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Author(s): Koen van Waerebeek and Andrew J. Read
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REPRODUCTION OF DUSKY DOLPHINS, *LAGENORHYNCHUS OBSCURUS,* FROM COASTAL PERU

KOEN VAN WAEREBEEK AND ANDREW J. READ

Centro Peruano de Estudios Cetológicos,
Asociación de Ecología y Conservación, casilla 1536, Lima 18, Peru (KVW)
Woods Hole Oceanographic Institution, Woods Hole, MA 02543 (AJR)

We examined the reproductive biology of 522 female and 330 male dusky dolphins, *Lagenorhynchus obscurus,* killed in Peruvian coastal fisheries between 1985 and 1990. Most births occurred in late winter (August, September, and October), although a few newborns were collected as late as February. Growth rate of fetuses was 0.261 cm/day; young were born at a mean length of 91 cm and mass of 9.6 kg. Gestation lasted for 12.9 months, followed by 12.0 months of lactation and a resting period of 3.7 months. The size of adult testes increased, reaching a maximum in September and October, in synchrony with the peak period of conception. The largest single-testis mass (with epididymis) was 5,120 g, and the maximum ratio of testis: body mass in mature males was 0.085, among the highest of any mammal. The large testes, relative sexual monomorphism, and apparent lack of aggressive behavior between males suggests a promiscuous mating system and sperm competition in this species.

Key words: *Lagenorhynchus obscurus,* dusky dolphin, Peru, reproductive biology

The reproductive biology of most dolphins and porpoises is poorly understood because of the difficulty of studying these animals at sea and problems in obtaining representative samples of carcasses (Perrin and Reilly, 1984). The genus *Lagenorhynchus* is especially poorly known, with reliable data available only for the Pacific white-sided dolphin, *L. obliquidens* (Walker et al., 1986), and a few scattered observations from other species (Harrison et al., 1972; Sergeant et al., 1980). Observations of the life history of the dusky dolphin, *L. obscurus,* have been limited to a preliminary description of age, growth, and reproduction from specimens from New Zealand (Cipriano, 1992; Webber, 1987) and a detailed study of the behavior of this species in Argentina (Würsig and Würsig, 1980).

In this paper, we describe aspects of reproduction in the dusky dolphin, based on observations of a large series of animals killed in Peruvian coastal fisheries. Several species of small cetaceans are captured both incidentally and directly in these fisheries, but the species most frequently taken is the dusky dolphin, with annual catches numbering into the thousands (Read et al., 1988; Van Waerebeek and Reyes, 1990). The impact of this mortality is unknown, but concern has been expressed over the population's ability to sustain such large removals (International Whaling Commission, 1991). Our intent in presenting these results is to improve the potential for management and conservation of the southeastern Pacific population of dusky dolphins (sensu Van Waerebeek, in press) by better understanding its basic life history.

We also were interested in examining the reproductive biology of this species because it inhabits an extremely unpredictable environment, the Peruvian coastal upwelling ecosystem, that is profoundly disturbed at irregular intervals by El Niño events. Our samples were collected in the years following the severe El Niño event during 1982–1983 (Barber and Chavez, 1983).

The present paper is limited to descriptions of seasonality and size at birth, estimation of the duration of the reproductive cycle of females, and observations of seasonal changes in reproductive status of males. Preliminary description of mean size and age at maturity may be found in Van Waerebeek (1992); a more detailed analysis of age-related, reproductive parameters is currently in preparation.

MATERIALS AND METHODS

We determined the reproductive status of 852 (522 females and 330 males) postnatal dusky dolphins. Most specimens were captured in coastal drift gillnets and landed at the central Peruvian ports of Pucusana (12°30′S), Cerro Azul (13°30′S), and Ancón (11°47′S) between January 1985 and April 1990. We examined dolphin carcasses at the fish markets in these coastal villages where they were eviscerated before being shipped to Lima (Read et al., 1988).

We recorded standard body length (taken from the tip of the upper jaw to the base of the fluke notch) and body mass from intact carcasses and obtained samples of reproductive tissues (ovaries and uterus from females, testes and epididymides from males) as the carcasses were eviscerated. We assessed lactation by exerting pressure on the mammary glands to express milk. Uteri were dissected in the field and carefully inspected for the presence of a fetus. Testes were weighed in the field with the epididymis still attached; we also recorded the linear dimensions (length, width, and height) of each testis. Final determination of reproductive status was made after considering the results of field necropsies and macroscopic examination of preserved tissues.

Females were considered sexually mature if at least one corpus luteum or corpus albicans was present on an ovary, or if the female was pregnant or lactating (Marsh and Kasuya, 1984; Perrin and Reilly, 1984). Females were considered pregnant only if we found a fetus in field dissections; early, pre-implantation pregnancies were not detected. We measured the mass and crown-rump length of fetuses during field examinations. Mature females neither pregnant nor lactating were classified as resting, a category that may include females with small, pre-implantation embryos as well as individuals truly between cycles (Perrin and Reilly, 1984).

We estimated the duration of gestation using the method of Hugget and Widdas (1951) as modified by Read (1990). The lengths of lactation (T_L) and resting periods (T_R) were estimated by assuming that the proportion of mature females in each reproductive condition was directly proportional to the relative length of time an individual spent in that condition (Perrin and Reilly, 1984). Thus, with an estimate of gestation period (T_G), it is possible to estimate the duration of lactation and resting periods:

$$T_L = T_G \times L/P \text{ and}$$

$$T_R = T_G \times R/P$$

where L represents the proportion of mature females lactating, P is the proportion pregnant, and R is the proportion resting. The annual pregnancy rate was defined as P/T_G, with T_G expressed in years (Perrin et al., 1976). We estimated mean size at birth from a sample of near-term fetuses and neonates using the 50% interpolation method, first with linear regression (Perrin and Reilly, 1984; Sergeant, 1962), and also using a second-order polynomial function with smoothed data.

The assessment of sexual maturity in males is complex, and several criteria have been used in previous research (Perrin and Henderson, 1984; Perrin et al., 1977*a*, 1977*b*; Sergeant, 1962). Due to the limitations imposed by field conditions, we used the method described by Sergeant (1962) and assessed functional maturity by the presence of seminal fluid in a gross field examination of the epididymis. This stage of maturity occurs somewhat later in ontogeny than that at which spermatogenesis can be detected histologically (Sergeant, 1962).

Several specimens with pathological reproductive organs were deleted from the dataset, as were a few females of dubious maturity status. Considerable variation exists in the sample sizes of specimens assessed for each reproductive condition because working conditions required us to collect incomplete data from many specimens.

RESULTS

Gestation and birth.—Reproduction was highly seasonal, resulting in synchrony of conception, fetal growth, and parturition. Seasonal growth in fetal length (Fig. 1) was described by a linear regression model ($F = 247$, $P < 0.0001$, $r^2 = 0.72$, $n = 96$; y

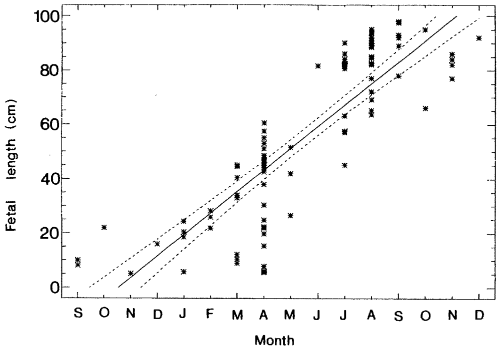

FIG. 1.—Temporal distribution of the size of 96 fetuses of dusky dolphins from Peru. The line representing the regression of fetal size on month is indicated with 95% *CI*.

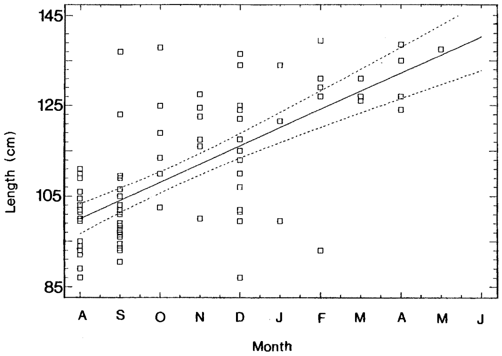

FIG. 2.—Temporal distribution of the size of 87 neonates of dusky dolphins from Peru. The line representing the regression of neonatal size on month is indicated with 95% *CI*.

= 11.59 + 7.92x), where y is standard length (cm) and x represents the median day of each month (January = 1, February = 2, and so on for year of parturition; November = −1 and December = 0 for the first months after conception). Fetal growth rate, thus, was estimated at 7.92 cm/month (*SE* = 0.50) or 0.261 cm/day. The length of neonates (animals <140 cm) also was significantly correlated with month ($F = 71.6$, $P < 0.0001$, $r^2 = 0.46$, $n = 87$; y = 67.83 + 4.02x; Fig. 2), where y is standard length (cm) and x represents the median day of each month (August = 8, September = 9 in the year of birth, to June = 18 in the second year). The low correlation coefficient of this relationship, compared with that of the fetal-growth equation, represents the additive effects of variation in birth date, birth size, and postnatal-growth rates.

We encountered most neonates ($n = 87$) and near-term fetuses ($n = 96$) in August, September, and October (Figs. 1 and 2), which appears to be the peak birth period of dusky dolphins in Peru during normal (i.e., non-El Niño) years. Our observations suggest that the onset of parturition is sudden, as we did not find neonates prior to August. The termination of the birth season is much less sharply defined, as we found a few near-term fetuses and neonates in December; single neonates were collected as late as February.

Mean length at birth was estimated from 96 fetuses and 87 neonates as 92.1 cm using the linear technique (Table 1) and as 90.7 cm using the smoothed polynomial (Fig. 3). We consider the arithmetic means of both values, 91.4 cm, as the best estimate of length at birth. Mean body mass at birth was estimated as 9.6 kg by substituting mean length at birth into a length-mass regression equation ($F = 12{,}630$, $P < 0.0001$, $r^2 = 0.99$) derived from 83 fetuses and neonates <105 cm in length (Fig. 4).

Mammalian fetal growth in length is curvilinear for the period immediately after conception and linear thereafter (Hugget

TABLE 1.—*Frequency distributions of the length of fetal and neonatal Peruvian dusky dolphins used to estimate mean length at birth.*

Class range (cm)	Midpoint	Total sample	Number of fetuses	Number of neonates	Proportion of neonates
80.5–84.5	82	12	12	0	0.00
84.5–88.5	86	7	5	2	0.29
88.5–92.5	90	11	8	3	0.27
92.5–96.5	94	16	5	11	0.69
96.5–100.5	98	15	2	13	0.87
100.5–104.5	102	13	0	13	1.00

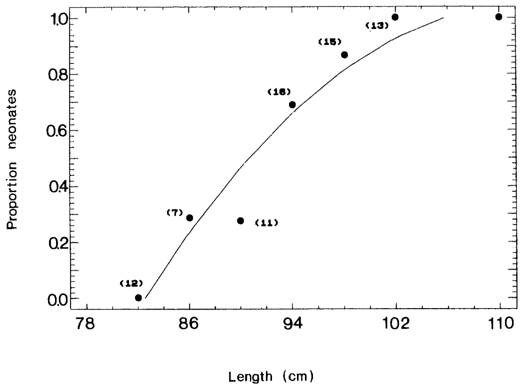

FIG. 3.—Proportion of neonatal dusky dolphins by standard length classes. The proportion of neonates refers to the number of neonates divided by the combined number of fetuses and neonates in each length class. Class sample sizes are denoted in brackets. Data (closed symbols) were smoothed by a second-order polynomial.

and Widdas, 1951). The total period of gestation (T_G) thus constitutes the initial curvilinear growth phase (t_0) and the later period of linear growth. The duration of t_0 may be derived from the allometric equation provided by Calder (1982):

$$t_0 = 7.25M^{0.19}$$

where M is mass at birth (g). Substituting the estimate of 9,600 g for mass at birth yields an estimate of 41.4 days, or 1.36 months, for t_0. We estimated the duration of linear fetal growth by substituting length values corresponding to the start of this phase (when fetal length is assumed to be 0.0) and to the mean birth length (91.4 cm) into the equation describing fetal growth. This yields an estimate of 11.53 months for the duration of linear fetal growth. Total gestation, therefore, lasts for 11.53 + 1.36 or 12.9 months (392 days). This computation also provided estimates of mean birth date (2 October) and mean conception date (5 September). This mean conception date is in agreement with the seasonal maximum in testis size, which is reached in September.

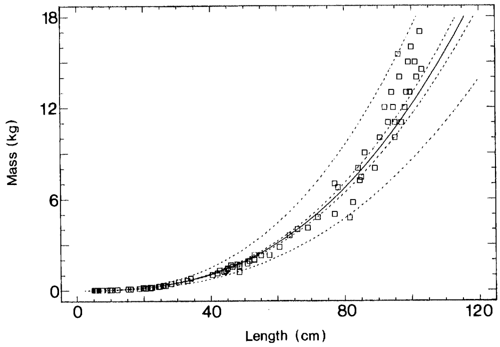

FIG. 4.—Relationship between body mass and standard length for fetal and neonatal (<105 cm) dusky dolphins from Peru. The dashed lines closest to the regression line represent 95% *CI* for the least-squares regression; the outer pair of dashed lines represent 95% estimation intervals for individual values.

We did not encounter multiplets in any pregnancy ($n = 96$). Following Kasuya and Marsh (1984), we determined the gender of fetuses >9 cm in crown-rump length. The fetal sex ratio was 1:1.33 ($n = 84$) in favor of females (95% *CI* 0.87—2.09). The neonatal sex ratio was 1:1.32 ($n = 86$) in favor of females (95% *CI* 0.87—2.08). The combined fetal and neonatal samples had a sex ratio of 1:1.32 ($n = 170$), which was not statistically different from 1:1 ($\chi^2 = 3.39$, $d.f. = 1$, $P = 0.066$).

Reproduction by females.—Of the 175 mature females checked for lactation, 87 were producing milk (L = 0.497). A fetus was found in 88 of 165 mature females ($P = 0.533$). Fifteen of 153 mature animals were simultaneously pregnant and lactating, and 22 of 144 were classified as resting (R = 0.153). The annual pregnancy rate (P/T_G) was, therefore, 0.555.

With a lactating-to-pregnant ratio of 0.497:0.533 and a gestation period of 12.9 months, we estimate that the average lactation period (T_L) lasted 12.0 months. The average time females spent in a resting period (T_R) was 3.7 months (12.9 months × 0.153/0.533). Thus, the mean length of the reproductive cycle ($T_G + T_L + T_R$) was ca. 28.6 months. The estimated duration of the resting period (T_R) was probably positively

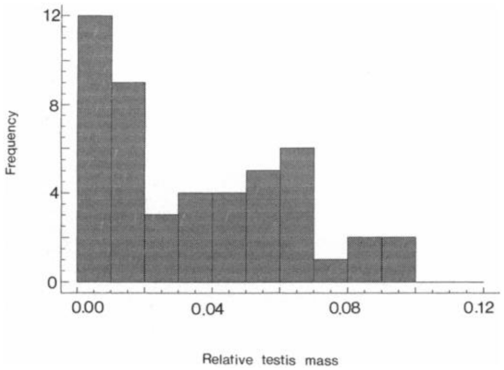

FIG. 5.—Frequency histogram of mass of testis and epididymis combined relative to body mass in 48 mature, male dusky dolphins from Peru. Data were pooled over all seasons.

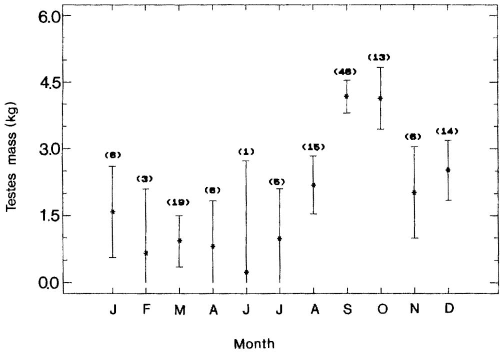

FIG. 6.—Seasonal variation in mass of testis and epididymis combined of sexually mature, male dusky dolphins from Peru; 95% *CI* based on pooled standard errors are shown. Monthly sample sizes are in brackets.

biased because females experiencing preimplantation pregnancy were grouped in this category. It is likely that the true resting period was extremely short and that the average reproductive cycle lasted for ca. 2 years, divided roughly equally between gestation and lactation. Other bias in these estimates is possible if females of different reproductive condition experienced differential probabilities of capture.

Reproduction by males.—In dusky dolphins from Peru, the mass and length of mature testes (with epididymides attached) ranged as follows: left testis 53–5,120 g ($\bar{X}$ = 1,464 g; $n = 125$) and 12.3–58.5 cm ($n = 132$); right testis 53–4,930 g ($\bar{X}$ = 1,486 g; $n = 125$) and 13.5–58.0 cm ($n = 133$). The maximum mass of testis and epididymis combined was 9,730 g. The heaviest pair of left and right immature testes ($n = 38$) weighed and measured 300 and 310 g and 23.0 and 24.0 cm, respectively. No difference was detected between the mean mass of left and right mature testes ($t = -0.128$, $P = 0.90$, *d.f.* = 123). The correlation between mass (y) and length (x) of left testis was highly significant ($F = 3{,}581$, $P < 0.0001$, $r^2 = 0.96$) and is expressed by $\log y = -10.86 + 3.02 \log x$.

The ratio of mass of the testis and epididymis combined : body mass in mature males, pooled over all seasons and years, ranged from 0.003 to 0.094 ($\bar{X} = 0.035$, $SD = 0.027$, $n = 48$; Fig. 5). The mass of the testis proper accounted for 90.6% ($SD = 4.9$, $n = 18$) of the mass of the testis and epididymis combined in adult males so that the maximum testis : body mass ratio (sensu Kenagy and Trombulak, 1986) in dusky dolphins from Peru was 0.085.

The mass of the testis of adult males increased in August, reached a maximum in September and October, and then decreased again in November (Fig. 6) in synchrony with the timing of ovulation and conception. The majority (20 of 24) of mature males that we examined in September and October had copious seminal fluid in their epididymides. An analysis of covariance demonstrated that the mass of the testis and epididymis combined of 51 mature males varied significantly among months, with body mass as covariate ($F = 2.18$, *d.f.* = 9,40, $P < 0.05$). Mass of testes combined was significantly correlated ($F = 43.9$, *d.f.* = 1,40, $P < 0.0001$) with total body mass. A second analysis of covariance with mass of the left testis as the response variable and body length as covariate employed a considerably greater sample ($n = 134$), resulting in statistically more significant seasonal variation ($F = 7.07$, $d.f. = 1,10$, $P < 0.0001$).

With few exceptions, males of adult size examined in all months of the year had some seminal fluid in their epididymides. This suggests that a complete cessation of testicular activity is rare, even outside the breeding season.

DISCUSSION

Reproduction in dusky dolphins from Peru is highly seasonal. Births are synchronized, with most occurring in September and October. After a gestation of almost 13 months, young of dusky dolphins are born at a mean length of ca. 91 cm and mass of 9.6 kg. After parturition, female dolphins nurse their young for ca. 1 year before mating again. During August and September, in the peak breeding season, male dolphins possess extremely large testes, which regress considerably during other periods of the year.

We are confident that our estimates of the timing and size at birth are accurate reflections of reproduction in this population of dusky dolphins. Likewise, our estimate of the duration of gestation seems well founded on empirical observation of fetal-growth rates. However, our estimates of the duration of lactation and resting periods depend on the proportion of females in our sample in each of these reproductive categories. These proportions are subject to bias if females of different reproductive status experience different probabilities of capture. For example, female dolphins with newborns might be more (or less) susceptible to capture than resting individuals unaccompanied by dependent offspring. Unfortunately, we have no information on differential capture susceptibility in the coastal, drift-net fishery that took the majority of our sample. In Argentina, female dusky dolphins of different reproductive status exhibit segregation, including the formation of nursery groups composed primarily of lactating females and their dependent offspring (Würsig and Würsig, 1980). Such segregation could increase the potential bias in our estimates of the duration of lactation and the resting period. Resolution of these potential problems must await a more detailed examination of the age and reproductive history of individual females in our sample.

If our estimates of the duration of the lactation and resting periods are accurate, dusky dolphins in Peru exhibit a shorter reproductive cycle and a higher fecundity than other dolphins of similar size (Perrin and Reilly, 1984). It is possible that this is a population response to large removals by the fishery or perhaps a reproductive strategy evolved in response to the extreme unpredictability of the Peruvian upwelling system. El Niño events severely disrupt the oceanography of the Peruvian coastal ecosystem at irregular intervals (Bohle-Carbonell, 1989; Brink et al., 1983), severely reducing food availability to upper-trophic-level predators (Barber and Chavez, 1983; Gunther, 1936; Muck et al., 1989). In particular, El Niños deplete the population of anchoveta, *Engraulis ringens,* the main prey of dusky dolphins (McKinnon, 1988). Records of the severe El Niño during 1982–1983 are present in the dentine of adult, female dusky dolphins from Peru, presumably reflecting the nutritional stress experienced by these animals (Manzanilla, 1989). Pinnipeds and seabirds experience widespread mortality and reproductive failure during severe events (Barber and Chavez, 1983; Trillmich and Limberger, 1985; Trillmich et al., 1986), and it is likely that dusky dolphins suffer a similar fate.

The timing of reproduction was fairly consistent over the study period (1985–1990), although some of the spread in average fetal and neonatal growth trajectories (Figs. 1 and 2) probably is due to slight interannual variation in the timing of reproduction. Our preliminary observations from the 1991–1992 season (not included here) indicate that the breeding season shifted, with most births occurring in late spring and early summer (J. C. Reyes, pers.

comm.), and small fetuses appearing in May. This shift in reproductive timing was likely related to the appearance of a medium-strength El Niño event in Peruvian coastal waters.

In Argentina, most births of dusky dolphins occur during the austral summer, based on observations of small young from November to February (Würsig and Würsig, 1980). Thus, the widely separated populations of dusky dolphins in the southeastern Pacific and southwestern Atlantic appear to exhibit reproductive segregation. Observations of dusky dolphins in New Zealand indicate that parturition there also occurs during summer, between November and January, the season when dolphins are found closest to shore (Cipriano, 1992). The movements of dusky dolphins in Peru have not been studied, but the directed dolphin fishery is highly seasonal in nature, with the largest number of animals landed during the period of parturition (Read et al., 1988), suggesting that dolphins may be more vulnerable to capture during this season.

Little quantitative information exists on size at birth in other populations of dusky dolphins. The three smallest young examined by Cipriano (1992), including two neonates, ranged from 97 to 102 cm. Another newborn male from New Zealand measured 83 cm in length with a body mass of 9.1 kg (specimen ZMA 14.764, Zoological Museum of Amsterdam; P. J. H. van Bree, pers. comm.). Adult dusky dolphins from New Zealand are smaller than their Peruvian counterparts (Cipriano, 1992; Van Waerebeek, 1992), but it is not known whether this difference is accompanied by a smaller mean size at birth.

The mass of testes of male dusky dolphins from Peru, 8.5% of body mass, is among the highest of all mammals (compare with data from Kenagy and Trombulak, 1986). Similar observations of the relative size and seasonal regression of testes of dusky dolphins have been made from New Zealand (Cipriano, 1992). The largest relative size of testes reported from other odontocetes, that of the harbor porpoise *Phocoena phocoena,* comprises "only" 4% of body mass (Harrison, 1969; Read, 1990). In many mammals, a functional relationship exists between the relative size of testes and the mating system (Kenagy and Trombulak, 1986). Testes typically are small in single-male breeding systems (monogamy or extreme polygyny) and large in multi-male systems, where several males may mate with a single female in estrus. In these latter cases, the evolution of large testes may be attributed to the competition of sperm from different males for fertilization of the same female that requires a high copulation frequency and high levels of sperm production (Harcourt et al., 1981; Kenagy and Trombulak, 1986). A high degree of sexual dimorphism in size and striking secondary sexual characteristics have been correlated with a polygynous mating system and relatively small testes in mammals (Jefferson, 1990; Kenagy and Trombulak, 1986; Ralls, 1977; Ralls et al., 1980). In contrast, the low level of sexual dimorphism (Van Waerebeek, 1992) the enormous testes, and the low degree of scarring on males that might reflect agonistic behavior (Van Waerebeek, 1992) point to a promiscuous mating system in *L. obscurus,* as also suggested by Cipriano (1992). This type of mating system would function well in a gregarious species like the dusky dolphin, which exhibits a high degree of reproductive synchrony and, thus, many opportunities for mating in a relatively short period.

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