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THE LIFE HISTORY OF FREE-RANGING ATLANTIC SPOTTED DOLPHINS (*STENELLA FRONTALIS*): AGE CLASSES, COLOR PHASES, AND FEMALE REPRODUCTION

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ABSTRACT

Atlantic spotted dolphins (*Stenella frontalis*) were observed underwater and from the surface from 1985 to 1996 and photographed through successive years. Individuals were categorized into age classes by their degree of spotting and color phases. Dolphins spent an average of 3 yr in the two-tone color phase, 5 yr in the speckled phase, 7 yr in the mottled phase and up to 10 yr or more in the fused phase.

Sex ratios were close to parity, with old adults skewed towards females and juveniles and young adults skewed towards males. The average calving interval for 24 females was 2.96 years with a range of 1–5 yr. Females whose calves survived the first year had a significantly longer calving interval (3.56 years). The ages of first parturition for five females were estimated to be 10–12 yr. The age at sexual maturation was estimated to range from 8 to 15 yr.

Pregnancy rate fluctuated annually, with an average rate of 0.25 (range 0.07–0.57). Annual average birth rate was 0.08 (range 0.06–0.14), average calf production was 0.33 (range 0.06–0.52), average fecundity was 0.23 (range 0.13–0.30), and average recruitment was 0.06 (range 0.03–0.08). Most females who lost a calf conceived the same or following year.

Lactation lasted up to 5 yr, and 45% of visibly pregnant females were also lactating. Age of first parturition was associated with the mottled color phase. Average first-year mortality rate of calves was 0.24.

Key words: *Stenella frontalis,* spotted dolphin reproduction, mortality, age class, sex composition, sexual maturity, color phase.

By systematically observing free-ranging and undisturbed populations over a long term, one can collect relatively unbiased life-history information. For cetaceans, which can usually be observed just briefly at the surface, underwater observation can aid in collecting such information. For example, researchers have explored the underwater lives of humpback whales *Megaptera novaeangliae* (Glockner-Ferrari and Ferrari 1990), spinner dolphins *Stenella longirostris* (Öst-

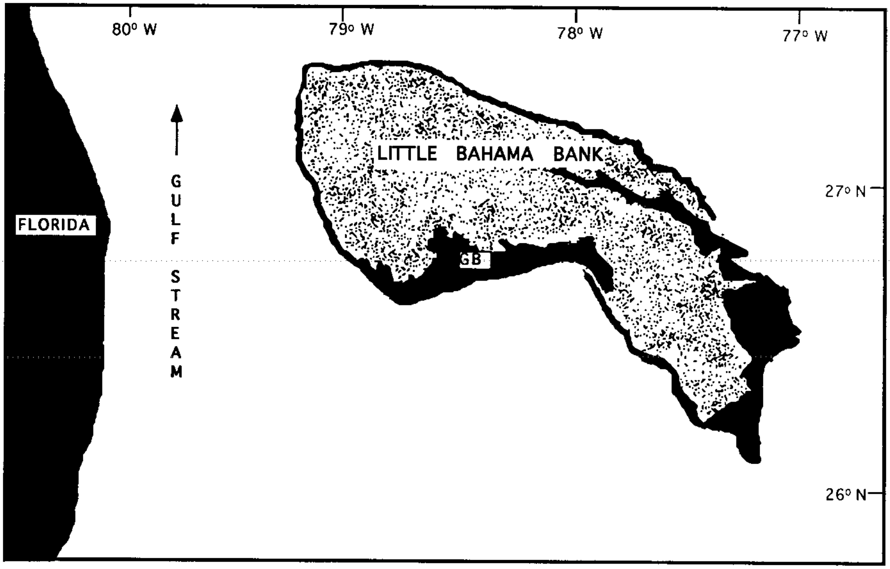

Figure 1. Chart of study area. Darkened area represents land masses and shaded area represents the submerged sandbank outlined by the 20-m depth contour. GB = Grand Bahama Island.

man 1994), and killer whales *Orcinus orca* (Simila and Ugarte 1993). This paper describes the ontogenetic development of color patterns, sex ratios, and reproductive parameters of Atlantic spotted dolphins (*Stenella frontalis*, previously *S. plagiodon*; Perrin *et al.* 1987) from 1985 to 1994 in the Bahamas, based on such observations. Little has been known about the life history of Atlantic spotted dolphins, but since the early 1970s a free-ranging community of spotted dolphins in the northern Bahamas has been habituated to humans, allowing long-term studies of behavior and communication (Herzing 1996). The habituated dolphins permitted human swimmers to approach them closely underwater, allowing researchers to identify individuals and classify them to age category, determine their gender, and monitor their behavior and reproductive status.

Materials and Methods

Atlantic spotted dolphins were encountered over shallow sandbanks, ranging in depth from 6–16 m, north of Grand Bahama Island in the Bahamas (Fig. 1). Dolphins were observed 1,140 times from the surface and underwater during May through September, 1985–1994 (Table 1). These dolphins have been habituated to human presence in the water since the 1970s. For some analyses, additional data from 1995–1996 were included.

Several types of vessels were used as anchored observation or survey platforms during this study (principally a 4-m motorboat and a 20-m catamaran). Beginning in 1985 the observation platform was anchored for 1-wk periods

Table 1. Encounter information for Atlantic spotted dolphins in the Bahamas, 1985–1994.

	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	Total
Days at sea	21	52	100	100	100	100	100	100	100	100	873
Days with encounters	19	46	55	36	51	52	63	64	84	71	541
# of encounters	54	103	143	56	101	100	130	127	182	144	1,140
Average encounters per day	5	2	3	4	2	2	2	2	2	2	
Hours in water	12	42	45	26	50	50	76	101	103	81	586
Average duration of encounter (min)	21	26	19	28	30	30	35	48	34	34	

in primarily one location on the edge of Little Bahama Bank. The vessel also surveyed between the island and the site twice each week. In 1990 the surveys were expanded to include the western third of Little Bahama Bank and deeper waters south of Grand Bahama Island (Fig. 1). Surveys were conducted opportunistically (about every 7–10 d) when the sea state was Beaufort 2 or less. Two observers searched for 2-hr periods by eye, supplemented with binoculars. The height of the observation platform changed through the years from 5 m (1-km visibility) to over 15 m (2-km visibility). Transects included both north and south searches and zig-zag movements across the edge of the sandbank.

Underwater still photography and video were used to document the dorsal fin, flukes, scars, and spot patterns of 153 dolphins. Pictures were taken using Nikonos III and V cameras with 35-mm lenses. Underwater video cameras, a Sony CCDV9 8-mm and a Yashica KXV1u Hi8-mm, with attached Labcore 76 hydrophone, were used for identifying individuals and simultaneously recording behavior and vocalizations.

Determining Sexes and Age Classes of Individuals

It is critical in dolphin life-history studies to know the sex and age of individuals. In the case of the pantropical spotted dolphin (*S. attenuata*) in the eastern tropical Pacific, age estimates from the teeth of the carcasses recovered from purse-seine nets have been used (Perrin *et al.* 1976, Barlow and Hohn 1984, Myrick *et al.* 1986). Caldwell and Caldwell (1966) described the ontogenetic development of the spotting pattern of Atlantic spotted dolphins, as Perrin (1970) has done for pantropical spotted dolphins. Other studies have suggested that the degree of spotting may be used to broadly define age classes. For example, behavioral observations within tuna nets have utilized age-class divisions based on color phase to describe social structure (Pryor and Kang-Shallenberger 1991). Color phase has also been suggested as an indicator of sexual maturity for female spotted dolphins (Myrick *et al.* 1986, Chivers and Myrick 1993). Kasuya *et al.* (1974) speculated that color phase may be influenced by reproductive hormones, suggesting that spotting is correlated with

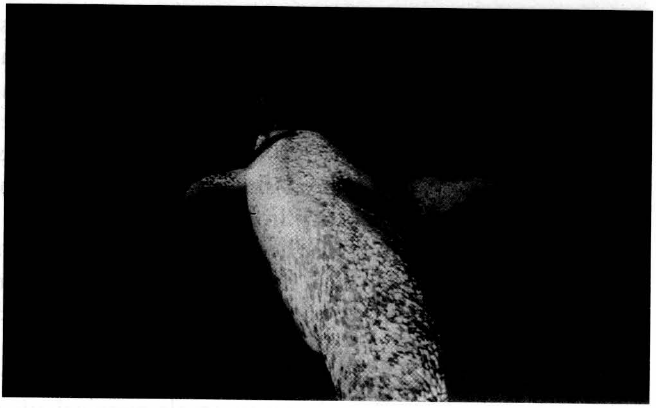

Figure 2. Lactating mother (foreground) is beak-to-genital with her calf. Her swollen mammaries, indicating lactation, can be seen in her genital region.

the process of sexual maturation The degree of spotting has also been correlated with age in Indian Ocean bottlenose dolphins, *Tursiops* sp. (Ross and Cockroft 1990, Smolker *et al.* 1992).

Sex was determined by observation of the genital area. Age classes were estimated initially by using the ontogenetic classification system for the pantropical spotted dolphin, which correlates color/spotting phase with maturity (Perrin 1970, Perrin *et al.* 1976). By closely monitoring individuals over the years, the development of these color patterns and the durations of the phases could be used to categorize dolphins by age class. Individuals with "bounded" age-class intervals were those that had been observed throughout an entire color phase. Actual ages were known only for those dolphins known since birth. "Unbounded" intervals had incomplete data available by which to determine transition years into and out of the color phase. Data collected for each group included number of individuals present, group size, age classes, time of day, environmental factors, and behavioral activity. Using video analysis, the lengths of calves were estimated as a proportion of the mother's length.

Determining Reproductive States

Reproductive status was determined for females by underwater visual inspection. Females were classified as reproductively active when they were observed to be visibly pregnant or showed obvious signs of lactation, *i.e.,* distended mammaries (Fig. 2) or repeated nursing of a calf. Visibly pregnant females often appeared slightly swollen in May and increased in girth over the 5-mo field season. Over 90% of the time these females were resighted the following spring with calves larger than other newborns who belonged to females whose state of pregnancy was not obvious by the fall. Connor *et al.* (1992) report that swelling is visible 2–3 mo prior to parturition in Indian Ocean bottlenose dolphins.

I believe that mid-term pregnancies of spotted dolphins are visible during regular, close-up underwater observations made during a longitudinal study of known individuals. Although more sophisticated methods (hormone analysis from blood samples, ultrasonic imaging) are currently used to detect pregnancies in captive dolphins (Schroeder 1990), the high rate of postpregnancy verification found in this study suggests that mid-term pregnancies can be detected visually with relative reliability in spotted dolphins.

The gestation period is unknown for the Atlantic spotted dolphin. Because the gestation is estimated to last 11.5 mo for pantropical spotted dolphins (Perrin *et al.* 1976) and one year for bottlenose dolphins (Schroeder 1990), I assumed a one-year gestation for Atlantic spotted dolphins.

The cycle of gestation, birth, and lactation was monitored for all mature and maturing female dolphins, and calving intervals were calculated. Calving intervals were calculated from data collected over a period of 10 yr for 24 females that were (1) observed in two or more consecutive years, and (2) mature or became sexually mature between 1985 and 1994. Potential bias exists, however, if females that were not habituated to our presence, and therefore not closely observed, had different reproductive parameters (see Discussion).

Results

Color phases—Atlantic spotted dolphins displayed the four color phases described by Perrin (1970) for the pantropical spotted dolphin: two-tone (Fig. 3a), speckled (Fig. 3b, c), mottled (Fig. 4a, b), and fused (Fig. 4c). Because of the long duration of each color phase and the continuous changes in color pattern, phases were subdivided into early and late stages to better describe the ontogeny of the pattern (Table 2). The average durations of these phases are presented in Table 3.

Two-tone = neonate/calf—The dolphins are born gray-white, without spots. Dolphins with one spot or none were considered to be in the two-tone phase; this phase included neonates and older calves. We observed 21 dolphins (11 female, 10 male) who passed from this phase at birth into the next phase (Table 3). This phase lasted from 2–6 yr for both males and females, with an average of 3.43 yr. Calves remained with their mothers for at least 3 yr or until a new calf was born.

Speckled = juvenile—Dolphins were classified as speckled when they developed black spots (at least two) on the ventral surface and a few light gray spots on the dorsal surface. Ventral spotting usually started at between 3 and 4 yr of age (range 2–6 yr) and increased throughout this phase. Five bounded intervals (1 female, 4 male) were recorded, with a mean of 5.0 yr and a range of 4–7 yr (Table 3). Young speckled dolphins were typically independent, although some remained with their mothers if the mother had not given birth to another calf.

Mottled = young adult—Dolphins were classified as mottled when they developed extensive and merging gray and white spots on the dorsal surface and continued to gain black spots on the ventral surface. Typically at age 8 or 9,

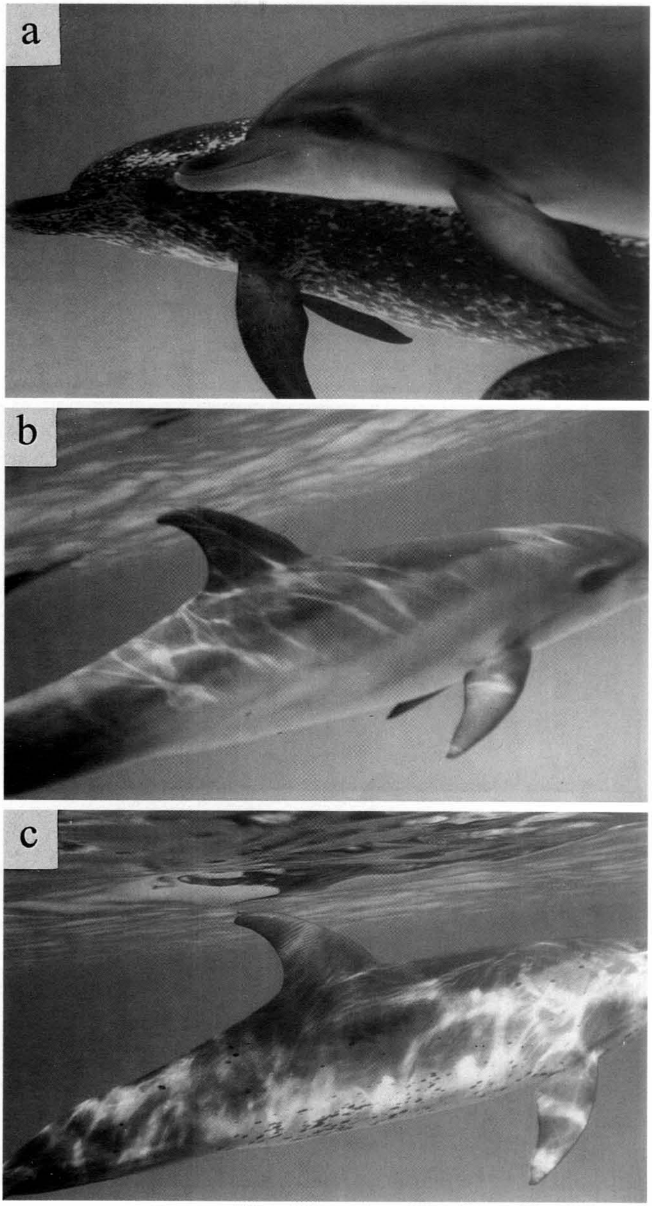

Figure 3. (a) A two-toned Atlantic spotted dolphin (foreground) with his adult mother (background). (b) An early speckled male Atlantic spotted dolphin at age 5. (c) A late speckled male Atlantic spotted dolphin at age 8.

development of spots accelerated. This spotting category was dramatic in its onset; some individuals developed from late speckled to early mottled within a 6- to 7-mo period (October–April). Eight individuals (3 female, 5 male) had bounded intervals, with an average interval of 7.13 yr and a range of 4–10

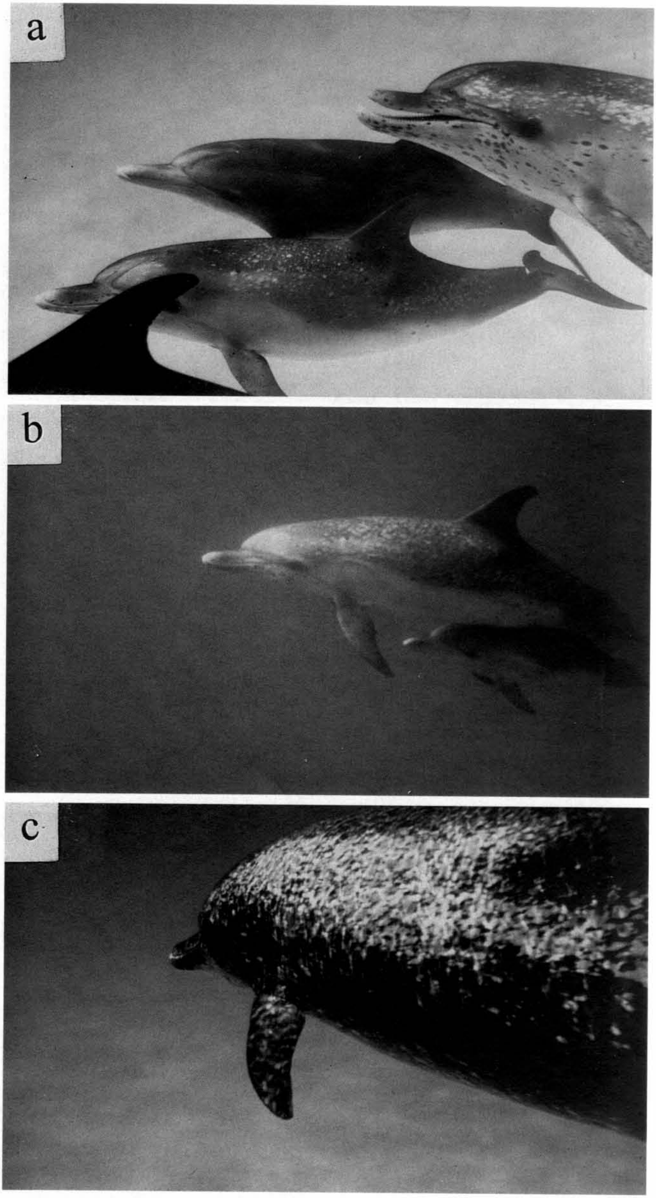

Figure 4. (a) An early mottled female Atlantic spotted dolphin at age 9 (middle). (b) A late mottled female Atlantic spotted dolphin at age 12 with her first offspring. (c) A fused male Atlantic spotted dolphin.

yr. Female spotted dolphins did not give birth until after they had reached the mottled color phase.

Fused = adult—Dolphins were classified as fused when dark and white spots became extensive and coalesced on the ventral and dorsal surfaces. Old males

Table 2. Age classes and color phases for Atlantic spotted dolphins in the Bahamas.

Age class	Relative size	Coloration	Affiliation and behavior
Neonate 1–3 mo	¼–⅓ of mother	Two-tone No spots. Gray-white with fetal folds visible.	With mother or multiple mother/calf pairs. Awkward swimming/surfacing.
Calf 3 mo–3+ yr	⅓–¾ of mother By first year, ¾ of mother's length. Older calves fill out in girth.	Two-tone–early/late Still gray-white with no more than one ventral black spot on older calves.	Usually seen with mother for the first two years. Older calves can be with young juvenile groups.
Juvenile 4–9+ yr	¾–⅞ of mother	Speckled–early/late Two or more black spots on ventral surface. Older juveniles have extensive ventral spots and a few white spots on dorsal surface.	Usually in juvenile subgroup of varying ages. Early speckleds may still be with mother if she has no new offspring. Late speckleds with younger juveniles when adults are not present.
Young adult 9–16+ yr	⅞ to adult size	Mottled–early/late Extensive black spots on ventral, white spots on dorsal surface.	With other mottleds, speckleds, or juvenile subgroups. Males in tight coalitions. Females may conceive and give birth for first time.
Old adult 16+ yr	Full adult size	Fused Black and white spots fusing. Males and old females with white tipped rostrum.	Old males in tight coalitions or with mothers with young offspring. Females with offspring or with old males.

Table 3. Bounded color-phase intervals for Atlantic spotted dolphins in the Bahamas, 1985–1996. Intervals assume no differences between the sexes. Dolphins with bounded intervals were those animals which were observed during the transitions both into and out of the color phase.

	Color phase			
	Two-tone	Speckled	Mottled	Fused
No. of individuals	21	5	8	0
Mean	3.43	5.00	7.13	n/a
Minimum years	2	4	4	n/a
Maximum years	6	7	10	n/a

and females had pronounced white rostrum tips similar to those reported for pantropical spotted dolphins (Pryor and Kang-Shallenberger 1991). Observations of both male and female dolphins in this color phase have spanned up to 10 yr.

Color phase durations—Although there may be considerable variation, the color phases exhibit the following general pattern: two-tone (birth through 3 or 4 yr), speckled (ages 4–9 yr), mottled (ages 10–16 yr), and fused (from age 16 yr).

Sex ratios by color phase—The age-class/color-phase composition of female and male spotted dolphins based on ten years of observations is summarized in Figures 5 and 6, respectively. Sex ratios were calculated for 4 yr based on resighting data (Table 4). (Because of concern about possible unequal "catchability" and photodocumentation of all age classes and both sexes during the early years, the analysis of sex ratios was limited to data from 1991 to 1994.) Potential bias in the sex ratios is still possible if there are differences between

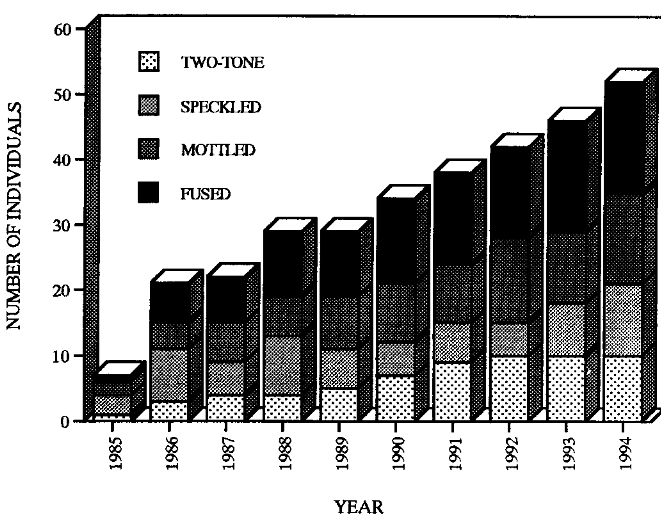

Figure 5. Female color phases, 1985–1994.

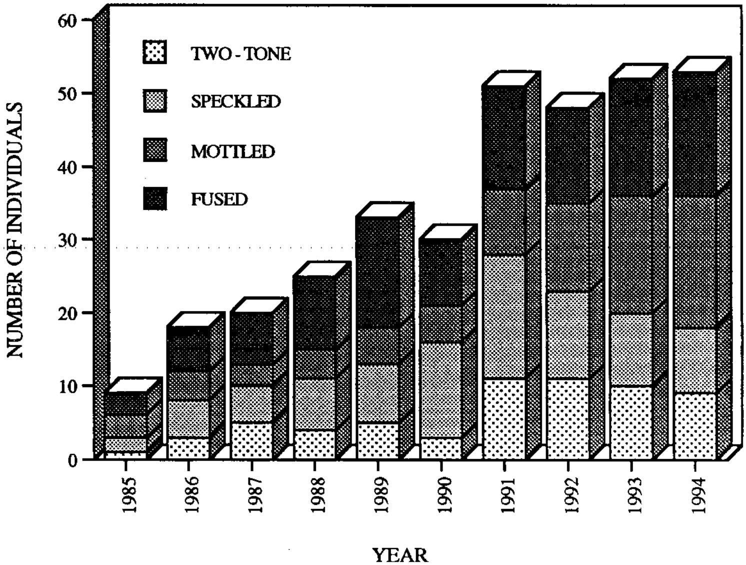

Figure 6. Male color phases, 1985–1994.

the sexes in the numbers of years spent in a given color phase. Sex ratios were close to parity (Table 4); differences within age classes were not statistically significant ($P = 0.54$, chi-square). The ratio was skewed towards males in juvenile and young adult age classes, but was near parity in adults.

Reproductive seasonality and calving intervals—Based on observations of pregnancy stages of females at the end of the summer season and the size of accompanying newborns in the spring, I conclude that the peak calving periods are early spring and late fall. Mating and courtship behaviors were observed during all stages of development (including in neonates), but young

Table 4. Sex and age composition of Atlantic spotted dolphins in the Bahamas, 1991–1994. Given are the numbers of males and females and, in parentheses, the sex ratios (m:f).

	1991	1992	1993	1994	Total
Adult	14:14	13:14	16:17	17:17	60:62
(fused)	(1:1)	(0.93:1)	(0.94:1)	(1:1)	(0.97:1)
Young adult	9:9	12:13	16:11	18:14	55:47
(mottled)	(1:1)	(0.92:1)	(1.45:1)	(1.29:1)	(1.2:1)
Juvenile	17:6	12:5	10:8	9:11	48:30
(speckled)	(2.8:1)	(2.4:1)	(1.3:1)	(0.82:1)	(1.6:1)
Calf	11:9	11:10	10:10	9:10	41:39
(two-tone)	(1.2:1)	(1.1:1)	(1:1)	(0.9:1)	(1.1:1)
Total	51:38	48:42	52:46	53:52	204:178
	(1.3:1)	(1.1:1)	(1.1:1)	(1:1)	(1.2:1)

adult females were most frequently observed engaged in copulation with mottled or fused males.

The reproductive histories of 24 females are summarized in Table 5. The average calving interval was 2.96 yr (SD = 1.224) with a range of 1–5 yr (Fig. 7a). All three of the 1-yr intervals and four of the five 2-yr intervals were from females who had lost a calf and became pregnant the following or same year. Three of the lost calves were males, two were females, and six were unsexed. The average calving interval for females whose calves survived (Fig. 7b) was 3.56 yr (n = 16, SD = 0.892) and was significantly longer than the average for all females (P = 0.016, two-tailed t-test).

Sexual maturity and age of first parturition—The age at sexual maturation (ASM), the age at which a female first ovulates, is unknown for Atlantic spotted dolphins. Evidence of pregnancy, parturition, and lactation could be detected and recorded, but behavioral observations could not detect first ovulation. Because of the long maturation time, only one female, Katy, has been monitored since birth and observed through her first parturition. Born in 1986, Katy became pregnant in 1995 and lost her first offspring in the 1996 field season to unknown causes. Therefore, she was 10 yr old at first parturition and became sexually mature at 9 yr old or earlier.

Four other females (Paint, Rosemole, FlyingA, LittleGash) that were first observed in the middle of the speckled phase provided less direct evidence of ASM. If it is assumed that they were, on average, 3 yr old when they entered the speckled phase and had spent 2.5 yr in the speckled phase (one-half the mean), then they would have been 5 yr old when first identified. These females matured into the early mottled phase 1–2 yr prior to giving birth to their first calves. If the assumptions are correct, then the estimated age of parturition would be 10 yr for Paint, 11 yr for Rosemole, and 12 yr for FlyingA and Little Gash (Table 5). Sexual maturation would have occurred at least one year prior to first parturition at 9–11 yr of age or possibly earlier due to our inability to observe or measure ovulations not followed by pregnancy. If, however, we use the minimum and maximum durations instead of the mean for the two-tone phase (2 and 6 yr) and the speckled phase (0.5×4 and 0.5×7 = 2 and 3.5 yr), we obtain a range for ASM of 8–15 yr.

Pregnancy rate, annual birth rate, calf production/mortality—Annual rates of pregnancy, calf production, fecundity, birth, calf mortality, and recruitment are presented in Table 6. The annual pregnancy rate is the average fraction of mature females that are pregnant divided by the gestation period (in years). Pregnant female spotted dolphins were either directly observed in the later stages of gestation or inferred pregnant based on known births in the following year. Although mid-to-late pregnancies were visually detectable by an increase in girth, early pregnancies were not detectable, so it is likely that the pregnancy rate is underestimated and should be considered a minimum rate. Rates of calf production, birth, and mortality are minimum estimates because calves may have been born and lost before we were able to observe them. Minimum (visible) pregnancy rates were higher than calving rates the subsequent year as would be expected given fetal or neonatal mortality (Figure 8).

Table 5. Reproductive histories of female Atlantic spotted dolphins in the Bahamas. Preg* = inferred from birth, Preg = pregnant, N/O = not observed, L&N = lactating and nursing, C-M/F = Calf, male or female, NRA = no reproductive activity visible, C-L = lost the calf, C-L/P = lost the calf and then became pregnant.

Name (resightings)	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	Total calves (mortality in %)
Fused females											
Blotches (51)	Preg*	C-F	L&N	L&N	Preg*	C-F	L&N	Preg	C-M	L&N	3 (0)
Bumper (13)	N/O	N/O	NRA	N/O	N/O	NRA	Preg*	C-L	Preg	C-M	2 (50)
Dos[1] (97)	N/O	NRA	NRA	NRA	NRA	Preg	C-L	Preg	C-M	L&N	2 (50)
Double Gash (18)	N/O	NRA	N/O	N/O	Preg	C-M	L&N	L&N	L&N	L&N	1 (0)
Flashlight (18)	N/O	N/O	N/O	N/O	N/O	NRA	NRA	Preg	C-F	L&N	1 (0)
Gemini[2] (120)	Preg*	C-F	L&N	L&N	L&N	Preg	C-M	L&N	L&N	L&N	2 (0)
Hedley (90)	N/O	NRA	NRA	NRA	Preg	C-L/P	C-M	L&N	L&N	Preg	2 (50)
Hook (35)	N/O	N/O	N/O	NRA	NRA	NRA	NRA	NRA	NRA	NRA	0 (0)
L Ridge (38)	N/O	NRA	Preg*	C-L	Preg	C-M	L&N	L&N	NRA	NRA	2 (50)
Luna (132)	C-M	L&N	Preg	C-F	L&N	Preg	C-M	L&N	L&N	Preg	3 (0)
Medley (15)	N/O	N/O	N/O	N/O	N/O	N/O	N/O	Preg*	C-F	L&N	1 (0)
PR1 (70)	Preg*	C-M	L&N	L&N	L&N	Preg	C-L	Preg	C-M	L&N	3 (33)
PR2 (67)	Preg*	C-M	L&N	L&N	L&N	Preg	C-L	NRA	Preg	C-F	3 (33)
Snowflake (56)	N/O	Preg	C-F	L&N	L&N	Preg	C-M	L&N	Preg	C-M	3 (0)
Stoplight (30)	N/O	NRA	NRA	N/O	NRA	Preg*	C-M	L&N	Preg	C-M	2 (0)
Mottled females											
Blaze (94)	NRA	NRA	NRA	NRA	NRA	Preg	C-L/P	C-L/P	N/O	N/O	2 (100)
Lilly (56)	N/O	L&N	N/O	NRA	NRA	Preg*	C-M	Preg	C-L/P	C-L	3 (66)
Mugsy (135)	N/O	NRA	NRA	NRA	NRA	Preg	C-L/P	C-M	L&N	L&N	2 (50)
Nippy (123)	C-F	L&N	L&N	Preg	C-F	L&N	Preg	C-F	L&N	Preg	3 (0)
Transition females (*year of transition from speckled to mottled*)											
Flying A (20)	spec	spec	spec	spec	spec	N/O	Preg*	C-M	L&N	Preg	1 (0)
Little Gash (213)	N/O	spec	spec	spec	spec	mott	mott	Preg	C-F	L&N	1 (0)
Paint (115)	spec	spec	spec	spec	Preg	C-F	L&N	L&N	Preg	C-F	2 (0)
Rosemole (191)	spec	spec	spec	spec	mott	Preg	C-F	L&N	Preg	C-F	2 (0)
Whitepat (190)	N/O	spec	mott	NRA	NRA	NRA	NRA	NRA	NRA	Preg	0 (0)

[1] Transition from mottled to fused in 1990.
[2] Transition from mottled to fused in 1987.

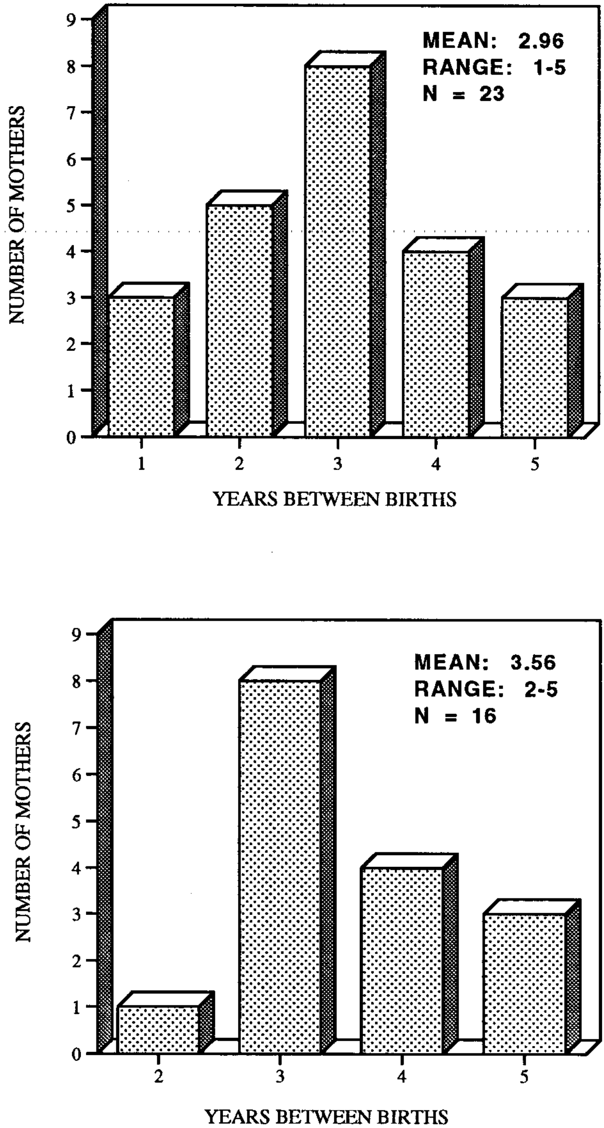

Figure 7. (a) Calving intervals for all females, including those whose calves died within the first year. (b) Calving intervals for females whose calves survived more than one year.

Lactation and nursing—For the 23 calving intervals calculated, all females were lactating throughout the duration of their cycle or until they were visibly pregnant with another fetus. Of 38 females whose pregnancies were fully observed (48 pregnancies minus 10 inferred pregnancies), 17 (45%) were observed lactating at the same time. Older offspring were observed to suckle during the mid-stages of the mother's pregnancy, after which nursing was no

Table 6. Summary of reproductive and calf mortality rates of Atlantic spotted dolphins. Pregnancy rate is the number of pregnant females divided by the number of mature females. Birth rate is the number of observed births divided by the number of mature females. Calf mortality rate is the first-year mortality divided by the number of births. Per capita birth rate is the number of births divided by the minimum population size. Fecundity is the number of calves surviving one year divided by the number of mature females. Recruitment is the number of calves surviving one year divided by the minimum population size. Pregnant and lactating rate is the number of pregnant and lactating females divided by the number of sexually mature females. The means were weighted by annual sample size for 1991–1994 and a binomial variance was used to calculate the standard deviation for the calf mortality rate; 1985–1994 data were included because both early and later years were thought to be reliable for this parameter. The minimum population represents identified individuals only.

	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	Mean	SD
Minimum population	—	—	—	—	—	—	89	90	98	105		
Mature females	7(4)	12	15	15	18(1)	22(3)	23(2)	24(1)	23	23		
( ) = inferred from following-year pregnancy												
Pregnant females	4	1	2	1	5	12	4	7	7	5		
Pregnancy rate	0.57	0.08	0.13	0.07	0.28	0.55	0.17	0.29	0.30	0.22	0.25	0.045
Birth rate	2	4	1	2	1	5	12	5	7	7		
	0.29	0.33	0.07	0.13	0.06	0.23	0.52	0.21	0.30	0.30	0.33	0.049
Calf mortality rate	0	0	0	1	0	1	5	2	1	1		
	—	—	—	0.50	—	0.20	0.42	0.40	0.14	0.14	0.24	0.063
Per capita birth rate	—	—	—	—	—	—	0.14	0.06	0.07	0.07	0.08	0.014
Fecundity	—	—	—	—	—	—	0.30	0.13	0.26	0.26	0.23	0.043
Recruitment	—	—	—	—	—	—	0.08	0.03	0.06	0.06	0.06	0.012
Pregnant and lactating	—	—	1/15	1/15	1/17	4/19	1/21	1/23	4/23	4/23		
rate	—	—	0.07	0.07	0.06	0.21	0.05	0.04	0.17	0.17	0.11	0.025

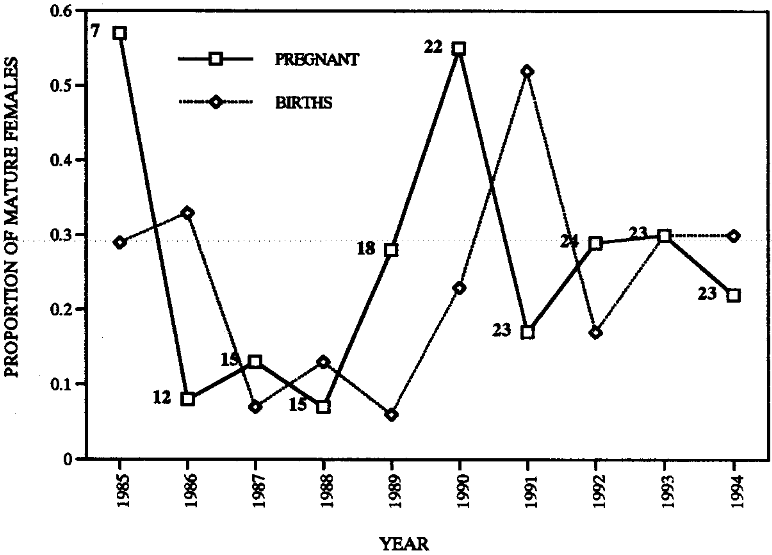

Figure 8. Pregnancy and calving rates, 1985–1994.

longer observed. It thus appeared that lactation and pregnancy occurred simultaneously in almost half of the pregnant females and that lactation could continue up through the mid-period of gestation. Visually observed pregnancies not associated with simultaneous lactation (n = 21) included four that were either first pregnancies or pregnancies that occurred following the loss of a calf. Six of seven females that had lost a calf apparently stopped lactating and became pregnant in the same or the following year.

Mortality and other population losses—Calf mortalities per female (Table 5) and per year (Table 6) were highly variable. Out of 46 calves born, 11 (24%) did not survive their first year. Non-fatal fresh sharkbites were observed on 12 dolphins, 8 of which were 3 yr old or younger (Table 7).

Immigration and emigration rates could not be calculated, but individuals of all age classes have been lost over the years for unknown reasons. Others were resighted after absences of 1–2 yr. For example, during the 1990 and 1991 seasons, one female (FlyingA) was not sighted in the area. In 1992 she was sighted with a calf 32 km away from her previous location.

Discussion

Potential bias in studying habituated dolphins—Because these dolphins are habituated to human presence in the water, there may be potential biases if certain age classes or individuals are more amenable to human approach. From 1985–1990, the observation platform mainly remained at anchor in one location on the shallow sandbanks. This allowed the dolphins to become familiar with, and to approach, the platform and humans. During this initial six-year period, juveniles and mothers with calves frequently approached the boat and

Table 7. Years of non-fatal shark bites and known or approximate ages for 12 Atlantic spotted dolphins.

Dolphin	Year	Age attacked	Sex
Bimini	1994	Newborn	Female
Zigzag	1990	1 yr	Male
Lucaya	1994	1 yr	Male
Brush	1992	2 yr	Female
Geo	1993	2 yr	Male
Havana	1993	2 yr	Male
Nassau	1991	2 yr	Female
Uno	1994	3 yr	Female
Rosemole	1986	6 yr	Female
Mugsy	1986	8 yr	Female
Gemini	1989	20+ yr	Mother of 4-yr-old
Luna	1992	20+ yr	Mother of 1-yr-old

were resighted, but other identifiable dolphins, particularly mottled and fused males, were resighted less frequently.

In 1991, however, we expanded our study area to determine the gender of less-familiar individuals in order to increase the probability that our study animals were of equal "catchability" and representative of the larger population. At the same time, we observed an increased tolerance by the dolphins to our presence in the water. The expanded coverage and increased tolerance resulted in improved access to previously unfamiliar individuals, followed by a decrease in new animal identifications and increased periods of time (up to four hours) during which groups of dolphins allowed us to observe their behavior.

Accustoming animals to the presence of observers has been done successfully in field and laboratory studies on primates and other mammals, and criteria for levels of habituation have been described (Davis and Balfour 1992). Long-term studies of dolphins have relied on habituation of study animals to the presence of researchers in small boats (*e.g.,* Scott *et al.* 1990, Smolker *et al.* 1992). In this study I assumed that these dolphins were representative of the population because: (1) the proportion of new animals identified declined from 19% in 1991 to 4% in 1995, suggesting that a large proportion of the population had been identified; (2) over 80 known individuals have been resighted every season since 1991, indicating that these dolphins were long-term, stable residents of the area; (3) individuals of all age and sex classes had high resighting rates after 1991, indicating that they could be regularly observed without apparent bias; and (4) after six years of habituation to our activities, dolphins often ignored our presence and engaged in behaviors such as courtship and mating, foraging, play, and aggressive conflicts. The question of bias in habituated populations still remains, however, and should be further examined in future studies of this population.

Sex ratios and age class—Overall sex ratios were near parity over ten years, although small differences between age classes were observed. Male to female ratios increased during the juvenile and young-adult stages and then decreased in the adult stage, when the ratio reached parity. A similar trend of increasing and decreasing ratios in subadults, maturing males, and adults has been observed in the Sarasota Bay bottlenose dolphin community, possibly due to higher mortality of males (Wells *et al.* 1987). Adult sex ratios are close to parity in other *Stenella* species (Perrin and Reilly 1984).

Calving intervals—The calving cycle includes gestation, lactation, and sometimes a resting period. The mean calving interval of 2.96 years found in this study is similar to that reported for other species. A calving interval of 3.03 yr (Myrick *et al.* 1986) and intervals ranging from 2.5–3.9 yr (Perrin and Reilly 1984) have been reported for pantropical spotted dolphins. Scott *et al.* (1996) reported a mode of 5 yr and a range of 2–10 yr for bottlenose dolphins in Sarasota Bay.

Three- and four-year interbirth intervals seem to be normal for Atlantic spotted dolphin mothers with surviving offspring. Shorter calving intervals were typically due to the loss of a calf.

Lactation/pregnancy—Some Atlantic spotted dolphins (average of 11% of mature females, 1985–1994) were observed lactating and nursing after the birth of one offspring until the birth of another. Lactation lasted an average of over 3 yr, with some females continuing to nurse for as long as 5 yr. This compares with an average length of lactation for pantropical spotted dolphins of 1.66 yr (northern offshore stock: Myrick *et al.* 1986), and prolonged lactation periods of up to 7 yr for bottlenose dolphins (Scott *et al.* 1996). The percentage of mature females that were simultaneously pregnant and lactating in this study (11%) can be compared to values found for pantropical spotted dolphins (6% by Chivers and Myrick 1993 and similar values by Barlow 1985). However, all females in our study who stopped lactating before the birth of the next calf did so following the loss of a calf. In addition, given our inability to detect early pregnancies, it is likely that the rate of females simultaneously pregnant and lactating may actually be higher than calculated.

Pregnancy rates—Annual pregnancy rates averaged 0.32 and ranged from 0.07 to 0.57. Pregnancy rates were likely underestimated due to the inability to detect early pregnancies. Studies of exploited populations show annual pregnancy rates of 0.63 for bottlenose dolphins in the Black Sea, 0.25–0.40 for pantropical spotted dolphins and 0.30–0.35 for spinner dolphins (Perrin and Reilly 1984, Chivers and Myrick 1993).

Annual birth rates, fecundity, and recruitment—Annual birth rates averaged 0.08 and ranged from 0.06–0.14. These estimates fall within the range of values for other delphinids, including bottlenose dolphins (0.06; Wells and Scott 1990) and exploited populations of pantropical spotted dolphins (range 0.10–0.20; Perrin and Reilly 1984). Mean fecundity (0.23) and recruitment rates (0.06) were also comparable to those described for bottlenose dolphins (0.144 and 0.048, respectively; Wells and Scott 1990).

Ages at sexual maturation and first parturition—Direct and indirect evidence indicates that five dolphins first gave birth when 10–12 yr old. A range for ASM of 8–15 yr is similar to the ranges for female pantropical spotted dolphins of 7–16 yr (mean 11.1) from the more-exploited northern offshore stock in the ETP and 6–11 yr (mean 9.8) from the less-exploited southern offshore stock (Chivers and Myrick 1993). The age at sexual maturation for female bottlenose dolphins ranges from 5 to 12 yr (Schroeder 1990).

Calf mortality—First-year mortality rates for spotted dolphin calves averaged 0.24 and ranged between 0 and 0.50. In comparison, Sarasota bottlenose dolphins had a 0.19 first-year mortality rate (Wells and Scott 1990). Loss of calves may have been due to shark attacks. Potential predators such as tiger (*Galeocerdo cuvieri*), bull (*Carcharhinus leucas*), and hammerhead (*Sphyrna* sp.) sharks inhabit this area (Wood *et al.* 1970), and calves and juveniles were observed with severe but non-fatal sharkbites.

Conclusions

This study is unusual in that it combines long-term longitudinal monitoring of known individuals, habituation of the dolphins to the presence of human swimmers and boats, underwater examination of individuals to determine gender and to detect pregnancies and lactation, and categorization by color phases to estimate approximately the ages of individuals. This approach produced values for life-history parameters similar to those from other studies using different methods, although a more rigorous comparison among studies will require more years of data. However, refining conclusions and improving methods are integral parts of long-term studies of dolphins in the wild. With time, this approach can better examine the potential biases that may exist in a study of habituated dolphins, can provide more known-age data by identifying newborn calves and observing them throughout their lives, and may allow the influence of habitat on life history to be examined through comparisons with other dolphin populations.

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