



Long-term interspecies association patterns of Atlantic bottlenose dolphins, *Tursiops truncatus*, and Atlantic spotted dolphins, *Stenella frontalis*, in the Bahamas

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ABSTRACT

With the exception of primates, detailed interspecies behavioral studies are rare in mammalian species and for cetaceans, most are anecdotal descriptions. This study is the first long-term study on interspecies associations of regularly interacting groups. In the Bahamas Atlantic bottlenose (*Tursiops truncatus*) and spotted dolphins (*Stenella frontalis*) regularly form mixed species encounters (MSE). Both species show strong site fidelity with high resighting rates. During MSE, the majority (>65%) of spotted dolphins (especially males) were continually resighted; however bottlenose dolphins had comparatively low resighting rates (<17%). During MSE group size was significantly larger for spotted dolphins (13.0 ± 11.0) than bottlenose dolphins (4.8 ± 3.5) ($F = 93.803$, $df = 1$, $P < 0.001$). This difference was largest during aggressive encounters, due to the increased spotted dolphin group size (t -test, $t = 4.75$, $df = 184$, $P < 0.0001$), but no difference in bottlenose dolphin group size. Strong associations (greater than twice the community average) were primarily between male spotted dolphins. Male alliances were prevalent for spotted dolphins but rare for bottlenose dolphins. These species differences were also observed in lagged association rates. These results highlight the differences involved in alliance formation and function for regularly interacting sympatric species and reveal insights into possible ecological and social reasons for these group formations.

Key words: interspecies, associations, *Stenella frontalis*, spotted dolphin, *Tursiops truncatus*, bottlenose dolphin, male alliances, SOCPROG, social structure, sympatric species.

Over 33 cetacean species have been documented in interspecific associations around the world, however, few have been well investigated in the field (reviewed in Bearzi 2005). The majority of these are anecdotal descriptions of singular or short-term events. This is primarily due to the fact that most cetacean interspecies associations are relatively brief (Baraff and Asmutis-Silvia 1998) and/or do not occur on a regular or consistent basis. In contrast, detailed interspecies behavioral studies have been described for avian species (*e.g.*, mixed species foraging flocks: Dolby and Grubb

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1998, Sasvari and Hegyi 1998), but are rare in mammals except for primates (Stensland *et al.* 2003).

The function of interspecies associations/groups is usually attributed to foraging advantages and predator avoidance that may give functional advantages and evolutionary benefits to the participants (Stensland *et al.* 2003, Bearzi 2005). These interspecies associations may also occur because of social factors, especially for social mammals like primates and cetaceans, including territory defense, practicing of behaviors (often sexual), or reproduction and dominance (Herzing and Johnson 1997, Stensland *et al.* 2003). Agonistic interactions are generally the predominant behavior in cetacean interspecies groups with the larger species dominant over the smaller (Ross and Wilson 1996, Herzing and Johnson 1997, Baird 1998, Patterson *et al.* 1998, Herzing *et al.* 2003, Psarakos *et al.* 2003, Wedekin *et al.* 2004, Acevedo-Gutiérrez *et al.* 2005, Herzing and Elliser 2013) although temporary reversals have been documented such as Atlantic spotted dolphins (*Stenella frontalis*) being aggressive toward bottlenose dolphins (*Tursiops truncatus*) (Herzing *et al.* 2003, Cusick and Herzing 2014). This predominance, however could be a sampling artifact because agonistic behavior is often more overt and the easiest to observe. Nonaggressive, or affiliative, behaviors (including grooming, play, and copulation) have also been documented in cetaceans and primates (Herzing and Johnson 1997, Stensland *et al.* 2003). The interspecies studies listed have documented behaviors and may indicate a species' tendency to form interspecies groups, but little is known about which individuals are involved, their associations, and whether they are resighted in interspecies groups over time.

Associations between interspecific individuals across years are rare for cetaceans (Baraff and Asmutis-Silvia 1998), but have been documented for an individual common dolphin (*Delphinus delphis*) with bottlenose dolphins (Bearzi 1997), an individual spinner dolphin (*Stenella longirostris*) with bottlenose dolphins and an individual long-finned pilot whale (*Globicephala melas*) with Atlantic white-sided dolphins (*Lagenorhynchus acutus*) (Baraff and Asmutis-Silvia 1998), and individual Risso's dolphins (*Grampus griseus*) with striped dolphins (*Stenella coeruleoalba*) and common dolphins (Frantzis and Herzing 2002). These associations range from 2 to 6 yr in length, but little detailed information is available about the nature of these interactions. Interspecific associations are often temporary and opportunistic, however, in areas where sympatric species show strong site fidelity and regular interactions, they may be less random and may be socially complex (Frantzis and Herzing 2002, Quérouil *et al.* 2008, May-Collado 2010).

Long-term, regular interspecies interactions between sympatric Atlantic spotted dolphins and Atlantic bottlenose dolphins in the Bahamas have been observed consistently every summer since 1985 as part of the research conducted by the Wild Dolphin Project (WDP). 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 and social structure (Herzing and Brunick 1997; Rossbach and Herzing 1999; Rogers *et al.* 2004; Elliser and Herzing 2011, 2012, 2014a, b). Both species show social structure characteristics similar to other well studied bottlenose dolphins where long-term affiliations are correlated with age, sex, and reproductive status. The spotted dolphins show strong site fidelity and high resighting rates, live in one community with three interacting social clusters, have female associations influenced by reproductive status, calf care and social familiarity and male associations influenced by age, female access and alliance formation (Elliser and Herzing 2012, 2014a). The bottlenose dolphins also show strong

site fidelity and high resighting rates, live in one community and have female associations influenced by reproductive status and male associations influenced by alliance formation (Elliser and Herzing 2011). Of particular interest to this study are the male alliances of both species and their interactions during MSE. Spotted dolphins form both first order (2–3 individuals) and second order alliances (associations between two first order alliances) similar to those seen in Shark Bay Australia (Connor and Mann 2006, Connor *et al.* 2011, Elliser and Herzing 2014a). Bottlenose dolphins show both long-term and short-term alliances usually between two males (Rogers *et al.* 2004, Elliser and Herzing 2011), similar to those seen in other bottlenose dolphin populations (Wells 1991, Connor *et al.* 1992, Owen *et al.* 2002, Krützen *et al.* 2003, Lusseau 2007).

In the Bahamas, the Atlantic spotted and bottlenose dolphins spend 15% of their time in mixed species groups, and are involved in a wide range of behavioral activities including affiliative (foraging, traveling, play, alloparental care) and aggressive behaviors (Herzing and Johnson 1997). Although the interactions (including those of male alliances) have been described (Herzing and Johnson 1997, Herzing and Elliser 2013, Cusick and Herzing 2014), little is known about the individual associations during these regular mixed species encounters (MSE). The primary goal of this study was to describe the long-term association patterns of regularly interacting groups of bottlenose dolphins and spotted dolphins during MSE in the Bahamas between 1993 and 2004.

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 km². 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*).

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). Detailed analysis of long-term intraspecies social structure has been published for these spotted dolphins (Elliser and Herzing 2012, 2014a) and bottlenose dolphins (Rogers *et al.* 2004). For comparative purposes with the interspecies data reported in this paper some data from the intraspecies studies have been presented in the results section. Social structure analysis in the current study (see below) follows the same protocol as analyses of the long-term intraspecies social structure (for detailed analyses of that work see Rogers *et al.* 2004; Elliser and Herzing 2012, 2014a).

Data were collected between May and early September each year, 1993–2004 (for effort 1991–2002 see Elliser and Herzing 2012 and for 2002–2007 see Elliser and Herzing 2014b) aboard a 19 m power catamaran research vessel. Observations for sighting dolphin groups were conducted in all but rough weather conditions (over

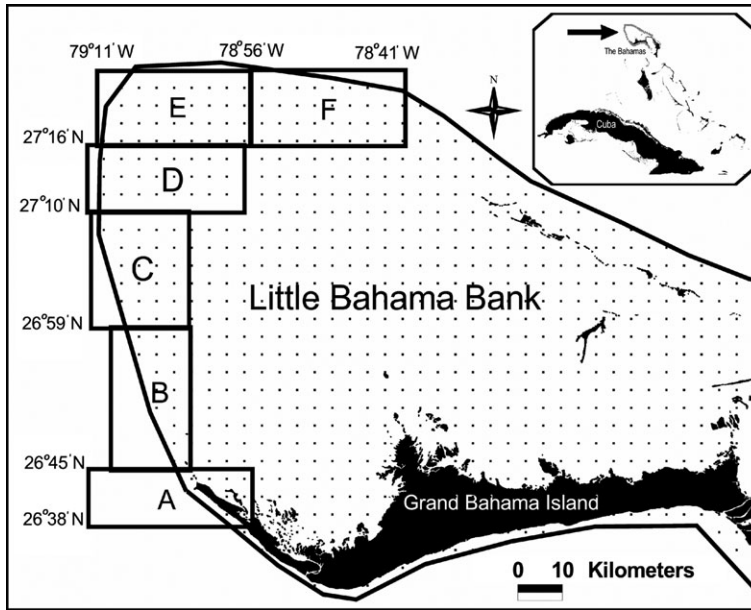


Figure 1. Arrow on the insert indicates Bahamas study area. The area was broken into six segments: A, B, C, D, E, and F for effort analyses, see Elliser and Herzog (2014a).

Beaufort 3 and/or intense rain squalls) from 0700 to 2000 in one person/one hour shifts or two person/two hour shifts, scanning forward 180° while the boat was underway, and 360° while anchored.

A group was defined as all dolphins in sight, moving in the same direction, typically involved in the same activity (*e.g.*, group; 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 photographs were taken of bottlenose dorsal fins to identify the bottlenose dolphins present using a Canon EOS 35 mm or a digital camera. Subsequently two to five researchers entered the water. One to three researchers had underwater video and Nikon V 35 mm or Sony cybershot digital cameras to document individual identification (see description for spotted dolphins below) 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 Herzog 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 so were not considered a new encounter (Elliser and Herzog 2014a). 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). Data collected before 1993 were used to show site fidelity and age class information.

Bottlenose dolphins were individually identified by nicks and scars on the dorsal fin, whereas spotted dolphins were identified by their spotting patterns. Additional

body marks were also used for both species, including marks and scars on the dorsal fins, flukes, pectoral fins and 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 was 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 (HWI, Cairns and Schwager 1987) with the software program SOCPROG 2.3 (Whitehead 2009). The HWI was chosen because it accounts for the bias that it is more difficult to record the presence of two dolphins in a sighting than one, and for comparisons with many other social structure studies, including previous work on this population. 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. The number of years to be pooled was greater than in other intraspecies studies of this study group (Rogers *et al.* 2004; Elliser and Herzing 2011, 2012, 2014*a, b*) due to the comparatively small number of MSE per year. Data were pooled by years into two data sets: 1993–1998 and 1999–2004. This break up of years was chosen because the 6 yr time span allowed for increased sample size of encounters. 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.*, ≥ 4 yr).

CoAs were determined for pairs of noncalf individuals of known sex sighted at least five times per pooled period for both species. The five sighting criterion was chosen to provide representative results while including as many individuals as possible, taking into consideration the longer pooling time and fewer MSE/year compared to intraspecies encounters. The precision of CoA analyses revealed there was enough data to be representative of the true social system (see power and precision of CoA analysis below). Calves were not included in these analyses as their associations are dependent upon their mother. Observed associations were defined as all nonzero CoAs. Strong associations were defined as greater than twice the average CoA of the study group (Gero *et al.* 2005, Whitehead 2008*a*). All CoAs labeled as strong adhered to this definition.

SOCPROG was used to conduct permutation tests to determine if associations were nonrandom and if there were preferred/avoided companions with a sampling period of “day” (Christal and Whitehead 2001, Whitehead 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). The “permute groups within samples” test was used, to account for lack of individuals due to birth, death, migration, *etc.* that could occur due to the pooling of years for each data set. Significantly high standard deviation (SD) or coefficient of variation

(CV) of the real association indices indicates long-term 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 power and precision of the CoA analysis was determined using SOCPROG by calculating the social differentiation (S), $S^2 \times H$ (H is the mean number of observed associations per individual), and the correlation coefficient (CC) between the true and calculated association indices (Whitehead 2008*a, b*). This information revealed how reliable the results were and whether there was enough data (including number of sightings) to be representative of the true social system. Standard errors (SE) were calculated from 1,000 bootstrap replications. Data sets with social differentiation of intermediate ($S \sim 0.5$) to high (S close to or above 1.0) require far fewer associations to detect preferred companionship than data sets with low differentiation. These statistics indicated that the sighting criteria used were sufficient to reject the null hypothesis of no preferred or avoided companionship and gave a "good" representation of the social structure.

Lagged (LAR) and null association rates were calculated to determine the temporal stability of the associations. LAR is the estimated probability of two individuals that are currently associating being associated various time lags later (Whitehead 1995). The null association rate is the expected value of the LAR if there are no preferred associates, or random associations (Whitehead 2009). LARs (overall and by species) were determined for each pooled period, utilizing all of the data (*e.g.*, no restrictions on number of sightings or sex of individuals) (Whitehead 2008*a*). A moving average of 30,000 associations was used for the overall and spotted only LAR; a moving average of 1,000 associations was used for the bottlenose only and mixed species LAR due to the lower number of bottlenose dolphin sightings in MSE. The overall LAR was compared with models of social organization and the best fitted model(s) was selected based on maximum likelihood and binomial loss techniques (Whitehead 1995). Jackknifing 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. Each pooled data set was analyzed separately for group size (\pm SD), similar results were obtained (data not shown), thus all years were combined for analysis.

RESULTS

Resighting

In any given year there were, on average, roughly 100 individuals of each species in this study site. More than 65% of the spotted dolphin community members were regularly involved in MSE; in contrast to only 14% of the bottlenose dolphin community members. Spotted dolphins had higher resightings (Table 1) than bottlenose dolphins during MSE. Despite there being a roughly 1:1 female:male sex ratio in the

Table 1. Resighting (average number of times individuals were seen) \pm SD for bottlenose (Bn) and spotted (Sp) dolphins per pooled data set. Bold indicates highest resightings.

Year	Bn males	Bn females	Sp males	Sp females
1993–1998	7.3 \pm 1.5	8.4 \pm 3.7	13.3 \pm 5.9	9.3 \pm 3.1
1999–2004	7.0 \pm 2.9	7.1 \pm 1.8	12.8 \pm 4.4	9.4 \pm 4.2

spotted dolphin population (Elliser and Herzing 2012, 2014a), male spotted dolphins were resighted much more than female spotted dolphins and both male and female bottlenose dolphins during MSE (Table 1).

Of all spotted dolphins involved in MSE, forty four (65%) were seen in MSE during both pooled periods, with almost twice as many males than females. Thus most of the spotted dolphins, especially males, resighted in MSE participated consistently through both pooled periods. Of all bottlenose dolphins involved in MSE, only six (38%) individuals were seen in MSE during both pooled periods.

Group Size

Number of MSE per year ranged from 6 to 29 ($\bar{x} = 15.6 \pm 6.9$). Taking into account all encounters for all years (intra- and interspecies combined), 14.8% of spotted dolphin encounters were MSE and 16.9% of bottlenose dolphin sightings were MSE. Total mixed species group size ($n = 186$, $\bar{x} = 17.9 \pm 11.6$) ranged from 3 to 82. An ANOVA showed that spotted dolphin group size in MSE was significantly larger ($\bar{x} = 13.0 \pm 11.0$) than bottlenose dolphin group size ($\bar{x} = 4.8 \pm 3.5$; $F = 93.803$, $df = 1$, $P < 0.001$). Figure 2 shows the distribution of group sizes in relation to species and behavior. During aggressive encounters ($n = 86$, $\bar{x} = 22.3 \pm 13.3$), total mixed species group size was significantly larger than during affiliative encounters ($n = 100$, $\bar{x} = 14.1 \pm 8.2$; t -test: $t = 5.15$, $df = 184$, $P < 0.0001$). Spotted dolphin group size during aggressive encounters ($\bar{x} = 16.9 \pm 13.1$) was significantly larger than during affiliative encounters ($\bar{x} = 9.7 \pm 7.3$; t -test: $t = 4.75$, $df = 184$, $P < 0.0001$). Bottlenose dolphin group size did not differ significantly between aggressive ($\bar{x} = 5.4 \pm 2.9$) *vs.* affiliative encounters ($\bar{x} = 4.4 \pm 3.9$; t -test, $t = 1.86$, $df = 184$, $P = 0.064$). Affiliative group sizes were similar to those seen during intra-species encounters for each species (Rogers *et al.* 2004, Elliser and Herzing 2014a).

Associations

The total number of noncalf individuals, males and females, association data for each data set (spotted and bottlenose dolphin individuals of known sex, seen at least five times per period) and test statistics are given in Table 2. Social differentiation was intermediate to high (>0.50). The correlation coefficients were high, indicating the CoA matrix was a good representation. The power to be able to detect preferred associations was more than sufficient. All these statistics indicate the data were representative. Permutation tests for both data sets revealed nonrandom associations, indicating preferred and/or avoided companions (Table 2).

For both periods the CoA ranged from 0.06 to 1.00, with the majority in the lower range. Strong associations (over twice the population average of 0.15 for 1993–1998 and 0.21 for 1999–2004) made up 21.5% and 14.9% of associations respectively. The majority and strongest of associations were between spotted dolphins (Table 3).

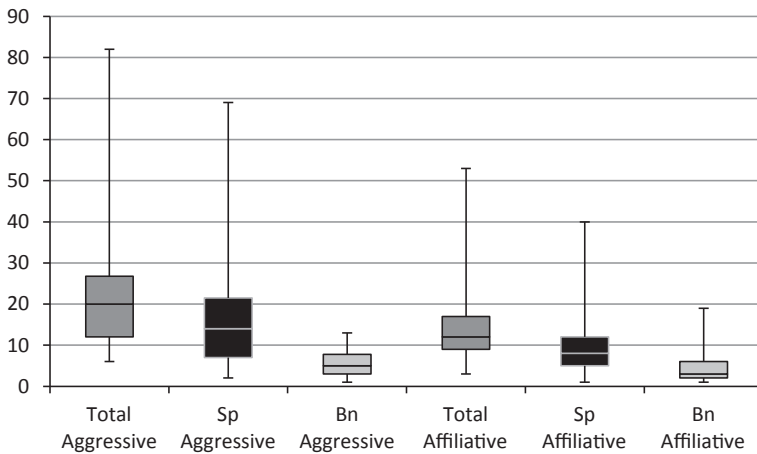


Figure 2. Group size broken down by behavior and species for all years 1993–2004. Sp = spotted dolphin, Bn = bottlenose dolphin, Total = both species in either aggressive or affiliative MSE. Total group size and spotted dolphin group size were significantly larger during aggressive encounters than affiliative, there was no significant difference in bottlenose group size in relation to behavior.

A Mantel test revealed that associations were stronger for within species associations than between species, specifically for spotted-spotted dolphin associations (Table 3) and were stronger within age class than between age class for spotted dolphins ($P < 0.001$). A Mantel test (including both species) revealed that CoAs were significantly higher for within sex associations than between sex, particularly for male-male CoAs (Table 4). Spotted dolphin mean CoA were higher during MSE, whereas bottlenose dolphin mean CoA were higher during intraspecies encounters (Table 3); intraspecies encounter data are also given in the table for comparison.

The majority of the strong CoAs involved spotted dolphin male-male pairs. All male-male CoAs above 0.55 (over $2 \times$ the 1993–1998 male-male average CoA; almost twice the 1999–2004 male-male average CoA) were between spotted dolphin males. The majority of these strong male-male associations involved adults of the mottled and fused age classes. This is similar to intraspecies encounters where strong male associations (above 0.45, Elliser and Herzing 2014a) of first and second order alliances (enduring cooperative relationships over years with strong CoA, over twice the community average) were usually between males of the same age class, mottled or fused. Both first and second order alliances were present during MSE. In addition males had strong associations outside of their first and second order alliances that were not seen during intraspecies encounters. The strongest bottlenose dolphin male associations were between 0.40 and 0.55, which is about half of the strongest spotted male alliance, and lower than the level of alliances seen in bottlenose dolphin intraspecies encounters (Rogers *et al.* 2004). Contrary to the spotted dolphins, no known bottlenose dolphin male alliance was seen consistently in MSE.

Only one male bottlenose dolphin and four male spotted dolphins had strong same-sex mixed species CoAs over both pooled periods. The majority of the strong mixed-sex bottlenose-spotted dolphin associations were between male bottlenose dolphins and female spotted dolphins, evenly distributed amongst speckled, mottled, and fused females.

Table 2. Number of individuals (Bn = bottlenose, Sp = spotted), males and females, P -value for permutation test results (significant P -value indicating preferred and/or avoided companions), social differentiation (S), number of associations per individual (H), correlation coefficient (CC), and power to detect preferred associations ($S^2 \times H$).

Year	No. individuals	Males	Females	Mean CoA \pm SD	P -value	$S \pm SE$	H	CC \pm SE	$S^2 \times H$
1993–1998	80 (12 Bn, 68 Sp)	44 (7 Bn, 37 Sp)	36 (5 Bn, 31 Sp)	0.15 \pm 0.15	$P < 0.001$	0.83 \pm 0.10	136.3	0.74 \pm 0.03	92.77
1999–2004	83 (16 Bn, 67 Sp)	45 (7 Bn, 38 Sp)	38 (9 Bn, 29 Sp)	0.21 \pm 0.15	$P < 0.001$	0.62 \pm 0.14	189.5	0.68 \pm 0.04	72.16

Table 3. Mean CoA \pm 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. Mantel test *P*-value indicates 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
1993–1998	0.15 \pm 0.15	0.12 \pm 0.06 (1.6%)	0.10 \pm 0.05 (19.6%)	0.17 \pm 0.06 (78.8%)	<i>P</i> < 0.001
mean during intraspecies encounters ^a		0.16 \pm 0.12	NA	0.11 \pm 0.12	
1999–2004	0.21 \pm 0.15	0.11 \pm 0.03 (2.1%)	0.12 \pm 0.06 (25.3%)	0.26 \pm 0.06 (72.6%)	<i>P</i> < 0.001
mean during intraspecies encounters ^a		0.14 \pm 0.08	NA	0.12 \pm 0.13	

^aData 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); spotted dolphin: Elliser and Herzing (2014a).

Table 4. Mean CoA \pm SD for sex class associations including both species: male-male (MM), male-female (MF) and female-female (FF) for non-calf individuals. Mantel test *P*-value indicates higher within-sex associations than between. Bold indicates the significantly higher mean CoA.

Year	MM	MF	FF	Mantel test
1993-1998	0.20 \pm 0.07	0.13 \pm 0.05	0.14 \pm 0.05	<i>P</i> < 0.001
1999-2004	0.29 \pm 0.09	0.18 \pm 0.06	0.19 \pm 0.06	<i>P</i> < 0.001

Temporal Analysis

Both pooled periods showed similar LAR indicating preferred associations over all timescales, even though association rates fell, they leveled out above the null association rate (Fig. 3a and 4a). For both periods there were two models that showed substantial support (Table 5, difference in QAIC between the models was less than 2, Whitehead 2009). The best fit model was “2 levels of casual acquaintances,” with the second model incorporating rapid disassociation. The most striking result is seen in the species specific LAR (Fig. 3b, 4b). Spotted-spotted associations were the highest, and resembled their intraspecies LAR of rapid disassociation, constant companions and casual acquaintances (Elliser and Herzing 2014a). There was a spike in the interspecies LAR at the shorter time lags (around 1–2 field seasons), and then a large drop off leveling out close to or below the null. The bottlenose-bottlenose LAR however was at or below the null, indicating no preferred companions during MSE.

DISCUSSION

Resightings and group size of each species were strikingly different in MSE. Bottlenose dolphin participation in MSE was more individualized, whereas spotted dolphin participation was widespread throughout the community, particularly for

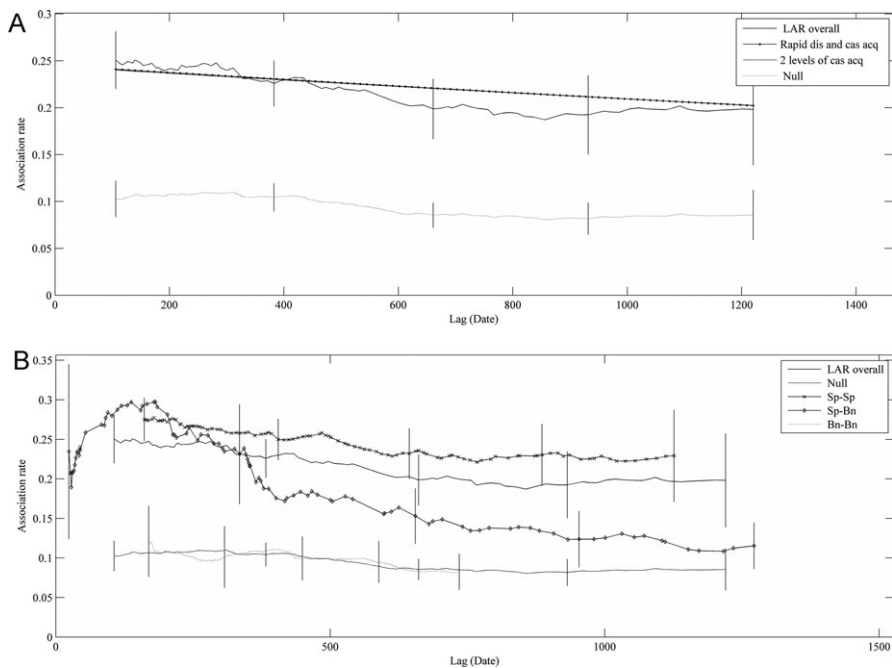


Figure 3. Lagged association rates for 1993–1998. A. Overall LAR with fitted models and null association rate (dis = disassociation, cas = casual, acq = acquaintance) with 30,000 association moving average and jackknifing over 30 d periods. B. Species specific LAR with overall and null association rates. Sp = spotted dolphin, Bn = bottlenose dolphin. A 30,000 association moving average was used for Sp-Sp, 1,000 association moving average used for Sp-Bn and Bn-Bn.

males who were resighted more than any other category (male/female for either species). Group size was also heavily weighted to the spotted dolphins, over 2.5 times larger than bottlenose dolphin group size.

The association data revealed interesting differences between the species as well. Compared to intraspecies associations, spotted dolphin CoA were higher and bottlenose dolphin CoA were lower during MSE. All the association data (regarding species, age class, and sex) revolved around the spotted dolphin male alliances, mostly composed of adult males (mottled and fused). Previously documented long-term first order alliances and shorter term second order alliances of male spotted dolphins seen during intraspecies encounters (Elliser and Herzing 2014a) were present during MSE. Contrary to intraspecies associations however, individual males also had more strong associations with males other than just their first and second order alliance partners during MSE. Unlike the spotted dolphins, alliances for bottlenose dolphins did not carry over to MSE and the strongest bottlenose dolphin male associations were between 0.40 and 0.55, which is about half of the strongest spotted male alliance.

The temporal analysis supports these data and highlights the differences between the species during MSE. The best fitted model for the overall LAR, two levels of casual acquaintances, describes a social organization with two levels of disassociation

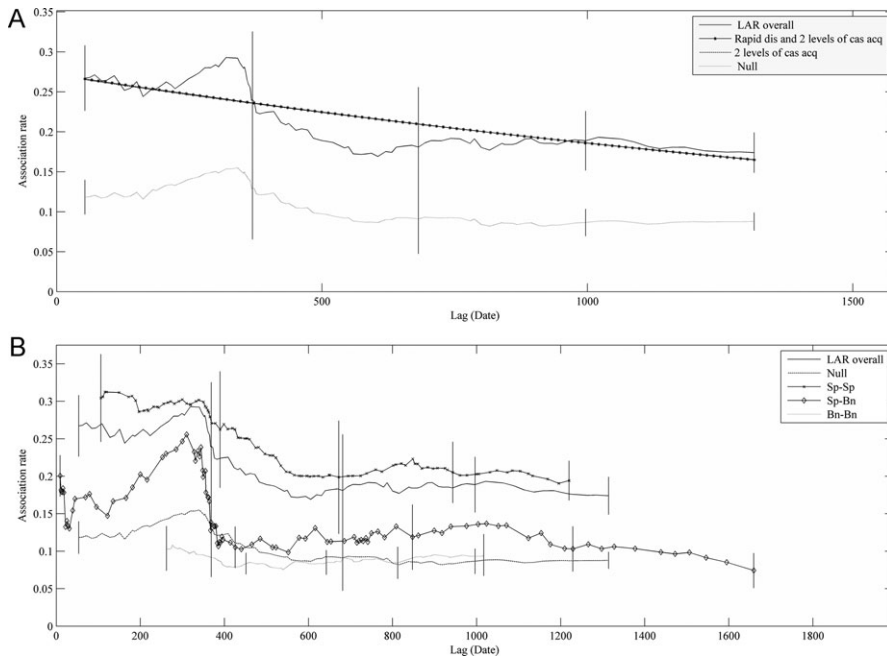


Figure 4. Lagged association rates for 1999–2004. A. Overall LAR with fitted models and null association rate (dis = disassociation, cas = casual, acq = acquaintance) with 30,000 association moving average and jackknifing over 30 d periods. B. Species specific LAR with overall and null association rates. Sp = spotted dolphin, Bn = bottlenose dolphin. A 30,000 association moving average was used for Sp-Sp, 1,000 association moving average used for Sp-Bn and Bn-Bn.

at different time scales, where the associations eventually decay completely (Whitehead 2008a); however the results showed that these MSE associations did level off above the null association rate. This difference can be explained by looking at the species specific LAR. The spotted-bottlenose LAR spiked and then dropped at shorter time lags (around one to two field seasons), before a more permanent dropping off close too or below the null association rate, confirming no long-term interspecies associations. Spotted-spotted associations were the highest, and resembled their intraspecies LAR, including sex differences (data not shown) where males showed the rapid disassociation and constant companion model and females the rapid disassociation and casual acquaintance model (Elliser and Herzing 2014a). Bottlenose dolphins showed basically random associations during MSE at all time lags, being at or below the null association rate, even though they have preferred/avoided companions in intraspecies associations (Rogers *et al.* 2004, Elliser and Herzing 2011).

Spotted dolphins displayed larger group sizes, maintained their intraspecies association patterns and male alliances when involved in MSE, but bottlenose dolphins did not. The question becomes why is there such a difference between the species (and in particular for male spotted dolphins) regarding MSE? What drives a species to join an interspecies group may vary among the species involved (Stensland *et al.* 2003, Querouil *et al.* 2008), and may be influenced by both ecological and social factors.

Table 5. Results of model fitting to overall LAR. Model parameters are a1, a2, a3, and a4 and lag is represented by td. Standard errors were calculated by jack-knifing over 30 d periods. LAR were calculated using a 30,000 association moving average. For both pooled periods two models had QAICs within 2 points of each other, showing both models had substantial support, thus both are given in the table. The model common to both periods was the two levels of casual acquaintances, which are bolded in the table.

Year	a1 (SE)	a2 (SE)	a3 (SE)	a4 (SE)	Best fit model association rate
1993–1998	0.00015741 (0.00037537) 1.958 (3.1759)	0.24506 (0.03718)	NA	NA	$0.24506 * \exp(-0.00015741 * td)$
1999–2004	3.7529 (28.4764) 1.8651 (27.1409)	0.00015152 (0.00039442) 0.00037967 (0.00030704)	0.75641 (0.042652) 4.2554 (23.5464)	NA (0.064299)	$0.75641 * \exp(-1.958 * td) + (1 - 0.75641) * \exp(-0.00015152 * td)$ $4.2554 * \exp(-3.7529 * td) + 0.27172 * \exp(-0.00037967 * td)$
		0.00037488 (0.00032625)	0.72943 (0.068073)	NA	$0.72943 * \exp(-1.8651 * td) + (1 - 0.72943) * \exp(-0.00037488 * td)$

The regularity in which MSE were observed in this study is consistent with previous documentation where the species spent 15% of their time together (Herzing and Johnson 1997). This regularity over so many years indicates that these encounters are an important part of their society, allowing the two species to live sympatrically. The MSE are usually observed after two species have come together, thus it is often unclear how the groups are formed, *i.e.* are spotted dolphins recruited when bottlenose dolphins are present, or are bottlenose dolphins more attracted to larger spotted dolphin groups? However it is likely that physical differences between the species influence the grouping patterns observed during MSE. Bottlenose dolphins (up to 3.9 m) can be almost twice the size of spotted dolphins (up to 2.2 m) (Herzing and Johnson 1997). Being much smaller, the spotted dolphins may need to form larger group sizes, and individuals return more often, to be able interact with the bottlenose dolphins (who are almost always the aggressors, Herzing and Elliser 2013) on a more equal level. Indeed behaviorally it has been shown that it takes 6–7 spotted dolphins to chase away one bottlenose dolphin, and without this number advantage, the spotted dolphin remains passive to the dominant behavior of the bottlenose dolphin (Herzing and Johnson 1997). Thus the resightings and group size differences may be at least partially due to the physical size difference between the species.

Behavioral studies (Herzing and Johnson 1997, Herzing and Elliser 2013, Cusick and Herzing 2014) reveal complex social interactions during MSE. Are there social reasons that may account for some of the differences between species observed in this study? The differences between spotted and bottlenose dolphins are highlighted during aggressive encounters. Spotted dolphin group size was larger during aggressive MSE compared to affiliative encounters. Aggression between these species is primarily one way, with bottlenose dolphins being the aggressors (Herzing and Elliser 2013), unless the spotted dolphins significantly outnumber them (Herzing and Johnson 1997) and often requiring synchrony of male spotted dolphin behavior (Cusick and Herzing 2014) and acoustics (Herzing 1996). Among closely related species, the degree of dominance may depend on the phylogenetic relation, ecological similarity, and size of the species involved (Wilson 2000). Between these sympatric, closely related, ecologically similar species, the degree of individual dominance will be heavily weighted to the larger bottlenose dolphins. Dominant mounting behavior (Östman 1991) by male bottlenose dolphins towards spotted dolphins (particularly males) has been seen consistently through 2004 (Herzing and Elliser 2013).

The larger group sizes and the prevalence/cooperation of first and second order alliances may be necessary for spotted dolphins to compete with the physically larger and more dominant bottlenose dolphins. For the same reason the bottlenose dolphins may not need increased numbers or alliance partners during these encounters. This behavior could be a form of social reinforcement of ecological partitioning, such as differences in prey and habitat that allows the species to live sympatrically. However some characteristics of these encounters point towards reproduction and female access as a driving factor.

Male alliances in primates, African lions (*Panthera leo*), dolphins, and birds are primarily attributed to increased access to females through herding/coercing/guarding of females (*e.g.*, Packer *et al.* 1991; Watts 1998; Connor *et al.* 2000*a, b*). During MSE, these relationships may occur primarily for defense of females, rather than active competition for consortships. The mixed sex/species CoA that occurred were highly skewed towards male bottlenose dolphins associating with female spotted dolphins. Mating between bottlenose dolphin males and spotted dolphin females in this study area has been documented (Herzing and Johnson 1997). Evidence from captiv-

ity (*e.g.*, Sylvestre and Tanaka 1985) and Great Bahama Bank (Herzing *et al.* 2003) indicates that bottlenose dolphins can and do hybridize with many different species. Spotted dolphin male fitness could be reduced if bottlenose dolphin males successfully mate with female spotted dolphins. Increased group size and male alliance cooperation may be vitally important for spotted dolphins during MSE, particularly during aggressive encounters, to be able to defend females and repel bottlenose dolphins during attempted copulation attempts with females.

Spotted dolphin males had strong associations with males other than their first and second order alliance members during these encounters. Behavior analysis has shown ritualized behaviors during aggressive interactions both within and between male spotted dolphin alliances that were critical in determining the outcome of many aggressive MSE (Herzing and Johnson 1997, Cusick and Herzing 2014). This indicates some level of cooperation for a common goal and relationship between the individuals (Elliser and Herzing 2014a). This is similar to Shark Bay where second order alliances have been seen to associate regularly and amicably with other groups, indicating a possible third order alliance formation (Connor 2007, Connor *et al.* 2011). It is unclear whether these more complex male spotted dolphin associations seen during MSE are indeed a third level of alliance structure or temporary coalitions (Elliser and Herzing 2014a), but they are an important aspect of these encounters.

The question arises, if access to females is a driving factor, why are bottlenose dolphin male alliances not important during MSE, when they do maintain them in intraspecies encounters? Reproductive seasonality seems to be similar for both species, having birthing peaks in the spring and fall. Therefore it is unlikely that the bottlenose dolphins would participate in MSE in order to supplement their reproductive opportunities outside of the peak of their mating season. Interestingly some males even temporarily leave their alliance partner to participate in MSE. Alliance formation is based on the costs and benefits related to maintaining that relationship (Whitehead and Connor 2005). One of the main benefits of an alliance is increased access to females (and thus mating opportunities). However, during MSE this may not be a benefit for bottlenose dolphins. In fact their participation could lower their reproductive success because there is less time available to gain access to conspecific females, which may be exacerbated by the fact that females may mediate gene flow in the Bahamas (Parsons *et al.* 2006) so there may be fewer females available to begin with, and/or through mating with a female of another species (which may or may not be fertile). This has been documented in the female choices of mates of sympatric fur seals (Goldsworthy *et al.* 1999). Costs like these can alter alliance formation because in certain cases (which affect the success of an alliance) it may benefit an individual to leave an alliance, either permanently or temporarily (Whitehead and Connor 2005). Thus individuals may associate highly with others during particular behavioral events (Gero *et al.* 2005), instead of forming stable long-term bonds, depending on the costs and benefits of the situation. In this study, the costs of interspecific mating may outweigh the benefits of maintaining alliances for bottlenose dolphins during MSE.

For bottlenose dolphins that are not members of a male alliance, their participation in MSE could be due to their social status. It is possible that the males involved in MSE are ostracized or unable to compete with other males, but can compete with less dominant spotted dolphins. Low-ranking males may be expected to pursue less costly alternative mating strategies, as seen in brown hyenas (*Hyaena brunnea*, Owens and Owens 1996) and hamadryas baboons (*Papio hamadryas*, Strier 2002). Alternatively, it is possible that individuals, particularly subadults, use multispecies groups to practice for future social interactions within their own species (Stensland *et al.* 2003). In

many of these encounters socio-sexual behaviors have been documented (Herzing and Johnson 1997). This could indicate that practice behavior may be a reason for individual bottlenose dolphins to join these groups, and thus alliances would not necessarily be important in this context.

Conclusion

This is the first study of long-term association patterns of interspecies groups and reveals there are obvious species differences regarding participation in MSE, likely relating to body size, dominance, female access and male alliances. The results presented in this paper reveal the complexity and species differences in the cost and benefits of participation in MSE and male alliance formation for regularly interacting sympatric species. Future work should involve detailed behavioral study on these MSE to further our understanding of the association patterns described in this paper.

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