Analyzing the Strength of Male Bottlenose Dolphin (*Tursiops truncatus*) Associations In North Carolina

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Introduction

Background

The common bottlenose dolphin (*Tursiops truncatus*) inhabits temperate and tropical waters worldwide (Leatherwood and Reeves, 1983). The Northwest Atlantic populations of common bottlenose dolphins are categorized into two distinct ecotypes: coastal and pelagic (Waring et al. 2015). Coastal bottlenose dolphins reside in nearshore coastal waters, such as gulfs, bays, sounds and river mouths (Waring et al. 2015). Additionally, these dolphins are lighter grey in color and smaller in size compared to their pelagic counterparts.

Bottlenose dolphins live in fission-fusion societies (Mann, 2000), where individuals regularly split and rejoin, making group membership highly fluid (Wilson et al. 1999). However, adult male bottlenose dolphins tend to form first-order alliances comprised of two to three individuals, which can persist for several years and are meant to increase mating success with receptive females (Connor *et al*. 1992). Two first-order alliances may combine to form a second-order alliance, which allows the males to overtake a female being herded by another first-order alliance or defend one or more females from other potential mates (Connor et al. 1992a). First-order alliances between males have been reported in bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida (Wells et al. 1987; Owen et al. 2002) and the St. Johns River near Jacksonville (Gibson and Brightwell 2017), as well as in bottlenose dolphins (*Tursiops aduncus*) in Port Stephens, Australia (Möller et al. 2001) and Shark Bay, Australia (Connor et al. 1992), yet second-order alliances have only been documented at the Jacksonville and Shark Bay sites. Some males, however, remain solitary, and the strength and duration of male pair associations varies across locations (Kappeler 2000; Whitehead & Connor 2005; Gehrt 2008; Ermak *et al*, in review).

Hamilton (1964a, b) argued that cooperation among related individuals may be favored by kin selection because individuals can increase their inclusive fitness by assisting relatives' reproduction, even if the direct benefit of increased reproductive success applies to only one or a few of the cooperating individuals. However, in most cases, genetic analyses and observational data from long-term studies of dolphins reveal that members of a male pair are often not closely related (Duffield & Wells, 2002; Möller *et al*. 2001). The only known exception is the population of bottlenose dolphins that reside in Shark Bay, Australia. According to a study by Krützen *et al*. (2003), it was discovered that males who cooperated in stable first-order alliances were, on average, significantly more closely related to each other than expected by chance. They also discovered that males in Shark Bay were significantly related to their second-order alliance partners as well, but the average relatedness among all super-alliance members was not significantly different from the average relatedness of all males, implying a negative association between relatedness and group size.

Male pairs are much more prevalent than female or mixed sex pairs. Generally, adult females with newborns or juvenile calves will form loose networks of associates with other female mothers, so their calves can develop critical social skills and become successful adults (Gibson & Mann, 2008a; Wells 2003; Wells *et al*. 1987). It is much more likely to see males and females together within a group than as a pair, as they typically only pair briefly to reproduce (Smolker *et al*., 1992; Wells *et al*. 1987).

Male bottlenose dolphins show affiliation through spatial proximity, physical contact and synchronous movements (Connor 2000). Spatial proximity, or how close together the individuals are upon sighting, is the best-known method to measure the strength of association between them (Ginsberg & Young, 1992; Whitehead 2008). The most common measure of association is termed the half-weight index, which is calculated from a mathematical equation based on the number of times individuals are observed together as well as apart (Kovacs *et al*. 2013). The greater the COA value, the more likely a relationship exists (Brager *et al*., 1994; Connor *et al*. 2000).

Photo-identification, a non-invasive mark-recapture technique, is used to identify individual dolphins by analyzing their distinctive dorsal fin markings such as nicks, notches, scars and rake marks. Through this technique, it is possible to acquire more knowledge about dolphin distribution, movement patterns, social associations, health and behavior over time. Photo-identification may also be combined with tagging and genetic studies to further study populations (Irvine *et al*., 1982; Scott *et al*., 1990; Waring *et al*. 2015).

This present study was conducted through the Outer Banks Center for Dolphin Research (OBXCDR), an organization that has conducted a long-term photo-identification monitoring study of bottlenose dolphins in the northern Outer Banks of North Carolina since 2008. Several prior studies have identified seasonal exchange in individuals between the northern Outer Banks and Beaufort, NC (Mason and Taylor, 2016; Fuentes and Taylor, 2015; McKeowan and Taylor, 2014).

Objectives

Our objectives were to investigate whether males in the northern Outer Banks formed and maintained first-order alliances, speculate as to whether second order alliances may exist, and examine the strength of these same associations at a study site in Beaufort.

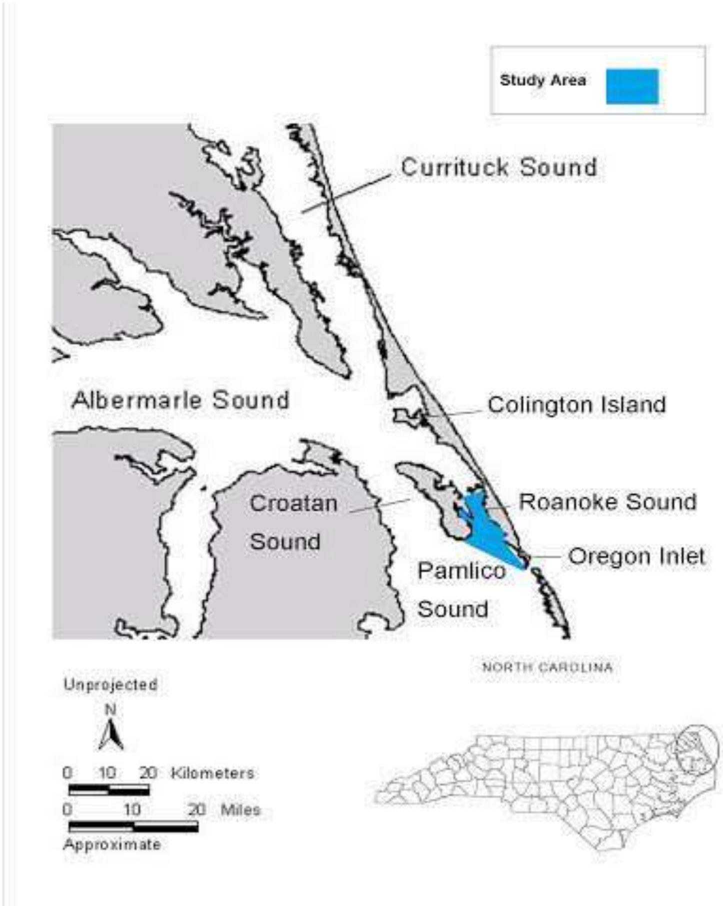
Methods

Study Areas

The Roanoke Sound is a narrow body of water that separates Roanoke Island from Nags Head. It encompasses approximately 41 square miles, extending from the northern tip of Roanoke Island to the northern tip of Oregon Inlet (Figure 1). On average, this body of water is slightly greater than 1 meter in depth, so a man-made channel was dredged to allow large vessels to travel along the Intracoastal Waterway. The Roanoke

Sound is ideal for recreational and commercial fishing, as well as family activities such as boating and watersports.

Figure 1. Roanoke Sound Study Area



The Beaufort study area encompasses the coastal waters of Beaufort, NC and is located approximately 177 miles southwest of the Roanoke Sound (Figures 2 and 3). The Cape Lookout Studies Photo-Identification Program maintains a long-term photo-identification study of the bottlenose dolphins that inhabit those waters (Table 1), and regularly collaborates with other researchers along the east coast to examine their seasonal movement patterns and social associations.

Figure 2. Beaufort Study Area

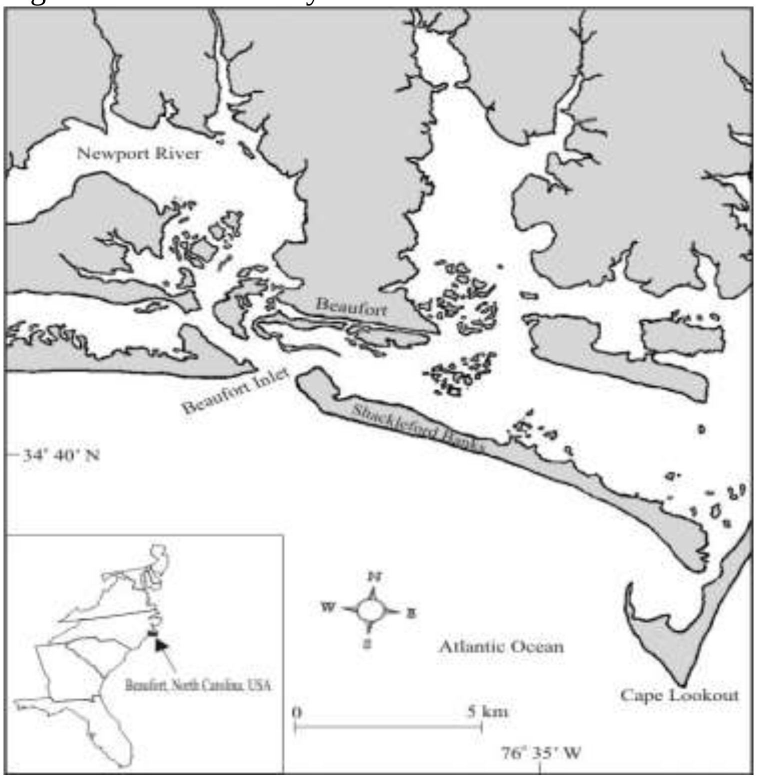


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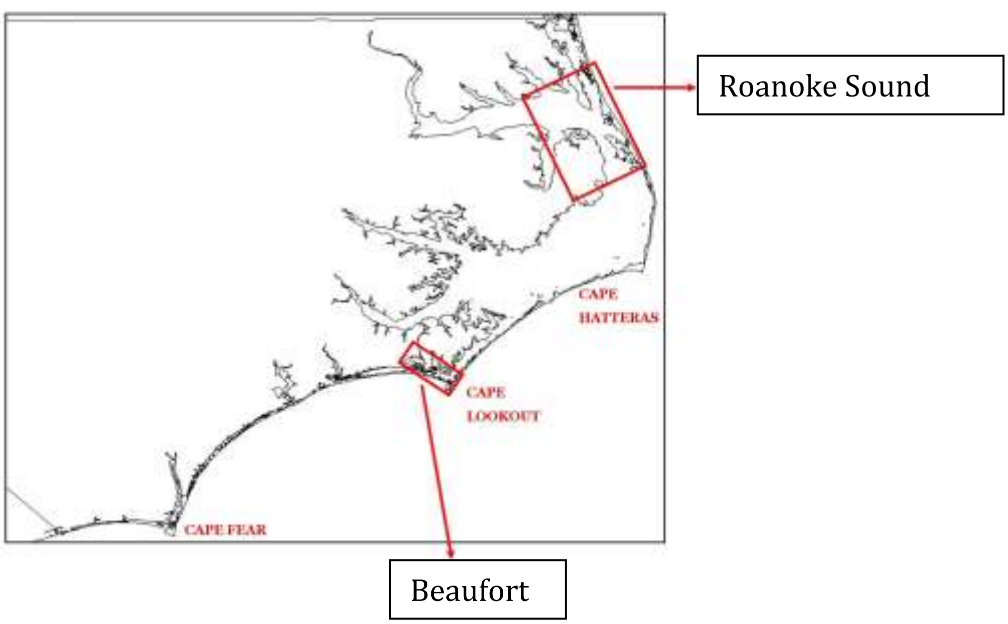
Figure 3. Aerial view of Roanoke Sound and Beaufort study areas



Data Collection

The Outer Banks Center for Dolphin Research regularly conducts dedicated and opportunistic photo-identification surveys of bottlenose dolphins (*Tursiops truncatus*) within the Roanoke Sound (Figures 4 and 5). Exploratory surveys were conducted in the southernmost part of the sighting area during October 2007. Dedicated photo-identification surveys were conducted at least once per month during June – August 2008, February 2009, and May – October 2009, 2010 and 2011. In November 2011, a standardized transect route was created with MapSource and uploaded to a GPS unit so the entire sighting area could be surveyed. Surveys were conducted from a small 16' or 17' outboard vessel under a General Authorization (GA) Permit, LOC-13416, LOC-17988 awarded to J. Taylor. Once a group of dolphins was sighted, the vessel left the trackline to begin a sighting. During the sighting, standard photo-identification techniques were conducted (Würsig & Würsig, 1977). Data such as the written location, GPS coordinates, weather (i.e. cloud cover, visibility, sightability, and precipitation) and water conditions (i.e. swell, Beaufort sea state, temperature and salinity) were recorded. The sighting lasted until all dolphins in the group were photographed, the dolphins were lost, or dolphins exhibited repeated avoidance behaviors. Once the sighting was concluded, the research vessel returned to the transect line and continued along the specified route until another group of dolphins was spotted or until the route was completed.

Opportunistic surveys were conducted onboard the Nags Head Dolphin Watch from May 2008 – October 2014. Upon sighting a group of dolphins, the captain would abide by the National Marine Fisheries Service (NMFS) Viewing Code of Conduct for bottlenose dolphins in the southeast region, established in accordance with the Marine Mammal Protection Act. Sightings were therefore limited to 30 minutes and dolphins were approached at a distance of no closer than 50 yards (NOAA 2012). Photographic and behavioral data were collected using the same protocol as the dedicated surveys.

Figure 4. Annual field survey effort of dedicated and opportunistic surveys 2008-2014

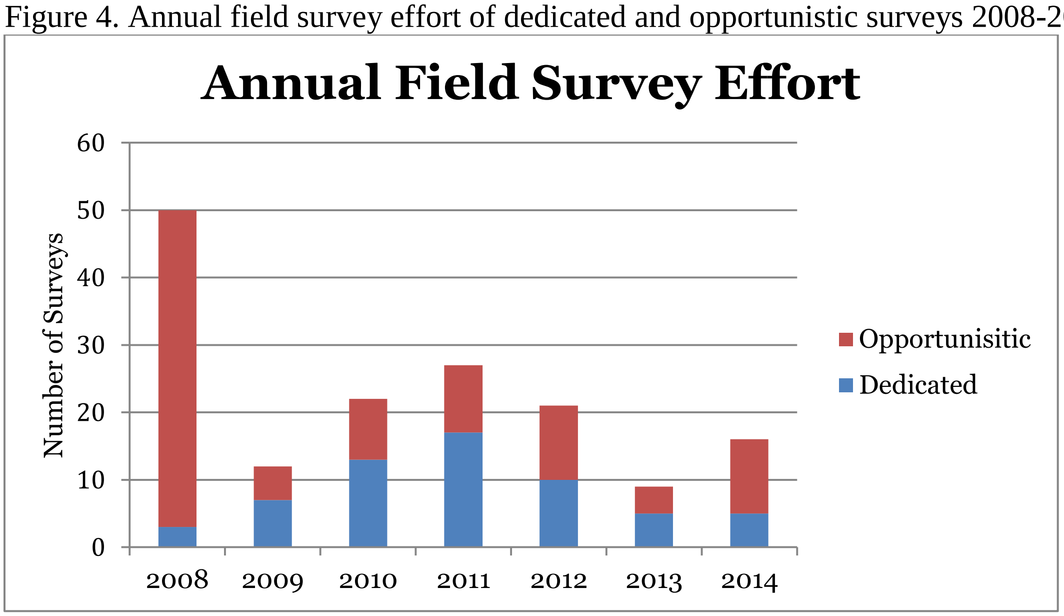
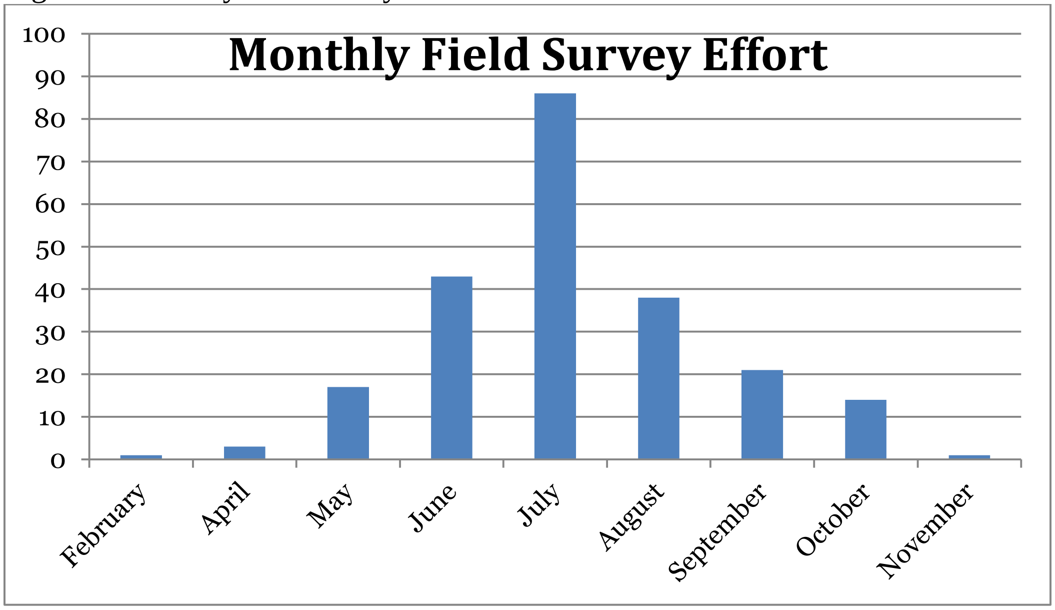


Figure 5. Monthly field survey effort 2008-2014



Data Analysis

The program FinBase (Adams et al. 2006) was utilized to process the photo-identification images and sighting data collected in the Roanoke Sound. Dorsal fin images from dedicated and opportunistic surveys were sorted, graded for photo quality, and matched to the NC-OBXCDR photo-identification catalog, which spans from October 2007 – October 2014. Once a researcher matched an individual to the catalog, another individual would verify the match to minimize error.

A matrix was created using FinBase to calculate the half-weight coefficient of association (COA) for each individual observed in Roanoke Sound with every other individual in the Roanoke Sound catalog. The COAs were calculated using the following equation: $\frac{X}{X+1/2(N_a+N_b)}$ where X is the number of times both individuals were observed together, N_a is the number of times that Individual A was seen without Individual B, and N_b is the number of times Individual B was seen without Individual A. The resulting value is indicative of the amount of time two individuals spend together, hence the strength of their pair bond (Kovacs *et al*. 2013). A value of 0 signifies that the two individuals were never sighted together, and a value of 1 means that they were always sighted together. Each COA was categorized as a low (0.3-0.39), medium (0.4-0.69), or high (≥0.7) association (Kovacs *et al*. 2013).

A sample of the Roanoke Sound population was previously sexed during routine health assessments and/or tagging studies in Beaufort, NC (Waring et al. 2015); the known males from this sample were selected for analysis of association patterns. Sex determination was also available for a few individuals that stranded during the study period based upon necropsy results. These males were included in the analysis as well. Lastly, a sample of probable males was included in the dataset, and those individuals were selected based on the following conditions: 1) the CoA between a known male and an individual was higher than between the known male and the remaining individuals, 2) two individuals (sex unknown) had a higher CoA with one another exclusively, 3) an individual frequently associated with other known or probable males, according to their CoA measurements and 4) the individual was an adult never seen with a dependent calf for at least 5 years. The COAs of the male pairs with high-level associations in Roanoke Sound were calculated in Beaufort using sighting data collected from the NC-NCMM catalog. Summary statistics spreadsheets were created to visually display sighting details of the males and probable males in Roanoke Sound and in Beaufort.

Table 1. Catalogs used to Assess Male Pairs in Roanoke Sound and Beaufort

Catalog	**Contributor / Affiliation**	**Study Area**	**Catalog Size**	**Catalog Dates**
NC-OBXCDR	Jessica Taylor / Outer Banks Center for Dolphin Research	Roanoke Sound	837	2007-2015
NC-NCMM	Keith Rittmaster / NC Maritime Museum	Beaufort, NC	3,237	1989-2016

Results

<u>Roanoke Sound</u>

Of the 19 males in the sample (Table 2), four were confirmed based upon necropsy results and three were confirmed from health assessment/tagging studies. The remaining twelve individuals were presumed to be males. OBX135 was sighted most frequency (n=173), whereas OBX541 was sighted the least (n=15 sightings). The average number of sightings was 103.4.

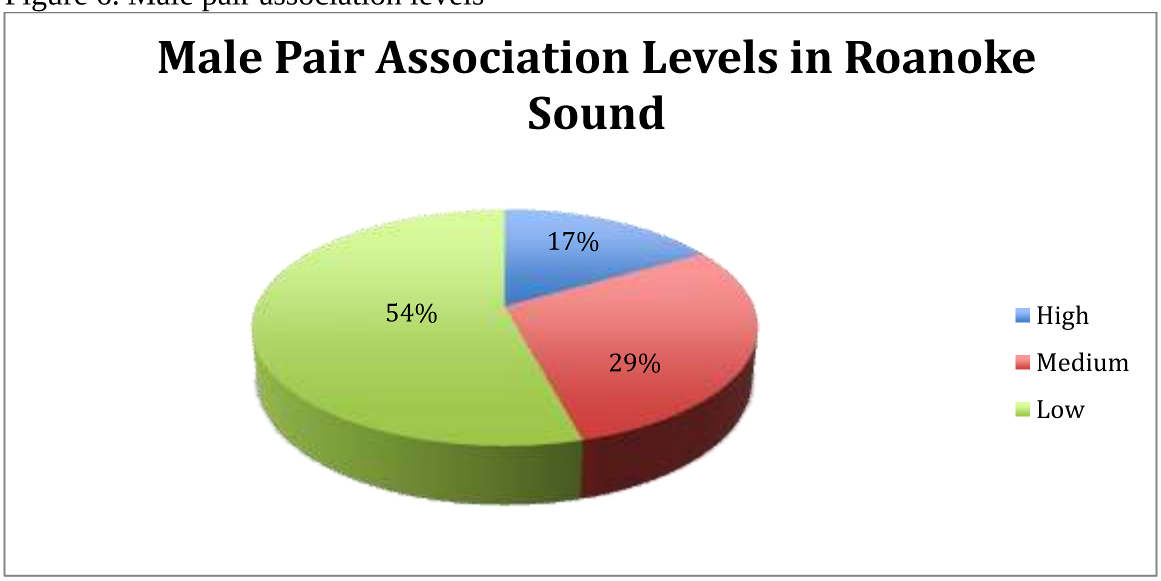
Table 2. Individual Males from the NC-OBXCDR Catalog

NC-OBXCDR ID Number	Alias/Name	1st Sighting	Total Times Sighted	Sex
1	Mohammed	10/7/2007	122	Male (Necropsied)
9	Buddha	10/7/2007	91	Male (Necropsied)
7	Onion	10/7/2007	119	Probably Male
8	Pinchers	10/7/2007	106	Male (Necropsied)
317	708	7/29/2008	131	Male (Freeze Brand)
318	Sequoia	6/5/2008	124	Probably Male
112	Rake	6/14/2008	135	Probably Male
135	92	6/20/2008	173	Probably Male
13	Sprite	10/7/2007	93	Probably Male
561	Cola	6/23/2010	55	Probably Male

128	Moose	6/17/2008	85	Probably Male
221	Tetris	6/25/2008	53	Probably Male
90	Lilo	6/5/2008	144	Probably Male
89	Stitch	6/5/2008	101	Probably Male
553	Curly	6/30/2009	42	Male (Necropsied)
541	Mo	9/11/2009	15	Probably Male
18	Skylar	10/7/2007	146	Male (Freeze Brand)
126	Rainbow	6/17/2008	125	Male (Freeze Brand)
240	Kerner	7/5/2008	105	Probably Male

The COAs calculated for each male pair spanned between 0.3 and 0.9; OBX01 and OBX09 (deceased since 2015) were measured to have the greatest level of association (COA = 0.86), whereas OBX126 and OBX07 were measured to have the weakest level of association (COA = 0.31). Of the 24 total associations, 54% of the associations were measured as low (n=13), nearly 30% of the associations were measured as medium (n=7), and 17% of the associations were measured as high (n=4) (Figure 6).

Figure 6. Male pair association levels



Of the twenty-two associated males in the medium and high-level categories, eight were associated with at least one other male besides their actual pair member (Figures 7-9), suggesting that male pairs do not associate with only each other. According to the COA values, these males would associate with 2-4 other males. In addition, three males did not appear to have a pair member, as they shared similar low-level COAs with a small group of 4-5 males (see figures 8-9, numbers OBX18, OBX126 and OBX240).

Figure 7. Male pairs with COAs measured within the high-level range (≥.7)

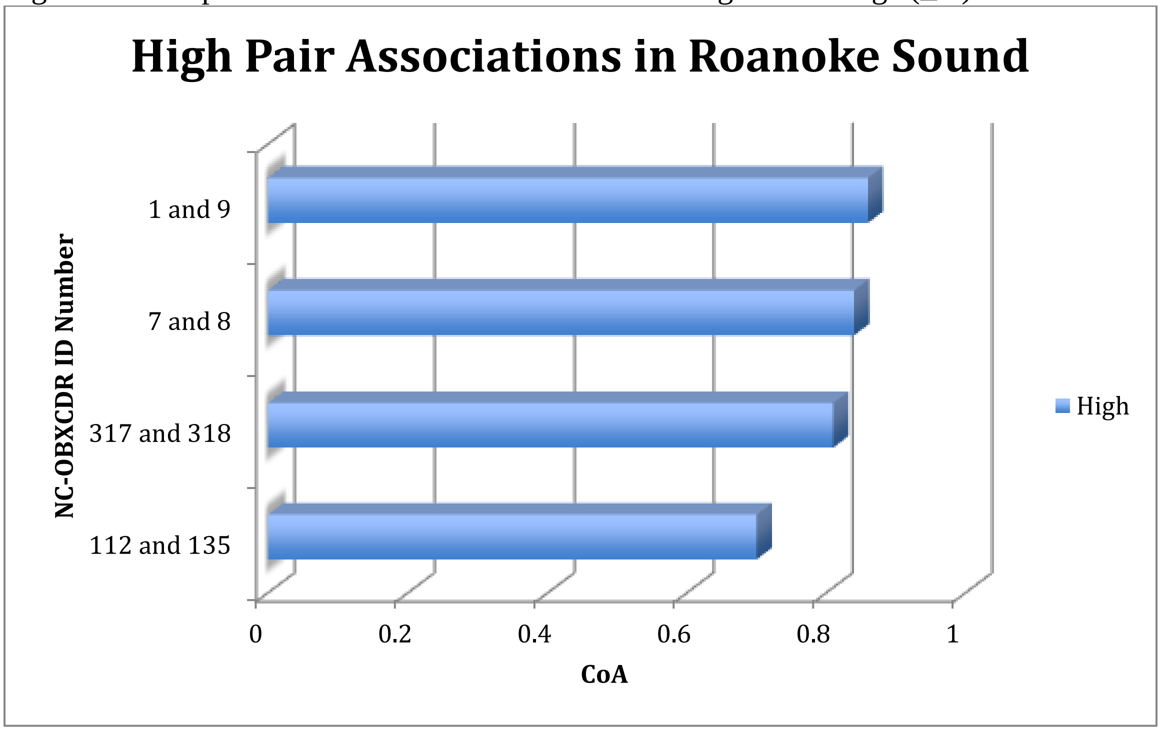


Figure 8. Male pairs with COAs measured within the mid-level range (0.4-0.69)

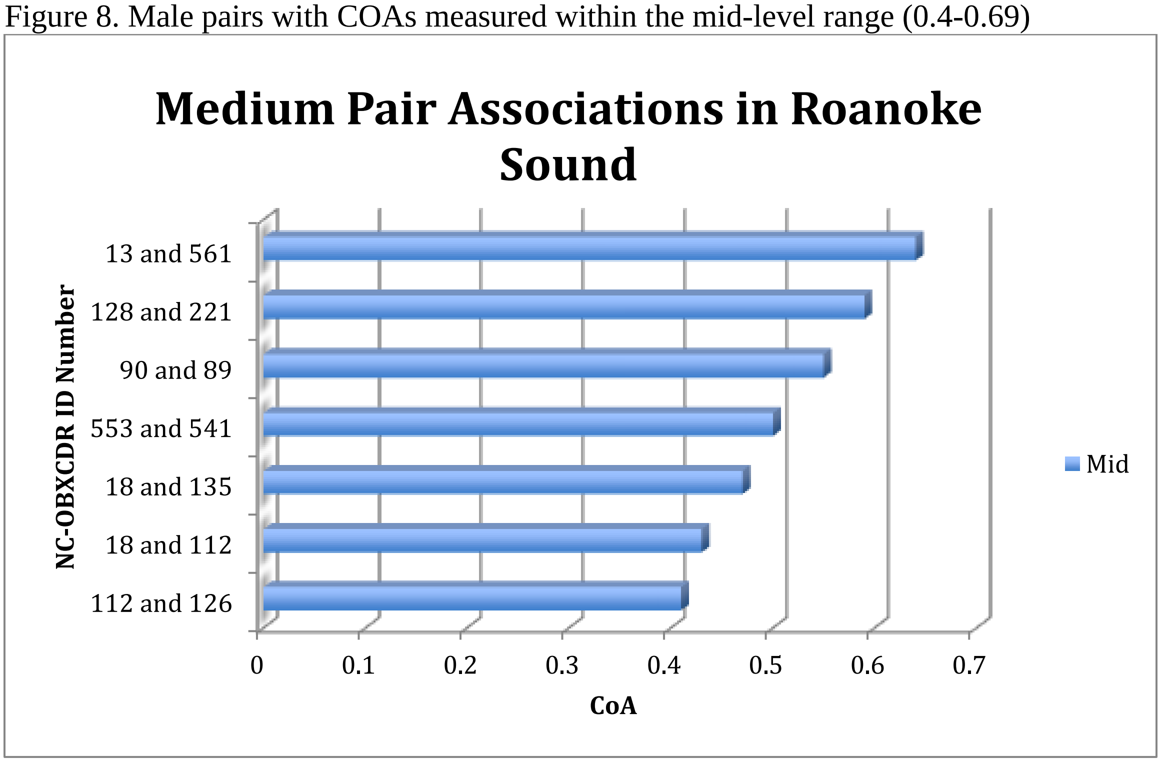
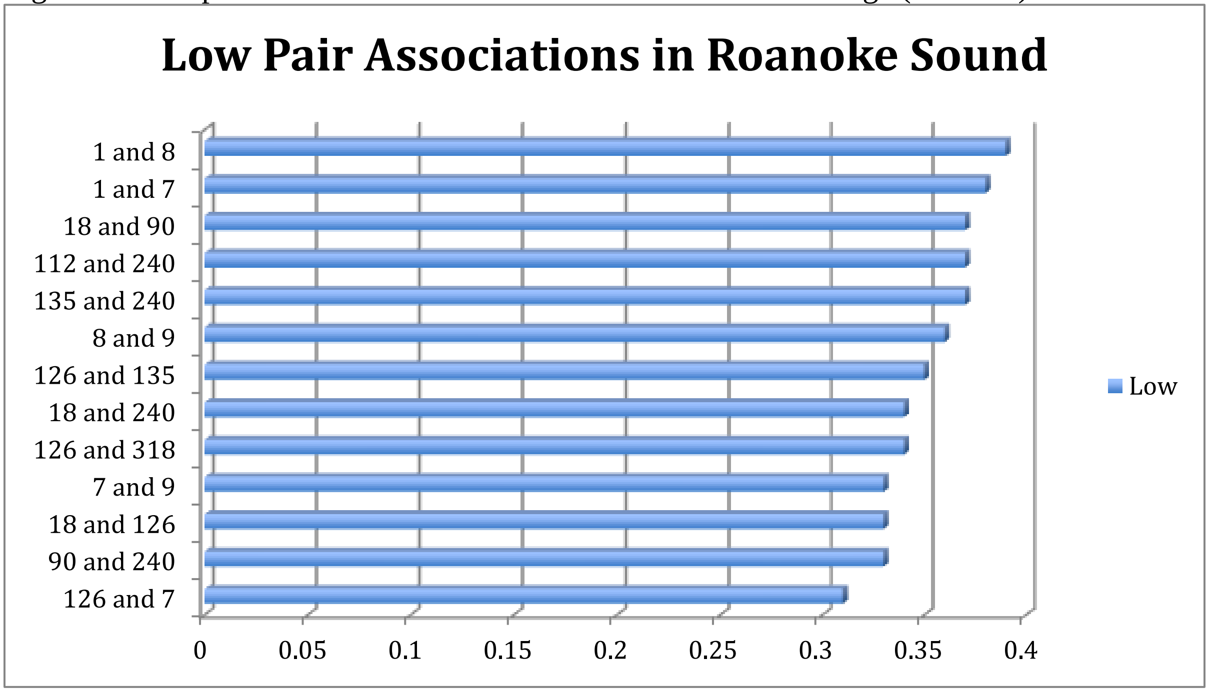


Figure 9. Male pairs with COAs measured within the low-level range (0.3-0.39)



Beaufort

The eight highly associated males from the NC-OBXCDR catalog were examined for pair stability in Beaufort using the NC-NCMM catalog (Table 3). NCMM0026 (OBX07) had the greatest number of sightings (n=128) and has been seen in the area since 1993, whereas NCMM1188 (OBX318) had the least number of sightings (n=13) and has been seen in the area since 1997.

Table 3. Individual Males from the NC-NCMM Catalog

NC-NCMM ID Number	NC-OBXCDR ID Number	Alias/Name	1st Sighting	Total Times Sighted
0618	01	Mohammed	1/30/1992	99
1142	09	Buddha	3/29/1994	93
0026	07	Onion	4/23/1990	128
0271	08	Pinchers	12/31/1993	103
1356	317	708	7/11/1995	35
1188	318	Sequoia	10/12/1997	13
1870	112	Rake	2/24/1996	14
2039	135	92	10/12/1997	24

Male pairs 1 and 2 were calculated as having nearly identical COAs in both Roanoke Sound and Beaufort (MP1 COAs = 0.86 and 0.89; MP2 COAs = 0.84 and 0.89), whereas a greater variation in COAs was observed between each area for male pairs 3 and 4 (Table 4). The COAs corresponding to male pairs 3 and 4 remained in the high-level category while the individuals were observed in the Roanoke Sound. In Beaufort however, the COA of male pair 3 dropped to the mid-level category, and the COA of male pair 4 dropped so substantially that it was not even within the range of the low-level category.

Table 4. Highly Associated Male Pair COA values in Roanoke Sound and Beaufort Study Areas

Male Pairs	NC-NCMM ID Numbers	NC-OBXCDR ID Numbers	Times Observed Together	Roanoke Sound COA	Beaufort COA
1	0618 and 1142	01 and 09	85	0.86	0.89
2	0026 and 0271	07 and 08	103	0.84	0.89
3	1356 and 1188	317 and 318	10	0.81	0.42
4	1870 and 2039	112 and 135	2	0.70	0.11

Discussion

This present study builds upon two previous male pair association studies conducted by Bowles and Rittmaster (1998) and Taylor *et al.* (2011). The COA values of male pairs 1 and 2 in 1998 were calculated as 0.77 and 0.89, respectively, and in 2011 these males still maintained a high level of association with each other (COAs = 0.89 and 0.91). The COAs for male pairs 1 and 2 calculated in 2011 resemble those recorded in 2017, with the exception of male pair number 4. In 2011 and 2017, male pair 4 was highly associated in the Roanoke Sound. In Beaufort, however, their COA dropped to mid-level in 2011 (COA = 0.58) and then dropped substantially in 2017 (COA = 0.11) (Table 5).

Table 5. Male pair stability in both study areas between 1998-2017

Male Pairs	NC-NCMM ID Numbers	NC-OBXCDR ID Numbers	Year	COA (Beaufort)	COA (Roanoke Sound)
1	0618 and 1142	01 and 09	1998	0.77	
2	0026 and 0271	07 and 08	1998	0.89	

1	0618 and 1142	01 and 09	2011	0.89	0.9
2	0026 and 0271	07 and 08	2011	0.91	0.95
4	1870 and 2039	112 and 135	2011	0.58	0.92
1	0618 and 1142	01 and 09	2017	0.89	0.86
2	0026 and 0271	07 and 08	2017	0.89	0.84
4	1870 and 2039	112 and 135	2017	0.11	0.7

Wells (2003) defined males as pair members if their COA remained ≥0.8 over time. Although only four high-level associations seem to exist in the Roanoke Sound, two of those associations have maintained a COA >0.8 over the past 19 years. This strongly suggests that long-term male pair associations do exist in this area. The remaining two highly associated pairs in the present study were not included in the 1998 study, so it cannot be determined whether they have maintained long-term associations with each other since then. However, the later study conducted in 2011 does include one of those pairs (OBX112-OBX135), and reveals that those individuals have maintained similar, high-levels of association in the Roanoke Sound, yet lower and much more variable COAs in Beaufort. Neither study has included the fourth and final highly associated pair (OBX317-OBX318) in their analyses, so those individuals should be included in a follow-up study to determine their stability as a pair.

There are a few specific factors that could explain the inconsistent COA values observed between the male pairs analyzed in 2011 and 2017. One factor is the lack of sightings in Beaufort; perhaps these individuals typically remained outside the borders of the study area. Each study area is likely unique in environmental, ecological, and reproductive pressures that affects the dolphins. Environmental pressures may include variation in available food sources between the study areas, which could have also have implications for availability of potential mates as well. If food sources were scarcer in the Beaufort study area, perhaps male pairs 3 and 4 moved beyond the study area for foraging. Predation risk may vary between study areas as well; a greater predation risk may exist in the Roanoke Sound area, influencing the formation of second-order alliances for increased protection. Lastly, in terms of reproductive pressures, the Beaufort study area may provide males with higher encounter rates with receptive females, reducing the need for cooperation in pairs. Future studies should focus on expanding study areas, especially to the coastal waters in the Outer Banks, to better increase sightings of these individuals and to gain more insight into the driving forces behind the changes in their associations.

In Roanoke Sound, the presence of medium and low-level associations could suggest that future first-order alliances are currently developing, or that second-order alliances exist within the population. In second-order alliances, males are known to regularly change their first-order alliance partners and exhibit significant partner preferences and avoidances (Connor *et al*. 1999, 2001). Evidence does exist for second-order alliances in the Roanoke Sound. For instance, OBX01 and OBX09 are a highly associated male pair, but according to their COA values, are also loosely associated with OBX07 and OBX08 (average COA = 0.36, respectively), another highly associated male pair. Additionally, their COA values show that they typically do not associate with other males, suggesting preference and avoidance of certain individuals. Future studies should focus on more detailed observations of male pairs in Roanoke Sound by using focal follows, increasing the sighting dataset size to better quantify association patterns, and constructing dendrograms to better analyze association patterns and further examine the presence of second-order alliances within known populations.

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