



Long-term social structure of a resident community of Atlantic spotted dolphins, *Stenella Frontalis*, in the Bahamas 1991–2002

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ABSTRACT

Long-term social structure data on small delphinids is lacking for most species except the bottlenose dolphin. This study describes the long-term social structure of one community of Atlantic spotted dolphins, *Stenella frontalis*, divided into three social clusters. Data from 12 yr were analyzed using SOCPROG 2.3. Coefficients of association (CoA) were calculated using the half-weight index. The overall mean community CoA ranged from 0.09 to 0.12. Temporal analyses and mantel tests revealed significant differences between sex class associations due to high male-male CoA (0.12–0.23) compared to female-female and mixed sex CoA (0.08–0.10). Female associations were strongly influenced by reproductive status, calf care, and social familiarity, but not by age class. Male associations were strongly influenced by age, access to females, and alliance formation. Males showed two levels of alliance formation, long-term first order pairs/trios (CoA 0.70–1.00) and shorter-term second order alliances between two or more first order alliances (CoA 0.45–0.69), and a possible third level during interspecies interactions. Mating strategies, sex, and cluster formation shaped the social structure in this spotted dolphin community. Similar to many bottlenose dolphin studies, long-term affiliations for spotted dolphins were correlated with age, sex, and reproductive status.

Key words: Atlantic spotted dolphins, *Stenella frontalis*, social structure, coefficients of association, SOCPROG, behavioral ecology, alliances, social familiarity, lagged association rates.

The social structure of a population is based on the interactions and relationships between individuals and categories (*e.g.*, age and sex) of individuals (Hinde 1976). The nature and course of each interaction is influenced by the history of past interactions as well as their expectations for future interactions; therefore it is crucial to collect data on these over time (Hinde 1976). The majority of long-term information

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available on the social structure of small delphinids comes from decades of research conducted on coastal bottlenose dolphins (*Tursiops sp.*) in Sarasota Bay, Florida (Wells 1991) and Shark Bay, Australia (Connor *et al.* 1992, Smolker *et al.* 1992). Other long-term studies in the Indian River Lagoon, FL (Kent *et al.* 2008) and the Bahamas (Rogers *et al.* 2004) have recently contributed long-term data sets on coastal ecotype bottlenose dolphins to the literature. This type of detailed long-term information is lacking for other small delphinid populations.

The fission/fusion dynamics (Aureli *et al.* 2008) of coastal bottlenose dolphins include many fluctuating low-level, short-term associations, with some strong long-term associations between preferred companions. Interactions may involve many combinations of age and sex of individuals, but long-term affiliations are correlated with age, sex, reproductive status, and kinship (Wells *et al.* 1999). These characteristics are quite common across most bottlenose dolphin populations that have been studied, despite differences in habitat (Quintana-Rizzo and Wells 2001, Rogers *et al.* 2004). However in areas with extreme ecological differences (deep water *vs.* shallow) and geographic isolation, selection pressures may be sufficiently different, allowing distinctive association patterns and social structure to develop (Lusseau *et al.* 2003).

Shorter-term studies (no more than a few years) have documented considerable variability in the fission/fusion dynamics of other small delphinids that often differ from well-studied bottlenose dolphin populations. A study of Hector's dolphins, *Cephalorhynchus hectori*, revealed an organization broadly similar to coastal bottlenose dolphins (Slooten *et al.* 1993). In marine tucuxi dolphins, *Sotalia guianensis*, there was a lack of consistency of group membership and lack of stable associations between individuals (Santos and Rosso 2008). In short-beaked common dolphins (*Delphinus delphis*) a fluid dynamic was documented, but little evidence for any long-term bonds (Bruno *et al.* 2004). Populations of spinner dolphins (*Stenella longirostris*) generally band together at night to feed in deep water, separate into smaller groups in shallow bays during the day (Würsig *et al.* 1994), and have some long-term associations (Marten and Psarakos 1999). Similar to the bottlenose dolphins described above, geographic isolation of spinner dolphins can produce extreme differences in social structure between populations, where the fluidity of the fission-fusion dynamics is replaced with long-term group fidelity and social stability (Karczmarski *et al.* 2005). The general pattern of the socioecology of mammalian groups shows considerable behavioral flexibility, indicating that social variability is a common response to environmental variability (see Karczmarski *et al.* 2005).

It is known that the spotted dolphin is closely related to *Tursiops aduncus* (LeDuc *et al.* 1999). They live in a similar habitat (Herzing 1997) and share some social structure characteristics (Herzing and Brunnick 1997, Welsh and Herzing 2008) with that of coastal bottlenose dolphins. However detailed sex-specific associations and social structure have yet to be explored, including male associations. Behavioral evidence over many years of research shows cooperative (including monopolization of females) and agonistic interactions between males (Herzing and Johnson 1997), but until now quantitative analyses have not been conducted. Of particular interest is whether the males of this species form long-term strong associations and if so, are they similar to alliances seen in bottlenose dolphins of Sarasota, FL (*T. truncatus*, Wells *et al.* 1987) and the sympatric bottlenose dolphins in the Bahamas (*T. truncatus*, Rogers *et al.* 2004) or the more complex multi-level alliance structure of their closely related cousins in Shark Bay, Australia (*T. aduncus*, Connor *et al.* 1992).

This community of Atlantic spotted dolphins has been observed by the Wild Dolphin Project (WDP) since 1985 (Herzing 1996, 1997). The purpose of this study

was to provide a detailed analysis of association patterns in relation to factors such as cluster designation (one community made up of the Northern, Central, and Southern clusters; Elliser and Herzing 2012), sex, and age class bonds. This study offers a unique look at the social structure and sex-specific bonds in a species other than the well-studied bottlenose dolphin, providing insight into the behavioral flexibility and ecological variability of social structure in small delphinids.

METHODS

Study Area

Little Bahama Bank (LBB) is 64 km from the east coast of Florida, and north of West End, Grand Bahama Island (Fig. 1). The study area spans 60 km north to south and 8 km east to west and encompasses 480 km². The sandbank is shallow, between 6 m and 16 m deep, and is surrounded by deep water (steep drop off to over 500 m into the Gulf Stream). It has a primarily sandy bottom, scattered with areas of rock, reef, and patches of seagrass (*Thalassia testudinum*). The entire study area was divided into six sections roughly equal in area, A–F (Fig. 1). Effort was not evenly distributed throughout the areas (% of total effort: A = 3.5%, B = 10.2%, C = 31.8%, D = 51.4%, E&F = 3.1%, Elliser and Herzing 2012) due to physical attributes of the environment as well as rough weather that prohibited boat movement. This type of varied effort is typical in other social analysis studies in similarly sized study areas (Shane 2004, Lusseau *et al.* 2006, Kent *et al.* 2008).

Data Collection

Atlantic spotted dolphins show the four developmental color phases described by Perrin (1970) for the pantropical spotted dolphin (*Stenella attenuata*) and adapted

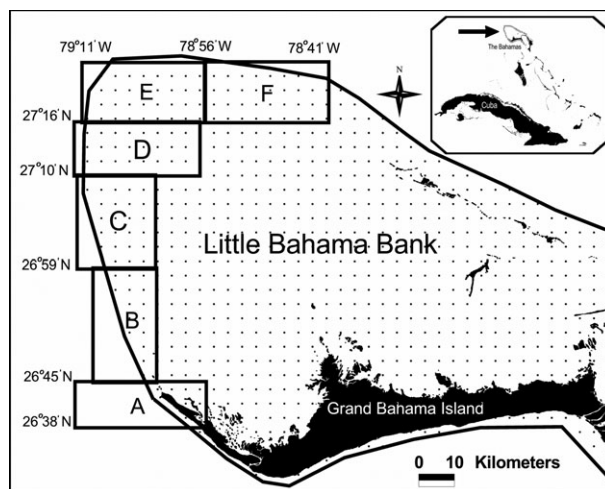


Figure 1. Study area broken into six segments: A, B, C, D, E, and F. Arrow on the insert indicates the Bahamas study area.

for Atlantic spotted dolphin by Herzog (1997). The four age classes include: two-tone (calves, ≤ 4 yr), speckled (juveniles, 4–9 yr), mottled (young adult, 10–16 yr) and fused (adult, ≥ 16 yr). This community is comprised of about 100 individuals in any given year, although over 330 have been identified over the past 28 yr total. All individuals have been identified in this community using their spotting patterns and coloration phases. Every identified individual is assigned to an age class and these data are updated each year. Individual identification was accomplished by comparing spotting patterns between individuals. Additional body marks were also used, including nicks and scars on the dorsal fin, flukes, and pectoral fins as well as marks or scars on the body. Females were sexed by observation of mammary slits or observation of nursing by a calf. Males were sexed by a gap between the genital slit and the anus, or observation of an erection. Sex was determined for 98.5% of the community and verified multiple times for all individuals seen more than once.

These dolphins are habituated to the presence of boats and people in the water. Data for this study were collected from May to September each year between 1991 and 2002. Opportunistic observations were made in every other month (October–April) over the years and known individuals were resighted in these months, indicating year round residency. Observations were conducted in all but rough weather conditions (over Beaufort 3 and/or intense rain squalls) from 0700 to 2000 in shifts of one person/one hour, or two person/two hours. Observers scanned an arc of 180° while underway and 360° while anchored.

A group was defined as all dolphins in sight, moving in the same direction and typically involved in the same activity (Shane 1990). Upon sighting, group size was determined from the surface. Individuals were considered associated when identified with the group. Two to five researchers then entered the water with underwater video and Nikon V 35 mm cameras to begin an encounter to document dolphin behavior and vocalizations.

Encounters were only included for analysis if the group of dolphins were observable underwater for more than 2–3 min. While the group size generally remained the same throughout the encounter, sometimes animals would join or depart from the group but these changes did not alter the group size substantially, so they were not considered a new group of dolphins or new encounter. Group size estimates were updated throughout the encounter and the largest estimate was used as the provisional group size. Photo-identification was used after the encounter to confirm identified individuals or reveal individuals not identified during the encounters. The final group size for an encounter was a product of in-water identification and photo-identification afterwards.

The end of an encounter occurred when the dolphins moved away or were unable to be observed reliably (*e.g.*, if they were traveling or swimming against a strong current). The researchers moved on to search for another group. Sometimes dolphins from a previous encounter would be sighted again shortly afterwards with other individuals. If the majority of the animals were the same, the researchers resumed the previous encounter. Only if the composition of the group changed by 50% or more, were they considered a different group and a new encounter began.

Data Analysis

Only groups where more than 50% of individuals were identified were included in analyses. If an individual was resighted twice or more in the same day, they were

included in analysis only if there was at least a 50% difference in group composition. Calves were not included in analyses as their associations are dependent on their mothers' associations.

Coefficients of association (CoAs) were calculated using the half-weight index (Cairns and Schwager 1987) with the software program SOCPROG 2.3 (Whitehead 2009). CoAs were calculated for pooled years 1991–1993, 1994–1996, 1997–1999, and 2000–2002. These pooled years permit enough individuals to be included, while giving representative results. The last year, 2002, was chosen as a cut-off point in the long-term data set because the area was impacted by hurricanes in 2004, after which about 30% of the population was lost (Elliser and Herzing, in press). In the same study area, significant changes in community/social structure were documented in the sympatric bottlenose dolphin population following similar losses of individuals and influx of new immigrants (Elliser and Herzing 2011).

CoAs were calculated for pairs of noncalf individuals of known sex using two sighting criteria: (1) those sighted at least six times per pooled period or (2) at least 10 times per pooled period. Similar results were found for both sighting criteria (Elliser and Herzing 2012). The results did not differ using the higher sighting criterion, so we used the six sightings criterion because it allowed for the inclusion of more individuals. In a concurrent study (Elliser and Herzing 2012), SOCPROG was used to conduct permutations to test the null hypothesis of random associations and no preferred/avoided companions (Christal and Whitehead 2001, Whitehead 2009). The power and precision of the calculated CoA matrices were determined using social differentiation (S , which indicates the variability of association indices within a population), $S^2 \times H$ (H is the mean number of observed associations per individual) and the correlation coefficient (CC) (Whitehead 2008*a, b*). 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*). The results of that study revealed that the social differentiation was high ($S > 0.87$), correlation coefficient showed good representation ($CC > 0.73$) and $S^2 \times H (> 90)$ met the criterion to reject the null hypothesis of no preferred companions (Elliser and Herzing 2012). Thus all the criteria for data inclusion were sufficient and the results were a good representation of the true social system and more detailed analysis of the associations could be conducted.

Age class is an important determinant of an individual's associations. The speckled age class lasts the shortest amount of time, an average of 4–5 yr. The 3 yr pooled categories allowed almost all individuals to be included under one age class for analysis. If an individual changed class within the pooled period, they were classified according to which class they were in for two of the three years. SOCPROG was used to conduct Mantel tests to examine whether differences in association occur between classes (*e.g.*, age and sex classes). Strong associations were defined as being greater than twice the mean CoA of the study group (Gero *et al.* 2005, Whitehead 2008*a*). All CoAs labeled as strong associations adhered to this definition.

The temporal stability of the associations was measured by calculating the lagged and null association rates. The lagged association rate (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 no preferred associates (*e.g.*, random associations) (Whitehead 2009). LARs were determined utilizing all of the data from the population (*e.g.*, no restrictions on number of sightings of individuals and using all years, no pooling)

(Whitehead 2008a), using a moving average of 50,000 associations. The LAR was compared with models of social organization and the best fitted model was selected based on maximum likelihood and binomial loss techniques (Whitehead 1995). Estimates of the precision of the LAR were determined using the jackknife method in which the analysis is done many times omitting one or more sampling periods each time (Whitehead 2009). The grouping factor was set to 30 sampling periods (days).

RESULTS

Overall Associations

The total number of encounters, noncalf individuals, males, and females that were included in analysis (based on restrictions stated in the methods) as well as the mean CoA for each data set are given in Table 1. The percentage of strong associations and associations between same *vs.* mixed sex and age classes are also shown in Table 1. Results were consistent over all pooled periods. The majority (>75%) of associations were low, with 20%–25% measured as strong associations. Of these strong associations, the majority (68%) were between same-sex pairs. Over all periods, male-male pairs (774 total associations) accounted for twice as many strong CoAs as female-female pairs (373 total associations). The percentage of same sex *vs.* mixed sex associations fluctuated closely around 50/50. The majority of associations (61%–65%) were between individuals of different age classes.

Mantel tests revealed that for all pooled periods, CoAs within sex class were greater than between sex class ($P < 0.003$). Table 2 reveals that this is due to the high level male-male associations, as female-female and mixed sex associations were similar in strength and below the overall average. Same age class associations were significantly stronger than mixed age class associations (Table 2) for all years even though the majority of associations involved mixed age classes (Table 1). This again is due to the high level of male-male associations that were significantly stronger within age class than between. There was no significant difference due to age class in female-female associations (Table 2). Within sex class CoA were significantly stronger than between sex class for fused individuals in all years, for mottled individuals in three of four pooled periods and for speckled individuals only two out of four pooled periods; again this is attributed to the high level of male-male associations in each age class with significant Mantel results (Table 2).

Table 1. Number of encounters, number of individuals total and by sex (M = male, F = female) included in the analysis and overall mean CoA for each pooled period. Percentage of strong CoA (greater than twice the overall average), same *vs.* mixed sex and age class CoA; note (in bold) % of CoA between mixed age classes was consistently higher.

Year	No. encounters	No. individuals	M/F	Mean CoA	Strong CoA	Same/mixed sex CoA	Same/mixed age class CoA
1991–1993	287	58	28/30	0.09	23.7%	48.8%/51.2%	34.3%/ 65.7%
1994–1996	230	87	44/43	0.11	20.6%	51.0%/49.0%	34.6%/ 65.4%
1997–1999	232	77	36/41	0.11	20.9%	49.3%/50.7%	39.0%/ 61.0%
2000–2002	190	79	35/44	0.12	24.2%	51.2%/48.8%	36.0%/ 64.0%

Table 2. CoA values and Mantel tests for sex and age class combinations. Fused (adult), mottled (young adult), speckled (juvenile). Bold indicates significantly high CoA and significant Mantel test results.

Year	Sex class	Fused- fused (SD)	Mottled-mottled (SD)	Speckled-speckled (SD)	Within age class	Between age class	Mantel
1991–1993 Mean (SD): 0.09 (0.09)	MM	0.24 (0.06)	0.18 (0.07)	0.15 (0.06)	0.19 (0.07)	0.10 (0.05)	$P < 0.001$
	MF	0.06 (0.03)	0.09 (0.05)	0.11 (0.07)	–	–	–
	FF	0.06 (0.03)	0.10 (0.02)	0.07 (0.04)	0.07 (0.03)	0.08 (0.04)	$P = 0.84$
1994–1996 Mean (SD): 0.11 (0.12)	Mantel	$P < 0.004$	$P < 0.02$	$P = 0.17$	0.23 (0.08)	0.13 (0.05)	$P < 0.001$
	MM	0.23 (0.06)	0.24 (0.10)	0.20 (0.07)	–	–	–
	MF	0.08 (0.03)	0.13 (0.06)	0.11 (0.06)	0.11 (0.03)	0.09 (0.03)	$P = 0.08$
1997–1999 Mean (SD): 0.11 (0.12)	FF	0.09 (0.03)	0.11 (0.04)	0.12 (0.03)	–	–	–
	Mantel	$P < 0.001$	$P < 0.003$	$P < 0.03$	0.23 (0.09)	0.15 (0.06)	$P < 0.001$
	MM	0.30 (0.04)	0.16 (0.07)	0.15 (0.06)	–	–	–
2000–2002 Mean (SD): 0.12 (0.13)	MF	0.10 (0.04)	0.10 (0.06)	0.09 (0.04)	0.09 (0.04)	0.20 (0.08)	$P < 0.02$
	FF	0.09 (0.03)	0.05 (0.04)	0.10 (0.03)	–	–	–
	Mantel	$P < 0.001$	$P = 0.16$	$P < 0.05$	0.27 (0.12)	0.10 (0.05)	$P = 0.06$
		0.28 (0.09)	0.40 (0.07)	0.14 (0.04)	–	–	–
		0.11 (0.07)	0.10 (0.07)	0.13 (0.04)	–	–	–
		0.07 (0.03)	0.10 (0.04)	0.14 (0.05)	0.10 (0.05)	0.09 (0.03)	$P = 0.06$
		$P < 0.002$	$P < 0.02$	$P = 0.18$	–	–	–

Males Associations

The percentage of observed (CoA >0) male-male associations between individuals ranged between 72.8%–86.9%, depending on the pooled period. The majority of the strong CoAs were male-male associations. Figure 2 shows sociograms for males with CoA of 0.45 and above during each pooled period. The CoA of 0.45 was chosen as a cut-off point because it represents associations at least twice the mean male-male CoA of each pooled period (for some pooled periods it was three times the mean). Over the entire 12 yr period there were 15 groupings of males, some were consistently present in every pooled period, while others were present in one, two, or three of the pooled periods.

The strongest associations (with CoAs ≥ 0.70) were between pairs or trios of males, with reciprocating strongest CoA values between members (the strongest CoA for each individual was with another member of the pair or trio). In a trio, two of the individuals have reciprocating highest CoA, and the third male (odd male) has lower CoA with the main pair. These associations were stable over many years, lasting up to at least 12 yr. The majority of individuals in the core pairs/trios were mottled and fused and almost all pair/trio members were of the same age class and cluster (except for one pair Rivet-Groucho, Northern-Central). Other associations were temporary

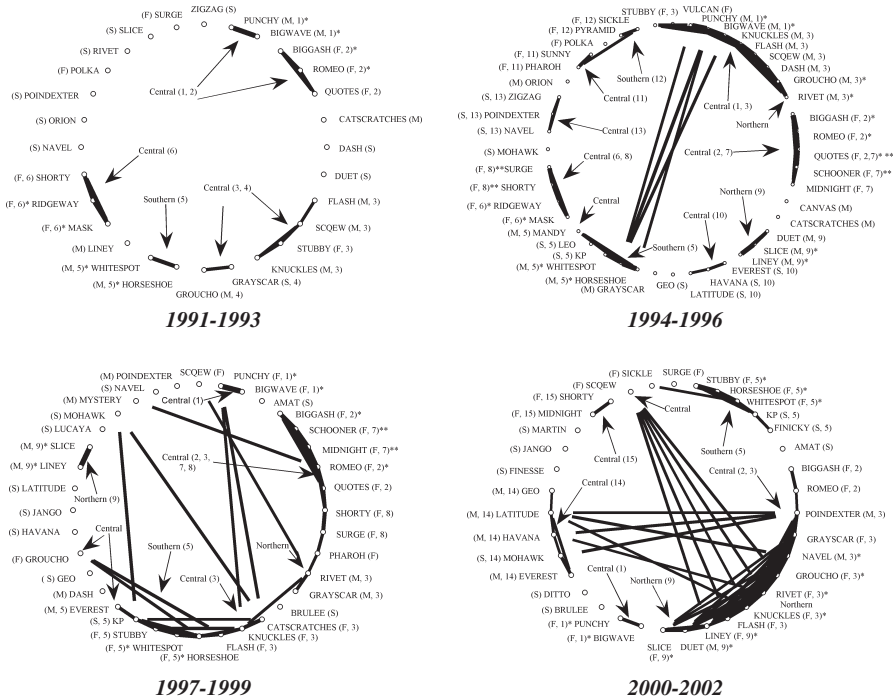


Figure 2. Sociograms of male associations of CoA = 0.45 and higher for each pooled period. Thicker lines indicate stronger associations. Arrows indicate social cluster, small arrow indicates individual of another cluster in alliance. Letters in parentheses indicate age class F = fused, M = mottled, S = speckled. Number in parentheses indicates alliance number. * indicates alliance pairs/trios with CoA 0.70 and above.

groupings lasting no more than three years at a time. These associations were often between the stable pairs/trios and had CoAs between 0.45 and 0.69. Generally these larger groups did not last more than one pooled period as membership changed between years, but the core pair/trios remained consistent. Associations between male pairs/trios occurred even between clusters, but these did not last more than one pooled period.

Figure 3 illustrates the evidence for both persistence and change among these strong male associations. In groupings 1, 2, 5, and 9 there were pairs of males that had consistent reciprocating highest CoA values (≥ 0.70) for 9–12 yr. Grouping 1 demonstrates a long-term consistent pair with no changes. Groupings 2, 5, and 6 demonstrate that changes occurred from loss of individuals or movement of an individual to another male pair/trio. Grouping 9 shows that CoAs between males grow stronger with age as they become mottled and fused. There is evidence of movement between clusters by an individual (Stubby-Central cluster to grouping 5-Southern cluster) and an entire male pair/trio (grouping 7: Northern cluster to Central cluster). Although most strong associations were between male pairs/trios or between two or three male groupings, there was evidence for a less stable grouping of males. This association had varying membership, (five fused, two mottled) with no stable pair/trio, however, a few males have been associated consistently over many years within this group (Fig. 2).

The majority of males not involved in these strong association groupings were speckled. Two groups of speckled individuals appeared in 1994–1996, however these groups did not persist. Generally, when these individuals became mottled, they

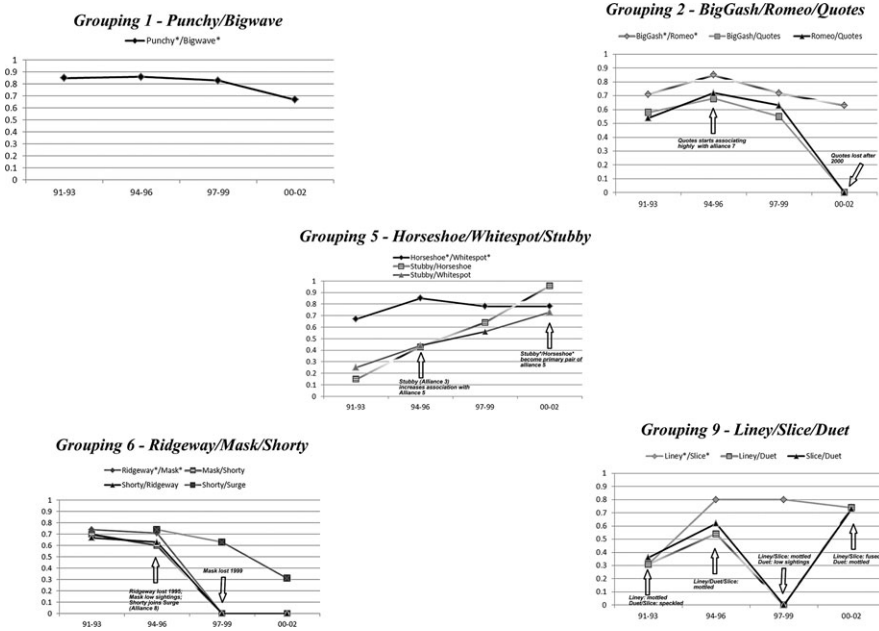


Figure 3. CoA of male groupings 1, 2, 5, 6, and 9 as described in the text. */* indicates the primary pair of an alliance. Low sightings indicates that the number of sightings for that individual was too low to be included in analysis for that time period.

appeared in a male grouping. These speckleds often had lower associations with some of their future partners (example: grouping 9, Fig. 2, 3). Only one speckled individual, KP, was in a strong association with mottled and fused individuals for more than one pooled period.

Female Associations

Out of all possible combinations of female-female associations between individuals, 53.6%–60.0% were observed ($\text{CoA} > 0$). Females remained in their natal cluster. Female-female associations had much lower CoA averages, far fewer strong associations and less consistency than males. Females generally associated with most other females in their cluster, creating a bigger network (an interconnected group or association of individuals) of weaker associations, compared to male-male associations. There were only a few strong associations between females in different clusters. There were more associations between Northern-Central and Southern-Central than Northern-Southern clusters. One Central female, Blotches, had some strong ties to the Southern cluster and after 1997 was associating more with the Southern cluster than the Central cluster. This was the only evidence of a move between clusters. The only consistent membership in strong associations across years were associations delineating clusters and between females and older offspring within clusters.

Over all the years strong associations ranged from 0.19 to 0.94. Some of the highest CoAs were between fused females and their older speckled female offspring (which remained in their mother's cluster). These older offspring often had strong associations with their mother's female associates and their older offspring. One speckled female lost her mother after 2000 and subsequently had strong associations (up to 0.74) with three other females in the Southern cluster. One strong association between a fused mother and her mottled female offspring was observed and this pair had strong associations throughout the offspring's development into adulthood (minimum $\text{CoA} = 0.37$, three times the population average). The majority of associations (59.0%–74.0%) were between different age classes in all years except 1997–1999, when it was 50.0%. Strong associations between speckled individuals were prevalent in all years except 1991–1993.

CoA results indicated that reproductive status may have influenced strong female associations. In each pooled period, an average of about 30% of the strong female associations involved two reproductively active mottled and fused females. The majority (81%) of the strong associations were between reproductively active females in the same reproductive state (*i.e.*, both had calves (majority), or both were pregnant, during that time period). However there was no difference in average CoA of same reproductive state *vs.* different reproductive state (average CoA for both ~ 0.36).

Mixed Sex Associations

Out of all the possible combinations of mixed sex associations between individuals, 63.2%–68.0% were observed ($\text{CoA} > 0$). This was higher than observed female-female associations, but lower than observed male-male associations. Strong CoAs ranged from 0.19 to 0.97, with the two highest (and several lower strong CoAs) between females and their older speckled male offspring. The majority of associations were mixed age class (between 58.3%–72.9%) through 1999, but in 2000–2002 mixed age class associations comprised only 46.6%.

Generally, strong mixed sex associations were between individuals of the same cluster. Only 21.3% of the observed mixed sex associations were between individuals from different clusters. One Northern male, Rivet, had strong associations with Central females in every pooled period, and one association with a Southern female in 2000–2002. No other Northern-Southern strong associations were observed. Although other Northern and Southern males had a few strong associations, the majority of cross cluster associations were between Southern or Northern females and Central males. There were speckled and young mottled males involved in cross cluster associations but the vast majority involved fused males. The percentage of males involved in mixed sex associations (85.7%–100.0%) was always larger than the percentage of females involved (73.1%–84.1%).

Few consistent mixed sex associations across pooled years were present, though this could be due to the pooling of data and the fact that reproductive status may change annually. Those that were evident were within cluster associations. This was particularly evident for the Southern cluster and was most likely due to the fewer number of individuals observed (and thus fewer choices in association) as compared to the Northern and Central clusters. Within a given pooled period, few male groupings had strong associations with certain females, and these were not consistent across pooled periods. Most associations with females varied between male group members, *i.e.*, CoA strength with a particular female often varied between association members, indicating they were not always together when with the female. The composition of the few males not involved in strong mixed sex associations during a given pooled period were: an entire male grouping, one member of a grouping (the other member(s) were involved) and a few individuals not in any male grouping. This was not consistent across pooled periods as noninvolvement did not last more than one pooled period for any individual or male group.

Temporal Analysis

The observed LARs for all years and individuals combined and between sex class indicated preferred associations over all timescales because even though the association rates fell, they leveled out above the null association rate (Fig. 4, 5). For all individuals the best-fitted model was the combination of rapid disassociation (within one sampling period or one day), constant companions (remained associated permanently) and casual acquaintances (individuals dissociate over time and may reassociate) (Fig. 4, Table 3). This combination of association types resulted from association differences between the sexes. The rapid disassociation and casual acquaintance model best fit both female-female and mixed sex LAR, with the female-female LAR being slightly higher than the mixed sex (Fig. 5, Table 3). Male-male associations showed a markedly different LAR where the best fit model was the rapid disassociation and constant companion model, in which their associations remained relatively stable over all time lags, with no decline as seen with the female-female and mixed sex LAR (Fig. 5, Table 3).

DISCUSSION

This community of Atlantic spotted dolphins exhibits fission/fusion dynamics very similar to that of the association patterns of coastal bottlenose dolphins and

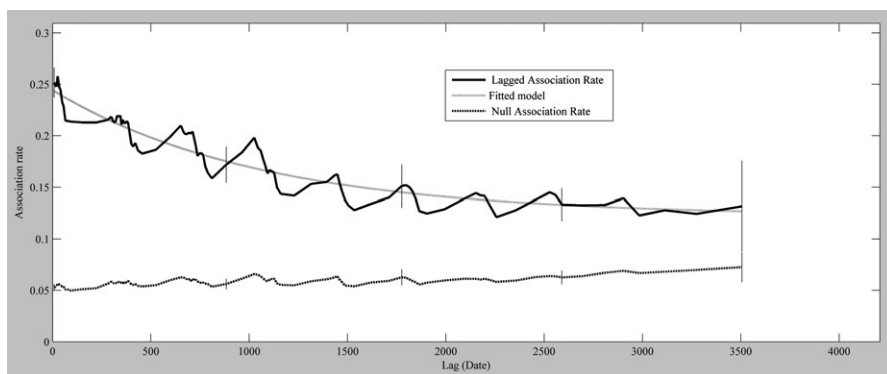


Figure 4. 1991–2002 Lagged association rate for all individuals (no restrictions), null association rate and best fit model (rapid disassociation, constant companions and casual acquaintances). Moving average was set to 50,000 associations. Standard errors were calculating by jack-knifing over 30 d periods.

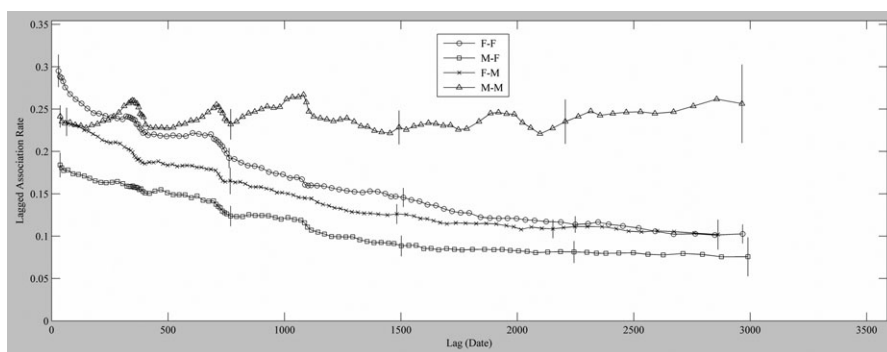


Figure 5. 1991–2002 Lagged association rates for each sex-class. M = male, F = female. The moving average was set to 50,000 associations. Standard errors were calculating by jack-knifing over 30 d periods.

Table 3. Results of model fitting for all LAR (all combined and by sex class). Model parameters are a_1 , a_2 , and a_3 and lag is represented by td . Standard errors were calculating by jack-knifing over 30 d periods. LAR were calculated using a 50,000 association moving average. M = male, F = female. NA indicates that parameter was not used in the given model.

Sex class	a_1 (SE)	a_2 (SE)	a_3 (SE)	Best fit model
M-M	0.24207 (0.01483)	NA	NA	a_1
M-F	0.00036 (7.2043e-005)	0.22111 (0.01887)	NA	$a_2 * \exp(-a_1 * td)$
F-M	0.00035 (9.826e-005)	0.1746 (0.01641)	NA	$a_2 * \exp(-a_1 * td)$
F-F	0.00039 (4.4187e-005)	0.27048 (0.01348)	NA	$a_2 * \exp(-a_1 * td)$
All combined	0.00095 (0.00249)	0.12255 (0.07335)	0.12171 (0.06491)	$a_2 + a_3 * \exp(-a_1 * td)$

chimpanzees (see Connor *et al.* 2000). Strongest associations were between the same sex and age classes, though some variations were found. Males formed strong associations within and between male pairs/trios that remained evident over all time lags, while females had preferred casual acquaintances that disassociate over time and were affected by reproductive status and social familiarity. Mixed sex pairs showed similar patterns to female-female associations, though they were weaker and less stable over time even though mixed sex groups were common. Rapid disassociation (within one day) was a common theme in all LAR indicating a level of daily fluidity within the more stable associations of this community. The overall LAR reported here supports the community structure documented previously of three interacting social clusters (Elliser and Herzing 2012) because this type of LAR can be produced by a social system of permanent social units that associate temporarily (Whitehead 2008a). Combined with the fact that all sex class associations leveled out above the null association rate, this indicates a community with distinct interacting social clusters along with differential association patterns due to sex. The detail of this study reveals how sex and age class interact in their influence on associations and social structure.

Male Associations

The pattern of male associations was consistent with the rapid disassociation and constant companion model, where although there will be some rapid disassociation on a daily basis, males remained with their preferred companions consistently over all time lags. Socio-ecological factors determine female grouping and association patterns that in turn determine the options (regarding socio-sexual strategies, male associations/relationships and dispersal) left for males because they compete primarily for access to fertile females (Hill and Van Hooff 1994, Van Hooff and van Shaik 1994). The male spotted dolphins in this study show long-term strong associations between individuals and pair/trios of males, but are these male coalitions and/or alliances? de Waal and Harcourt (1992) define a coalition as a joining of forces by two or more parties during a conflict of interests with other parties, and an alliance as an enduring cooperative relationship in which repeated coalitions are formed. Male alliances in primates, lions and dolphins are primarily attributed to increased access (directly or indirectly) to females (*e.g.*, Packer *et al.* 1991, Watts 1998, Connor *et al.* 2000).

Herzing (1996) described male coalitions (as defined above) of spotted dolphins consisting of three to four dolphins that chased and surrounded a female and eventually mated with her. This monopolization involves tending/following a female in apparent estrus, surrounding her, escorting her to the bottom during feeding bouts and fending off other male groups (Herzing and Johnson 1997; Herzing and Elliser, *in press*). The absolute duration of these behaviors is unknown, but females have been documented with the same male pair/trio during encounters (minutes to hours), multiple encounters in one day and in some cases across multiple days (DLH, unpublished data). Although this monopolizing behavior is not as overt as the herding by Shark Bay dolphins (Connor *et al.* 2000), or mate guarding in chimpanzees (Watts 1998), it seems to serve the same purpose: males cooperating to gain and maintain access to females. The importance of defense of females by first and second order alliances (discouraging attacks from other alliances) in these instances may have contributed to the selection pressure for use of coercion in consortships (Connor and Vollmer 2009). Cooperative behaviors within and between spotted dolphin male coalitions were also documented during intra and interspecific aggressive interactions, including synchronized swimming behavior, postures, and vocalizations (Herzing 1996,

Cusick 2012). Synchrony has been shown to be an important component of bottlenose dolphin male alliances, and may be a useful measure of alliance unity (Connor *et al.* 2006). The behavioral evidence combined with the long-term association analysis presented here indicates that these strong male associations are alliances because they represent enduring cooperative relationships, whose function is, at least partially, to gain access to females.

Spotted dolphin male alliances share with Sarasota and Shark Bay bottlenose dolphins the characteristic of long-term stability, lasting at least 12 yr. These were strong, long-term stable core pairs/trios with CoAs ≥ 0.70 , similar to first order alliances in Shark Bay (Connor *et al.* 1992) and pair alliances in Sarasota (Wells *et al.* 1987). The structure of spotted dolphin male alliances, however, more closely resembles that of the Shark Bay bottlenose dolphin alliances with at least two levels of alliance formation (Connor and Mann 2006, Connor *et al.* 2011).

There were groupings of two to three alliances, with lower CoAs ranging from twice the community average to 0.69 in a given pooled period and changing membership across pooled years. These groupings have been observed during courtship activities (Herzing 1996; Herzing and Johnson 1997; Herzing and Elliser, in press) as well as in both intra- and interspecies aggressive encounters (Herzing 1996; Cusick 2012; Herzing and Elliser, in press), suggesting enduring cooperative relationships indicative of alliance formation. These are similar in structure to the second order alliances of Shark Bay where there are strong associations between members of different alliances; however, the temporal stability of the second order alliances varies between the two species. In Shark Bay there can be shifts in membership over time, although many second order alliances in Shark Bay are very stable over many years (Connor *et al.* 1992; Connor 2007, 2010). The spotted dolphins seem to have less stability in second order alliances over longer periods (>3 yr). It is important to note that the pooling of data may have diluted the length of the associations we observed (they could be 4 to 5 yr long possibly); however, this is still shorter than the majority of stable second order alliances in Shark Bay. This difference in temporal stability between these two species may be due to varying social and ecological pressures, such that selection for long-term second order alliances is favored in Shark Bay, but not in the Bahamas.

While the majority of spotted dolphin second order alliances were between two stable core pairs, one larger group of males had more labile association patterns, similar to the 14 male bottlenose dolphin superalliance of Shark Bay (Connor *et al.* 1999). Although these male spotted dolphins (up to seven individuals) had varying associates within the group over the years, distinct partner preferences and avoidances were documented, similar to the superalliance (Connor 2007). However there were no associations between clear stable first order alliances as seen in the smaller second order alliances described above. The varied associations may also be influenced by competition for females and/or between other individuals/alliances. The superalliance members in Shark Bay joined forces and competed directly with smaller teams of stable alliances (Connor *et al.* 1999). It may be that these varied associations within this larger group are a result of dolphins associating with certain individuals during particular behavioral events (Gero *et al.* 2005). It is unclear what the purpose and significance are for this larger grouping of males in the Bahamas. Further behavioral research is needed to determine the function of this large grouping of males and how they interact with first and second order alliances.

Age class seems to be an important determinant in alliance formation as male association patterns were influenced heavily by the age of their associate. Alliance members were weakly associated during juvenile years when they were speckled, and the

majority of spotted dolphin males that were not part of any alliance were speckled. The bonds between males apparently grow from relationships developed in subadult groups or earlier (Wells 1991), where more affiliative associations between juveniles may indicate the early stages of alliance formation (Gero *et al.* 2005). Spotted dolphin CoAs strengthened as they became mottled, starting at 10 yr of age and older. The majority of alliance pairs involved mottled and fused males of the same age class; with the strongest CoAs of first order alliances between fused males aged ≥ 16 yr. This structure is similar to that seen in Sarasota, where the minimum age for pair formation was 7 yr old, and most male pair bonds formed in their early teens. As males increase in age (15–20 or more years), so does the probability that the male was currently paired, or has had a partner in the past (Owen *et al.* 2002). Males became more restricted in their associations with other males of the same age class after the onset of sexual maturity (Wells *et al.* 1987).

There is preliminary evidence that these alliances of older, sexually mature males are important to successful reproduction in this population. In a recent genetic study, seven males were assigned paternity (for 10 calves). BigGash and Romeo (a long-term first order alliance), each had two calves and two other males (siring three calves) were in first order alliances. The final three males were within the larger more labile alliance. All paternities were assigned to fused males (≥ 16 yr old) (Green *et al.* 2011). Although limited sample size precludes absolute support, these results are similar to Shark Bay, where reproductive success was significantly skewed toward members of first order alliances (Krützen *et al.* 2004).

Access to females may not be the only reason for spotted dolphin male alliances. Regularly occurring interspecies encounters reveal more complex spotted dolphin male interactions. Spotted dolphins spend 15% of their time together with sympatric bottlenose dolphins. In many instances during aggressive interspecies interactions, coalitional male behavior by the spotted dolphins was critical in determining the outcome, needing six spotted dolphins to chase away one bottlenose dolphin (Herzing and Johnson 1997). First order and second order alliances were prevalent during these interspecies encounters, however, their associations were more complex; males had strong associates other than their first and second order alliance members (Elliser 2010). This has some similarities (though for a different purpose) to a possible third order alliance structure seen in Shark Bay where second order alliances have been seen to associate in amicable, regular low-level associations with other male groups in contests for females (Connor 2007, Connor *et al.* 2011). The need for allies to defend females may explain the formation of third order alliances if former allies were no longer present (Connor *et al.* 2011). For spotted dolphins the need for allies may be for defense against bottlenose dolphins. The function of these interspecies interactions is not fully understood, but alliance behavior has been seen to ward off and intercept matings between the species and defend individual males against the physical dominant behavior of the bottlenose dolphins (Herzing and Johnson 1997). Detailed behavioral analysis has documented focused, synchronized behavior within and between alliances during aggressive encounters towards bottlenose dolphins (Herzing and Johnson 1997, Cusick 2012), indicating cooperation for a common goal and some level of relationship between the individuals (at least during these encounters). Although de Waal and Harcourt (1992) define alliances/coalitions as interactions between members of the same species, the context of these interspecies encounters often mirrors that of intraspecies interactions (access to females, directly or indirectly). This is a unique case where the terms alliance and coalition can be used when describing interactions within and between species. Interestingly the spotted and bottlenose

dolphins have also formed temporary interspecies associations while defending against third party intruders (such as a shark or offshore ecotype bottlenose dolphin [nonresident]), indicating cooperation even beyond intraspecies alliances/coalitions.

The question becomes, are these relationships during these encounters alliances or coalitions? Shorter-term coalitions often form during agonistic interactions in many populations (e.g., *Tursiops* sp.: Connor *et al.* 1999, Lusseau 2007; primates: Goodall 1986, Noë 1994, Silk 1999). It is evident that first and second order alliances for spotted dolphins, at the very least, form temporary coalitions during aggressive interactions with the larger, more dominant bottlenose dolphins. It is unclear whether these coalitions are indeed temporary and inconsistent between encounters, or are enduring cooperative relationships that constitute a third level of alliance formation. Future behavioral and association pattern research will help to illuminate the complex male relationships in this population and their regular interactions with the sympatric bottlenose dolphins.

Females Associations

Spotted dolphin females also showed rapid disassociation on a daily basis but contrary to the males, females had preferred casual acquaintances that disassociated and then may have re-associated again over time. These associations leveled out above the null association rate (and mixed sex LAR), most likely due to their consistent associations with other females in their social cluster (from 5 to 25 females). They had low-level associations in a network of females, but with no long-term consistent subsets of individuals. Generally bottlenose dolphin females have this type of "network," rather than the specific subgroups of two to three individuals seen in male-male associations (Wells *et al.* 1987, Smolker *et al.* 1992, Connor *et al.* 2000, Rogers *et al.* 2004). There is evidence for increased relatedness of spotted dolphin females within clusters (genetic differentiation, Green 2008). This has also been documented in bottlenose dolphins (e.g., Wells 1991). Increased relatedness between females may reduce the fitness cost of competing/sharing resources, while also gaining the benefits of receiving aid in rearing young (Sterck and Watts 1997). This may encourage females to remain in their natal cluster, as the potential costs of emigration/immigration (such as increased aggression, decreased foraging and energetic travel costs) may be high, as seen in chimpanzees (Kahlenberg *et al.* 2008).

Strong associations between females were correlated with reproductive status and past social familiarity, supporting previous work on female associations (Herzing and Brunnick 1997). Female fitness and reproductive success are dependent on the successful rearing of young, and females will use social relationships to achieve their reproductive goals, as described in primates (Sterck and Watts 1997). Benefits to female grouping may be ecological in nature, such as increased predator protection and food distribution (Sterck and Watts 1997), or social, including calf care and social learning (Miles and Herzing 2003, Bender *et al.* 2008, Gibson and Mann 2008). Results indicate that familiarity and reproduction are strong influences in female sociality. Adaptive value of sociality is described for female bottlenose dolphins in a unique approach by Frère *et al.* (2010), showing that sociality influences the fitness trait in a wild population, consistent with the results of many social analyses (like this study) that show strong associations between females of the same reproductive status, and between non-related individuals. Thus genetic and social effects on fitness are intertwined, both important in determining female success (Frère *et al.* 2010).

Contrary to male-male associations, age was not a significant factor in female only associations. Female-female CoAs within and between age class were not significantly different and the majority of associations were between age classes. Spotted dolphin females had strong associations across age classes within their cluster because they associate highly with their older speckled and even mottled offspring. They also associate with other females and their older offspring, with whom they have had previous associations. It is obvious that females would have strong associations across classes between adults and calves, due to dependency during the first few years of the calves' life. Subsequently mother/calf associations tend to drop significantly between calf years three and four (spotted dolphins: Herzing and Brunnick 1997; bottlenose dolphins: Wells *et al.* 1987, Smolker *et al.* 1992), however, this study shows that some strong associations can remain, through adulthood of the offspring.

Consistent mother-offspring associations up to 11 yr were documented in both this study and previously (Herzing and Brunnick 1997), indicating strong relationships through at least three age classes of the offspring (up to mottled). While the mother and offspring are closely associated, the offspring will be exposed to and have relationships with their mother's associates and their offspring. Female associates may be daughters of their mother's close associates, with whom they spent part of their infancy or juvenile period (Wells *et al.* 1987, Möller and Harcourt 2008). The sociability of Shark Bay bottlenose dolphin female calves has been shown to mirror that of their mothers (Gibson and Mann 2008). This parity may translate into adulthood, continuing on the "network" of female relationships. The formation of the Northern, Central, and Southern clusters may be influenced by both kinship and social familiarity between females, while reproduction and social familiarity affect the patterns of within-cluster associations.

CONCLUSION

This community of spotted dolphins, like many bottlenose dolphin populations, has long-term affiliations that are often correlated with factors such as age, sex, and reproduction. Mating strategies and sex are the primary factors shaping social structure. Reproduction and social familiarity strongly influence female associations, whereas age and alliance formation strongly affect male associations. Future work should focus on defining the function of male alliances more definitively through behavioral analysis, genetics (relatedness and more paternity studies), and ranging patterns. Combining association data with behavioral, genetic and ranging analysis will help illuminate the function of both female networks and male alliances.

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