Reproductive Seasonality in Pelagic Dolphins (*Stenella* spp.): Implications for Measuring Rates

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ABSTRACT

This paper examines the patterns of reproductive seasonality in two species of dolphin in the eastern tropical Pacific: *Stenella attenuata* and *S. longirostris*. These are the principal species used by tuna purse seiners in locating schools of yellowfin tuna in this area. Birthdate distributions are calculated from the lengths-at-capture of fetuses and calves killed in fishing operations, the dates of captur~, and the estimated growth curves for these species. Although births were found to occur at all times of the year, distinct modes could be seen in the distributions. Geographic differences in patterns of seasonality could be distinguished on the basis of the strength of the observed modes, the number of modes, and their timing. The northern stock of *S. attenuata* has a diffuse bimodal pattern in annual reproduction with peaks in spring and autumn. The southern stock of this species has a strong unimodal pattern whose timing corresponds to the spring peak in the northern stock. The eastern spinner form of *S. longirostris* also has a single annual peak in reproduction, between March and June, with regional differences in the timing of this mode. The whitebelly spinner form of *S. longirostris* shows a bimodal pattern with peaks in spring and autumn. These seasonal patterns in reproduction can affect reproductive rate measurements by changing our concept of stock boundaries or by introducing biases due to time of sampling. If the mating season is short, this can also limit the rate at which females can be inseminated after an aborted pregnancy, calf death, or weaning.

INTRODUCTION

This report examines the seasonal patterns of reproduction in pelagic dolphins of the eastern tropical Pacific. Four dolphin stocks are considered: the 'northern offshore' and 'southern offshore' forms of the spotted dolphin (*Stenella attenuata*) and the 'eastern' and 'northern whitebelly' forms of the spinner dolphin (*Stenella longirostris*) (see Perrin (1975) and Perrin, Sloan and Henderson (1979) for stock delineations). Stock boundaries for these species are given in Smith (1979); Figs 1, 2, and 3 show approximate ranges. A statistical method is presented for comparing distributions of birthdate, and this method is used to test geographic differences in birthdate distributions within the same species.

S. attenuata and *S. longirostris* are the principal species used by tuna purse-seiners in locating schools of yellowfin tuna. Historical kills of dolphins incidental to this fishery have been large, totaling several millions (Smith, 1979), which has prompted management efforts in recent years. This paper will also consider the implications of seasonal reproduction in measuring the reproductive rates of Cetacea. These implications may prove important in the management of eastern Pacific dolphin stocks.

Previous work on reproductive patterns of these dolphin stocks has shown two broad peaks in calving (one in spring and one in autumn) for spotted dolphins (Perrin, Coe and Zweifel, 1976) and a rather diffuse pattern of seasonality for eastern spinners (Perrin, Holts and Miller, 1977). Perrin *et al.* (1977) found one birth mode in late January of 1974 for eastern spinners, but noted that the timing of births appeared to vary from one area to another. Work on a different stock of *S. attenuata* off the coast of Japan indicated perhaps three peak periods of parturition (Kasuya, Miyazaki and Dawbin, 1974). Similarly Miyazaki (1977) interpreted data on a closely related species (*S. coeruleoalba*) as indicating three annual modes in births.

Of the small toothed whales, strong patterns of reproductive seasonality are most evident in the temperate and subarctic species. The common porpoise (*Phocoena phocoena*) in the North Atlantic (Fisher and Harrison, 1970), the common dolphin (*Delphinus delphis*) off California's coast (Harrison, Boice and Brownell, 1969), the white whale (*Delphinapterus leucas*) off Baffin Island (Brodie, 1971) and the white-sided dolphin (*Lagenorhynchus obliquidens*) off California (Harrison *et al.*, 1969) all show a single period of parturition during the year. Tropical species such as *S. attenuata* and *S. longirostris* and more cosmopolitan species such as *Tursiops truncatus* (Harrison and Ridgway, 1971) may have multiple breeding seasons or diffuse patterns of reproductive seasonality.

MATERIALS AND METHODS

The data upon which this report is based were gathered between 1968 and 1978 by the National Marine Fisheries Service (NMFS) scientific technicians aboard tuna purse-seiners. The sample represents dolphins that were killed as a result of the tuna purse-seining operations. Seining for yellowfin tuna was seasonal during these years, both in its intensity and its areas of operation. Typically, the US fleet concentrated its effort near the coastline for the first several months of the year. Later in the year, fishing intensity slackened and the fleet's efforts were concentrated more offshore.

Extensive life history data were gathered by the NMFS technicians. The items of principal interest in this report were the date, lengths, and collection localities of young dolphins and fetuses that died in the purse seines.

Patterns of reproductive seasonality are most easily summarized by the frequency distribution of birthdates. Two methods were used to estimate birthdates, one from prenatal dolphins and the other from postnatal. These methods are similar to those used by Kasuya *et al.* (1974) and Perrin *et al.* (1976).

Table 1

Postnatal and fetal growth rates used in the projection of birthdate distributions. Postnatal growth parameters are as defined by Perrin *et al.* (1976)

Population	Length at birth (cm)	Postnatal growth parameters		Fetal growth rate (cm/month)	Reference
		a	*α*		
Offshore spotted dolphin	82	0.963	1.414	8.28	Perrin *et al.* (1976)
Eastern spinner dolphin	77	0.995	1.365	8.37	Perrin *et al.* (1977)
Whitebelly spinner dolphin	77	0.950	1.290	8.37	Perrin and Henderson (1979)

The first method involves the forward projection of birthdates from fetal lengths and dates of capture. Fetal growth parameters were taken from Perrin *et al.* (1976, 1977) (Table 1). The fetal growth rate of the whitebelly spinner dolphin was assumed to be the same as its conspecific, the eastern spinner; likewise the fetal growth rate of the southern offshore spotted dolphin was taken to be the same as that of the northern offshore spotted dolphin. Only fetuses greater than 10 cm long were used, and growth rates were assumed to be constant. If gestation were significantly less than 1 year, seasonality in sampling could affect the birthdate distributions projected by this method. Since gestation is estimated to be 11.5 and 10.6 months respectively for *S. attenuata* and *S. longirostris* (Perrin *et al.*, 1976, 1977), this effect should be insignificant. No correction was made for the time of sampling.

The second method involves the back projection of the birthdates of postnatal dolphins from their lengths and dates of capture. Postnatal growth rates were taken from Perrin *et al.* (1976, 1977) and Perrin and Henderson (1979). Growth was assumed to follow the Laird/Gompertz model (Laird, 1966).

$$L(t) = L_0 \cdot \exp\left[(a/\alpha) \cdot (1 - \exp(-\alpha \cdot t))\right].$$

The values used for the parameters above are given in Table 1. These values correspond to the hypothesized 2.0, 1.5, and 1.36 dentinal growth layers in the first year respectively for spotted dolphins (Perrin *et al.*, 1976), eastern spinner dolphins (Perrin *et al.*, 1977), and whitebelly spinner dolphins (Perrin and Henderson, 1979).

The back-projection method was only applied to animals estimated to be less than 1 year old (less than 132 cm for *S. longirostris* and 138 cm for *S. attenuata*). In practice, this method is only useful for young animals, for which growth is rapid relative to individual variation in growth rate. The 1-year age interval was chosen to minimize the potential bias from seasonality in sampling.

Statistical methods used for comparing birthdate distributions are a variation of the Kolmogorov/Smirnov (K/S) one- and two-sample tests. These are nonparametric tests for goodness of fit based on cumulative distributions. Birthdate distributions are, however, circular (Fig. 4), and therefore the results of a conventional K/S test could depend on which month is taken as the beginning of the distribution. The modifications made by Kuiper (1960) and discussed by Batschelet (1965) allow the unambiguous use of these tests on circular distributions. The statistic used for the one sample test is the sum of the maximum positive and negative deviations of the observed cumulative distribu-
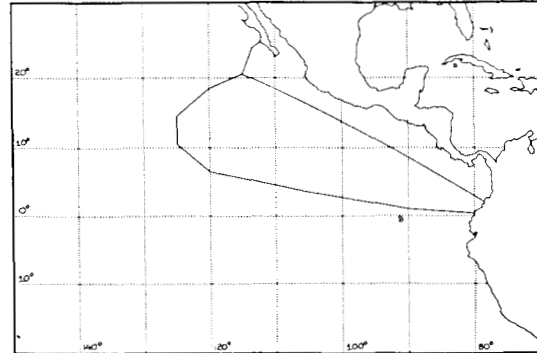

Fig. 1. Geographic distribution of eastern spinner dolphins (*Stenella longirostris*) in the eastern tropical Pacific. Inshore/offshore regions are defined by diagonal line.
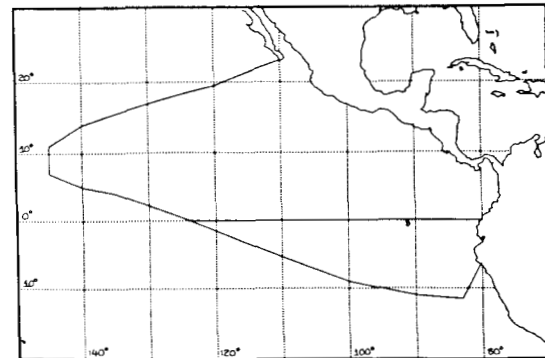

Fig. 2. Geographic distribution of offshore spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific. Northern and southern regions are defined by the equator.
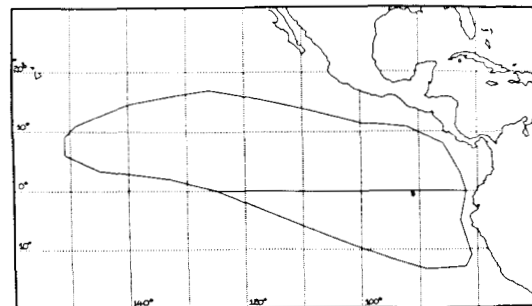

Fig. 3. Geographic distribution of whitebelly spinner dolphins (*Stenella longirostris*) in the eastern tropical Pacific. Northern and southern regions are defined by the equator.
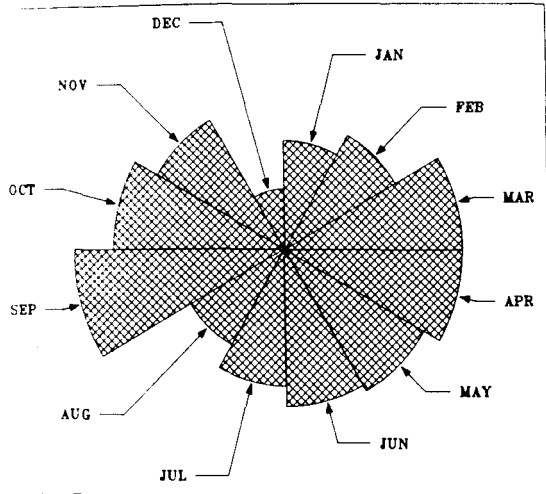
Fig. 4. Birthdate distribution of northern offshore spotted dolphins (*Stenella attenuata*) projected from lengths of fetuses. Length of each ray is proportional to the number of births expected in the given month.

tion from the expected cumulative distribution. Similarly, the statistic for the two sample test is the sum of the maximum positive and negative deviations of one cumulative distribution from the other. The critical values for the two-sample version of this test have not been tabulated for unequal sample sizes. For this reason, statistical comparisons were made only when sample sizes were roughly equal, and in such cases, the smaller sample size was used, which makes the test conservative.

To examine geographic variability in birthdate distributions, where sample size permitted, the samples were stratified by geographical areas. Because Perrin *et al.* (1977) noted an inshore/offshore difference in seasonality for the eastern spinner dolphin, this stock was divided into inshore and offshore ranges by a line drawn roughly parallel to the coastline (Fig. 1). To facilitate statistical comparisons, the line was drawn so as to provide approximately equal sample sizes. The offshore spotted dolphins were divided into a northern and a southern stock by a line drawn along the equator (Fig. 2). In order to better understand the latitudinal variability of reproductive seasonality in this species, the sample of northern spotted dolphins was further divided into those caught between the equator and 5° N and those caught north of 5° N. Due to small sample sizes, geographical stratification of the northern whitebelly spinner range (Fig. 3) was not attempted. Also the southern whitebelly spinner was not considered due to its small sample size.
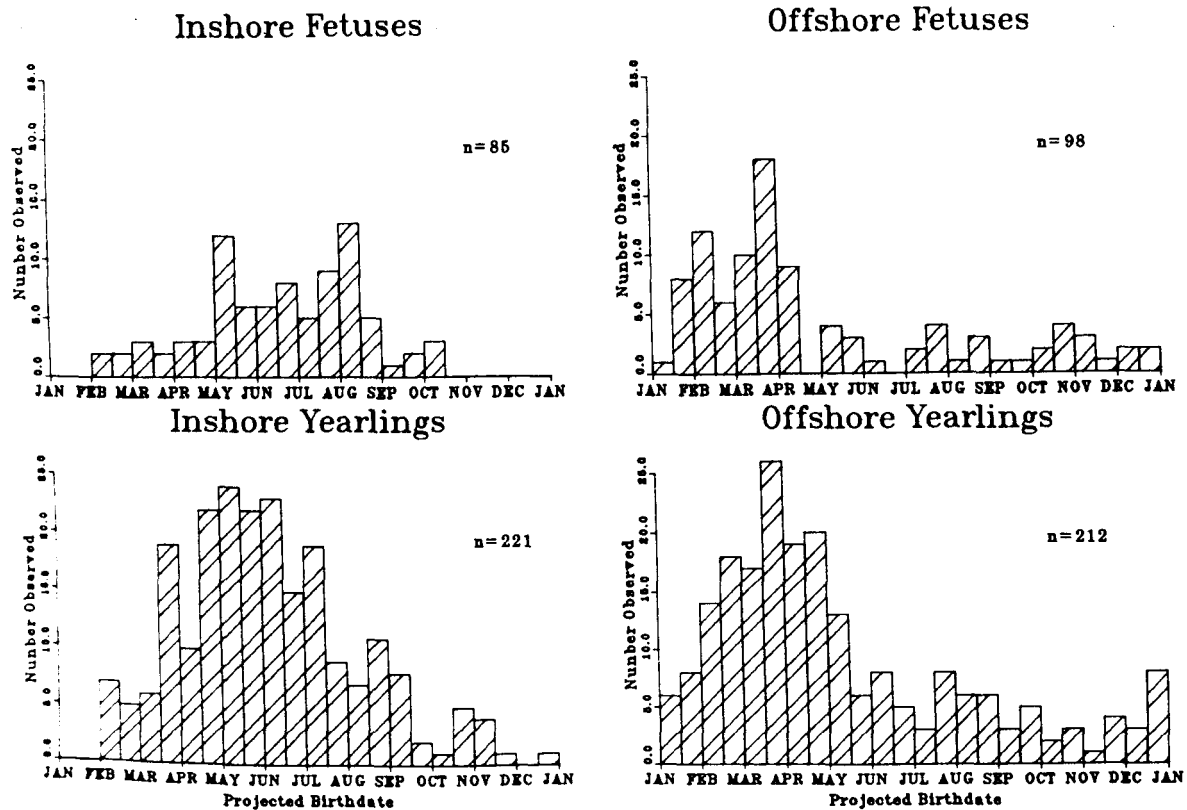

Fig. 5. Birthdate distributions of eastern spinner dolphins (*Stenella longirostris*) projected from lengths of fetuses (top) and calves (bottom). Inshore/offshore geographic stratification is as shown in Fig. 1.
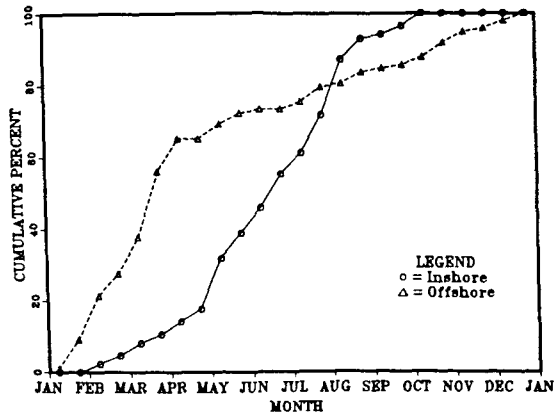
Fig. 6. Cumulative birthdate distributions of inshore and offshore groups of eastern spinner dolphins (*Stenella longirostris*) projected from lengths of fetuses. Geographic stratification is as shown in Fig. 1.

To avoid possible confounding of data for the 'offshore' and 'coastal' forms of the spotted dolphin (Perrin, 1975), only those individuals classified as belonging to the 'offshore' group and found more than 100 km from the coastline were included.

RESULTS

Eastern spinner dolphin

A single, strong peak can be seen in the birthdate distributions projected for the eastern spinner dolphin (Fig. 5). Although similar peaks are evident for both inshore and offshore areas, a regional difference can be noted in the timing of these peaks. For both the forward and back projection methods, the peak calving period occurs earlier in the year for the more offshore group.

The regional differences in seasonality were compared with the two sample K/S test described above (illustrated in Fig. 6 for the projection from fetal lengths). For both projection methods the differences were statistically significant ($P < 0.01$). Although differential growth rates in the two regions could contribute to apparent differences in birthdate distributions, this explanation is unlikely because the forward and back projection methods corroborate each other's results. For growth rate variations to bias the result in the same way for both of the projection methods, the fetal and postnatal growth rates would have to differ in a reciprocal manner. A regional difference in reproductive seasonality is thus indicated for the eastern spinner dolphin.

Whitebelly spinner dolphin

The birthdate distributions for the whitebelly spinner appear to be bimodal when projected from fetal lengths (Fig. 7). The modes are approximately 6 months apart. The birthdate distribution obtained from the lengths of postnatal dolphins shows no evidence of this bimodal pattern (Fig. 7). The two sample K/S test indicates that the two estimated birthdate distributions are significantly different ($P < 0.05$). If a one sample K/S test is applied, the results indicate that the birthdate distribution
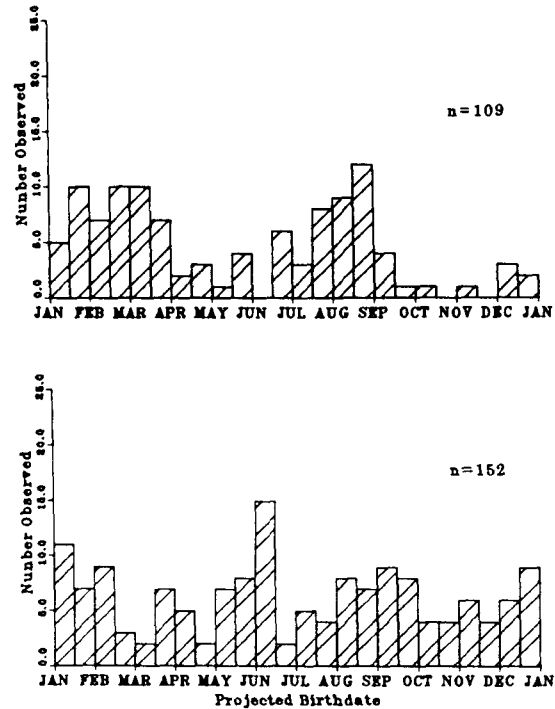

Fig. 7. Birthdate distributions of northern whitebelly spinner dolphins (*Stenella longirostris*) projected from lengths of fetuses (top) and calves (bottom). The equator was taken as the lower limit of their geographic distribution.

projected from fetal lengths is significantly different from a uniform birthdate distribution ($P < 0.01$), but that projected from calf lengths is not ($P < 0.1$).

Northern offshore spotted dolphin

The birthdate distribution derived from the northern offshore spotted dolphin (Fig. 8) showed a rather even distribution of reproduction throughout the year. Using a one sample K/S test, the observed distributions can be shown to be significantly different from a uniform distribution for both methods of birthdate projection ($P < 0.01$, illustrated in Fig. 9 for projections from fetal lengths). Although the apparent seasonality is not strong, there is a tendency for more births to occur in spring and autumn than in other times of the year. This pattern of seasonality may not be constant from year to year. Perrin *et al.* (1976) suggested that annual changes in the season of peak reproduction might be occurring, and additional evidence for this was presented by Barlow (1979).[1]

Southern offshore spotted dolphin

The distribution of birthdates from the southern stock of the offshore spotted dolphin (Fig. 8) is very different from that of the northern stock of this species. For the southern

[1] Barlow, J. 1979. Reproductive seasonality in pelagic dolphins of the eastern tropical Pacific. NMFS, Southwest Fisheries Center, Status of the Porpoise Stocks Workshop Doc. 26, La Jolla, California, 27–31 August 22 pp.

Northern Fetuses

Southern Fetuses

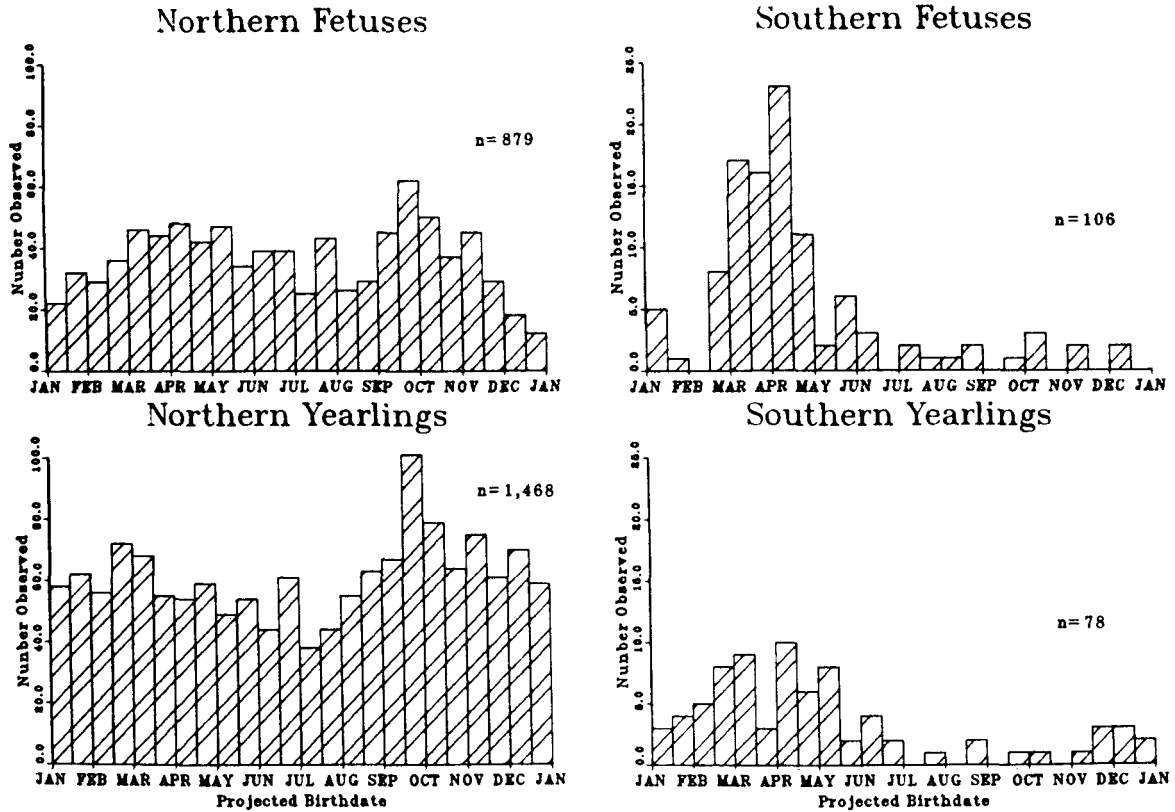## Northern Yearlings

Southern Yearlings

Fig. 8. Birthdate distributions of offshore spotted dolphins (*Stenella attenuata*) projected from lengths of fetuses (top) and calves (bottom). North/south geographic stratification is as shown in Fig. 2.
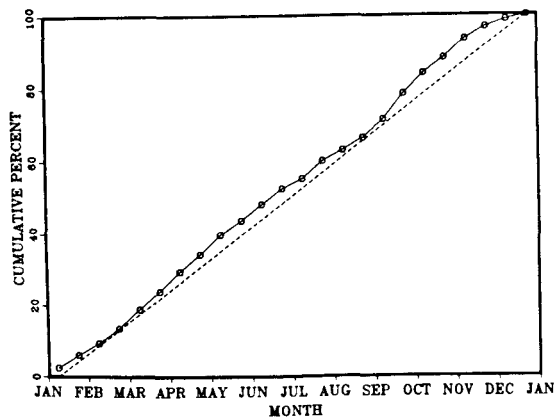
Fig. 9. Cumulative birthdate distribution of northern offshore spotted dolphins (*Stenella attenuata*) projected from lengths of fetuses. Broken line indicates expected cumulative distribution if births were uniformly distributed throughout the year.

stock, the season of parturition is quite short, with most births occurring from March through May. Indeed this group shows the strongest pattern of seasonality of any of the stocks considered here. Sample sizes for the southern population were small, so no attempt was made

to divide its range into sub-regions to examine finer geographic differences in birthdates.

Having shown distinct differences between the timing of reproduction in spotted dolphins north and south of the equator, it would be helpful to know whether these changes occur over a narrow range of latitude or whether there is a gradual change from a diffuse bimodal pattern in the north to a strong unimodal pattern in the south. The sample of northern spotted dolphins was therefore stratified into a group taken between the equator and 5° N and a group taken north of 5° N (Fig. 10). Although the sample size is small, those spotted dolphins caught between 0–5° N appear to have a diffuse pattern of seasonality but with one peak from March to June. Two sample K/S tests show this pattern to be significantly different from both that taken from south of the equator (Fig. 8) and that taken from north of 5° N (Fig. 10).

DISCUSSION

As with other dolphin species that have been studied to date, the stocks of *Stenella attenuata* and *S. longirostris* in the eastern tropical Pacific show seasonal patterns in their reproduction. Unlike the strict seasonality of temperate and subarctic species, seasonality in these tropical dolphins is manifest as one or more calving peaks per year, with some parturition occurring throughout the

Fetuses from Equator to 5° N
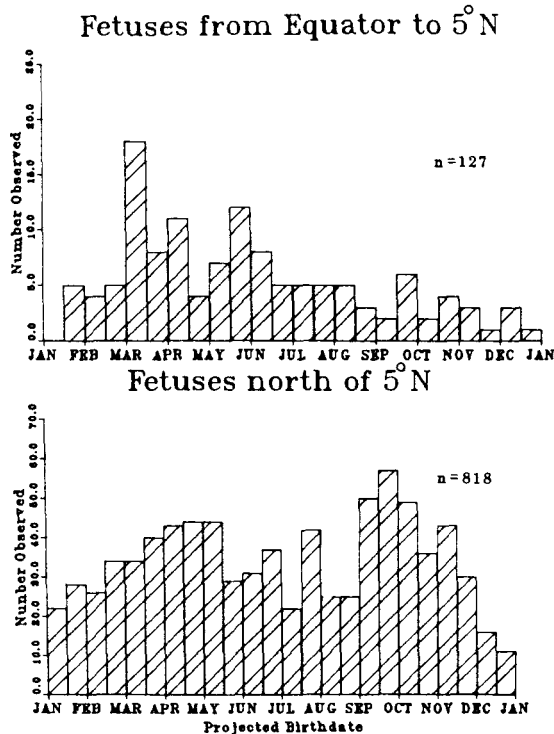

Fetuses north of 5° N

Fig. 10. Birthdate distributions projected from fetuses of northern spotted dolphins (*Stenella attenuata*) grouped by latitude at time of capture.

year. The reproductive seasonality of these species can be characterized by the strength of the observed modes, the number of modes, and their timing. Based on these criteria, there are significant differences in reproductive patterns between dolphin populations that have previously been identified based on morphological criteria, and there is evidence of significant geographic differences in seasonality within these recognized stocks.

The eastern and whitebelly stocks of *S. longirostris* were originally separated on the basis of morphology (Perrin, 1975). This distinction is corroborated by the differences noted here in reproductive seasonality. The eastern spinner (Fig. 5) has a single peak in births, and the whitebelly spinner (Fig. 7) shows at least two modes. It should be noted that the modes in both cases show a sharper definition when projected from fetus lengths. This may attest to the greater precision of the fetal birthdate projection method (despite smaller sample sizes). This would be expected if fetal growth shows less individual variability than that of postnatal animals, or if the estimated growth curves are more accurate for fetuses than for calves.

Within the eastern group, additional geographic differences in seasonality (discussed above) may indicate that a further subdivision of this species would be meaningful. Although both the inshore and offshore groups of eastern spinners show a single annual mode in parturition, this mode occurs significantly earlier in the offshore area. Distributional studies of these dolphins indicate that there are inshore and offshore population

centers for eastern spinners with a paucity of sightings in between (Fig. 5 in Au, Perryman and Perrin, 1979). These two observations suggest that the eastern spinner stock might consist of two populations. Regional differences in the timing of a reproductive cycle could be due, of course, to local differences in the seasonality of environmental factors, such as food supply. If this were the case for eastern spinners, reproductive isolation of the inshore and offshore groups would not necessarily result. Before these groups could be identified as separate stocks, further work would be required to determine the degree of isolation, perhaps by means of tagging, genetic, or morphometric studies.

The patterns of seasonality in the northern whitebelly spinner are more difficult to interpret. Although the birthdate distribution projected from fetuses shows a bimodal pattern, that projected from calf lengths shows no clear pattern at all (Fig. 7). Perrin and Henderson (1979) showed that for whitebelly spinners, variations in male testis weight were seasonal, with two modes. The peak periods of testis weight correspond well to the expected breeding seasons given the birthdate distributions taken from fetuses. As noted above, the birthdate distributions taken from fetuses tend to show better definition than those estimated from calves. For these reasons, two annual peaks in reproduction are taken to be the most likely pattern. The absence of these modes in the birthdate distributions projected from calves may be simply due to the combination of sampling error and the high degree of variance associated with this projection method. Alternatively, the difference could be due to misidentification of calves to stock in the area of overlap with the eastern spinner dolphin, or to error in estimating length at birth or postnatal growth rate for this stock. Larger sample sizes may help resolve this apparent discrepancy.

The offshore spotted dolphins were originally considered a single population (Perrin, 1975); however, more recent evidence (Perrin et al., 1979) has supported the consideration of a separate population south of the equator. Evidence presented here for marked seasonal differences in reproduction supports this view. The transition from a diffuse bimodal pattern in the north to a strong unimodal pattern in the south may not be abrupt. Dolphins taken between the equator and 5° N show a single mode synchronous with that of the animals to the south, but they show a more diffuse pattern of seasonality similar to that of the northern spotted dolphins. The explanation of this gradual change is not known. If seasonality in reproduction is determined by the timing of oceanographic or trophic factors, the change could reflect a geographical change in the timing of these physical determinants. Alternatively, the area between 0° and 5° N could represent an area where two separate populations can both occur with the birthdate distribution from that area being a composite of two different distributions. A hiatus in spotted dolphin sightings has been used to determine the boundary between the northern and southern stocks; this region is just south of the equator (Perrin et al., 1979). If this proves to be an accurate boundary, the latter hypothesis could be rejected.

Seasonal patterns of reproduction have been examined for the populations of *Stenella* off the coast of Japan.

Three annual periods of parturition were shown for both *S. attenuata* (Kasuya, Miyazaki and Dawbin, 1974) and *S. coeruleoalba* (Miyazaki, 1977). These estimates were based, however, on the back calculation of birthdates from animals that were up to 2 years old. Individual variation in growth would almost certainly act to obscure seasonal patterns estimated from the older animals. Using only the birthdate distributions taken from fetuses, the data indicate a single mode in the births of *S. attenuata* (Fig. 33 in Kasuya *et al.*, 1974) and an obvious bimodal pattern for *S. coeruleoalba* (Fig. 16 in Miyazaki, 1977).

The reason for the observed differences in reproductive seasonality within the genus *Stenella* are not clear. One possible explanation is that density-dependent changes occurred as a result of exploitation. The southern spotted form of *S. attenuata* has been exploited only lightly (Smith, 1979). This population shows a single strong peak in reproduction, which I will, for purpose of discussion, assume to be the 'natural state' for this genus. Given that all mating occurs at the same time each year, the calving cycle must be an integral number of years: say, for example, 3 years. As exploitation decreases population size, the calving interval might decrease to 2.5 years due to density-compensatory effects. This calving interval would not be consistent with a single annual season of births, hence a bimodal pattern might result. Such a pattern was found in *S. coeruleoalba* off the coast of Japan, in the northern spotted form of *S. attenuata*, and in the northern whitebelly form of *S. longirostris*, all of which have been exposed to moderately heavy exploitation (Kasuya, 1976; Smith, 1979). If the calving period were reduced further, say to 2 years, a single annual mode in births would again be possible. This pattern was seen in the eastern spinner form of *S. longirostris* which has been subject to very heavy exploitation (Smith, 1979). Although speculative, this explanation is consistent with the observed patterns of seasonality in this genus. These predicted patterns can be tested as accurate estimates of calving period become available for these stocks.

Regardless of their cause, the observed patterns of reproductive seasonality can affect our estimation of birth rates for these dolphins in several ways. First, reproductive seasonality, once established, can impose barriers to reproduction and hence change our concept of what constitutes a stock or population. Clearly this is of importance in the management of marine mammals.

Another aspect of seasonality of importance in management is the introduction of bias in the estimation of reproductive rates due to seasonality of sampling effort. For instance, the fraction of pregnant females in a population could be underestimated if sampling of that population were predominantly during the time between the period of peak births and that of peak conceptions. If gestation were 10 months, this time interval would be 2 months. A method for correcting this sort of sampling bias was presented by Barlow (1979). In general, if gestation is close to 1 year (as it is for most dolphins), and if reproductive peaks are somewhat diffuse (as they are for most tropical species), this bias will be small.

The final aspect of reproductive seasonality to be discussed here is a consequence of the synchrony it imposes. If births are restricted to a short season, as in

the case of the southern spotted dolphins, then the inter-birth period will necessarily be an integral number of years. This does not mean that the average calving period will be an integer since some individual variability may exist in lactation times and since not all females may become pregnant during the first breeding season after weaning. For birth rate estimates that only involve mean calving interval, synchrony need not affect the resulting estimate of birth rate. However, if the estimation of reproductive rates involve more mechanistic considerations (such as spontaneous abortions and calf mortality) the rate at which females become reinseminated becomes important. If, as was shown by Perrin and Henderson (1979), male fertility is also seasonal, a female that loses her calf might not become pregnant again until the next breeding season. This simple scenario is complicated by the fact that some males always have active sperm production and that conception can occur at any time of the year. Regardless, a model could be developed that would take such seasonal effects into consideration.

ACKNOWLEDGMENTS

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