (2009). Behavioral ontogeny in humpback whale (*Megaptera novaeangliae*) calves during their residence in Hawaiian waters. *Marine Mammal Science*, *25*(3), 659-680. https://doi.org/10.1111/j.1748-7692.00286.x

Chilvers, B. L., Corkeron, P. J., & Puotinen, M. L. (2003). Influence of trawling on the behaviour and spatial distribution of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Moreton Bay, Australia. *Canadian Journal of Zoology*, *81*(12), 1947-1955. https://doi.org/10.1139/z03-195

Clementini, E., Di Felice, P., & van Oosterom, P. (1993, June). A small set of formal topological relationships suitable for end-user interaction. *Proceedings of the Third International Symposium on Advances in Spatial Databases*, Singapore. https://doi.org/10.1007/3-540-56869-7_16

Coastal Planning and Engineering. (1997). *Indian River Lagoon bathymetric survey. A final report to St. Johns River Water Management District* (Contract #95W142). Palatka, FL: Coastal Planning and Engineering.

Connor, R. C. (2000). Group living in whales and dolphins. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 199-218). Chicago, IL: University of Chicago Press.

Connor, R. C., Smolker, R. A., & Richards, F. A. (1992a). Dolphin alliances and coalitions. In A. H. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 415-443). Oxford, UK: Oxford University Press.

Connor, R. C., Smolker, R. A., & Richards, A. F. (1992b). 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., Richards, A. F., Smolker, R. A., & Mann, J. (1996). Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behaviour*, *133*(1/2), 37-69. https://doi.org/10.1163/156853996X00026

Connor, R. C., Watson-Capps, J. J., Sherwin, W. B., & Krützen, M. (2011). A new level of complexity in the male alliance networks of Indian Ocean bottlenose dolphins (*Tursiops* sp.). *Biology Letters*, *7*(4), 623-626. https://doi.org/10.1098/rsbl.2010.0852

Connor, R. C., Cioffi, W. R., Randić, 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*(1), Article 46354. https://doi.org/10.1038/srep46354

Constantine, R., Brunton, D. H., & Dennis, T. (2004). Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Biological Conservation*, *117*(3), 299-307. https://doi.org/10.1016/j.biocon.2003.12.009

Cunningham-Smith, P., Colbert, D. E., Wells, R. S., & Speakman, T. (2006). Evaluation of human interactions with a provisioned wild bottlenose dolphin (*Tursiops truncatus*) near Sarasota Bay, Florida, and efforts to curtail the interactions. *Aquatic Mammals*, *32*(3), 346-356. https://doi.org/10.1578/AM.32.3.2006.346

Duffield, D. A., & Wells, R. S. (1991). The combined application of chromosome protein and molecular data for the investigation of social unit structure and dynamics in *Tursiops truncatus*. *Reports of the International Whaling Commission*, Special Issue 13, 155-170.

Durden, W. N. (2005). The harmful effects of inadvertently conditioning a wild bottlenose dolphin (*Tursiops truncatus*) to interact with fishing vessels in the Indian River

Lagoon, Florida, USA. *Aquatic Mammals*, *31*(4), 413-419. https://doi.org/10.1578/AM.31.4.2005.413

Durden, W. N., Stolen, M. K., Adams, D. H., & Stolen, E. D. (2007). Mercury and selenium concentrations in stranded bottlenose dolphins from the Indian River Lagoon system, Florida. *Bulletin of Marine Science*, *81*(1), 37-54.

Durden, W. N., St. Leger, J., Stolen, M., Mazza, T., & Londono, C. (2009). Lacaziosis in bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon, Florida, USA. *Journal of Wildlife Diseases*, *45*(3), 849-856. https://doi.org/10.7589/0090-3558-45.3.849

Fair, P. A., & Becker, P. R. (2000). Review of stress in marine mammals. *Journal of Aquatic Ecosystem Stress and Recovery*, *7*(4), 335-354. https://doi.org/10.1023/A:1009968113079

Fair, P. A., Adams, J., Mitchum, G., Hulsey, T. C., Reif, J. S., Houde, M., . . . Bossart, G. D. (2010). Contaminant blubber burdens in Atlantic bottlenose dolphins (*Tursiops truncatus*) from two southeastern U.S. estuarine areas: Concentrations and patterns of PCBs, pesticides, PBDEs, PFCs, and PAHs. *Science of the Total Environment*, *408*(7), 1577-1597. https://doi.org/10.1016/j.scitotenv.2009.12.021

Fair, P. A., Adams, J. D., Zolman, E., McCulloch, S. D., Goldstein, J. D., Murdoch, M. E., . . . Bossart, G. D. (2006). *Protocols for conducting dolphin capture-release health assessment studies* (NOAA Technical Memorandum NOS NCCOS 49). Charleston, SC: National Oceanic and Atmospheric Administration.

Fury, C. A., Ruckstuhl, K. E., & Harrison, P. E. (2013). Spatial and social sexual segregation patterns in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *PLOS ONE*, *8*(1), e52987. https://doi.org/10.1371/journal.pone.0052987

Gazda, S., Iyer, S., Killingback, T., Connor, R., & Brault, S. (2015). The importance of delineating networks by activity type in bottlenose dolphins (*Tursiops truncatus*) in Cedar Key, Florida. *Royal Society Open Science*, *2*(3), 140263. https://doi.org/10.1098/rsos.140263

Gibson, Q. A., & Mann, J. (2008). Early social development in wild bottlenose dolphins: Sex differences, individual variation and maternal influence. *Animal Behaviour*, *76*(2), 375-387. https://doi.org/10.1016/j.anbehav.2008.01.021

Gilmore, R. G., Jr. (1977). Fishes of the Indian River Lagoon and adjacent waters, Florida. *Bulletin of the Florida State Museum, Biological Science*, *22*(3), 101-147.

Ginsberg, J. R., & Young, T. P. (1992). Measuring association between individuals or groups in behavioural studies. *Animal Behaviour*, *44*(Part 2), 377-379. https://doi.org/10.1016/0003-3472(92)90042-8

Greene, W. E., Melillo-Sweeting, K., & Dudzinski, K. M. (2011). Comparing object play in captive and wild dolphins. *International Journal of Comparative Psychology*, *24*, 292-306.

Hanson, M. T., & Defran, R. H. (1993). The behaviour and feeding ecology of the Pacific coast bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals*, *19*(3), 127-142.

Hedrick, M. S., & Duffield, D. A. (1991). Haematological and rhetological characteristics of blood in seven marine mammal species: Physiological implications for diving behaviour. *Journal of Zoology*, *225*(2), 273-282. https://doi.org/10.1111/j.1469-7998.1991.tb03816.x

Hohn, A. A., Scott, M. D., Wells, R. S., Sweeney, J. C., & Irvine, A. B. (1989). Growth layers in teeth from known-age, free-ranging bottlenose dolphins. *Marine Mammal Science*, *5*(4), 315-342. https://doi.org/10.1111/j/1748-7692.1989.tb00346.x

Irvine, A. B., Scott, M. D., Wells, R. S., & Kaufmann, J. H. (1981). Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin*, *79*(4), 671-688.

Jefferson, T. A. (2000). Population biology of the Indo-Pacific humpbacked dolphin in Hong Kong waters. *Wildlife Monographs*, *144*, 1-65.

Kenney, R. D. (1990). Bottlenose dolphins off the northeastern United States. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 369-386). San Diego, CA: Academic Press. https://doi.org/10.1016/B978-0-12-440280-5.50025-1

Kramer, B. J., Davis, T. W., Meyer, K. A., Rosen, B. H., Goleski, J. A., Dick, G. J., . . . Gobler, C. J. (2018). Nitrogen limitation, toxin synthesis potential, and toxicity of cyanobacterial populations in Lake Okeechobee and the St. Lucie River Estuary, Florida, during the 2016 state of emergency event. *PLOS ONE*, *13*(5), e0196278. https://doi.org/10.1371/journal.pone.0196278

Leatherwood, S. (1979). Aerial survey of the bottlenosed dolphin, *Tursiops truncatus*, and the West Indian manatee, *Trichechus manatus*, in the Indian and Banana Rivers, Florida. *Fishery Bulletin*, *77*(1), 47-59.

Lusseau, D. (2003). The effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. *Conservation Biology*, *17*(6), 1785-1793. https://doi.org/10.1111/j.1523-1739.2003.00054.x

Lusseau, D. (2004). The hidden cost of tourism: Detecting long-term effects of tourism using behavioral information. *Ecology and Society*, *9*(1). Retrieved from www.ecologyandsociety.org/vol9/iss1/art2

Lusseau, D. (2006). The short-term behavioral reactions of bottlenose dolphins to interactions with boats in Doubtful Sound, New Zealand. *Marine Mammal Science*, *22*(4), 802-818. https://doi.org/10.1111/j.1748-7692.2006.00052.x

Lusseau, D., Schneider, K., Boisseau, O. J., Haase, P., Slooten, E., & Dawson, S. M. (2003). The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. *Behavioral Ecology and Sociobiology*, *54*(4), 396-405. https://doi.org/10.1007/s00265-003-0651-y

Mann, J. (1999). Behavioral sampling methods for cetaceans: A review and critique. *Marine Mammal Science*, *15*(1), 102-122. https://doi.org/10.1111/j.1748-7692.1999.tb00784.x

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 effect. *Behavioral Ecology*, *11*(2), 210-219. https://doi.org/10.1093/beheco/11.2.210

Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. J., & Singh, L. O. (2012). Social networks reveal cultural behavior in tool-using dolphins. *Nature Communications*, *3*(1181), 1-7. https://doi.org/10.1038/ncomms1983

Mann, J., Sargeant, B. L., Watson-Capps, J. J., Gibson, Q. A., Heithaus, M. R., Connor, R. C., & Patterson, E. (2008). Why do dolphins carry sponges? *PLOS ONE*, *3*(12), e3868. https://doi.org/10.1371/journal.pone.0003868

Mares, M. A., Willig, M. R., & Bitar, N. A. (1980). Home range size in eastern chipmunks, *Tamais striatus*, as a function of number of captures: Statistical biases of inadequate sampling. *Journal of Mammalogy*, *61*(4), 661-669. https://doi.org/10.2307/1380311

Marley, S. A., Salgado Kent, C. P., Erbe, C., & Parnum, I. (2017). Effects of vessel traffic and underwater noise on the movement, behavior and vocalisations of bottlenose dolphins in an urbanised estuary. *Scientific Reports*, *7*(1), 13437. https://doi.org/10.1038/s41598-017-13252-z

Mattson, M. C., Thomas, J. A., & St. Aubin, D. (2005). Effects of boat activity on the behavior of bottlenose dolphins (*Tursiops truncatus*) in waters surrounding Hilton Head Island, South Carolina. *Aquatic Mammals*, *31*(1), 133-140. https://doi.org/10.1578/AM.31.1.2005.133

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.

Mazzoil, M., McCulloch, S. D., Defran, R. H., & Murdoch, 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. S., McCulloch, S. D., Youngbluth, M. J., Kilpatrick, D. S., Murdoch, M. E., Mase-Guthrie, B., . . . Bossart, G. D. (2008a). Radio-tracking and survivorship of two rehabilitated bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon, Florida. *Aquatic Mammals*, *34*(1), 54-64. https://doi.org/10.1578/AM.34.1.2008.54

Mazzoil, M., Reif, J. S., Murdoch, M. E., Bechdel, S. E., Howells, E., Youngbluth, M., . . . Bossart, G. D. (2008b). 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

McDonald, T. L., Hornsby, F. E., Speakman, T. R., Zolman, E. S., Mullin, K. D., Sinclair, C., . . . Schwacke, L. H. (2017). Survival, density, and abundance of common bottlenose dolphins in Barataria Bay (USA) following the Deepwater Horizon oil spill. *Endangered Species Research*, *33*(1), 193-209. https://doi.org/10.3354/esr00806

McFarland, M. (1986). Ecological determinants of fission–fusion sociality in *Ateles* and *Pan*. In J. G. Else & P. C. Lee (Eds.), *Primate ecology and conservation* (pp. 181-190). Cambridge, UK: Cambridge University Press.

McHugh, K. A., Barleycorn, A. A., & Wells, R. S. (2011). Severe *Karenia brevis* red tides influences juvenile bottlenose dolphin (*Tursiops truncatus*) behavior in Sarasota Bay, Florida. *Marine Mammal Science*, *27*(3), 622-643. https://doi.org/10.1111/j.1748-7692.2010.00428.x

Mech, L. D. (1983). *A handbook of animal radio-tracking*. Minneapolis: University of Minnesota Press.

Miketa, M. L., Krzyszczyk, E., & Mann, J. (2017). Behavioral responses to fishing line entanglement of a juvenile bottlenose dolphin in Shark Bay, Australia. *Matters*. https://doi.org/10.19185/matters.201711000011

Mulligan, T. J., & Snelson, F. F., Jr. (1983). Summer season population of epibenthic marine fishes in the Indian River Lagoon system, Florida. *Florida Scientist*, *46*(3/4), 250-276.

Mullin, K. D., McDonald, T., Wells, R. S., Balmer, B. C., Speakman, T., Sinclair, C., . . . Schwacke, L. H. (2017). Density, abundance, survival, and ranging patterns of common bottlenose dolphins (*Tursiops truncatus*) in Mississippi Sound following the Deepwater Horizon oil spill. *PLOS ONE*, *12*(10), e0186265. https://doi.org/10.1371/journal.pone.0186265

Murdoch, M. E., Reif, J. S., Mazzoil, M., McCulloch, S. D., Fair, P. A., & Bossart, G. D. (2008). Lobomycosis in bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon, Florida: Estimation of prevalence, temporal trends and spatial distribution. *EcoHealth*, *5*(3), 289-297. https://doi.org/10.1007/s10393-008-0187-8

Myrick, A. C., Hohn, A. A., Sloan, P. A., Kimura, M., & Stanley, D. D. (1983). *Estimating age of spotted and spinner dolphins (*Stenella attenuata *and* Stenella longirostris*) from teeth* (NOAA Technical Memo NOAA-TM-NMFS-SWFC-30). La Jolla, CA: National Oceanic and Atmospheric Administration.

National Oceanic and Atmospheric Administration (NOAA) Fisheries. (2013). *Marine mammal stock assessment reports (SARs) by species/stock: Bottlenose dolphin (*Tursiops truncatus*) Indian River Lagoon estuarine system stock*. Retrieved from www.nmfs.noaa.gov/pr/sars/2013/ao2013_bottlenose-irl-estuarine.pdf

Neumann, D. R. (2001). The activity budget of free-ranging common dolphins (*Delphinus delphis*) in the northwestern Bay of Plenty, New Zealand. *Aquatic Mammals*, *27*(2), 121-136.

Noke, W. D., & Odell, D. K. (2002). Interactions between the Indian River Lagoon blue crab fishery and the bottlenose dolphin *Tursiops truncatus*. *Marine Mammal Science*, *18*(4), 819-832. https://doi.org/10.1111/j.1748-7692.2002.tb010750x

Norman, S. A., Hobbs, R. C., Foster, J., Schroeder, J. P., & Townsend, F. I. (2004). A review of animal and human health concerns during capture-release, handling and tagging of odontocetes. *Journal of Cetacean Research and Management*, *6*(1), 53-62.

Norris, K. S. (1961). Standardized methods for measuring and recording data on the smaller cetaceans. *Journal of Mammalogy*, *42*(4), 471-476. https://doi.org/10.2307/1377364

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Potgieter, B., Harwood, L., Litovka, D., . . . Mahoney, B. (2018). Migratory culture, population structure and stock identify in North Pacific beluga whales (*Delphinapterus leucas*). *PLOS ONE*, *13*, e0194201. https://doi.org/10.1371/journal.pone.0194201

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). San Diego, CA: 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

Pirotta, E., Merchant, N. D., Thompson, P. M., Barton, T. R., & Lusseau, D. (2015). Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity. *Biological Conservation*, *181*, 82-89. https://doi.org/10.1016/j.biocon.2014.11.003

Powell, J. R., & Wells, R. S. (2011). Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine Mammal Science*, *27*(1), 111-129. https://doi.org/10.1111/j.1748-7692.2010.00401.x

QGIS Development Team. (2016). *QGIS Geographic Information System* (Open Source Geospatial Foundation Project). Retrieved from http://qgis.org

Quinn, T., & Brodeur, R. D. (1991). Intra-specific variation in the movement patterns of marine animals. *American Zoologist*, *31*(1), 231-241. https://doi.org/10.1093/icb/31.1.231

Quintana-Rizzo, E., & Wells, R. S. (2001). Resighting and association patterns of bottlenose dolphins (*Tursiops truncatus*) in the Cedar Keys, Florida: Insights into social organization. *Canadian Journal of Zoology*, *79*(3), 447-456. https://doi.org/10.1139/cjz-79-3-447

Read, A. J., Urian, K. W., & Wilson, B. (2003). Abundance of bottlenose dolphins in the bays, sounds, and estuaries of North Carolina. *Marine Mammal Science*, *19*(1), 59-73. https://doi.org/10.1111/j.1748-7692.2003.tb01092.x

Reif, J. S., Mazzoil, M. S., McCulloch, S. D., Varela, R. A., Goldstein, J. D., Fair, P. A., & Bossart, G. D. (2006). Lobomycosis in Atlantic bottlenose dolphins from the Indian River Lagoon, Florida. *Journal of the American Veterinary Medical Association*, *228*(1), 104-108. https://doi.org/10.2460/javma.228.1.104

Ridgway, S. H., Green, R. F., & Sweeney, J. C. (1975). Mandibular anesthesia and tooth extraction in the bottlenosed dolphin. *Journal of Wildlife Diseases*, *11*(3), 415-418. https://doi.org/10.7589/0090-3558-11.3.415

Rigley, L. (1983). Dolphins feeding in a South Carolina salt marsh. *Whalewatcher*, *17*(2), 3-5.

Sarasota Dolphin Research Program (SDRP). (2006). *Manual for field research and laboratory activities*. Retrieved from http://sarasotadolphin.org/wp-content/uploads/2012/01/SDRP_Manual-for-Field-Research-and-Laboratory-Activities.pdf

Sargeant, B. L., Mann, J., Berggren, P., & Krützen, M. (2005). Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). *Canadian Journal of Zoology*, *83*(11), 1400-1410. https://doi.org/10.1139/z05-136

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J., & Gitzen, R. A. (1999). Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management*, *63*(2), 739-747. https://doi.org/10.2307/3802664

Sergeant, D. E., Caldwell, D. K., & Caldwell, M. C. (1973). Age, growth, and maturity of bottlenosed dolphin (*Tursiops truncatus*) from northeast Florida. *Journal of the Fisheries Research Board of Canada*, *30*(7), 1009-1011. https://doi.org/10.1139/f73-165

Shane, S. H. (1990). Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 245-265). San Diego, CA: Academic Press. https://doi.org/10.1016/B978-0-12-440280-5.50016-0

Shippee, S. F. (2014). *Movements, fishery interactions, and unusual mortalities of bottlenose dolphins* (Doctoral dissertation). University of Central Florida, Orlando. Retrieved from http://stars.library.ucf.edu/etd/4763

Shippee, S., Zolman, E., Durden, W. N., Townsend, F., & Bossart, G. D. (2008, March). High-flyers and low-riders: A performance analysis of radio tag attachments. *Proceedings of the Southeast and Mid-Atlantic Marine Mammal Symposium*, Charleston, SC.

Silber, G. K., & Fertl, D. (1995). Intentional beaching by bottlenose dolphins (*Tursiops truncatus*) in the Colorado River Delta, Mexico. *Aquatic Mammals*, *21*(3), 183-186.

Smolker, R. A., Richards, A. F., Connor, R. C., & Pepper, J. W. (1992). Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, *123*(1), 38-69. https://doi.org/10.1163/156853992X00101

South Florida Water Management District. (1998). *Indian River Lagoon-St. Lucie Estuary bathymetry*. Retrieved from http://apps.sfwmd.gov/gisapps/sfwmdxwebdc/dataview.asp?query=unq_id=1801

St. Johns Water Management District. (2012). *Indian River Lagoon 2011 Superbloom Plan of Investigation*. Retrieved from https://www.sjrwmd.com/static/waterways/irl-technical//2011superbloom_investigationplan_June_2012.pdf

Stockin, K. A., Lusseau, D., Binedell, V., Wiseman, N., & Orams, M. B. (2008). Tourism affects the behavioural budget of the common dolphin *Delphinus* sp. in the

Hauraki Gulf, New Zealand. *Marine Ecology Progress Series*, *355*, 287-295. https://doi.org/10.3354/meps07386

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, from 1977-2005. *Florida Scientist*, *70*(1), 45-54.

Stolen, M. K., Odell, D. K., & Barros, N. (2002). Growth of bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon system, Florida, U.S.A. *Marine Mammal Science*, *18*(2), 348-357. https://doi.org/10.1111/j1748-7692.2002.tb01042.x

Stolen, M. K., Durden, W. N., Mazza, T., Barros, N., & St. Leger, J. (2013). Effects of fishing gear on bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon system, Florida. *Marine Mammal Science*, *29*(2), 356-364. https://doi.org/10.1111/j.1748-7692.2012.00575.x

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

Titcomb, E. M., Reif, J. S., Fair, P. A., Stavros, H. C. W., Mazzoil, M., Bossart, G. D., & Schaefer, A. M. (2017). Blood mercury concentrations in common bottlenose dolphins from the Indian River Lagoon, Florida: Patterns of social distribution. *Marine Mammal Science*, *33*(3), 771-784. https://doi.org/10.1111/mms.12390

Tremain, D. M., & Adams, D. H. (1995). Seasonal variations in species diversity, abundance, and composition of fish communities in the northern Indian River Lagoon, Florida. *Bulletin of Marine Science*, *57*(1), 171-192.

U.S. Environmental Protection Agency (EPA), National Estuary Program. (1996). *Indian River Lagoon Comprehensive Conservation and Management Plan* (IRLCCMP). Retrieved from www.irlcouncil.com/uploads/7/9/2/7/79276172/irl_ccmp.pdf

Urian, K. W., & Wells, R. S. (1996). *Bottlenose Dolphin Photo-Identification Workshop* (NOAA Technical Memo NMFS-SEFSC-393). Charleston, SC: 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 Memo NMFS-SEFSC-425). Beaufort, NC: National Oceanic and Atmospheric Administration.

Wells, R. S. (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 199-225). Berkeley: University of California Press.

Wells, R. S. (2003). Dolphin social complexity: Lessons from long-term study and life history. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 32-56). Cambridge, MA: Harvard University Press. https://doi.org/10.4159/harvard.9780674419131.c4

Wells, R. S., & Scott, M. D. (1999). Bottlenose dolphin (*Tursiops truncatus*). In S. H. Ridgway & R. Harrison (Eds.), *Handbook of marine mammals. Volume 6: The second book of dolphins and the porpoises* (pp. 137-182). San Diego, CA: Academic Press.

Wells, R. S., Hofmann, S., & Moors, T. L. (1998). Entanglement and mortality of bottlenose dolphins, *Tursiops truncatus*, in recreational fishing gear in Florida. *Fishery Bulletin*, *96*, 647-650.

Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In H. H. Genoways (Ed.), *Current mammalogy, Vol. I* (pp. 407-416). New York: Plenum Press. https://doi.org/10.1007/978-1-4757-9909-5_7

Wells, R. S., Hansen, L. J., Baldridge, A., Dohl, T. P., Kelly, D. L., & Defran, R. H. (1990). Northward extension of the range of bottlenose dolphins along the California coast. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 421-434). New York: Academic Press. https://doi.org/10.1016/B978-0-12-440280-5.50028-7

Wells, R. S., Allen, J. B., Hofmann, S., Bassos-Hull, K., Fauquier, D. A., Barros, N. B., . . . Scott, M. D. (2008). Consequences of injuries on survival and reproduction of common bottlenose dolphins (*Tursiops truncatus*) along the west coast of Florida. *Marine Mammal Science*, *24*(4), 774-794. https://doi.org/10.1111/j.1748-7692.2008.00212.x

Wells, R. S., Rhinehart, H. L., Hansen, L. J., Sweeney, J. C., Townsend, F. I., Stone, R., . . . Rowles, T. K. (2004). Bottlenose dolphins as marine ecosystem sentinels: Developing a health monitoring system. *EcoHealth*, *1*(3), 246-254. https://doi.org/10.1007/s10393-004-0094-6

Whitehead, H. L., Rendell, L., Osborne, R. W., & Würsig, B. (2004). Culture and conservation of non-humans with reference to whales and dolphins: Review and new directions. *Biological Conservation*, *120*(3), 427-437. https://doi.org/10.1016/j.biocon.2004.03.017

Wilson, B. (1995). *The ecology of bottlenose dolphins in the Moray Firth, Scotland: A population at the northern extreme of the species' range* (Doctoral dissertation). University of Aberdeen, Aberdeen, Scotland. Retrieved from http://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.261914

Wiszniewski, J., Brown, C., & Möller, L. M. (2012). Complex patterns of male alliance formation in a dolphin social network. *Journal of Mammalogy*, *93*(1), 239-250. https://doi.org/10.1644/10-MAMM-A-366.1

Woodward-Clyde Consultants. (1994). *Biological resources of Indian River Lagoon* (Final Technical Report, Project Number 92F274C). Melbourne, FL: Indian River Lagoon National Estuary Program.

Wrangham, R. W. (1986). Ecology and social relationships in two species of chimpanzee. In D. I. Rubenstein & R. W. Wrangham (Eds.), *Ecological aspects of social evolution* (pp. 352-378). Princeton, NJ: Princeton University Press.

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