# Community structure and cluster definition of Atlantic spotted dolphins, *Stenella frontalis*, in the Bahamas

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## ABSTRACT

Fission-fusion dynamics typical of many delphinid populations allow for a variety of social grouping patterns. Identifying these groupings is crucial before conducting a detailed social structure analysis. This study analyzed the structure of a population of Bahamian spotted dolphins, *Stenella frontalis*. Through long-term observations and preliminary analysis, three clusters were defined: Northern, Central, and Southern. To quantitatively investigate these delineations, we conducted analysis on 12 yr of sighting data using SOCPROG 2.3. Coefficients of association (CoA) were calculated using the half-weight index, with individuals sighted six or more times per pooled period (3 yr each). Nonmetric multidimensional scaling (MD), hierarchical agglomerative cluster analysis and Mantel tests were conducted to determine if any divisions were present. Mantel tests and MD plots analysis supported the delineations into the three clusters. Cluster analysis showed cluster groupings, but with less clear distinctions between the clusters. The amount and strength of associations were significantly higher within clusters than between clusters. Based on behavioral and geographic overlap, these clusters did not meet the definition of separate communities and thus were termed social clusters. These fine scale, within community divisions, are biologically and socially important aspects of their community and are crucial in understanding the dolphins' social structure.

Key words: *Stenella frontalis*, Atlantic spotted dolphins, community structure, social structure, association patterns, coefficients of association, SOCPROG.

Dolphin societies exhibit large variation in the spatial cohesion and individual membership in a group over time (fission-fusion dynamics: Aureli *et al.* 2008). Interactions among delphinids 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). Patterns can differ between populations, but generally there is some combination of fluctuating low-level, short-term associations, and some strong long-term associations between preferred companions, often centered around sex-specific bonds. These detailed individual associations, however, may be influenced by larger overall grouping patterns that define the population structure.

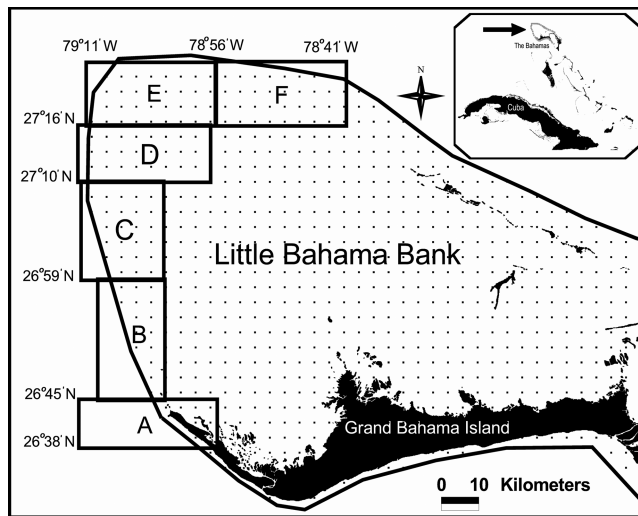[1]Corresponding author (e-mail: cindy.elliser@gmail.com).

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

These delineations may show the groups to be completely separate communities, or defined social clusters within one community. For any population, it is first important to document the occurrence, number and composition of social groupings because this analysis can reveal association preferences of individuals and is a prerequisite for determining the social structure of a population (Whitehead 1997).

The first step is to determine whether more than one community exists, and then whether there are any important groupings within that community. Many of the terms describing populations have been used interchangeably without being completely defined in each context or population. Recent studies have tried to limit the ambiguity in nomenclature, and those definitions will be used here. Dolphin community structure is usually defined by associations of individuals with long-term site fidelity to a particular area (Urian *et al.* 2009). Communities are generally thought to be largely behaviorally self-contained over all relevant time scales, so that nearly all interactions and associations occur within, rather than between communities (Whitehead 2008*a*). Within a community, a social unit is a set of individuals in (nearly) permanent mutual association, by some reasonable definition of association (Whitehead 2008*a*).

The subject of this study was a resident population of Atlantic spotted dolphins (*Stenella frontalis*) found far from shore on a shallow sandbank north of Grand Bahama Island. These dolphins have been part of the long-term scientific observation of the Wild Dolphin Project (WDP) since 1985 (Herzing 1996, 1997). Long-term observations and data collection, genetic analysis (Microsatellite genotypes, Green 2008; also see paternity analyses: Green *et al.* 2011) and preliminary association analyses (Welsh 2007) suggest that these dolphins live in one community divided into three clusters (similar to units described above). These clusters were previously termed the Northern (areas D, E, F, some C), Central (areas C, D) and Southern (areas A, B, but seen on occasion in all areas A–F) clusters by WDP researchers. The names were chosen according to the general geographic areas (see Fig.1) that the individuals

*Table 1.* Effort calculations for 1991–2002. Observations of dolphins occurred when the boat was either underway or anchored.

| Season | # Days at sea | Encounters | # Days with encounters | Total hours | % Hours underway (anchored) |
|--------|---------------|------------|------------------------|-------------|------------------------------|
| 2002 | 73 | 50 | 34 | 895 | 54.0(46.0) |
| 2001 | 74 | 61 | 34 | 771.5 | 59.2(40.8) |
| 2000 | 82 | 107 | 50 | 956 | 44.8(55.2) |
| 1999 | 87 | 97 | 56 | 1,010.25 | 38.6(61.4) |
| 1998 | 78 | 91 | 45 | 916 | 27.5(72.5) |
| 1997 | 92 | 109 | 55 | 1,026.25 | 28.5(71.5) |
| 1996 | 81 | 63 | 39 | 834.5 | 33.3(66.7) |
| 1995 | 96 | 78 | 46 | 1004 | 41.4(58.6) |
| 1994 | 100 | 110 | 63 | 1,093.25 | 38.9(61.1) |
| 1993 | 103 | 137 | 77 | 1154 | 44.0(59.0) |
| 1992 | 80 | 97 | 59 | 943.75 | 43.0(57.0) |
| 1991 | 92 | 93 | 52 | 1075 | 39.0(61.0) |

were observed in over long-term data collection (unpublished data). Encounters with groups containing individuals of different clusters were not uncommon and there was a degree of geographic overlap suggesting that the clusters were not separate communities (Welsh 2007). The goal of this study was to quantitatively define, through the analysis of long-term association data, whether any distinct groupings were present within this population of spotted dolphins.

METHODS

*Study Area*

Little Bahama Bank (LBB) is located 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 km$^2$. The sandbank is shallow, between 6–16 m and is surrounded by deep water (steep drop off to over 500 m into the Gulf Stream). It has a mostly sandy bottom, scattered with areas of rock, reef, and patches of sea grass (*Thalassia testudimum*). The entire study area was divided into six sections roughly equal in area, A–F (Fig. 1). Effort was not evenly distributed throughout every area (% of total effort: A = 3.5%, B = 10.2%, C = 31.8%, D = 51.4%, E and F = 3.1%) due to physical attributes of the environment as well as rough weather which prohibits 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*

Data for this study were collected between May and September each year, 1991–2002 (Table 1). Observations were conducted in all but severe weather conditions (Beaufort >3 and/or intense rain squalls) from 0700 to 2000 in one person/one hour shifts, or two person/two hour shifts, scanning 180° while 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 or pod Shane 1990). Upon sighting, group size was determined from the surface. These dolphins are habituated to the presence of boats and people in the water. Between two and five researchers entered the water with video and Nikon V underwater 35 mm cameras to document individual identification and behavior. The majority of encounters occurred while the boat was underway but some occurred when dolphins approached the boat while it was anchored, usually in the early morning before the boat was underway for the day or in the early evening when the boat was anchored for the night.

An encounter was defined as a group of dolphins that were observable underwater for more than 2–3 min. Mean ($\pm$ SD) encounter duration was 30.3 $\pm$ 35.6 min (range 2–300 min). Generally the group size remained the same throughout the encounter. Occasionally there would be some additions to and departures from the group during the encounter, but these did not alter the group size substantially, and thus were not considered a new encounter (or new group of dolphins). Group size estimates were updated throughout the encounter and the largest estimate was used as the provisional group size. Photo-identification after the encounters confirmed identified individuals and sometimes revealed individuals not identified in the water by the researchers. The final group size for an encounter was a product of in-water identification and photo-identification afterwards. Individuals were considered associated when identified with the group.

The end of an encounter was generally dictated by the dolphins, when they left the area or the researchers were no longer able to observe them underwater (*e.g.,* if they were traveling or swimming against a strong current). The researchers then left that area in search of another group. Sometimes dolphins from a previous encounter would be sighted again shortly afterwards with other individuals. 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*

A discovery curve was generated to determine the rate of new individuals identified each year, and when the majority of the population had been identified. Based on this analysis, 1991 was the first year used in this analysis because the majority of new individuals after this date were new calves born into the community, not newly identified noncalf individuals (Fig. 2). Absence of new individuals in 1996–1998 and a larger than average influx in 1999 may be an artifact due to a change in protocol by WDP (Fig. 2). During 1997–1998 it would have been less likely to identify previously unidentified individuals as the range of area the boat was covering was reduced. Thus, in 1999 a large influx of new individuals was more an artifact of the sampling (as WDP began normal surveying of the study area), rather than an actual influx of new individuals. Mean resighting rates were determined for all individuals sighted at least twice per time period.

Differences in group size were analyzed in relation to calf presence with ANOVA and Tukey tests using SPSS 16 software. All groups were included in group size analysis. Consensus on group size estimates between researchers throughout the encounter limited the bias of unidentified individuals being documented more than once.
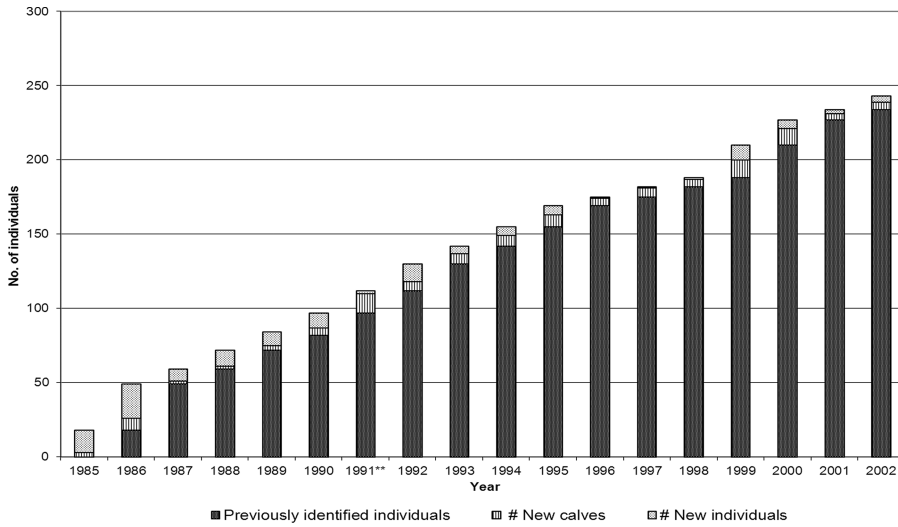
*Figure 2.* Discovery curve for 1985–2002. 1991**indicates the first year of data used in this study. From 1991 on, the majority of newly identified individuals were new calves born into the population, not newly identified noncalf individuals.

Analysis of associations was conducted by calculating coefficients of association (CoA) 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. In association studies, there is a trade-off between including as many animals as possible and ensuring data are reliable, *i.e.,* there are enough sightings per individual to be representative of their associations (Bejder *et al.* 1998). These years were pooled to allow enough individuals to be included in each analysis, particularly for the Northern and Southern clusters where there are fewer sightings per individual. Pooling data also enables comparison between years to determine the stability or instability of any delineation found throughout this long-term study. Finally pooling allows comparison with detailed social structure analysis conducted concurrently. The last year, 2002, was chosen because the area was impacted by hurricanes in 2004, after which about 36% of the population was lost (Elliser 2010). In the same study area, significant changes in community and social structure were documented in the sympatric bottlenose dolphin population following similar losses of individuals and influx of new immigrants (Elliser and Herzing 2011). It was not possible to pool another three years (2003–2005) without incorporating a year following the hurricanes. Therefore to get a clear picture of the community structure prior to the hurricanes we ended the analysis in 2002.

Only encounters where more than 50% of individuals were identified were included in the CoA analyses. If an individual was resighted twice or more in the same day, the group was included in the analysis only if there was at least a 50% difference in group composition of individuals. Due to these restrictions, the number of encounters used in the CoA analysis was less than the total number of encounters. Calves were not included in these analyses as their associations are dependent on their mothers' associations. In a study in Tampa Bay, Urian *et al.* (2009) documented

that community level structure of bottlenose dolphins (*Tursiops truncatus*) could be determined with a small sample size of 10 resightings per individual. We began by using this criterion of 10 resightings per pooled period. In an effort to include more individuals (particularly for the Northern and Southern clusters) analyses were also conducted using the criteria of individuals with six resightings per pooled period. Results revealed no differences between the two data sets, therefore the later six resighting limit/pooled period was presented here. If the ratio of number of years per number of resightings is compared, the two studies are similar. Urian *et al.* 2009 used 10 resightings in 6 yr; in this study we are using six resightings in 3 yr, both close to an average of two sightings per year. Individuals were not included in every period of analysis, if they did not meet the sighting criteria for the given time frame.

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 sampling period was set to day. 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, which accounts for situations where not all individuals are present in each sampling interval (due to birth, death, migration, *etc.*). Significantly high SD or CV of the real association indices indicates long-term preferred companionship (Whitehead 2009).

The power and precision of the calculated CoA matrices were determined using social differentiation (*S*), $S^2 \times H$ (*H* is the mean number of observed associations per individual) and the correlation coefficient (CC) (Whitehead 2008*a*, *b*). This information reveals how reliable the results were, and if there were enough data to be representative of the true social structure of the population. Standard errors (SE) were calculated from 1,000 bootstrap replications. Data sets with intermediate (*S* ∼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 level of social differentiation, average number of observed associations per dyad, and individual calculated by SOCPROG indicated that the limit of six sightings per individual per pooled period was sufficient to reject the null hypothesis of no preferred or avoided companionship and gave a "good" representation of social structure (Whitehead 2008*a*).

To test for the long-term presence of the Northern, Central, and Southern clusters Nonmetric multidimensional scaling (MD) analysis was conducted with SOCPROG 2.3. In a MD plot, strongly associated individuals will be plotted together and weakly associated individuals will be farther apart (Whitehead 2009). A plot with stress <0.10 is considered a good ordination (Whitehead 2008*a*). The starting configuration was set to random. The number of dimensions was increased until the stress was below 0.10. The plots produced were similar in ordination, and a representative plot for each pooled period was chosen for the figure. Hierarchical agglomerative cluster analysis, using the average-linkage method produces a dendrogram where the individuals are arranged on one axis and their degree of association on another (Whitehead 2009). A cophenetic correlation coefficient (CCC) of >0.80 indicates the dendrogram is a good match to the association matrix (Whitehead 2008*a*). Mantel tests were performed to determine whether there were more associations within clusters (if found) than between, indicating the discreteness of the clusters.

<div align="center">RESULTS</div>

*Resightings*

In 965 d at sea between 1991 and 2002, spotted dolphins were observed on 576 d with a total of 1,093 encounters (Table 1). A total of 199 individuals seen more than once were identified. There were 99 females, 97 males, and 3 of unknown sex. The majority of new individuals seen during this time period were new calves born into the community; immigration was low (Fig. 2). Both male and female calves remained in the study area from birth through adulthood, up to 22 yr of age.

Individuals in this community were regularly resighted. Eighty-six individuals (43.2%) were sighted in every year of this study that was possible for that individual (*i.e.,* they had not disappeared or had not been born yet). Of individuals that were missing years, but were resighted, 15 had 1 yr missing. Seven individuals had 2–4 yr missing, with no more than 2 yr per missing period. Three individuals had a group of 3 yr missing between sightings. The rest of the individuals, 84 (42.2%) had missing periods of no more than 2 yr, before being lost (never resighted), indicating regular resightings before disappearing. The final four individuals had a missing period of 3–4 yr before being lost.

*Group Size*

There were a total of 1,071 groups where group size was recorded, ranging from 1 to 60 individuals. The majority of groups (68.8%) included nine or fewer individuals ($\bar{x} = 8.8 \pm 7.2$) Out of all possible age class combinations, groups that included all age classes (two-tone [calves], speckled [juveniles], mottled and fused [adults]) occurred the most comprising 27%–36% of the total for each pooled period. An ANOVA (df = 1, $F = 19.911$, $P < 0.001$) indicated that group size was larger with calves ($n = 714$, $\bar{x} = 10.3 \pm 7.5$) than without ($n = 357$, $\bar{x} = 5.8 \pm 5.3$).

*Defining Clusters*

The total number of encounters, noncalf individuals, males and females, and test statistics for each data set are given in Table 2 (number of encounters differs from Table 1 due to sighting restrictions for CoA analysis, see Methods). For all data sets, permutation tests revealed nonrandom associations with significantly higher real association SD and CV *vs.* random permutation SD and CV ($P < 0.001$, Table 2), indicating preferred and/or avoided companions. The data were a good representation of the true social system with high social differentiation ($S$) and correlation coefficients for all pooled years (Table 2).

The presence of the Northern, Central, and Southern social clusters within one community was confirmed through multidimensional scaling for all years. Figure 3 contains a representative MD plot from each pooled period. The Southern cluster is the most distinctive (separated) in all plots. The Northern and Central clusters are less distinct and have some individuals close to the edges of clusters, indicating some associations across clusters. The Central cluster is the largest having between 40 and 57 individuals included in analysis for each time period (out of a total of 103 individuals over all years). The Southern and Northern clusters have far fewer individuals included in the analysis, 5–16 and 12–14, respectively (out of a total of 61 and 37 individuals over all years, respectively).

*Table 2.* Number of encounters, individuals, mean CoA (across all individuals in all clusters), SD and CV test statistics for the real associations (real) and random permutation tests (perm.) and test statistics for power and precision of social structure analysis. Significance of high real association SD and CV *vs.* random permutations was $P < 0.001$ for all years. M = males, F = females. $S$ = Social differentiation with standard error (SE). $S > 0.50$ = well differentiated society, CC = correlation coefficient with standard error (SE). CC = 0.40 CoA matrix is somewhat representative, CC = 0.80 CoA matrix is a good representation, and $S^2 \times H > 5$, good ability to reject the null hypothesis of no preferred companions.

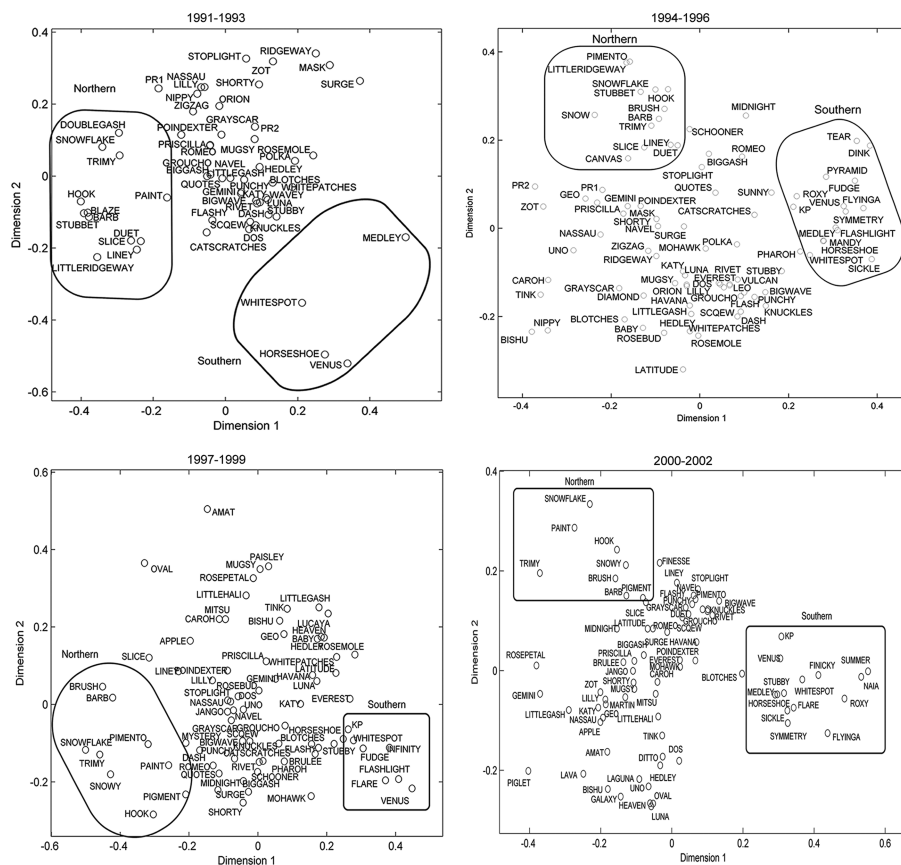| Year | No. encounters | No. individuals | M/F | Mean CoA | SD real/ perm. | CV real/ perm. | $S \pm$ SE | $H$ | CC $\pm$ SE | $S^2 \times H$ |
|---|---|---|---|---|---|---|---|---|---|---|
| 1991–1993 | 287 | 58 | 28/30 | 0.09 | 0.110/0.099 | 1.211/1.086 | 1.27 ± 0.08 | 132.8 | 0.89 ± 0.01 | 213.8 |
| 1994–1996 | 230 | 87 | 44/43 | 0.11 | 0.124/0.107 | 1.105/0.945 | 1.01 ± 0.09 | 174.8 | 0.82 ± 0.02 | 178.3 |
| 1997–1999 | 232 | 77 | 36/41 | 0.11 | 0.124/0.108 | 1.128/0.987 | 0.88 ± 0.13 | 118.4 | 0.74 ± 0.02 | 90.9 |
| 2000–2002 | 190 | 79 | 35/44 | 0.12 | 0.140/0.123 | 1.149/1.018 | 0.89 ± 0.15 | 115.9 | 0.74 ± 0.02 | 91.9 |

*Figure 3.* Nonmetric multidimensional scaling plots for each of the pooled years, showing three social clusters. Circles indicate cluster membership relating to previous cluster attributions by WDP researchers. Individuals not encircled are of the Central social cluster. MD scaling was produced using 200 iterations, in six dimensions stress <0.10.

Hierarchical cluster analysis produced plots that were close to the good representation threshold of CCC = 0.80 (Fig. 4). In contrast to the MD plots, cluster definition was not as clear from the dendrograms due to the borderline CCC and the fact that the modularity did not reach the critical 0.30 threshold of good definition, so care must be taken when analyzing these results. Although definite conclusions about clusters cannot be made, the data show interesting trends that support the MD plot results.

In all pooled years the individuals in the Northern and Southern clusters were tightly associated in their respective clusters, though they were sometimes found within a clustering of Central individuals. The discrepancies are due to male alliances. In 1997–1999 the Southern cluster looks to be split due to the grouping of Horseshoe, Stubby, and Whitespot; and in 2000–2002 the Northern cluster looks to be split due to the grouping of Slice, Duet, and Liney (Fig. 4). Both of these groupings are

*Figure 4.* Hierarchical cluster analysis plots for each of the pooled years. These are borderline representative with CCC (cophenetic correlation coefficient) close to 0.80 (1991–1993 CCC = 0.814; 1994–1996 CCC = 0.768; 1997–1999 CCC = 0.748; 2000–2002 CCC = 0.773). Encircled groups indicate cluster membership relating to previous cluster attributions by WDP researchers.

*Table 3.* Mean and SD resighting rates overall and by cluster for males and females seen at least twice per time period given. Bold indicates higher average resighting rates *vs.* other sex for that period.

|  |  | 1991–1993 | 1994–1996 | 1997–1999 | 2000–2002 | All years |
|---|---|---|---|---|---|---|
| Overall | Males | 20.5 ± 10.8 | 17.8 ± 7.4 | 13.9 ± 5.7 | 11.1 ± 3.5 | 30.0 ± 28.9 |
|  | Females | **24.7 ± 16.7** | **18.7 ± 9.9** | **16.7 ± 9.1** | **15.2 ± 9.1** | **37.7 ± 35.9** |
| Central | Males | 22.3 ± 11.1 | 19.2 ± 7.2 | 14.0 ± 5.9 | 11.1 ± 3.7 | 16.5 ± 8.4 |
|  | Females | **31.7 ± 16.1** | **23.2 ± 10.5** | **20.2 ± 9.1** | **18.2 ± 9.9** | **22.6 ± 12.3** |
| Northern | Males | **18.0 ± 5.7** | **15.4 ± 7.2** | **11.3 ± 1.9** | 11.6 ± 2.1 | **14.2 ± 5.7** |
|  | Females | 13.8 ± 8.1 | 13.2 ± 2.6 | 10.9 ± 2.8 | 11.7 ± 4.2 | 12.4 ± 5.1 |
| Southern | Males | **11 ± 3.7** | **12.9 ± 4.8** | **15.3 ± 2.9** | **10.4 ± 3.0** | **12.3 ± 4.3** |
|  | Females | 7.5 ± 1.5 | 11.4 ± 3.7 | 8.0 ± 1.7 | 9.1 ± 2.9 | 9.3 ± 3.6 |

actually long-term male alliances (Elliser 2010). The results in these plots may be better understood by looking at overall group composition and associations.

The majority of the encounters (62.5%) contained only Central cluster individuals. A small percentage of encounters contained only Northern (5.0%) or only Southern (2.2%) individuals. Mixed cluster encounters were not uncommon between Northern/Central (17.8%) and Southern/Central (10.4%), however, there were no Northern/Southern only encounters. In the majority of these cross cluster encounters the composition of the group is mainly individuals from one cluster, with a single individual (sometimes two) from another cluster. There were few encounters containing individuals from each of the Northern, Southern, and Central clusters (2.1%). Table 3 shows that individuals were regularly resighted and that overall, females had consistently higher resighting rates than males in each pooled period as well as over all years. When broken down by cluster, this trend was evident for the Central cluster; however, males in the Northern and Southern clusters had higher resighting rates than females (except in 2000–2002, Table 3).

Mantel tests were conducted for each pooled period for within *vs.* between cluster association levels to indicate the discreteness of the clusters. Associations within clusters (mean CoA range 0.15–0.21) were stronger than between clusters (mean CoA range 0.05–0.08) for every pooled period (1991–1993 $t = 8.86$; 1994–1996 $t = 8.79$; 1997–1999 $t = 5.52$; 2000–2002 $t = 7.92$; all $P < 0.001$). Within cluster associations were almost double that of the community overall averages for each pooled period (mean CoA range 0.09–0.12).

## DISCUSSION

*Group Size*

The majority of groups included nine or fewer individuals. The group size for spotted dolphins in our study area was larger than many coastal bottlenose dolphin populations including Sarasota ($\bar{x} = 7$, Wells *et al.* 1987), Shark Bay ($\bar{x} = 4.8$, Smolker *et al.* 1992), and bottlenose dolphins sympatric with these spotted dolphins ($\bar{x} = 4.58$, Rogers *et al.* 2004). Spotted dolphin groups containing

calves was significantly larger than those without calves, which appears to be a generalized characteristic of coastal bottlenose dolphins (Campbell *et al*. 2002), although the varying definition of a group between populations may affect direct comparisons.

*Defining clusters*

This spotted dolphin population is behaviorally self-contained and includes long-term associations and site fidelity which meets the criteria to be defined as one community. Although definitions of community may vary to some degree between studies, most agree that nearly all interactions and associations occur within, rather than between communities (Whitehead 2008*a*) and communities are usually defined by associations of individuals with long-term site fidelity to a particular area (Urian *et al.* 2009). Some individuals have been seen regularly since 1985, indicating up to 23 yr of site fidelity to the study area, as of 2007. Almost 45% of individuals were seen in every year possible for that individual, there was natal philopatry of both sexes and immigration was low (only a few individuals per year). Observations for this study were made during May–September (summer); however, opportunistic trips have been made in every other month of the year. Positive identification matches have been made in nonsummer months (DLH, unpublished data), suggesting that at least some individuals are year round residents. Similar long-term site fidelity and natal philopatry of both sexes have been documented in the two longest running bottlenose dolphin field studies (>20 yr) in Sarasota, Florida (*Tursiops truncatus*, Wells 1991) and Shark Bay, Australia (*Tursiops aduncus*, Connor *et al*. 2000).

The social analysis revealed that despite overlapping ranges, there was subdivision within this community. Compared to community distinctions, these subdivisions may be harder to document *i.e.,* they may not be as clearly definable with conventional analyses, particularly if there is some level of interaction between the clusters. It has been shown that communities can overlap in ranges (from small to large amounts), but still be distinct social entities despite lack of physiographic barriers to movement (Chilvers and Corkeron 2001, Lusseau *et al.* 2006, Urian *et al.* 2009, Wiszniewski *et al*. 2009). This may also occur between clusters within a community, as found in this study, where there is no physiographic barrier. The ability to detect differences between communities will be fairly straight forward and detectable given a requisite number of sightings per individual. However, the levels of associations within clusters of a community may not be as easily definable using the same criteria for the presence of distinct groupings, as seen in the results of this study.

So the question is community, or cluster? In social terrestrial animals the term community refers to a social group with defined boundaries. Such identifiable delineations are often absent in cetacean populations, which often lack any physiographic barriers. In Sarasota, Florida, 17% of groups involved individual dolphins from outside of the community (Wells *et al.* 1987). In Tampa Bay five communities have been described, with small to large overlaps in ranging patterns and distinct association values (though the amount of association overlap was not determined) (Urian *et al.* 2009). The methods, delineation criteria and results are similar to the results of this study of spotted dolphins. The question then becomes, are the interactions really behaviorally self-contained enough to warrant being called separate communities? Or are they social clusters, defined as a set of individuals in (nearly) permanent mutual association (Whitehead 2008*a*), within one community? Based on the definitions

stated above and the level of social overlap documented in this study, we determined that these were social clusters within one community.

There was quantitative evidence for the delineation of individuals into the three previously designated clusters (Northern, Central, and Southern). It is important to note that in previous work another group was defined called the "roaming group." These were individuals that did not seem to fit into a particular cluster based on Principal Coordinate Analysis (Welsh 2007, Green *et al.* 2011). This group of 10 (all but two were male) included a male alliance of three individuals that included one Central individual who began associating with two Southern males. This alliance remained in the Southern cluster, but with close links to the Central cluster (Elliser 2010). The inability to assign these individuals to a cluster by Welsh (2007) may be due to transitions among and between alliances, but also the shorter term scope of the study. The 12 yr, long-term data described in this paper allowed these individuals to be positively identified in a specific cluster, thus there were only the Northern, Central and Southern clusters.

Although mixed cluster groups (involving Northern or Southern and Central individuals) were not uncommon, the majority (69.7%) of groups consisted of individuals from one cluster only. These were mostly encounters of Central individuals, as there were few encounters with only Northern (5.0%) or Southern individuals (2.2%). This was most likely due to the fewer number of individuals in those clusters as well as the lower boat effort in those areas. Mantel tests showed that there were significantly stronger associations within than between clusters and the MD plots showed consistent separations.

MD plots consistently grouped the Southern animals distinctly separate from the Central animals and a lower degree of separation between the Northern and Central animals, although the degree of separation varied between pooled periods. The hierarchical cluster analysis supported the trend that individuals within clusters associated highly with one another. There were tight groupings of both the Northern and Southern individuals, except for two male alliances that seemed to be separate in two of the pooled years. The separation of these alliances from their main groupings, and links to the Central cluster, may be due to their ranging patterns which are influenced by male mating strategies. Alliances in primates, lions, and dolphins are primarily attributed to increased access to females through herding, coercing, and guarding of females (*e.g.,* Watts 1998, Packer *et al.* 1991, Connor *et al.* 2000). Association patterns (Elliser 2010) and paternity information (Green *et al.* 2011) indicate that males do mate outside of their cluster, thus they may have more associations with individuals outside their cluster. Due to the limited size of the Northern and Southern clusters in particular, individuals may need to mate outside of their cluster to maintain enough genetic diversity (Green *et al.* 2011).

The cluster analysis also showed that these groupings seem to be imbedded within associations with the Central cluster. It may be that with more effort in the Northern and Southern areas, hierarchical cluster analysis may show more definitive clusters, as more of their "in cluster" associations would be captured. There may also be other individuals with which they associate that were not documented due to the lower effort in those areas. However it could also be that this type of hierarchical analysis may not be the best way to represent the data for this community structure (indicated by the low modularity and borderline CCC). Interactions between individuals of different clusters are common, and it may be very difficult to tease apart the complicated interwoven community structure in a hierarchical fashion.

All clusters contained both females and males, and remained fairly consistent (though some changes in cluster composition did occur). Detailed association analysis revealed that female-female associations were generally constrained within their respective clusters (Elliser 2010). Similar cluster formation within one community was documented in a bottlenose dolphin population Port Stephens, Australia (Wiszniewski *et al.* 2009). Those clusters were generally affiliated with previously identified female social clusters (Möller *et al.* 2006) and grouped together with several adult males. Relatively low modularity and change in subgroup clustering is consistent with fission-fusion social structures within communities (Wiszniewski *et al.* 2009). Shared foraging strategies can also influence philopatry, especially in females. In some populations of bottlenose dolphins, foraging strategies may be culturally transmitted along matrilines (Mann and Sargeant 2003, Krützen *et al.* 2004). Although specific strategies have not been linked to matrilines in this spotted dolphin population, teaching of foraging techniques from mother to offspring has been documented (Bender *et al.* 2008). It is possible that cultural transmission may influence female philopatry and cluster formation in this population.

Cluster natal philopatry of both sexes was also observed. Overall, females were consistently resighted more than males; however, when broken down by cluster, this remained evident for only the Central cluster. Males in the Northern/Southern clusters were generally resighted slightly more often than Northern/Southern females. Males with larger ranging patterns than females could account for this discrepancy. If males are ranging outside their clusters, males from the Northern/Southern clusters will be seen more and Central males will be seen less in the Central area where boat effort was highest.

There is also evidence of genetic differentiation between social clusters and for geographically close male dispersal and reproductive success across clusters in this community (Green 2008, Green *et al.* 2011). Spotted dolphin males may be ranging farther across clusters to increase their reproductive success through increased access to a variety of females. These males may serve as a vector for genetic exchange as seen in Sarasota bottlenose dolphins (Wells 1991). Males in many other bottlenose dolphin populations also show larger home ranges than females (*e.g.,* Smolker *et al.* 1992, Quintana-Rizzo and Wells 2001). Although for bottlenose dolphins on LBB (including this study area), genetic work found that if a sex bias in dispersal exists, it is in the direction of females rather than males (Parsons *et al.* 2006). It may be that the two sympatric species on LBB have differing sex dispersal strategies.

*Conclusion*

Through association analyses this study revealed a spotted dolphin community made up of three social clusters, whose definition is also supported by preliminary geographic (Welsh 2007) and genetic work (Green 2008, Green *et al.* 2011). Defining clusters within a community can prove to be difficult; however, the increasing variety of tools and analyses available now allows researchers to begin to tease apart the intricacies of the complex society of social animals. Care should be taken in this type of research so as not to dismiss possible biologically significant results that may not be visible at first glance. This study indicates these social clusters were as clearly defined as some communities are, and for these spotted dolphins, they are a biologically and socially significant part of their community. Defining the community structure is a vital prerequisite before delving into a detailed social structure analysis. This study

has provided the ground work for an in-depth analysis of long-term spotted dolphin social structure.

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