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Changes in interspecies association patterns of Atlantic bottlenose dolphins, *Tursiops truncatus*, and Atlantic spotted dolphins, *Stenella frontalis*, after demographic changes related to environmental disturbance

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Abstract

Animal populations can be affected by environmental disturbances in many ways including demographic and behavioral changes. This can affect interspecies associations for regularly interacting sympatric species, like bottlenose and spotted dolphins in the Bahamas (observed since 1985 and interspecies associations analyzed since 1993). After two hurricanes in 2004 each species lost roughly 30% of their respective communities resulting in differing social structure and behavioral changes. During mixed species encounters (MSE) group sizes for spotted dolphins ($\bar{x}$ = 14.1 ± 9.2) were significantly larger than bottlenose dolphins ($\bar{x}$ = 6.0 ± 7.3; $F = 11.74$, df = 1, $P < 0.001$), however, t-tests revealed no differences between aggressive *vs.* affiliative encounters. Sexual/aggressive behavior regularly seen previously was not observed posthurricanes and aggressive encounters were greatly reduced. Generally results were similar to prehurricane data including high resightings of spotted dolphins with male alliances prevalent (including new juvenile alliances seen only posthurricane), and individualized bottlenose participation with few male alliances. However temporal associations varied compared to prehurricane. Interspecies association and behavior patterns were altered and likely affected by the changes in intraspecies association patterns following the hurricanes. However both species still participated in MSE, suggesting this is an important component of their ability to coexist as sympatric species.

Key words: *Stenella frontalis*, *Tursiops truncatus*, interspecies, associations, SOCPROG, environmental disturbance, spotted dolphin, bottlenose dolphin, behavioral ecology.

Environmental disasters can alter animal populations in a variety of ways, including changes in behavior, death, emigration/immigration, food abundance/distribution, and social structure (Elliser and Herzing 2014*b*). In particular, losses of individuals can subtly or greatly affect associations and social structure (chimpanzees, *Pan troglodytes verus*, Lehmann and Boesch 2004; bottlenose dolphins, Elliser and

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Herzing 2011; spotted dolphins, Elliser and Herzing 2014*b*; killer whales, *Orcinus orca*, Matkin *et al.* 2008). For sympatric species these changes may also influence their interspecies interactions; however, this is difficult to document for multiple reasons. Lack of long-term baseline data limits the ability for researchers to document damages, particularly for cetaceans (Matkin *et al.* 2008). This becomes especially true for interspecific interactions. Although 33 cetacean species have been documented in interspecific interactions, few have been well investigated in the field (reviewed in Bearzi 2005). None to the authors' knowledge addresses the effects of environmental disturbance on interspecies interactions, beyond possible affects due to distribution changes related to climate change (MacLeod *et al.* 2005, Smith *et al.* 2009). Combining the rarity of a disturbance occurring in a place where long-term data on interspecific interactions has been conducted, data on how population changes in sympatric species may affect interspecies interactions is lacking.

The Wild Dolphin Project (WDP) has observed regularly interacting sympatric Atlantic spotted dolphins (*Stenella frontalis*) and Atlantic bottlenose dolphins (*Tursiops truncatus*) in the Bahamas every summer since 1985. Much is known about both species including life history (Herzing 1997), correlating sound with behavior (Herzing 1996, 2000), genetics (Green *et al.* 2011, 2015), and community definition and social structure (Herzing and Brunnick 1997; Rossbach and Herzing 1999; Rogers *et al.* 2004; Elliser and Herzing 2011; Elliser and Herzing 2012, 2014*a*, *b*). Both species show social structure characteristics similar to other well studied bottlenose dolphin studies where long-term affiliations are correlated with age, sex, and reproductive status. Males associate based on age, access to females and alliance formation (first and second order alliances for spotted dolphins, first order only for bottlenose dolphins) and females associate based on reproductive status and social familiarity (Rogers *et al.* 2004, Elliser and Herzing 2014*a*).

These sympatric species spend 15% of their time in interspecies encounters (Herzing and Johnson 1997). The function of mixed species groups/associations like these is often attributed to advantages related to foraging benefits and predator avoidance that may give evolutionary benefits to the participants (Stensland *et al.* 2003, Bearzi 2005). However particularly for sympatric species, there may be social factors that influence these associations, including territory defense, practicing of behaviors (often sexual), or reproduction and dominance (Herzing and Johnson 1997, Stensland *et al.* 2003). Analyses of the interspecies associations (Elliser and Herzing 2015) and behavior (Herzing and Johnson 1997, Cusick and Herzing 2014) of this study population of spotted and bottlenose dolphins reveal complex social interactions during mixed species encounters (MSE). Obvious species differences have been documented. Spotted dolphins have high resighting rates (especially males), larger group sizes (particularly for aggressive encounters), prevalence of male alliances (including first order, second order, and possible third order involving associations outside of those alliances), and intraspecies associations during MSE similar to their intraspecies interactions (Elliser and Herzing 2015). Bottlenose dolphins show more individualized participation, smaller group sizes, few male alliances and intraspecies associations during MSE much different than their intraspecies interactions, including random associations during MSE (Elliser and Herzing 2015). Aggressive behavior during agonistic encounters was usually unidirectional with bottlenose dolphins being the aggressors (Herzing and Elliser 2013), unless the spotted dolphins significantly outnumbered them (Herzing and Johnson 1997), often with synchrony of male spotted dolphin behavior (Cusick and Herzing

2014) and acoustics (Herzing 1996). These species difference likely relate to body size and social factors such as dominance, female access, and male alliances (Elliser and Herzing 2015).

In 2004 two major hurricanes directly impacted the area and are thought to be the likely cause of demographic changes (loss of individuals and subsequent immigration of bottlenose dolphins) that occurred. It is unknown whether the loss of individuals observed for both species was due to mass mortality, displacement, or other correlated events (including environmental changes such as prey abundance or distribution) (Elliser and Herzing 2014*b*); however, none of the lost individuals have been resighted to date.

The bottlenose dolphin community lost many individuals (30%), including 14 females, 10 males, and 6 unknown sex, but subsequently gained 27 new individuals which remained in the area, including 5 females, 10 males, and 12 unknown sex (Elliser and Herzing 2011). The community split into two distinct social units each with increased social cohesion, but varying association patterns: unit A (strikingly homogeneous) and unit B (association patterns more similar to prehurricane years); associations between units were rare (Elliser and Herzing 2011). Bottlenose dolphin immigrants assimilated well into the community (particularly males), and the difference of the sexes in acceptance of immigrants may have been the driving force for the changes in social structure (Elliser and Herzing 2011).

The spotted dolphin community suffered the greatest loss of individuals (36%), including 16 females and 20 males, with no subsequent immigration. Although the losses were fairly consistent over age classes, the percentage loss per age class decreased with increasing age (Elliser and Herzing 2014*b*). Community structure (consisting of three social clusters), sex preferences and overall association patterns remained consistent with previous long-term analyses, however some changes did occur (Elliser and Herzing 2014*b*). Decreased social differentiation and increased cohesion within social clusters and across age class, reduced prevalence of second-order alliances, and unprecedented juvenile alliance level associations were documented, revealing social structure changes within overall stability after the demographic changes (Elliser and Herzing 2014*b*).

The demographic changes altered the communities of these two sympatric species in different ways, revealing the social plasticity of both species and that responses to these type of events may vary by species and depend greatly on the original social structure of the community or population. The goal of this study was to show how the altering of each species' social structure following hurricane disturbance affected interspecies interactions in 2005–2007.

METHODS

Study Area

Little Bahama Bank (LBB) is about 64 km from the east coast of Florida (Fig. 1). The study area spans 60 km north to south from West End, Grand Bahama, and 8 km east to west, encompassing 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 seagrass (*Thalassia testudinum*).

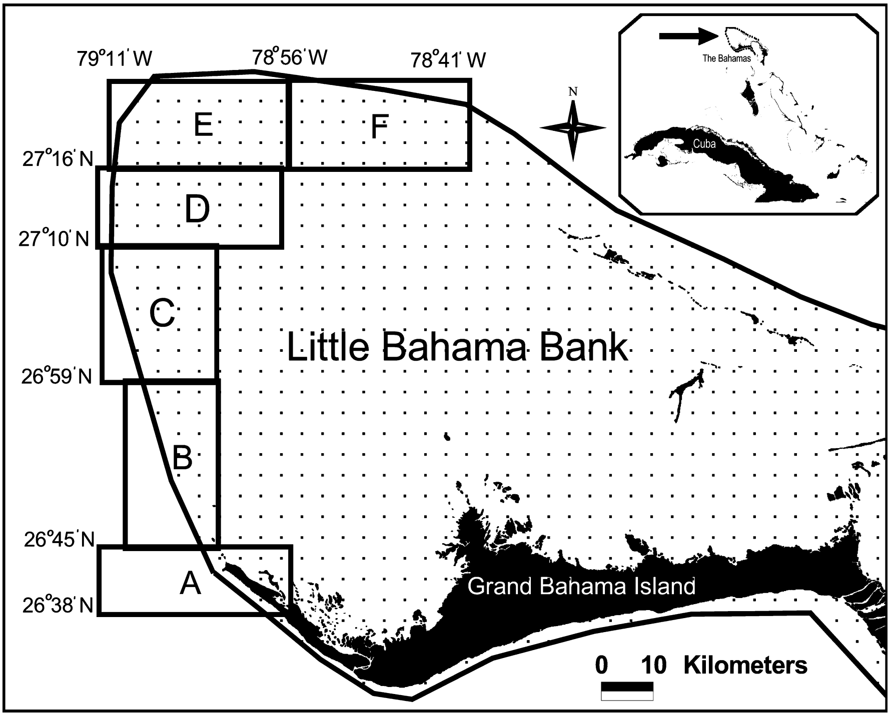

Figure 1. Arrow on the insert indicates Bahamas study area. The area was broken into six segments: A, B, C, D, E, and F for effort analyses, see Elliser and Herzing 2014*b*.

Hurricane History

In 2004 the study area was directly hit 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 Island 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). Because the maximum lifespan of most dolphins averages 40–50 yr (Connor *et al.* 2000), this population of dolphins has not encountered storms of this intensity before.

Data Collection

Individuals of both species are continually and consistently resighted within and between field seasons over long periods, up to at least 22 yr (Rogers *et al.* 2004, Elliser and Herzing 2012). Data were collected between May and early September each year, 2005–2007 (for effort 2002–2007 see Elliser and Herzing 2014*b*) aboard a 62 ft power catamaran research vessel. Observations for sighting dolphin groups were conducted in all but rough weather conditions (over Beaufort 3 and/or intense rain squalls) from 0700 to 2000 in one person/one hour shifts, scanning forward 180° while the boat was underway, and 360° while anchored. Field time was more limited than previous years due to poor weather conditions (strong winds, rough seas, and storms) in years following the hurricanes of 2004.

A group was defined as all dolphins in sight, moving in the same direction, typically involved in the same activity (Shane 1990). When a mixed species group was sighted, an estimate of group size for each species was determined from the surface. Individuals were considered associated when identified with the group. Surface dorsal fin photographs were taken to identify the bottlenose dolphins present using SLR digital cameras. Subsequently two to five researchers entered the water where one to three researchers had underwater digital cameras to document individual identification and behavior (for both species). These dolphins have been habituated to the presence of boats and people in the water over the decades, allowing underwater observations. An encounter was defined as a group of dolphins that were observable underwater for more than 2–3 min (Elliser and Herzing 2012). Group size generally remained consistent during an encounter; however, sometimes animals would join or depart the group, but these did not alter the size substantially and therefore was not made a new encounter (Elliser and Herzing 2014*a*). Final group size was determined from initial surface estimate (including any nonmarked individuals), in-water identification, and surface and underwater photo-identification after the encounter (which would also include photographs of any nonmarked individuals).

Individual identification for bottlenose dolphins was accomplished by comparing and matching natural markings, including nicks and scars on the dorsal fin. For spotted dolphins identification was accomplished by comparing spotting patterns between individuals. Additional body marks were also used, including nicks and scars on the dorsal fin, flukes, pectoral fins and marks or scars on the body. For both species, females were identified by observation of mammary slits or observation of nursing by a calf and males were identified by a gap between the genital slit and the anus, or observation of an erection.

Bottlenose dolphins were classified as adult or calf (individual that is two-thirds the length of an adult, often in echelon position). Individuals were only classified as juveniles if their birth year was known. Atlantic spotted dolphins show the four developmental color phases described by Perrin (1970) for the pantropical spotted dolphin (*Stenella attenuata*) and have been adapted for the Atlantic spotted dolphin by Herzing (1997). The four age classes include: two-tone (calves, 0–3 or 4 yr), speckled (juveniles, 4–9 yr), mottled (young adult, 10–16 yr) and fused (adult, 16+ yr). Every identified individual is assigned to an age class and these data were updated each year.

Data Analysis

Coefficients of association (CoAs) were calculated using the half-weight index (Cairns and Schwager 1987) with the software program SOCPROG 2.3 (Whitehead 2009). For both species data were pooled in order to obtain sufficient sightings per individual, and to be able to include enough individuals in the study. Data after the hurricanes were pooled into one data set: 2005–2007. Detailed age class information was available for spotted dolphins (see above). An individual spotted dolphin was placed in the age class category that they were in for the majority of the pooled time frame (*i.e.*, two or more years).

CoAs were determined for pairs of noncalf individuals of known sex sighted at least three times per pooled period for both species. Calves were not included in these analyses as their associations are dependent upon their mother. The period after the hurricanes is shorter than the prehurricane pooled data sets (Elliser and Herzing 2015), therefore a lower sighting criterion was used. Both pre and posthurricane criteria average to roughly one sighting/year; so the posthurricane data are comparable in terms of sampling effort. Strong associations were defined as greater than twice the average CoA of the study group (Gero *et al.* 2005, Whitehead 2008*a*).

Permutation tests were conducted permuting the groups within samples using SOCPROG to evaluate whether associations were nonrandom or there were preferred/avoided companions with a sampling period of "day" (Whitehead 2008*a*, 2009). The number of permutations was increased until the *P*-value for the standard deviation (SD) stabilized at 10,000 permutations, with 100 flips per permutation (Whitehead 2009). This test accounted for potential demographic effects (*e.g.*, entrance and exit of individuals due to birth, death, migration, *etc.*) due to the pooling of years for each data set. Significantly high SD or coefficient of variation (CV = SD/mean) of the observed association indices indicated longer-term (*i.e.*, between sampling periods) preferred companionship and nonrandom associations (Whitehead 2009). If associations were found to be nonrandom, Mantel tests were conducted to examine whether differences in association occur between classes (*e.g.*, sex and age classes, where appropriate).

The precision (SD, SE) of the CoA was estimated with bootstrap techniques (1,000 replications). The correlation coefficient (CC) between the true and calculated association indices (Whitehead 2008*a*, *b*) was used to infer how reliable the results were and if there was enough data (including number of sightings) to be representative of the true social system. Data sets with social differentiation of intermediate ($S \sim 0.5$) to high (S close to or above 1.0) require fewer associations to detect preferred companionship than data sets with low differentiation (Whitehead 2008*b*). The statistical power of the permutation test was estimated with the Social Differentiation (S, the CV of the true association indices) and the mean number of observed associations per individual (H), given that $S^2 \times H > 5$ suggests sufficient power (Whitehead 2008*b*).

The temporal stability of the associations was investigated using Lagged (LAR) and null association rates. LAR is the estimated probability of two individuals currently associating being associated various time lags later (Whitehead 1995). The null association rate is the expected value of the LAR if there are random, or no preferred, associations (Whitehead 2009). LARs (overall and by species) were determined utilizing all of the data (*e.g.*, no restrictions on number of sightings or sex of individuals) (Whitehead 2008*a*). A moving average of 8,000 associations was used for the overall LAR; 6,500 associations for the LAR of only spotted dolphins; 2,000 associations for LAR of mixed species; and 900 associations for LAR of only bottlenose dolphins. Different moving averages were needed based on the lower number of bottlenose dolphin sightings in MSE. The overall LAR was compared with models of social organization given in SOCPROG: (1) rapid disassociation and constant companions (some associations decay rapidly within one sampling period, then LAR is stable with no decay); (2) casual acquaintances (animals associate for a certain time period, then never again, LAR decays to zero); (3) rapid disassociation and casual acquaintances (disassociations within a single sampling period, but those that do persist eventually fall to zero); (4) rapid disassociation and constant companions and casual acquaintances (association rates initially fall, but then level off above zero); (5) constant companions and casual acquaintances (rapid disassociation within one sampling period and association rates initially fall, but then level off above zero); (6) rapid disassociation and two levels of casual acquaintances (rapid disassociation within one sampling period and two levels of disassociation at shorter and longer time lags with rates eventually decaying to zero); (7) two levels of casual acquaintances (two levels of disassociation at shorter and longer time lags with rates eventually decaying to zero) (more detailed descriptions can be found in Whitehead 2008*a*). The best fitted model(s) was selected based on lowest quasi-Akaike Information Criterion (QAIC), which tries to account for overdispersion of the association data (Burnham and Anderson 2002). The differences in QAIC (ΔQAIC), in relation to the best fit model, were calculated, where 0–2 shows substantial support, 4–7 shows considerably less support, and >10 shows essentially no support (Whitehead 2009). The ΔQAIC, likelihood and relative QAIC weights ($e^{(-0.5*\Delta QAIC)}$) were calculated and give an indication of how well the data support the less favored models (Burnham and Anderson 2002). Jacknifing was used to estimate the precision of the LAR (Whitehead 2009), with a grouping factor set to 30 sampling periods (days).

Group size and behavior comparisons were conducted in order to help understand group composition and the role of each species during these MSE. Group size analyses used parametric tests; residuals showed a normal distribution. Behavior was recorded for each encounter and categorized as affiliative (foraging, travel, courtship, play, nursing, discipline) or aggressive (open mouth, S posture, chasing, side mounting, hits) for data analysis. Group size was analyzed in relation to species and aggressive/affiliative encounters with ANOVAs and *t*-tests using SPSS 16 software.

RESULTS

Resightings

Despite the reduction of community size by more than 30% for the spotted dolphins (Elliser and Herzing 2014*b*), over 60% of the remaining spotted dolphin community was regularly involved in MSE, almost equal to the 65% in the prehurricane results (Elliser and Herzing 2015). The bottlenose dolphin community size did not change due to an almost equal number of lost individuals (30) and immigrants (27) (Elliser and Herzing 2011). Only 14% of the bottlenose dolphin community were involved in MSE, which is consistent with prehurricane results (Elliser and Herzing 2015). Spotted dolphins had higher resightings (average number of times individuals were seen) than bottlenose dolphins, though not as drastic as prehurricane results. Male ($\bar{x} = 6.5 \pm 2.3$) and female ($\bar{x} = 6.4 \pm 2.3$) spotted dolphins were resighted almost equally and more than both male ($\bar{x} = 5.0 \pm 1.9$) and female ($\bar{x} = 4.3 \pm 1.4$) bottlenose dolphins. For bottlenose dolphins this is a reduction of 32% for males and 45% for females from prehurricane years. For spotted dolphins this is a reduction of 50% for males and 32% for females from prehurricane years. These reductions may be due to the shorter pooling time frame posthurricane (3 yr *vs.* 6 yr); however it is interesting to note that the spotted dolphin males showed the largest reduction, with female bottlenose dolphins a close second.

Lack of continuity in resightings following the hurricanes was not due to individual choices to stop participating, but because of their absence from the community (due to death or possible emigration). The majority of spotted dolphins not seen again in posthurricane encounters (85.2%) were lost prior to or following the hurricanes and thus unable to be present. Only one bottlenose dolphin individual (female) was seen in both pre- and posthurricane MSE. Six bottlenose dolphin individuals in posthurricane MSE were immigrants.

Group Size

Number of MSE per year ranged from 6 to 11 ($\bar{x} = 8.3 \pm 2.1$). Taking into account all encounters (intra- and interspecies combined), spotted dolphins spent 9.1% of their time, and bottlenose spent 14.4% of their time in MSE. Posthurricane total group size ($n = 25$, $\bar{x} = 20.2 \pm 9.3$) ranged from five to 37. An ANOVA showed that spotted dolphin group size in MSE was significantly larger ($\bar{x} = 14.1 \pm 9.2$) than bottlenose dolphin group size ($\bar{x} = 6.0 \pm 7.3$; F=11.74, df = 1, $P < 0.001$). Figure 2 shows the distribution of group sizes in relation to species and behavior. During aggressive encounters, total group size was significantly larger ($\bar{x} = 23.6 \pm 8.8$) than during affiliative encounters ($\bar{x} = 14.1 \pm 7.0$; t-test: $t = 2.75$, df = 23, $P = 0.011$). However both spotted and bottlenose dolphin group sizes did not differ significantly between aggressive (spotted: $\bar{x} = 15.6 \pm 10.2$; bottlenose: $\bar{x} = 7.9 \pm 8.5$) and affiliative encounters (spotted: $\bar{x} = 11.4 \pm 6.9$; t-test: $t = 1.09$, df = 23, $P = 0.287$; bottlenose: $\bar{x} = 2.7 \pm 2.1$; t-test: $t = 1.81$, df = 23, $P = 0.084$). For spotted dolphins group sizes in affiliative MSE were similar to those seen during intraspecies encounters ($\bar{x} = 10.9 \pm 8.9$, Elliser and Herzing 2014*b*), however, for bottlenose dolphins group sizes in affiliative MSE were lower than intraspecies encounters ($\bar{x} = 6.2 \pm 6.1$, Elliser and Herzing 2011).

Associations

The total number of noncalf individuals, males and females for each data set (spotted and bottlenose dolphin individuals of known sex, seen at least three times) are given in Table 1. The statistical power to detect preferred associations was

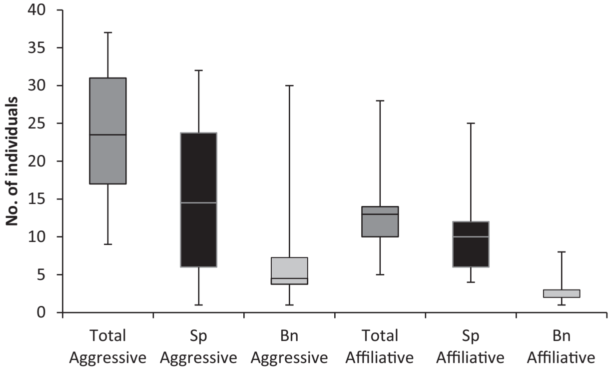

Figure 2. Group size broken down by behavior and species posthurricane 2005–2007 in a standard box plot (boxes contain from the first to third quartiles, line in the box is the median, whiskers are the minimum and maximum). Sp = spotted dolphin, Bn = bottlenose dolphin and Total = both species in either aggressive or affiliative MSE. Total group size was significantly larger during aggressive encounters than affiliative, however, there was no significant difference in spotted or bottlenose dolphin group size in relation to behavior.

more than sufficient (S^2 x $H > 5$, Table 1). Permutation tests revealed nonrandom associations, indicating preferred and/or avoided companions (Table 1). However, social differentiation was only close to intermediate differentiation at 0.437; and the correlation coefficient was moderate (CC = 0.50, Table 1), indicating the CoA matrix was "somewhat" representative, indicating the data were less representative compared to prehurricane results with $S > 0.60$ and CC > 0.67 (Elliser and Herzing 2015).

CoA ranged from 0.13 to 1.00, with a mean of 0.27 ± 0.20 and the majority in the lower range. The overall, spotted-spotted, and bottlenose-bottlenose mean CoA were higher than prehurricane years (Table 2). Strong associations (over twice the population average of 0.27) made up 13.5% of all associations, a similar number of strong associations to prehurricane results. The majority and strongest of associations were intraspecies between spotted dolphins; however, this percentage decreased by 18% (compared to 1993-1998) and 12% (compared to 1999-2004) from the prehurricane analyses (Elliser and Herzing 2015). There were more bottlenose-bottlenose dolphin associations (increase of about 4%) that had a higher mean (which was similar to the spotted dolphin mean) than prehurricane results. Interestingly, spotted dolphin intraspecies CoA were lower than CoA during MSE (consistent with prehurricane data), however, the intraspecies bottlenose dolphin CoA were lower than CoA during MSE, which is opposite of prehurricane results (Elliser and Herzing

Table 1. Permutation test statistics including SD and CV of real and permuted (random) data, P-value for permutation test results, social differentiation (S), number of associations per individual (H), correlation coefficient (CC), and power to detect preferred associations ($S^2 \times H$). There were 55 individuals (14 bottlenose dolphins [Bn], 41 spotted dolphins [Sp]): 30 males (8 Bn, 22 Sp) and 25 females (6 Bn, 19 Sp).

Year	SD	CV	P	$S \pm$ (SE)	H	CC ± (SE)	$S^2 \times H$
2005–2007	0.202 (random) 0.203 (real)	0.745 (random) 0.750 (real)	0.0086 0.0091	0.44 ± (0.15)	94.2	0.50 ± (0.07)	17.97

Table 2. Mean CoA ± SD: overall, bottlenose dolphin only (Bn-Bn), mixed (Bn-Sp), spotted dolphin only (Sp-Sp), with percentage of total associations for each type given in parenthesis (%) for posthurricane years 2005–2007. Mantel test P-value and correlation coefficient (CC) indicate that within species associations were significantly higher than between species. Bold indicates the significantly higher mean CoA.

Year	Overall	Bn-Bn	Bn-Sp	Sp-Sp	Mantel test
2005–2007	0.27 ± 0.20	**0.32 + 0.08 (6.3%)**	0.18 ± 0.08 (33.1%)	**0.33 ± 0.08 (60.5%)**	CC = 0.342; $P < 0.001$
Mean intraspecies encounters[a]		0.16 ± 0.05	N/A	0.24 ± 0.16	

[a] Data retrieved from previous work, pooled years were not directly compatible but averages were similar across most years, mean is best estimate for current pooled analysis. Bottlenose dolphin: Rogers *et al.* (2004) and Elliser and Herzing (2011). Spotted dolphin: Elliser and Herzing (2014*a*, *b*).

2015) (Table 2). A Mantel test revealed that associations were significantly stronger for within species associations than between species associations, as seen in the prehurricane years even though both spotted and bottlenose dolphins had similar, higher, within-species CoAs (Table 2).

Posthurricane sex associations were similar to prehurricane results. A Mantel test revealed that CoAs were significantly higher for within sex associations than between sex (including both species), particularly because of spotted dolphin male-male CoAs (mean CoA: male-male = 0.30 ± 0.09; male-female = 0.25 ± 0.08; female-female = 0.27 ± 0.06; $P < 0.003$) although the difference in CoAs was smaller than prehurricane associations (Elliser and Herzing 2015).

The majority (80.6%) and strongest (up to 0.92) of the male-male associations were between spotted dolphins, although bottlenose dolphin male pairs also had very strong associations (up to 0.83, similar to that seen in alliances during intraspecies encounters, Rogers *et al.* 2004), contrary to prehurricane results. Mottled and/or fused male spotted dolphin individuals comprised 80% of the spotted-spotted male pairs and all of the mixed-species male pairs. A Mantel test revealed that CoAs for spotted dolphins were significantly higher within ($\bar{x} = 0.35 \pm 0.10$) than between ($\bar{x} = 0.25 \pm 0.08$) age classes (CC = 0.21, $t = 7.08$, $P < 0.001$), particularly for the mottled/fused age classes.

Spotted dolphin alliances between long-term associates, and new alliances of speckled and mottled individuals that were observed during intraspecies encounters in the same time frame (Elliser and Herzing 2014*b*) were also documented in posthurricane MSE. The alliances of speckled individuals are of particular interest as this level of association between juveniles was not seen previous to the hurricanes, in intra or interspecies interactions. In addition, strong associations between members of different alliances were also observed, indicating persistence of second order alliances in MSE after the hurricanes.

There were five strong bottlenose-bottlenose CoAs (0.60–0.83), comparable to the spotted male-male CoAs, involving six bottlenose dolphin males (two residents and four immigrants). These CoAs were the strongest ever seen for bottlenose dolphins in any interspecies encounter. However, no previously known bottlenose dolphin male alliance was seen in the posthurricane MSE, despite at least three of these alliances present in bottlenose dolphin intraspecies encounters during the same time.

The few strong mixed-sex bottlenose-spotted dolphin associations were between male bottlenose dolphins (a trio with CoAs 0.80 and up) and fused female spotted dolphins. There were no mixed-species male associations that were also seen in prehurricane years because all the male bottlenose dolphins (both resident and immigrant) were not seen previously in MSE.

Temporal Analysis

LAR indicated preferred associations over all timescales, even though association rates fell, they leveled out above the null association rate (Fig. 3a). There were three models that showed substantial support (Table 3, difference in QAIC between the models was <2, Whitehead 2009). The best fit model was rapid disassociation and casual acquaintance, with both the rapid disassociation and two levels of casual acquaintances and two levels of casual acquaintances showing substantial support. The differences were striking between species, as seen in the species specific LAR (Fig. 3b). Spotted dolphin only associations were the highest, fitting the rapid

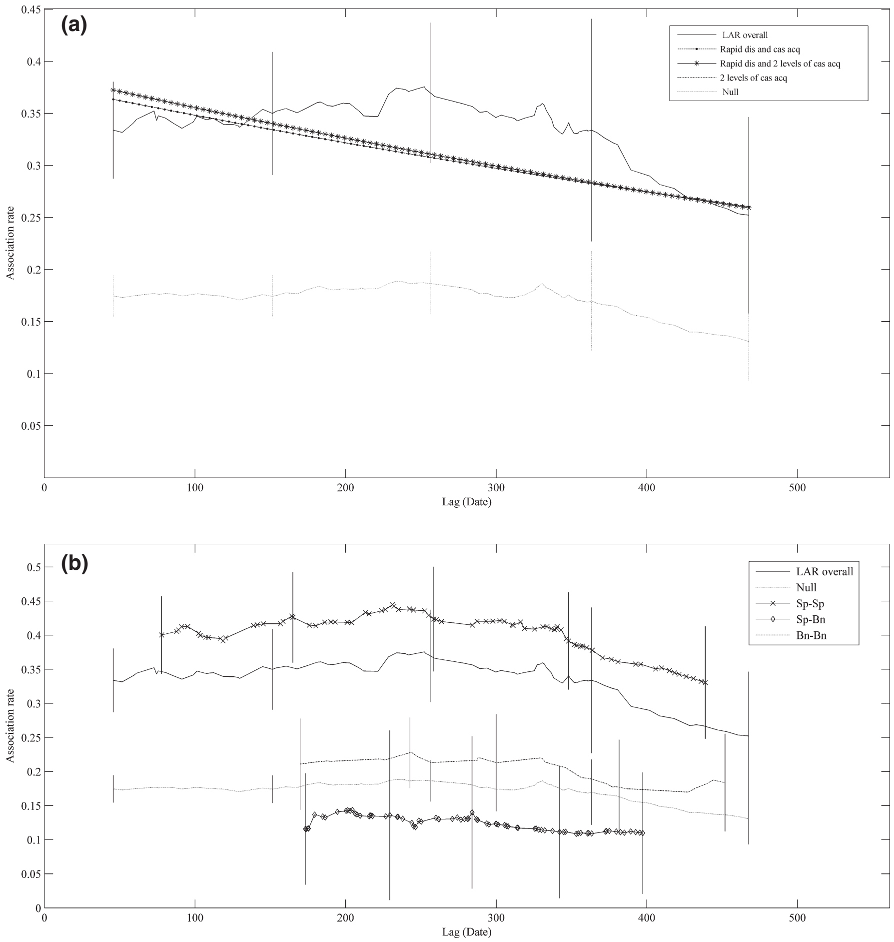

Figure 3. (a) 2005–2007 overall LAR with fitted models and null association rate (dis = disassociation, cas = casual, acq = acquaintance) with 8,000 association moving average and jackknifing over 30 d periods. (b) 2005–2007 species specific LAR with overall and null association rates. Sp = spotted dolphin, Bn = bottlenose dolphin. A 6,500 association moving average was used for Sp-Sp, 2,000 association moving average used for Sp-Bn, and 900 association moving average used for Bn-Bn.

disassociation and casual acquaintances model, similar to their intraspecies LAR of rapid disassociation, constant companions and casual acquaintances (Elliser and Herzing 2014*a*, 2015). Contrary to prehurricane data, however, bottlenose-bottlenose dolphin LAR was above the null association rate, and had multiple LAR model support (including Rapid disassociation and constant companion, rapid disassociation and casual acquaintances, constant companion and casual acquaintances, and two levels of casual acquaintances). Interestingly, the mixed-species LAR was well below the null association rate, contrary to prehurricane results (Elliser and Herzing 2015).

Table 3. Results of model fitting to overall LAR (dis = disassociation and acq = acquaintance(s)). Lag is represented by td. LAR were calculated using a 8,000 association moving average. The bolded model is the best fit, the other two showing substantial support are in italics, with difference in QAIC between the models being equal or less than 2.

LAR Model	Description	QAIC	QAIC	QAIC weight	Likelihood
$\mathbf{g(td) = 0.38 * e(-0.00079 * td)}$	**Rapid dis and casual acq**	**1,894.78**	**0**	**0.56**	**1**
$g(td) = -0.23 * e(-0.49 * td) + 0.39 * e(-0.00086 * td)$	*Rapid dis and two levels of casual acq*	*1,896.62*	*1.84*	*0.23*	*0.4*
$g(td) = 0.62 * e(-30.19 * td) + (1 - 0.62) * e(-0.00079 * td)$	*Two levels of casual acq*	*1,896.78*	*2*	*0.21*	*0.37*
$g(td) = e(-0.0050 * td)$	Casual acq	2,914.17	1019.39	0	0
$g(td) = 0.31 + -0.39 * e(-1.5 * td)$	Rapid dis, constant companions, casual acq	1,915.17	20.39	0	0
$g(td) = 0.31$	Rapid dis and constant companions	1,911.93	17.15	0	0
$g(td) = 0.31 + (1 - 0.31) * e(-32.09 * td)$	Constant companions and casual acq	1,913.93	19.15	0	0

DISCUSSION

It is evident that interspecies interactions are an important component of the social interactions between these sympatric species; despite social restructuring for both species following the demographic changes, they continued to participate in MSE. While the overall association patterns during MSE remained similar to prehurricane analyses (including similar LAR, consistent spotted dolphin resightings and importance of male alliances, individualized bottlenose dolphin participation and lack of male alliances, and lack of long-term interspecies associations), there appeared to be less social differentiation, slightly less representative associations and some association differences posthurricane. These results may indicate a decrease in strongly preferred associations in MSE posthurricane and may be explained by the differences between the species in their association patterns both during and outside of MSE.

Based on the average 15% of their time spent in MSE prehurricane (Elliser and Herzing 2015), spotted dolphins decreased their time (9.1%), whereas bottlenose dolphins remained close to the average (14.4%). LAR for spotted dolphins remained remarkably similar to their prehurricane LAR (Elliser and Herzing 2014*a*, 2015). However interspecies associations were well below the null association rate for all time lags (suggesting random associations) indicating that even though there did seem to be some preferred associations at shorter time lags between species in prehurricane years (Elliser and Herzing 2015), this was not evident posthurricane. The LAR for bottlenose dolphins showed associations consistently above the null association rate (indicating preferred associations during MSE), whereas in prehurricane years they were below the null association rate at all time lags (Elliser and Herzing 2015). Thus, although there is stability in the continuation of MSE, there are changes that may be influenced by the differential demographic changes between the species and their behavioral responses.

Behavioral and social variability can be a common response to environmental variability in cetaceans (Karczmarski *et al.* 2005), and are not limited to intraspecies associations. The differences observed during MSE are likely linked to the behavioral and social changes that occurred following the hurricanes. The spotted dolphin community remained relatively stable, with no drastic changes in social structure (Elliser and Herzing 2014*b*), whereas the bottlenose dolphin community had an influx of immigrants and large restructuring of their social structure (community spilt into two distinct social units) (Elliser and Herzing 2011). There may have been more focus, for each species, on maintaining/creating their intraspecies associations during this time of recovery and restructuring; increased cohesiveness within units/clusters for both species was observed (Elliser and Herzing 2011, 2014*b*). Thus the bottlenose dolphins, which experienced more drastic changes to social structure, may have more of a need for maintaining relationships in MSE during this time (compared to prehurricane) to solidify old and new relationships. Consequently relationships between the spotted and bottlenose dolphins participating may not have had time to become established.

Spotted dolphin male alliances (both first and second order) were prevalent, consistent with prehurricane results, likely needed for spotted dolphins to compete with the physically and more dominant bottlenose dolphins, including defense of spotted dolphin females (Elliser and Herzing 2015). The most interesting change in these alliances was that juvenile males had an increase in their mean association levels during MSE. This increase correlates with what occurred in their intraspecies associations during the same time period, where juvenile male associations reached alliance level strength (Elliser and Herzing 2014*b*). Normally male alliances crystallize during sexual maturity, but these dynamics may have been altered during/after the hurricanes, possibly speeding up the development of male alliances (Elliser and Herzing 2014*b*). The increased strength of association may indicate that participation in these MSE is an important aspect of male spotted dolphin alliance development. However it may be more important now only because of the loss of individuals in the community and social changes after the hurricanes. Alternatively, the increased strength of association between young males may be due to the lack of individuals after the hurricanes; with fewer choices, individuals may increase their associations to a stronger level (Elliser and Herzing 2014*b*), regardless of other influences.

Another significant change was that group size during aggressive encounters was no longer larger for spotted dolphins and their amount of time spent in MSE decreased. This correlates with observed behavioral changes including regular sexual/aggressive behavior in which bottlenose males dominate and side mount spotted dolphin males. Although aggressive encounters still occurred, this type of overt behavior was not seen at all since the hurricanes, until the field season of 2009 (CRE and DLH, unpublished observations), thus larger spotted dolphin group size (and more time spent in MSE) may not have been as necessary for defense from the dominant bottlenose dolphins. However, spotted dolphin male alliances (which were still present) may still have been necessary for female defense in a less overt manner. Regardless of the method of aggression, spotted dolphins are physically smaller and require six individuals to chase away one bottlenose dolphin (Herzing and Johnson 1997), thus maintenance of alliances may be prudent for spotted dolphins regardless of the absence of aggressive physical behavior.

There continued to be a general lack of male alliances (though a few were present) and lower resightings for bottlenose dolphins in MSE, but contrary to prehurricane results there were nonrandom associations among bottlenose dolphins and random interspecies associations. This may be due to the demographic changes that seemed to skew which bottlenose dolphins were involved. The bottlenose dolphin community split into two units with differing association patterns. Unit B had association patterns similar to the prehurricane population, whereas unit A was much more homogenous in nature (Elliser and Herzing 2011). All the bottlenose dolphins involved in MSE were from Unit B, none were from Unit A. Specialized behaviors by certain individuals or groups within a population have been documented (*e.g.*, intentional stranding to capture pinnipeds, Guinet 1991; "sponge-carriers," Smolker *et al.* 1997; cooperation with artisanal fisherman, Daura-Jorge *et al.* 2012). It is possible that involvement in MSE may be restricted to individuals in one unit due to their association patterns, or their social familiarity with local spotted dolphins. This could indicate a greater social and behavioral split in the bottlenose dolphin community than previously reported through associations alone (Elliser and Herzing 2011).

Although the two species were each undergoing social restructuring following the hurricanes (Elliser and Herzing 2011, Elliser and Herzing 2014*b*) they were still involved in MSE, though with altered association and behavior patterns and reduced frequency. The spotted dolphins remained the most stable in their association patterns, whereas the bottlenose dolphins varied (likely causing the differences seen in interspecies associations) between pre- and posthurricane years. It may be that the changes in the bottlenose dolphin social structure had a greater impact on associations during MSE than that of the spotted dolphin social structure. The decreased aggression and altered associations patterns seen during MSE posthurricane indicate that the time following the hurricanes may have been a rebuilding and restructuring of the relationships between these two species, and it may take some time to return to behaviors normally observed in the past (such as the mounting dominance behavior), and may depend on the resiliency (and species differences) of the communities involved. The consistency with which these MSE are observed, even through drastic demographic changes, indicates MSE are an integral part of how these two resident communities of sympatric dolphins live together.

Conclusion

The results of this paper reveal how demographic upheaval can alter interspecies association and behavior patterns, but also that MSE seem to be a critical component of the society of these sympatric species. Environmental changes and disasters will likely increasingly effect animal populations as climate change continues. Effects of shifting habitat and demographic upheaval can greatly alter communities and how they interact with one another in the ecosystem. This study is an example of the mechanisms and time frame involved in reestablishing wild dolphin communities after traumatic environmental events.

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