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THE SOCIAL STRUCTURE OF BOTTLENOSE DOLPHINS, *TURSIOPS TRUNCATUS*, IN THE BAHAMAS

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ABSTRACT

The social structure of coastal ecotype bottlenose dolphins, *Tursiops truncatus*, is largely unknown as they inhabit regions far from shore. This study reports on a community of bottlenose dolphins $\geq$ 27 km from Grand Bahama Island (May–September, 1993–2002). Resident and non-resident dolphins occurred in the area. Some dolphins traveled over 320 km between communities; others showed long-term site fidelity up to 17 yr. Average group size was 3–5, and was significantly larger with calves present and significantly smaller when traveling. The half-weight index was used to determine coefficients of association (COA) for individuals of known sex annually and for pooled years. Permutation tests revealed non-random associations and presence of preferred/avoided companions in all data sets. Annual COAs were low: female-female $x = 0.31$, male-male $x = 0.30$, and mixed-sex $x = 0.26$. Mother–calf associations showed the highest values. Some males formed strong, long-term bonds. Female COAs fluctuated with reproductive status. Using pooled data, COAs were lower and the same basic trends were evident. However, strong associations seen in the annual data were not evident in pooled data. Bottlenose dolphins that inhabit offshore, shallow water show many of the same social structure characteristics as in well-studied coastal populations.

Key words: bottlenose dolphin, *Tursiops truncatus*, coefficients of association, group size, site fidelity, social structure.

Studies of demography and social structure of bottlenose dolphins, *Tursiops* sp., are typically conducted within a few kilometers of shore (up to 5 km, Wells *et al.* 1987; up to 5.5 km, Ballance 1990; up to 0.4 km, Hansen 1990; up to 1 km, Würsig and Harris 1990, Smolker *et al.* 1992; up to 2 km, Quintana-Rizzo and Wells 2001; up to 2 km, Gubbins 2002*a*, Krützen *et al.* 2003). However, little research has focused on bottlenose dolphin populations that occur more than a few kilometers off the coast, such as occur in the Bahamas. This study provides a unique look at coastal ecotype bottlenose dolphins (*Tursiops truncatus*) living far from shore.

Similarities in social structure of odontocetes in similar habitats reveal that ecological forces act strongly on the social behavior of cetaceans (Wells *et al.* 1980). In comparison to marine environments, extensive data have been collected on terrestrial social systems and ecology, allowing in-depth analysis on the evolution and ecology of sociality (Wells *et al.* 1980). Studies on many birds and terrestrial mammals have correlated social structure with various ecological parameters (Crook 1970, Eisenberg *et al.* 1972, Crook *et al.* 1976, Rubenstein and Wrangham 1986). Advances and more detailed research in GIS, mapping, and habitat analysis in the marine environment have provided additional insight into the correlation between cetacean sociality and ecology in recent years. Our study offers a look into the similarities and differences of the social structure of this relatively unstudied coastal ecotype in a unique habitat that occurs far from land, and allows comparisons with other well-studied coastal populations and habitats.

This population of bottlenose dolphins inhabits the western edge of Little Bahama Bank (LBB) north of Grand Bahama Island (Fig. 1). The dolphins observed are divided into two types based on coastal proximity, close to shore (from West End, Grand Bahama up to 19 km) and $\geq$27 km offshore. Rossbach and Herzing (1999) determined that these two communities of dolphins (both close and far from shore) were of the single coastal ecotype, as they inhabit warm, shallow waters and are relatively small (about 2.4 m in length) compared to dolphins of the offshore ecotype seen in the Gulf Stream of the Straits of Florida found farther to the west. This coastal ecotype in the Bahamas was termed the Northern ($\geq$ 27 km offshore) and Southern (closer to shore) communities based on association and range patterns (Rossbach 1997, Rossbach and Herzing 1999) (Fig.1).

The overall objective of this study was to determine the social structure of the Northern community of coastal ecotype bottlenose dolphins occurring far from shore. Our specific objectives were to: (1) determine whether these dolphins are resident, by showing long-term site fidelity and regular resightings; (2) calculate the average group size and does it change in relation to behavior and presence/absence of calves; (3) calculate association indices of individuals of known sex, both annually and pooled over 5- and 10-yr periods; (4) determine whether the dolphins show non-random associations and if there are preferred and/or avoided companions; (5) compare COA values between same sex and mixed-sex pairs; and (6) compare these results to the social structure of other well-studied coastal populations.

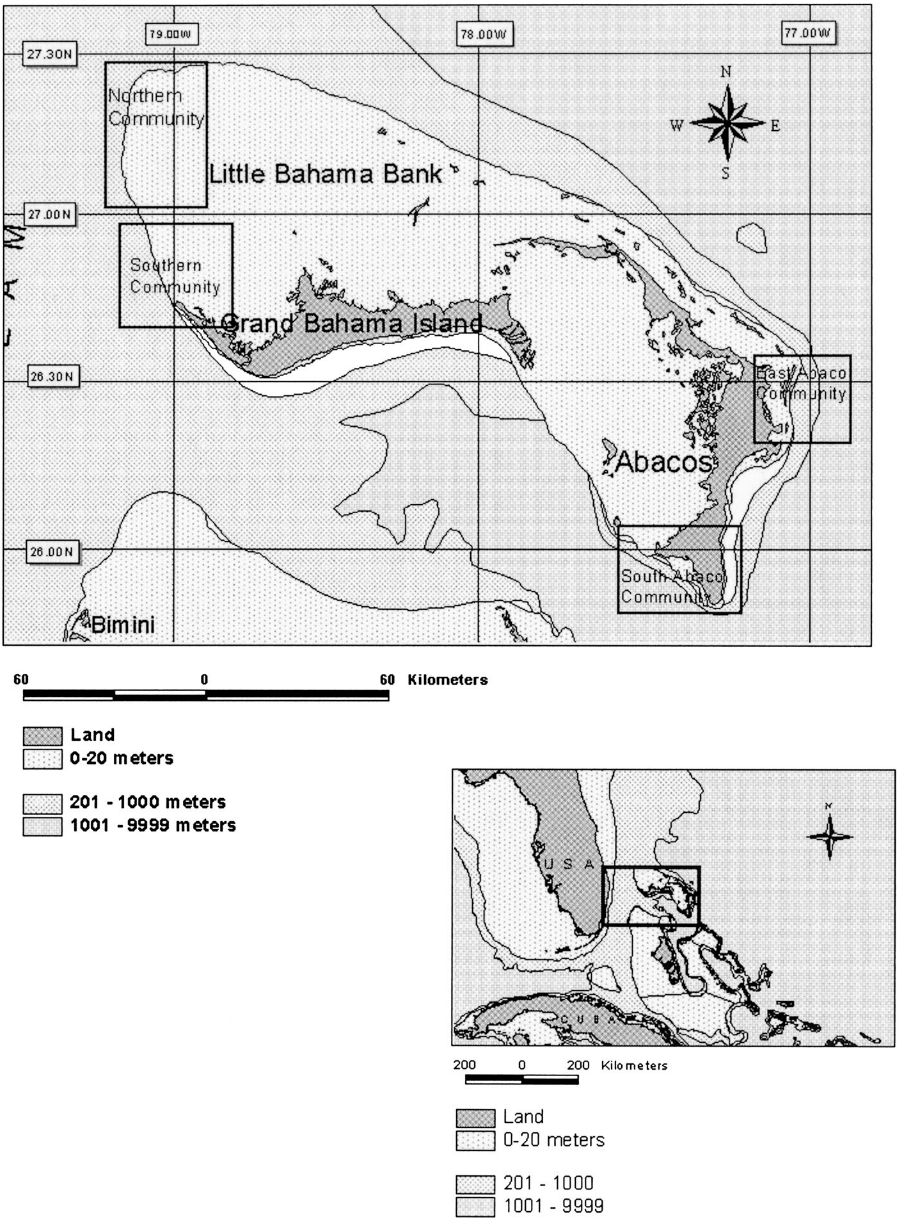

Figure 1. Geographic distribution of dolphin communities. The box in the insert represents the large and more detailed map of the Bahamas, including Grand Bahama Island and the Abacos. Small inset boxes represent the four different dolphin communities present on LBB: Northern, Southern, East Abaco, and South Abaco.

METHODS

Study Area

The study area is 280 km^2 and spans 56 km north to south and 5 km east to west and encompasses the Northern and Southern dolphin communities on LBB (Fig. 1). The $CaCO_3$ bank is shallow, (6–16 m), but is surrounded by deep water. The area is characterized by a sandy bottom with patches of *Thalassia testudimum* and scattered with areas of rock and reef. LBB extends over 160 km from West End, Grand Bahama to Abaco, where Parsons (2002) has described two other dolphin communities, East and South Abaco (Fig. 1). Our study focuses on the dolphins of the Northern community of LBB, ranging north of latitude 27°03′00″.

Data Collection

Since 1985, The Wild Dolphin Project (WDP) has conducted an on-going study of spotted dolphins (*Stenella frontalis*) that inhabit LBB (Herzing 1997, Brunnick 2000). Data on bottlenose dolphins were also collected from May to September (1993–2002) aboard the WDP vessel, *Stenella*, a 20-m power catamaran. Observations were conducted from 0700 to 1900, in one-person/one-hour shifts, scanning 360° while on the bridge in all but severe weather conditions.

All dolphins, moving in the same direction and usually involved in the same activity were considered a group (group or pod, Shane 1990). For each group we recorded: date, start and end time, start and end latitude and longitude, number of bottlenose dolphin adults and calves, number of spotted dolphins, water depth, behavior (defined as travel, social, feeding, or other), film roll and frame numbers, photographer, and the names of any immediately identified dolphins.

Primary identification was done by comparing and matching natural markings, including nicks and scars on the dorsal fin, to all previously photographed fins with the aid of a 10× magnifying loupe (Würsig and Würsig 1977, Würsig and Jefferson 1990). Additional markings on the body of the dolphin were also used to aid in positive identifications of individuals. If we identified more dolphins in a group than we had in the group size estimate, then the estimate was raised to reflect the actual number of dolphins present. Some photographs from 1985 to 1992 were used to investigate site fidelity for certain individuals. Underwater video from 1993 to 2002 aided in identification and sex determination. Sex was determined by direct observation of the genital region. Males were identified by a gap between the genital slit and the anus, lack of mammary slits or observation of an erection. Females were identified by observation of mammary slits, or regular accompaniment of a smaller animal presumed to be her calf.

Data Analysis

Although this study describes the social structure of dolphins of the Northern community on LBB, dolphins labeled as members of the Northern community were not restricted to this area and have been sighted in the Southern area. In order to get a complete look at their social structure and associations, groups from the entire study area (encompassing the Northern (n = 808) and Southern (n = 129) areas, total n = 937) were included. The terms Northern area and Southern area refer to the ranges by which the respective communities are defined (Northern is north of

27°03′00″, and the Southern is south of 26°54′00″ as described by Rossbach and Herzing 1999). Many dolphins have been seen only once in the study. These animals are not considered a part of this community (and are possible transients from other communities), and are therefore eliminated from this analysis.

Coefficients of association (COA), ranging from 0.00 (two dolphins never seen together) to 1.00 (two dolphins always seen together), were determined using the half weight index (HWI):

$$2N/(N_a + N_b)$$

where N is the number of sightings that included both dolphins a and b, N_a is the number of sightings that included dolphin a but not dolphin b, and N_b is the number of sightings that included dolphin b but not dolphin a (Cairns and Schwager 1987). The calculated COAs were grouped into three catagories: low $\leq$ 0.39, moderate 0.40–0.79, and high $\geq$ 0.80 (modified from five categories used by Wells *et al.* 1987, Quintana-Rizzo and Wells 2001).

Annual COAs were determined every year for each pair of dolphins of known sex, seen three or more times within that year. Individuals included in one year were not included in analysis of other years if they did not meet the sighting criteria. When choosing sighting criteria, there is a trade-off between including as many animals as possible and ensuring data are reliable (Bejder *et al.* 1998). Other studies have used a variety of sighting criteria for calculating COAs, from two sightings per individual (Slooten *et al.* 1993), to five (Wells *et al.* 1987) to ten (Quintana-Rizzo and Wells, 2001). We chose three as our limit because it permitted enough individuals to be included in the analysis, while allowing the results to be comparable with other studies.

Data were also pooled over two 5-yr periods (1993–1997 and 1998–2002) and the entire 10-yr period. Pooling data over years to obtain sufficient number of sightings for individuals is common in dolphin studies (*e.g.*, Wells *et al.* 1987, Rossbach and Herzing 1999) and will enable these data to be compared more easily to other studies of dolphin associations. COAs were calculated for every pair of dolphins of known sex seen $\geq$5 times in each pooled period. These data were then compared to the annual COA values, to determine if any difference in observed trends occurred.

COAs were calculated using the Helix Rade relational database, as well as with SOCPROG 1.3 (Whitehead 1999). Mantel and permutation tests were conducted using SOCPROG 1.3. Mantel tests were calculated to determine whether significant differences in COAs occurred between sexes (*i.e.*, are mixed-sex associations significantly different than same sex associations). Permutation tests were conducted using a daily sampling period, and were performed to determine whether the distribution of associations from the real data was significantly different from that of the permuted (random) data, indicating whether or not the dolphins were associating randomly. If some individuals preferentially associate with other individuals (indicating non-random associations), then the Standard Deviation (SD) of the real association indices will be significantly higher than the SD calculated in the random data (Whitehead 1999, Christal and Whitehead 2001). For the annual analysis, the "permute all groups" test was chosen to test the null hypothesis that there were no preferred or avoided companions, given the total number of groups each animal was seen in during that year (Whitehead 1999). This test does not account for situations such as birth, death, and migration. This bias was considered

Table 1. Field effort (days at sea, days with sightings and number of sightings per year for 1993–2002).

Year	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	Total
Days at sea	100	100	100	97	92	80	92	87	71	78	897
Days with sightings	35	56	54	35	32	34	46	44	31	34	401
Sightings per year	53	153	120	97	65	57	108	95	90	99	937

negligible for the annual data sets, as the field season for each year is short (May–September), and most of the animals used in each analysis are present in the study area for the duration of our field season. The pooled data have a considerably longer time frame (over many years), therefore the "permute groups within samples" test was used, with a daily sampling period. This test accounts for the fact that some individuals are not present in each sampling interval due to birth, death, and migration.

If overall associations are non-random, then individual dyads can be considered separately. The permutation tests determine which, if any, individual dyad COAs are significantly higher or lower than their random values. The tests also calculate the number of expected significant dyads. If the observed number is close to or smaller than the expected, then the observed significant dyads should be considered cautiously. If the observed number is larger than the expected, then those dyads can be described separately (Whitehead 1999). All descriptive statistics, Kruskal Wallis and Mann Whitney *U* tests, were performed with Statistica software. SD is reported with means.

RESULTS

Effort and Discovery Rate

In 897 d at sea, bottlenose dolphins were sighted on 401 d (Table 1). The total number of individual dolphins identified was 170. Thirty-eight of these dolphins were observed once in the 10-yr period, and were not included in this analysis. Of the 132 individuals observed more than once, sex was determined for 53%. There were 29 known males (22%), 41 known females (31%), and 62 individuals of unknown sex (47%). In the first three years of the study 49 new individuals were discovered, excluding neonates and calves. By 1996, 71% of the observed non-calf animals in this Northern community were identified. Generally, the discovery rate of new animals decreased after 1996 (Fig. 2).

Resighting and Site Fidelity

Total number of sightings of 29 males ranged from 2 to 68, $x = 18.45 \pm 17.14$. Sightings per year for individual males ranged from 0 to 14. Total number of sightings for 41 females ranged between 2 and 78, $x = 18.63 \pm 16.49$. Sightings per year of individual females ranged between 0 and 28.

Based on earlier photographs taken before this study began, some individual dolphins showed site fidelity for up to 17 yr. Although no individual dolphin has been seen in every field season since 1985, many have been resighted in nearly every

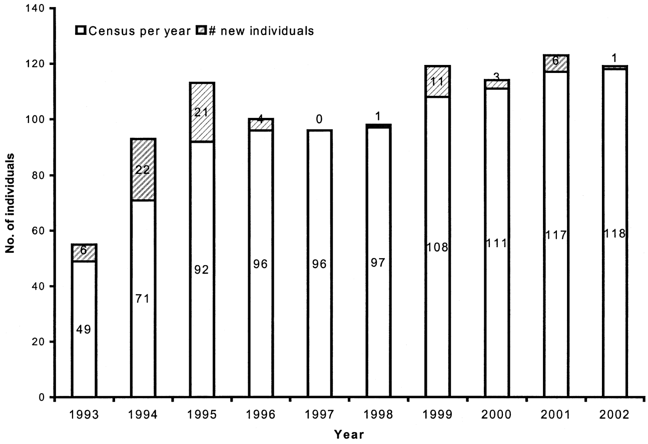

Figure 2. Discovery curve of new non-calf individuals (excluding births). True field effort for sighting bottlenose dolphins was low in years 1997 and 1998 due to a change in protocol by WDP, which may bias new individual sighting numbers to be low in 1997 and 1998, and consequently high in 1999.

year since their first sighting, as far back as 1986. Of dolphins resighted in the study period, 26 have been photographed previously between 1985 and 1992. Sighting patterns were separated into four categories. Thirty dolphins have been seen every year since they were first sighted. Thirty-two individuals have one set of consecutive years missing (range 1–6 yr, with one animal missing 11). Thirty-eight dolphins have more than one set of years missing (each set ranging from 1 to 5 yr). Finally, 32 individuals have not been seen for three or more years since their last sighting.

The dolphins in this study are primarily based in the Northern area, however many have been seen in the Southern area, from as few as one sighting, to almost half the individual's total sightings. Of the 132 individuals, 52 have been seen at least once in the Southern area. Of these, 20 are female, 12 are male, and 20 are of unknown sex. In addition, seven matches (one male, one female, five of unknown sex; Parsons 2002) between this study area and Abaco, Bahamas (a >320 km round trip), indicate that some dolphins travel long distances periodically and remain in either community for years at a time.

Group Size

Fully identified groups—Group size was calculated from groups where all dolphins were identified, $n = 150$ out of a total of 937 groups. Group size ranged from 1 to 22 individuals, $\bar{x} = 3.45 \pm 3.65$. Groups containing only one or two animals comprised 89 of 150 groups (59%). Behavior was defined for 69 of these groups and size did not vary significantly between feeding, social, or travel behaviors (Kruskal Wallis $P > 0.05$). The number of calves per group ranged from 0 to 3, $\bar{x} = 0.23 \pm 0.60$. Calves were present in 23 sightings (15%). Mean group size with calves present ($\bar{x} = 6.86 \pm 4.49$) was significantly higher than without calves ($\bar{x} = 2.83 \pm 3.11$, $n = 127$) (Mann Whitney $U = 544.5$, $P < 0.001$).

All sightings—Data on all sightings were also analyzed where estimates for group size were available ($n = 916$). Size ranged from 1 to 25 individuals, $\bar{x} = 4.58 \pm 3.99$. Sightings containing only one or two dolphins comprised 372 of 916 groups (41%). Group size in all sightings did vary significantly between behaviors (Kruskal Wallis $P < 0.05$) and groups were significantly larger when socializing ($\bar{x} = 5.90 \pm 4.03$, Mann Whitney $U = 5{,}844$, $P = 0.01$) or feeding ($\bar{x} = 6.16 \pm 4.81$, Mann Whitney $U = 6{,}006$, $P = 0.01$) than when traveling ($\bar{x} = 4.92 \pm 4.43$). There was no significant difference in group size between feeding and socializing groups (Mann Whitney $U = 8{,}954$, $P = 0.89$). The number of calves per sighting (447 sightings where presence or absence of calves was reported) ranged from 0 to 4 calves, $\bar{x} = 0.60 \pm 0.90$. Calves were present in 174 sightings (39%). Group size was significantly larger with calves, $\bar{x} = 7.28 \pm 4.29$, than without calves ($n = 273$), $\bar{x} = 3.29 \pm 2.61$ (Mann Whitney $U = 9{,}024$, $P < 0.001$).

Annual Coefficients of Association

Overall associations—Permutation test P values stabilized at 20,000 permutations, and were replicated five times for each year (Table 2). In 1997 the number of associations observed were too low to conduct permutation tests. Seven years showed significantly higher SD of the real association indices than the random association indices, indicating non-random associations. Two years revealed the dolphins were associating randomly (Table 2). The majority of associations (53%) were between individuals of the same sex. Mantel tests determined that in three years, mixed sex COAs were significantly smaller than same sex pairs (Table 3). All other years showed no significant differences.

Mother-calf—Seven known mother-calf associations were analyzed. COA values, ranging from 0.55 to 1.00, were among the highest in the study and were significantly higher than those of their random associations. The first year (birth year of the calf) generally revealed the highest association value ($\bar{x} = 0.80$). For the few pairs with information on year two of the calf, COAs were generally lower than year one. However some mothers and calves continued to associate for years after the birth and subsequent weaning of the calf.

Female-female associations—Of the 41 identified females, 34 met the criteria to be used in COA analysis. Female–female associations represented 31% ($n = 288$) of the total associations ($n = 915$). Total possible female associates was 33 over 10 yr. Females had a range of observed associates, 1–23, $\bar{x} = 11.32 \pm 6.19$ (Table 4). The majority of associations were low, however some high level associations were observed.

Some changes in COA values occurred between females, in relation to their reproductive status. The majority of moderate to high COAs between females occurred in years when calves were born. In 1995 Doppler had a calf, Dizzy. Associations between this mother and calf and four other females ranged from 0.43 to 0.84, $\bar{x} = 0.60$, well above the average female-female COA. These females had associated to a much lower extent and inconsistently in previous and subsequent years. In 2002 Amy had a calf Aragon, and Nose had a calf, Nozzle. These mothers and calves had moderately high COAs with four other females (and each other), ranging from 0.33 to 0.78, $\bar{x} = 0.58$. These females include juveniles (determined juveniles because their birth year was known) and adults, both related and unrelated to the mothers. They had associated with each other inconsistently and with much

Table 2. Number of individuals, mean *P* value (over five replicate random permutations) for the SD of association indices, range of the number of significant dyads, and number of expected significant dyads for each period of COA analysis, annual and pooled.

	1993	1994[a]	1995[a]	1996[a]	1997	1998[a]	1999	2000[a]	2001[a]	2002[a]	(1993–1997)*	(1998–2002)[a]	(10 yr)[a]
No. Individuals	12	27	33	14	6	9	21	18	22	27	45	39	63
Mean *P* value	0.3	<0.001	<0.001	<0.001	—	0.03	0.16	<0.003	<0.001	<0.001	<0.001	<0.001	<0.001
No. significant dyads	1–2	21–24	30–34	10–11	—	1	4–6	2–3	11–13	26–30	3–4	8–12	14–17
No. expected significant dyads	3	16	25	4	—	1	10	7	11	16	47	35	95

[a] Significantly higher SD of the real associations compared to the SD of the random associations.

Table 3. Results of Mantel tests for each COA analysis, annual and pooled: *t* value, *P* value and matrix correlation coefficient (*r*).

Year	1993	1994	1995	1996	1997	1998	1999	2000	2001[a]	2002	(1993–1997)	(1998–2002)[a]	10 yr[a]
t	−0.8	2.73	2.26	0.37	−0.65	1.17	−0.08	0.30	2.69	1.25	1.07	2.92	2.91
P	0.79	0.00	0.01	0.36	0.74	0.12	0.53	0.38	0.004	0.11	0.14	0.002	0.002
r	−0.15	0.14	0.11	0.04	−0.17	0.2	−0.01	0.03	0.18	0.09	0.04	0.12	0.07

[a] Mixed-sex associations are significantly smaller than same-sex associations.

Table 4. Non-zero COA ranges, means and SD, sample size and frequency distribution for low (L), moderate (M) and high (H) for each association type for annual and pooled data.

Association type	Annual COA	Pooled COA (1993–1997)	Pooled COA (1998–2002)	Pooled COA 10 yr
Female-female	0.06–1.00 ($\bar{x} = 0.31 \pm 0.18$) L = 74.65%, M = 23.27%, H = 2.08% $n = 288$	0.03–1.00 ($\bar{x} = 0.17 \pm 0.14$) L = 92.72%, M = 6.62%, H = 0.66% $n = 151$	0.03–0.49 ($\bar{x} = 0.16 \pm 0.11$) L = 91.67%, M = 8.33%, H = 0% $n = 120$	0.02–1.00 ($\bar{x} = 0.12 \pm 0.11$) L = 98.00%, M = 1.60%, H = 0.40% $n = 247$
Male-male	0.11–0.93 ($\bar{x} = 0.30 \pm 0.17$) L = 79.80%, M = 17.70%, H = 2.50% $n = 198$	0.04–0.76 ($\bar{x} = 0.16 \pm 0.13$) L = 93.48%, M = 6.52%, H = 0% $n = 92$	0.04–0.53 ($\bar{x} = 0.15 \pm 0.10$) L = 94.55%, M = 5.45%, H = 0% $n = 55$	0.02–0.59 ($\bar{x} = 0.12 \pm 0.09$) L = 98.04%, M = 1.96%, H = 0% $n = 150$
Mixed-sex	0.06–1.00 ($\bar{x} = 0.26 \pm 0.14$) L = 85.31%, M = 14.23%, H = 0.46% $n = 429$	0.03–0.50 ($\bar{x} = 0.14 \pm 0.09$) L = 98.76%, M = 1.24%, H = 0% $n = 242$	0.03–0.61 ($\bar{x} = 0.13 \pm 0.10$) L = 96.27%, M = 3.73%, H = 0% $n = 134$	0.02–0.62 ($\bar{x} = 0.10 \pm 0.08$) L = 99.20%, M = 0.80%, H = 0% $n = 180$

lower COA values in previous years. In both 1995 and 2002 these females had significantly higher COAs with each other than those of their random associations. In all other years the number of significantly high female dyads ranged from one to four. However, there were 16 and 23 significantly high female dyads in 1995 and 2002, respectively. Pregnant females, Amy and Nose, had a moderate COA of 0.55 in 2001. Two other pregnant females (who previously associated at a low level), had a moderate COA value of 0.62 in 2002. Both of these associations also had significantly higher COAs than their random associations.

Male–male associations—Of the 29 males identified, 25 met the criteria to be used in COA analysis. Male–male associations represented 22% ($n = 198$) of the total associations. Each male had 24 possible associates over the 10-yr period. The number of male associates ranged from 0 to 18, $\bar{x} = 9.12 \pm 5.22$ (Table 4).

Two males, Face and Clip, had consistently moderate to high COA values from 1994 to 1996 and from 1998 to 1999 (0.57–0.92, $\bar{x} = 0.73$). They also associated in 1993 and 1997, but these associations could not be included in COA analysis due to low sightings. After 1999, Clip was not seen, and Face was seen (in 2001 and 2002) in moderate associations with another male, Loop (0.40 and 0.71, respectively). Face and Loop had previously low associations ($\bar{x} = 0.29$) in 1993–1995 and 1999. Loop had a strong association from 1993 to 1996 with another male Sawtooth (0.18–0.93, $\bar{x} = 0.68$) who disappeared after 1996. All of these male–male dyads had significantly higher COAs than those of their random associations. Another pair, Sly and Max, appeared to have a consistent low to moderate association from 1994 to 1995, and again from 1999 to 2002 (0.17–0.58, $\bar{x} = 0.35$). They also associated in 1996 and 1998, but could not be included due to low sightings. Sly and Max had a significantly higher COA than random in 1995 only. There were other significantly higher male-male associations compared to their random values, however these dyads were not consistently the same over the years. The majority of other associations were of a lower value (≤ 0.39), and no other consistent trends over the 10-yr period were observed (Table 4).

Mixed sex—Mixed sex associations represented 47% ($n = 429$) of the total associations, and the majority fell into the low category of associations (Table 4). A variety of mixed-sex dyads had significantly high associations compared to their random values, however these were different dyads each year, with no consistent pairs observed over the years. Males had a range of female associates, 1–26 ($\bar{x} = 10.24 \pm 8.47$), while females had a lower number of male associates ranging 0–18 ($\bar{x} = 7.47 \pm 4.94$).

Pooled COA

Twenty six males and 37 females were used for the 10-yr pooled data analysis (Table 4). The majority of COA values were low, with only one high association observed, and a small amount of moderate associations compared to the annual results. Permutation P values stabilized at 20,000 permutations, and five replicates were conducted for each period (Table 2). Pooled data also showed evidence of non-random associations for this community, with the SD of real associations being higher than those in the random data. Same sex associations comprised 69% of total associations (total $n = 577$). A Mantel test revealed that mixed-sex associations were significantly lower than same sex associations (Table 3).

The number of observed significant dyads was much lower than the expected number, and therefore the associations should be regarded cautiously (Table 2).

Three were mother/calf, three were male-male dyads discussed earlier, and seven were female-female associations involving some of the female dyads mentioned in the annual results.

Data were also pooled into two 5-yr periods. In 1993–1997 there were 45 dolphins, 27 females, and 18 males used in the analysis. For 1998–2002 there were 39 individuals, 24 females and 13 males (Table 4). The majority of associations were in the low category, with only one high COA in either period, and again a much smaller amount of moderate associations compared to the annual data.

Both periods revealed non-random associations, as the SD of the real associations was significantly higher than the SD of the random data. Same sex associations comprised 50% (for 1993–1997) and 57% (for 1998–2002) (Table 2). There was no significant difference between mixed-sex COAs and same sex COAs in 1993–1997. However, in 1998–2002, mixed-sex associations were significantly lower than same sex (Table 3). The number of significant dyads was smaller than the expected number for both periods and should be considered cautiously (Table 2). The dyads in 1993–1997 were all male-male (including two dyads described earlier), and in 1998–2002, one was a male-male association discussed earlier, and the six female-female associations were the same as some of the significant dyads described in the annual analysis.

DISCUSSION

Resighting Patterns and Site Fidelity

Our observations were made only from May to September. Thus, the presence of animals in other months has not been investigated primarily due to weather conditions in the winter. However, this study does include one trip in March of 1996 to the study site, where seven animals were sighted, indicating that at least some dolphins may be year round residents of the area. The spotted dolphins that live in the same area show year-round residency as well (Herzing, unpublished).

The Northern community of dolphins on LBB showed varying resighting patterns. The discovery rate of new non-calf individuals did begin to level off towards the end of the study. However, this does not include the 38 dolphins seen only once. Many dolphins had varying amounts of resightings, some were not observed in several subsequent years, then returned; others having oscillating resighting patterns over many years. This may be an indication that some dolphins are not residents, or that the study area on LBB is part of a larger population. At least 30 individuals have been seen every year since their first sighting, and indicate that at least these dolphins are residents (many of them had been seen prior to the onset of this study, between 1985 and 1992). Some of the animals, missing only one or two years, were also seen prior to this study, and are most likely residents as well.

Other dolphins with more varying resighting patterns may not be residents of the area. Some of these dolphins are from the Southern community, or from adjacent communities (such as the Abacos). In fact, seven individuals have been matched with photographs from the Abaco study site (Parsons 2002). One of these seven was seen only once in the Northern area and, therefore, not included in this analysis. The others have been resighted in our study area between 3 and 11 times. One matched female has been seen every couple of years in the Northern area, in the last two sightings (2000 and 2002) she was also observed with a calf. No Abaco match has been seen every year in this study area, but they do appear to visit the area on occasion for varying lengths of time (Rogers 2003).

There appear to be both residents and non-residents (both one time and periodic visitors) present in this community. Other studies have shown dolphins with different patterns of disappearance for both residents and non-residents (Würsig and Würsig 1977, Wells *et al.* 1987, Wells 1991, Rossbach and Herzing 1999, Quintana-Rizzo and Wells 2001, Gubbins 2002*b*). This Northern community on LLB seems to have a relatively closed resident population (as seen in the declining discovery rate), however many non-residents either pass through the area, or make visits periodically. Therefore this community must be considered open because of an abundance of non-resident visitors.

Long-term site fidelity is a characteristic of many bottlenose dolphin populations (Wells *et al.* 1987, Smolker *et al.* 1992, Maze-Foley and Würsig 2002), and the population of spotted dolphins inhabiting LBB (Herzing 1997, Brunnick 2000). This study supports the findings of Rossbach (1997) and Rossbach and Herzing (1999) documenting this bottlenose dolphin community, and further shows, through regular resightings, that some dolphins have long-term site fidelity of up to 17 yr.

Although home ranges were not determined for these dolphins, observations of movement were made. Generally in bottlenose dolphin communities males have a larger home range than females, indicating a male-mediated gene flow (Wells *et al.* 1987, Scott *et al.* 1990, Wells 1991, Smolker *et al.* 1992, Quintana-Rizzo and Wells 2001, Krützen *et al.* 2004). In Sarasota Bay, FL, males visited the extreme limits of the community range more frequently than did females (Wells *et al.* 1987); and in Shark Bay, males ranged over a larger territory than females (Krützen *et al.* 2004). However, in the Bahamas, Parsons (2002) used molecular genetic analysis and found evidence of female mediated gene flow in bottlenose dolphins on LBB. Interestingly, of the Northern community dolphins, which have also been sighted in the Southern area, there were almost twice as many females than males. Half of the known females (20 out of 41 total) and 40% (12 out of 29 total) of the known males have been sighted in the Southern area. This may be a preliminary indication that, contrary to most bottlenose studies, females may range farther than (or equal to) males, supporting the female basis for genetic flow. Further evidence for this extended range for females is that at least one female has been seen in Abaco, a round trip of over 320 km. This female dolphin has been resighted every couple of years in the Northern study area, recently with a calf. Although it is evident that some males range between communities (one male has also been matched with the Abaco study census), this is evidence that female bottlenose on LBB also range between communities, supporting a female-mediated gene flow.

The ecology of LBB is different from most bottlenose dolphin communities where male-mediated gene flow is present (*e.g.*, Wells 1991). LBB is a habitat suitable for coastal ecotype bottlenose dolphins, however it is unusual because of its relatively continuous habitat over a large distance (Parsons 2002). This unusual ecology of a large sheltered sandbank may allow for a different genetic mechanism for reproductive success, such as the female-mediated gene flow found by Parsons (2002), that would not work under different ecological pressures.

The importance of kinship in establishing strong male associations (alliances) has been demonstrated for other dolphin communities (Krützen *et al.* 2003) and for the dolphins in Abaco, on LBB (Parsons *et al.* 2003). When levels of cooperation between male kin are high, female dispersal may occur (Pusey 1987). This contributes to the possible reasons for female-mediated gene flow found on LBB.

Differences in mating strategies between different bottlenose dolphin populations show the cultural and ecological diversity of the *Tursiops* sp. (Parsons *et al.* 2003) and reveal how similarities and differences in ecology can affect cetacean social organization.

Group Size

Group sizes reported from other studies range from 1 to over 100, but are commonly between 2 and 15 (Shane *et al.* 1986). Most coastal studies reveal relatively small groups ($\bar{x} = 4$–5, Wells *et al.* 1980; $\bar{x} = 7$, Scott *et al.* 1990; $\bar{x} = 2$–7 varying with activity, Shane 1990; $\bar{x} = 4.8$, Smolker *et al.* 1992; $\bar{x} = 4.4$, Bräger *et al.* 1994) compared to other coastal studies ($\bar{x} = 15$, Würsig and Würsig 1977; $\bar{x} = 15$, Ballance 1990; $\bar{x} = 19.8$, Weller 1991). Spotted dolphins that share the bank also show small group sizes, $\bar{x} = 5.8$ (Brunnick 2000). Overall group size was also small in this Northern community.

Group size is influenced by factors such as predation and food availability (Johnson and Norris 1986). Observations of shark bites (scars) and missing pieces of fluke or pectoral fins have been noted on some individual bottlenose and spotted dolphins on the LBB, indicating a significant predation pressure from sharks (Herzing and Johnson 1997). Small group size would not be expected when risk of predation is high, as one of the primary advantages of schooling (larger number of animals) is reduced predation (Würsig 1986, Norris and Dohl 1980). However, the bottlenose and spotted dolphins have been observed interacting in aggressive, affiliative, and occasional foraging behaviors together, with a significantly larger group size than single species encounters. These larger groups could be an indication of greater protection for both species from predators, as the larger number of animals and combined mass may be more effective at detecting, deterring, or repelling predators (Herzing and Johnson 1997). Interspecies associations (like these) may show another level of organization to meet the ecological pressures faced by the species (Wells *et al.* 1999).

Food availability can also influence group size and may be determined by factors such as food distribution in time and space, and communication ability of the species (Rodman 1988). Bottlenose dolphins are often seen crater feeding on the sandy bottom (Rossbach and Herzing 1997), and also foraging along edges of small patchy *Thallasia testudimum* beds. Greater foraging efficiency might occur in small groups in this type of area, as prey occurs in a smaller area (or smaller schools), and thus may not support larger group size (Wells *et al.* 1999). Bottlenose dolphins and spotted dolphins on the bank exhibit different foraging tactics, feed on different prey species, and are rarely seen foraging together (Herzing and Johnson 1997). Mixed-schools are common when dolphins are feeding on a single prey species (Norris and Dohl 1980). Mixed groups are significantly larger than single species groups on LBB (Herzing and Johnson 1997), but are rarely seen foraging together. Single species groups feeding on patchy prey will likely be small in this habitat.

Groups containing calves were significantly larger than non-calf groups in both fully identified and all sightings. Many delphinid species show this trend (Wells *et al.* 1987, Weller 1991, Brunnick 2000, Maze-Foley and Würsig 2002). Risk of predation is significant in our study area, and so larger group sizes may provide greater protection of the young calves. Larger group size with calves can also be related to the fact that long-lived mammals such as bottlenose dolphins share parenting responsibilities with related and unrelated individuals (Weller 1991). Some of the female associations observed in our study suggest allomaternal care. Allomaternal care has been documented for other bottlenose dolphin communities (Wells *et al.* 1987, Shane 1990), and interspecies allomaternal care has been noted between a female spotted dolphin and bottlenose calf in our study area (Herzing and Johnson 1997).

Annual Coefficients of Association

Overall associations—Permutation tests revealed that in seven of the nine years (excluding 1997 when tests could not be conducted) the dolphins were associating non-randomly, indicating individuals have preferred/avoided companions throughout the majority of the study period. This is further revealed by the fact that in the majority of years the number of observed significant dyads was larger than the expected number, indicating these dyads were significant and could be considered and described individually.

Over half (53%) of the total associations seen were between individuals of the same sex. Although not every year revealed significantly lower COA values for mixed-sex pairs, the majority of significant dyads found each year were between same sex individuals. In many dolphin populations the majority and strongest associations are between same-sex individuals. Interactions may involve many combinations of age and sex of individuals, but long-term affiliations are correlated with age, gender, reproductive status, and kinship (Wells *et al.* 1999). This sex segregation tends to be a general rule in dolphin societies as, regardless of habitat, these trends are evident (Wells *et al.* 1987, Connor *et al.* 1992*b*, Smolker *et al.* 1992, Rossbach and Herzing 1999, Brunnick 2000, Quintana-Rizzo and Wells 2001).

Mother-calf—A calf's first year revealed the highest COA value with its mother, (and were significantly higher than their random associations), after which the value began to decline. The second year of the calf's life marked a decrease in the COA value between the mothers and calves. For the few mother-calf pairs with information beyond two years, the trend of decreasing association remained evident. Although some mother-calf associations ended after 3–4 yr, others had consistent associations for up to at least seven years (Rogers 2003).

The mother-calf bond is the strongest association found in most dolphin societies (Wells *et al.* 1987, Smolker *et al.* 1992, Herzing and Brunnick 1997, Brunnick 2000, Quintana-Rizzo and Wells 2001). High associations are predictable since calves are highly dependent upon their mothers and, therefore, they will strongly associate with each other (Wells 1991). For both bottlenose dolphins (Wells *et al.* 1987, Smolker *et al.* 1992) and spotted dolphins (Herzing and Brunnick 1997, Brunnick 2000) mother-calf associations are consistent, or slowly decline, until the calf reaches 3–4 yr of age, when the calf becomes more independent and the mother often has another offspring. However, some individual calves may continue to associate with their mothers after this period (Wells *et al.* 1987, Wells 1991, Smolker *et al.* 1992, Herzing and Brunnick 1997).

Female associations—The associations between females were generally of a low level between a variety of individual female associates, although no individual was seen with every other female in the community. Some female dyads did show significantly higher associations than random, however, they were not as strong or consistent over years as some of the male-male associations observed, as seen in other bottlenose dolphin communities (Wells *et al.* 1987, Smolker *et al.* 1992). Rossbach and Herzing (1999) believed that the north-central group on LBB could be a female band (see Wells 1991) belonging to the Northern or Southern communities; however this is most likely not the case, because one of the five animals, Zee, is male.

The high female associations seen (especially the large numbers of significantly high associations in 1995 and 2002) can be related to the reproductive status of the individuals. In most cases the females of similar reproductive condition associated with each other, to a lesser extent, in years previous to their current reproductive condition. When their reproductive statuses changed, their highest COA values were with other similar status females. Other delphinid studies have also shown this type of segregation (Wells *et al.* 1987) and temporal pattern (Herzing and Brunnick 1997, Brunnick 2000). Our study also showed that adult and juvenile females, both related and unrelated to the mothers, began to associate highly with the mothers and calves. This high association, with the calves especially, suggests that allomaternal behavior is occurring in this community. The younger and nulliparous females may be learning about taking care of a calf. Allomaternal behavior has been documented for other bottlenose populations (Wells *et al.* 1987, Shane 1990).

Male associations—Male dolphins had a range of associates, although no individual was seen with every male or female. However, males associated more with multiple females than females did with multiple males, thus increasing the males' chance of reproductive success. About 40% (12/29) of Northern males were seen in the Southern area, indicating that some males range throughout both communities. This large range is usually attributed to increased access to females, as seen in Wells *et al.* (1987), where males tended to visit the extreme limits of the community range, therefore being able to interact with more females and increasing chances of mating opportunities.

Most male-male associations were of low level, however some did show significantly higher COAs than their random associations. It is apparent that some individuals do maintain moderate to high level bonds that can last for at least seven years (Rogers, 2003). In addition, males had a smaller network of associates (compared to females), and some of these associations remain constant over years, unlike female associations. When a member of a male pair died, or disappeared, the surviving individual formed a bond with another male, as reported in other studies (Wells *et al.* 1987, Smolker *et al.* 1992). These strong associations, termed alliances, have been found in many dolphin populations (Wells *et al.* 1987, Connor *et al.* 1992*a*,*b*, Smolker *et al.* 1992, Brunnick 2000, Connor 2000, Quintana-Rizzo and Wells 2001, Maze-Foley and Würsig 2002, Krützen *et al.* 2003). Reasons for these alliances in other communities are usually attributed to increased reproductive access to females; *i.e.*, herding/coercing females (Wells 1991, Connor *et al.* 1992*a*).

Male alliances in interspecies interactions—In most studies on bottlenose dolphin coastal communities, bottlenose dolphins are the only prevalent marine mammals. Dolphins in this study live in a unique environment, are sympatric with spotted dolphins and often interact with them. Alliances between males may be an important aspect in the social organization and interaction of both species. Pairs and groups of both bottlenose and spotted dolphins have been seen associating in affiliative and aggressive encounters (Herzing and Johnson 1997). It appears that alliances from both species may be involved in many of the encounters, and could be important in maintaining and creating the bonds and complex social interactions that allow the two species to live together on LBB.

Interspecific mating has been observed, however this can often escalate into aggressive encounters. Members of either species (which can involve male alliances) can intervene and chase the other species away (for specific observations see Herzing and Johnson 1997). There are no obvious hybrids present in this community, despite the observed interspecific mating. However, a hybrid has been reported in a study site in Bimini, Bahamas (Herzing *et al.* 2003). These two species on LBB are sympatric, with no geographical or physical barriers separating them, therefore it may be that these alliances function as a behavioral mechanism of reproductive isolation between the species, at least during a majority of interspecific mating encounters.

Pooled associations

The 10-yr pooled COA values are much lower than the annual analysis (with only one high-category COA, and few moderate), but many of the same trends were observed. The dolphins were associating non-randomly, the majority of associations were between same sex individuals (69%), and mixed-sex COA values were significantly lower than same sex associations. The majority of significant dyads were same sex pairs, including the male-male associations and some of the female-female associations discussed earlier. However, the number of significant dyads was much smaller than the expected, and must therefore be treated cautiously.

Some similarities and differences were observed in the two 5-yr pooled data sets. The dolphins showed non-random associations in both; but only in 1998–2002 was the majority of associations between same sex individuals and mixed-sex COAs significantly lower than same sex COAs. The significant dyads found in both periods involved the male-male and some of the female-female associations described earlier, however, as in the 10-yr pooled data, the number of observed significant dyads was much smaller than the expected.

A major difference between the pooled *vs.* annual data is the lack of strong associations observed in any of the pooled COA values. Although the pooled data revealed significant dyads, their individual COAs, when looked at separately, where not in the high category (and few were in the moderate category), and therefore may be overlooked as not significant. When data are pooled subtle changes may be lost. For example, the few years of random associations, and years where the mixed-sex COAs were not significantly lower, were diluted and not detected in the pooled data. This can be a problem when looking at data that have been pooled over many years since associations between dolphins are not static from day to day, or year to year.

Some strong associations that are present will not be detected in pooled data. For example, the male alliances found in this study lasted up to seven years. However when the data are pooled these values are lowered because of the lack of associations in later years (due to disappearance of one of the pair, or change in associate), and the resulting COA value was lower, masking the strong association during some of the pooled years. Females tended to vary associations based on reproductive status, which changes year to year. By pooling data these changes are not detected. Although pooling data may reveal the same basic trends, the strong and/or long-term associations may not be shown, therefore not illuminating the true nature of the community structure.

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