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Replacement dolphins? Social restructuring of a resident pod of Atlantic bottlenose dolphins, *Tursiops truncatus*, after two major hurricanes

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ABSTRACT

Environmental variations can influence the structure of ecological communities that in turn alter the grouping and association patterns of social communities. This study compares the social structure of bottlenose dolphins in the Bahamas before and after two major hurricanes. Approximately 30% of regularly seen individuals disappeared after the hurricanes, with an equal number of immigrants arriving afterwards. The primary goal of this study was to quantitatively describe social structure changes occurring after this large-scale emigration (or death) and subsequent immigration of individuals using the social analysis program, SOCPROG 2.3. The pre-hurricane results revealed one community with association patterns that were consistent with previous work on this population as well as other well-documented populations. Post-hurricane associations revealed that the community split into two distinct units, whose members associated highly within, but rarely between units. Association patterns varied between units. Immigrants assimilated well into the population, especially males. Over half of the post-hurricane associations involved immigrants, the majority between residents and immigrants, and primarily involving immigrant males. The costs/benefits of choosing to associate with an immigrant individual differ between males and females and may have been the driving force for the changes in social structure that occurred.

Key words: bottlenose dolphin, *Tursiops truncatus*, immigration, emigration, climate variations, behavioural ecology, social structure, coefficients of association, SOCPROG.

Knowledge of emigration and immigration patterns is important for understanding the origin and structure of social groups (Baker and Dietz 1996, Brockelman *et al*. 1998). Dispersal, including immigration and emigration, has been studied in many species including birds (Ward 2005), cooperatively breeding primates (Baker and Dietz 1996, Lazaro-Perea *et al.* 2000), chimpanzees, *Pan troglodytes* (Kahlenberg *et al.* 2008), gibbons, *Hylobates lar* (Brockelman *et al.* 1998), screech-owls, *Otus kennicottii* (Ellsworth and Belthoff 1999), and mole-rats, *Cryptomys hottentotus hottentotus* (Spinks *et al.* 2000). However, research on dispersal, and specifically immigration, is hindered by difficult logistics involved in following individuals (Bowler and Benton 2005). Even for well-studied species like chimpanzees, little is known about immigration events because they are rare (Kahlenberg *et al.* 2008). Past research on the effects of immigration has focused on primates (*e.g.*, Baker and Dietz 1996, Schaffner and French 1997, Brockelman *et al.* 1998, Henzi *et al.* 1998, Lazaro-Perea *et al.* 2000, Kahlenberg *et al.* 2008) and avian species (*e.g.*, Clobert *et al.* 1988). Due to logistical problems and rarity, not much is known about the effect of immigration and emigration on dolphin associations and social structure.

The amount of immigration, and the ability of these individuals to assimilate into a population, can have substantial implications for social structure. It is important in understanding the origin and structure of social groups and the interpretation of individual behaviour (Baker and Dietz 1996). The differential responses of males and females to immigrants of either sex are derived from the differences between male and female sociality and their drive to increase their inclusive fitness. Choices in association made by resident individuals help determine if the immigrants are accepted into the population (Baker and Dietz 1996, Kahlenberg *et al.* 2008) and how grouping patterns and social structure may change as a result.

Bottlenose dolphins form complex fission/fusion societies like those of chimpanzees, where membership in groups is continually changing (Connor *et al.* 2000) but some long-term associations are evident. Social interactions may involve many age and sex combinations of individuals, but long-term affiliations are generally correlated with age, sex, reproductive status, and kinship (Wells *et al.* 1999). Despite differences in habitat between populations, these aspects of bottlenose dolphin social organization are somewhat uniform (Quintana-Rizzo and Wells 2001). However, in extreme habitats, some populations have shown much different social structure, with increased social cohesion and long-term bonds between sexes (Lusseau *et al.* 2003, Karczmarski *et al.* 2005). Other variations include multiple communities or social units within a population (Lusseau *et al.* 2006, Urian *et al.* 2009, Wiszniewski *et al.* 2009). Although different, the structure of all these populations, to the best of our knowledge, has remained stable over many years as no changes in social or community structure have been documented.

Demographic changes can affect social organization and fission/fusion dynamics (Lehmann and Boesch 2004). Immigration, emigration, and death may have important effects on the social structure of a population through limitations or availability of potential associates. In chimpanzees, decreasing community size resulted in increasing group size and decreasing flexibility of the fission–fusion system (Lehmann and Boesch 2004). Network analysis on a population of bottlenose dolphins revealed that some individuals may be more important to the connectivity of the network and their removal may cause a disproportionate effect on the population (Lusseau and Newman 2004). Intense natural disasters, such as hurricanes, can similarly alter social interactions through loss of individuals and immigration following the storms. These events can change grouping and association patterns and ultimately the social structure of a population.

In this study we present how a large-scale emigration (or death) and immigration event affected the social structure of a small, resident population of bottlenose dolphins, *Tursiops truncatus*, following multiple hurricanes. The study population is resident, has shown a stable social structure over more than 10 yr, with small amounts of yearly immigration (Rogers *et al*. 2004). The study area was directly impacted by two major hurricanes within 3 wk of each other in September of 2004. An unprecedented 30% of the population disappeared and have not been resighted. Roughly the same number of individuals subsequently immigrated into the population. This event provided a unique opportunity to study the effect of a large-scale emigration (or death) and immigration of individuals on the social structure of a previously stable population.

METHODS

Study Area

Little Bahama Bank (LBB) is about 64 km from the east coast of Florida, and just north of West End, Grand Bahama Island. The study area spans 60 km north to south and 8 km east to west and encompasses 480 km^2. The sandbank is shallow, between 6 and 16 m, and is surrounded by deep water (steep drop off to over 500 m into the Gulf Stream). It has a mostly sandy bottom, scattered with areas of rock, reef, and patches of sea grass (*Thalassia testudimum*). The entire study area was divided into six sections, A–F (Fig. 1), based on the study area described in previous work on this population (Rogers *et al.* 2004). Effort was not evenly distributed throughout

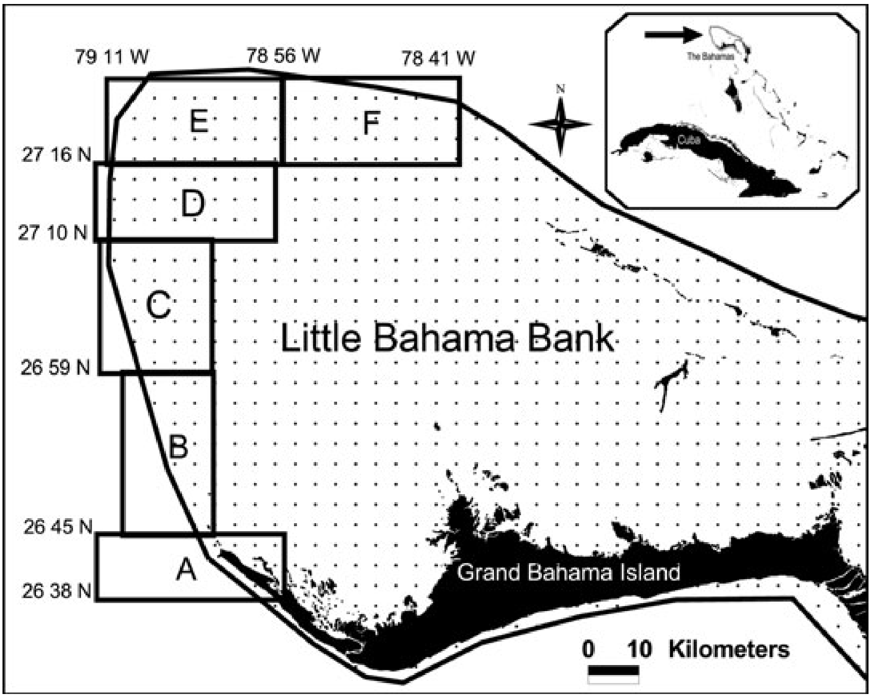

Figure 1. Study area broken into six segments: A, B, C, D, E, and F. Arrow on the insert indicates the Bahamas study area.

every area due to physical attributes of the environment as well as rough weather, which prohibits boat movement. This type of varied effort is evident in other social analysis studies in similar size study areas (Shane 2004, Lusseau *et al.* 2006, Kent *et al.* 2008).

Hurricane History

In 2004, the study area was hit directly by two major hurricanes: Frances and Jeanne. On 3 September 2004, Frances weakened from a category 3 to a strong category 2 hurricane as it slowly passed, after a 12 h stationary period, directly over Grand Bahama and the study area. Three weeks later, hurricane Jeanne passed over the same area on 25 September 2004 as a category 3 hurricane. In 2005, Hurricane Wilma passed just above the study area on 24 October 2005 as a category 2 storm. Although storms are not uncommon during hurricane season in the Caribbean, there has not been a direct hit to this specific area by a hurricane since at least the early 1900s (National Hurricane Center: http://www.nhc.noaa.gov/HAW2/english/history.shtml). The maximum lifespan of most dolphins averages 40–50 yr (Connor *et al.* 2000). Therefore, this population of dolphins has not encountered storms of this intensity before.

Data Collection

The Wild Dolphin Project began a focused study on Atlantic bottlenose dolphins in 1993 (Rossbach and Herzing 1999, Rogers *et al.* 2004) in conjunction with their on-going study of Atlantic spotted dolphins (*Stenella frontalis*) resident to LBB (Herzing 1996, 1997). Data were collected between May and early September each year. Observations were conducted during random transects, in all but severe weather conditions (over Beaufort 3 and/or intense rain squalls) from 0700 to 2000 in one person/hour shifts, scanning forward 180° while underway, and 360° while anchored.

A group was defined as all dolphins in sight and usually involved in the same activity (*e.g.*, group or pod Shane 1990). Once dolphins were found, a sighting sheet was filled out and photographs of dorsal fins were taken with a Canon 35 mm camera between 2002 and 2004 or a Canon EOS-1D Mark II digital camera between 2004 and 2007.

Individual identification was accomplished by comparing and matching natural markings, including nicks and scars on the dorsal fin to all previously photographed fins (Würsig and Jefferson 1990). Sex was determined by a variety of methods from long-term life history monitoring, including both surface and underwater observations (Herzing 1996, Herzing and Johnson 1997, Rossbach and Herzing 1999, Rogers *et al.* 2004). Females were identified by observation of mammary slits, or regular accompaniment of a smaller animal presumed to be her calf. Males were identified by a gap between the genital slit and the anus, or observation of an erection. Bottlenose dolphins in this study were classified as adult or calf (individual less than two-thirds the length of an adult and often swimming in echelon position). Individuals were classified as juveniles only if their birth year was known. Regularly seen resident individuals were defined as dolphins seen in at least four of the last 5 yr before 2005 or animals seen consistently since 1993 with no more than 2 yr between sightings.

Data Analysis

All coefficients of association (COAs) were calculated using the half-weight index (Cairns and Schwager 1987) with the software program SOCPROG 2.3 (Whitehead 2006). Calves were not included in these analyses because their associations are dependent on their mothers' associations; however mother–calf associations were described separately. Annual COAs were calculated for pairs of noncalf individuals of known sex that were sighted three or more times within that year. Pooled COAs were calculated for pairs of noncalf individuals of known sex that were sighted six or more times per pooled period (pre-hurricane 2002–2004, post-hurricane 2005–2007). All individual association values were categorized as low $\leq$0.39, moderate 0.40–0.79, and high $\geq$0.80 (following Rogers *et al.* 2004). Alternatively, some studies define strong associations as being greater than twice the average COA of the population (Gero *et al.* 2005, Whitehead 2008*a*); therefore, this categorization was also used in the analyses.

SOCPROG was used to conduct permutation tests (10,000 permutations, with 100 flips per permutation) to test for nonrandom associations and preferred/avoided companions (Christal and Whitehead 2001, Whitehead 2006). The sampling period was set to daily for all analyses. The "permute all groups" test was chosen for the annual analyses and the "permute groups within samples" test was used for pooled analyses (Whitehead 2006). If associations were found to be nonrandom, Mantel tests were conducted to examine whether differences in association occur between classes (*e.g.*, sex or resident/immigrant status).

The power and precision of the calculated COA matrices were determined using social differentiation (S), $S^2 \times H$ (H is the mean number of observed associations per individual) and the correlation coefficient (CC) (Whitehead 2008*a*, *b*). This information reveals how reliable the results were, if there was enough data to be representative and aided in determining which data set (annual or pooled) was more representative. Standard Errors (SE) were calculated from 1,000 bootstrap replications. Data sets with intermediate ($S \sim 0.5$) to high (S close to or above 1.0) social differentiation need far fewer associations than data sets with low differentiation to detect preferred companionship (Whitehead 2008*a*).

To correctly analyze the calculated COA, it is important to determine whether the individuals in the analysis belong to one or more unit/community. A community is defined as "a set of individuals that is largely behaviourally self-contained over all relevant time scales, so that nearly all interactions and associations occur within, rather than between communities" (Whitehead 2008*a*). Community structure is usually defined by associations of individuals with long-term site fidelity to a particular area (Urian *et al.* 2009). A social unit is a set of individuals in (nearly) permanent mutual association, by some reasonable definition of association and may be embedded within a larger community (Whitehead 2008*a*).

Nonmetric multidimensional (MD) scaling and hierarchical agglomerative cluster analysis were conducted with SOCPROG 2.3 to determine if there was more than one community/unit. In a MD plot, strongly associated individuals will be plotted together and weakly associated will be farther apart (Whitehead 2006). A plot with stress $<$0.1 is considered a good ordination (Whitehead 2008*a*). Hierarchical agglomerative cluster analysis produces a dendrogram where the individuals are arranged on one axis and their degree of association on another (Whitehead 2006). The average-linkage method was used. The cophenetic correlation coefficient (CCC) determines how well the dendrogram matches the association matrix. A CCC of $>$0.8 indicates a good match, (Whitehead 2008*a*). If separate units were detected,

Table 1. Field effort (May to early September) and number of sightings for 2002–2007, by year and pooled years pre-hurricane (2002–2004) and post-hurricane (2005–2007).

Year	# Days at sea	# Sightings	# Days with sightings	Total hours at sea	% Hours underway (anchored)
2002	73	84	39	895	54.0 (46.0)
2003	71	69	41	779	59.5 (40.5)
2004	73	58	35	793.5	62.9 (37.1)
2002–2004	217	211	115	2,467.5	58.6 (41.4)
2005	55	50	32	592	70.4 (29.6)
2006	60	49	26	619.75	65.4 (34.6)
2007	61	51	35	654	68.5 (31.5)
2005–2007	176	150	93	1,865.75	68.1 (31.9)
Total	393	361	208	4,333.25	62.7 (37.3)

then a Mantel test was performed to determine whether there were more associations within units than between, indicating the discreteness of the units.

The pooled data were the best representation of the social structure (see "Results"), so all analyses after COA calculation (Mantel tests, MD, and cluster analysis) were conducted only on the pooled data. However, the yearly COA analysis gave a good representation and was used to help describe the COA patterns in detail. ANOVA tests were conducted with the statistics program, SPSS 16. Standard deviations (SD) are given after means.

Results

Resighting

In 393 d at sea between 2002 and 2007, dolphins were sighted on 208 d with a total of 361 sightings (Table 1). A total of 190 dolphins were identified during this study. Of these, 61 were females, 52 were males, and 77 were of unknown sex. Rogers *et al.* (2004) reported that 71% of the individuals in the population were identified by 1996, and discovery of new individuals decreased through 2002. Following that study, matches were found with previously unidentified photographs between years 1999 and 2002, increasing the number of new individuals found per year. The discovery rate of new individuals per year ranged from 8 to 10, with an average of eight between 1999 and 2004. After the hurricanes, there was a large increase in new individuals, 27 (5 females, 10 males, and 12 unknown sex), that returned to an average of 8 in 2007 (Fig. 2). The majority of these new dolphins (70.4%) were resighted in at least 2 yr post-hurricane. This influx of individuals doubled the average rate to 16 new individuals between 2005 and 2007.

Out of 60 regularly seen individuals, 30 (14 females, 10 males, and 6 unknown sex) have not been sighted since 2004 (Fig. 2). The sex ratio of the new individuals did not greatly change the makeup of the population, except for possibly fewer females present (though this is not certain due to the number of unknown sex). Residents that remained after the storms increased their presence in post-hurricane years. For almost half of these dolphins, their resighting rates and overall number of sightings doubled (Table 2).

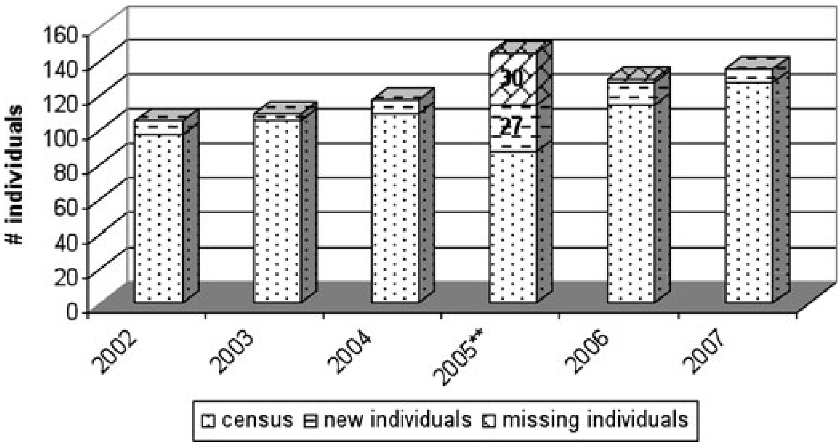

Figure 2. Discovery curve of new and missing noncalf individuals. **indicates the year after hurricanes Frances and Jeanne.

Table 2. Average resighting rates (average number of times individuals were seen) for immigrants (13 males, 6 females, 30 unknown sex), residents (24 males, 28 females, 20 unknown sex) and residents that doubled their overall number of sightings post-hurricane. Ranges are given in parentheses. ND = no data.

	Pre-hurricane	Post-hurricane
Immigrants	ND	5.56 (1–18)
Residents	3.51 (0–17)	6.89 (0–23)
Residents with double # resightings	2.72 (0–12)	12.15 (3–23)

Group Size

Group size ranged from 1 to 35 individuals and was significantly larger post-hurricane (Table 3). Groups were generally small: 40% contained only one or two individuals and 80% containing seven or fewer individuals. ANOVA revealed that groups were larger with calves than without calves for both data sets, were larger post-hurricane (especially for groups with calves) than pre-hurricane and there was a

Table 3. Group size mean (SD) for all groups, only groups without calves and only groups with calves pre- and post-hurricane. Bold indicates significantly larger group size with calves and post-hurricane. ANOVA showed significant differences for presence of calves ($P < 0.001$), pre- and post-hurricane ($P < 0.001$), and calves/hurricane interaction ($P < 0.03$).

Groups	Pre-hurricane $n = 194$	Post-hurricane $n = 149$
All, $n = 343$	4.43 (4.25)	**6.15 (6.08)**
No calves, $n = 211$	2.78 (2.61)	3.39 (3.89)
With calves, $n = 132$	**7.3 (4.98)**	**10.15 (6.46)**

significant interaction between calf presence and pre-/post-hurricanes on group size (Table 3).

Pre-Hurricane Associations

The total number of noncalf individuals, males and females for each data set are given in Table 4. In 2003, the number of individuals included for analysis and the subsequent number of associations was small and therefore tests could not be conducted. Permutation tests revealed nonrandom associations, indicating preferred and avoided companions, for all other years (Table 4). Results indicated intermediate to highly differentiated social systems for all analyses, with the pooled years having the highest differentiation (S) and power to detect preferred associations, $S^2 \times H$. The CC showed the pooled matrix to be the best representation. Data presented hereafter are from the pooled years data unless otherwise stated, when annual results were used to help describe the COA patterns in detail.

Table 5 shows the total percentage of observed associations, low, moderate, high, and by sex class. Associations were generally low, with over 55% between same-sex individuals. Male–male COAs had the highest average, however, a Mantel test revealed no significant difference between same-sex *vs.* mixed-sex associations (Table 6). Over a third of the associations were greater than twice the average, and these associations were most prevalent in same-sex associations, especially males (Table 7).

MD scaling (Fig. 3) and hierarchical agglomerative cluster analysis (Fig. 4) both show one community, with no discreet social units and some moderate to high associations between individuals.

Detailed COA

Strong associations that were greater than twice the average COA comprised 37.5% of the total and were more prevalent in same-sex associations (Table 7). The four highest COAs (>0.55, over four times the population average) were two adult male and two adult female pairs (Fig. 4).

Almost half (49%) of possible female–female associations were observed. Every female had at least one association that was greater than twice the average COA, and the majority had moderate level associations as well. Some older juvenile females had strong associations with their mother, as well as their mother's associates. Annual associations showed that the strength of these relationships and the individuals involved fluctuated between years.

All males had at least one association greater than twice the overall average COA and 71% of possible male–male associations were observed. Two alliances were evident with COA greater than five times the average (Fig. 4). These pairs had strong moderate to high associations (ranging from 0.50 to 0.80) throughout the annual analyses. Other male pairs had strong associations (ranging from 0.35 to 0.80) in a given year; however, they fluctuated in strength and individual membership.

Fifty-six percent of possible mixed-sex associations were observed. All males had at least one association with a female that was greater than twice the population average. Eight females had at least one association greater than twice the average with a male, and these were the same individuals with moderate female–female associations. Consequently, many of the male–female associations were males with females and their close female associates. On an annual basis, two patterns emerged.

Table 4. Number of groups, noncalf individuals, males, females, mean COA, P for permutation tests, social differentiation (S), number of associations per individual (H), CC, and test for sufficient data to detect preferential associations ($S^2 \times H$). $S \sim 0.5 =$ intermediate differentiation, S close to or above $1 =$ high differentiation. A CC of 0.4 indicates that the COA matrix is somewhat representative; a CC of 0.8, indicates the COA matrix is a good representation. If the $S^2 \times H > 5$, this indicates a good ability to reject the null hypothesis of no preferred companions. I in 2005–2007 indicates the number of immigrants. ND = no data.

Year	Groups	Individuals	Males	Females	Mean COA ± SD	P	S ± SE	H	CC ± SE	$S^2 \times H$
2002	39	23	7	16	0.20 ± 0.10	<0.001	0.68 ± 0.19	16.9	0.57 ± 0.08	7.83
2003	25	13	5	8	ND	ND	ND	ND	ND	ND
2004	31	19	8	11	0.15 ± 0.05	<0.001	0.62 ± 0.23	10.1	0.42 ± 0.11	3.88
2002–2004	99	25	7	18	0.12 ± 0.05	<0.001	0.86 ± 0.13	29.2	0.69 ± 0.04	21.4
2005	38	26	14	12	0.13 ± 0.06	<0.001	1.23 ± 0.23	14.92	0.69 ± 0.07	22.5
2006	34	26	15	11	0.23 ± 0.10	<0.001	0.45 ± 0.15	30.85	0.45 ± 0.10	6.25
2007	44	29	18	11	0.20 ± 0.05	<0.001	0.63 ± 0.22	24.83	0.51 ± 0.12	9.92
2005–2007	108	35	20 (7I)	15 (3I)	0.16 ± 0.05	<0.001	0.92 ± 0.11	61.3	0.78 ± 0.03	51.7

Table 5. Percentage distribution of nonzero (observed) associations for pre-, post-hurricane, and Units A and B. MM = male–male, FF = female–female, and MF = mixed sex. Low = ≤ 0.39, Moderate = 0.40–0.79, High $\geq$ 0.80. Units A and B have unusually high percentages of observed associations (bold).

Year	Observed	Low	Moderate	High	MM	MF	FF	Same sex
2002–2004	53.30%	88.80%	11.20%	0%	9.40%	43.70%	46.90%	56.30%
2005–2007	66%	81.30%	18.50%	0.20%	34.30%	49.60%	16.10%	50.40%
Unit A	**99%**	70.40%	29.60%	0%	32.60%	51.80%	15.60%	48.20%
Unit B	**81%**	77.40%	21.80%	0.80%	31.50%	52.40%	16.10%	47.60%

The two male pairs with very strong associations had between four to six consistent female associates in two or three of the pooled years, with the majority being greater than twice the average. Other males did not show consistent relationships with females. The majority of associations were at least twice the population average, but associates between years varied.

Post-Hurricane Associations

The total number of individuals, males, and females for each data set are given in Table 4. Permutation tests revealed nonrandom associations, indicating preferred and avoided companions, for all data sets, $P < 0.05$. Results indicate intermediate to highly differentiated social systems for all years except 2006, which was very close at $S = 0.45$. The pooled years had the highest differentiation (S) and power to detect preferred associations, $S^2 \times H$. The CC showed the pooled matrix to be the best representation (Table 4). Data presented hereafter are from the pooled years unless otherwise stated, when annual results were used to help describe the COA patterns in detail.

Table 5 shows the total percentage of observed associations, low, moderate, high, and by sex class. Associations were generally low, with just over 50% between same-sex individuals. Female–female COAs had the highest average, however, a Mantel test revealed no significant difference between same-sex *vs.* mixed-sex associations (Table 6). About a quarter of the associations were greater than twice the average, and these associations were most prevalent in female–female associations (Table 7).

Over half of the associations involved at least one immigrant, with the majority between residents and immigrants. Only one immigrant female associated with residents (20% of the associations). Over half (54.8%) of mixed-sex associations involved an immigrant (the majority involving new males with resident females) and 62% of male–male associations involved an immigrant (the majority between immigrant males and resident males).

MD scaling (Fig. 5) and hierarchical agglomerative cluster analysis (Fig. 6) revealed two distinct units (A and B) within the community, with two immigrant female individuals on the edges of the units that were difficult to assign to either unit. There were some moderate to high associations between individuals within each unit. A Mantel test ($P < 0.001$) revealed that within unit COAs (Table 6) were significantly higher than between unit COAs ($\bar{x} = 0.06 \pm 0.05$).

Table 6. Average COA overall and for sex and resident/immigrant classes. MM = male–male, FF = female–female, and MF = mixed sex. R-R = resident–resident, R-I = resident–immigrant, and I-I = immigrant–immigrant. Highest COA averages for each set of years or unit and significant Mantel test results are in bold. ND = no data.

Year	COA (SD)	MM (SD)	MF (SD)	FF (SD)	Mantel test	R-R	R-I	I-I	Mantel test
2002–2004	0.12 (0.05)	**0.21 (0.04)**	0.11 (0.07)	0.12 (0.06)	$P > 0.17$	ND	ND	ND	ND
2005–2007	0.16 (0.05)	0.16 (0.04)	0.16 (0.05)	**0.18 (0.06)**	$P > 0.11$	ND	ND	ND	ND
Unit A	0.32 (0.06)	0.29 (0.08)	0.30 (0.06)	**0.43 (0.05)**	$P > 0.10$	0.34 (0.06)	0.28 (0.09)	0.28 (0.08)	$P = 0.07$
Unit B	0.22 (0.08)	**0.27 (0.08)**	0.19 (0.11)	0.21 (0.10)	$\mathbf{P < 0.05}$	0.26 (0.09)	0.20 (0.09)	0.13 (0.04)	$P = 0.14$

Table 7. Percentage of COA that were greater than twice the overall average COA (strong associations) and the percentage of strong associations in each sex class: MM = male–male, FF = female–female, and MF = mixed sex. Highest sex class percentage for each set of years is in bold.

Year	% Twice average	% of MM	% of MF	% of FF
2002–2004	37.50%	**46.70%**	31.40%	41.30%
2005–2007	26.60%	22.90%	25.00%	**37.70%**

Unit A

All possible associations were observed, except one male–male pair. The number of moderate associations was larger than any other data set (Table 5). The average COA for Unit A was higher than Unit B, and it was more than double that of pre-hurricane years. Mantel tests showed there was no significant difference in COAs in regard to sex or resident status (Table 6). Only four COAs (three female–female and one mixed-sex pair) were greater than twice the average COA, with two male pairs just below. These results indicate a more homogeneous unit than previously observed in this population.

Female–female associations had the strongest COAs (Table 6) and centered around two females with calves, the highest between the mothers (Fig. 6). This trend was consistent through the annual analysis, though the strength of the COAs fluctuated between years. The two strong male–male associations involved three resident males (Fig. 6). These pairs had strong associations in the annual analysis as well. Other male pairs had strong associations; however, they fluctuated in strength and individual membership in different years. These three males were involved in over half the mixed-sex associations and one of the pairs associated strongly with the mothers with calves. Other associations varied in strength and membership in the annual analysis.

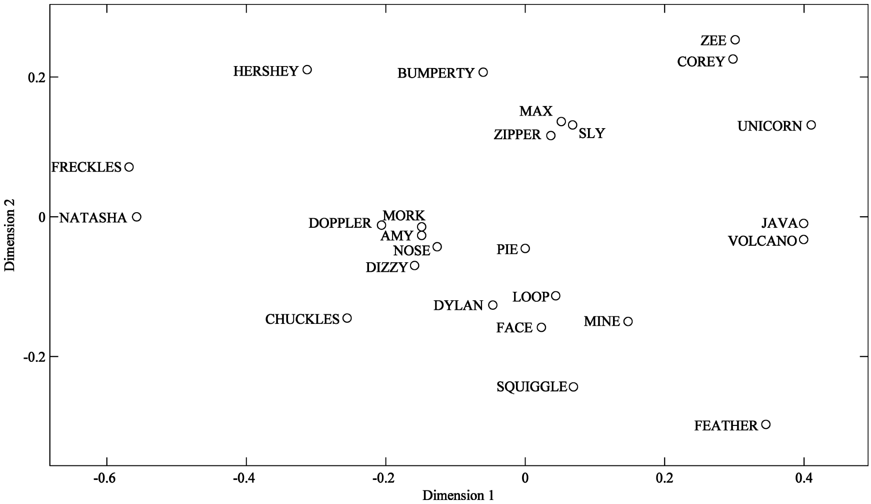

Figure 3. Representative plot of multidimensional scaling showing one community for the 2002–2004 pooled years. Stress = 0.07. Stress < 0.10 is a good ordination.

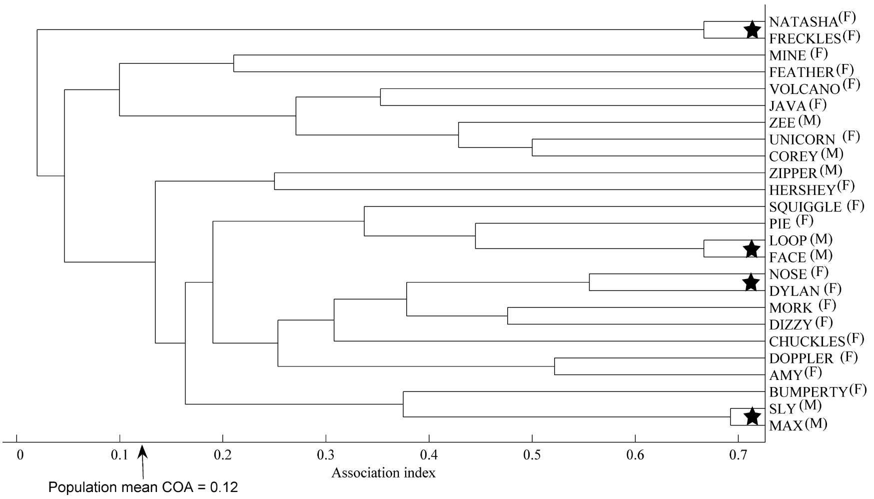

Figure 4. Hierarchical agglomerative cluster analysis for pooled years 2002–2004. Stars indicate strong associations. CCC = 0.81. CCC > 0.8 is a good representation.

Unit B

The number of observed associations was higher than pre-hurricane, but not as high as Unit A. The number of moderate associations was also lower than Unit A (Table 5). The average COA was almost double that of pre-hurricane years, but not as high as Unit A (Table 6). More strong associations (17%) were observed in Unit B, and these occurred more often between same-sex pairs. Mantel tests showed that same-sex COAs were significantly higher than mixed-sex, especially for males and that there was no significant difference in COAs regarding resident status (Table 6). The highest COAs, three times the population average, were between same-sex pairs/trios involving seven males and four females (Fig. 6).

Over 70% of the possible female–female associations were observed, and 20% of these were strong COAs and involved six of the eight females of Unit B. The two highest female–female COAs were between resident females (Fig. 6). One pair showed strong associations over more than 1 yr, others varied in strength and individual membership between years. Over 85% of possible male–male associations were observed. Strong associations between males involved juvenile and adult residents, as well as adult residents and immigrants (Fig. 6). Annual analysis showed two male pairs with consistently strong associations, others varied in strength and individual membership between years. Over 80% of the possible mixed-sex associations were observed. All but two pairs had strong associations, involving more than half the males, and less than half the females. Each member of the male pair Mimic/Gemtwist had an equally strong COA with all these females, indicating they were always together with the females. Only one member of the juvenile pair Nightmare/Koi had strong associations with females. These results were consistent in the annual analysis, other associations varied in strength and individual membership between years.

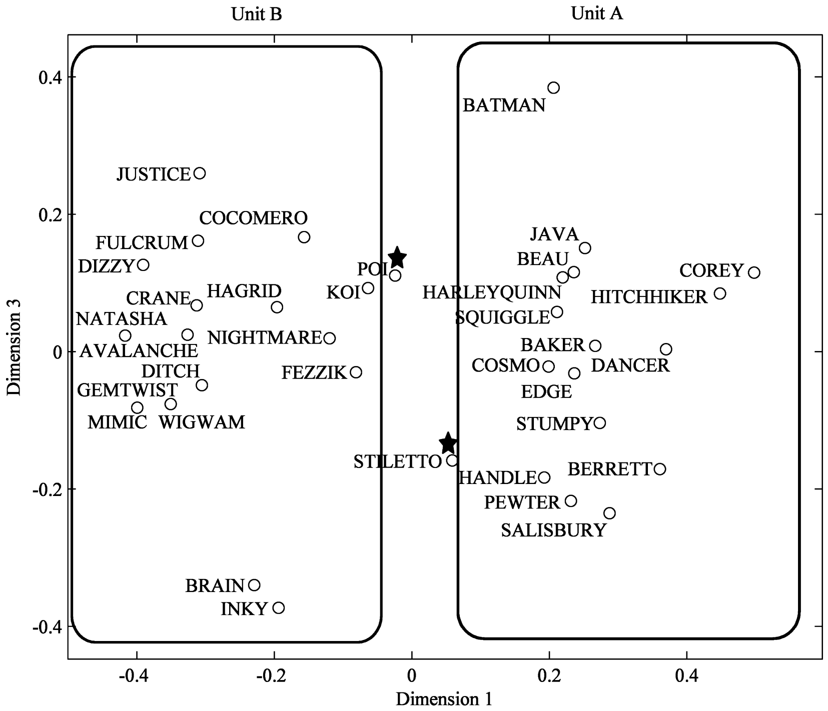

Figure 5. Representative plot of multidimensional scaling pooled years 2005–2007. Stars indicate immigrant females on the edge of the units that were difficult to assign to either unit. Stress = 0.06. Stress < 0.10 is a good ordination.

DISCUSSION

Community structure is defined by associations among dolphins with long-term fidelity to particular areas (Urian *et al.* 2009). For over 10 yr this population has shown a consistent social structure, comprised of one community (Rogers *et al.* 2004), and this remained evident prior to the hurricanes. Following the hurricanes and the immigration/emigration (or death) of many individuals, two distinct units emerged, each comprised of both residents and immigrants. The shorter time frame of this study following the hurricanes precludes us from determining if the two units were actually separate communities.

Association patterns of most bottlenose dolphin populations are primarily based on the sex of the individuals and include male alliances, variations with female reproductive status and the majority of associations being between same-sex pairs (Wells *et al.* 1987, Connor *et al.* 1992, Smolker *et al.* 1992, Rossbach and Herzing 1999, Quintana-Rizzo and Wells 2001, Rogers *et al.* 2004). However, there is behavioural flexibility between dolphin populations in different habitats as some show less fluidity and increased social cohesion (Lusseau *et al.* 2003, Karczmarski *et al.* 2005), indicating that social variability is a common response to environmental variability (Karczmarski *et al.* 2005). Thus social plasticity is important to be able to exploit a variety of habitats (Lusseau *et al.* 2003), but may also be important in surviving environmental or demographic changes.

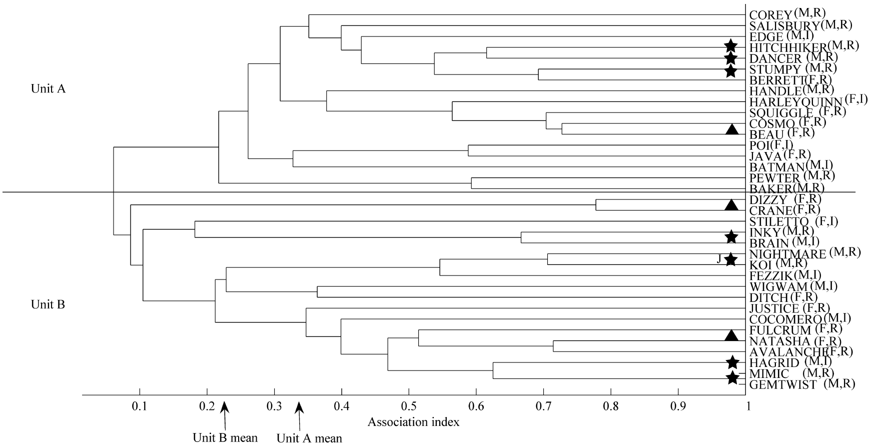

Figure 6. Hierarchical agglomerative cluster analysis for pooled years 2005–2007. Stars indicate strong male associations (alliances), J indicates a juvenile pair and triangles indicate strong female associations. CCC = 0.84. CCC > 0.8 is a good representation.

The results of this study provide evidence for the social plasticity of bottlenose dolphin social structure within a population, not just between. Although multiple social units/communities within one dolphin population occur elsewhere (Lusseau *et al.* 2006, Urian *et al.* 2009, Wiszniewski *et al.* 2009), a split in a previously stable community has not, to our knowledge, been documented before.

In this study, a stable community split into two new units with increased social cohesion (intensity varied between units), however sex and reproductive status preferences in associations remained. These association patterns within the two units were contrary to other dolphin populations that showed increased social cohesion. In these other populations there were also strong inter-sex bonds and less social fluidity, which were shaped by the ecological constraints of their geographic isolation (bottlenose dolphins, Lusseau *et al.* 2003; spinner dolphins, Karczmarski *et al.* 2005). Interestingly, a large-scale (60 individuals) immigration event occurred in the spinner dolphin population in a remote Hawaiian atoll (Karczmarski *et al.* 2005). The immigrants and residents rarely interacted (even though in close proximity, 2–3 km). When they did interact, original group membership was restored (no individuals ever switched groups) and some aggression was observed as residents chased away immigrants. This is in stark contrast with the results of our study, where immigrants were well integrated within the resident population. In addition to the different social structure characteristics, the study area for our population, LBB, is a very different habitat than the atolls and fjords in the studies mentioned above. The more fluid social structure and the lack of geographic isolation on LBB may explain why this extreme form of social cohesion was not observed and why immigrants were more accepted.

Variations in the social cohesion of the two new social units were observed. Differences in social cohesion within one population have been documented and related to the variation in habitat (marine *vs.* estuarine) between the two communities (Wiszniewski *et al.* 2009). On LBB there are no such stark differences in habitat that could account for the differences in social cohesion observed, although it is unknown whether smaller changes in habitat (*e.g.*, bottom type) could produce similar results. Thus it is most likely that the impetus for the observed changes was demographic. The new social structure was influenced by the choices of association between residents and immigrants and how they differed between the sexes.

Fission of the Community

The loss of so many individuals within the population may have disrupted the communication between individuals, facilitating the split of the community. Certain individuals, termed "centralized brokers," may play a more important role in the connectivity within a network, and their removal may cause a disproportionate effect on the community even though many redundant paths of communication between members of the network may be present (Lusseau and Newman 2004). It may be that some of the individuals lost after the hurricanes were "brokers." Even if individual "brokers" were not present, the sheer number of individuals lost could produce the same lack of communication between individuals, facilitating a split in the community. There is evidence for the possibility of new "brokers," as two immigrant females seem to be at the edge of their respective units, possibly facilitating a link between the two units. They, or other individuals, may play an important role in the future structure of the community.

Immigration

The results of this study support the findings that dispersal can have profound effects on the structure and stability of a population (Bowler and Benton 2005). The presence of immigrants can induce change in local social organization (Lin *et al.* 2004), in combination with loss of resident individuals. Results show that immigrants assimilated well into the population. Male immigrants were far more accepted into each of the two units than female immigrants. When an immigrant arrives, there is a conflict of interest between resident males and females, in whether to accept or fight off new individuals of either sex. These conflicts are widespread in polygynous mating systems (Davies 1989). Both males and females may find resistance from resident individuals of one (usually same-sex) or both sexes (*e.g.*, Pereira and Weiss 1991, Baker and Dietz 1996, Schaffner and French 1997, Lazeo-Perea *et al.* 2000, Kahlenberg *et al.* 2008), and these behaviours may depend on the mating strategies and social structure of the population. In some cases this means that female immigrants may find more resistance, while male immigrants may find less from residents (Baker and Dietz 1996, Schaffner and French 1997). This type of immigration acceptance is supported by the results presented here.

Strong associations were more prevalent in resident female–female associations than in any other sex class after the hurricanes, particularly in Unit A, and there were few associations between immigrant and resident females. Female immigrants may compete with female residents for physical resources (food, space) and mating opportunities with males, negatively impacting the fitness, and reproductive success of resident females. Thus, in many species, immigrant females are often aggressively chased away by resident females (Baker and Dietz 1996, Schaffner and French 1997, Lin *et al.* 2004, Kahlenberg *et al.* 2008, Pusey *et al.* 2008). In some populations males will also chase immigrant females (Baker and Dietz 1996). In many cases it may be more difficult for females to immigrate into new areas due to aggression from both male and female residents. Although it is unknown whether female immigrants were met with aggression or actively chased away, the association patterns of the resident and immigrant females indicate resistance to female immigrants.

Female associations may also depend on social familiarity (Möller and Harcourt 2008). Female associates may be daughters of their mother's close associate, with who they spent part of their infancy or juvenile period together (Wells *et al.* 1987, Möller and Harcourt 2008). This type of association was also seen in this population, as daughters associated highly with their mother and her new calf, as well as their mother's close associate (which often also had a calf). Thus resident females would not associate or form strong bonds with immigrant females.

Contrary to females, male immigrants seemed to assimilate easily into the population, with over half the post-hurricane associations involving immigrant males (especially male–male associations). Bottlenose dolphin males tend to have larger home ranges (Wells *et al.* 1987, Quintana-Rizzo and Wells 2001, Gubbins 2002), including this population (Rogers *et al.* 2004). Therefore, it is not uncommon for males and females to interact with immigrant or visiting males, which may allow immigrant males to be more readily accepted into the population.

Alliances were present between residents and residents/immigrants with some having consistent membership and strong COA over the pooled years, while others seemed short-term and varied between years. In chimpanzees, males have been shown to change reproductive strategies depending on the size and composition of the community (Lehmann and Boesch 2004). If the male reproductive strategy favors alliance formation in a population, the benefits of alliance membership (including increased access to females, protection from predators, increased foraging) must outweigh the cost of lowered mating chances due to the fact that the allied males must share all of the opportunities. In this scenario, males would not suffer much fitness loss by allowing males into the population, especially because many males were lost previously and competition would not be greater after the hurricanes than before.

Male bottlenose dolphins in this study showed varying alliance strategies, which has been documented for other populations as well (Owen *et al.* 2002, Krützen *et al.* 2003, Lusseau 2007). In Shark Bay, second-order alliances (generally lasting no more than a few years) are involved in both agonistic interactions as well as during consortships and may cooperate or oppose each other in different contexts (Connor *et al.* 1999). Short-term alliances (temporary coalitions) form during agonistic interactions in a population of bottlenose dolphins in Doubtful Sound, New Zealand (Lusseau 2007). Short-term coalitions are also evident in primates (*e.g.*, Watts 1998). These coalitions may be important during interspecific interactions with Atlantic spotted dolphins in this study area (Herzing and Johnson 1997, Rogers *et al.* 2004). Short-term relationships may be behaviourally specific preferred associations (Gero *et al.* 2005). Residents may benefit from partnering with immigrant males through increased access to females or aid during intra- and interspecies agonistic interactions. Strong immigrant males may be seen as advantageous partners.

Kinship is often thought to be important in bottlenose dolphin alliance formation. However, in some cases, factors other than kin selection seem to govern male alliance formation (Möller *et al.* 2001). It is unknown if alliances seen in this study are correlated with relatedness; however, the association patterns between residents and immigrants indicates that relatedness may not be the major factor determining alliance formation in this population, especially after the demographic changes resulting from the hurricanes.

Environmental Changes

The altered community structure, grouping and association patterns that occurred after the hurricanes in this study may, in part, be due to shifts in prey related to the disturbance of the hurricanes. Changes in prey populations have been linked to ecological variations and can influence the structure of ecological communities (Genner *et al.* 2004, MacLeod *et al.* 2005). Choices of individuals to stay with or leave groups will affect association patterns, and may be related to the group size and abundance of prey, which can be altered by climatic variations (Lusseau *et al.* 2004). Although it is unclear whether prey abundance and/or distribution changed in the study area, limitations in food availability cannot entirely explain the altered social structure observed in this study. It is possible that the individuals that were lost had emigrated due to a decrease in prey abundance following the hurricanes. However, this seems unlikely since an almost equivalent number of individuals immigrated into the population, and the majority of them remained in the study area.

Conclusion

Demographic changes (including community size and composition) can affect the social system of a species and the results presented here further indicate how flexible the fission/fusion system is, how it can respond quickly to environmental change and how reproductive strategies can influence these dynamics (Lehmann and Boesch 2004). To our knowledge, this is the first study to document changes in dolphin social structure after a natural disaster and resulting demographic upheaval. It showed that environmental variations, which may become more severe or frequent with the current climate changes, may alter the structure of mammal societies through demographic upheaval. Survival of populations may depend on their social structure and the social adaptability of the species. Future work should focus on behavioural interactions within and between sex classes, home range and distribution patterns, habitat use and changes, and prey availability and distribution to illuminate further the reasons behind the social structure fluctuations.

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