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Patterns of Social Affiliation and Group Composition for Bottlenose Dolphins (*Tursiops truncatus*) in San Luis Pass, Texas

KATHERINE MAZE-FOLEY AND BERND WÜRSIG

Group sizes, group composition, and association patterns of bottlenose dolphins (*Tursiops truncatus*) were investigated in the San Luis Pass area (Sep. 1995–Aug. 1996) of the Galveston Bay Estuary to examine differences in community structure of individuals inhabiting different portions of the estuary. Group sizes ($n = 83$) ranged from 1 to 29 ($\bar{x} = 10.6$) and were seasonally variable, with the largest groups occurring in spring ($\bar{x} = 16.3$) and the smallest groups during the fall ($\bar{x} = 6.3$). Seventy-one individuals were identified using photoidentification, and the sex of six dolphins (three males, three females) was determined. At least 31 (48.4%) groups were of mixed sex. Twenty-nine dolphins that were identified five or more times were used to calculate half-weight coefficients of association (COAs), which ranged from 0.00 to 0.83 ($\bar{x} = 0.46$). Coefficients of association for male pairs were higher than COAs for female and mixed-sex pairs. Permutation tests were performed to test for nonrandom associations and presence of preferred or avoided companions. The null hypothesis of random association was rejected, indicating that dolphins preferentially associated with some individuals and avoided others. In all replicates, three known-male pairs had significantly large COAs. These preliminary results suggested that, excluding mother–calf pairs that were not examined, male pairs formed the most stable social bonds.

Research was initiated to examine differences in community structure of bottlenose dolphins (*Tursiops truncatus*) inhabiting different portions of the Galveston Bay Estuary (GBE). The GBE is situated along the northern Texas coast and is the second largest estuary in Texas (Fig. 1). Averaging 2.1 m in depth, it consists of approximately 1,600 km² of mostly brackish water (Armstrong, 1987; Wermund et al., 1988). Since 1990, various researchers have studied bottlenose dolphins in this estuary; however, most of this research has taken place in the northeastern (NE) portion of the estuary, which we refer to as “Galveston Bay.” Henningsen (1991) and Henningsen and Würsig (1991) conducted surveys encompassing the entire estuary, which included sightings of bottlenose dolphins in the San Luis Pass (SLP) area in the southwestern (SW) portion of GBE. Because no sightings were made in the central or NE portions of West Bay during these surveys, we hypothesized that animals from opposite ends of GBE do not regularly travel back and forth or associate with dolphins from the opposing end and that they compose a separate community. In addition (based on aerial survey sighting data), the National Marine Fisheries Service (NMFS) separates bottlenose dolphins within GBE into two separate bay, sound, and estuary stocks: the West Bay stock (SW portion of GBE); and the Galveston Bay, East Bay, and Trinity Bay (NE

portion of GBE) stock (Blaylock and Hoggard, 1994; Blaylock et al., 1995; Waring et al., 2001). We initiated surveys in the SLP area of GBE to more closely examine the hypothesis that this was a separate community or stock of dolphins from those inhabiting the NE portion of GBE.

Previously, we reported on occurrence patterns, site fidelity, habitat use, and movement patterns for bottlenose dolphins inhabiting SLP during a 12-mo study (1995–96) period (Maze and Würsig, 1999). The 71 dolphins identified consisted of both the year-round residents and occasional transients, and comparisons with photographs from 1990 suggested that some individuals exhibit long-term site fidelity to the area. Seasonal shifts in distribution within the study area were observed for resident dolphins, with animals most commonly sighted in inner bays during summer and in the nearshore Gulf of Mexico during winter. Coastal movements between SLP and Galveston Bay were detected at a low level. Overall, these data supported that a resident community of dolphins inhabited the SLP area that was separate from the Galveston Bay community. Protecting long-term resident communities, which are at the greatest risk from geographically localized effects, has been suggested as the starting point for managing bay, sound, and estuary stocks (Waring et al., 2001). In addition to its importance as supporting a resident community, the SLP area is unique

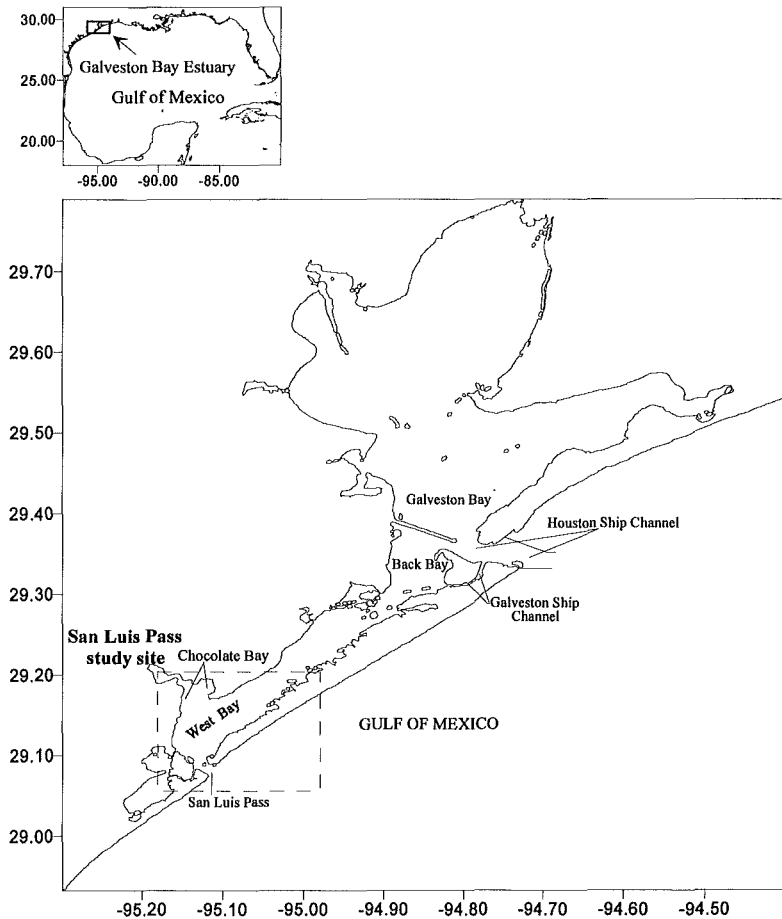


Fig. 1. The San Luis Pass study area, located in the SW portion of the GBE.

among Texas study sites because it is relatively undisturbed and maintains a natural pass connecting the inner bays and Gulf (in contrast to the dredged channels and jetties of other areas). This may account for some of the major differences in findings between SLP and other Texas study sites, such as the low number of animals identified in SLP (see Maze and Würsig, 1999).

In addition to studying occurrence patterns, site fidelity, habitat use, and movement patterns in SLP and comparing these with those of portions of GBE, we also examined the group and social structure of dolphins inhabiting SLP, which we report here. In lieu of the uncertainty regarding stock structure, it has been suggested that the criteria to better define and manage stocks in this region should integrate multiple approaches, including social patterns (Waring et al., 2001). Previous findings from Galveston Bay have indicated that group sizes are small for bay waters (mean sizes

from 3 to 8), and group composition is fluid as shown by the majority of low coefficient of association indices (most below 0.20) (Henningson and Würsig, 1991; Bräger et al., 1994; Fertl, 1994a).

To study group and social structure, we had the following objectives: (1) to examine group sizes and composition; (2) to determine association indices for 29 dolphins identified five or more times in the SLP area during 1995–96; (3) to test for nonrandom associations and presence of preferred or avoided companions; (4) to examine association indices of known-sex individuals; and (5) to compare findings from SLP with previous findings from within GBE and from well-studied areas, such as Sarasota Bay, Florida, and Shark Bay, Australia.

Many field studies have described social relationships among individual bottlenose dolphins by using association indices. Recently, this method has been criticized because it does not distinguish whether individuals co-occur

due to preferred associations or due to chance alone. This is a severe limitation of using association index values in a descriptive manner. Bejder et al. (1998) developed a method to test associations of pairs of animals (diads) against those occurring by chance, using a Monte Carlo randomization algorithm developed for a similar ecological problem (Manly, 1995). The benefits of this technique include the ability to examine the overall pattern of associations within a population and compare it with the distribution of random associations to determine whether they differ significantly from chance and to do the same with associations of individual diads (Bejder et al., 1998; Bräger, 1999; Whitehead, 1999a, 1999b). Whitehead (1999a, 1999b) developed a series of programs, SOCPROG, building on the technique of Bejder et al. (1998), to test observed association patterns against those expected from random associations. We used these techniques to test association patterns of bottlenose dolphins inhabiting the SLP area of GBE.

METHODS

Study site description.—The SLP study site, situated in the SW portion of GBE, consisted of Chocolate Bay, the SW third of West Bay, and the SLP area including adjacent nearshore Gulf of Mexico waters (~65 km²) (Fig. 1). Bay floors are predominately flat and dominated by thick accumulations of mud and silt; however, oyster reefs are well developed in the Chocolate Bay area. Adjacent Gulf of Mexico waters are dominated by a sand bottom (Wermund et al., 1988; Britton and Morton, 1989). For a more detailed description, see Maze and Würsig (1999).

Data collection.—Data were collected during boat-based, photoidentification surveys conducted for 12 mo from 1 Sep. 1995 to 31 Aug. 1996 (see Maze and Würsig, 1999 for details). Seasons were defined as the fall (Sep.–Nov.), winter (Dec.–Feb.), spring (March–May), and summer (June–Aug.) (e.g., Gruber, 1981; Shane, 1990; Fertl, 1994a; Bearzi et al., 1997; Weller, 1998). Dolphin groups were defined using the definition of “parties” by Smolker et al. (1992) as dolphins with relatively close-knit spatial cohesion, with each member within 10 m of any other member (10-m “chain” rule). Group size estimates included the total number of adults, calves, and neonates. Calves were defined according to Shane (1987, 1990) and Fertl (1994a) as individuals judged by eye to be two-thirds or less the length of an adult,

swimming beside or slightly behind an adult. Neonates were distinguished by visible fetal folds, charcoal color, and uncoordinated surfacings.

Data analysis.—Maze and Würsig (1999) reported 102 group sightings; however, only 83 of these groups were used for analyses of group size and social structure. Eight groups were deleted on the basis of duration of observation. Group size estimates were based on field observations; therefore, groups in which animals were seen at the surface only once and groups that were observed for less than 5 min were omitted from analyses. Eleven additional groups were deleted following the rules of Smolker et al. (1992): (1) exclude a group if any member had been sighted <1 hr previously or if all members had already been sighted that day; and (2) exclude groups from the same day unless the group had changed by 30% of its original composition (i.e., dolphins had joined or departed). Thus, it was possible for an individual to appear in more than one group per day, but in the majority of cases, each dolphin’s associations were sampled only once per day.

The term affiliate is used for an individual that was sighted in the same group as a specified individual. The total number of affiliates of each identified individual was calculated.

Twenty-nine dolphins that were sighted five or more times were used to calculate coefficients of association (COAs). Different cutoff levels have been used for including individuals in COA analyses, ranging from two sightings per individual (e.g., Slooten et al., 1993; Bräger, 1999) to 10 sightings (e.g., Smolker et al., 1992; Quintana-Rizzo and Wells, 2001), with various intermediates, such as five and greater than eight sightings per individual (e.g., Félix, 1997; Chilvers and Corkeron, 2001). We chose five as a cutoff because we thought it was appropriate for the size of our dataset and would facilitate comparison with other studies within GBE and Texas with the same or similar cutoffs (Bräger et al., 1994; Würsig and Lynn, 1996). Coefficients of association were calculated using the half-weight index (Cairns and Schwager, 1987): $2ab/(a + b)$, where a = total number of times individual a was seen, b = total number of times individual b was seen, and ab = total number of times a and b were seen together. Resulting coefficients for pairs of individuals range from 0.00 (never sighted together) to 1.00 (always sighted together). Association was defined, following Cairns and Schwager (1987), as the frequency with which

two individuals are present in the same social group at the same time. The half-weight index was chosen because it is least biased when pairs are more likely to be seen when separate than when together. Because small groups dominated the sightings in this study area, and typically only one or two groups were sighted on any given day, any given pair of the 29 dolphins included in this analysis was more likely to be sighted apart than together. This index has been used frequently in studies of association patterns of bottlenose dolphins (e.g., Wells, 1986; Wells et al., 1987; Weller, 1991; Connor et al., 1992a, 1992b; Smolker et al., 1992; Bräger et al., 1994; Félix, 1997).

Association data were analyzed using SOCPROG1.3 (Whitehead, 1999a, 1999b). A 1-hr sampling period was used. Permutation tests were performed to test the hypothesis that the distribution of association indices from the empirical data was not different from that of the permuted data sets. The number of permutations was increased until the *P* value stabilized and confidence intervals decreased, following the methods of Bejder et al. (1998) and Whitehead (1999a). The permutation test chosen, "permute all groups," tests the null hypothesis that there were no preferred or avoided companions, given the total number of groups each animal was seen in during the study. This test takes into account that individuals sighted in many groups are likely to group together at random. A bias of this test is that it does not account for situations such as birth, death, and migration; however, given the short duration of this study (1 yr), and the year-round presence in the study area of most of the 29 dolphins included in the analyses, this bias was considered negligible. Permutation tests also generated standard deviations of association indices for both empirical and random data. A dendrogram (using average linkage cluster analysis) of associations was generated with SOCPROG1.3. SOCPROG1.3 generates COAs using means; therefore, means are reported despite nonnormal distributions and are used for comparisons with those of previous studies.

For group size analyses, descriptive statistics, one-way ANOVAs, all-pairwise multiple comparisons, Kolmogorov–Smirnov normality tests, Levene Median (equal variance) tests, and Mann–Whitney rank sum tests were performed using SigmaStat 1.0 (Jandel Scientific Software, 1993). If the data passed the tests of normality and equal variance, parametric tests were used. If the data failed a test of normality but passed an equal variance test, parametric tests were used because of robustness of AN-

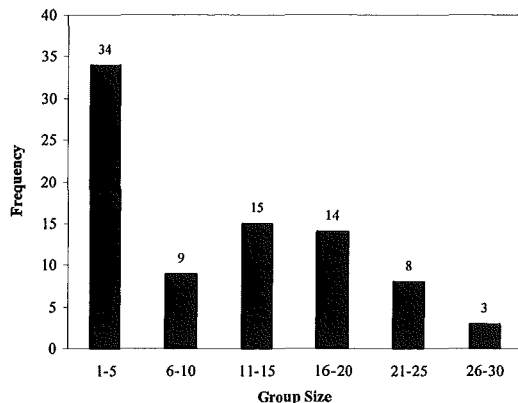


Fig. 2. Frequency distribution of group sizes ($n = 83$).

OVA. If the data failed both tests, nonparametric tests were used. Means and standard deviations or medians are reported.

RESULTS

Survey effort and sightings.—Eighty-three surveys were conducted during the 12-mo study period. Survey effort totaled 349.4 hr, of which 94.3 hr were spent observing and photographing dolphin groups. The 83 sightings used for analyses were made throughout the year, with 18 groups sighted in the fall (21.7%), 12 in winter (14.4%), 16 in spring (19.3%), and 37 in summer (44.6%).

Identified individuals.—Seventy-one bottlenose dolphins were photographically identified during the 12-mo study period. These 71 animals fell into two groups: 34 Gulf animals—those sighted only in the Gulf of Mexico and sighted only on 1 d of the study—and 37 Bay animals—those sighted in the bays only or those moving back and forth between bay and Gulf waters and typically sighted the year round (see Maze and Würsig, 1999).

Group sizes—group composition.—Group sizes ranged from 1 to 29, with $\bar{x} = 10.6 \pm 8.23$ (median = 10; Fig. 2). The most frequently encountered groups contained 1–5 individuals. Groups with 15 or fewer individuals comprised 70% of all sightings, whereas groups of 20 or fewer comprised 87% of all sightings.

Group sizes differed seasonally (ANOVA, $F_{3,79} = 4.79$, $P = 0.004$, $n = 83$), with the largest groups occurring during spring ($\bar{x} = 16.3 \pm 7.86$), intermediate group sizes during summer and winter ($\bar{x} = 10.4 \pm 8.56$ and 10.1 ± 7.46 , respectively), and the smallest groups during the fall ($\bar{x} = 6.3 \pm 5.55$). An all-pairwise

multiple comparison (Student-Newman-Keuls method) found group sizes for the fall and spring to be significantly different ($P < 0.05$).

Fifty-five (66.3%) of the 83 groups had one or more calves present. Groups containing calves, both excluding calves from the analysis (median = 12) and including calves (median = 15), were significantly larger than groups without calves (median = 2) ($P < 0.001$, Mann-Whitney U-test). Calves were sighted the year round, with 44.4% of the fall groups, 75.0% of winter groups, 75.0% of spring groups, and 70.3% of summer groups containing calves. Twelve (14.5%) of the 83 groups had one or more neonates present. All groups with one or more neonates also contained one or more calves. Neonate sightings occurred only between 31 March and 13 July 1996, indicating a calving peak from early spring to midsummer. Neonates were present in 47.6% of spring groups and 13.3% of summer groups. The majority of neonates were sighted in April, May, and June (March—2 neonates; April—7; May—4; June—6; and July—2).

Three Bay animals were positively identified as males by simultaneous observation of a dorsal fin and penis (SLP001, SLP002, and SLP012). Many animals were suspected to be females based on consistent association and synchronized surfacings with a calf. Three Bay animals were observed and photographed in close association with a calf during 7–13 group sightings and were presumed to be females (SLP004, SLP006, and SLP020). Animals that had been observed in close association with calves on fewer than seven occasions (other animals were sighted 1–3 times in close association with a calf) were not assumed to be females because of the possibility that they were “babysitting” calves, as has been noted by Fertl (1994b).

Of the 83 group sightings, 64 resulted in usable photographs of identifiable individuals. Calves and neonates were not identifiable, but nearly every adult in the study area was identifiable. For these 64 groups, we estimated 833 individuals that were encountered, of which 674 were adults ($\bar{x} = 10.5$ adults/group). We photoidentified 636 animals ($\bar{x} = 9.9$ adults/group). The 64 sightings were examined for the occurrence of all-male, all-female, and mixed-sex groups. Thirty-one (48.4%) groups were confirmed as being composed of mixed sexes, as indicated by the presence of at least one known male and one known female. All the 31 groups also contained calves, further indicating groups of mixed composition because calves typically accompany their mothers for

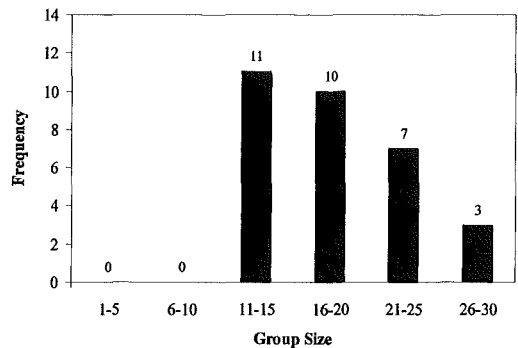


Fig. 3. Frequency distribution of group sizes for known mixed-sex groups ($n = 31$).

several years (Wells et al., 1987). One additional group was composed of one mother-calf pair. The composition of the remaining 33 groups could not be determined. For the 31 confirmed mixed-sex groups (median = 17), group sizes were significantly larger than those reported for all 83 groups (median = 10) ($P < 0.001$, Mann-Whitney U-test). The range of mixed-sex group sizes, 11–29, was narrower and shifted toward larger groups (Fig. 3).

Affiliates.—Number of affiliates ranged from 1 to 46, with a median of 21. For affiliates of Bay animals only, the range was also 1–46, with a median of 36. When considering only Bay affiliates of Bay animals, median number of affiliates was 31. Bay animals with five or more sightings had at least 27 Bay affiliates. One Bay animal had 35 Bay affiliates, and hence was sighted with all other Bay animals except one. It was rare for a frequently sighted Bay animal not to have Gulf affiliates, and on all days in which new groups of Gulf animals were sighted, at least one Bay animal was a member of the group.

Association patterns.—The 406 pairwise comparisons of 29 individuals were generated using SOCPROG1.3. The distribution of COAs failed a test of normality (K-S distance = 0.0454, $P = 0.0438$). Coefficients of association ranged from 0.00 to 0.83, with $\bar{x} = 0.46 \pm 0.157$ (median = 0.47). The most frequently occurring levels were 0.40–0.49 and 0.50–0.59 (Fig. 4a). The distributions of the mean COA and the maximum COA for each dolphin were generated (Fig. 4b,c). The mean COA for each dolphin was calculated by averaging that dolphin’s 28 COAs (each dolphin is used in 28 pairwise comparisons). Mean COAs ranged from 0.19 to 0.58. The maximum COA for each dolphin ranged from 0.30 to 0.83.

P values for permutation tests stabilized at 20,000 permutations, ranging from 0.005 to 0.029 with $\bar{x} = 0.016 \pm 0.0074$ for the 10 replicates. This was evidence of nonrandomness in the association of each pair of dolphins, and therefore, the null hypothesis of random association was rejected, and each diad was considered separately. Each permutation generated significant diads at a two-sided significance level of $\alpha = 0.05$. For each permutation, the expected number of significant diads was 19, but the observed number ranged from 38 to 43, indicating diads with significantly high or low associations. In all 10 replicates, the three known-male pairs had significantly high associations, indicating that their association indices were higher than 97.5% of their random association indices. No known-female pairs had significantly high or low association. In all 10 replicates, SLP006, a known female, had significantly low associations with all three known males, indicating that the observed association indices were less than 2.5% of their random indices. The standard deviation of the association indices was higher in the observed data than in the random data sets, but the difference was not significant (observed SD = 0.157, random SD = 0.139, $P = 0.998$).

As mentioned previously, three animals were identified as males, SLP001, SLP002, and SLP012, and three animals were presumed to be females, SLP004, SLP006, and SLP020. Coefficients of association for the three male pairs ranged from 0.75 to 0.82, and COAs for the three female pairs ranged from 0.50 to 0.65 (Table 1). Coefficients of association for the known mixed-sex pairs ranged from 0.38 to 0.72 (Table 2). Coefficients of association for the three male pairs were among the highest of all observed COAs.

A dendrogram was generated using average linkage cluster analysis of the association data (Fig. 5). The cluster analysis grouped SLP001, SLP012, SLP017, SLP005, and SLP002 together, SLP004 and SLP007 together, and SLP013 and SLP020 together as the individuals most closely affiliated based on COAs (Fig. 5). The second highest COA was between the pair SLP012, a known male, and SLP017. SLP017 was never seen in close association with a calf. The third and fourth highest COAs were between SLP002 and SLP012 and between SLP001 and SLP012, respectively, the three known males. SLP005 was also never seen in close association with a calf. However, the highest COA was for a known female, SLP004, and an unidentified animal, SLP007. SLP007 was observed in close association with a calf on at

least three occasions, so it is likely that the highest COA was for a female pair. In all 10 replicates, SLP004 and SLP007 had significantly high associations. SLP020, a known female, and SLP013, of unknown sex, also had significantly high associations in all replicates. It is important to note that most calves were not identifiable, and therefore, COAs for mother-calf pairs were not estimated.

Long-term social bonds.—To look for evidence that individuals form long-term social bonds, the SLP dorsal fin catalog was compared with dorsal fin photographs taken in 1990 by Henningsen (1991). In this earlier study, 20 surveys passed through part or all of the SLP study area, sighting 16 groups and producing usable photographs of 13 groups (107 animals were photographed, resulting in 67 individuals with resightings). SLP071 and SLP075 were sighted only once during each study period but were seen together during both sightings (9 July 1990 and 9 June 1996). In 1990, SLP007 and SLP008 were each sighted five times, and they were sighted together during four of these five sightings. In 1995–96, the COA for this pair was 0.73, the 15th highest COA reported for the study, and they were each other's second closest associate. A similar situation existed when sightings of SLP007 and SLP008 were compared with sightings of SLP020. SLP020 was seen seven times during 1990, including five sightings with SLP007 and five sightings with SLP008 (four sightings with both). In 1995–96, the COAs for 007/020 and 008/020 were 0.72 and 0.69, respectively. SLP029 was sighted six times in 1990, all of which were joint sightings with SLP020. The pair's COA in 1995–96 was 0.65.

DISCUSSION

Association patterns.—The results of the permutation tests indicated that dolphins were associating nonrandomly. Because sexes were determined for only six (20.7%) of the 29 animals used in the association analyses, it is not possible to conclude that these preferred and avoided associations resulted from preferences to associate with the same or opposite sex. However, these preliminary results suggest that male pairs formed very tight bonds, perhaps tighter bonds than did female pairs or male-female pairs. Results also suggested that SLP017 and SLP005, the two animals grouped together with three known males by the cluster analysis, are also males and that these five males formed the tightest group among Bay

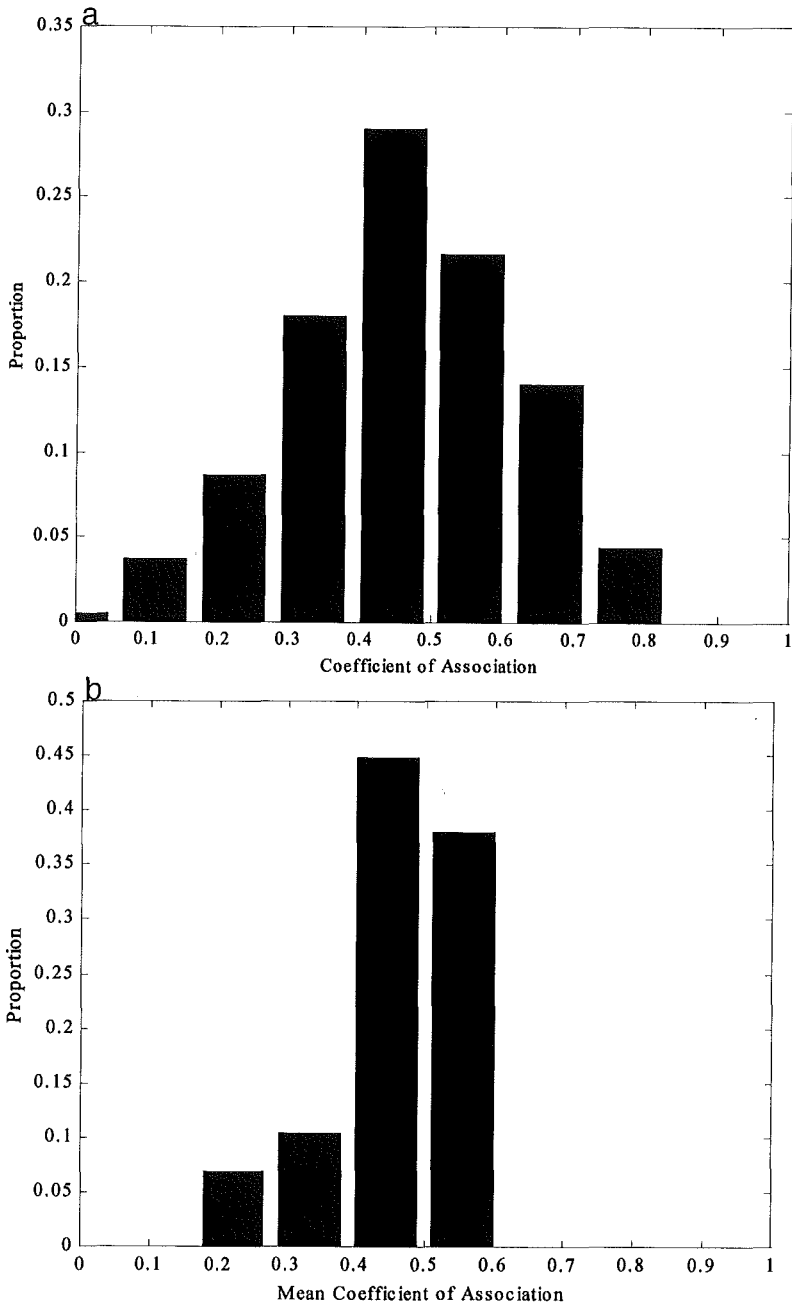
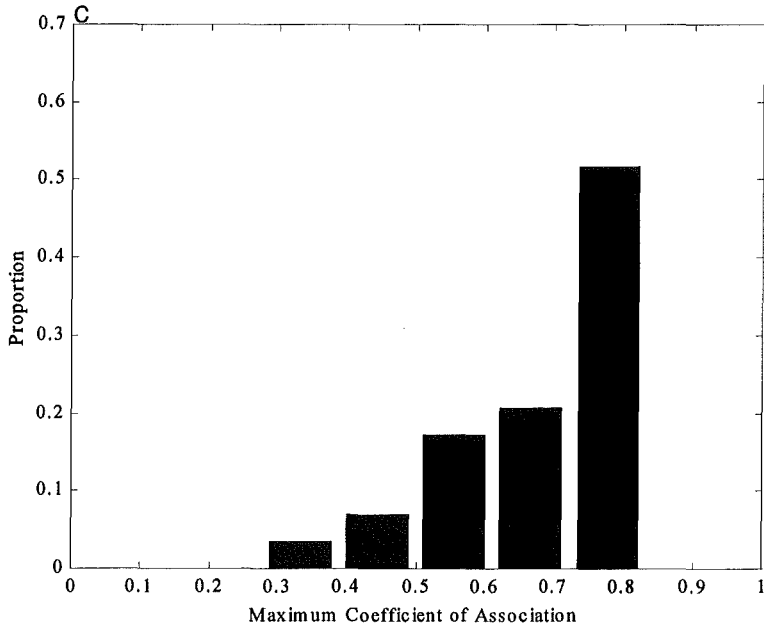


Fig. 4. (a) Distribution of COAs for all pairwise comparisons of 29 individuals identified five or more times ($n = 406$). (b) Distribution of mean COAs for 29 individuals identified five or more times. (c) Distribution of maximum COAs for 29 individuals identified five or more times.

animals in SLP. However, the highest COA observed in the population was likely for a female pair. Comparing COAs of known male–female pairs, it is interesting that one female, SLP006, had low associations with all three males and probably was avoiding them, based on the permutations, whereas SLP020, another female,

had fairly high associations with all three males.

Coefficients of association have been well studied among the Sarasota Bay bottlenose dolphin community, but comparisons with the area are difficult. In Sarasota Bay, age and sex information is known for most dolphins, so



Continued.

most COA information has been partitioned into age and sex classes (Wells et al., 1987; Connor et al., 2000). Despite the paucity of data on ages and sexes of SLP individuals, both study sites reported high COAs for male pairs. A similar situation has been reported for *T. aduncus* in Shark Bay, Australia, where male pairs accounted for most of the COAs in the two highest classes (88% of 61–80 class and 94% of 81–100 class) (Smolker et al., 1992). Despite varying population sizes, study area sizes, and habitat features among the three study sites, each study found high or the highest COAs among male pairs. This reinforces suggestions by previous authors that, excluding mother–calf pairs, male pairs form the most stable social bonds in some coastal *Tursiops* sp. communities.

In Shark Bay, males cooperate in pairs and triplets, termed alliances, to aggressively herd estrous females (Connor et al., 1992a, 1992b; Connor et al., 2000). In Sarasota Bay, males also form strongly bonded pairs, which have been observed separating individual females from groups (Wells et al., 1987; Connor et al., 2000). In SLP, it has not been determined whether male pairs or trios herd females; however, we made observations on three different days that resembled descriptions of herding attempts in Shark Bay.

Comparing association indices without regard for difference from random, the values from this study are higher than those from Galveston Bay (Bräger et al., 1994) and some other areas, like northern San Diego County, CA

TABLE 1. Coefficients of association (COA) for known male pairs and female pairs.

COA	ID no.	ID no.
Males		
0.75	SLP001	SLP002
0.80	SLP001	SLP012
0.82	SLP002	SLP012
Females		
0.50	SLP006	SLP020
0.59	SLP004	SLP020
0.65	SLP004	SLP006

TABLE 2. Coefficients of association (COA) for known male and female pairs.

COA	Male ID no.	Female ID no.
0.38	SLP001	SLP006
0.37	SLP012	SLP006
0.45	SLP002	SLP006
0.58	SLP012	SLP004
0.62	SLP012	SLP020
0.60	SLP001	SLP004
0.66	SLP002	SLP004
0.68	SLP001	SLP020
0.72	SLP002	SLP020

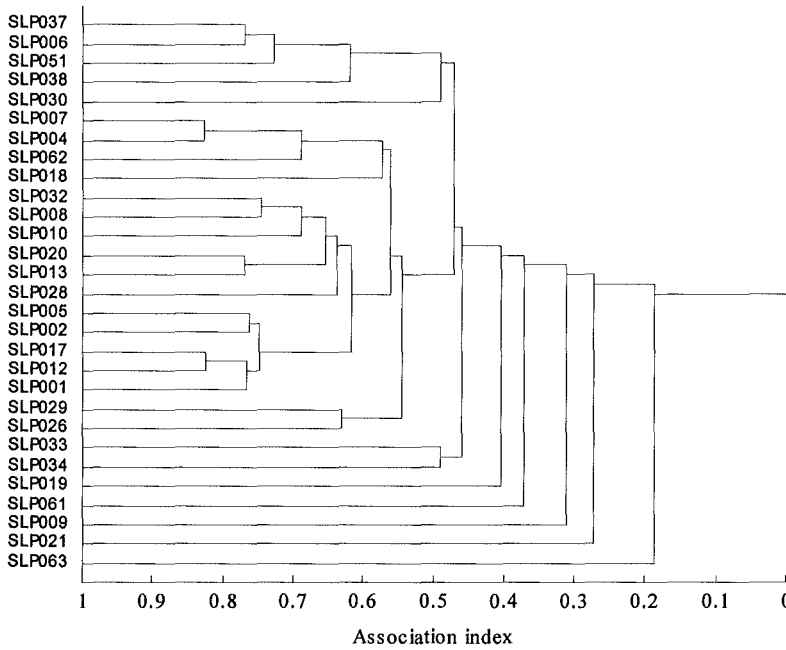


Fig. 5. Dendrogram generated using average linkage cluster analysis of 29 individuals identified five or more times.

(Weller, 1991), where dolphins are highly mobile and display no residency trend. However, our findings were very similar to those from the Sado Estuary, Portugal, where 72% of COAs were ≥ 0.40 (Harzen, 1989 from Bräger et al., 1994). As the dataset from this study site grows, it may be appropriate to increase the cutoff level for including individuals in COA analyses from five to 10 or more to determine whether the COA values were inflated by our small sample size.

Affiliates.—The “resident” Bay animals associated regularly, but they probably did not represent a genetically isolated population. Each sighting of Gulf animals contained at least one Bay animal. Genetic exchange may occur when Bay animals mate with transients that pass through the SLP area.

Wells et al. (1987) reported that Sarasota residents associate with a large number of community members. They are also known to associate with members of adjacent communities, and these groups tended to occur along the home range peripheral areas more frequently (Scott et al., 1990). Sightings of Bay animals mixing with transient groups in SLP were not frequent enough to determine seasonality of occurrence, but all such sightings occurred in the Gulf, presumably somewhere

near the periphery of the Bay animals’ home range.

Long-term social bonds.—In both 1990 and 1995–96, several dolphin pairs and triplets were frequently sighted together. We hypothesize that animals exhibit site fidelity to this area and that social bonds remained strong during the intervening years. This is further suggested by more recent work in SLP during 1997–2000, which showed that many animals continued displaying fidelity to the area (L. J. Irwin-Smith, pers. comm.).

Würsig and Harris (1990) also reported site fidelity for dolphins frequenting the SE portion of Golfo San José, Chubut, Argentina. Animals identified during a study in 1974–76 were resighted in 1984, and two dolphins from subgroup A and three from subgroup B, both subgroups that were found together consistently during 1974–76, were again found together. According to the authors, this indicated that these individuals had formed long-term social bonds and were probably together during at least part of the years during which no data were available.

Group sizes.—Range and frequency distribution of group sizes were similar to those reported previously by other researchers. In the Sado Es-

tuary, Portugal, dos Santos and Lacerda (1987) found a mean group size of 13.7, with about 67% of groups containing 15 or fewer and about 82% of groups containing 20 or fewer individuals (in SLP the mean was 10.6 with 70% of groups containing 15 or fewer and 87% containing 20 or fewer individuals). The study sites are similar in some respects, as the inner part of Sado Estuary is shallow with extensive mud flats, and mud and sand banks are present in places. In the Northern Adriatic Sea, Bearzi et al. (1997) found a mean group size of 7.4, with the most frequently encountered groups containing 1–5 individuals and most groups (90.3%) containing fewer than 15 individuals. Much larger groups have been reported for more open habitats, such as Kino Bay, Mexico, where group sizes ranged from 1 to 125, with a mean of 15 (Ballance, 1990), and north San Diego County, CA, where group sizes ranged from 2 to 90, with a mean of 19.8 (Defran and Weller, 1999).

Studies in Galveston Bay have found groups ranging in size from 1 to 30 with a mean of 4.4 (Bräger et al., 1994) and from 1 to 70 with a mean of 8.3 (unpubl. data). For the Galveston Ship Channel, Fertl (1994a) found groups sizes ranging from 1 to 10 for groups without calves ($\bar{x} = 3.2$) and from 1 to 15 for groups with calves ($\bar{x} = 2.9$, excluding calves). Overall, group size findings for SLP were within ranges of previous findings for the Galveston Bay area.

In the SLP study area, the largest groups were observed during spring and the smallest groups during the fall. Seasonal differences in group size have not been examined in detail for Galveston Bay but they have for other Texas study sites. Gruber (1981) also found the smallest group sizes during the fall but found the largest during summer in the Pass Cavallo area of Matagorda Bay. Groups in Aransas Pass were largest in the fall and smallest in summer (Weller, 1998). For the Matagorda-Espiritu Santo Bay area, Würsig and Lynn (1996) found no strong seasonal trends in group size.

Group size for small cetaceans is a complicated interaction of various factors, such as predation pressure, feeding, body size, and potential for social interactions (Wells et al., 1999; Ballance, 2002). No clear patterns emerged to explain why group sizes would differ seasonally in this area; however, we hypothesize that larger groups during spring might have been related to increased social activity during this season. Socializing was the most frequently observed behavior during spring (Maze, 1997). With a 12-mo gestation period and an observed calving peak during spring to midsum-

mer, spring is probably a time of increased mating–socializing activity for this area, which may result in larger group sizes. It is also possible that differences in group sizes were an artifact of how we defined our seasons. We used four seasons so that we could compare our findings with those of previous studies, but two seasonal weather patterns with transitional periods between them more accurately describe the climatology of the central and western Gulf of Mexico.

Group composition.—Because the sex of only six individuals (adults) was determined, it was difficult to evaluate the composition of all groups encountered. However, each of these six individuals was sighted 28–40 times, making it possible to determine that almost half the groups had both sexes. When compared with all groups, mixed-sex groups were larger, containing at least 11 animals. However, based on chance alone the probability of a mixed-sex group existing will increase with group size, and not all mixed-sex groups were identified. Every group, except the mother–calf pair and groups containing only one individual, could have been composed of both males and females, but this seems highly improbable. A more likely scenario is that single-sex groups, including mothers with calves of either sex, were smaller and that these groups frequently fused to form larger mixed-sex groups.

Wells et al. (1987) reported that sexual segregation was a distinct feature of group composition in the Sarasota Bay community between 1970–76 and 1980–84. For two samples, 20% and 31% of sightings were of mixed composition. It is very likely that single-sex groups are a feature of the SLP area as they are for Sarasota Bay but to what degree is unknown. Mixed-sex groups composed a higher percentage of samples in SLP than in Sarasota Bay; however, sample sizes were much lower for SLP, and information on sex was only determined for six individuals. Despite this, over half the sightings in SLP that produced usable photographs contained mixed-sex groups, and this is certainly a minimum estimate. The situation in SLP seems closer to that of *T. aduncus* in Shark Bay, Western Australia, in which 49% of groups contained adults of mixed composition (Smolker et al., 1992). The Shark Bay population is also resident the year round and exhibits seasonal shifts in habitat use, as do the SLP and Sarasota populations. Shark Bay is also a shallow bay, but it is more open than the Sarasota and SLP study sites.

Calving.—Neonate sightings were confined to spring and early summer, beginning in late March and ending in mid-July. Births could have occurred earlier in March and been missed due to the fact that no surveys were conducted between 12 March and 29 March 1996. This is contrary to Fertl's (1994b) findings from the Galveston Ship Channel, where newborn calves were sighted the year round, but similar to the late-spring peak reported by Shane (1977) for the Aransas Pass area of Texas. However, Shane's (1977) first neonate sighting of the year occurred on 27 Jan., much earlier than in SLP, and she suggested that young are born in Texas the year round due to sightings of very small dolphins in almost every month of the year. Although the peaks coincided, no neonates were sighted outside the peak season for the SLP area. Neonate strandings along the Texas coast are highly seasonal, with a peak in March (Urian et al., 1996; Fernandez and Hohn, 1998). However, as noted by Fernandez and Hohn (1998), stranding patterns may not correctly reflect actual calving, and neonates that do not survive may be those born earlier or later than those that do survive. The observed calving peak for SLP was later than the neonate stranding peak in Texas. An estimate of date of birth from stranded neonates that was earlier than estimates made from field studies was also found for the central-west coast of Florida, including Sarasota Bay (Urian et al., 1996; Fernandez and Hohn, 1998). Fernandez and Hohn (1998) suggested that a lack of detection of neonates that stay very close to their mothers might be one source of bias.

A short 3-mo peak for births just before the warmest temperatures of the year, with an extended season of lower numbers of birth, is very similar to what Mann et al. (2000) reported for *T. aduncus* in Shark Bay, where the peak birth months are Oct.–Dec. Mann et al. (2000) comment that birth seasons appear to be more pronounced for *Tursiops* sp. in some study sites than in others; however, they caution that different sampling methods may account for the differences. Ongoing work in the SLP area should further elucidate seasonality of calving.

CONCLUSIONS

Additional study has taken place in SLP from 1997 to the present. We plan to compare and combine more recent data with data from our study to examine temporal variability in association of individual diads and to further examine group composition by including addi-

tional data on ages and sexes of identified individuals. Analysis of this larger dataset will allow an assessment of our preliminary findings of nonrandom associations and preferred companions among male pairs with longer-term trends, perhaps further elucidating the social structure of Texas coastal bottlenose dolphins.

Our findings indicate that a possibly long-term, resident community of bottlenose dolphins inhabits the SLP area (West Bay stock), and is separate, but not isolated from the Galveston Bay community (Galveston Bay, East Bay, and Trinity Bay stock). Co-occurrence of resident and nonresident dolphins was found within the SLP area, and obviously much uncertainty still remains regarding stock structure. However, for the present, we recommend that NMFS should continue managing the communities or stocks in GBE separately, and we suggest that protection and additional study of this area is needed.

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- MARINE MAMMAL RESEARCH PROGRAM, TEXAS A&M UNIVERSITY AT GALVESTON, 4700 AVENUE U, BUILDING 303, GALVESTON, TEXAS 77551. PRESENT ADDRESS (KM-F): JOHNSON CONTROLS, INC./NATIONAL MARINE FISHERIES SERVICE, 3209 FREDERIC STREET, PASCAGOULA, MISSISSIPPI 39567. Date accepted: June 24, 2002.