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Summer Movement Patterns of Bottlenose Dolphins in a Texas Bay

SPENCER K. LYNN AND BERND WÜRSIG

Radiotracking of 10 bottlenose dolphins (*Tursiops truncatus*), from 9 July 1992 to 13 Sep. 1992, was conducted in Matagorda Bay, Texas. The mean range size was 140 km² (SD = 90.7). Males and females had similar range sizes, though males visited the extremities of their ranges more frequently. Several generalities were observed: (1) dolphins were capable of traversing their range in several hours; (2) dolphins traveled widely on some days, whereas on other days, movement was very confined, within 1–2 km²; (3) dolphins tended to spend about 1–4 d in a particular portion of their range; (4) movement tended to be more confined at night than during daytime; and (5) dolphins tended to visit the extremes of their ranges only in the daytime. Individually, dolphins showed preferences for geographic regions within the bay; ranges overlapped strongly for some dolphins, yet only at range boundaries for others. Photoidentification surveys between May 1992 and June 1993 indicate that some individuals probably reside in Matagorda Bay for one or more years, whereas other individuals do not and can be found in other Texas bays. Limited ranging within the bay system and a lack of movement offshore may indicate that some of the dolphins are susceptible to localized anthropogenic and naturally occurring toxins. Examples of movement between bays, though few in the present data set, indicate that on the Texas coast, within-bay dolphin populations are probably not truly isolated.

In March and April 1992, 111 bottlenose dolphin (*Tursiops truncatus*) carcasses were recovered from the area between Matagorda and Aransas bays of the central Texas coast. This represented an unusually high mortality, compared with a mean of 14 (SD = 7.7, range = 5–23) carcass recoveries in this area during March–April calculated from the previous 5 yr (Texas Marine Mammal Stranding Network database, E. M. Haubold, pers. comm.). The die-off raised questions about dolphin movement patterns and site fidelity on the Texas coast and on the ability of potentially depleted local stocks to recover through immigration.

Consequently, to assess the impact of the spring 1992 die-off, a National Marine Fisheries Service-sponsored capture effort from 7–19 July 1992 resulted in collection of physiological information from 36 dolphins from Matagorda and Espiritu Santo bays, Texas (Fig. 1) (Sweeney, 1992). Thirty-five dolphins were freeze-branded with numbers on both sides of the upper dorsum, dorsal fin, or both (Sweeney, 1992), 10 were fitted with radio transmitters, and 27 of 36 dolphins received roto-tags in the dorsal fin (the exceptions were nine radio-tagged dolphins).

In previous studies on the Texas coast, bottlenose dolphins have shown fidelity to study sites during research lasting 6–35 mo (Shane, 1980; Gruber, 1981; Bräger et al., 1994; Fertl, 1994; Weller, 1998; Maze and Würsig, 1999),

and researchers have hypothesized that some Texas coastal dolphins may spend many years in the same general area, similar to those in Sarasota Bay, Florida (Wells, 1991). However, Texas coastal dolphins have also been shown to travel as far as 622 km between bays in similar time frames (Jones, 1991; B. Würsig, unpubl. data). Contrary to Gunter's (1942) claim, seasonal density changes have been found, near the mouths of Texas bays (Shane, 1980; Gruber, 1981; Jones, 1988; McHugh, 1989; Fertl, 1994; Weller, 1998), but nothing is yet known about the source of the arriving dolphins or the destination of those departing. Thousands of bottlenose dolphins can be found on the continental shelf, outside the bay systems (Mullin et al., 1990; Scott, 1990). It is not known whether inshore density changes reflect migration inshore between bays, coastally alongshore, or directly offshore, or whether the local dolphins may simply be congregating seasonally near the deepwater passes. It is also not known if the between-bay movement represents a separate population, following a different life history strategy, or if perhaps those dolphins are roving males in search of mating opportunities, for instance, within one coastal population. Clearly, little is yet known, and more data are needed to ascertain how the long-range movement exhibited by some dolphins interleaves with possible long-term residency to relatively small geographic ranges of other individuals along Texas shores.

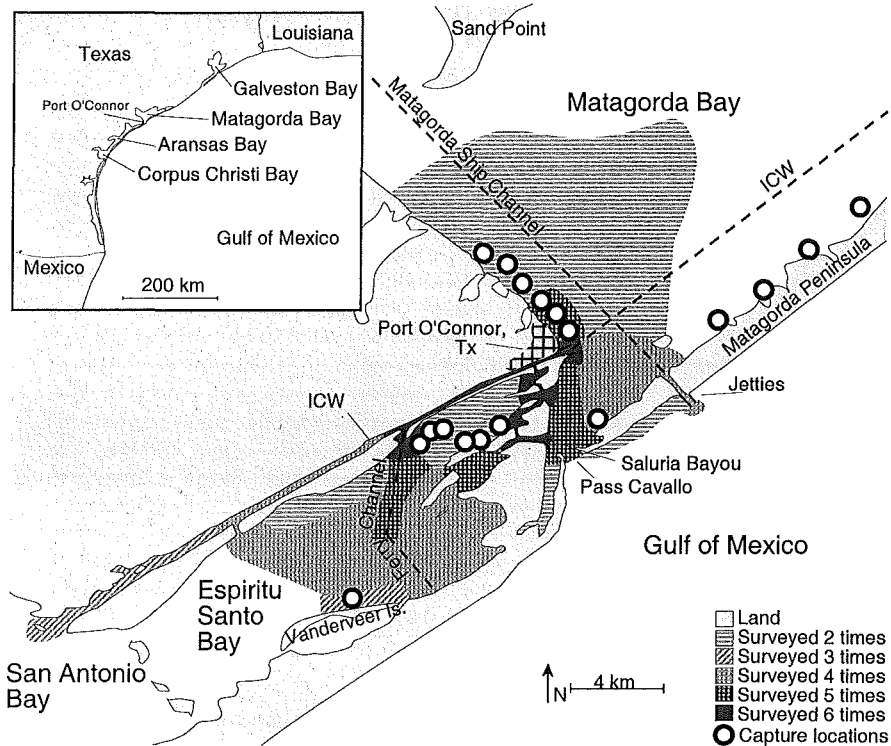


Fig. 1. Chart of the Port O'Connor area of Matagorda Bay, Texas, dolphin capture locations (Sweeney, 1992), and photographic survey effort, May 1992–June 1993. Surveys from July 1992–Sep. 1992 are excluded because they are biased for radiotracking. The May 1993 survey is excluded because it ended early because of rain. Shading indicates the number of surveys in which a region was visited out of a total of six surveys.

The primary objectives of the present study were to address these issues by gathering information on movements and site fidelity, via radiotracking and photographic surveys. Dolphins were radio-tracked from 9 July 1992 to 13 Sep. 1992. These data are supplemented with data from sightings of freeze-branded dolphins during photographic surveys between May 1992 and June 1993.

MATERIALS AND METHODS

Radio package specifications and mounting.—The radio transmitters (built by Telonics, Inc., Mesa, AZ) consisted of aluminum tubes 8.0-cm long and 1.6 cm in diameter, with a 0.1-cm thick and 39.0-cm long stainless steel antenna, topped by a 0.3-cm ball to prevent injury by the tip of the antenna (configuration MOD-050 transmitter package with TAGL antenna). Transmitters broadcasted in the frequency range of 148–150 MHz, at a pulse rate of 90/min, pulse duration of 400 msec, bandwidth of 16.2 Hz, and power output of approximately 10–20 mW. Power was provided by sealed lith-

ium batteries designed to last for approximately 6 wk.

The transmitters were attached to a rectangular 12.5-cm long, 4.0-cm high, and 0.12-cm thick aluminum plate rounded at the four corners and backed by 0.4-cm thick open-cell “wetsuit” neoprene. Transmitters were attached to both the aluminum–neoprene plate and the dolphin dorsal fin by two 0.64-cm diameter bolts fabricated from Teflon[®] rods. On the radio side, the Teflon[®] bolts were threaded with a stainless steel lock-tight nut. On the opposite side of the fin, the bolts were threaded with a fabricated magnesium alloy nut. The magnesium nuts were backed by 3.5-cm aluminum washers, also fitted with neoprene against the skin surface. Between the magnesium nut and the aluminum washer was a 3.5-cm steel washer to interact electrolytically with the magnesium and salt water. The magnesium nuts were designed to corrode to disappearance within about 4 wk in water 25–30 C and about 20–30 ppt salinity. The magnesium nuts were 2.6 cm in diameter and approximately 1.0–1.3-cm thick, with the rear nut slightly thin-

ner (by 0.1 cm) than the front nut, so that the front bolt would tend to hold the package a few hours longer than the rear bolt and not cause an adverse turning and increased drag of the radio package, likely if the rear bolt held longer.

The radio was mounted on the dorsal fin by the Teflon[®] bolt and aluminum–stainless-steel–magnesium nut assemblies. Two 0.60-cm bolt holes were punched through the fin with a standard stainless steel laboratory cork borer disinfected with Betadine[®]. Before hole punching, a veterinarian sterilized the site with alcohol, examined the chosen location for absence of major arteries with an 18-gauge needle, and administered a local anesthetic of 1.8 cc Lidocaine[®] (Sweeney, 1992). Slight bleeding occurred about one-half of the time and always stopped upon insertion of the tight-fitting Teflon[®] bolts. The bolts were custom-fit to each dorsal fin by snipping off excess bolt material with wire cutters. The magnesium alloy nuts were finger-tightened and then pressure-cripped with a Vice-grip[®].

Signal reception system.—Dolphin radio-transmitter signals were received with Telonics TR-2 handheld receivers and Telonics TS-1 handheld automatic frequency scanning receivers. These were used with antennas ranging from handheld “H” or two-element antennas ($\pm 20^\circ$ directional accuracy) to five-element Yagi-Uda antennas ($\pm 5^\circ$ directional accuracy) on aluminum poles up to 8-m high. Receiving systems were used from a 5.5- and 7-m outboard vessel, a pickup truck, several secondary land-based stations, and two five-element antennas on the second story balcony of a house in Port O’Connor, at the southern end of Matagorda Bay (28°27.05’N, 96°25.12’W). The total height of the two home-based antennas was approximately 14 m above sea level, and the approximate range of reception varied from 10 to 20 km. For aerial tracking, twin “H” antennas also were mounted on the wing struts of Cessna 172 and Piper Cub aircraft and on the footsteps of a Cessna 177. The usual range was at least 50 km from an altitude of 800–1,500 m. Details of tracking from stationary and mobile antenna arrays can be found in Mech (1983).

Data collection and analyses.—Radio-telemetered data included directional bearings taken on each dolphin every 4–6 hr for the life of the transmitter. Bearing entries included notes on signal quality (strength and signal-to-background noise), estimated distance and location (based on operator experience), environmen-

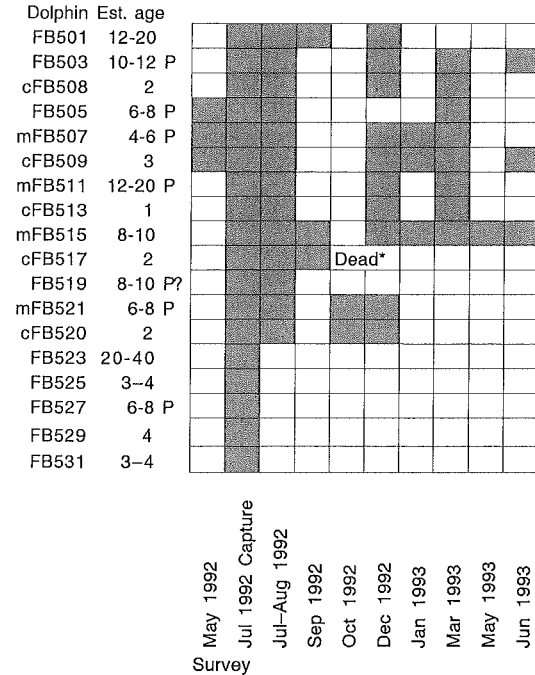
tal conditions, and a 30-min sample of surfacing intervals when signal quality allowed for reliable data. Bearings were often taken simultaneously from more than one location, allowing for triangulated positions. During daylight hours, one of the vessels often approached tagged animals by homing in on the signal. At such times, behavioral observations, photographs, and HI8 video recordings were made; exact positions, useful for comparisons with estimated and triangulated positions, were obtained. These sightings also allowed radio operators at remote locations to calibrate their distance and location estimates, and we believe the positional data presented here to be accurate to within 2 km.

Radio-track analysis consisted of plotting telemetered locations onto a map and visually inspecting for movement patterns, distances traveled, and geographic ranges (the area over which an individual moved in the course of the study). Ranges (Fig. 3) were plotted with Canvas[®] 3.5 for Macintosh[®] (Deneba, 1992) by drawing a continuous area covering all telemetered and visually sighted positions. Range sizes were calculated with Canvas’ “Calculate Area” command and were compared between males and females, pregnant and nonpregnant females, and females with calf and those without (Mann–Whitney U); and age and number of days tracked for each dolphin (regression).

To investigate potential differences in range use between males and females, we compared variance about the “mean position.” The mean horizontal and vertical x–y coordinate was determined for each radio-tagged dolphin. Horizontal and vertical deviations from the mean were calculated for each telemetered and visually sighted position for each animal and compared by a variance ratio F-test (Zar, 1984).

Photographic survey methods.—Meandering photoidentification surveys, designed to encounter as many dolphins as possible, were conducted from May 1992 through June 1993 in 5.5- and 7-m outboard vessels. Areas with particularly high survey effort were western Matagorda Bay, from Sand Point south to the Matagorda Ship Channel Jetties and west to eastern Espiritu Santo Bay, including Vanderveer Island and the Ferry Channel. This area also includes the Intra-Coastal Waterway (ICW) near Port O’Connor and Pass Cavallo (Fig. 1). Upon encountering a dolphin group, behavioral and environmental data were collected, and dorsal fin photographs were attempted for individual recognition of all animals in the group (Würsig

Females and mother-calf pairs



Males

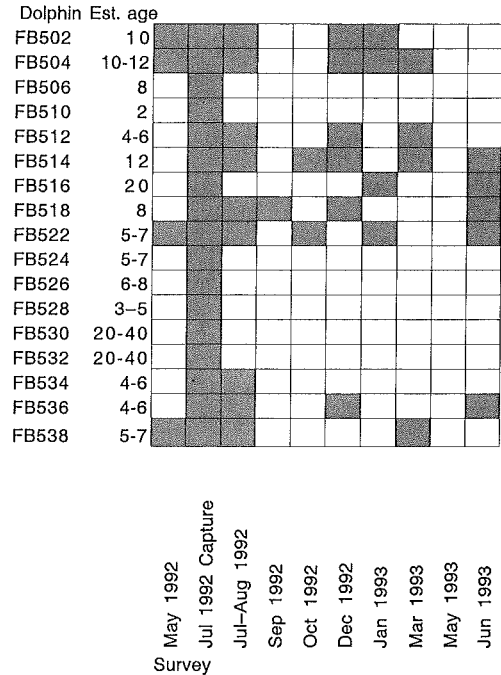


Fig. 2. Sightings of freeze-branded dolphins across surveys. "m" and "c" denote mother-calf pairs, "P" denotes a pregnant dolphin. Sex and length-based age estimates from Sweeney (1992). *FB517, calf of FB515, was found dead on 13 Sep. 1992. Necropsy showed that it died from an intestinal infarction unrelated to the study (TMMSN, 1992).

and Jefferson, 1990). Roto-tags, freeze-brands, and radio transmitters (and subsequent transmitter bolt hole marks) provided reliable means of photographic recognition for those 36 dolphins that had been captured in July 1992. Sighting locations of individuals were plotted on charts of the area and examined for range patterns and site fidelity.

RESULTS

Thirty-five dolphins were captured and marked (Figs. 1, 2). Based on observations at capture and resightings, five mother-calf pairs were caught. Six (possibly seven) pregnant females were estimated to be in their first trimester, based on ultrasound analysis (Sweeney, 1992). Five males and five females were radio-tracked (Table 1). The radio-tagged dolphins had partially to almost completely overlapping ranges. The mean range size was 140 ± 90.7 (SD) km^2 (Table 1). Radio-tagged dolphins ranged no more than ca. 17 km from Port O'Connor in all but three cases (Fig. 3a-c). The exceptions were FB501, adult female (Fig. 3a), FB502, adult male (Fig. 3a), and FB504, adult male (Fig. 3b). Dolphins FB504 and

FB502 spent most of their time near Port O'Connor and not far from their capture sites but traversed 20–35 km southwest into western Espiritu Santo Bay and San Antonio Bay on 4 of 21 d and 5–11 of 39 d, respectively. (On 5 of the 11 d, we located FB502 in western Espiritu Santo Bay–San Antonio Bay; on the remaining 6 d, we could not locate him in the Port O'Connor area, and we assume that he was in the western Espiritu Santo Bay–San Antonio Bay area, out of receiver range, but we did not search there.) FB501, however, spent about one-half of her time (18–45 of 59 d) in San Antonio Bay, often close to the Aransas National Wildlife Refuge (ANWR). She traveled rapidly between sites on at least three occasions and spent time either at the northeastern (near Port O'Connor) or at the southwestern (near ANWR) portion of her range. On one occasion, she traveled overnight at least 55 km in 12 hr, at an average speed of 4.2 km/hr. The other seven dolphins showed more confined ranges, traveling within a usual radius of about 12 km from Port O'Connor (Fig. 3b,c).

No differences were found in range size by age, sex, or reproductive condition. A regres-

TABLE 1. Summary of radiotracking effort for dolphins in Matagorda Bay, Texas, 9 July–13 Sep. 1992 (sex and length-based age estimates from Sweeney, 1992).

Radio	Freeze-brand	Date mounted	Date of last regular signal	Useful life span (d)	#Positions obtained	Area of range (km ²)	Sex	Age (yr)
1	502	9 July 1992	16 Aug. 1992	39	144	235	M	10
2	504	9 July 1992	29 July 1992	21	120	100	M	10–12
3	501	10 July 1992	6 Sep. 1992	59	76	329	F	12–20
4	505	11 July 1992	23 July 1992	13	64	191	F	6–8
5	511	12 July 1992	1 Aug. 1992	21	102	92	F	12–20
6	515	14 July 1992	3 Aug. 1992	21	84	88	F	8–10
7	514	14 July 1992	1 Aug. 1992	19	98	61	M	12
8	518	15 July 1992	13 Sep. 1992	61	225	180	M	8
9	521	15 July 1992	9 Aug. 1992	27	125	49	F	6–8
10	522	17 July 1992	11 Aug. 1992	26	116	77	M	5–7
				Mean	30.7	115		
				SD	16.85	45.5		
						140		
						90.7		

sion of range size on number of days tracked showed a moderate linear correlation ($P = 0.02$, $R^2 = 0.53$, $n = 10$), indicating that range estimates for some individuals might have benefited from further tracking. However, range sizes did not change appreciably for most dolphins past the first week of data collection. In addition, from subsequent photosurveys described later, we believe that the duration of the radio-tracking effort was sufficient to describe the ranges of most of the radio-tagged dolphins during the study period.

On only three occasions did we obtain evidence of radio-tagged dolphins leaving the confines of the bay system to swim in the open Gulf of Mexico. All three positions were within 1 km offshore of Pass Cavallo, based on signal strength and bearing. FB518 (approximately 8-yr-old male) [age estimated from length (Sweeney, 1992)] was positioned offshore on 20 July 1992 and FB522 (approximately 5- to 7-yr-old male) on 23 July and 29 July 1992. On 29 July, FB522 may have been offshore for 6–7 hr, based on the inability to detect a signal following his initial offshore positioning. Because of errors inherent in positioning dolphins by triangulation and the changing influences of habitat structure and climate on signal strength (Mech, 1983), movement offshore could in reality have occurred somewhat more or less often.

Males were found in the extremities of their ranges more often than females (for horizontal and vertical coordinates $P < 0.0001$, $n = 863$ male positions, $n = 455$ female positions, variance ratio F-test). FB501 was excluded from this analysis because her “dual home range” movement pattern differed from that of the other radio-tagged dolphins (see subsequent-

ly). Similar results for random equal subsamples of male and female positions indicate that the higher male variance is not simply because of larger sample sizes. No differences in geographic distribution were found for pregnancy, with-calf, or age class, perhaps because of small sample sizes. No differences in geographic distribution were found for group size class, behavior, or time of day. That is, mother-calf pairs or feeding dolphins, etc., were not found in particular, different, areas of the study site.

Diurnality and week-by-week movement patterns were similar within and among most dolphins throughout the study. The basic patterns were exemplified by FB518, an approximately 8-yr-old male tracked for 61 d. He ranged between the southwest portion of Matagorda Bay, from Sand Point to Pass Cavallo, and the northeast of Espiritu Santo Bay (Fig. 3c). He was never tracked beyond 13 km from Port O'Connor and ranged within an area approximately 10 km in radius, centered at Port O'Connor. There was no strong shift in movement pattern by time of day (Fig. 4), and he showed no overall change in movement pattern throughout his 60-d tracking period (Fig. 5).

FB518 illustrates several general movement patterns seen in the radio-tracked individuals. (1) Dolphins were capable of, and often did, traverse their range in several hours. (2) A dolphin traveled widely on some days, perhaps crossing its range, whereas on other days, movement was very confined, within 1–2 km². This wide-ranging vs confined movement did not appear to have a regular temporal cycle. Nor was confined movement specific to a particular part of a dolphin's range or relative to a habitat characteristic (e.g., depth, distance

from shore). (3) Dolphins tended to spend about 1–4 d in a particular portion of their range. (4) Movement tended to be more confined at night than during daytime. (5) Dolphins tended to visit the extremes of their ranges only in the daytime. The assertions of (4) and (5) may be slightly biased as a result of less sampling effort at night, with fewer triangulations than during the day and no visual sightings. Nevertheless, we believe the overall pattern to be correct.

The ranging of FB501 differed from the patterns illustrated by FB518 because FB501 apparently had two main areas of habitat use (near Port O'Connor and ANWR, respectively) and traveled rapidly through the intervening ~30 km. While within one particular area, her movement patterns were similar to those of the other radio-tagged dolphins.

Nine photographic surveys were conducted between May 1992 and June 1993 (Table 2). Seven dolphins captured in June 1992 had been photoidentified the previous May. Survey effort was not geographically uniform (Fig. 1), but dolphins were found in all surveyed regions of the bay. Among noncalves, females and males did not differ in number of sightings (t-test) nor was number of sightings linearly dependent on age (regression). After 12–14 mo, freeze-brands became difficult to read on most adult dolphins; the calves' freeze-brands began fading 3–4 mo earlier.

Excluding the five known calves, whose sightings were not independent of sightings of their mothers, and FB519 and FB534, who were only resighted in the July–Aug. survey directly after the capture, 16 dolphins were resighted in from three to seven (of nine) surveys (Fig. 2). No well-defined seasonal pattern in individual freeze-branded dolphin's resightings was apparent.

Several animals stand out (Fig. 2, FB523–FB532, five males and five females). None of them was resighted in the year since they were captured and freeze-branded in July 1992. All were captured at the extreme northeast end of

the study area, 5.5–20 km northeast of the Matagorda Ship Channel Jetties on Matagorda Peninsula (the three northeast-most capture locations). Surveys in the year after the captures did not include that northeast section (Fig. 1). However, an amateur's sighting record from Nov. 1992 and sightings from July and Aug. 1993 surveys imply that FB530 periodically visited Saluria Bayou, an area we surveyed consistently. Data from Aug. 1993 and Nov. 1993 also contain sightings along Matagorda Peninsula of FB524 and FB528, respectively. These sporadic sightings indicate that dolphins FB523–FB532 may frequent Matagorda Bay but further northeast than we usually surveyed.

Evidence from resightings indicates interseasonal occurrence in the Matagorda–Espiritu Santo Bay areas for some dolphins: excluding calves and the 10 dolphins captured in the northeast, 12 dolphins were seen in three to four seasons, 4 in two seasons, and 4 in one season over the 13-mo study (Table 2 indicates seasons). We believe that at least some of the marked dolphins were resident to the area throughout the yearlong study.

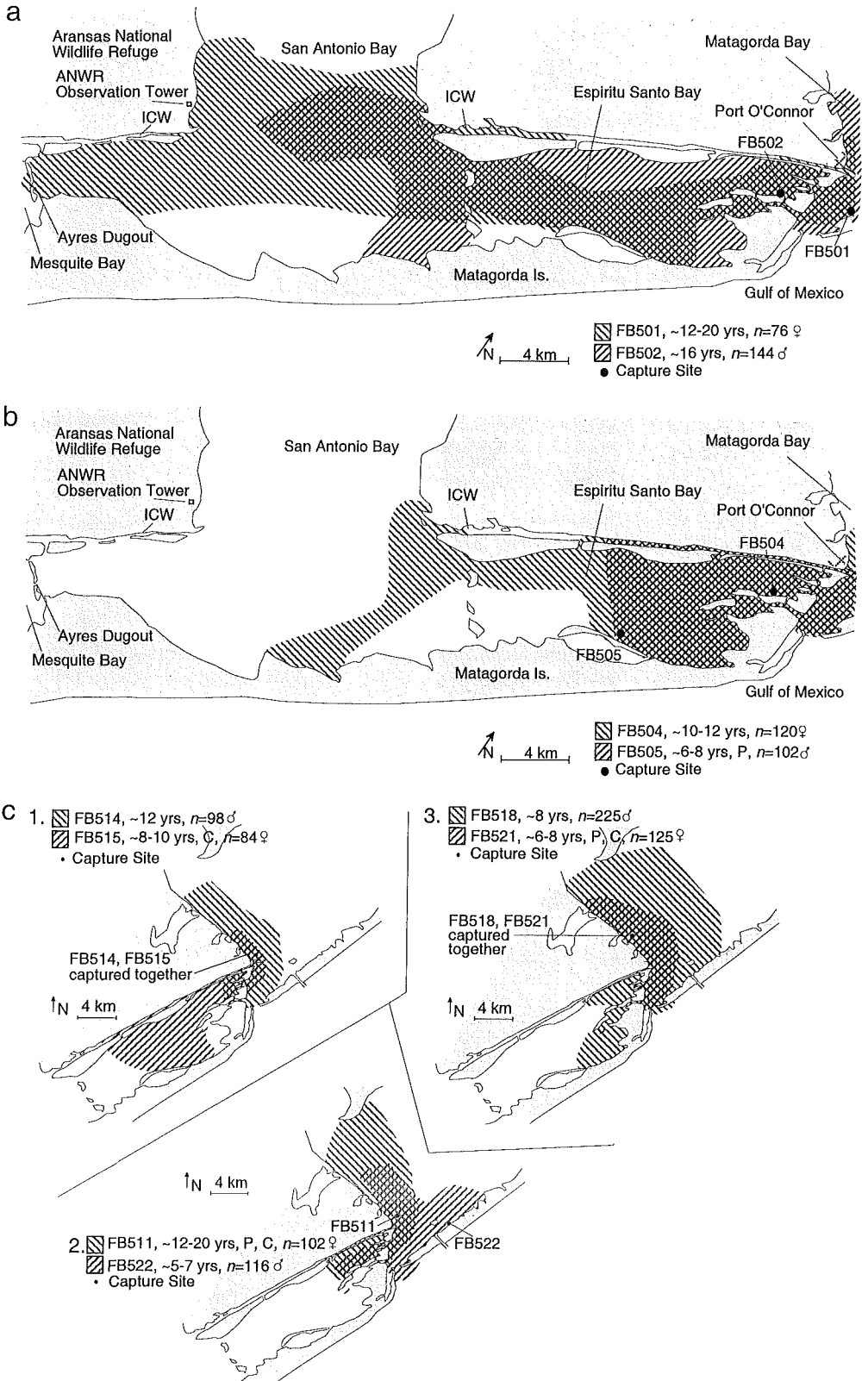
DISCUSSION

Radio transmitter life spans of 13–61 d made possible an analysis of individual ranges of 10 bottlenose dolphins in a warm temperate inshore ecosystem. Ranges overlapped strongly for all 10 of the radio-tagged dolphins and most of the 25 other freeze-branded dolphins, except for the 10 individuals caught in the extreme northeast of the study area. The latter 10 individuals apparently did not frequent the Port O'Connor area or eastern Espiritu Santo Bay. Short-term movement patterns (days to weeks) may be driven by resource distributions, such as prey density or mating opportunities. More confined movement at night may indicate rest. Nighttime rest was also indicated by radio-telemetered surfacing data (Lynn, 1995; Würsig and Lynn, 1996).

Whereas reports of residency of bottlenose

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Fig. 3. (a) Summary ranges (accurate to 2 km) for radio-tagged dolphins FB501 and FB502, from radio telemetry and sightings, May 1992–June 1993, with information on age and sex. "n" refers to the number of positions used to determine the ranges. (b) Summary ranges (accurate to 2 km) for radio-tagged dolphins FB504 and FB505, from radiotelemetry and sightings, May 1992–June 1993, with information on age and sex. "P" denotes a pregnant dolphin. "n" refers to the number of positions used to determine the ranges. (c) Summary ranges (accurate to 2 km) for radio-tagged dolphins FB514 and FB515 (1), FB511 and FB522 (2), and FB518 and FB521 (3), from radiotelemetry and sightings, May 1992–June 1993, with information on age and sex. "P" denotes a pregnant dolphin, "C" denotes "with calf." "n" refers to the number of positions used to determine the ranges.



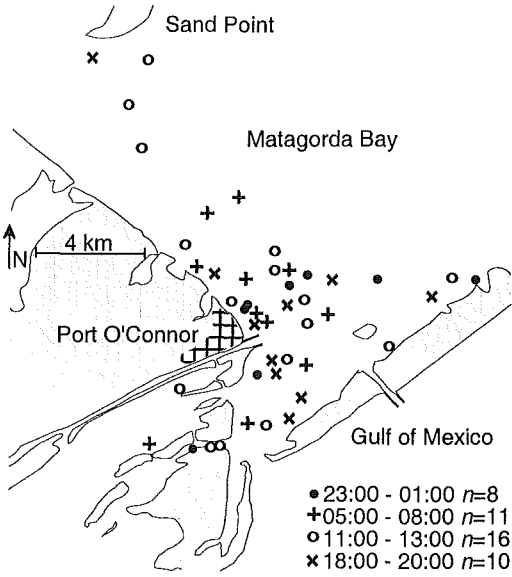


Fig. 4. Positions of FB518 by time of day, 15 June 1992–13 Sep. 1992, from radiotelemetry and sightings.

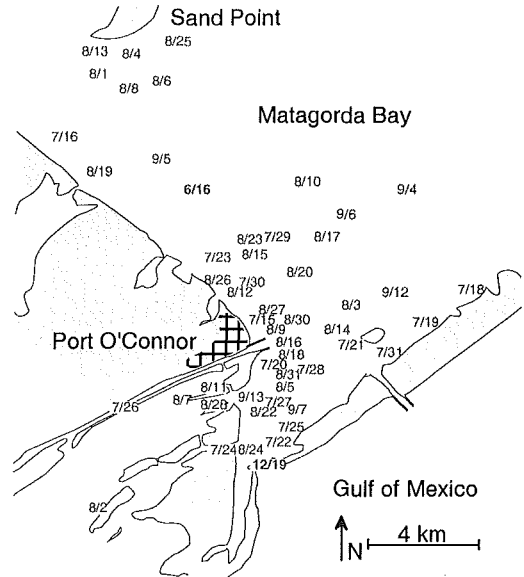


Fig. 5. Approximate noon positions ($n = 53$) for dolphin FB518, 15 June 1992–13 Sep. 1992, from radiotracking and sightings (two subsequent sightings in boldface).

dolphins are ubiquitous in the literature, measurements of geographic area commonly used by individuals are more rare. Researchers at two study sites have provided estimates of bottlenose dolphin ranges. On the Californian coast, individual dolphins commonly range over ≥ 50 –483 km of coastline in a 0.5-km-wide strip (Defran et al., 1999). On the Florida Gulf coast, the population is hypothesized to be structured into geographically adjacent “communities,” with some social mixing and geographic overlap (see summaries in Scott et al.,

1990; Wells, 1991). The Sarasota Bay area community consists of approximately 100 individuals, ranging over 100 km² to about 1 km offshore (Wells, 1991). Individuals in different age and sex classes have different sized “core use areas,” which seem to be on the order of 50–100 km² (Wells, 1991; Reynolds et al. 2000).

In the present study, the 10 radio-tagged dolphins had two distinct range areas (Fig. 3). This is consistent with Gruber’s (1981:52) hypothesized “extended herd home ranges” with

TABLE 2. Summary of photographic survey effort for dolphins in Matagorda Bay, Texas, 14 May 1992–18 June 1993.

Survey	Season ^a	Dates	Total# photos	#Dolphins seen	#Freeze-brands seen	#Hours on water	#Hours with dolphins	Mean group size	SD	n	ER ^b
1	SP	14–19 May 1992	792	230	8 ^c	41.9	14.0	3.9	3.32	58	5.5
2 ^d	SU	6 July–30 Aug. 1992	2,196	1,180	106	800	60.7	3.3	2.71	368	
3 ^d	FA	4–6 and 11–12 Sep. 1992	180	67	2	30.3	4.5	2.6	2.37	26	
4	FA	24–25 Oct. 1992	108	154	3	20.4	9.7	3.9	3.33	39	7.5
5	WI	19–21 Dec. 1992	324	210	13	19.8	13.3	4.0	3.56	52	10.6
6	WI	12–13 Jan. 1993	216	98	7	16.1	9.1	3.0	1.76	33	6.1
7	SP	19–21 March 1993	468	176	10	27.4	15.3	3.1	2.65	57	6.4
8 ^c	SP	24–25 May 1993	36	10	1	1.5	0.9	2.0	0.70	5	
9	SU	15–18 June 1993	252	111	8	25.7	8.9	4.4	3.79	25	4.3
Overall			4,572	2,236	158	983.1	136.4	3.5	2.86	648	6.5

^a Seasons defined following previous Texas coast studies (Shane, 1977; Gruber, 1981). SP, spring; SU, summer; FA, fall; WI, winter.

^b ER = encounter rate, #dolphins seen/#hours on water.

^c Eight photoidentifications (based on natural markings) of dolphins, which were captured and freeze-branded the following July.

^d Survey effort biased by radiotracking.

^e Ended early because of rain.

shared borders in the Port O'Connor area and suggests a consistency of habitat use and population substructure over a >12-yr period. For example, FB515 stayed mainly in the northeast section of Espiritu Santo Bay and FB514 in an adjoining area in southwest Matagorda Bay (Fig. 3c). Both were originally captured together in the small overlapping area. Ranges for FB518, FB521, FB511, and FB522 all overlap strongly. These dolphins were caught together (FB518, FB521) or in areas only 4 km apart (FB511, FB522). A third "extended herd home range" to the northwest along Matagorda Peninsula is suggested by the lack of resightings of 10 of the 11 individuals captured there. These 10 were not seen in the following year, perhaps because of a lack of effort northwest of our primary study area; data from later surveys indicate that at least some of them may have been present in the subsequent year. The 11th dolphin, FB522 (radiotag #10), seldom frequented that area in the remainder of his radio's life span. The hypothesized "extended herd home range" boundaries in this study correspond well with those of Gruber (1981).

Bottlenose dolphins in Matagorda Bay show intriguing parallels to the Sarasota Bay community, described by Wells (1991). The mean 140 ± 90.7 (SD) km² range size for individuals in the present study is similar to ranges in the Sarasota area. The Sarasota community is composed, in part, of several "bands" of females and their calves. In the Matagorda Bay area, evidence of several "extended herd home ranges" within at least 312 km², overlapping near Port O'Connor, might correspond to the adjacent communities hypothesized to reside along the Florida west coast (our study site is about three times larger than the Sarasota study site), to the female bands seen within the Sarasota dolphin community, or to an as yet undescribed pattern for bottlenose dolphins. Dolphin movement ranges in Matagorda, as revealed by radiotracking, appeared very similar to early radiotracking results in Sarasota Bay (Irvine et al., 1981). In both studies, individual dolphins used separate but somewhat overlapping regions of the bays, and individual ranges were on the order of 100 km². The radio-tracked ranges in Irvine et al. (1981) for Sarasota Bay corresponded generally to what, with more data, came to be recognized as female band ranges, described by Wells (1991) for the same area.

There was a greater geographic spread of male dolphin sightings (variance ratio F-test). If capture and sampling biases were small between the sexes, this pattern might have arisen

from one of two different behavioral traits: (1) males have larger ranges than females (not supported statistically) or (2) range sizes are similar for both sexes, but males visit more of their range more frequently and are therefore more likely to be found in a wider distribution. Male dolphins in Sarasota Bay have shown both traits (Wells et al., 1987; Wells, 1991). The "resident male pattern" was typified by lone males associating frequently with females and remaining in the relatively limited area within which females ranged. The "roving male pattern" was characterized by males who roamed throughout the community home range. The "resident males" were seen with reproductively receptive females more than the "roving males" (Wells et al., 1987). Range size and dolphin movement patterns have been hypothesized to be dependent upon reproductive or forage resources (or both) (Scott et al., 1990; Weller, 1991; Ballance, 1992). It is possible that these patterns have to do with sexual maturity and obtaining mating opportunities by polygamous males.

The radio-tagged dolphins of the present study were observed to leave the bay system only very infrequently (e.g., to feed in Gulf of Mexico waters). This is an important finding; if a large proportion of inshore dolphins remains in bay systems, these dolphins are potentially susceptible to localized anthropogenic and naturally occurring toxins. This susceptibility is compounded by the limited ranging displayed by some dolphins; however, the short seasonal duration of our radiotracking highlights the need for additional study. Shane (1977), Gruber (1981), and McHugh (1989) also reported very limited movement in either direction through passes linking Texas bays with the Gulf of Mexico. However, Maze and Würsig (1999) found a strong seasonal movement pattern of photographically identified individuals through San Luis Pass, 130 km north of our study site. The ca. 30 dolphins that were consistently sighted by Maze and Würsig in the Chocolate Bay-San Luis Pass area at the southwest end of Galveston Island were typically found on the Gulf side of the pass in winter (sometimes more than 3 km offshore) and in Chocolate Bay in warmer months. Maze and Würsig (1999) hypothesized that the dolphins were moving in response to temperature-dependent seasonal changes in prey densities. Dolphins in the Indian-Banana River system on the Florida east coast showed no movement offshore in surveys conducted between Aug. 1979 and Oct. 1981 (Odell and Asper, 1990).

Encounter rates (#dolphins seen/#hours on

water, Table 2) indicated an autumn increase in the number of dolphins in the Port O'Connor area. Gruber (1981), in the Port O'Connor area, and Shane (1980), McHugh (1989), and Weller (1998), in the Aransas Pass area 100-km south, found fall–winter increases and spring–summer decreases in dolphin numbers. In the Galveston area, 200-km north of Matagorda, Jones (1988) found higher summer–fall numbers. These changing abundances may be attributable to low-level, short-range migratory movements to warmer waters (Jones, 1988) or perhaps simply to a local (near–study site) reaction to changing prey densities (Gruber, 1981). Weller (1998) suggested a seasonal migration, northward in spring–summer and southward in fall–winter.

Bottlenose dolphin stocks on Texas shores.—Dolphins in and near Texas bay systems exhibit two residency patterns: long- and short-term site fidelity. There are some individual dolphins of long-term (multiseason, multiyear) in-bay residency (Fertl, 1994; Weller, 1998). Resident dolphins of Chocolate Bay travel frequently into the Gulf and relocate there during winter (Maze and Würsig, 1999), but such use of Gulf waters cannot be generalized to resident dolphins of other bay systems. Consistently across studies, some individuals (ca. 10–30) inhabit study areas from months to at least several years (e.g., Fertl, 1994; Maze and Würsig, 1999), whereas the majority of individuals (>1,000 in some studies) are sighted once or on a few consecutive days but are not present on subsequent surveys in the following months and years (e.g., Bräger et al., 1994; Weller, 1998). There are apparently 1–2 orders of magnitude more transient dolphins than resident dolphins.

All Texas bay systems studied have shown seasonal density changes. However, in most studies, the density estimates are based on encounter rates with dolphins during *photoidentification* surveys. On the Texas coast, dolphins are attracted to shrimp-fishing boats. In an attempt to maximize the number of dolphins photographically identified, researchers often seek out shrimp boats preferentially to surveying an area randomly or systematically. The shrimp fishery is somewhat seasonal and inconsistent within and among bays, with both inshore and offshore shrimping. Density estimates reported in many studies are thus biased, and the bias cannot be known unless the following of shrimp boats is somehow quantified. Shane (1980), Gruber (1981), and Maze (1997) are exceptional in utilizing transect

methods to obtain density estimates (in addition to separate surveys for photoidentification). Shane (1980) found a winter increase in dolphin numbers within Lydia Ann Channel, in the Corpus Christi Bay area. Gruber (1981) found fall–winter increases in dolphin numbers within Matagorda Bay near Port O'Connor. Neither Shane nor Gruber performed transects offshore in the Gulf. Though Maze (1997) found seasonal movements between subareas of her study site (inshore and offshore), she found no density changes for the study site as a whole. Additionally, because the dolphins were known to Maze individually, we know that it was the same individual dolphins being counted offshore in winter and inshore in summer that, in part, caused the subarea density changes. Overlaid on this seasonal movement of individuals is a long-shore movement of transient dolphins passing through the study site, consistent in number across seasons (Maze, 1997). Maze's work shows that the density changes suggested in other studies can be caused by movement of individuals within a local area, as hypothesized by Gruber (1981) and Jones (1988). However, Weller (1998), citing encounter-rate density estimates in part, detected a pattern suggestive of seasonal migration up and down the Texas coast. A third alternative is that Gulf coastal dolphins are moving closer to shore from the continental shelf. In their discussion, Maze and Würsig (1999) link such seasonal changes in habitat use to shifting prey availability.

All coastal bottlenose dolphin studies that have used some form of individual identification have shown resightings of individual dolphins (e.g., Würsig and Würsig, 1977; Shane et al., 1986). Across studies, there is variation in resighting rate, which seems to correlate with range size where such information is available (e.g., Weller, 1991; Wells, 1991; present study). In Texas, resightings for a few well-known individuals have spanned 5 yr [Galveston Ship Channel, Fertl (1994)], 11 yr [Chocolate Bay, southwest Galveston Bay, Irwin-Smith and Würsig (in prep.)], and 15 yr [Aransas Pass, Weller (1998), L. Price-May (pers. comm.)]. With other studies, our results indicate that long-term site fidelity is a habit of some within-bay bottlenose dolphins on the Texas coast. However, 15 of 31 (48%) noncalves captured in the present study were seen only in summer 1992. Although we believe that a few of those dolphins may have been resident in northeastern Matagorda Bay, others may indeed be infrequent visitors.

A corresponding attribute to short-term site

fidelity may be long-range movement. FB523 (not seen in the present study site since captured) was photographically documented in Galveston waters in May 1994 (190 km north), and a freeze-branded (number unknown) dolphin was reported at the Corpus Christi Ship Channel jetties (100 km south) in Nov. 1992. Other evidence of long-distance movements along Texas comes from several sources. Gruber (1981) describes a Matagorda Bay sighting of a dolphin originally identified by Shane (1977) in the Corpus Christi area. Jones (1991) describes two dolphins that were resighted at Gulf inlets 517 and 622 km from where they were initially identified. Jones (1991) found that 11 of 146 identified dolphins occurred at two or more inlets, and all but the above two long-distance movements were of distances <300 km. Our May 1992 and May 1993 Matagorda Bay surveys yielded identifications of two dolphins that had been previously photoidentified in the South Padre Island area, 285 km south.

The handful of examples of travel between Texas bays, in spite of the low-level monitoring effort that produced the observations, suggests to us that transient dolphins are moving along the coast, as in California, but dolphins might also move directly offshore, on and off the continental shelf. Dolphin abundances are higher near the dredged deepwater passes from Texas bays into the Gulf and along Gulf coastlines than within bays (Mullin et al., 1990). It is near these bay inlets, rather than within the bays proper, where short-term residents are most frequently encountered. Other survey data (Würsig, unpubl.) show that the inshore waterways (i.e., the 3-m-dredged Intracoastal Waterway that runs unbroken from Mexico to Florida and natural shallow connections between bays) connecting Gulf bays are rarely, if ever, used by dolphins for long-distance between bay travel. A long-term satellite tag study of dolphins captured offshore would shed light on movements of these transient dolphins.

The presence of between-bay travel and offshore movement suggests to us that the regional, within-bay, dolphin populations are not truly isolated. Maze (1997) found that resident bay animals were with offshore groups of transients when these bay animals were themselves offshore. We can therefore presume that residents and transients socialize in some manner. It remains unknown to what extent transients might interbreed or compete with residents. Though a resident-transient distinction seems to describe Texas dolphins, few details are known. For reasons outlined above, we pre-

sume that the two strategies do not reflect two separate genetic populations [though that is the case for killer whales (*Orcinus orca*) in the waters of the Pacific northwest coast (Baird, 2000)]. However, the distinction could reflect a cultural strategy, transmitted from mothers to calves (Rendell and Whitehead, 2001). Individuals might change strategies; we do not know how long resident dolphins are actually resident in bays.

With respect to mass mortalities, the Matagorda Bay dolphin population seems to be physically healthy (Sweeney, 1992) and numerically robust, occupying all surveyed regions of the bay. The resident dolphins are probably susceptible to local anthropogenic and naturally occurring toxins (Irwin-Smith and Würsig, in prep.). Post-1992 die-off population size appears not to have changed from Gruber's (1981) earlier estimate (Lynn, 1995; Würsig and Lynn, 1996). Travel between Texas bays and transient sightings inshore (Maze and Würsig, 1999) suggest to us that an individual Texas bay ecosystem could recover numerically from localized dolphin mortalities. However, these conclusions must be considered tentative. Despite the indicated nonisolated nature of the population, nothing is yet known about interactions between the apparently resident dolphins and the visitors, and it is not known if the dolphins that died in spring 1992 were resident. If the resident dolphins seldom mate with visitors, loss of all or most residents in an area could have significant impact on the genetic (and perhaps cultural) makeup of dolphins in the area.

Differences in range size, residency, and population size should be attributable to carrying capacity of the habitat. Several authors make this point for bottlenose dolphins but with scarce information on prey abundance and other habitat needs (e.g., Weller, 1991, 1998; Ballance, 1992). More thorough evaluations of habitat productivity, including primary productivity and prey availability patterns, are needed. The Texas coast, spanning 2.5° latitude, with its unique cycling of tropical and temperate conditions and sparse coastal beaches punctuated by productive estuaries, provides for an interesting, yet little understood, blend of bottlenose dolphin life history patterns.

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