

Association patterns of resident bottlenose dolphins (*Tursiops truncatus*) in a South Carolina estuary

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Abstract

Associations between individuals in most mammalian social systems result from complex interactions among internal and external factors. My objective was to relate associations among identifiable Atlantic coastal bottlenose dolphins (*Tursiops truncatus*) to their geographic, ecological, and social environments. From October 1994 through December 1998, I conducted 204 surveys in Calibogue Sound, South Carolina and adjoining coastal waters. Individual dolphins were identified by distinctive fin characteristics and were categorized as either year-round (resident) or occasional (transient) inhabitants of the area based on resighting patterns. A simple ratio index defined association patterns between pairs of resident dolphins. Cluster analysis identified two distinct social groups of resident dolphins, which corresponded to geographic concentrations of home ranges. Resident dolphins had many associations with transient dolphins, but neither resident social group was more likely to interact with transients. There were no significant changes in the association patterns of resident dolphins based on local environmental factors (season, habitat type, and tidal phase) or behavioral states (social versus asocial). Additionally, resident dolphins did not change their preferred associates when new dolphins entered their ranges. The association patterns of these dolphins are mainly based on geographic organization and are consistent with those of dolphins living in similar inshore communities not subject to the passage of large numbers of seasonally migrating dolphins.

Key words: association, bottlenose dolphins, photo-identification, simple ratio index, social structure, South Carolina, *Tursiops truncatus*.

Introduction

Around the world, association patterns of bottlenose dolphins (*Tursiops truncatus*) have been

related to ranging patterns (Rossbach & Herzing, 1999; Wells, 1991), environment (Brager *et al.*, 1994; Shane, 1980, 1987; Smolker *et al.*, 1992; Wells, 1978; Würsig, 1978; Würsig & Würsig, 1977, 1979) and behavior (Brager *et al.*, 1994; Connor *et al.*, 1992; Richards, 1996). Shared ranging patterns were hypothesized to partially determine social 'communities' of bottlenose dolphins in Sarasota, Florida by limiting potential associates to those with similar ranges (Wells, 1991). Broad features of the environment, such as water depth and coastline shape, have been related to association rates of bottlenose dolphins (Shane, 1980, 1987; Wells, 1978; Würsig, 1978; Würsig & Würsig, 1977, 1979). Open habitats were correlated with low fidelity between individuals (Würsig & Würsig, 1977, 1979; Würsig, 1978; Shane, 1980, 1987; Shane *et al.*, 1986; Brager *et al.*, 1994; Weller, 1991), while in 'closed' habitats, dolphins maintained stronger associations with long-term fidelity (Wells, 1978; Ballance, 1990). Other environmental factors might also affect dolphin association patterns. For instance, Smolker *et al.* (1992) reported that associations among female dolphins in Australia changed seasonally. Like ranging patterns, behavior may determine association rates of bottlenose dolphins by limiting the partners available for interaction (Brager *et al.*, 1994). Associations of both male and female bottlenose dolphins in Australia changed with behavior (Connor *et al.*, 1992; Richards, 1996). Similarly, Hector's dolphins (*Cephalorhynchus obliquidens*) in New Zealand changed their behavior from feeding to social (sexual) interactions when new associates were encountered (Slooten, 1994).

Few studies have examined geographic, social, and environmental factors and association patterns at the same time or in the same location. A small population of dolphins that occurs year round in a coastal estuary near the South Carolina-Georgia border (Gubbins, 2002; Gubbins *et al.* unpublished data; Petricig, 1994) offers an excellent opportunity to relate association patterns to all of these factors simultaneously. These year-round residents have home ranges that are concentrated into two

Table 1. Summary of research effort (surveys), groups observed, and dolphins counted, identified and added to the identification catalogue per year during this 5-year study. 'Identifications Made' includes initial and subsequent resightings of identifiable individual dolphins.

	Surveys	Groups observed	Dolphins counted	Identifications made	Individuals identified
1994	8	167	380	77	51
1995	45	661	1952	525	135
1996	32	372	1111	326	67
1997	48	503	1729	488	118
1998	72	808	2759	154	107
Total	205	2511	7931	1570	478

geographic hubs of overlapping individual ranges (Gubbins, 2002). The peripheries of the hubs overlap each other by <2 km. Abundance in this area regularly increases and decreases as some bottlenose dolphins move through the area seasonally, potentially altering the social dynamics of resident dolphins (Gubbins, 2000; Gubbins *et al.*, unpublished data; Petricig, 1994). The physical environment of this estuary varies, with three distinct habitats, seasonal changes in water temperature, and daily tidal cycles with up to 2.5-m tidal amplitude. Thus, the resident dolphins in South Carolina are regularly exposed to changing conditions of several factors known to be correlated with association rates. In this paper, I examine associations among identifiable bottlenose dolphins relative to their geographic, ecological, and social environments.

Materials and Methods

The study site was approximately 100 km² of inshore and coastal estuarine habitat including tidal creeks and marshes near Hilton Head Island, South Carolina (Fig. 1). The area was bordered at the north by the May River, at the south by the Atlantic Ocean, at the west by Savage Creek, and at the east by Hilton Head Island. The area included Broad Creek, which bisects Hilton Head Island. Nearshore (~2 km) ocean waters at the mouth of Calibogue Sound were included and were regularly surveyed and occasional surveys were made offshore (<10 km) and around the perimeter of Hilton Head Island. The study area included three distinct habitat types categorized as Sound (inshore sounds and tidal rivers >7 m deep and >30 m wide), Creek (inshore waterways <7 m deep and <30 m wide), and Ocean (coastal and offshore waters).

Data were collected from 29 October 1994 through 18 December 1998. Surveys were conducted quarterly for 1–8 weeks from 1994 to 1996

and twice weekly in 1997 and 1998. A 5-m powerboat was used on a standard transect to traverse the entire study area for each survey. A survey team consisted of a vessel operator, a data recorder, and a photographer. The vessel maintained a cruising speed of 30–40 km h until dolphins were encountered, at which time the boat was slowed. The time of initial observation, sea state, water depth, tidal phase, habitat type, and direction of movement of the group were recorded. The boat then moved parallel to the group and the location, number of dolphins, number of calves, and group behavioral state (travel, rest, feed, social, or unknown) were recorded. A dolphin group was defined as a collection of individuals that were estimated to be within 100 m of each other and engaged in the same behaviour while being observed. Dolphins separated by more than 100 m were recorded as separate groups.

Once location, group, environmental, and behavioral data were recorded, attempts were made to photograph the dorsal fin of each member of the group. Individual dolphins were identified by distinctive fin characteristics using standard photo-identification methods (Urian & Wells, 1996; Würsig & Jefferson, 1990). Based on overall resighting patterns between October 1994 and December 1998, I categorized each dolphin identified as a resident (year-round) or transient (seasonal) inhabitant of the area (Gubbins, 2000, 2002). Resident dolphins were seen in all four seasons of the year while transients were seen only in one or two seasons.

I used cluster analysis with average linkage to assess the association patterns of resident dolphins, testing the hypothesis that two distinct social groups with stronger associations within than between communities existed in the resident population (SOCPROG; Whitehead, 1997). I expected to find two social groups that corresponded to the two hubs (Creek and Sound) of overlapping resident dolphin home ranges (Gubbins, 2002). Strength of

association between pairs was represented by the simple ratio association index, which is statistically unbiased (Cairns & Schwager, 1987; Ginsberg & Young, 1992). The association index between pairs of individuals was calculated as:

$$SR = \frac{x}{(x + y_a + y_b)}$$

where,

x = total number of times that two dolphins were seen together,

y_a = number of sightings of the first dolphin without the second, and

y_b = number of sightings of the second dolphin without the first. SR can range from 0 (two dolphins never seen together) to 1 (two dolphins always seen together).

Because dolphins in the Sound were geographically closer to the ocean, where transient dolphins are hypothesized to travel during seasonal migrations up and down the coast, I expected them to have more transient associates than Creek dolphins. To determine whether Sound dolphins had significantly more transient associates than Creek dolphins, I tallied the number of associates of each resident dolphin from individual sighting records. An 'associate' was a dolphin sighted in the same group as the focal dolphin. I tested this hypothesis by comparing individuals in the two resident hubs for number of transient associates, employing a Student's t-test.

To test the hypothesis that environmental factors influence patterns of association among resident dolphins, I compared associations in different seasons, tidal phases, and habitat types. The first analysis compared association rates by season (winter and summer), based on significant differences in sea surface temperature. Water temperatures were obtained from the website (www.noaa.gov) of the National Oceanic and Atmospheric Administration weather stations for the dates surveyed. During summer (May–October), water temperature was $>18^\circ\text{C}$ (mean: 26.3°C ; range: 23.4 – 28.6°C). During winter (November–April), water temperature was $<18^\circ\text{C}$ (mean: 17.1°C ; range: 15.4 – 17.9°C). I calculated SR coefficients of association for pairs of resident dolphins in the two seasons, creating one matrix for winter and one for summer; I then compared these two matrices using a Mantel test with 1000 permutations to test for significant differences (SOCPROG; Whitehead, 1997).

To test the hypothesis that association rates varied with different tidal conditions, I used the same methods. Before beginning each survey, high and low tides for that survey period were recorded on the data sheet from a tide chart. The data recorder calculated the 4-h high and low tidal

phases by including the 2 h- before and -after the high and low tide peaks. Medium tides were between these two phases. These periods were chosen due to the clear environmental changes in the tidal marshes. During low tide, mudbanks were exposed in the tidal creeks and creek depth and volume were significantly reduced. During medium tides, the mudbanks were covered, but marsh grass was not, and during high tides, all mudbanks and marsh grass were covered or nearly so. For this analysis, I combined sightings during high and medium phases into one state corresponding to water covering the mudbanks and created an association matrix. Using a Mantel test with 1000 permutations, I compared this matrix to one constructed for associations during low tide when mudbanks were exposed. Since resident dolphins were never seen in the Ocean habitat (Gubbins, 2002), I compared association patterns in the two inshore habitat types, Sound and Creek, again constructing two association matrices (one for each habitat type) and comparing them with a 1000-permutation Mantel test.

Based on results of their study on the association patterns of bottlenose dolphins in Galveston Bay, Texas, Brager *et al.* (1994) proposed that bottlenose dolphins have preferred associates for different behaviors. To test this hypothesis for South Carolina dolphins, I compared associations during social behavior (social, travel, rest) and asocial behavior (feeding) to determine whether dolphins were socializing or feeding preferentially with certain members of the population (Slooten, 1994). Sightings in which the behavioral state of the group was recorded as 'unknown' were not included in this analysis. Two association matrices (social and feeding) were constructed in SOCPROG and compared with a Mantel test.

Results

Between 1994 and 1998, I completed 204 surveys, observing 7931 dolphins in 2511 groups. Dolphins were sighted in every month of the year and on every survey. From 8520 dorsal fin photographs, I made 1570 identifications of 478 individual dolphins (Table 1). I categorized 52 individuals as residents and 426 as transients. Individual resident dolphins were observed 10–116 times, while individual transients were observed 1–8 times during the 5-year study.

Two groups of resident dolphins, referred to here as 'Sound' and 'Creek' communities, were apparent from cluster analysis (Fig. 2). They consisted of 25 (Sound) and 27 (Creek) photographically identifiable dolphins. There was no difference in sighting rates between the two communities ($P=0.1$, Student's t-test). Dolphins in the Sound community

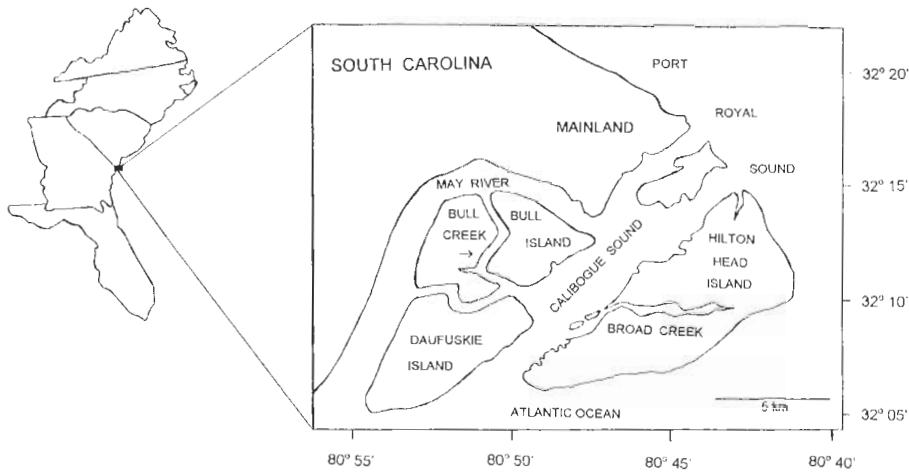


Figure 1. Study site, an area of approximately 100 km² of inshore and coastal waters near Hilton Head Island, South Carolina centred at 32°10'N and 80°50'W.

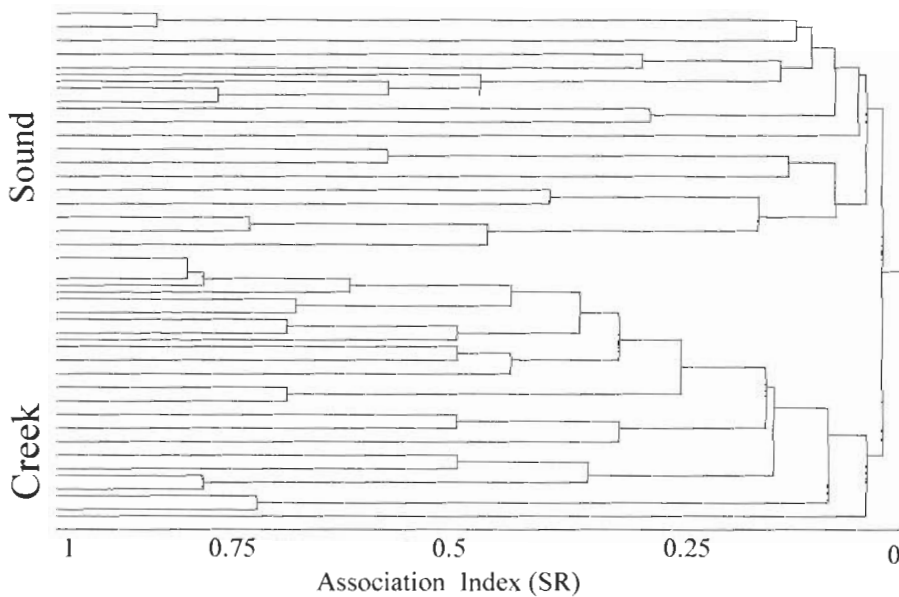


Figure 2. Cluster analysis of a simple ratio association index (SR) among pairs of 52 resident dolphins revealed two distinct social groups. Dolphins in each social group also had home ranges that strongly overlapped.

were seen 28 ± 25.3 times (mean \pm SD; range 11–116), while those in the Creek community were observed 18 ± 9.2 times (mean \pm SD; range 10–46). Resident dolphins had significantly more associates within their own community than in the other resident community ($t=11.4$, $df=51$, $P=0.00$), averaging 10 ± 5.2 associates in their community (range 1–21) and 2 ± 1.6 in the other community (range 0–6). Neither community was significantly more likely to interact with transients ($t= -1.32$, $df=40$,

$P=0.19$), although dolphins in the Sound community averaged 15 transient associates (range 2–39; SD 10.7), and those in the Creek community averaged 12 transient associates (range 1–26; SD 6.8).

Overall, resident dolphins displayed no significant difference in association patterns between seasons (matrix correlation=0.074, Mantel $t=1.36$, $P=0.9$), when in different habitat types (matrix correlation=0.067, Mantel $t=1.32$, $P=0.9$), or at

different tidal stages (matrix correlation = -0.05 , Mantel $t = -1.1$, $P = 0.14$). Behavior was not a determinant of association patterns of resident dolphins, i.e., there was no significant difference in association patterns during different behavioral states (matrix correlation = -0.037 , Mantel $t = -0.77$, $P = 0.22$).

Discussion

Dolphin communities are 'assemblages of dolphins that inhabit similar ranges and that interact socially more often with each other than with other adjacent assemblages' (Wells, 1986). Cluster analysis and associate data support the hypothesis that resident dolphins in this South Carolina estuary comprise two distinct communities. Dolphins in each community interacted significantly more frequently with other community members than with non-members. These two social communities corresponded to the two hubs of home range overlap reported by Gubbins (2002). Overlapping or adjacent ranges of social communities of bottlenose dolphins occur in Sarasota, Florida (Irvine *et al.*, 1981; Wells, 1986; Wells *et al.*, 1987) and in the Bahamas (Rossbach & Herzog, 1999), but this is the first evidence of such a pattern in the mid-Atlantic coastal bottlenose dolphin population between Florida and New Jersey.

While geography was related to association patterns within the two resident communities, it did not show a parallel relationship with residents' interactions with transient dolphins. Although dolphins in the Sound community ranged nearer the Atlantic Ocean than dolphins in the Creek community, dolphins in both communities had similar numbers of transient associates.

Ranging and association patterns of bottlenose dolphins in the western Atlantic Ocean are not well understood (Hohn, 1997; Wang *et al.*, 1994; Waring *et al.*, 2000). Inshore resident dolphins along the entire Atlantic coast were unaffected during a 1987-88 mass mortality event that led to the mortality of 50% of migrating (transient) dolphins (Scott *et al.*, 1988). At the time, it was unknown whether transients exposed resident dolphins to the pathogens that caused the die-off since there had been no studies of the ranging or association patterns of either resident or transient dolphins. It was believed that transient dolphins remained in coastal waters and did not venture into the inshore waters where residents were believed to reside. However, based on the association patterns presented here, transient dolphins do penetrate several km inland and interact with resident dolphins. South Carolina resident dolphins likely interacted with affected transients in 1987 and 1988 and were exposed to the morbillivirus (distemper virus) associated with the

die-off. Pre-existing immunity to the pathogen might account for the residents' survival, but there are no data on antibody titres among resident dolphins, either before or after the event. The similar association rates for Creek and Sound dolphins with transient dolphins suggest that the entire resident population is susceptible to future disease transmission from transient dolphins.

The two communities of resident dolphins were centred on two different types of waterways: the wide, deep Calibogue Sound and the narrow, shallow Bull Creek. However, each community range contained roughly an even mix of both Sound and Creek habitat types and nearly all 52 resident dolphins identified were observed in both Sound and Creek habitats during this study. Habitat type did not significantly affect their association patterns. Three explanations are possible. First, the two distinct habitat types I categorized were not perceived as different by the dolphins. Second, the habitat differences were less important than some other factor(s) in determining association patterns. Third, the geographic range of each community, rather than environmental factors, dictated the social structure, and thus association patterns of the resident population. As the following discussion illustrates, the latter is most likely the correct explanation.

Resident dolphins showed no change in association patterns during different seasons. Seasonal changes in association patterns have been reported among inshore bottlenose dolphins in Australia (Smolker *et al.*, 1992) and were expected in this South Carolina population since environmental conditions change significantly and there is a seasonal influx of transient dolphins during the summer. Although resident dolphins were observed in groups with transient dolphins, the strength of their associations with other resident dolphins was not significantly different between summer and winter. Groups in which residents and transients were sighted together were larger than those in which only residents dolphins were identified (Gubbins, 2000), suggesting that transient dolphins temporarily joined already-formed groups of resident dolphins.

Resident dolphins did not change their association patterns with different tidal states or when engaged in social versus feeding behaviors. Some resident dolphins employed a distinctive foraging behavior at low tide called 'strand feeding' (Hoese, 1971; Rigley *et al.*, 1981; Rigley, 1983) in which they swiftly hurled themselves out of the water, creating a pressure wall of water that carried any fish present onto exposed mudflats. Singly or in groups, dolphins came partially or completely out of the water, grasped fish from the mud, then slid back into the water. This behavior is likely learned within

a social group that is stable over time (Petricig, 1994). Similar stranding behavior is used by killer whales (*Orcinus orca*) to capture southern sea lions (*Otaria flavescens*) and elephant seals (*Mirounga leonina*) on beaches in Patagonia (Lopez & Lopez, 1985). Since associations did not change with tidal phase or behavior, specialized foraging behaviors used by social group members apparently occurred when associates were already gathered.

Among resident dolphins in this South Carolina estuary, associations with preferred individuals were probably based solely on community membership, with a range of behaviors performed with close associates within the community. In contrast, male bottlenose dolphin pairs in Australia changed alliances with other pairs, depending on behavioral context (herding or not herding females) and prior behavior (whether the second pair had assisted the first pair in herding; Connor *et al.*, 1992). Female dolphins in Australia formed pairs in response to male herding behavior (Richards, 1996) and associates changed seasonally (Smolker *et al.*, 1992).

Strong site and association fidelity are general features of coastal bottlenose dolphins living in the shallow, protected inshore waters of 'closed' habitats. These features are shared by bottlenose dolphin populations in Sarasota, Florida (e.g., Wells *et al.*, 1987), Sanibel Island, Florida (Shane, 1990), Shark Bay, Australia (Connor *et al.*, 1992; Smolker *et al.*, 1992) and the Bahamas (Rossbach & Herzing, 1999). In contrast, dolphins living along open coastlines with deep water in California (Defran *et al.*, 1999), South Africa (Tayler & Saayman, 1972), Mexico (Ballance, 1990) and Argentina (Würsig & Würsig, 1979) maintain larger groups with little site fidelity and low rates of association.

Resident dolphins in South Carolina displayed the strong site and association fidelity typical of bottlenose dolphins in protected coastal waters. Geography was the main correlate of the two resident communities, but it was not a determinant of whether residents interacted with transient dolphins moving through the area. There were no significant changes in the association patterns of resident dolphins based on local social and environmental factors, indicating that resident dolphins did not change their preferred associates when new dolphins entered their ranges or when external biotic and abiotic conditions changed. The association patterns of these dolphins appeared to be independent of variations in environmental and social conditions and consistent with those of dolphins living in similar inshore communities without a seasonal influx of migrating dolphins.

This is the first report on the association patterns and community structure of resident bottlenose

dolphins in the mid-Atlantic coastal population in the United States. With only a handful of published reports on the behavioral ecology (Jacobs *et al.*, 1993), distribution (Barco *et al.*, 1999; Blaylock, 1988), and ranging patterns (Gubbins, 2002) of coastal Atlantic bottlenose dolphins, little is known about their social structure (Waring *et al.*, 2000). Data presented here indicate discrete social communities exist within a single inshore resident population occurring in a small coastal estuary. Further, transient dolphins, previously thought to be restricted to coastal waters, ranged extensively into the inshore areas occupied by the residents, and interacted with them throughout those waters. Thus, there appears to be a strong potential for gene flow between resident and transient dolphins in South Carolina. Because their primary associations did not change with the influx of transients to their ranges, resident dolphins occupy a distinct social niche separate from transients. It is likely that inshore resident populations with similar community structure exist from Florida to North Carolina (Caldwell, 2001; Wang *et al.*, 1994). Currently, bottlenose dolphins occurring in inshore bays and estuaries along the US Atlantic coast are hypothesized to represent a separate management 'stock' from 'coastal migratory' and 'offshore' dolphins (Waring *et al.*, 2000). This position is supported by the behavioral data presented here. As behaviorally distinct populations, residents and transients should be considered separate management stocks. However, genetic data are insufficient at this time to confirm definite separation of these two putative stocks (Waring *et al.*, 2000) and the potential for gene flow between residents and transients complicates stock distinction. Because transient dolphins potentially range from Florida to New Jersey (Wang *et al.*, 1994), there may be genetic panmixure among the entire coastal bottlenose dolphin population from Florida to New Jersey. The clear social structure found within this geographically small area suggests a complex social structure exists at the geographic scale of the entire mid-Atlantic coastal bottlenose dolphin population. Meta-analysis of results from this and several similar studies conducted at a micro-geographic scale would help elucidate the social structure of the coastal/inshore population as well as the underlying principles guiding the social structure of the species.

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