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DIVING BEHAVIOR AND AT-SEA MOVEMENTS OF AN ATLANTIC SPOTTED DOLPHIN IN THE GULF OF MEXICO

Atlantic spotted dolphins (Stenella frontalis) are common in the Gulf of Mexico and typically inhabit shallow waters on the continental shelf within the 250-m isobath (Mullin et al. 1994, Perrin et al. 1994, Davis and Fargion 1996). Although they are similar to bottlenose dolphins in their preference for shallow-water habitats, Atlantic spotted dolphins are less common in near-shore waters. Despite their abundance and proximity to coastal regions in the Gulf of Mexico and along the Atlantic coast of the eastern United States, little is known of their life history, seasonal movements, or diving behavior.

The development of small satellite-linked time-depth recorders (SLTDRs) and recent advances in the design of dorsal fin saddles have enabled researchers to study the diving behavior and at-sea movements of small cetaceans (Jennings 1982, Tanaka 1987, Mate 1989, Mate et al. 1995, Scott et al. 1990b).

This technology has also provided information on habitat use and the distribution of marine mammals near distinctive oceanographic features such as eddies and seamounts (Tanaka 1987, Mate 1989, Merrick et al. 1994). We report here the diving behavior and daily movements of a rehabilitated Atlantic spotted dolphin that was tracked in the northwestern Gulf of Mexico for 24 d. This is the first time that this species has been monitored at sea using satellite telemetry.

An adult male Atlantic spotted dolphin stranded on Galveston Island, Texas (29°17′N, 94°50′W) on 10 February 1995. The animal (Identification No. GA678) was recovered by the Texas Marine Mammal Stranding Network and brought to the Fort Crockett research complex jointly operated by Texas A&M University at Galveston and the National Marine Fisheries Service. A vinyl pool (7 m in diameter, 1.5 m deep) was used to house the dolphin during its rehabilitation. By early March the animal was eating 10 kg of fish daily, exhibited normal blood chemistry and hematological values, and was deemed healthy enough to be released. On the day of release (17 March), the animal weighed 127 kg, which was within the normal range for this species (Perrin et al. 1994). The dolphin was released from a ship 16 km southeast of Freeport, Texas (28.79°N, 95.16°W) near the 20-m isobath.

We used the Service Argos satellite system to track the movements of the dolphin and receive data on diving behavior (for a detailed description of the Argos system see Mate 1989, Mate et al. 1992, Stewart et al. 1989). The satellite receivers pick up signals from Argos transmitters (termed Platform Transmitter Terminals or PTTs). A minimum of two messages must be received by the satellite during a pass for a location to be calculated. Service Argos uses the following classification to rank locations according to their accuracy. Class 2 (LC 2) locations are based on five contacts and have a predicted accuracy of 350 m. Class 1 (LC 1) locations are based on four contacts and are accurate to 1 km. Class 0 (LC 0) and Class A (LC A) locations are based on three contacts and Class B (LC B) on two contacts during a pass; Service Argos provides no predictions for the accuracy of the latter three categories. Location Class Z (LC Z) is considered unreliable and was not used in this study.

We used a Type 3 satellite-linked time-depth recorder (SLTDR) manufactured by Wildlife Computers (Woodinville, WA). The SLTDR (11 × 9 × 2.5 cm) consisted of a resin-encased PTT, electronics that monitored and stored data on diving behavior, a pressure transducer, batteries, and a 10-cm flexible antenna. The depth range for the SLTDR was 0–470 m, with a resolution of 2 m. The instrument was programmed so that the minimum depth to be considered a dive was 4 m, and the maximum depth to accumulate "at surface time" was 2 m. Data on maximum dive depths, dive durations, and the amount of time that the animal spent at certain depths were collected and encoded into histograms with programmable ranges of depth and time. The transmit buffer stored 24 hours of data in 6-h histogram periods that corresponded to night (2100–0259 CST), dawn (0300–0859 CST), day (0900–1459 CST) and dusk (1500–2059 CST). In order to prolong battery life, the



Figure 1. The TracPac[®] saddle containing the SLTDR and VHF transmitter mounted on the dorsal fin.

SLTDR was programmed to transmit a message only when at the surface. We also attached a small (8 cm long \times 1.6 cm in diameter; 39-cm flexible antenna) VHF transmitter (Model 050, Telonics, Inc., Mesa, Arizona) to the saddle for conventional radio tracking. The transmitter broadcast at 149.620 MHz at a pulse rate of 144/min and a power output of 10–20 mw.

The saddle (Fig. 1) was custom fabricated for the dolphin by Trac Pac[®] Inc. (Fort Walton Beach, Florida). A cast of the dorsal fin was made using quick setting, plaster-impregnated gauze. A positive model was then made of the cast using molding plaster. The saddle was vacuum formed from polyethylene thermoplastic using standard vacuum-forming techniques. The inside of the saddle was lined with neoprene rubber to prevent skin abrasion. The completed saddle measured 11.8 cm tall, 25.3 cm long, and 4.6 cm wide. Molded compartments along the sides held the SLTDR and VHF radio. The saddle with telemeters weighed 625 g in air and was positively buoyant.

On the day of release the dolphin was removed from the pool in a sling, placed on a foam mat on the ground, and lightly restrained by several handlers. The saddle was attached to the dorsal fin and held in place by three Delrin pins (Cadillac Plastic and Chemical Company, Houston, Texas) that were guided through 6.4-mm-diameter holes (one on the anterior edge and two on the posterior edge) cored through the fin. The coring device and pins were disinfected prior to use. There was little bleeding around the core holes because we avoided major blood vessels located near the center of the dorsal fin. Once

the saddle was attached, the Delrin pins were held in place with magnesium nuts (Metal Supply Co., Philadelphia, PA) that were 2.5 mm in diameter, 10 mm thick, and weighed 10.4 g each. The nuts were designed to dissolve in about three weeks when placed in seawater at 20°C. Without the nuts, the Delrin pins would fall out and release the saddle. Attachment of the saddle took approximately 20 min.

Dive data were analyzed with the SATPAK software from Wildlife Computers. Data were tested for normality using a Kolmogorov-Smirnov test (significance considered at P=0.05) available with STATISTICA[®] software. Locations were plotted using a Geographical Information System (Delta Data Systems, Picayune, MS). Bathymetry was based on the ETOPO-5 data set (Herring, 1993).

Sea surface temperature, current velocity, and current direction were obtained from the Texas General Land Office's Texas Automated Buoy System (TABS). TABS buoy B (28°59′N, 94° 54′W) and buoy C (28°49′N, 94°46′W) are located 30 km and 48 km south of Galveston, Texas, respectively. Oceanographic data were available for only the last seven days of the study because both buoys became operational on April 3, 1995. Buoy data were decoded and analyzed by N. Guinasso and W. Lee of the Geochemical and Environmental Research Group (GERG) at Texas A&M University. Sunrise on March 17 (day of release) occurred at 0607 CST and sunset at 1810 CST. By April 10 (last satellite transmission), sunrise occurred 29 min earlier and sunset 14 min later.

The mean number of daily satellite contacts during the 23.7-d monitoring period was 30.8 ± 11.7 SD (range = 17-58, n = 23). The mean number of daily locations was 5.5 ± 1.5 SD (range = 3-9, n = 23). Eighteen percent of the daily satellite contacts resulted in usable locations. Of these, 87.8% were LC 0, LC A or LC B (low-accuracy classifications); the remainder were LC 1 (1-km accuracy) except for one LC 2 (350-m accuracy). Of the 128 locations that were received between 17 March and 10 April, 124 (97%) were usable. We rejected three LC Z locations, and one LC B location that was on land. The number of satellite contacts and locations by hour of the day was variable, with peaks spaced 4-7 h apart at 0200, 0900, 1300, and 2000 CST. No contacts were received during 0300–0600, 1100, 1600–1800, and 2200 CST.

After release on March 17 the dolphin immediately moved eastward and remained between the 20-m and 40-m isobaths south of the area between Galveston Bay and Sabine Pass (Fig. 2). On 24 March (seven days after release), the dolphin began moving southwest along a line roughly parallel to the 20-m isobath. It remained in an area south of Matagorda Island between the 20-m and 60-m isobaths until the SLTDR fell off and stopped transmitting on 10 April. The last transmission was received 48 km southeast of Matagorda Island near the 60-m isobath. During 23.7 days of monitoring the dolphin traveled a minimum distance of 1,711 km at a mean transit speed of 0.8 m/sec (range = 0.08-5.69 m/sec, n = 123). The mean minimum distance traveled daily was 72 km. The animal ranged along 300 km of coastline from Sabine Pass

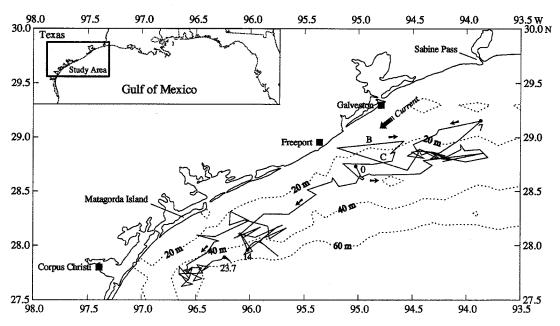


Figure 2. Plot of the dolphin's movements along the Texas coast. The box in the upper left shows the location of the study area in the northwestern Gulf of Mexico. Decimal latitude and longitude are shown along the edge of the map. Isobathymetry lines are in meters. The solid circles show the point of release (0) and time marks in 7-d increments up to the point of last contact with the SLTDR. Small arrows indicate the direction of the dolphin's movements. B and C indicate the locations of the two TABS buoys that provided data on sea surface temperature and surface current direction (indicated by the large arrow) and speed.

to Matagorda Island, with a mean distance offshore of 52 km \pm 16 SD (range = 17–97, n = 124). The mean ocean depth along the dolphin's track was 32.6 m (median 28 m, range = 12–63 m, n = 124).

Immediately following the dolphin's release, 52 min of surfacing-interval data were collected using a VHF receiver aboard the release vessel. Mean interval between surfacings was 14.4 sec (median 14, range 3-35 sec, n=204 intervals). Mean time at the surface was 1.2 sec (median 1.3 sec, range 0.4-5.8 sec, n=207 surfacings).

A total of 15,506 dives were recorded for maximum dive depth and 16,547 for dive duration. The number of dives for depth and duration differ because the histograms are encoded separately and not all of the 6-h periods were received by the satellite. The minimum estimated number of dives per day using the latter number was 698/d. There was no apparent diel pattern in the depth of dives, dive duration, or the time spent at a particular depth (Table 1 and Fig. 3). Most dives were shallow and of short duration, regardless of the time of day. On average, 58.1% of the dives were in the 4–10 m category, and 93.8% were to less than 30 m. The deepest dives (2.6% on average) were to 40–60 m. Throughout the monitoring period the dolphin consistently made dives that were deep enough to reach the ocean floor. An average of 93.3% of the dives were less than 2 min in duration, and only 6% were 2–3 min long (Table 1 and Fig. 3). Two dives were recorded in the range of 4–5 min, and one dive was 5–6 min long. On average, the dolphin spent 76.2% of the time

Table 1. The percentage of dives recorded for maximum dive depth (A) and duration (B) and the percentage of time recorded for time at depth (C). Data were divided into ranges of depth or time (left side) and into 6 h periods (top) corresponding to night (2100–0259 h CST), dawn (0300–0859 h CST), day (0900–1459 h CST), dusk (1500–2059 h CST). The 24-h mean was calculated as the mean of the four 6-h periods for each range of depth or time. n = 1 the number of dives recorded for each period.

	Period (hours)				
	2100-0259	0300-0859	0900-1459	1500–2059	24 h x̄
A. Max div	e depth (meters	s)			
4–10	59.1%	54.3%	61.3%	57.7%	58.1%
10-20	21.4%	21.8%	20.2%	17.2%	20.2%
20-30	16.1%	17.0%	11.3%	17.6%	15.5%
30-40	1.3%	2.2%	4.5%	6.5%	3.6%
40–60	2.1%	4.6%	2.8%	1.0%	2.6%
n	3,878	4,084	3,171	4,373	
B. Dive du	ration (minutes)			
0-1	79.8%	72.3%	68.0%	72.6%	73.2%
1–2	16.1%	21.7%	22.7%	19.8%	20.1%
2-3	3.6%	5.1%	8.5%	7.0%	6.0%
3-4	0.5%	0.8%	0.7%	0.6%	0.6%
4–5	0%	0.1%	0.1%	0%	0%
5–6	0%	0%	0%	0.02%	0%
n	4,342	4,441	3,584	4,180	
C. Time at	depth (meters)				
0–10	79.2%	71.7%	81.8%	72.4%	76.2%
10–20	11.4%	12.7%	9.6%	12.5%	11.4%
20–30	6.8%	9.8%	5.8%	10.8%	8.3%
30–40	1.0%	3.8%	2.9%	3.8%	2.9%
40–60	2.1%	2.7%	0.3%	0.6%	1.4%

at depths less than 10 m and 95.9% at depths less than 30 m. Only 2.9% of the time was spent at depths of 30-40 m and 1.4% at depths of 40-60 m.

To determine whether the dolphin's diving behavior changed over the duration of the study, we divided the data into three 8-d periods: Period 1 = days 1-8; Period 2 = days 9-16; Period 3 = days 17-24. The dolphin made increasingly deeper dives and spent a greater percentage of its time at deeper depths in Periods 2 and 3 than in Period 1 (Fig. 4). For example, dives deeper than 30 m did not occur until after the eighth day and increased to 14.7% of total dives by Period 3. The trend toward deeper dives corresponded with the animal's movement southwest where the continental shelf narrows and deeper water occurs closer to shore.

Sea-surface temperature ranged from 18–24°C from April 3–10 at the two automated buoys 30 and 48 km south of Galveston. The mean current velocity (longshore component) was 0.25 m/sec down (southwest direction) the coast.

This is the first time that an Atlantic spotted dolphin has been monitored at sea using satellite or radio telemetry. Although this rehabilitated animal appeared healthy at the time of release, we cannot be certain that its behavior

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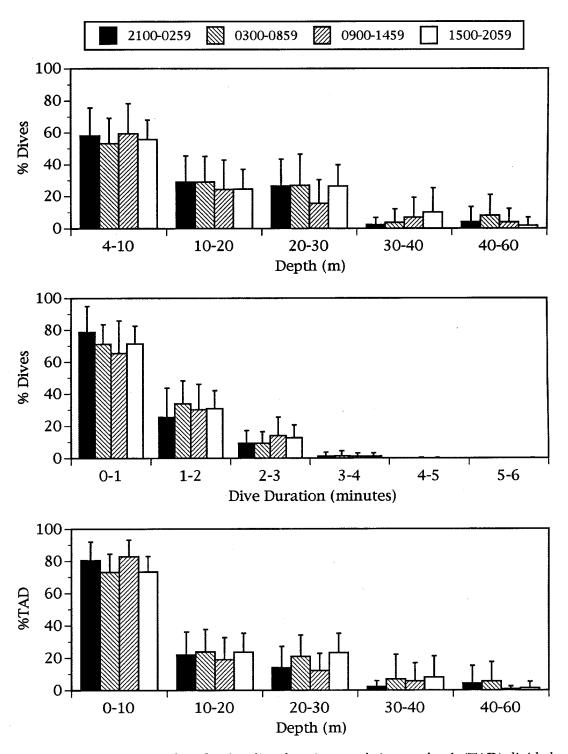


Figure 3. Maximum dive depths, dive durations, and time at depth (TAD) divided into 6-h periods corresponding to night (2100–0259 CST), dawn (0300–0859 CST), day (0900–1459 CST) and dusk (1500–2059 CST). The histograms show the mean percentage of dives or time at depth (TAD) \pm SD. Data were tested for normality using the Kolmogorov-Smirnov test.

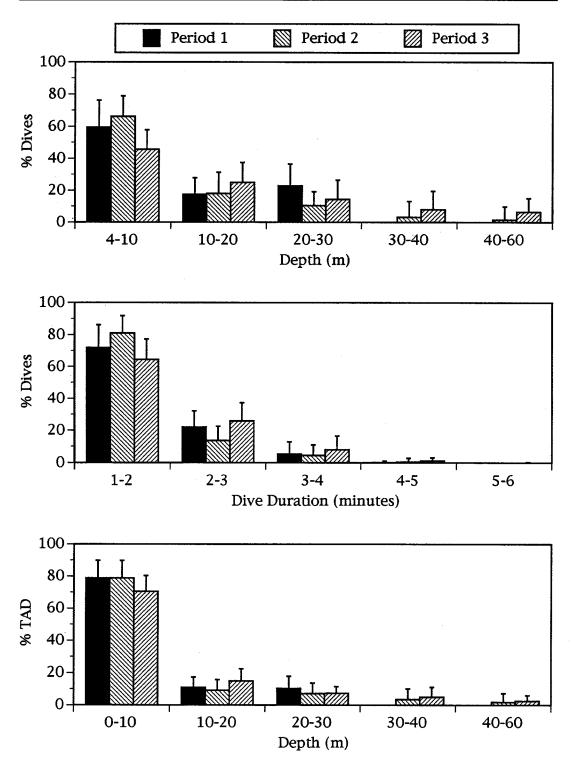


Figure 4. Maximum dive depths, dive durations, and time at depth (TAD) divided into three 8-d periods: Period 1 = days 1-8, Period 2 = days 9-16, and Period 3 = days 17-24. The histograms show the mean percentages of dives or time at depth (TAD) \pm SD.

was typical of this species, as there are no previous studies with which to compare our results. Nevertheless, the animal's diving behavior, mean transit speed, and minimum daily distance traveled are similar to those of other small odontocetes [e.g., bottlenose dolphins, common dolphins (Delphinus delphis), pantropical spotted dolphins (Stenella attenuata), spinner dolphins (S. longirostris), dusky dolphins (Lagenorhynchus obscurus), and humpback dolphins (Sousa chinensis)] that have been monitored using a theodolite on shore or by satellite and radio telemetry (Evans 1971, 1994; Saayman et al. 1972; Leatherwood and Ljungblad 1979; Perrin et al. 1979; Powers et al. 1979; Würsig and Würsig 1979; Irvine et al. 1979, 1981; Norris and Dohl 1980; Würsig and Würsig 1980; Würsig 1982; Tanaka 1987; Würsig et al. 1991; Mate et al. 1995). In addition, the dolphin's sustained dive frequency and tendency toward deeper dives toward the end of the monitoring period indicate that diving ability did not diminish due to poor health. Therefore, we assume that the animal was successfully feeding, able to sustain an active metabolism, and in reasonably good health.

The saddle containing the small satellite and radio transmitters attached easily to the dolphin's dorsal fin using three Delrin pins with magnesium nuts. An advantage of using the TracPac[®] saddle was that it was custom molded from a plaster cast of the dolphin's dorsal fin. This assured a proper fit and reduced the possibility of injury to the animal after the saddle was attached. The hydrodynamic shape of the saddle reduced drag-induced force on the dorsal fin that can cause tissue damage over time (Irvine et al. 1982, Tanaka et al. 1987). Nevertheless, we decided to minimize possible damage to the dorsal fin by using magnesium nuts that dissolved after 24 d and allowed the saddle to fall off.

Satellite contacts and locations were made each day during the monitoring period. However, analysis of the number of contacts and locations by hour of the day revealed four periods spaced 4–7 h apart when contacts were made, and four intervening periods with no contacts. This cyclical pattern results primarily from the geographical coverage of the northern Gulf of Mexico provided by the two polar-orbiting satellites with Argos receivers.

Only 18% of the total satellite contacts gave usable locations, which is less than the 50% reported by Tanaka (1987) for satellite tracking of bottlenose dolphins (Tursiops truncatus) along the coast of Japan. Nevertheless, the number of locations per day (i.e., 5–6) for this study was similar to that reported by Tanaka (1987) and Mate et al. (1995) for bottlenose dolphins and by Mate (1989) for pilot whales (Globicephala spp.). Most of our locations were LC 0, LC A, or LC B classifications for which Service Argos provides no predictions for their accuracy. Stewart et al. (1989) found the error of LC 0 locations to be variable with a mean of 15 km. However, our LC 1 or LC 2 contacts were consistent with the less-accurate location classes (LC 0, LC A, and LC B) and confirmed the general location of the animal on a daily basis. None of the low-accuracy locations resulted in unreasonable movement patterns that would have exceeded the maximum swimming speed of a dolphin of this size.

The dolphin spent 76.2% of its time at a depth of less than 10 m. These

shallow dives undoubtedly included surface swimming while the dolphin ranged along the coast. However, some of this time probably involved foraging as well. There were three separate periods in which the animal remained in an area for 4–5 d. These periods of more confined movement alternated with periods of directed movement, generally parallel to the 20-m isobath, in the direction of the longshore current, and within 30 km of the coast. Würsig and Würsig (1979) observed that bottlenose dolphins in shallow water also moved parallel to the depth lines and stayed in water of constant depth. It is possible that periodic movements in restricted areas take advantage of prey concentrations, while directed movement generally along an isobath is due to movement between food concentrations (Evans 1971).

The Atlantic spotted dolphin's mean transit speed of 0.8 m/sec or 72 km/d is similar to that recorded for satellite-tagged bottlenose dolphins (Tanaka 1987) and pilot whales (Mate 1989). These are minimum swim speeds, as it is likely that the animal did not swim in a straight line between consecutive satellite locations. Routine swim speeds for species of similar size (e.g., bottlenose dolphins, humpback dolphins, dusky dolphins, and pantropical spotted dolphins) range from 0.3 to 3.3 m/sec (Saayman et al. 1972; Irvine et al. 1979, 1981; Leatherwood and Ljungblad 1979; Würsig and Würsig 1979; Shane 1990; Mate et al. 1995), although maximum speeds for short durations approach 8 m/sec (Lang and Norris 1966).

Atlantic spotted dolphins in the northern Gulf of Mexico appear to prefer shallow water with a gently sloping bottom typical of the continental shelf, although they may also occur along the shelf break and upper continental slope (Davis and Fargion 1996). Their occurrence in shallow shelf waters may be related to prey preference and foraging strategies. Atlantic spotted dolphins are known to feed on small fish, cephalopods, and benthic invertebrates (Clarke 1986, Perrin et al. 1994). Fertl and Würsig (1995) reported on the coordinated behavior of Atlantic spotted dolphins feeding near the surface on a school of clupeid fish. Unlike odontocetes that live beyond the continental shelf and feed primarily at night on deep scattering layer organisms (Norris and Dohl 1980, Mate 1989, Würsig et al. 1991, Evans 1994), our study animal behaved more like nearshore bottlenose dolphins, which show little diel change in dive depth (Scott et al. 1990a). Most of the dives were shallow, in part because the animal remained on the continental shelf in shallow water close to shore. Nevertheless, the dolphin made a small percentage of dives that were deep enough to reach the ocean floor. Whether these deeper dives involved foraging on benthic organisms is unknown.

The aerobic dive limit (ADL) is the maximum dive duration during which a marine mammal can sustain aerobic metabolism using oxygen stored in the lungs, blood, and muscle. Williams et al. (1993) calculated the ADL to be about four minutes for a 145-kg bottlenose dolphin swimming at speeds ranging from 1.7 to 2.3 m/sec. Although measurements of oxygen stores and swimming metabolism have not been made for Atlantic spotted dolphins, the ADL for this species is probably similar to that of a comparably sized bottlenose dolphin. For the 127-kg animal in this study, 93.3% of the dives were

less than two minutes in duration and 99.9% were less than four minutes. It therefore appears likely that most dives were aerobic and that the dolphin did not rely on anaerobic metabolism.

Although this study has provided our first glimpse of the diving behavior and at-sea movements of an Atlantic spotted dolphin, it would be unreasonable to assume that the behavior of this animal is representative of the species. A sample size of one, especially a rehabilitated animal, makes conclusions premature. We do not know whether the dolphin rejoined a group of other animals because we were unable to re-approach it by following the VHF transmitter before the saddle fell off. Atlantic spotted dolphins are highly social, and a lone animal is not likely to exhibit totally natural cycles of behavior (Norris et al. 1994). Nevertheless, this dolphin behaved in a manner consistent with our current understanding of the species' preference for shallow-water habitats and short dives that are probably supported by aerobic metabolism. Throughout the monitoring period the animal showed no indication of failing health and continued diving until the saddle fell off as planned. Much remains to be learned about the at-sea behavior of Atlantic spotted dolphins, and they appear to be good candidates for further studies using satellite telemetry.

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