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Thesis of
Skylar L. Muller

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science
M.S. Marine Biology

Nova Southeastern University
Halmos College of Natural Sciences and Oceanography

April 2020

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NOVA SOUTHEASTERN UNIVERSITY

HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

Atlantic Spotted Dolphin (*Stenella frontalis*) and Bottlenose Dolphin (*Tursiops truncatus*) Nearshore Distribution, Bimini, The Bahamas

By:

SKYLAR L MULLER

Submitted to the Faculty of

Halmos College of Natural Sciences and Oceanography

in partial fulfillment of the requirements for

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Acknowledgments

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Abstract

Bimini, The Bahamas, includes two islands surrounded by a diverse assemblage of ecosystems and a large array of organisms, including two delphinid species, Atlantic spotted dolphins (*Stenella frontalis*) and common bottlenose dolphins (*Tursiops truncatus*, inshore ecotype). Within a predefined nearshore zone, individuals of both species had largely overlapping distribution from 2003-2018; Atlantic spotted dolphins tended to disperse farther to the north while bottlenose dolphins were located farther south. The distribution of both species varied significantly by year. Atlantic spotted dolphin sightings varied across years and months while bottlenose dolphin sightings varied by month, with differences between months April, June, July, and August from year to year. The proportion of female Atlantic spotted dolphins was higher than males, but sex identification of all individuals was not always possible with each sighting. Calf sightings decreased from April to August every year and mean counts and sightings of adults had a slight, but non-significant, increase during the last five years of the data.

Key words: Distribution, *Stenella frontalis*, *Tursiops truncatus*, Age class, Sex

Introduction

Long-term distribution studies have been used to monitor populations of delphinid species to determine seasonality patterns (Ridgway & Harrison, 1998; Wells & Scott, 1998; Sprogis et al., 2018), predation behavior and prey availability (Heithaus, 2001; Heithaus & Dill, 2002; Hastie et al., 2004), and habitat preferences (Toth et al., 2011; Toth et al., 2012; Rogan et al., 2017). This information can be used to assign marine protected areas (Hastie et al., 2003; Becker et al., 2016; Mannocci et al., 2016; Rogan et al., 2017) and monitor activities of populations including individual and/or group behavior (Folkens et al., 2002; Toth et al., 2011). Assessing changes in delphinid distribution may highlight changes in their environment, as top predators can reflect abiotic factors within an ecosystem (Toth et al., 2011; Mannocci et al., 2016).

Many dolphin species have been observed utilizing coastal habitats (*e.g.*, Scott et al., 1990; Bräger et al., 2003; Melillo-Sweeting et al., 2015). More than one species may be found using the same coastal habitat, for instance dusky dolphins (*Lagenorhynchus obscurus*) and common dolphins (*Delphinus delphis)* in the San Matias Gulf, North Patagonia, Argentina (Svendsen et al., 2015). Although both these dolphins reside in the same area with overlapping diets, segregation by habitat on a regional scale and differences with seasonality were observed. Common dolphins showed a preference for warm temperate, higher salinity waters. In the warm season, they are found in areas farther from the coast with temperate sea surface temperatures while in the cold season, areas of highly variable sea surface temperatures were preferred. Dusky dolphins had no seasonal preference and preferred the cold temperate waters of the steep slopes close to the coast (Svendsen et al., 2015).

Similar sympatric dolphin species often avoid competition by segregation of either spatial distribution, diet, and/or time (Bearzi & Standford, 2007; Praca & Gannier, 2008; Kiszka et al., 2011; Svendsen et al., 2015). Around the Falkland Islands, which is southeast of the San Matias Gulf in Patagonia, are sympatric populations of Commerson's dolphins (*Cephalorhynchus commersonii*) and Peale's dolphins (*Lagenorhynchus australis*), separated by differences in habitat preferences (Franchini et al., 2020). Commerson's dolphins often associated with nearshore waters near river mouths and outlets, along with areas of strong tidal mixing. Peale's dolphins preferred well-stratified, deep shelf waters. Peale's dolphins also were seen in the nearshore habitat in areas of extensive kelp beds and overlapped little with Commerson's dolphins (Franchini et al., 2020). Along Florida's Gulf coast between Tampa Bay and Charlotte

Harbor, populations of Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) demonstrate minimal spatial overlap. Atlantic spotted dolphins were observed in high salinity, low chlorophyll, mid-shelf waters while bottlenose dolphins occupied lower salinity, high chlorophyll, nearshore waters (Griffin & Griffin, 2003).

Differences in distribution by coastal dolphins can also be attributed to age class and sex (Heithaus & Dill, 2002; Hung & Jefferson, 2004; Weir et al., 2008; Chen et al., 2011; Jutapruet et al., 2015; Rossman et al., 2015; Sprogis et al., 2018). Distribution of Indo-Pacific humpback dolphins (*Sousa chinensis)* sighted within Pearl River Estuary, People's Rebublic of China, may differ by age class; younger individuals (calves and juveniles) occupy a smaller range within the estuary while adults maintain larger ranges (Hung & Jefferson, 2004). Another population near Xiamen, China, showed similar results but with subadults having slightly smaller ranges than adults (Chen et al., 2011). Off Donsak, Surat Thani, Thailand, adult Indo-Pacific humpback dolphins occurred in clear but deep water and younger individuals were found closer to the coast (Jutapruet et al., 2015).

Common bottlenose dolphins of Florida's Sarasota Bay have distinct home ranges; males preferred habitats with seagrass but utilized a larger home range while females used a variety of habitats but a smaller portion of the home range (Rossman et al., 2015). Indo-Pacific bottlenose dolphins (*T. aduncus*) in Bunbury, southwestern Australia, showed a preference in depth based on both sex and season. In the summer, males and females preferred shallow depths while only females occupied shallow depths in winter (Sprogis et al., 2018). Indo-Pacific bottlenose dophins within Shark Bay, Western Australia, not only showed a difference in habitat use by season, likely to avoid predation, but also showed differences in habitat use by age (Heithaus & Dill, 2002). Juvenile male Indo-Pacific bottlenose dolphins were observed in shallow waters more often than other age classes regardless of predation risk (Heithaus & Dill, 2002).

Reproductive females in Shark Bay also demonstrated seasonallity of shallow habitat use to increase calf survival (Heithaus & Dill, 2002). Preference for shallow water habitats by females with calves, in the form of nursery groups, has been observed in dusky dolphins as well, to potentially protect calves from predators and male harassment (Weir et al., 2008). Bottlenose dolphin calf abundance in Indian River Lagoon, Florida, fluctuated with season. Calf abundance was higher in fall and winter, suggesting birthing events peaking in spring and late summer. Overall abundance was higher in winter months near ocean outlets within the lagoon, further suggesting this population aggregates in areas of potentially high prey abundance after birthing events (Duren et al., 2011).

Sympatric Species Near Bimini, The Bahamas

Bimini, The Bahamas, is comprised of two islands that lie parallel and east of the Florida Straits, on the Great Bahama Bank (Voss & Voss, 1960; Morrissey & Gruber, 1993; Trave & Sheaves, 2014). Due to Bimini's location and interaction with oceanic processes, it has an assemblage of distinct ecosystem types. The ecosystems, or marine biotopes, observed around Bimini include a lagoon with mangrove forests and seagrass beds (Scoffin, 1970; Newman et al., 2007), coastal habitat with sand flats and banks (Newell et al., 1959; Voss & Voss, 1960), and coral reefs (Squires, 1958; Trave & Sheaves, 2014). Populations of sympatric Atlantic spotted and bottlenose dolphins frequent the nearshore habitat and are typically observed in depths less than 30 meters over shallow sand flats and banks. All age classes and both sexes of both species have been observed in the nearshore habitat (Melillo-Sweeting et al., 2015). Mixed species group interactions have also been observed in this area (Melillo et al., 2009).

Atlantic spotted dolphins are endemic to the Atlantic Ocean, ranging from tropical to warm temperate latitudes (Caldwell & Caldwell, 1966; Perrin et al.,1994; Perrin et al.,2009; Culik, 2011). They are typically found within a 250-meter depth contour, reaching waters as shallow as 20 meters (Perrin et al., 1994; Reynolds & Wells, 2003). They are not often found in open water but in coastal or continental shelf and slope waters (Perrin et al., 1994; Perrin et al., 2009). This species is generally absent from the Mediterranean Sea (Folkens et al., 2002; Shirihai et al., 2006) but is common in the Caribbean Sea and Gulf of Mexico (Griffin & Griffin, 2003; Reynolds & Wells, 2003). Diet includes fish, benthic invertebrates, and cephalopods (Perrin et al., 1994; Culik, 2011). Natural predators of Atlantic spotted dolphins include tiger sharks (*Galeocerdo cuvier*), bull sharks (*Carcharhinus leucus*), shortfin mako sharks (*Isurus oxyrinchus*), dusky sharks (*Carcharhinus obscurus*), possibly hammerhead sharks (*Sphyrna mokarran*), and, on rare occasion, killer whales (*Orcinus orca*) (Kinze & Christie, 2003; Melillo-Sweeting et al., 2015). The life expectancy of Atlantic spotted dolphins is not confirmed due to limited data, but multi-year field observations provide estimates of sexual maturity and calving rates (Herzing, 1997; Folkens et al., 2002; Kinze & Christie, 2003; Shirihai et al., 2006). Sexual maturity is believed to be reached between eight and 15 years (Herzing, 1997; Folkens et al., 2002; Kinze & Christie, 2003; Shirihai et al., 2006). Females have a single calf approximately every three to five years (Herzing, 1997; K. Melillo-Sweeting, pers. comm., 2018).

Common bottlenose dolphins are found in all oceans (Folkens et al., 2002; Kinze & Christie, 2003; Reynolds & Wells, 2003). Bottlenose dolphins are primarily found in coastal waters along the continental shelf and the shelf break, and they are often associated with oceanic islands and atolls in pelagic waters (Würsig & Würsig, 1979; Folkens et al., 2002). This species appears to inhabit waters ranging in surface temps from 10°C to 32°C (Ridgway & Harrison, 1998; Wells & Scott, 1998). Diet, which varies with region and prey availability, consists of 10 families of teleosts, including mackerel, houndfish, pinfish, striped mullet, pigfish, spot, five species of cephalopods, benthic invertebrates (Rossbach & Herzing, 1997; Rossbach, 1999), and one elasmobranch species (Wells et al., 1980; Ridgway & Harrison, 1998; Wells & Scott, 1998; Shirihai et al., 2006; Perrin et al., 2009). Known predators of bottlenose dolphins include tiger sharks, shortfin mako sharks, dusky sharks, bull sharks, bluntnose six gill sharks (*Hexanchus griseus*), sharpnose sevengill sharks (*Heptranchias perlo*), white sharks (*Carcharodon carcharias*), and occasionally killer whales (Würsig & Würsig, 1979; Shane et al., 1986; Wells & Scott, 1998; Heithaus, 2001; Heithaus & Dill, 2002; Perrin et al., 2009; Sprogis et al., 2018). Captive and long-term studies of bottlenose dolphins indicate that they live approximately 40 to 50 years with females averaging 50 years and males 40 to 45 years (Wells et al., 1980; Reynolds & Wells, 2003; Culik, 2011). However, recent survival comparisons of zoological facility and wild dolphins suggest bottlenose have an even longer life span than previously recorded (55 + years) (Jaakkola & Willis, 2019). Sexual maturation varies by geography and sex, with males estimated to reach maturity at nine to 14 years and females at five to 14 years (Ridgway & Harrison, 1998; Wells & Scott, 1998; Folkens et al., 2002; Kinze & Christie, 2003; Reynolds & Wells, 2003; Shirihai et al., 2006; Culik, 2011). Gestation is estimated to be 12 months after which females nurse a single calf for 18 to 20 months. Females will birth calves every three to six years (Ridgway & Harrison, 1998; Wells & Scott, 1998; Folkens et al., 2002; Kinze & Christie, 2003; Reynolds & Wells, 2003; Shirihai et al., 2006; Culik, 2011).

No single, specific use of the Bimini nearshore waters has been determined but the dolphins, which are often observed traveling and socializing and occasionally foraging, may be using the shallow waters as a refuge from predator attacks (Melillo-Sweeting et al., 2014; Danaher-Garcia et al., 2019; Melillo-Sweeting & Maust-Mohl, 2019; K. Melillo-Sweeting, pers.

comm., 2019). Understanding of prey preferences of dolphins near Bimini is incomplete. Atlantic spotted dolphins are occasionally observed preying on ballyhoo and mackerel, as well as small buried prey (K. Melillo-Sweeting, pers. comm., 2019). The bulk of their foraging may be done nocturnally on fish and squid in deep water near the Gulf Stream, similar to the Little Bahama Bank dolphin population (Herzing & Elliser, 2014). Bottlenose dolphins near Bimini have been recorded crater feeding for benthic prey items, such as wrasse, conger eels, and clinid species, in the shallow waters (Kaplan et al., 2019). These differences in possible prey choices and depth suggest differences in habitat utilization by sympatric species, despite evidence of mixed species group interactions in The Bahamas (Herzing & Johnson, 1997; Herzing et al., 2003; Melillo et al., 2009; Melillo-Sweeting et al., 2015)

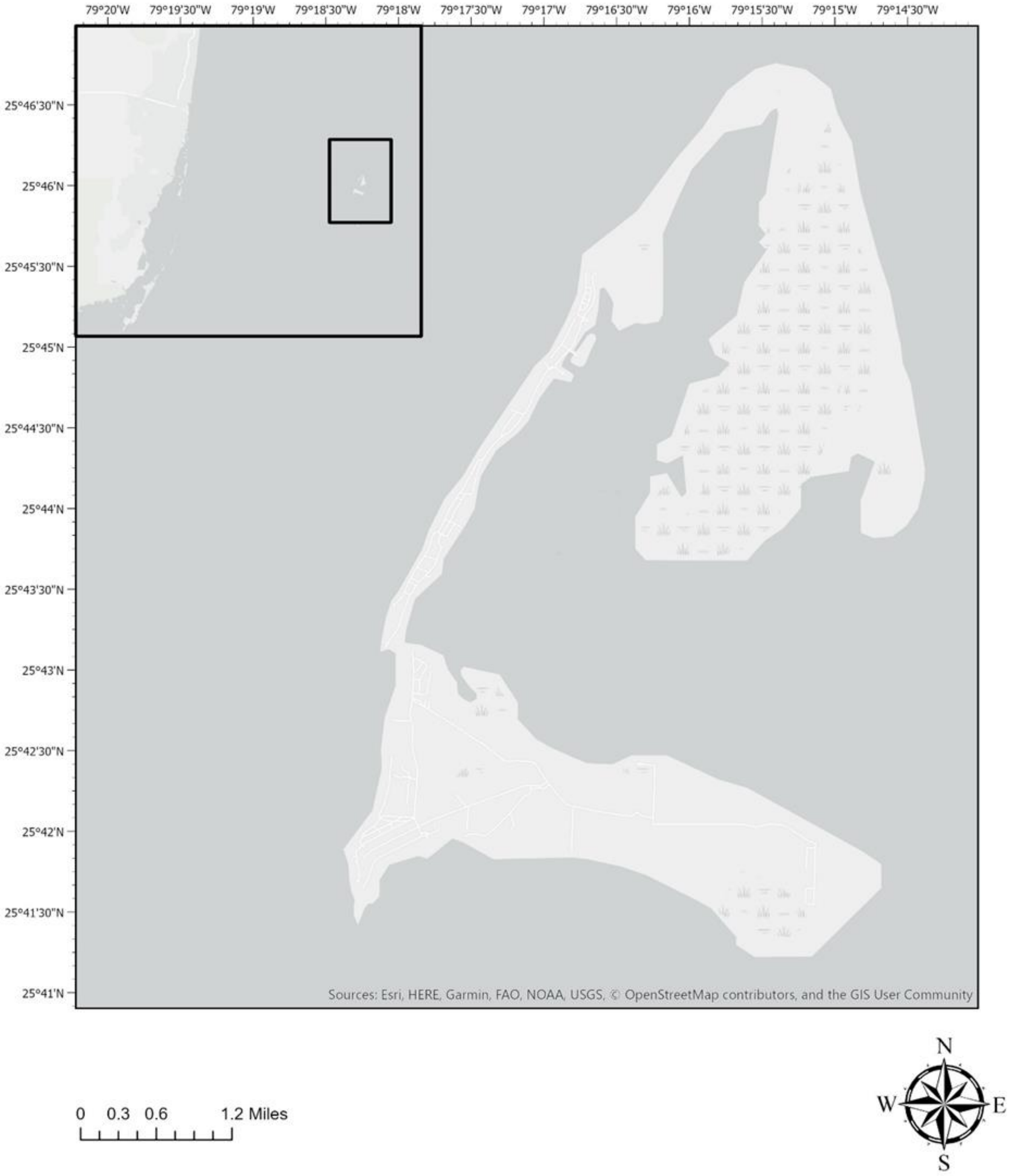
Assessing the presence of Atlantic spotted and bottlenose dolphins in nearshore/coastal habitats could provide insight as to how distribution may vary between these two protected marine mammal species. There is evidence that both species use the Bimini nearshore habitat as a possible refuge from predators but show differences in foraging behaviors. It was expected Atlantic spotted and bottlenose dolphins would show segregation by species by utilizing different areas to avoid competition while occupying the same nearshore habitat. Delphinid group composition and associations have been previously assessed for the coastal waters around Bimini (Melillo et al., 2009; Melillo-Sweeting et al., 2015; Danaher-Garcia et al., 2019), but age class and sex differences have not been refined. Assessing distribution of both species, as well as group composition by age class and sex, within the nearshore habitat of Bimini, could highlight differences and similarities in habitat preference and provide further insight into group morphology. With shifting environments in response to climate change, and habitat destruction by anthropogenic influences, it is important to investigate species distribution in order to better understand the use of their surrounding environment, potentially revealing other species' distribution and patterns. This information is key for conservation and management and would be useful for future assignment of a marine protected area.

Methods

To address habitat distribution of Atlantic spotted and common bottlenose dolphins in coastal Bimini waters, dolphin sighting data collected by the Dolphin Communication Project (DCP) were used. The Bahamas' Department of Marine Resources provides DCP's annual permit to conduct scientific research on the dolphins near Bimini, The Bahamas. Since 2001, DCP has conducted a continuous, long-term study of Atlantic spotted and bottlenose dolphins observed near Bimini, The Bahamas (Figure 1). This study utilized archived data of dolphins sighted between 25° 40.130’ N to 25° 47.976’ N from 2003-2018 (Figure 2). This subset of DCP’s larger study area is located between the western shoreline of North Bimini Island and the eastern edge of the Gulf Stream current using North Rock and North Turtle Rocks as natural north/south boundary markers.

Surveys were defined as any trip taken by vessel to search for and observe dolphins. Four mono-hull vessels (inboard and outboard motors), ranging from 11.5 to 12.8 meters (m), were used as the platform for data collection. The survey season was between April and September annually with a few surveys completed outside of season. Surveys were typically conducted during the four to five hours before sunset. Dolphin survey records follow a systematic protocol for data collection (K. Melillo-Sweeting, pers. comm., 2018). At least two on-effort passes were made within this subset study area during each data collection day, generally in depths averaging 8 to 12 m. On-effort is defined as researchers actively looking for dolphins; at least one DCP researcher visually searched for dolphins at all times. Photo-identification catalogs are maintained for both species by DCP. Environmental data collected during each sighting included percent cloud cover, Beaufort Sea State, wind direction and speed, and Global Positioning System (GPS) coordinates of dolphin sightings. Data specific to the dolphins included group size, species, age classes and sex (when confirmed), and catalog identification numbers of individuals present, when possible. Dolphins were not seen every survey.

All dolphins observed constitute a sighting but not every sighting led to an underwater encounter. Sightings were defined as observations of dolphins from the vessel. A short encounter was defined as any underwater observation of dolphins lasting between 30 and 180 s from the observer vantage in the water. An encounter was any underwater observation of dolphins lasting longer than 180 s, again with the observer in the water. Both species are considered habituated to boats and humans with bottlenose dolphins less tolerant than Atlantic spotted dolphins (Melillo et al., 2009; Danaher-Garcia et al., 2019). DCP does not provision dolphins and discourages human contact. A mobile video/acoustic system (MVA), consisting of a custom-made underwater housing that encloses a video camera with stereo audio, was used to record most encounters (Dudzinski et al., 1995).



Sources: Esri, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community

Figure 1: Bimini, The Bahamas, is located on the northwest corner of the Great Bahama Bank, immediately east of the Gulf Stream and approximately 50 miles east of South Florida, USA.

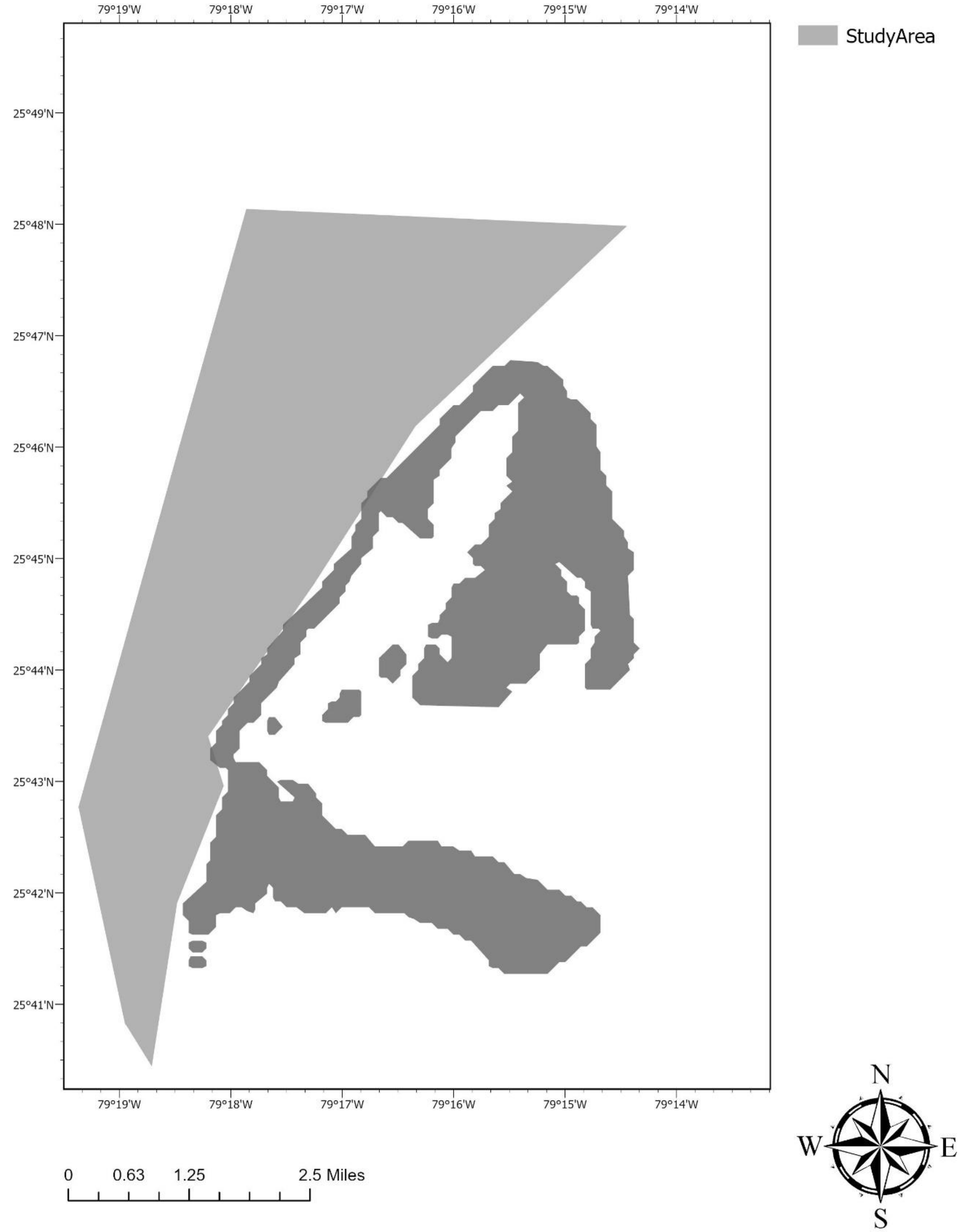


Figure 2: Shaded area (25° 40.130' N to 25° 47.976' N) is a subset of DCP's larger study area and deemed the nearshore habitat for this study.

The MVA is manually operated by the observer who focuses on one dolphin or a small group of dolphins; this protocol is a focal-follow (Altmann, 1974; Mann, 1999) during which all occurrences of behavior and interactions are documented for the focal dolphin(s). Focal follows began once the observer was underwater and in position to assess group composition. The focal individual was chosen randomly assuming all age classes and both sexes were present. The duration of a focal follow was determined by the dolphin's behavior; i.e., a dolphin was video recorded until it moved out of the camera's field of view, at which point a new focal individual was chosen at random.

Data on trip, location, species, and group size totals were obtained from sighting notes. Group sizes were documented for each sighting; group size was defined as all dolphins within visual range of the boat. Information on age class and sex were obtained from video logs of identified individual dolphins. Not all dolphins were identified at each sighting or encounter, so values for age class and sex did not always reflect the actual total(s). Re-sightings of individuals were not included within sightings but were within surveys. Data files were reviewed by two to three DCP researchers to ensure accuracy and consistency within and between years.

Statistical Analysis

Dolphin sightings were identified as either *Stenella frontalis* (Sf), *Tursiops truncatus* (Tt), or unknown (U). Mixed species observations (Sf and Tt interacting in the same group) were noted by DCP, but not used in this study. Sightings of unconfirmed species were excluded from all analyses. Atlantic spotted dolphin individuals were separated into four age classes (calf, juvenile, subadult, and adult) based on their pigmentation patterns (Perrin, 1970; Herzing, 1997) and categorized as counts. Though DCP has observed neonates, none were observed in the data used for this study. Atlantic spotted dolphin sex – male, female or unknown – were determined by viewing of the genital area of individuals and categorized as a count; the counts for unknown sex were not included in analyses. Bottlenose dolphins had limited recordings of individual age classes and sex and, therefore, these variables were excluded from further analysis. Sightings of both species were analyzed by year and month. Months outside the typical season (April-September) were removed for age class and sex analysis due to limited recordings. Statistical analyses were conducted with the software R (Version 3.5.2) (R Core Team, 2018). Multivariate multiple regression was used to assess effects of year, month, and species on location variables (latitude and longitude combined) (Johnson & Wichern, 2002; Fox & Weisberg, 2011). Generalized linear mixed models (GLMM) with negative binomial error distribution and zero inflation applied were created using the package glmmTMB (Magnusson et al., 2017) to assess the effects of year, month, and species on group size, age class counts, and sex counts. Zero inflation was removed for the variable group size that contained no zeros. Akaike information criterion (AIC) was used to determine which model best described the effect of independent variables on the dependent variable (counts). The model with the lowest AIC value was selected as the final model. Residual plots were created to validate the chosen model using package DHARMa (Hartig, 2018). Models were accepted as valid when no significant deviation was detected. Pairwise tests using the Tukey method were employed using the package Emmeans (Length et al., 2018) to explain significance within variables.

Results

Over a 16-year period (2003-2018), 368 surveys were completed within the nearshore habitat, resulting in a total of 633 sightings (mean: 39.56 ± 17 sightings per year). Atlantic spotted dolphins comprised 48% (N=304) of the sightings, while bottlenose dolphin sightings were 46% (N=289) and unknown species were 6% (N=40) of the total sightings (Table 1). Unknown, or unidentifiable, species were excluded from further analyses.

Distribution

A multivariate multiple regression determined that location (latitude and longitude) of the dolphin sightings differed significantly by species (df=1, p<0.001), year (df=15, p<0.001), and month (df=9, p<0.001) (Figure 3). Sightings of both species occurred from October through March, though not for each of the 16 years and so extraneous (out of normal field season) months were excluded. Atlantic spotted dolphin location significantly differed among both years (df=15, p=0.003) (Figure 4) and months (df=5, p<0.001) (Figure 5). Emmeans pairwise tests indicated that locations of year 2011 significantly differed from 2018 (df=252, p=0.022), and locations within April significantly differed from July (df=252, p=0.008) and August (df=252, p<0.001).

Table 1: Mean ± SD group size sightings by year, 2003-2018. *Stenella frontalis* labeled as Sf, *Tursiops truncatus* labeled as Tt.

Year	Sighting Total Sf	Sighting Total Tt	Mean ± SD Group Size Sf	Mean ± SD Group Size Tt
2003	5	6	5.80 ± 4.76	5.83 ± 5.46
2004	8	8	4.43 ± 3.10	6.38 ± 3.70
2005	4	12	3.50 ± 1.73	10.1 ± 3.60
2006	14	9	5.67 ± 2.71	6.25 ± 2.87
2007	14	19	6.55 ± 2.81	5.82 ± 3.92
2008	13	17	6.64 ± 3.04	6 ± 3.30
2009	10	18	7.10 ± 4.37	6.31 ± 4.08
2010	24	23	8.95 ± 6.23	4.30 ± 3.10
2011	18	23	8.50 ± 4.53	4.67 ± 2.83
2012	16	32	12.57 ± 6.58	4.63 ± 3.30
2013	21	15	6.80 ± 3.69	6.15 ± 3.29
2014	11	24	6.45 ± 6.64	7.52 ± 5.88
2015	26	23	11.15 ± 6.69	4.67 ± 3.94
2016	46	21	13.32 ± 10.76	4.11 ± 2.54
2017	20	20	6.94 ± 4.98	3.68 ± 2.69
2018	54	19	7.60 ± 6.40	4.75 ± 3
Totals	304	289		
Mean	19 ± 13.70	18.07 ± 6.80	7.62 ± 2.72	5.70 ± 1.57
Median	15	19	6.87	5.83
%	48%	46%		

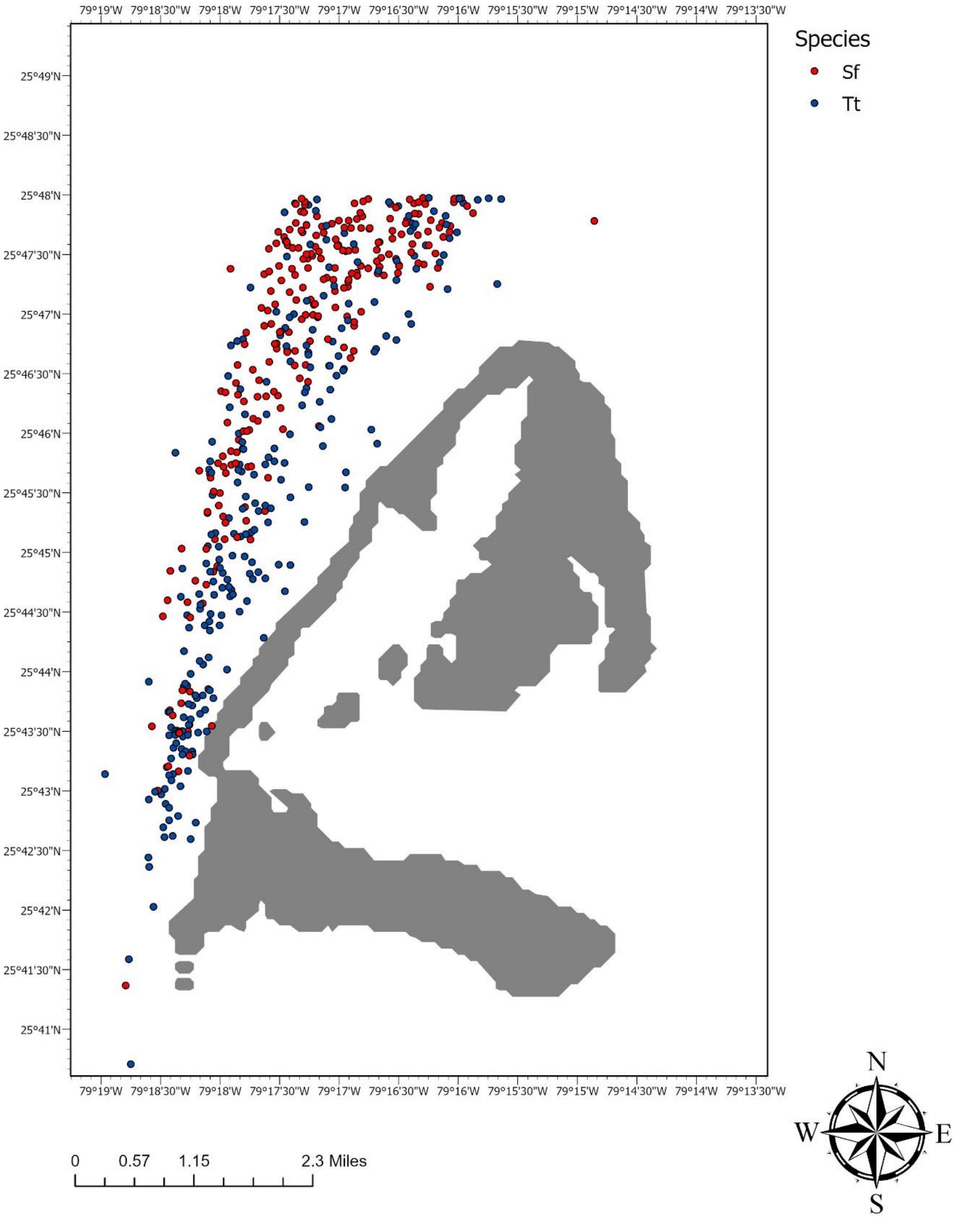


Figure 3: Both Atlantic spotted and bottlenose dolphin sightings extended north while bottlenose dolphin sightings extended further south, 2003 – 2018. (*Stenella frontalis* = Sf in red, *Tursiops trunctatus* = Tt in blue).

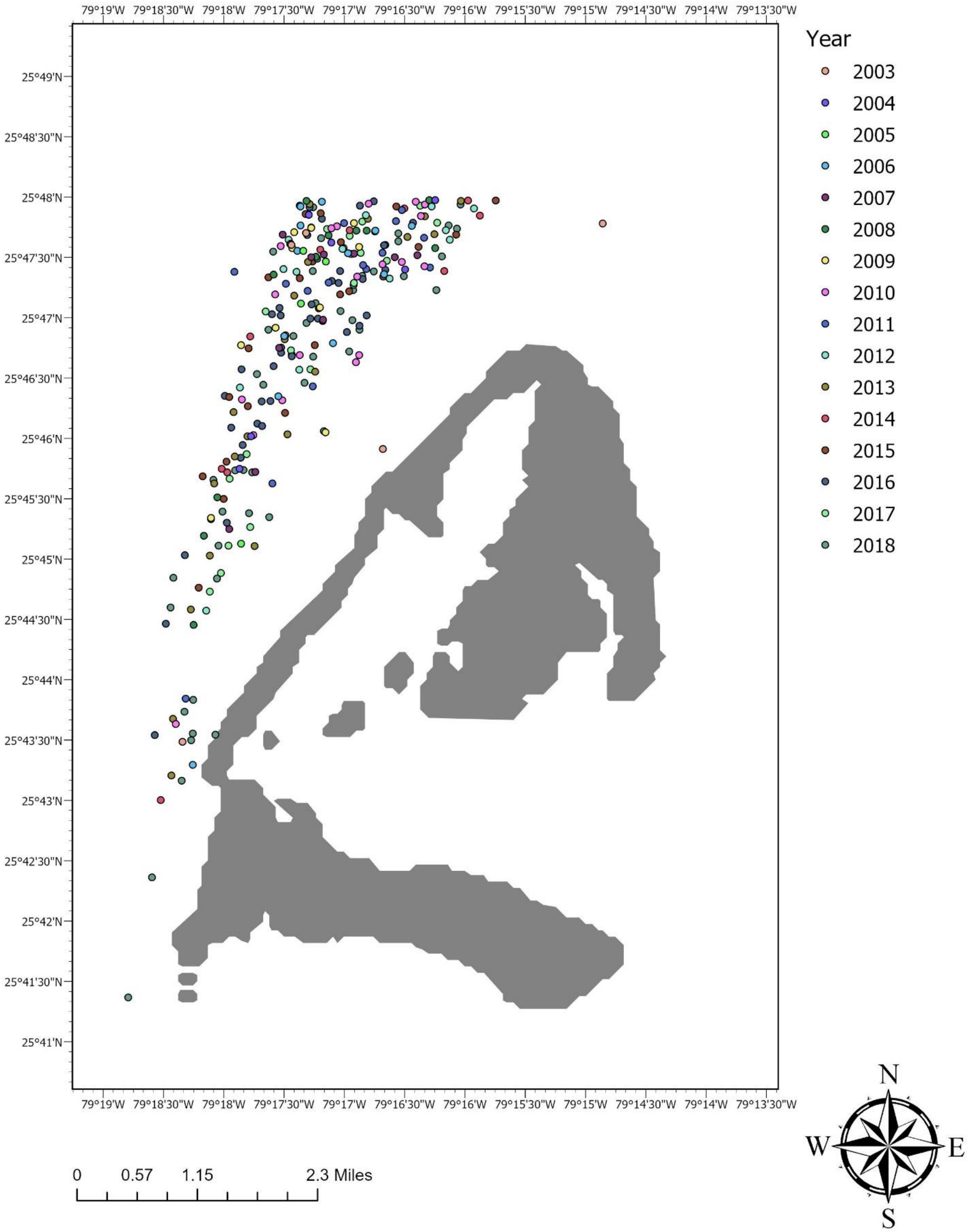


Figure 4: Atlantic spotted dolphin sightings distribution by year, 2003-2018.

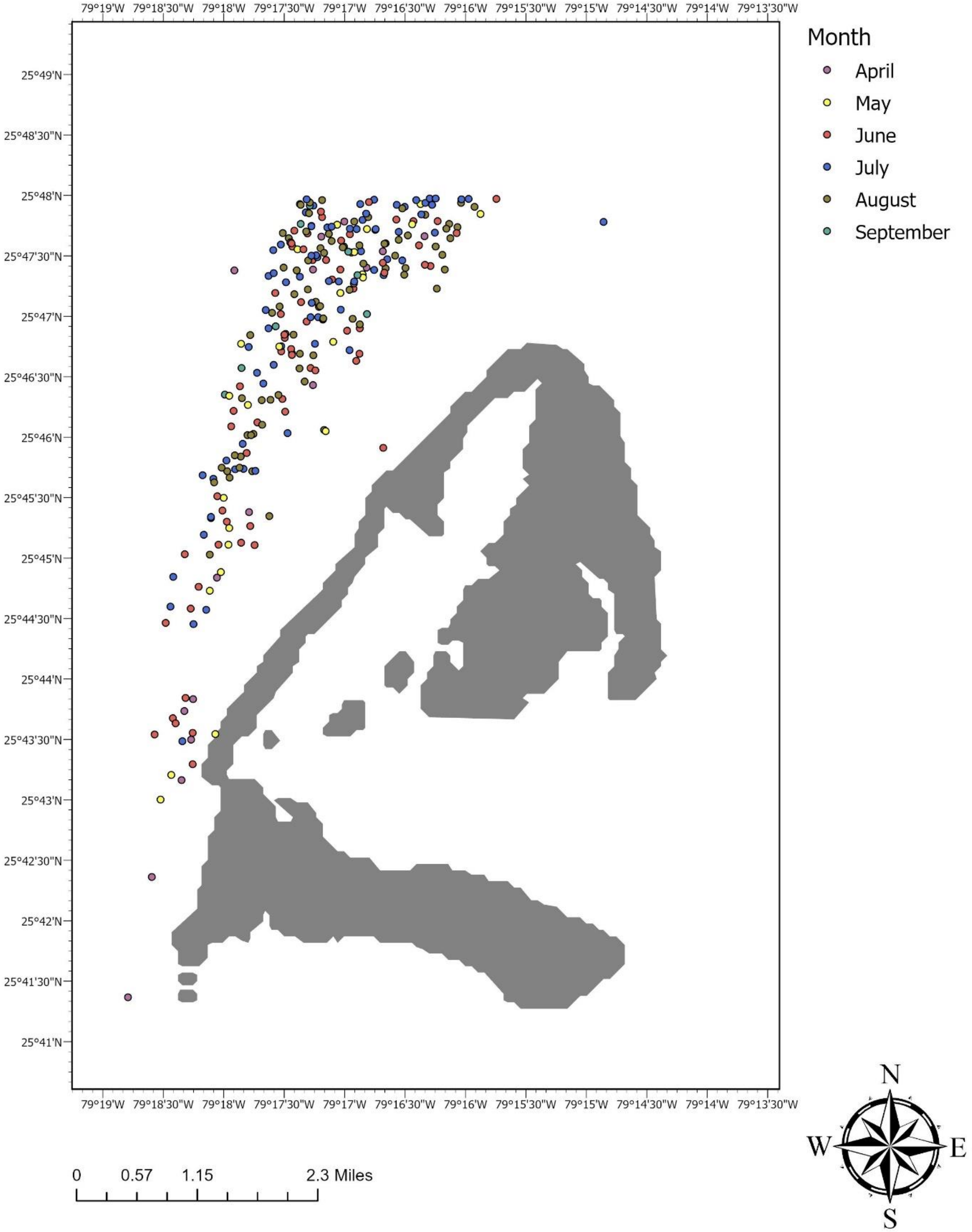


Figure 5: Atlantic spotted dolphin sightings distribution by month, 2003-2018.

The bottlenose dolphin sighting locations significantly differed by month only (*df*=5, *p*=0.036) (Figure 6). Locations in April significantly differ from June (*df*=236, *p*=0.005) and August (*df*=236, *p*=0.019).

Group sizes

GLM modeling determined that differences in group size were best described by two factors: species and year. The group size of Atlantic spotted dolphins (mean group size 7.62 ± 2.72) differed from bottlenose dolphins (mean group size 5.70 ± 1.57) (*df*=497, *p*<0.001) every year (Table 1). Emmeans pairwise test determined that spotted dolphin mean group size in 2016 was higher than mean group size totals in 2018 (*df*=259, *p*=0.031). Differences in group size of bottlenose dolphins are best described by year; Emmeans pairwise tests indicated year 2005 had a higher group mean than years 2010 (*df*=237, *p*=0.006), 2011(*df*=237, *p*=0.016), 2012 (*df*=237, *p*=0.008), 2015 (*df*=237, *p*=0.003), 2016 (*df*=237, *p*=0.006), 2017 (*df*=237, *p*<0.001), and 2018 (*df*=237, *p*=0.045) (Figure 7).

Age Class and Sex

Confirmation of sex was not possible for all members of all groups. Of the Atlantic spotted dolphins where sex was confirmed, 36% (N=336) were male and 64% (N=600) were female. As a result of limited sex confirmation, attempted GLM models did not converge so sex was excluded from further analyses. Observed age classes of Atlantic spotted dolphins were distributed roughly equally: 29.5% (N= 426) calves, 27.5% (N=397) juveniles, 20.3% (N=293) subadults, and 22.7% (N=328) adults (Table 2). GLM modeling determined differences in number of calves sighted were best explained by year and month. A declining mean number of calves was sighted from April through August though no significant trends in sightings were detected across all years (Figures 8 and 9). GLMM determined differences in number of adults were best described by year; specifically, 2013 had a lower mean number of adults than 2016 (*df*=258, *p*=0.004) (Figure 10). This too may be due to a difference in number of adults recorded. Year 2016 had 27 sightings with adults recorded and a higher mean number per sighting while 2013 only had six adult sightings (Figure 11). A slight increase in mean adult counts occurred over time but more individuals will need to be identified in other years to confirm age classes with each sighting.

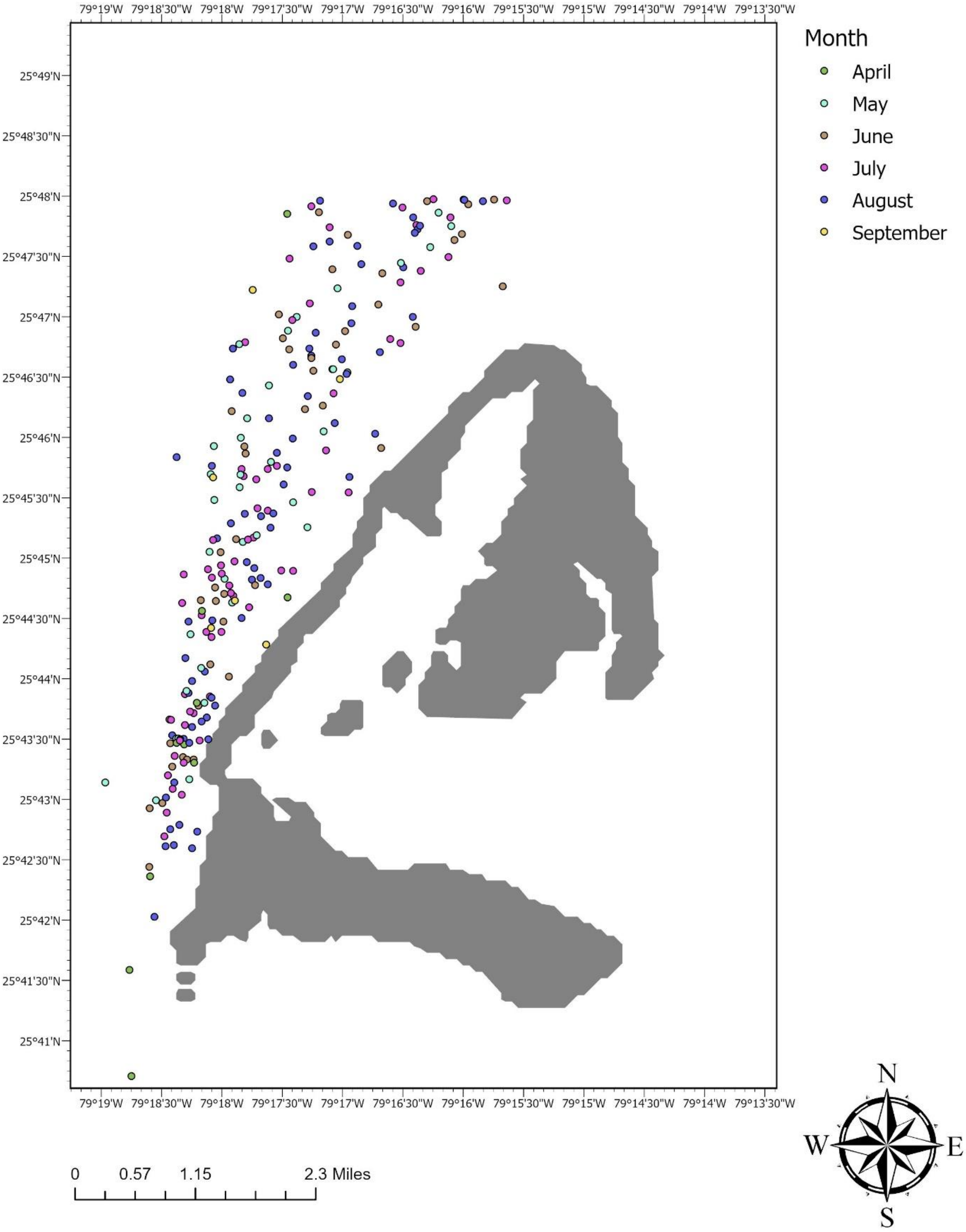
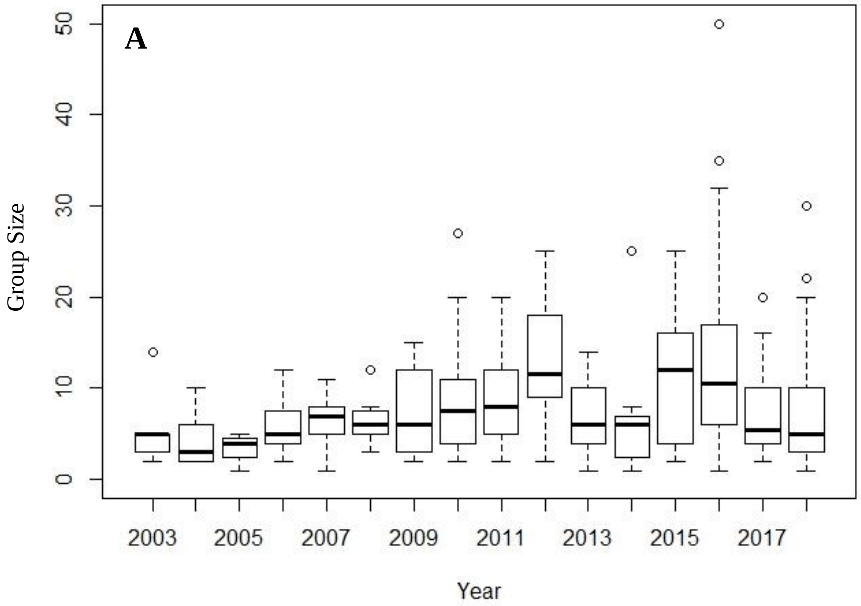


Figure 6: Bottlenose dolphin sightings distribution by month, 2003-2018.

Stenella frontalis



Tursiops truncatus

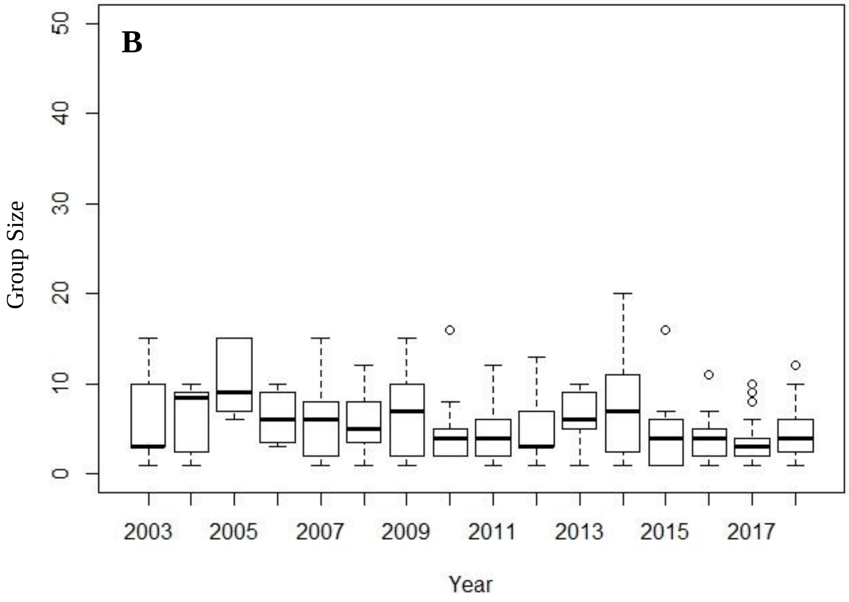


Figure 7: Annual mean ± SD group sizes for A) Atlantic spotted (*Stenella frontalis*) and B) bottlenose (*Tursiops truncatus*) dolphins by year, 2003-2018.

Table 2: Atlantic spotted dolphin age class and sex, 2003-2018. Annual re-sightings for each age class and both sexes were included.

Year	Calf	Juvenile	Subadult	Adult	Male	Female
2018	67	56	51	67	58	102
2017	15	28	19	21	22	47
2016	75	76	81	95	96	113
2015	46	72	34	34	52	73
2014	13	12	9	7	8	4
2013	23	12	6	8	5	15
2012	24	29	9	9	30	27
2011	35	25	16	13	18	38
2010	48	22	21	23	15	53
2009	12	9	6	7	2	26
2008	7	15	11	18	7	34
2007	21	13	14	9	6	31
2006	15	20	11	8	10	27
2005	3	2	2	2	3	3
2004	15	4	3	3	4	6
2003	7	2	0	4	0	1
Totals	426	397	293	328	336	600
Mean	26.63 ± 21.69	24.81 ± 23.33	18.31 ± 21.13	20.50 ± 25.59	21 ± 26.41	37.50 ± 33.67
Median	18	17.5	11	9	9	29

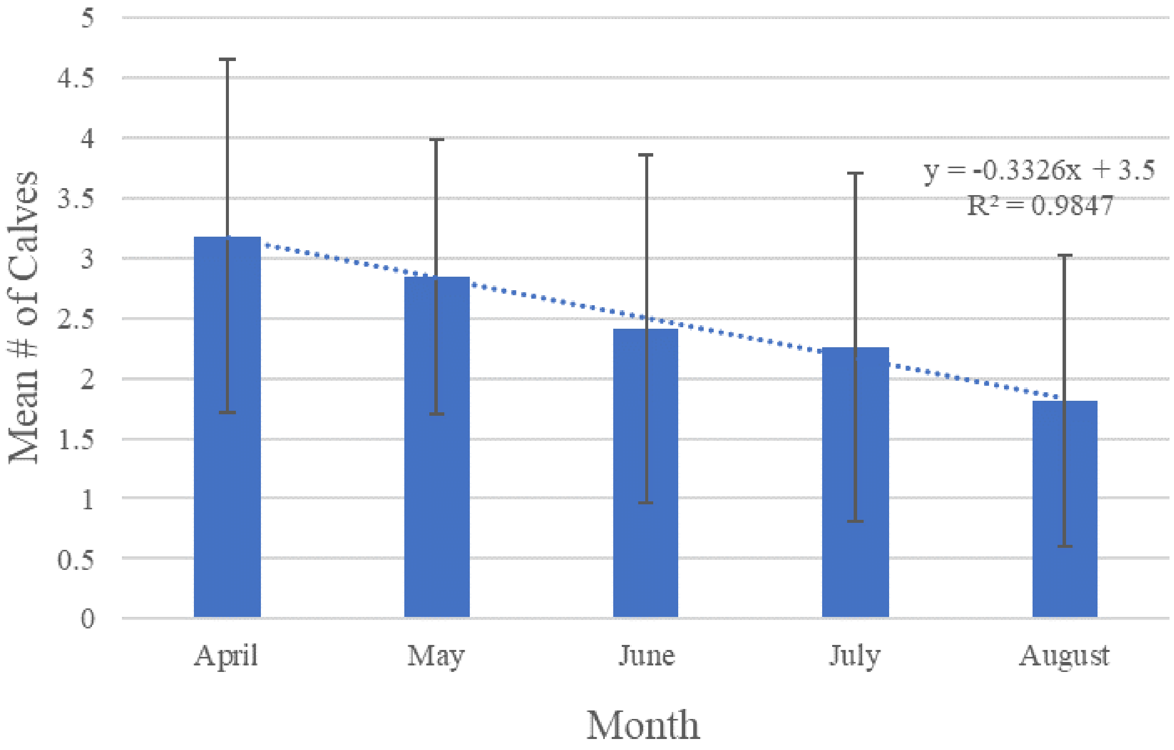


Figure 8: Monthly mean ± SD Atlantic spotted dolphin calves per sighting (April 2011 and 2018 through August 2003-2018). Mean number of calves decreased by month during the study period. Annual re-sightings were included.

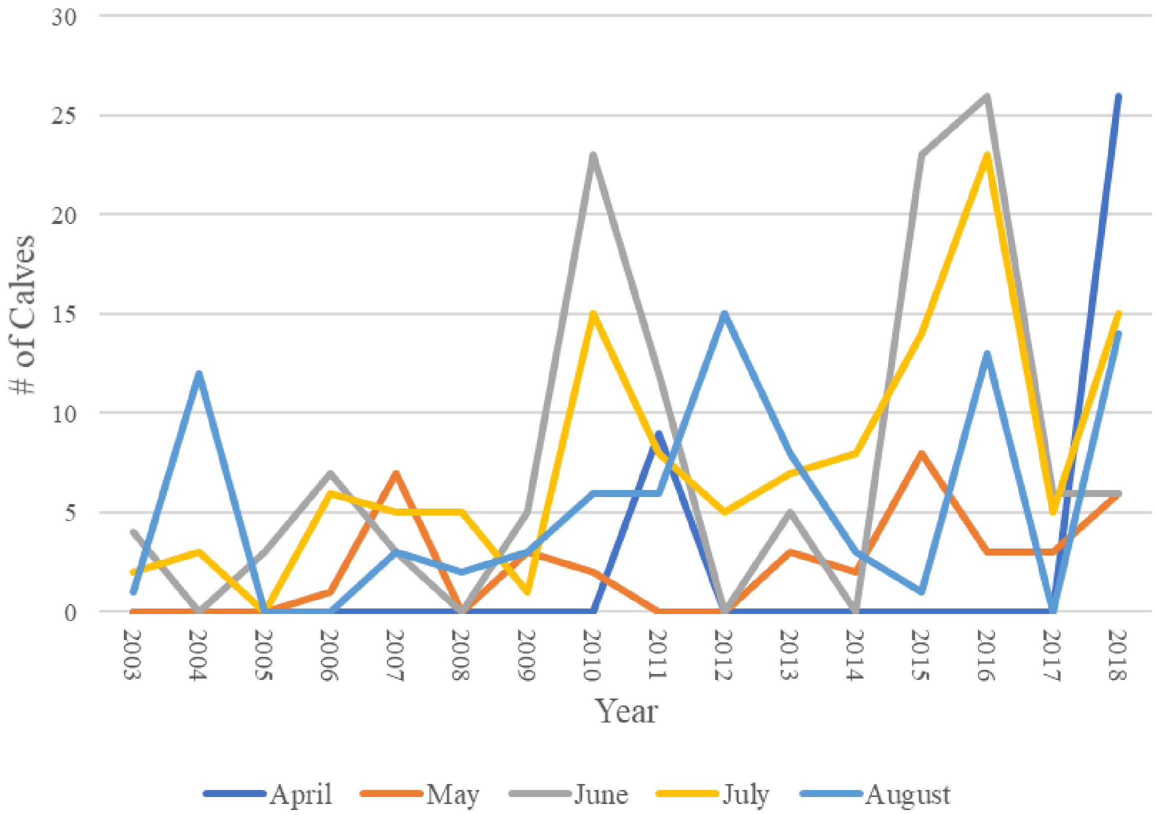


Figure 9: Total number of Atlantic spotted dolphin calves sighted by month, 2003-2018. Annual re-sightings were included.

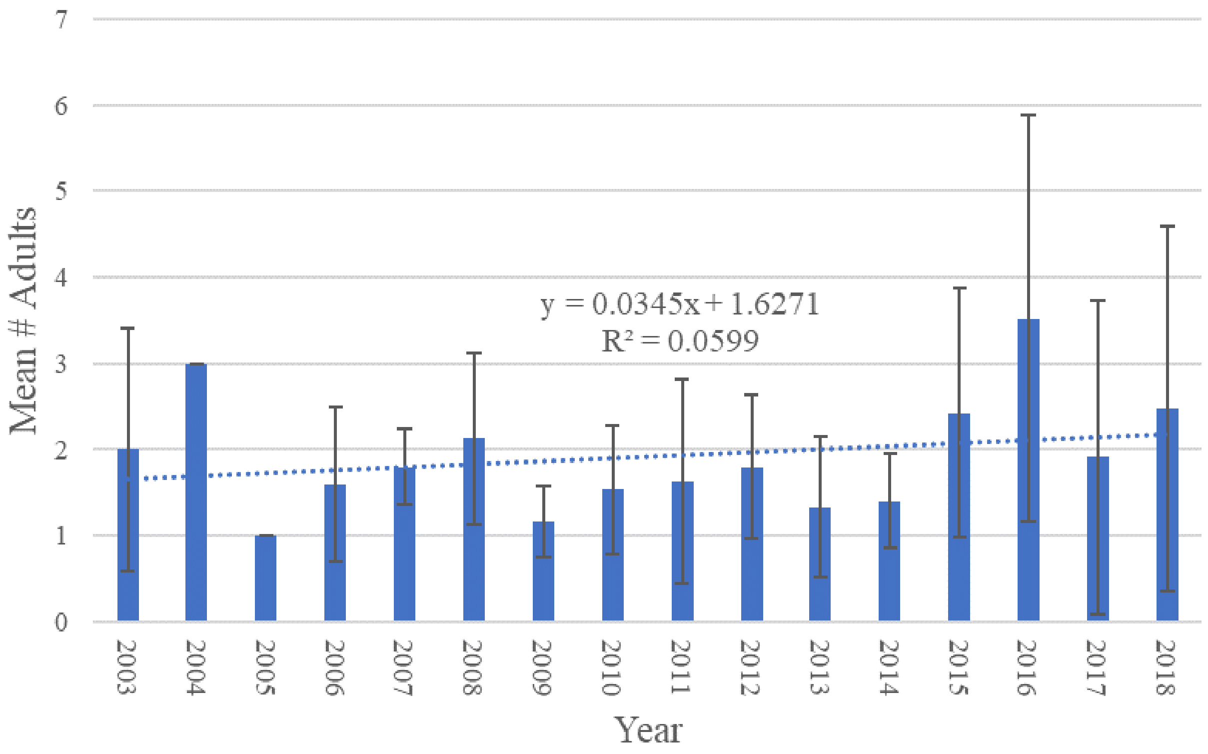


Figure 10: Annual mean ± SD adult Atlantic spotted dolphins, 2003-2018. Mean adult counts appear to increase with time, although insignificant. Annual re-sightings were included.

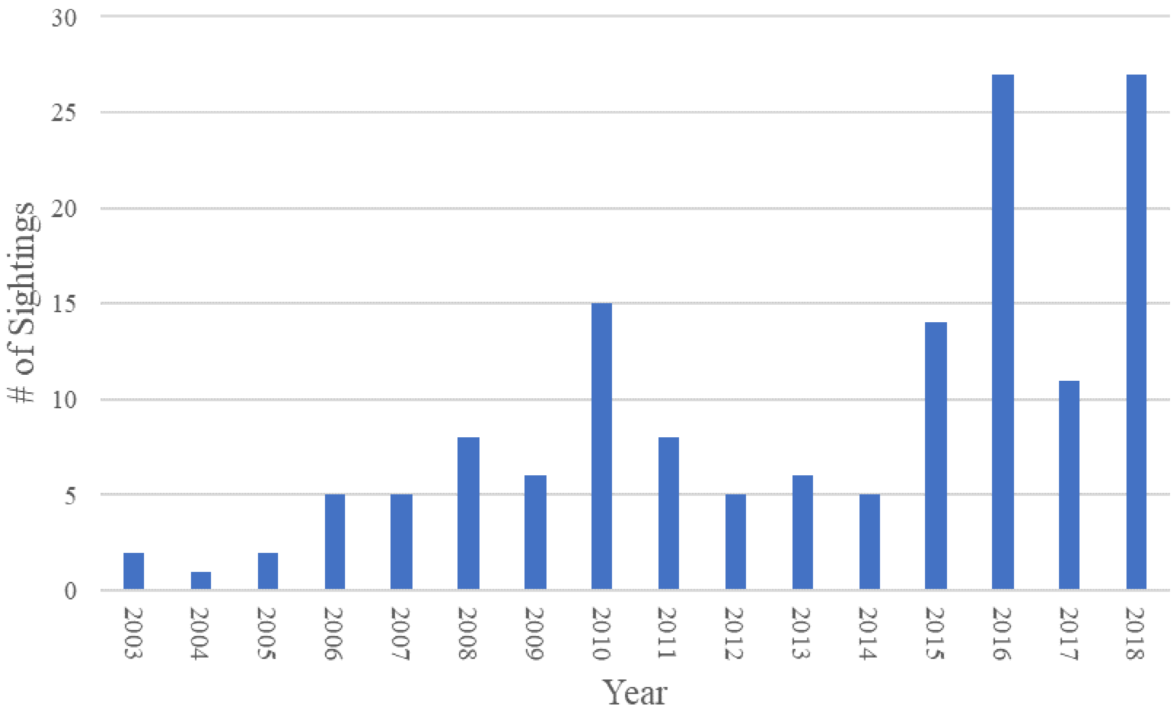


Figure 11: Annual sightings with adult Atlantic spotted dolphins, 2003-2018.

Discussion

The present study examined the distribution and group composition of single species sightings of Atlantic spotted and common bottlenose dolphins observed in the nearshore waters off Bimini, The Bahamas, across locations, months, years, age class, and sex. Investigating distribution and composition of groups has allowed for an examination of the potential effects of age and sex over time on sympatric species distribution.

Distribution

Any visual study on animal group composition will be influenced by environmental conditions, particularly on the water. Sea state and meteorological conditions from day to day could have influenced every aspect of this study – from the initial sighting of a dolphin group to species identification and individual counts. These same abiotic variables can also influence the quality of video recordings necessary for age class and sex identifications.

Locations (latitude and longitude) of dolphins had a significant difference for both species across all years and months. The nearshore habitat is parallel to North Bimini Island and is generally oriented north to south so a change in latitude is to be expected. Although there was an overlap in habitat distribution by both species, Atlantic spotted dolphins were more often observed farther from shore than bottlenose dolphins. In order to access the study area from Bimini Harbor, a sandbar located outside the entrance of the harbor must be avoided when exiting and entering the harbor. Dolphin surveys south of this sandbar were completed opportunistically or when weather precluded traveling north through the study area. Dolphins of either species could be utilizing the southern portion of the study area more than what is represented here.

Bathymetric or abiotic data were not assessed in this study to corroborate depth preferences, but similar distribution results were found by Griffin & Griffin (2003). In the Gulf of Mexico, bottlenose dolphins preferred the shallow, lower salinity, high chlorophyll waters closer to the shore, while Atlantic spotted dolphins preferred relatively deeper water with higher salinity and low chlorophyll content. Previous studies around Bimini have indicated that there are distinct water masses with varying salinities and an increase in salinity from the Florida Straits to the Great Bahama Bank. It is suggested this high variance in salinity may cause differing ecological conditions within a small area (Turekian & Newell, 1957; Trave & Sheaves, 2014). It is possible the dolphins in Bimini show a similar salinity preference to the populations in the Gulf of Mexico, resulting in similar distribution patterns. To test species preferences, salinity, chlorophyll, along with other abiotic and bathymetric data, would need be collected at the location dolphins are sighted during a survey.

The segregation shown by these sympatric species may be related to differences in prey niches in order to avoid competition. Little is known about the prey pursued specifically by Atlantic spotted dolphins near Bimini (Danaher-Garcia et al., 2019), but it is assumed that they do most of their foraging on fish and squid nocturnally in deeper water closer to the Gulf Stream, similar to the Little Bahama Bank population (Herzing & Elliser, 2014). This differs from the bottlenose dolphin populations at both locations in The Bahamas; they have been observed crater feeding for benthic prey (at Little Bahamas Bank, Rossbach & Herzing, 1997; Rossbach, 1999; near Bimini, Kaplan et al., 2019). This may also explain the differences in observed distances from shore by each species in this study. The northern extent of the study area is close to the deeper water where we see both dolphin species. Bottlenose dolphins are also observed more in the southern portion of the habitat, closer to the shallow channel entrance between the North and South Bimini Islands. Bottlenose dolphins crater feed at a variety of depths, optimizing use of the whole nearshore study area. Atlantic spotted dolphin regurgitation has revealed prey items, such as large squid pens, that surpass reef species sizes, further supporting the possibility of their foraging in deeper water, possibly on species that migrate with the deep scattering layer (Herzing & Elliser, 2014). Additionally, DCP generally conducts surveys in the 4-5 hours before sunset. It is possible Atlantic spotted dolphins utilize the whole study area during the day to forage on burrowing and schooling prey items (Herzing & Elliser, 2014), but are observed towards the outer range of the study site around sunset, perhaps as they prepare to leave the nearshore habitat for nocturnal foraging in deeper water. To test this hypothesis, distribution analysis would need to segregate sightings into incremental time periods throughout the day until just before sunset.

Attempted shark predation may also influence the daily use of the nearshore habitat by both species. A minimum of 15% of the cataloged Atlantic spotted dolphins (Melillo-Sweeting et al., 2014) and 28% of cataloged bottlenose dolphins (Melillo-Sweeting & Maust-Mohl, 2019) have shark bite scars as evidence for failed predation attempts. Although both species are subject to predation from several shark species, DCP has only rarely seen tiger sharks in Bimini's shallow water (Danaher-Garcia et al., 2019; K. Melillo-Sweeting, pers. comm., 2019). The lack of shark sightings within the study area suggests this area is a refuge from potential predators for both species during the day.

Environmental Impacts

The distribution of Atlantic spotted dolphins differed from April to July and August and bottlenose dolphins differed from April to June and August. Seagrass and faunal communities within the North Sound Lagoon and south of South Bimini Island have demonstrated seasonal changes in response to the wet season (May through October) and the dry season (November through April) (Newman et al., 2007). Temperatures reach a near-lethal range for fish species within the North Sound Lagoon during the wet season, suggesting fish utilize the North Sound Lagoon in the dry season but move to neighboring areas with lower temperatures in the wet season (Newman et al., 2007). The nearshore habitat is adjacent to the North Sound Lagoon and not directly connected for prey species to travel to, but it is possible these seasonal changes, along with changes in salinity within the various biotopes of Bimini, could cause seasonal movement of other prey items that can access the nearshore habitat. Perhaps the difference in location by month reflects seasonal movement of prey items that could influence seasonal movement of dolphins.

Between 2003 - 2018, many events occurred off North Bimini Island that likely altered the underwater, nearshore habitat, including continued and varied tourism and boat traffic, construction with dredging and pile driving components (Gruber & Parks, 2002; Weilgart, 2007; Pirotta et al., 2013; Trave & Sheaves, 2014: Grimmel et al., 2020), and hurricanes (Elliser & Herzing, 2011; 2014; Melillo-Sweeting et al., 2015; Herzing et al., 2017). The alterations on North Bimini Island may have caused changes to seagrass assemblages (Trave & Sheaves, 2014); there have been noted decreases in juvenile lemon shark (*Negaprion brevirostris*) survival (Jennings et al., 2008). The North Sound Lagoon acts as a nursery and refuge for a multitude of fish species until they can inhabit the neighboring biomes, including the western nearshore habitat of these dolphin species (Voss & Voss, 1960; Jennings et al., 2012; Grimmel et al., 2020). Even with recorded changes to the North Sound Lagoon, it is unclear how these events have impacted the dolphin populations utilizing Bimini’s nearshore habitat.

Hurricane Sandy moved through The Bahamas in 2012, but no hurricanes impacted The Bahamas in 2013. In 2012 and 2013, Little Bahama Bank experienced significant cooling along with a decrease in chlorophyll, potentially reducing production and available food (Herzing et al., 2017); it is unknown if the same changes occurred on the Great Bahama Bank. However, during these same years, known individual Atlantic spotted dolphins from Little Bahama Bank immigrated to the Bimini area of the Great Bahama Bank (Herzing et al., 2017). DCP observed 35 of these individuals off Bimini (Danaher-Garcia et al., 2019). It is still unknown how this immigration of new individuals has affected the dolphins that frequent Bimini. After two major hurricanes in 2004, Atlantic spotted and bottlenose dolphins residing near Little Bahama Bank experienced a large population loss as well immigration of new individuals (Elliser & Herzing, 2011; 2014; Herzing et al., 2017). These events caused changes in social structure, effectively splitting the population into new groups. Direct effects of the 2004 hurricanes to the underwater habitat are unknown. It is possible group compositions could change with the addition of these immigrated individuals to the Bimini population in 2013, potentially altering group sizes, habitat preferences, and distribution.

Movements of sediment on the ocean floor can alter available nutrients that control photosynthesis and resultant production throughout the food web (Chang et al., 2001; Schallenberg & Burns, 2004). Hurricanes can cause sediment resuspension (Chang et al., 2001) that can increase overall production (Schallenberg & Burns, 2004), affecting potential prey items and influencing dolphin distribution. During this study, other major hurricanes (e.g., Matthew in 2016, Irma in 2017) have impacted the nearshore area of Bimini. Data regarding anthropogenic impacts and natural forces have not been utilized in this study but should be considered in the future when assessing dolphin distribution.

Atlantic Spotted Dolphin Age Class and Sex Distribution

Age classes and sexes for spotted dolphins were obtained from confirmed dolphin identities during sightings. Not every dolphin's age class or sex could be identified so counts do not always reflect the entire group being observed. Of the identified dolphins, a similar number of all four age classes (calf, juvenile, subadult, adult) was observed with slightly more calves and juveniles than subadult or adult classes. When individuals of unknown sex were removed, females were also observed more often than males. On the Little Bahama Bank, births occur year-round with a peak in April and another in the late fall (Herzing, 1997), and it is assumed similar peaks may occur in the Bimini region of Great Bahama Bank (K. Melillo-Sweeting, pers.

comm., 2018). Because different-sized, first-year calves are seen throughout the summer, calving is likely to occur year-round off Bimini (DCP, unpublished data, 2003-2018). Mother-calf groups are consistently observed throughout the whole study area over the course of each field season (Danaher-Garcia et al., 2019). DCP has observed an adult spotted dolphin mother nursing her calf for over five years; however, a more typical nursing period is expected to be three to four years (DCP, unpublished data, 2003 – 2018). Females with their young may utilize the relatively safe shallows of Bimini during the day as a nursery and refuge, possibly explaining the higher counts of observed adult females, calves, and juveniles.

The mean number of Atlantic spotted dolphin calves from 2003-2018 was higher in April and decreased through August. However, sightings with calves recorded in April only occurred in two years, 2011 and 2018. Despite these two years having a higher mean number of calves than other months, we also see a decrease in mean number of calves by month from May to August across all years (2003-2018). Perhaps seasonal changes around Bimini described earlier, influence when calves are brought by their mothers to the nearshore habitat. More surveys need to be completed in April in order to confirm a higher number of calves during this month. Surveys within months outside the typical study period would allow for assessments by month throughout the year to see if other monthly fluctuations occur.

A difference in age class was also found when assessing counts of Atlantic spotted dolphin adults. The year 2013 had a lower mean number of adults than 2016; however, year 2016 had 27 sightings with adults recorded and a higher mean number per sighting, while 2013 only had six sightings of adults. When comparing mean number of adults over time (2003-2018), a slight increase is observed. Individuals that immigrated from the Little Bahama Bank population included many subadults and adults (Danaher-Garcia et al., 2019; DCP, unpublished data, 2012-2018). The identification of these immigrated individuals could have influenced the number of adults recorded in years after 2013. More adults would need to be identified in other years to see if this trend holds, as with other age classes.

Future Considerations

Comparison of age class and sex between the two species was limited by available data. DCP's bottlenose photo-identification catalog consists primarily of dorsal fin images taken above water from boats with limited underwater encounter footage available, leading to limited age class and sex confirmation. Distinguishing age classes and sex of either species from a boat is not always possible. Additional age class and sex identifications for both species should facilitate future analyses and comparisons.

While this study only focused on single species groups, these two species do occupy the same area over time. Interspecies sexual interactions have been observed, but no hybrids have been confirmed (Melillo et al., 2009). Bottlenose dolphins are, however, known hybridizers with a number of other dolphin species (Rough-tooth dolphin (*Steno bredanensis*), Dohl et al., 1974; Long-beaked common dolphin (*Delphinus capensis*), Zornetzer & Duffield, 2003; Guiana dolphin (*Sotalia guianensis*), Caballero & Baker, 2010; Risso's dolphin (*Grampus griseus*), Zhang et al., 2014). DNA samples are not collected so hybridization between these two species at Bimini has not been confirmed but is worth assessing in future research.

This study expands upon baseline data (Melillo-Sweeting et al., 2015) on the long-term habitat use by these dolphin populations. Further identification and data collection of both species should provide more in-depth comparisons for habitat distribution analysis. Refinement of these data to the individual level may potentially highlight preferences that could be applied to past and present behavioral data on individuals and groups. Understanding prey distribution relative to dolphins' habitat use could address foraging versus predator avoidance as motivating factors. Continued research should consider assessing areas of change or possible impact by both anthropogenic and natural forces, within the nearshore habitat, to better understand the influence these events may have on the faunal communities.

Literature Cited

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour, 49*(3-4), 227-266.

Bearzi, M., & Stanford, C. B. (2007). Dolphins and African apes: comparisons of sympatric socio-ecology. *Contributions to Zoology, 76*(4), 235-254.

Becker, E., Forney, K., Fiedler, P., Barlow, J., Chivers, S., Edwards, C., ... & Redfern, J. (2016). Moving towards dynamic ocean management: how well do modeled ocean products predict species distributions?. *Remote Sensing, 8*(2), 149.

Boss, S. K. J. G. (1996). Digital shaded relief image of a carbonate platform (northern Great Bahama Bank): scenery seen and unseen. *Geology, 24*(11), 985-988.

Bräger, S., Harraway, J. A., & Manly, B. F. J. (2003). Habitat selection in a coastal dolphin species (Cephalorhynchus hectori). *Marine Biology*, *143*(2), 233-244.

Caballero, S., & Baker, C. S. (2010). Captive-born intergeneric hybrid of a Guiana and bottlenose dolphin: Sotalia guianensis× Tursiops truncatus. *Zoo Biology, 29*(5), 647-657.

Caldwell, D. K., & Caldwell, M. C. (1966). Observations on the distribution, coloration, behavior and audible sound production of the spotted dolphin, Stenella plagiodon. *Los Angeles County Museum Contributions in Science, 104*, 1-28.

Chang, G. C., Dickey, T. D., & Williams III, A. J. (2001). Sediment resuspension over a continental shelf during Hurricanes Edouard and Hortense. *Journal of Geophysical Research: Oceans, 106*(C5), 9517-9531.

Chen, B. Y., Zheng, D. M., Ju, J. F., Xu, X. R., Zhou, K. Y., & Yang, G. (2011). Range Patterns of Resident Indo-Pacific Humpback Dolphins(Sousa chinensis, Osbeck 1765) in Xiamen, China: Implications for Conservation and Management. *Zoological Studies*, *50*(6), 751-762.

Culik, B. (2011). *Odontocetes – the Toothed Whales, CMS Technical Series No. 24*. Bonn, Germany: UNEP/CMS Secretariat.

Danaher-Garcia, N. A., Melillo-Sweeting, K., & Dudzinski, K. M. (2019). Social structure of Atlantic spotted dolphins (Stenella frontalis) off Bimini, The Bahamas (2003–2016): alternate reasons for preferential association in delphinids. *Acta Ethologica*, *23*, 9-21.

Dohl, T. P., Norris, K. S., & Kang, I. (1974). A porpoise hybrid: Tursiops× Steno. *Journal of Mammalogy, 55*(1), 217-221.

Dudzinski, K. A., Clark, C. W., & Würsig, B. (1995). A mobile video/acoustic system for simultaneous underwater recording of dolphin interactions. *Aquatic Mammals, 21*, 187-194.

Durden, W. N., Stolen, E. D., & Stolen, M. K. (2011). Abundance, distribution, and group composition of Indian River Lagoon bottlenose dolphins (Tursiops truncatus). *Aquatic Mammals, 37*(2), 175.

Elliser, C. R., & Herzing, D. L. (2011). Replacement dolphins? Social restructuring of a resident pod of Atlantic bottlenose dolphins, Tursiops truncatus, after two major hurricanes. *Marine Mammal Science, 27*(1), 39-59.

Elliser, C. R., & Herzing, D. L. (2014). Social structure of Atlantic spotted dolphins, Stenella frontalis, following environmental disturbance and demographic changes. *Marine Mammal Science, 30*(1), 329-347.

Feldheim, K. A., Gruber, S. H., DiBattista, J. D., Babcock, E. A., Kessel, S. T., Hendry, A. P., ... & Chapman, D. D. (2014). Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks. *Molecular Ecology, 23*(1), 110-117.

Folkens, P. A., Reeves, R. R., Stewart, B. S., Clapham, P. J., Powell, J. A., (Eds.). (2002). *Guide to Marine Mammals of the World*, New York, New York: National Audubon Society.

Fox, J., & Weisberg, S. (2011). An R companion to applied regression, 2nd edn Sage. *Thousand Oaks, CA.*

Franchini, F., Smout, S., Blight, C., Boehme, L., Munro, G., Costa, M., & Heinrich, S. (2020). Habitat Partitioning in Sympatric Delphinids Around the Falkland Islands: Predicting Distributions Based on a Limited Data Set. *Frontiers in Marine Science, 7*, 277.

Griffin, R. B., & Griffin, N. J. (2003). Distribution, habitat partitioning, and abundance of Atlantic spotted dolphins, bottlenose dolphins, and loggerhead sea turtles on the eastern Gulf of Mexico continental shelf. *Gulf of Mexico Science, 21*(1), 3.

Grimmel, H. M., Bullock, R. W., Dedman, S. L., Guttridge, T. L., & Bond, M. E. (2020). Assessment of faunal communities and habitat use within a shallow water system using non-invasive BRUVs methodology. *Aquaculture and Fisheries*.

Gruber, S., & Parks, W. (2002). Mega-resort development on Bimini: sound economics or environmental disaster? *Bahamas Journal of Science, 9*(2), 2-18.

Hartig, F. (2018). DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package v. 0.2. 0.

Hastie, G. D., Barton, T. R., Grellier, K., Hammond, P. S., SwIFT, R. J., Thompson, P. M., & Wilson, B. (2003). Distribution of small cetaceans within a candidate Special Area of Conservation; implications for management. *Journal of Cetacean research and Management*, *5*(3), 261-266.

Hastie, G. D., Wilson, B. E. N., Wilson, L. J., Parsons, K. M., & Thompson, P. M. (2004). Functional mechanisms underlying cetacean distribution patterns: hotspots for bottlenose dolphins are linked to foraging. *Marine Biology, 144*(2), 397-403.

Heithaus, M. R. (2001). Shark attacks on bottlenose dolphins (Tursiops aduncus) in Shark Bay, Western Australia: attack rate, bite scar frequencies, and attack seasonality. *Marine Mammal Science, 17*(3), 526-539.

Heithaus, M. R., & Dill, L. M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology, 83*(2), 480-491.

Herzing, D. L. (1997). The life history of free-ranging Atlantic spotted dolphins (Stenella frontalis): Age classes, color phases, and female reproduction. *Marine Mammal Science, 13*(4), 576-595.

Herzing, D.L., & Johnson, C. M. (1997). Interspecific interactions between Atlantic spotted dolphins (Stenella frontalis) and bottlenose dolphins (Tursiops truncatus) in the Bahamas. 1985-1995. *Aquatic Mammals 23*(2), 85-99.

Herzing, D. L., Moewe, K., & Brunnick, B. J. (2003). Interspecies interactions between Atlantic spotted dolphins, Stenella frontalis and bottlenose dolphins, Tursiops truncatus, on Great Bahama Bank, Bahamas. *Aquatic Mammals 29*(3), 335-341.

Herzing, D. L., & Elliser, C. R. (2014). Nocturnal feeding of Atlantic spotted dolphins (Stenella frontalis) in the Bahamas. *Marine Mammal Science*, *30,* 367-373.

Herzing, D. L., Augliere, B. N., Elliser, C. R., Green, M. L., & Pack, A. A. (2017). Exodus! Large-scale displacement and social adjustments of resident Atlantic spotted dolphins (Stenella frontalis) in the Bahamas. *PloS One, 12*(8), e0180304.

Hung, S. K., & Jefferson, T. A. (2004). Ranging patterns of Indo-Pacific humpback dolphins (Sousa chinensis) in the Pearl River estuary, Peoples Republic of China. *Aquatic Mammals, 30*(1), 159-174.

Jaakkola, K, & Wliis, K. (2019). How long go dolphins life? Survival rates and life expectancies for bottlenose dolphins in zoological facilities vs. wild populations. Marine Mammal Science, *35*(4), 1418-1437. DOI: 10.1111/mms.12601

Jennings, D. E., Gruber, S. H., Franks, B. R., Kessel, S. T., & Robertson, A. L. (2008). Effects of large-scale anthropogenic development on juvenile lemon shark (Negaprion brevirostris) populations of Bimini, Bahamas. *Environmental Biology of Fishes, 83*(4), 369-377.

Jennings, D. E., DiBattista, J. D., Stump, K. L., Hussey, N. E., Franks, B. R., Grubbs, R. D., & Gruber, S. H. (2012). Assessment of the aquatic biodiversity of a threatened coastal lagoon at Bimini, Bahamas. *Journal of Coastal Conservation, 16*(3), 405-428.

Johnson, R. A., & Wichern, D. W. (2002). *Applied multivariate statistical analysis* (Vol. 5, No. 8). Upper Saddle River, NJ: Prentice hall.

Jutapruet, S., Huang, S. L., Li, S., Lin, M., Kittiwattanawong, K., & Pradit, S. (2015). Population size and habitat characteristics of the Indo-Pacific humpback dolphin (Sousa chinensis) off Donsak, Surat Thani, Thailand. *Aquatic Mammals, 41*(2), 129-142.

Kaplan, J. D., Goodrich, S. Y., Melillo-Sweeting, K., & Reiss, D. (2019). Behavioural laterality in foraging bottlenose dolphins (Tursiops truncatus). *Royal Society Open Science*, *6*(11), 190929.

Kinze, C. C., & Christie, D. A. (Eds.). (2003). *Marine mammals of the North Atlantic*, Princeton, New Jersey: Princeton University Press.

Kiszka, J., Simon-Bouhet, B., Martinez, L., Pusineri, C., Richard, P., & Ridoux, V. (2011). Ecological niche segregation within a community of sympatric dolphins around a tropical island. *Marine Ecology Progress Series*, *433*, 273-288.

Lenth, R., Singmann, H., & Love, J. (2018). Emmeans: Estimated marginal means, aka least-squares means. *R package version*, *1*(1).

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., ... & Brooks, M. M. (2017). Package ‘glmmTMB’. *R Package Version 0.2. 0*.

Melillo, K. E., Dudzinski, K. M., & Cornick, L. A. (2009). Interactions between Atlantic spotted (Stenella frontalis) and bottlenose (Tursiops truncatus) dolphins off Bimini, The Bahamas, 2003-2007. *Aquatic Mammals*, *35*(2), 281.

Melillo-Sweeting, K., Turnbull, S. D., & Guttridge, T. L. (2014). Evidence of shark attacks on Atlantic spotted dolphins (Stenella frontalis) off Bimini, The Bahamas. *Marine Mammal Science, 30*(3), 1158-1164.

Melillo-Sweeting, K., Yeater, D., & Dudzinski, K. M. (2015). Dolphin sightings near the coast of Bimini, The Bahamas, 2003-2013. *Aquatic Mammals, 41*(3), 245.

Melillo-Sweeting, K., & Maust-Mohl, M. (2019, December). Examining shark bite scars on bottlenose dolphins (Tursiops truncatus) off Bimini, The Bahamas. *Proceedings of the World Marine Mammal Conference*, Barcelona, Catalonia, Spain.

Mann, J. (1999). Behavioral sampling methods for cetaceans: a review and critique. *Marine Mammal Science, 15*(1), 102-122.

Mannocci, L., Catalogna, M., Dorémus, G., Laran, S., Lehodey, P., Massart, W., ... & Ridoux, V. (2014). Predicting cetacean and seabird habitats across a productivity gradient in the South Pacific gyre. *Progress in Oceanography*, *120*, 383-398.

Morrissey, J. F., & Gruber, S. H. (1993). Home range of juvenile lemon sharks, Negaprion brevirostris. *Copeia*, 425-434.

Newman, S. P., Handy, R. D., & Gruber, S. H. (2007). Spatial and temporal variations in mangrove and seagrass faunal communities at Bimini, Bahamas. *Bulletin of Marine Science, 80*(3), 529-553.

Newell, N. D., Imbrie, J., Purdy, E. G., & Thurber, D. L. (1959). Organism communities and bottom facies, Great Bahama Bank. *Bulletin of the AMNH*, *117*, article 4.

Perrin, W. (1970). Color pattern of eastern Pacific spotted porpoise *Stenella-graffmani lonnberg* (Cetacea, Delphinidae). *Zoologica-New York*, *54*(4), 13.

Perrin, W. F., Caldwell, D. K., & Caldwell, M. C. (1994). Atlantic spotted dolphin Stenella frontalis (G. Cuvier, 1829). *Handbook of Marine Mammals*, *5*, 173-190.

Perrin, W. F., Würsig, B., & Thewissen, J. G. M. (Eds.). (2009). E*ncyclopedia of marine mammals*, San Diego, California: Academic Press.

Pirotta, E., Laesser, B. E., Hardaker, A., Riddoch, N., Marcoux, M., & Lusseau, D. (2013). Dredging displaces bottlenose dolphins from an urbanised foraging patch. *Marine Pollution Bulletin*, *74*(1), 396-402.

Praca, E., & Gannier, A. (2008). Ecological niches of three teuthophageous odontocetes in the northwestern Mediterranean Sea.

R Core Team (2018). R: A language and environment for statistical computing [Computer software manual]. *Vienna, Austria*.

Reynolds, J. E., & Wells, R. S. (2003). *Dolphins, whales, and manatees of Florida*, Gainesville, Florida: University Press of Florida.

Ridgway, S. H., & Harrison, R. J. (Eds.). (1998). *Handbook of marine mammals: Volume 6: The second book of dolphins and the porpoises,* San Deigo, California: Academic Press.

Rogan, E., Cañadas, A., Macleod, K., Santos, M. B., Mikkelsen, B., Uriarte, A., ... & Hammond, P. S. (2017). Distribution, abundance and habitat use of deep diving cetaceans in the North-East Atlantic. *Deep Sea Research Part II: Topical Studies in Oceanography, 141*, 8-19.

Rossbach, K. A., & Herzing, D. L. (1997). Underwater observations of benthic-feeding bottlenose dolphins (Tursiops truncatus) near Grand Bahama Island, Bahamas. *Marine Mammal Science, 13*(3), 498-504.

Rossbach, K. A. (1999). Cooperative feeding among bottlenose dolphins (Tursiops truncatus) near Grand Bahama Island, Bahamas. *Aquatic Mammals*, *25*, 163-168.

Rossman, S., Berens McCabe, E., Barros, N. B., Gandhi, H., Ostrom, P. H., Stricker, C. A., & Wells, R. S. (2015). Foraging habits in a generalist predator: sex and age influence habitat selection and resource use among bottlenose dolphins (Tursiops truncatus). *Marine Mammal Science, 31*(1), 155-168.

Schallenberg, M., & Burns, C. W. (2004). Effects of sediment resuspension on phytoplankton production: teasing apart the influences of light, nutrients and algal entrainment. *Freshwater Biology*, *49*(2), 143-159.

Scoffin, T. P. (1970). The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *Journal of Sedimentary Research, 40*(1), 249-273.

Shane, S. H., Wells, R. S., & Würsig, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: a review. *Marine Mammal Science*, *2*(1), 34-63.

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.*, (245-265). San Diego, California: Academic Press.

Shirihai, H., Jarrett, B., & Kirwan, G. M. (Eds.). (2006). *Whales, dolphins, and other marine mammals of the world*, Princeton, New Jersey: Princeton University Press.

Sprogis, K. R., Christiansen, F., Raudino, H. C., Kobryn, H. T., Wells, R. S., & Bejder, L. (2018). Sex-specific differences in the seasonal habitat use of a coastal dolphin population. *Biodiversity Conservation* 1-20.

Sprogis, K. R., King, C., Bejder, L., & Loneragan, N. R. (2018). Frequency and temporal trends of shark predation attempts on bottlenose dolphins (Tursiops aduncus) in temperate Australian waters. *Journal of Experimental Marine Biology and Ecology*, *508*, 35-43. doi:https://doi.org/10.1016/j.jembe.2018.08.008

Squires, D. F. (1958). Stony corals from the vicinity of Bimini, Bahamas, British West Indies. *Bulletin of the AMNH*, *115*, article 4.

Svendsen, G. M., Romero, M. A., Williams, G. N., Gagliardini, D. A., Crespo, E. A., Dans, S. L., & González, R. A. (2015). Environmental niche overlap between common and dusky dolphins in North Patagonia, Argentina. *PloS One*, *10*(6).

Toth, J. L., Hohn, A. A., Able, K. W., & Gorgone, A. M. (2011). Patterns of seasonal occurrence, distribution, and site fidelity of coastal bottlenose dolphins (Tursiops truncatus) in southern New Jersey, USA. *Marine Mammal Science, 27*(1), 94-110.

Toth, J. L., Hohn, A. A., Able, K. W., & Gorgone, A. M. (2012). Defining bottlenose dolphin (Tursiops truncatus) stocks based on environmental, physical, and behavioral characteristics. *Marine Mammal Science, 28*(3), 461-478.

Trave, C., & Sheaves, M. (2014). Bimini Islands: a characterization of the two major nursery areas; status and perspectives. *SpringerPlus, 3*(1), 270.

Urian, K., Duffield, D., Read, A., Wells, R., & Shell, E. (1996). Seasonality of reproduction in bottlenose dolphins, Tursiops truncatus. *Journal of Mammalogy, 77*(2), 394-403.

Voss, G. L., & Voss, N. A. (1960). An ecological survey of the marine invertebrates of Bimini, Bahamas, with a consideration of their zoogeographical relationships. *Bulletin of Marine Science, 10*(1), 96-116.

Weilgart, L. S. (2007). The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Canadian Journal of Zoology, 85*(11), 1091-1116.

Weir, J. S., Duprey, N. M. T., & Würsig, B. (2008). Dusky dolphin (Lagenorhynchus obscurus) subgroup distribution: are shallow waters a refuge for nursery groups? *Canadian Journal of Zoology, 86*(11), 1225–1234. https://doi org.ezproxylocal.library.nova.edu/10.1139/Z08-101

Wells, R., Irvine, A. B., & Scott, M. (1980). The social ecology of inshore odontocetes In L. M. Herman (Editor), *Cetacean Behavior: Mechanisms & functions* (pp. 263-317), Berkley and Los Angeles, California, University of California Press.

Wells, R., Scott, M., & Irvine, A. B. (1987). The Social Structure of Free-Ranging Bottlenose Dolphins, In H. H. Genoways (Editor), *Current Mammalogy* (Vol. 1., pp. 247- 305), New York, New York; Plenum Press.

Wells, R. S., & Scott, M. D. (1998). Bottlenose dolphin Tursiops truncatus (Montagu, 1821). In S. Ridgway & H. Richard (Eds.), *Handbook of Marine Mammals: The second book of dolphins and the porpoises* (Vol. 6., pp. 137-182), San Diego, California: Academic Press.

Würsig, B., & Würsig, M. (1979). Behavior and ecology of the bottlenose dolphin (*Tursiops truncatus*) in the South Atlantic. *Fishery Bulletin, 77*(2), 399-412

Würsig, B., & Harris, G. (1990). Site and Association Fidelity in Bottlenose Dolphins Off Argentina In S. Leatherwood & R.R. Reeves (Eds.), *The Bottlenose Dolphin* (pp. 361-365), San Diego, California: Academic Press.

Zhang, P., Han, J., Lu, Z., & Chen, R. (2014). Molecular Evidence of a Captive-Born Intergeneric Hybridization Between Bottlenose and Risso's Dolphins: Tursiops truncatus× Grampus griseus. *Aquatic Mammals*, *40*(1), 5.

Zornetzer, H. R., & Duffield, D. A. (2003). Captive-born bottlenose dolphin x common dolphin (Tursiops truncatus x Delphinus capensis) intergeneric hybrids. *Canadian Journal of Zoology*, *81*(10), 1755–1762. https://doi-org.ezproxylocal.library.nova.edu/10.1139/Z03-150