REPRODUCTIVE SEASONALITY OF WESTERN ATLANTIC BOTTLENOSE DOLPHINS OFF NORTH CAROLINA, U.S.A.

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ABSTRACT

We describe reproductive seasonality of bottlenose dolphins in North Carolina (NC), U.S.A., using strandings data from the entire coast of NC and sighting data from Beaufort, NC and by estimating dates of birth of known females. We found a strong peak of neonate strandings in the spring (April–May), and low levels of neonate strandings in the fall and winter. The distribution of neonate strandings was significantly different from a uniform distribution ($P < 0.001$, $K = 3.8$). We

found a unimodal distribution of 282 sightings of neonates with a diffuse peak in the summer. The temporal distribution of sightings of neonates departed significantly from a uniform distribution ($P < 0.001$, $K = 5.1$). Estimated birth dates of neonates from known females occurred in May ($n = 6$) and June ($n = 4$), with a single fall birth. These methods shed light on bottlenose reproductive patterns and underscore the value of using information from multiple types of data. Clarification of bottlenose dolphin reproductive patterns, such as the seasonality of birth, may enhance our understanding of the population structure of this species in the mid-Atlantic region.

Key words: reproduction, seasonality, strandings, photo-identification, circular analysis, bottlenose dolphins, *Tursiops truncatus*.

Many mammal species exhibit seasonality in reproduction (Bronson 1989). Ultimate factors, such as seasonal variation in food, precipitation, temperature, predation pressure, and proximate factors, such as changes in day length, interact in a complex manner to determine the timing of reproduction. For example, the reproductive cycles of baleen whales are tightly synchronized with their migratory patterns. These patterns of reproduction and migration are likely driven by ultimate factors such as seasonal variation in the availability of food at high latitudes (Evans 1987). Proximate factors act as cues to trigger events in mammalian reproductive cycles (Bronson 1989). For instance, changes in day length may stimulate humpback whales (*Megaptera novaeangliae*) to move toward the equator to breed (Dawbin 1966) and the implantation of blastocysts in pinnipeds (Temte 1991).

Seasonal reproduction is pronounced in many odontocetes, such as sperm whales (*Physeter macrocephalus*) (Best *et al.* 1984, Whitehead and Weilgart 2000), harbor porpoises (*Phocoena phocoena*) (Read and Hohn 1995), and many delphinids (Perrin and Reilly 1984). Distinct birth peaks are less obvious in tropical odontocetes (Perrin 1976, Whitehead and Mann 2000), although Barlow (1984) was able to discern modes in the parturition of tropical spotted (*Stenella attenuata*) and spinner dolphins (*Stenella longirostris*). Reproductive timing may also vary among populations within a species. For example, Urian *et al.* (1996) found that populations of bottlenose dolphins from North America and Europe (*Tursiops truncatus*) exhibited distinct seasonality of reproduction and that captive animals from these populations maintained the seasonality of their natal environments.

During a morbillivirus epizootic in 1987 and 1988, large numbers of bottlenose dolphins stranded along the mid-Atlantic coast of the United States, and the U.S. National Marine Fisheries Service listed these dolphins as a single depleted population under the Marine Mammal Protection Act (58 CFR 17789, 6 April 1993). Management actions designed to address incidental takes of bottlenose dolphins in fishing gear (Wang *et al.* 1994) have prompted the National Marine Fisheries Service to reexamine the population structure of bottlenose dolphins along the eastern seaboard of the United States (Hohn 1997). The picture emerging from this recent analysis is one of a complex of populations, some resident and others migratory, along the Atlantic coast from Florida to New Jersey. This view has evolved from analyses of strandings (Mead and Potter 1995, Fernandez and Hohn 1998, McLellan *et al.* 2003) and sightings (Urian *et al.* 1996). An understanding of reproductive seasonality may help to clarify the stock structure of bottlenose dolphins in North Carolina.

Here we examine the seasonality of reproduction in the bottlenose dolphin from the Atlantic coast of North Carolina. We analyze data supplied by the North

Carolina marine mammal stranding network, photo-identification efforts (Barco *et al.* 1999, Urian *et al.* 1999, Wang *et al.* 1994), and information from recent live captures (Hansen and Wells 1996).

METHODS

Strandings

We analyzed data collected from stranded dolphins along the coast of North Carolina from 1992 to 1999. We defined neonates as those individuals having at least three of five of the following characteristics (Dearolf *et al.* 2000): rostral hairs (Cockroft and Ross 1990, Mcbride and Kritzler 1951), floppy dorsal fin (Mead and Potter 1990, Mcbride and Kritzler 1951), floppy tail flukes (Mcbride and Kritzler 1951), floppy or folded peduncle, and a partially healed umbilicus (Cockroft and Ross 1990). Additional characters such as unerupted teeth, caudal blowhole dent, fetal folds or fetal lines (Mann and Smuts 1999), and tongue papillae were noted, although we did not use these as defining characteristics. Only neonates in condition codes 2 or 3, using the Smithsonian Institution's scale, where 1 = alive, 2 = freshly dead, 3 = moderately decomposed, 4 = severely decomposed, and 5 = skeletal remains (Geraci and Lounsbury 1993) were considered. Total body length, date of stranding, location, condition code, sex, and date of data collection were noted for all stranded animals. We took straight-line measurements from the tip of the rostrum to the fluke notch to determine the length of each carcass. Experienced personnel from the University of North Carolina at Wilmington, Duke Marine Laboratory, or the Beaufort National Ocean Services and National Marine Fisheries Laboratory examined animals. For this study we defined non-neonates as all dolphins equal to or greater than 125 cm in length (see below).

Sightings

We used eight years (1992–1999) of data from photo-identification surveys in the Beaufort, NC, area (Fig. 1). We employed small (4–12 m) boats in sea states of Beaufort ≤3. When dolphins were sighted, we estimated school size, then approached the school and continued on a course parallel to the dolphins' apparent course to obtain photographs. Schools were defined as aggregations of animals engaged in similar behavior within 100 m of one another (Wells *et al.* 1987, Connor *et al.* 1998). We recorded date, location, school size and composition, environmental conditions, behavior, and whether any individuals displayed neonatal features. We surveyed in both estuarine and coastal ocean waters. Estuarine waters were defined as those inside barrier islands. Coastal waters were defined as those outside barrier islands. We surveyed within 100 m of shore.

Dolphin dorsal fins were photographed using standard photo-identification techniques (Würsig and Würsig 1977, Würsig and Jefferson 1990) using cameras with 100–400-mm lenses. Both black and white print film (ISO 400) and color slide film (ISO 64) were used. Images were labeled and cataloged according to fin features such as nicks, notches, and scars.

Features for identifying neonates in the field included body size less than half the size of the proximate adult (Cockroft and Ross 1990), dark color (Cockroft and Ross 1990), floppy dorsal fin (Mead and Potter 1990), extreme buoyancy (Cockroft and
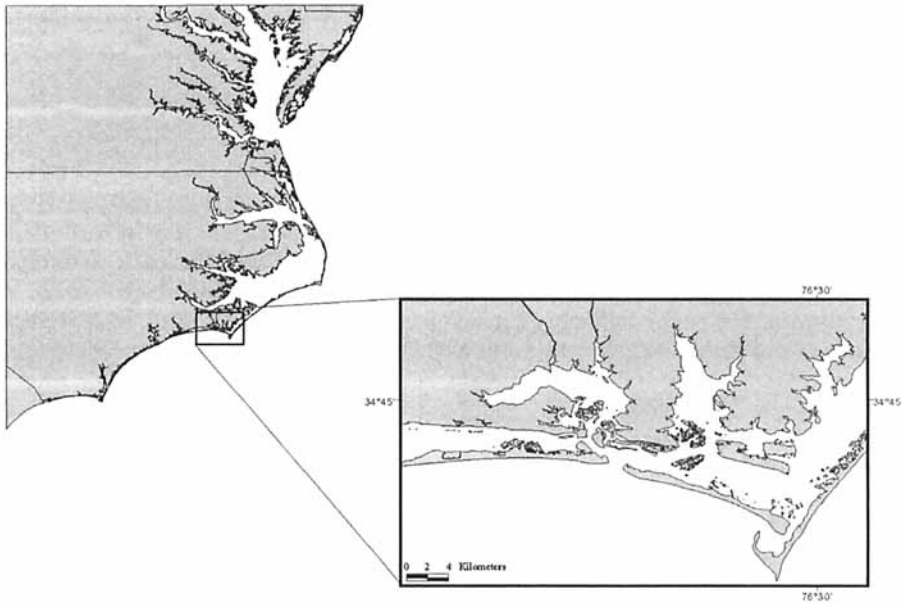
Figure 1. Map of study area for strandings (entire state of NC) and for photo-identification effort in Beaufort, NC. Inset shows study area.

Ross 1990), rostrum-first surfacing, and echelon swimming position (Mann and Smuts 1999). We used a minimum of three of the above features to score the animal as a neonate. We noted the presence of fetal lines (Mann and Smuts 1999), but did not use these as a defining feature. We could not score infant position, as defined by Mann and Smuts (1999) due to lack of water clarity. Non-neonates were defined as all dolphins that did not exhibit the above neonatal characters.

Estimates of Birth Dates

We estimated dates of birth to known females from field sightings. In this study animals were identified as recently parturient females only when photographed with a calf in echelon position (Mann and Smuts 1999) on ≥ 3 d. Estimated birth dates were calculated as the midpoint between the last sighting of a known female without young and the first sighting with a neonate within a 31-d period (Wells *et al.* 1987, Urian *et al.* 1996). Some individuals were sighted with a neonate after not being sighted for more than 31 d. Estimates derived from these sightings were considered rough birth dates.

Water Temperature

Water temperatures have been collected weekly at the NOS/NMFS laboratory docks in Beaufort for the last three decades.[1] The temperature probe is at a depth of

[1] Personal communication from William Hettler and Peter Crumley, NOS/NMFS Beaufort Laboratory, March 2002.

1.5 m, which varies with tides. For this study we averaged the weekly temperatures from 1992 to 1999 to derive mean monthly temperatures and correlated these data with estimated births.

Analysis

We analyzed stranding and sighting data for neonates and non-neonates using circular statistics (Batschelet 1981, Zar 1984). We used circular statistics rather than the Kolmogorv/Smirnov (K/S) test because seasons are circular and analysis using a standard K/S test could introduce bias, depending on which month is chosen as the beginning of the distribution (Barlow 1984). Specifically, we used a variation of the K/S non-parametric test for goodness of fit based on cumulative distributions, the Kuiper's test (Batschelet 1981). We compared each category separately (stranded neonates, stranded non-neonates, sighted neonates, sighted non-neonates) to a uniform distribution and to a Von Mises circular normal distribution, using the one-sample Kuiper's test. We then compared neonates to non-neonates for strandings and sighting using a two-sample Kuiper's test. Standard deviation is given with means.

<div align="center">RESULTS</div>

Strandings

We documented 19 stranded neonates plus one near-term fetus that exhibited at least three of five of the neonatal features described above. These 20 animals ranged in size from 95 to 124 cm, with a mean of 108.2 ± 7.3 cm. We then examined the seasonal distribution of strandings of these neonates, plus an additional 49 calves that ranged in size from 96 to 122 cm with a mean of 108.6 cm $\pm$ 5.9 cm, but for which the presence of neonatal features had not been assessed by experienced personnel using the same criteria that we used for the 20 that we examined. We believed these 49 to be neonates, according to the size of the animals and the notes on the data sheets. We found a strong peak of stranded neonates in the spring (April–May), and low levels of neonatal strandings in the fall (October–November) and winter (January–February) (Fig. 2a). The distribution of neonatal strandings was significantly different from a uniform distribution ($P < 0.001$, $K = 3.8$), and from a circular normal Von Mises distribution ($P < 0.05$, $K = 22.2$). Strandings of 223 other dolphins occurred most frequently during the spring and fall, and less frequently from June through August (Fig. 3a). The distribution of non-neonates was significantly different ($P < 0.05$, $K = 3.6$) from a uniform distribution, and from a circular normal Von Mises distribution ($P < 0.001$, $K = 2.3$). The seasonal distribution of neonate strandings was significantly different from that of non-neonates ($P < 0.05$, $K = 4.8$). Spatial distribution of strandings by season is provided in Figure 4.

Sightings

We found a unimodal distribution of sightings of 282 neonates with a diffuse peak extending from the late spring into the fall (Fig. 2b). The temporal distribution of sightings of neonates departed significantly from a uniform distribution ($P < 0.001$, $K = 5.1$), and from a Von Mises circular normal distribution ($P <$
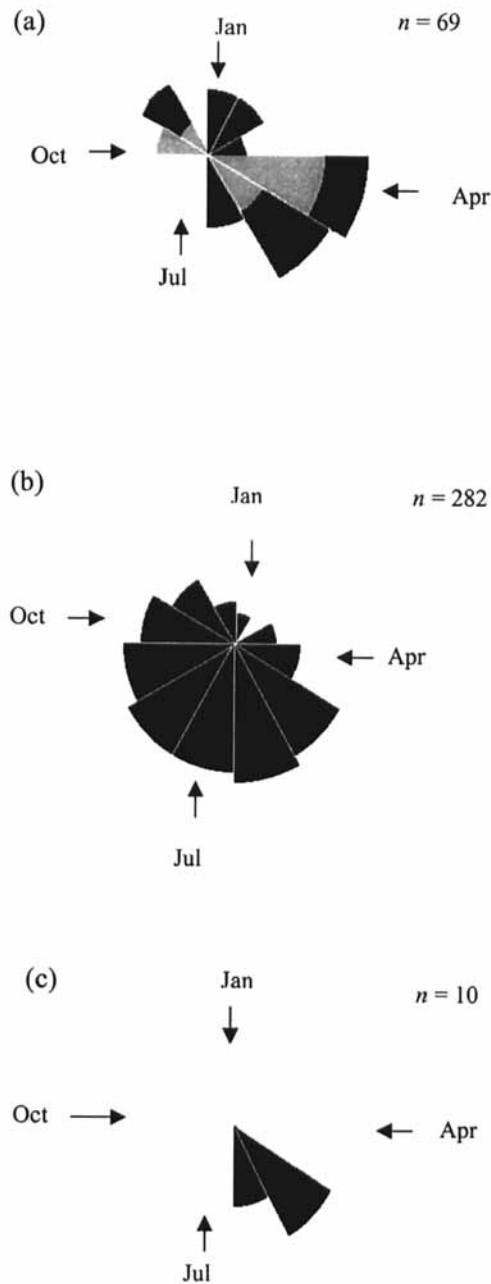
Figure 2. Monthly distribution of (a) neonate strandings. Light area represents monthly distribution of neonates (95–124 cm) examined by experienced observers. Darker area represents neonates within that size range (96–122 cm) scored as neonates but not quantitatively evaluated by experienced observers. Monthly distribution of (b) neonate sightings, and (c) estimated birth dates of neonates born to known females, from 1992 to 1999. Area of each wedge is proportional to the number of neonate dolphins that month.
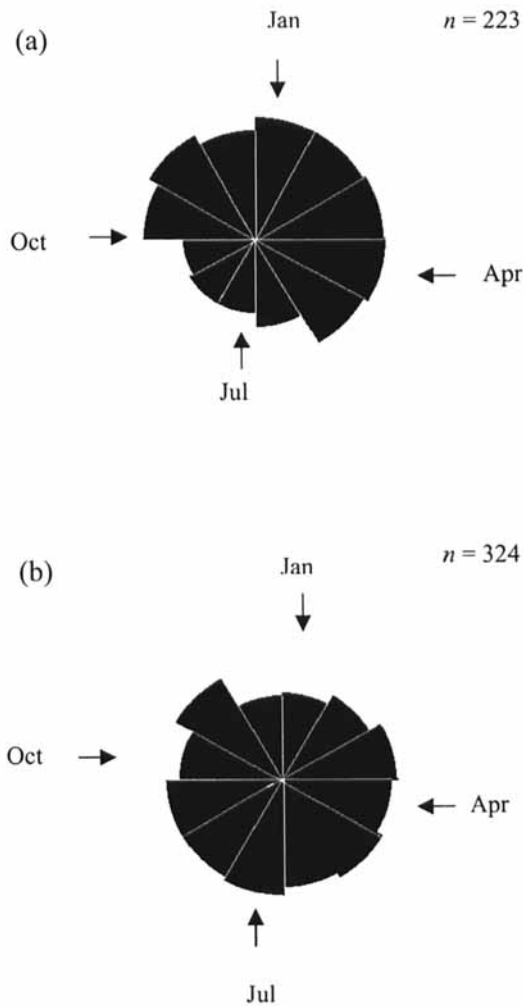
Figure 3. Monthly distribution of (a) non-neonate strandings, and (b) non-neonate sightings, from 1992 to 1999. Area of each wedge is proportional to number of non-neonate dolphins that month.

$0.05, K = 1.9$). The distribution of sightings of 324 non-neonate dolphins was not uniform ($P < 0.001, K = 2.4$) (Fig. 3b) and exhibited a weak peak in the fall. The degree of concentration of sightings was not great enough to allow estimation of Kappa (Batschelet 1981, table D1). Hence, we could not fit a Von Mises circular normal distribution to the data. The temporal distribution of sightings of neonates was significantly different from that of other dolphins ($P < 0.05, K = 17,074.8$).

Estimated Birth Dates of Young to Known Females

We were able to estimate birth dates for 10 neonates from eight female dolphins (two females gave birth more than once). Six births occurred in late spring (May)
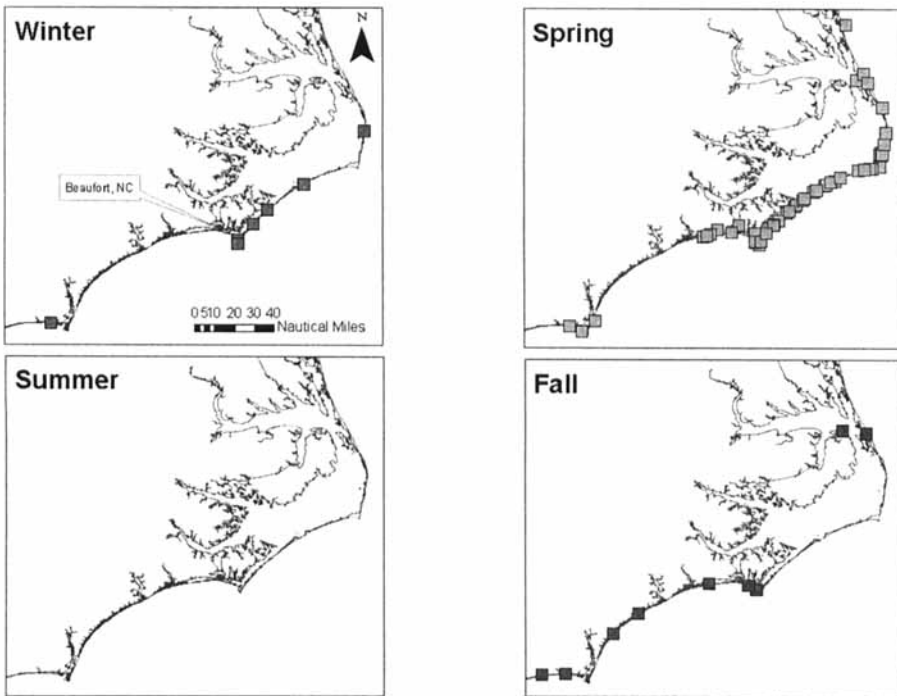
Figure 4. Figures showing locations of stranded neonates by season. Winter is defined as January–March, Spring is defined as April–June, Summer is defined as July–September, and Fall is defined as October–December.

and four occurred in early summer (June) (Fig. 2c). The mean date for the estimated births was May 27 ($\pm$ 11.8 d). We estimated one other birth for which the interval between the last sighting without a calf and the first sighting with a neonate was more than 31 d. This female gave birth in the fall. The animal was captured on 20 July (Hansen and Wells 1996) and was pregnant at the time, and then was seen on November 23 with a young of the year. The estimated date of birth of this calf was 21 September.

Water Temperature

Water temperatures collected in the estuary at the NOS/NMFS Beaufort laboratory docks were highest in August, followed by July and September. Mean water temperatures throughout the year ranged from a low in February of 9.25°C to a high in July of 34.9°C.

DISCUSSION

Based on state-wide stranding records, bottlenose dolphins in North Carolina exhibit a strong birth peak in the spring; low levels of neonatal strandings were observed at other times (Fig 2a). Sightings data indicate a diffuse peak from late spring to early fall, and births to known females occurred during May and June.

Some of this variation may be due to the existence of multiple populations in NC with different reproductive schedules. For example, the fall and winter neonates observed in strandings may reflect the existence of populations that are present for different periods along the beaches of NC (Fig. 4). In addition, strandings were collected most often on ocean beaches, whereas most sightings of neonates were observed in estuarine areas. Further information on the population structure of dolphins in this area is required before we can fully address these sources of variation.

Estimates of reproductive seasonality derived from strandings data could be biased toward an earlier date if the strandings include prenatal mortality. In our samples, neonate strandings (April–May) preceded neonate sightings (May–September). Urian *et al.* (1996) used similar methods to examine reproductive seasonality in this species and defined stranded neonates as animals that were 100–120 cm in length. In their study in Sarasota, Florida, the mean date of estimated birth from stranding data was 16 d earlier than that estimated from sighting data. Fernandez and Hohn (1998) found most neonate strandings in Texas occurred from February through June, with a smaller number occurring in November and December. These authors stated that stranded neonates may not reflect true reproductive seasonality, because they may represent individuals that suffered mortality because they were born *outside* the peak birth season.

Sightings of neonates occurred most frequently during summer (Fig. 2b). This peak is diffuse, and likely reflects the fact that our criteria for identifying neonates in the field were not conservative, as young dolphins might have been classified as neonates for periods of a month or more. Inclusion of older animals would broaden the apparent peak of neonate sightings, and result in a positively biased estimate of mean birth date. It is more difficult to recognize neonatal features in the field than in stranded specimens, and it is easy to miss newborns in the field (Caughley and Caughley 1974, Fernandez and Hohn 1998). Some features, such as fetal lines, may last months (Cockroft and Ross 1990), resulting in positively biased estimates of mean birth date. We did not use the presence of fetal lines as an identifying neonatal feature for this reason. Standard photo-identification techniques may not be precise enough to: (1) discern the presence of newborns, (2) assign each new-born to its presumed mother, and (3) allow enough time in the field to rule out the possibility of mistakenly identifying other dolphin mothers as mothers of newborns. Grellier (2000) discussed some difficulties encountered in assigning mothers to calves in the field and used association indices to identify the closest associate of young calves. The assignment of newborns to presumed mothers during longitudinal studies can help researchers track reproductive parameters such as calf survival, interbirth intervals, and reproductive seasonality.

Estimated births to known females occurred primarily during May and June. One individual gave birth in the fall. Therefore, we believe a spring peak and a smaller number of fall births may reflect the reproductive seasonality pattern of one of the populations of dolphins that frequent North Carolina estuarine waters. This spring peak may reflect a population of dolphins that is primarily estuarine in North Carolina during the summer months, although these animals are occasionally photographed in the nearshore ocean.

Seasonality of reproduction may reflect variation in food availability (Barros and Odell 1990, Urian *et al.* 1996), water temperature (Wells *et al.* 1987), loss of a dependent calf, duration of lactation (Barlow 1984), and presence of predators (Wells *et al.* 1987, Mann and Smuts 1998). Newborns may also have increased

survival if born when water temperatures are warmer and when food supply is adequate for lactating mothers (Wells *et al.* 1987, Mann *et al.* 2000); thus, those born early may not survive. In Virginia, Barco *et al.* (1999) recorded sightings of dolphins only when water temperatures were greater than 16°C. Although in Sarasota (Wells *et al.* 1987) found that births tended to occur when water temperatures exceeded 27°C, mean water temperatures in the Beaufort study area range from 16.7°C in April to 24.6°C in September, when we have estimated birth dates to known dolphins.

Whitehead and Mann (2000) postulated that newborn animals might have greater chances of survival in warmer waters that are less likely to contain predators. Wells *et al.* (1987) stated that the relatively low percentage of shark bite wounds on calves and juvenile dolphins in Sarasota indicates that either the young are well protected by their mothers or that the attacks are fatal (Wells and Scott 1999). In North Carolina's coastal waters, sharks are most prevalent in the nearshore ocean waters during the spring, although bull sharks (*Carcharhinus leucus*) are known to frequent estuarine waters (Castro 1993).

We believe the best method to determine reproductive seasonality in wild populations of bottlenose dolphins is to estimate birth dates of known females by using focal animals sampling methods (Altmann 1974, Whitehead and Mann 2000). Repeated focal observations offer the most precision in estimating birth dates, if field methods are rigorous enough to assign young to appropriate adult females. Even young calves spend time with escorts, away from their mothers (Mann and Smuts 1998), so researchers should adjust their definitions of mothers to include several sightings of the suspected females with neonates or young calves. Increasing the amount of time spent observing suspected females should reduce the possibility of mistaking escorts for the actual mothers.

Cockroft and Ross (1990) described the longevity of some neonatal features in captivity, but inherent difficulties in the field (murky water conditions, protective behavior of new mothers and their newborns) continue to hamper attempts to quantify neonatal characters in areas where water clarity is lacking. Although neonatal characteristics have been described in wild bottlenose dolphins from Shark Bay (Mann and Smuts 1999), the duration of these characteristics remain unclear for bottlenose dolphins from the western Atlantic. Thus, the longevity of neonatal features observed in wild populations remains unknown.

The analysis of several types of data to examine reproductive seasonality can also highlight differences from varying methods. Discrepancies between sightings of neonates during routine photo-identification studies and focal female studies eventually may be used to quantify the longevity of neonatal features. Similarly, the comparison of neonate stranding dates to dates of the first sightings of neonates born to known females eventually may be used to quantify the relative survival of calves born at different times of the year. Improved quantitative evaluation of neonatal characteristics, through the continued collaboration with stranding networks and the use of multiple sources of data from strandings, surveys, and focal individual follows, will strengthen our understanding of reproductive seasonality in wild bottlenose dolphin populations.

LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49: 227–267.

BARCO, S. G., W. M. SWINGLE, W. A. MCLELLAN, R. N. HARRIS AND D. A. PABST. 1999. Local abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia Beach, VA. Marine Mammal Science 15:394–408.

BARLOW, J. 1984. Reproductive seasonality in pelagic dolphins (*Stenella* spp.): Implications for measuring rates. Report of the International Whaling Commission (Special Issue 6):191–198.

BARROS, N. B., AND D. K. ODELL. 1990. Food habits of bottlenose dolphins in the southeastern United States. Pages 309–328 *in* S. Leatherwood and R. Reeves, eds. The bottlenose dolphin. Academic Press, London.

BATSCHELET, E. 1981. Circular statistics in biology. Academic Press, London.

BEST, P. B., P. A. S. CANHAM AND N. MACLEOD. 1984. Patterns of reproduction in sperm whales, *Physeter macrocephalus*. Report of the International Whaling Commission (Special Issue 6):51–79.

BRONSON, F. H. 1989. Mammalian reproductive biology. The University of Chicago Press, Chicago, IL.

CASTRO, J. I. 1993. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environmental Biology of Fishes 38:37–48.

CAUGHLEY, G., AND J. CAUGHLEY. 1974. Estimating median date of birth. Journal of Wildlife Management 38:552–556.

COCKCROFT, V. G., AND G. J. B. ROSS. 1990. Early development of a captive calf. Pages 461–478 *in* S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, San Diego, CA.

CONNOR, R. C., J. MANN, P. L. TYACK AND H. WHITEHEAD. 1998. Social evolution in toothed whales. Trends in Ecology and Evolution 13:228–232.

DAWBIN, W. H. 1966. The seasonal migratory cycle of humpback whales. Pages 145–170 *in* K. S. Norris, ed. Whales, dolphins and porpoises. University of California Press, Berkeley and Los Angeles, CA.

DEAROLF, J. L., W. A. MCLELLAN, R. M. DILLAMAN, D. FRIERSON, JR. AND D. A PABST. 2000. Precocial development of axial locomotor muscle in bottlenose dolphins (*Tursiops truncatus*). Journal of Morphology 244:203–215.

EVANS, P. G. H. 1987. The natural history of whales and dolphins. Facts on File, New York, NY.

FERNANDEZ, S., AND A. A. HOHN. 1998. Age, growth, and calving season of bottlenose dolphins, *Tursiops truncatus*, off coastal Texas. Fisheries Bulletin, U.S. 96:357–365.

GERACI, J. R., AND V. J. LOUNSBURY. 1993. Marine mammals ashore: A field guide for strandings. Texas A&M University Sea Grant College Program, Galveston, TX.

GRELLIER, K. 2000. Reproductive biology of bottlenose dolphins (*Tursiops truncatus*) using the Moray Firth, Scotland. M.Sc. thesis, University of Aberdeen. 73 pp.

HANSEN, L. J., AND R. S. WELLS. 1996. Bottlenose dolphin health assessment: field report on sampling near Beaufort, NC, during July 1995. NOAA Technical Memorandum. NMFS-SEFSC-382. 24 pp.

HOHN, A. A. 1997. Design for a multiple-method approach to determine stock structure of bottlenose dolphins in the mid-Atlantic. NOAA Technical Memorandum. NMFS-SEFSC-401. 22 pp.

MANN, J., AND B. B. SMUTS. 1998. Natal attraction: Allomaternal care and mother-infant separations in wild bottlenose dolphins. Animal Behavior 55:1097–1113.

MANN, J., AND B. B. SMUTS. 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops sp.*) Behavior 136:529–566.

MANN, J., R. C. CONNOR, L. M. BARRE AND M. R. HEITHAUS. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): Life history, habitat, provisioning, and group-size effects. Behavioral Ecology 11:210–219.

MCBRIDE, A. F., AND H. KRITZLER. 1951. Observations on pregnancy, parturition, and post-natal behavior in the bottlenose dolphin. Journal of Mammalogy 32:251–266.

MCLELLAN, W. A., A. S. FRIEDLAENDER, J. G. MEAD, C. W. POTTER AND D. A. PABST. 2003. Analysing 25 years of bottlenose dolphin (*Tursiops truncatus*) strandings along the Atlantic coast of the USA: Do historic records support the coastal migratory stock hypothesis? Journal of Cetacean Research Management. 4:297–304.

MEAD, J. G., AND C. W. POTTER. 1990. Natural history of bottlenose dolphins along the central Atlantic coast of the United States. Pages 165–195 *in* S. Leatherwood and R. Reeves, eds. The bottlenose dolphin. Academic Press, San Diego, CA.

MEAD, J. G., AND C. W. POTTER. 1995. Recognizing two populations of the bottlenose dolphin (*Tursiops truncatus*) off the Atlantic coast of North America: Morphologic and ecologic considerations. IBI Reports 5:31–44.

PERRIN, W. F. 1976. Growth and reproduction of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. Fisheries Bulletin, U.S. 74:229–69.

PERRIN, W. F., AND S. B. REILLY. 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. Report of the International Whaling Commission (Special Issue 6):97–133.

READ, A. J., AND A. A. HOHN. 1995. Life in the fast lane: The life history of harbor porpoises from the Gulf of Maine. Marine Mammal Science 11:423–440.

TEMTE, J. L. 1991. Precise birth timing in captive harbor seals (*Phoca vitulina*) and California sea lions (*Zalophus californianus*). Marine Mammal Science 7:145–156.

URIAN, K. W., D. A. DUFFIELD, A. J. READ, R. S. WELLS AND E. D. SHELL. 1996. Seasonality of reproduction in bottlenose dolphins, *Tursiops truncatus*. Journal of Mammalogy 77:394–403.

URIAN, K. W., A. A. HOHN AND L. J. HANSEN. 1999. Status of the photo-identification catalog of coastal bottlenose dolphins of the western North Atlantic: Report of a workshop of catalog contributors. NOAA Administrative Report NMFS-SEFSC-425. 24 pp.

WANG, K. R., P. M. PAYNE AND V. G. THAYER. 1994. Coastal stocks of Atlantic bottlenose dolphin: Status review and management. NOAA Technical Memorandum. NMFS-OPR-4. 120 pp.

WELLS, R. S., AND M. D. SCOTT. 1999. Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). Pages 137–182 *in* S. H. Ridgway and R. Harrison, F. R. S., eds. Handbook of marine mammals. Academic Press, London.

WELLS, R. S., M. D. SCOTT AND A. B. IRVINE. 1987. The social structure of free-ranging bottlenose dolphins. Current Mammalogy. 1:247–305.

WHITEHEAD, H., AND J. MANN. 2000. Female reproductive strategies of cetaceans. Pages 219–

246 *in* J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead, eds. Cetacean societies: Field studies of dolphins and whales. University of Chicago Press, Chicago, IL.

WHITEHEAD, H., AND L. WEILGART. 2000. The sperm whale: Social females and roving males. Pages 154–172 *in* R. C. Mann, P. L. Connor, P. L. Tyack and H. Whitehead, eds. Cetacean societies: Field studies of dolphins and whales. The University of Chicago Press, Chicago, IL.

WÜRSIG, B., AND T. A. JEFFERSON. 1990. Methods of photo-identification for small cetaceans. Reports of the International Whaling Commission (Special Issue Number 12):43–52.

WÜRSIG, B., AND M. WÜRSIG. 1977. The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science 198:399–412.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J.