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Use of Gulf of Mexico Coastal Waters by Distinct Assemblages of Bottlenose Dolphins (*Tursiops truncatus*)

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Abstract

Management and conservation decisions affecting coastal bottlenose dolphins (*Tursiops truncatus*) benefit from consideration of population parameters such as population size, stability, distribution, habitat use, and gene flow, as well as social organization patterns. Long-term study of bottlenose dolphins in inshore areas suggested population units are based on the social structure and habitat use of resident dolphins, but little is known about dolphins in open coastal waters just offshore. This study examined the stock structure of bottlenose dolphins in an open coastal habitat, made comparisons to adjacent inshore population units, and evaluated interactions between dolphins in these two regions. We conducted a 14-mo boat-based photographic identification study along 93 km of the west coast of Florida, extending 9.3 km offshore. We identified 580 individual dolphins in the study area and designated these individuals as "Inshore" (long-term bay residents) or "Gulf" (observed predominantly in Gulf waters) regional population units. Dolphins used the Gulf habitat differently, depending on season and regional designation. Sighting frequencies of "Gulf" dolphins suggested patterns of seasonal residency, extended geographic range out of the study area, or transience, with fewer individuals displaying year-round residence. In general, dolphins in this coastal region appear to divide into overlapping communities defined by preferred geographic ranges, habitat use patterns, and social associations.

Key Words: bottlenose dolphin, *Tursiops truncatus*, Florida, Gulf of Mexico, stock structure, habitat use, distribution

Introduction

Requisite information on population size, stability, distribution, habitat use, and gene flow is lacking for many stocks of coastal bottlenose dolphins (*Tursiops truncatus*) (Waring et al., 2000). These data are critical for deciphering cetacean stock structure and making responsible management and conservation decisions (Scott et al., 1990a). Long-term study and the ability to recognize individuals provide the opportunity to evaluate distribution patterns and interactions among individuals and groups to examine stock structure and social organization. The U.S. Marine Mammal Protection Act of 1972 (MMPA) defined the term "population stock" as a group of animals that share a common space and interbreed. Bottlenose dolphin populations, in the strictest sense of the term relative to reproductive isolation, have yet to be discriminated through the complex of continuous coastal and inshore dolphin assemblages. Herein, we refer to less strictly defined population units, or "communities" as defined by Wells (1986): "distinct assemblages of dolphins that inhabit similar ranges and that interact socially more with each other than with adjacent assemblages" (p. 19). Communities are not necessarily reproductively isolated (Wells et al., 1999).

Research to date has demonstrated that the bottlenose dolphin is a highly adaptable species, with variable social organization patterns throughout their range (see Shane et al., 1986, for review; Wells & Scott, 1999). Home range size, average group size, and residence patterns are thought to vary depending on habitat (Shane et al., 1986; Ballance, 1990). The use of home ranges by bottlenose dolphins was first suggested by Caldwell (1955), and has since been supported by a number of studies showing various sizes of home ranges and degrees of site fidelity within these ranges (e.g., Würsig, 1978; Shane, 1980; Wells et al., 1980, 1987, 1996a, 1996b, 1997; Shane et al., 1986; Scott et al., 1990a; Ballance, 1992; Defran & Weller, 1999). The ranging patterns of individual dolphins and their associates can provide information on potential boundaries between population units along the coast (Wells, 1986; Urian, 2002). Bottlenose dolphin distribution and social organization patterns are thought to reflect the physical environment such as topography and water temperature (Hansen, 1990; Wells & Scott, 1990; Barco et al., 1999), as well as local prey distribution and abundance and predation pressures (Ballance, 1990). Overlapping geographic ranges of population units may or may not indicate gene flow; therefore, information regarding reproductive seasonality and social interactions is valuable in addition to information on movement patterns (Dizon et al., 1992; Urian et al., 1996; Wells, 2003).

Evaluation of interactions between population units can provide for informed management of this species. While a number of studies have provided information on inshore population units of bottlenose dolphins (those that reside in bays, sounds, and estuaries) and have suggested their designations as stocks (Wells & Scott, 1999; Urian, 2002; Wells, 2003), little has been done in the Gulf of Mexico to examine adjacent population units immediately offshore in open waters without clear geographical features to limit animal movements (Wells, 1986; Quintana-Rizzo & Wells, 2001).

Resident dolphins in Sarasota Bay, Florida, have been the subjects of research since 1970. A community of about 150 dolphins shows a strong degree of site fidelity within a fairly distinct, long-term home range, and are part of a mosaic of home ranges through the bays, sounds, and estuaries of the west coast of Florida, with dolphins inhabiting waters to the north, south, and coastal Gulf of Mexico (Wells, 1986, 1991; Wells et al., 1996a, 1996b, 1997). An extensive database includes gender, age, and genetic relationships for most individuals using Sarasota Bay. Mixing with non-resident individuals is well-documented within the Sarasota community (Wells, 1986). High levels of heterozygosity within the community, along with genetic determinations of a high proportion of calves apparently sired by non-resident males, suggest extensive genetic exchange with other communities (Duffield & Wells, 1991, 2002; Wells et al., 2001). The coastal Gulf of Mexico adjacent to Sarasota Bay is a potential area for genetic exchange and population mixing with the inshore community. We examined bottlenose dolphins in the eastern coastal Gulf of Mexico offshore of three well-studied inshore habitats—Sarasota Bay, Tampa Bay, and Charlotte Harbor/Pine Island Sound—to establish relative abundance indices for the Gulf region, and to define the ranging patterns and interactions of coastal and inshore dolphins using these waters.

Materials and Methods

Study Area

The Gulf of Mexico includes a wide, gradually sloping continental shelf that extends approximately 200 km offshore of the central west coast of Florida. The Gulf study area for this project extends 9.3 km offshore onto this shelf and borders 93 km of highly productive estuarine coastline (Figure 1). This coastline is broken by natural passes, which allow movement between deeper water offshore and shallow bays, sounds, and estuaries. The study area encompasses an open water habitat, with little physical protection from environmental conditions and predators. Depths range up to 14 m. Water temperatures vary depending on location and season, with a mean summer temperature of 29° C and mean winter temperature of 19.5° C (range 15.5° C to 33.8° C). The extent of the study area was determined by logistical and safety concerns associated with using a small vessel in open coastal waters.

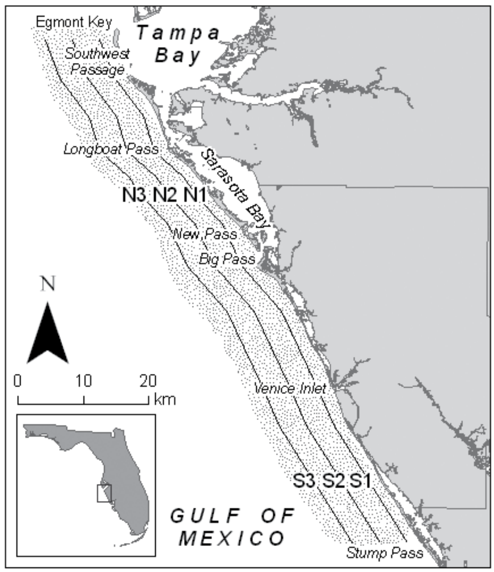

Figure 1. The stippled area indicates the Gulf of Mexico study area off Sarasota, Florida; lines indicate transect routes at 1.9 km, 5.6 km, and 9.3 km offshore.

Data Collection

Photo-identification surveys were conducted from a 6-m outboard-powered vessel during 14 consecutive months from July 1997 through August 1998 (Table 1). We spent 122 days searching for dolphins, including 251 hours actively observing and photographing dolphin groups. The number of survey days per month ranged from 4 to 15, determined mostly by weather. We attempted to spend at least one day per month surveying each of four transects: near the coast and paralleling the coast at distances of 1.9, 5.6, and 9.3 km offshore.

Transect routes were maintained at the specified distance from shore by using a GPS. We attempted to survey the entire study area each month by systematically completing all transects, as weather conditions allowed. In some cases, after all transects were completed within a calendar month, additional surveys were conducted using alternate routes that covered portions of the study area between transect lines.

While searching for dolphins, the boat was operated at a constant speed, moving at the minimum speed necessary to maintain the vessel on a plane (approximately 35 km/h). At least three observers watched for dolphins so that a forward field of view of at least 90° to each side of the bow was under surveillance at all times. Sighting conditions were graded according to sea state, weather, and surface glare (Urian & Wells, 1996).

When a group of dolphins was sighted, the boat approached slowly and paralleled the group's movements. In general, a sighting was defined as all of the dolphins within view; often, many of the dolphins were engaged in the same activity. The terms "group" and "sighting" are used interchangeably (some "groups" contained only a single dolphin). We attempted to photograph the dorsal fin of each animal in the group, using a 35-mm camera with databack, motordrive, 75- to 300-mm zoom lens, and color slide film. Data were collected on time, location (latitude and longitude), dolphin identification (if any were recognized in real time), number of dolphins and calves in the group, environmental conditions, and general dolphin activity.

A dolphin was assumed to be a female if it was seen on at least three occasions with a smaller animal in the typical "calf position" alongside. Calves were determined by relative size of the animal and their positions in the group. Unmarked calves were given identifications based on repeated proximity to their presumed mothers. Because calves may be up to several years old, young of the calendar year (YOY), determined by small size, position in the group, nonrigid dorsal fin, and presence of neonatal folds, were recorded as a separate category.

Two additional survey opportunities supplemented regular photo-identification surveys. Data collection methods for these projects were the same as those used in our surveys. Monthly photo-identification surveys, focusing on the dolphins resident to the bays, sounds, and estuaries, surveyed Gulf waters within approximately 1 km of shore up to 8 times each month. Survey teams also accompanied a Mote Marine Laboratory red-tide sampling boat 55 km offshore once per month. The sampling boat stopped for photo-identification and data collection when dolphins were sighted.

Photo-Identification

Proven photo-identification methods were used to produce a catalog of identifiable animals for comparison to other catalogs developed for the Florida west coast and inshore waters (Scott et al., 1990b; Würsig & Jefferson, 1990; Urian & Wells, 1996). A distinctive fin was defined as a dorsal fin with visible markings such as nicks, gashes, and permanent scars, which can be identified and tracked over time. Each distinctive dorsal fin was compared to the more than 2,000 dolphins in established fin catalogs for the Sarasota Bay (SB), Tampa Bay (TB), and Charlotte Harbor/Pine Island Sound (CH/PIS) study areas (Wells et al., 1996a, 1996b, 1997).

Each individual dolphin identified in the Gulf was categorized by a regional range designation for analysis purposes, based on prevalence of sightings in Gulf vs inshore waters. Sighting histories for dolphins seen prior to our project are composed of records from survey and behavioral observation efforts since 1970 (Scott et al., 1990a; Wells, 1991). Frequencies of sightings in each region were adjusted relative to survey efforts in each region. For the period up through 1996, a ratio of 9 inshore surveys for each Gulf survey was used as a guideline when considering an individual's distributional history prior to this project. This proportion was calculated by examining the number of kilometers surveyed for inshore and Gulf regions during surveys in a typical year since relative effort was similar each year during this time. For example, survey effort may have covered 225 km in inshore waters, but only 25 km in Gulf waters during a given time period. During these efforts, an individual dolphin sighted nine times in inshore waters and two times in Gulf waters would be given an adjusted proportional sighting record of one inshore to two Gulf sightings due to the 9:1 survey effort ratio. Inshore and Gulf surveys were conducted concurrently between July 1997 and August 1998, so effort was considered equal during this time for these regions.

Each dolphin was categorized into a regional designation using three factors: (1) total number of sightings prior to and during this study, (2) proportion of sightings which occurred in Gulf vs inshore waters compared to the approximate survey effort in each region at the time of the sighting (prior to or during this study), and (3) location of each sighting in relation to each region's approximate geographic bounds.

Individuals associating consistently (> 75% of sightings relative to adjusted effort) within one of the inshore, estuarine regions of SB, TB, or CH/PIS were grouped into one "Inshore" regional designation for these analyses. If an individual was sighted consistently (> 75% of sightings relative to adjusted effort) in open Gulf of Mexico waters with < 25% of their sightings inshore of the barrier islands, it was considered a "Gulf" dolphin. These regional designations agree with those defined by Wells (1986) for TB, SB, and Gulf communities. For individuals with sightings more evenly distributed between inshore and Gulf regions (< 75% in both regions relative to adjusted effort), we analyzed the location of each sighting record in relation to each other. Those individuals that had Gulf sightings occurring only in shallow coastal waters (< 5.48 m) directly bordering the region where their inshore sightings occurred were given the "Inshore" regional designation. If the individual had sightings both in more offshore Gulf waters and Inshore regions, it was given a "Both" regional designation.

Each sighting was given a regional designation based on the composition of identified individuals in that group. If all identified individuals in a group were designated as either "Inshore" or "Both," it was considered an "Inshore" group. If all identified individuals in a group were determined to be of "Gulf" designation, it was considered a "Gulf" group. If there was a mixture of "Gulf" dolphins with either "Inshore" dolphins or "Both" dolphins, it was categorized as a "Mixed" group. When determining a group to be mixed, only individual dolphins with five or more sightings in their histories were considered. This minimum number was selected to increase confidence in the categorization of each individual while at the same time provide a sufficient number of individuals for consideration of general patterns.

Data Analysis

Data were entered into a relational database with GIS mapping capabilities, containing more than 18,000 records of group sightings from 1975 to 2000. Only sightings from surveys within the Gulf study area were used for analysis. Opportunistic sightings obtained offshore, or to the north or south of the outlined study area, were used in making identification matches but were not included in data analyses. In addition, only sightings offshore of barrier islands, west of a line connecting the westernmost tips of land of the adjacent keys at each pass, were used for analysis.

Two seasons were designated for the purposes of our analyses—"summer," May through October; and "winter," November through April. These definitions were based on water temperature data for the Gulf study area during the time of this project. The greatest change in water temperature between months occurred quickly from October to November when temperatures decreased from over 26.6° C to under 21.1° C. Temperatures increased from below 21.1° C in March to above 26.6° C in June.

The number of dolphins sighted per km of transect surveyed (d/km) was used to determine relative overall abundance, abundance of each regional group type, and seasonal fluctuations in abundance. Typically, we sighted dolphins reliably within 1 km of either side of the survey transect. We examined dolphin distribution patterns in relation to water depth, distance from shore, and season. Dolphin distribution also was analyzed relative to distance from passes leading to inshore waters—the major physiographical features in the study area. Using GIS mapping software, numbers of sightings and dolphins were determined for each 1-km increment away from a pass. These values were then related to the proportion of the study area within each increment. The expected number of sightings for each increment from a pass was calculated by multiplying the total number of sightings by the relative area contained within that increment. The observed and expected values were compared using chi-square analysis. The null hypothesis assumed uniform distribution of dolphins throughout the study area. Statistical analyses were performed at $\alpha = 0.05$ significance level, using *SPSS*® statistical software.

Interactions between Gulf dolphins and the adjacent inshore communities were evaluated by examining the frequency and seasonality of mixed-group occurrences. Sightings of known SB resident dolphins in the Gulf were examined throughout the study period.

Results

Dolphins were sighted during every survey conducted under good or excellent conditions, and they were observed in all parts of the study area. The number of dolphin groups sighted per month during favorable conditions ranged from 6 to 52, with a total of 493 groups sighted in the

Table 1. Monthly summary of Gulf of Mexico surveys for bottlenose dolphins conducted between July 1997 and August 1998

	1997						1998								Total
	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	
Number of survey days	12	11	8	12	8	5	7	5	7	4	12	8	15	8	122
Number of dolphin groups sighted	52	35	43	49	31	10	38	13	26	6	51	46	51	42	493
Number of dolphins sighted	261	331	220	364	219	46	147	69	198	26	305	341	404	220	3,151

Gulf during the entire project (Table 1). Of these 493 groups, 300 were sighted while on a specific transect, and the remaining 193 were sighted between transect lines or while running alternate courses such as a saw-tooth or zigzag course across the study area.

A total of 609 individuals was cataloged during Gulf of Mexico surveys. These dolphins were identified 1 to 14 times each (median = 2; mean = 2.8; SD = 2.30) during the course of these surveys. Of these identified dolphins, 230 (37%) were first identified during previous photo-identification efforts. New catalog additions included 337 (55%) distinctive dolphins, along with 42 (6.8%) of their unmarked calves. Sightings of 29 cataloged individuals were restricted to large passes, leaving 580 individuals included in the Gulf analyses. Overall, we identified an average of 53% of the dolphins in each sighting. The size of the catalog increased throughout the study period, indicating the probability that all distinctive individuals using the study area were not identified.

We examined each identified dolphin's sighting history followed by the composition of each group to provide regional designations for both individuals and the groups in which they traveled. "Inshore" regional designation was given to 131 individuals (TB, $n = 57$; SB, $n = 57$; CH/PIS, $n = 17$), comprising a total of 23% of the 580 dolphins identified in Gulf waters. Of the remaining 77%, 432 individuals received a "Gulf" designation and 17 received a "Both" designation. Of the 493 dolphin groups sighted in the Gulf, 205 (42%) contained only dolphins of the "Gulf" regional type, 71 (14%) were "Mixed" groups, and 107 (22%) contained only "Inshore" dolphins. The remaining 110 (22%) sightings were "unknown," representing those sightings with no identified dolphins.

Distribution

Dolphin distribution patterns throughout the study area varied by region. Groups containing only "Gulf" dolphins were seen throughout the study area (mean distance from shore = 4.8 km, SD = 3.52, range 0.10 to 14.69 km, $n = 205$), while groups made up entirely of "Inshore" dolphins were seen closer to shore (mean distance from shore = 0.8 km, SD = 1.03, range 0.01 to 5.31 km, $n = 107$), often just outside passes. Average distance from shore was significantly different for these two groups (Mann-Whitney U-Wilcoxon Rank Sum W Test, $p < 0.001$). "Mixed" groups were intermediate between "Inshore" and "Gulf" groups (mean distance from shore = 1.9 km, SD = 1.03 km, range 0.16 to 9.52 km, $n = 71$). The average depth for each group type followed a similar pattern and also was significantly different for "Inshore" and "Gulf" groups (Mann-Whitney U-Wilcoxon Rank Sum W Test, $p < 0.001$). "Gulf" groups were seen throughout the depth range of the study area, except in very shallow waters (mean depth = 8.4 m, SD = 2.63, range 2.13 to 13.11 m, $n = 204$). "Inshore" groups were found in shallower water (mean depth = 3.8 m, SD = 2.07, range 0.64 to 9.75 m, $n = 107$), and "Mixed" groups were intermediate (mean depth = 6.0 m, SD = 2.45, range 1.55 to 11.89 m, $n = 71$).

Distribution of dolphins relative to passes leading to inshore waters showed a significant difference by region (Figure 2). For "Gulf" types, relatively uniform distribution was displayed throughout the study area, supporting the null hypothesis that the percent of total sightings is equal to the percent of study area for each 1-km increment away from a pass ($X^2 = 12.65$, DF = 15, $p = 0.63$). In contrast, the "Inshore" regional group types showed a strong preference toward areas closer to passes, leading to rejection of the null hypothesis ($X^2 = 645.42$, DF = 15, $p < 0.001$). No "Inshore" groups were found beyond 9 km from a pass, and no mixed groups were found beyond 10 km from a pass.

Abundance

Abundance indices for the Gulf of Mexico study area indicated seasonal variation in dolphin density in the Gulf of Mexico. Abundance estimation was based on 6,531 km of on-transect survey data. An average of 0.3 d/km surveyed was found for the entire duration of the study (SD = 0.13), with a decrease in abundance over winter months indicated by the lowest estimate of 0.10 d/km in December and the highest estimate of 0.52 d/km in August 1997. Winter abundance indices (mean = 0.2 d/km, SD = 0.10) differed significantly from summer abundance indices (mean = 0.4 d/km, SD = 0.10) (Mann Whitney U-Wilcoxon Rank Sum W Test, $p < 0.05$).

Regional group type abundance indices revealed complementary summer and winter patterns (Figure 3). A decrease in abundance during winter months for "Gulf" groups was in contrast to an increase in abundance for "Inshore" groups. This trend was most apparent during the months of December, January, and February, when "Gulf" abundance indices were < 0.05 d/km and "Inshore" indices were > 0.05 d/km. Summer abundance indices compared to winter abundance indices were significantly different within both "Inshore" and "Gulf" regional group types (Mann Whitney U-Wilcoxon Rank Sum W Test, $p < 0.05$).

The average abundance index for calves in the study area was 0.04 calves per km, including an average of < 0.01 YOY per km. The monthly proportion of calves within the Gulf study area ranged from 6 to 20%, with an overall average of

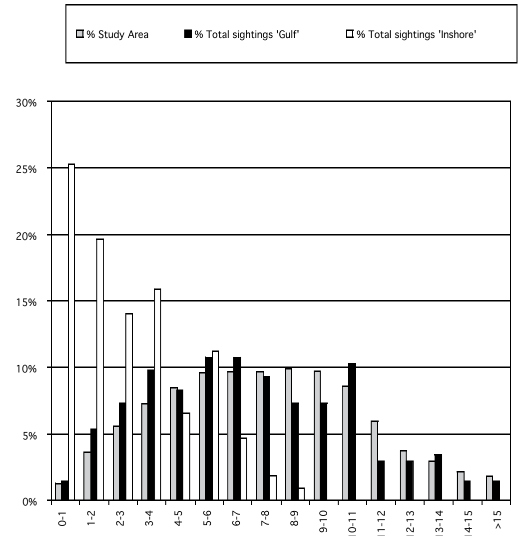

Figure 2. Distribution of bottlenose dolphin sightings for "Gulf" and "Inshore" regional groups in relation to distance from the nearest pass

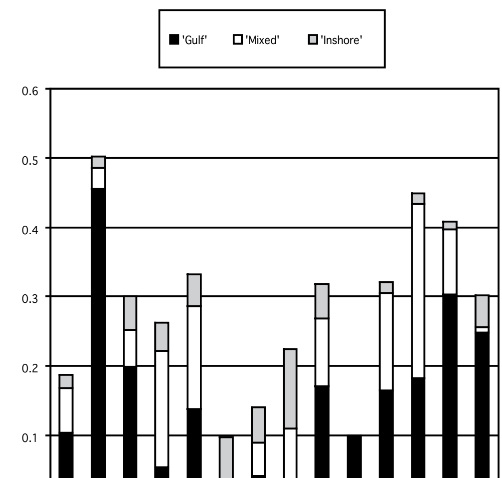

Figure 3. Monthly abundance indices, shown as number of bottlenose dolphins sighted per kilometer (d/km) surveyed, for three regional group types

13% of the total dolphin estimates. The number of calves sighted decreased during the winter months due to the complete absence of calves in "Gulf" groups between December and February. The overall proportion of calves was not significantly different between "Gulf" and "Inshore" groups. YOY sightings made up 1 to 4% of total dolphins sighted. The distribution of YOY is seasonal, with the first newborns appearing in May, and an increase in YOY sightings during the fall months. Most YOY sightings in Gulf waters belonged to "Gulf" groups rather than "Inshore" groups, with "Inshore" YOY appearing in the Gulf during only one month of the study. No YOY were sighted between December and April (by definition YOY abundance would be expected to be reduced at the beginning of a calendar year before the calving season).

Site Fidelity and Seasonality

Of the 580 dolphins identified in Gulf waters during this study, 226 (39%) were sighted only once. The remaining 354 (61%) were seen 2 to 14 times. A total of 210 dolphins had sighting histories in the Gulf predating this project. Of these, 34 individuals (16%) had initial sightings dating back at least 10 y. Fifteen of these (41.6%) were of the "Inshore" regional designation, 4 (11.8%) were "Both," and 15 (41.6%) were of the "Gulf" regional designation.

We examined sighting patterns for "Gulf" and "Both" dolphins with five or more sightings (n = 89, 20%) to gain a better understanding of seasonal occurrence within the study area. Some dolphins (n = 23, 26%) displayed seasonal patterns, occurring only in summer months, while the remaining dolphins (n = 66, 74%) were seen during both the winter and summer months. No dolphins were present in the study area during only winter months.

Individual Range Patterns and Community Overlap

Sighting locations of "Gulf" dolphins with at least ten sightings during this project (n = 7) were plotted to examine ranging patterns within the study area. Two general patterns emerged. Three of the seven dolphins showed a typical range within the northern 71% (66 km) of the study area, with only one sighting of one dolphin south of Venice Inlet in the remaining 27 km of the study area. The other four dolphins showed a typical range pattern within the southern 78% (73 km) of the study area, with no sightings north of Longboat Pass in the remaining 20 km of the study area.

Exceptional movements were noted by one group of dolphins. Four individuals sighted in the Gulf on 19 November 1997 as part of a large group (n = 25) traveling south 0.28 km off Longboat Pass also were sighted on 30 July 1998 traveling north near the same location, 1.73 km offshore, again as part of a large group (n = 35). These dolphins were observed inside CH/PIS on 16 August 1990, as well as inside TB on 19 June 1991 (Wells et al., 1996a). This constituted a minimum 138-km swimming distance between the farthest points of their observed sightings, and it represents the longest distance movements recorded during the

35-y history of the Sarasota Dolphin Research Program, passing through at least four different community ranges.

During nine opportunistic red-tide survey trips (plus one offshore radio-tracking trip during which survey data were collected), 144 dolphins were sighted. Of these, 83 were identified. Six of these dolphins were matched to the catalog produced from within the Gulf study area, within 9.3 km of shore. Five of these dolphins were observed in one sighting on 10 November 1997, 11.1 km offshore of New Pass (the midportion of the study area). The sixth dolphin was sighted 23.15 km offshore of this same pass on the same day.

In total, 57 SB resident dolphins were identified in Gulf waters during the study period. The majority of these sightings occurred in near-shore waters immediately west of passes, but a few dolphins were sighted up to 5.6 km offshore and to the northern and southern extents of the study area. The sighting locations for SB residents indicated a seasonal pattern, with summer sightings distributed along the shoreline and winter sightings clustered near passes. Distribution patterns for female ($n = 105$) and male ($n = 104$) SB resident sightings showed no obvious differences.

"Mixed" groups made up 14% of all Gulf sightings. These groups occurred during both winter and summer months, with the most frequent occurrence during the months of October, November, May, and June.

Discussion

The near-shore waters of the eastern coastal Gulf of Mexico are used by a complex system of bottlenose dolphin population units, exhibiting a variety of social organization, distribution, and residency patterns (Wells, 1986). The Gulf study area appears to border a number of inshore dolphin communities in TB, SB, and CH/PIS. Dolphins from the inshore communities primarily used the inshore system of bays, sounds, and estuaries, and they were occasionally observed in Gulf near-shore waters adjacent to their inshore range. Dolphins in these regions have displayed long-term, year-round residency patterns (Wells et al., 1980, 1996a, 1996b; Wells, 1986, 1991, 2003; Scott et al., 1990a). "Gulf" dolphins were found primarily in open Gulf of Mexico waters, with some displaying seasonal variations in use of the study area. A few individuals displayed sighting patterns with consistent use of both the inshore and open Gulf waters and were given a "Both" regional designation.

The Gulf of Mexico study area is a range apparently shared by several dolphin population units. "Inshore" dolphins used waters closer to shore, and "Gulf" dolphins moved throughout the range, but made greater use of waters offshore of those used by "Inshore" dolphins. Odell & Reynolds (1980) found dolphins distributed evenly over the gently sloping continental shelf; whereas, other studies of coastal bottlenose dolphin distribution indicated a preference for regions near passes and river or estuarine mouths (Ballance, 1992; Felix, 1994), and for regions close to shore (Würsig & Würsig, 1979; Blaylock, 1988; Defran & Weller, 1999). While we found dolphins distributed throughout our study area, the ability to recognize individuals in this study allowed us to categorize distribution patterns regionally. We determined that they were not all distributed evenly; rather, specific individuals used Gulf waters as a function of season and regional designation.

Distribution of "Inshore" dolphins in the Gulf of Mexico apparently was affected by several factors, including group composition, season, depth/distance from shore, and proximity to passes leading to inshore waters. It is difficult to discern the cues these dolphins may use in the Gulf, such as whether water depth or distance from shore determines the offshore limits of their range. With a uniform sloping bottom, such as our study area, water depth and distance from shore figures might be expected to follow similar patterns, as seen in our results. Seasonal patterns in distribution and range may also follow cues from factors such as water temperature, fish migrations, predator distribution, and social organization. The few sightings of "Inshore" dolphins with YOY in the Gulf may indicate a preference to stay inside the barrier islands, rather than using the more open and less protected Gulf habitat during the summer months when accompanied by very young calves and when predatory sharks are most abundant in Gulf waters (Wells et al., 1980). The SB resident dolphins' different distribution patterns in winter and summer may indicate that these dolphins are using the Gulf waters for different reasons seasonally, or it may indicate a difference in prey distribution with season. The migration of spawning mullet during the winter months may be one factor leading to a general shift in inshore dolphin distribution away from shallow seagrass meadows and into passes leading to the Gulf (Irvine et al., 1981; Waples, 1995; Barros & Wells, 1998). This phenomenon may also draw "Inshore" dolphins away from shallow coastal beaches in the Gulf and toward the passes to take advantage of the concentrated prey source during the winter months.

"Gulf" regional dolphins showed no preference for waters in proximity to passes as seen for "Inshore" regional dolphins, and there were no apparent physical barriers to distribution along the shore or offshore. The Gulf study area likely comprises only a part of the total home range of these dolphins. Abundance indices and seasonal movements of identified individuals indicate that a portion of the "Gulf" dolphin community moves out of the study area during the winter months and that their destination is unknown. The absence of calves in "Gulf" regional groups during some winter months may indicate variable seasonal distribution patterns of "Gulf" dolphins by social unit, with female/calf groups leaving the study area, while others remain year-round. Odell (1975, 1976) noted an increase in abundance in the Florida Everglades National Park during the winter months. Aerial surveys in the CH/PIS area revealed an apparent increase in abundance during the winter months (Thompson, 1981; Scott et al., 1989). A similar increase in abundance inshore of the barrier islands near Port Aransas, Texas, during the winter months was noted by Shane (1980).

For the TB and CH/PIS communities, the catalogs have been based largely on late summer to early autumn surveys (Wells et al., 1996a, 1996b). Current seasonal photographic identification surveys in CH/PIS are examining the possibility that the seasonal inshore increases suggested by aerial surveys may be due to an influx of dolphins from the Gulf. Seasonal movements of dolphins out of the study area could reflect lower productivity of this region during the winter months, causing dolphins to leave the area in search of better food resources. While the tendency toward seasonal migration for some coastal bottlenose dolphins in northern latitudes is clear (Shane et al., 1986; Barco et al., 1999; Wells & Scott, 1999), long distance seasonal movements in the Gulf of Mexico have not yet been documented (Quintana-Rizzo & Wells, 2001).

Dolphins of the "Both" regional designation ranged more widely between inshore and Gulf waters than other types. The 17 dolphins given this designation represent 2.9% of dolphins identified in the Gulf during this study. Further analysis of these individuals may clarify community designations or provide additional support for a grouping of dolphins that does not identify with a single regional grouping, but rather, uses a variety of geographical regions.

It is important to note that a strong El Niño weather pattern was in effect during the study period. An unusually wet and windy winter was one effect of this global weather event. These conditions interfered with survey efforts by reducing opportunities to complete surveys in the Gulf. The possibility of effects on the behavior and distribution of dolphins in the area must be considered, although consistent data from opportunistic long-term observations in the study area suggest such effects may have been minimal.

A pattern emerges for dolphins with at least ten sightings, suggesting that the Gulf study area may contain the southernmost end of a home range for some dolphins and the northernmost end of a home range for others. These home ranges widely overlap, but likely extend beyond the limits of our study to the north and south, and perhaps west (offshore). These overlapping range patterns could indicate preferred areas of usage for some individuals as seen in the SB community where many individuals are rarely seen in the southern portion of the range, and many others are rarely seen in the northern portion of the range (Wells, 1986). Another possibility could be the existence of two or more overlapping but separate "Gulf" communities using the study area. At least one small group of dolphins is known to travel the entire coastal extent of the study area. This is the longest observed travel distance for any dolphins in this region and could have implications for genetic exchange, community structure, and home range analyses. This small group accounted for only a very small portion (0.65%) of the dolphins observed during our study, however. Identifications of dolphins during surveys offshore of our study area suggest some limited use of these offshore waters; however, data from distances greater than 9.3 km from shore are few and only provide a small glimpse of offshore ranging patterns.

Social interactions among dolphin communities are important for stock discrimination and management (Wells, 1986). Community overlap between regional dolphin types occurred year-round in Gulf waters. Taken together, some SB resident dolphins used Gulf of Mexico waters over as much as the entire 93-km length of the study area, but they tended to remain near to shore. "Mixed" groups occurred most frequently in early summer and in the fall months; these months have previously been identified as peak reproductive months for SB inshore dolphins (Wells et al., 1987; Urian et al., 1996). The proportion of "Mixed" group sightings found in the Gulf (14%) is comparable to the 17% "Mixed" group proportion found by Wells (1986) when examining mixing relative to the SB community.

When evaluating dolphins along Florida's west coast for stock management purposes, this assemblage of dolphins should be viewed as one displaying some geographic overlap in ranging patterns with no obvious barriers to reproductive mixing. The occurrence of some degree of overlap supports the idea that while these communities may have preferred geographic ranges and social associations, they perhaps are not closed, reproductively discrete populations. The amount of genetic exchange between communities will affect how these dolphins are viewed as population units. The level and timing of community mixing found in this study suggest a high potential for genetic exchange. Recent research comparing the genetic compositions of SB resident dolphins and Gulf of Mexico dolphins demonstrated significant genetic differentiation between these regions, but this differentiation falls short of indicating reproductive isolation (Duffield & Wells, 2002; Sellas et al., in press). In spite of the lack of complete reproductive isolation, distinctions based on genetic differentiation combined with multi-generational patterns of social associations and habitat use suggest these communities may be important functional elements of their ecosystem, and therefore should be managed as separate stocks (Dizon et al., 1992).

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Literature Cited

Ballance, L. T. (1990). Residence patterns, group organization, and surfacing associations of bottlenose dolphins in Kino Bay, Gulf of California, Mexico. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 267-283). San Diego: Academic Press.

Ballance, L. T. (1992). Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. *Marine Mammal Science, 8*(3), 262-274.

Barco. S. G., Swingle, W. M., McLellan, W. A., Harris, R. N., & Pabst, D. A. (1999). Local abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia Beach, Virginia. *Marine Mammal Science, 15*(2), 394-408.

Barros, N. B., & Wells, R. S. (1998). Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Journal of Mammalogy, 79*(3), 1045-1059.

Blaylock, R. A. (1988). Distribution and abundance of the bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), in Virginia. *Fishery Bulletin*, *86*(4), 797-805.

Caldwell, D. K. (1955). Evidence of home range of an Atlantic bottlenose dolphin. *Journal of Mammalogy, 36*(2), 304-305.

Defran, R. H., & Weller, D. W. (1999). Occurrence, distribution, site fidelity, and school size of bottlenose dolphins (*Tursiops truncatus*) off San Diego, California. *Marine Mammal Science*, *15*(2), 366-380.

Dizon, A. E., Lockyer, C., Perrin, W. F., DeMaster, D. P., & Sisson, J. (1992). Rethinking the stock concept: A phylogeographic approach. *Conservation Biology*, *6*, 24-36.

Duffield, D. A., & Wells, R. S. (1991). The combined application of chromosome, protein and molecular data for the investigation of social unit structure and dynamics in *Tursiops truncatus*. In A. R Hoelzel (Ed.), *Genetic ecology of whales and dolphins* (Report of the International Whaling Commission, Special Issue 13) (pp. 155-169). Cambridge, UK: IWC.

Duffield, D. A., & Wells, R. S. (2002). The molecular profile of a resident community of bottlenose dolphins, *Tursiops truncatus*. In C. J. Pfeiffer (Ed.), *Molecular and cell biology of marine mammals* (pp. 3-11). Melbourne, FL: Krieger Publishing Company.

Felix, F. (1994). Ecology of the coastal bottlenose dolphin *Tursiops truncatus* in the Gulf of Guayaquil, Ecuador. *Investigations on Cetacea*, *25*, 235-236.

Hansen, L. J. (1990). California coastal bottlenose dolphins. In S. Leatherwood & R. R. Reeves (Ed.), *The bottlenose dolphin* (pp. 403-420). San Diego: Academic Press.

Irvine, A. B., Scott, M. D., Wells, R. S., & Kaufmann, J. H. (1981). Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin*, *79*(4), 671-688.

Odell, D. K. (1975). Status and aspects of the life history of the bottlenose dolphin, *Tursiops truncatus*, in Florida. *Journal of the Fisheries Research Board of Canada, 32*, 1055-1058.

Odell, D. K. (1976). Distribution and abundance of marine mammals in South Florida: Preliminary results. In A. Thorhaug (Ed.), *Biscayne Bay: Past/present/future* (pp. 203-212). Miami: University of Miami Sea Grant Special Report.

Odell, D. K., & Reynolds, J. E. (1980). *Abundance of the bottlenose dolphin*, *Tursiops truncatus*, *on the west coast of Florida.* (U.S. Marine Mammal Commission Final Report MM5AC026).

Quintana-Rizzo, E., & Wells, R. S. (2001). Associations and habitat use of resident and non-resident bottlenose dolphins, *Tursiops truncatus*, in the Cedar Keys, Florida: Insights into social organization. *Canadian Journal of Zoology*, *79*, 447-456.

Scott, G. P., Burn, D. M., Hansen, L. J., & Owen, R. E. (1989). *Estimates of bottlenose dolphin abundance in the Gulf of Mexico from regional aerial surveys* (Report to the National Marine Fisheries Service, Southeast Fisheries Center, CRD-88/89-07).

Scott, M. D., Wells, R. S., & Irvine, A. B. (1990a). A long-term study of bottlenose dolphins on the west coast of Florida. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 235-244). San Diego: Academic Press.

Scott, M. D., Wells, R. S., Irvine, A. B., & Mate, B. R. (1990b). Tagging and marking studies on small cetaceans. In S. Leatherwood & R. R. Reeves (Eds.), *The bottlenose dolphin* (pp. 489-514). San Diego: Academic Press.

Sellas, A. B., Wells, R. S., & Rosel, P. E. (In press). Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. *Conservation Genetics*.

Shane, S. H. (1980). Occurrence, movements, and distribution of bottlenose dolphin, *Tursiops truncatus*, in southern Texas. *Fishery Bulletin*, *78*(3), 593-601.

Shane, S. H., Wells, R. S., & Würsig, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: A review. *Marine Mammal Science*, *2*(1), 34-63.

Thompson, N. B. (1981). *Estimates of abundance of* Tursiops truncatus *in Tampa Bay, Florida* (Fishery Analysis Division Report). Miami: National Marine Fisheries Service – SEFL, Miami Laboratory. 14 pp.

Urian, K. W. (2002). *Community structure of bottlenose dolphins* (Tursiops truncatus) *in Tampa Bay, Florida, USA*. Master of Science thesis, University of North Carolina, Wilmington. 26 pp.

Urian, K. W., & Wells, R. S. (1996). *Bottlenose Dolphin Photo-identification Workshop: March 21-22, 1996, Charleston, South Carolina* (NOAA Technical Memorandum, NMFS-SEFSC-393). Washington, DC: U.S. Fish and Wildlife Services.

Urian, K. W., Duffield, D. A., Read, A. J., Wells, R. S., & Shell, E. D. (1996). Seasonality of reproduction in bottlenose dolphins, *Tursiops truncatus*. *Journal of Mammalogy*, *7*(2), 394-403.

Waples, D. M. (1995). *Activity budgets of free-ranging bottlenose dolphins* (Tursiops truncatus) *in Sarasota Bay, Florida*. Master of Science thesis, University of California at Santa Cruz. 61 pp.

Waring, G. T., Quintal, J. M., Swartz, S. L. (2000). *U.S. Atlantic and Gulf of Mexico marine mammal stock assessments – 2000* (NOAA Technical Memorandum NMFS-NE-162). Washington, DC: U.S. Fish and Wildlife Services. Available online: www.nefsc.noaa.gov/nefsc/publications/tm/tm162/. Downloaded 2 May 2006.

Wells, R. S. (1986). *Structural aspects of dolphin societies*. Ph.D. dissertation, University of California at Santa Cruz. 234 pp.

Wells, R. S. (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In K. Pryor & K. S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 199-225). Berkeley: University of California Press.

Wells, R. S. (1994). Determination of bottlenose dolphin stock discreteness: Application of a combined behavioral and genetic approach. In K. R. Wang, P. M. Payne, & V. G. Thayer (Compilers), *Coastal stock(s) of Atlantic bottlenose dolphin: Status review and management* (NOAA Technical Memorandum, NMFS-OPR-4). Proceedings and Recommendations from a Workshop held in Beaufort, NC, 13-14 September 1993. 120 pp.

Wells, R. S. (2003). Dolphin social complexity: Lessons from long-term study and life history. In F. B. M. de Waal & P. L. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 32-56). Cambridge, MA: Harvard University Press.

Wells, R. S., & Scott, M. D. (1990). Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. *Report of the International Whaling Commission*, (Special Issue 12), 407-415.

Wells, R. S., & Scott, M. D. (1999). Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). In S. H. Ridgway & R. Harrison (Eds.), *Handbook of marine mammals. Vol. 6*: *The second book of dolphins and porpoises* (pp. 137-182). San Diego: Academic Press.

Wells, R. S., Boness, D. J., & Rathbun, G. B. (1999). Behavior. In J. E. Reynolds, III & S. A. Rommel (Eds.), *Biology of marine mammals* (pp. 324-422). Washington, DC: Smithsonian Institution Press. 578 pp.

Wells, R. S., Duffield, D. A., & Hohn, A. A. (2001). *Reproductive success of free-ranging bottlenose dolphins: Experience and size make a difference*. 14th Biennial Conference on the Biology of Marine Mammals, Vancouver, BC.

Wells, R. S., Irvine, A. B., & Scott, M. D. (1980). The social ecology of inshore odontocetes. In L. M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp. 263-318). New York: John Wiley.

Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In H. H. Genoways (Ed.), *Current mammalogy* (pp. 247-305). New York and London: Plenum Press.

Wells, R. S., Bassos, M. K., Urian, K. W., Carr, W. J., & Scott, M. D. (1996a). *Low-level monitoring of bottlenose dolphins*, Tursiops truncatus, *in Charlotte Harbor, Florida 1990-1994* (NOAA Technical Memorandum, NMFS-SEFSC-384). Washington, DC: U.S. Fish and Wildlife Services.

Wells, R. S., Urian, K. W., Read, A. J., Bassos, M. K., Carr, W. J., & Scott, M. D. (1996b). Low-level monitoring of bottlenose dolphins, *Tursiops truncatus*, in Tampa Bay, Florida 1988-1993 (NOAA Technical Memorandum, NMFS-SEFSC-385). Washington, DC: U.S. Fish and Wildlife Services.

Wells, R. S., Bassos, M. K., Urian, K. W., Shane, S. H., Owen, E. C. G., Weiss, C. F., et al. (1997). *Low-level monitoring of bottlenose dolphins,* Tursiops truncatus*, in Pine Island Sound, Florida: 1996* (Contract Report to National Marine Fisheries Service, Southeast Fisheries Center, Contract No. 40-WCNF601958).

Würsig, B. (1978). Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine Bay. *Biological Bulletin*, *154*(2) 348-359.

Würsig, B., & Würsig, M. (1979). Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. *Fishery Bulletin*, *77*(2) 399-412.

Würsig, B., & Jefferson, T. A. (1990). Methods of photo-identification for small cetaceans. *Report of the International Whaling Commission*, (Special Issue 12), 43-52.