Growth and Reproductive Rates in Two Populations of Spinner Dolphins, *Stenella longirostris*, with Different Histories of Exploitation[1]

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ABSTRACT

A model of density-dependent change in net reproductive rate (births minus deaths) has been used in assessing status of dolphin stocks in the eastern tropical Pacific. The eastern spinner population has been estimated to be at a lower fraction of original size (17–25%) than is the population of whitebelly spinners (58–72%). Higher reproductive rates would be expected in the former than in the latter on the basis of the density-dependent model, provided the latter is above its level of maximum net production. Based on analyses of over 4,000 specimens collected through 1978: (1) there is a relative paucity of fully adult males in the eastern spinner population (possibly resulting in lower average fertility), (2) the eastern spinner female attains sexual maturity about one tooth-layer unit (probably one year) earlier than does the whitebelly spinner, (3) ovulation rate in young females is lower in the eastern spinner population, and (4) the proportion of all females which are sexually mature is lower in the eastern spinner population. Gross annual reproductive rates (proportion female × proportion of females mature × pregnancy rate) are not different in the two populations (about 8–10% in both cases). This comparison does not confirm the hypothesis that a density-dependent increase in gross reproduction occurs in the spinner dolphin.

INTRODUCTION

Tuna seiners operating in the eastern tropical Pacific (ETP) kill dolphins incidentally during fishing operations (Perrin, 1969; Fox, 1978). The incidental kill has reduced the abundance of some geographical forms, by as much as 83% (Smith, 1983). The basic model used in assessing the status of stocks and estimating net production has been based on density-dependent change in gross production, i.e. that reproductive rates go up as density goes down (loc. cit.). Such a change has not been observed in a dolphin population; its use in dolphin assessment and management has been based on observations of populations of terrestrial mammals, pinnipeds and two baleen whales (Fowler, 1981). This paper presents the results of a comparative study of two populations estimated to be at different proportions of their initial sizes, in an attempt to validate the assumption of density-dependent change in reproductive rates.

At least four morphologically differentiated stocks of spinner dolphins, *Stenella longirostris* (Gray, 1828), exist in the eastern tropical Pacific (Perrin, 1975a and b; Perrin, Sloan and Henderson, 1979; and Au, Perryman and Perrin, 1979). The two forms treated in this paper are the 'eastern spinner dolphin', which occurs from close to the coast of Mexico and Central America to several hundred kilometers offshore, and the 'northern whitebelly spinner dolphin', which is a more high-seas form, found north of the equator and ranging west to about 150° W long. In 1979, the population of eastern spinners was estimated to be 17–25% (central estimate 20%) of its initial size, whereas the population of northern whitebelly spinners was estimated to be 58–72% (central estimate 65%) of initial size (Smith, 1983). In assessment and management of the ETP dolphin stocks, maximum net productivity level (MNPL, in numbers of individuals) has been assumed to occur at population size somewhere between 50 and 80% of initial size (Smith, 1983). If it is assumed that the two rather similar populations had similar reproductive rates prior to exploitation, then from the population-dynamics theory outlined above, the current reproductive rates should be higher in the eastern spinner population than in the whitebelly spinner population, providing that MNPL is below 65% and that the form of the density-dependent response is not strongly curvilinear (see Fowler, 1984, for discussion of the form of the density-dependent response). Alternatively, no detectable difference in the reproductive rates could mean that both populations are below (or above) MNPL, that the form of the response is strongly curvilinear, that the two populations had different rates initially, or that density-dependence may exist but act on some other life history parameter. The purposes of this paper are to present estimates of growth and reproductive parameters for the northern whitebelly spinner, as was done for the eastern spinner (Perrin, Holts and Miller, 1977), and to compare the estimates for the two populations.

MATERIALS AND METHODS

The field program

Most of the data and specimens were collected by NMFS scientific technicians aboard commercial tuna seiners. The collection procedures were the same as previously described for the spotted dolphin, *Stenella attenuata* (Perrin, Coe and Zweifel, 1976). Data were collected on 1 cruise in 1968, 4 in 1971, 12 in 1972, 21 in 1973, 33 in 1974, 30 in 1975, 48 in 1976, 72 in 1977 and 74 in 1978. Some specimens were also collected by personnel of the Inter-American Tropical Tuna Commission aboard chartered purse seiners.

In 1971 and early 1972, when the field program was

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[1] An earlier version of this paper was working Document SOPS/79/30 prepared for the Status of Porpoise Stocks Workshop, 27–31 August 1979 at the Southwest Fisheries Center, La Jolla, California, and SWFC Admin. Rep. LJ-79-29 (1979).

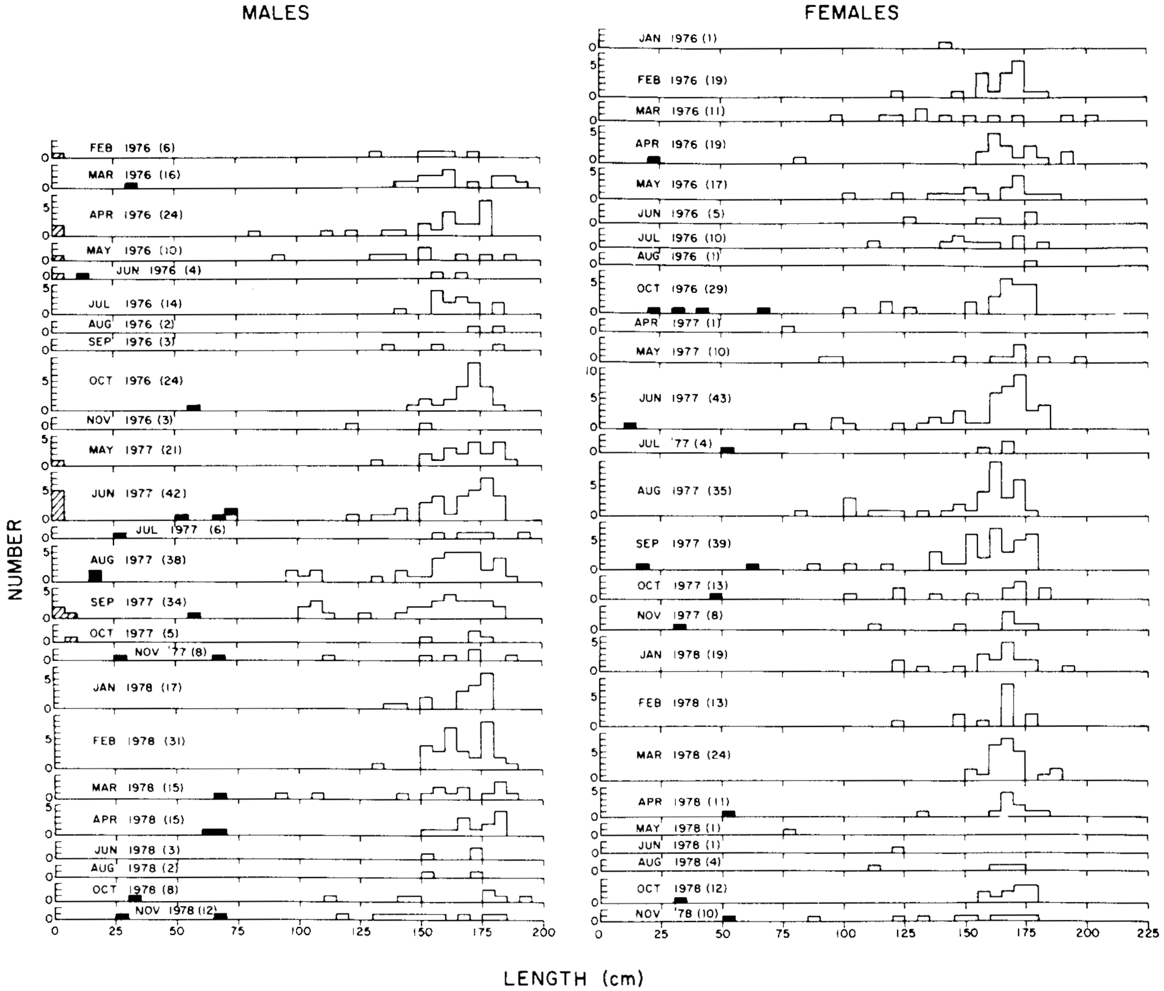

Fig. 1. Length frequency distributions by month and year of eastern spinner dolphins collected 1976–78 and included in the present study. (Sample sizes in parentheses.) Solid squares represent foetuses; hatched squares represent foetuses of undetermined sex (plotted with males).

very limited, adult female specimens were preferentially selected for dissection when available, and the samples for those periods are therefore biased with respect to the age and sex structures of the kill. In 1968 and on cruises from October 1972 on, no selection was done in determining which animals were to be examined (the attempt was made to examine all the animals in small-kill sets – less than about 30 – and the first 30 or so that came to hand in large-kill sets), and those samples are assumed to be cross-sectional with respect to the kill. Foetuses were not collected in 1968.

The sample of animals for which life history data including, but not limited to, sex and body length were collected includes over 4,000 specimens. Length-frequency data by month and sex were presented for eastern spinner specimens collected before 1976 in Perrin *et al.* (1977); length-frequency data for the balance of the eastern spinner material (1976–78) and the whitebelly spinner specimens are presented in Figs 1 and 2. Charts showing collection localities are presented in Henderson, Perrin and Miller (1980).

The morphological differences between the two races of spinner dolphins are average differences, with considerable overlap, and their geographical ranges overlap, so schools and single-school groups of specimens are identified at sea based on their model characteristics. In case of single specimens or small series of specimens coming from the area of geographical overlap and for which information on the nature of the entire school is minimal, the danger exists of erroneous identification. Such error would tend to obscure any differences between the two populations in reproductive parameters. We were conservative in reviewing identification of such specimens to race, and designated many as 'unidentified spinner dolphins' (excluded from the present study).

Laboratory procedures were the same as reported for the studies of the eastern form of *S. longirostris* (Perrin *et al.*, 1977) and of the spotted dolphin (Perrin *et al.*, 1976).

The NORMSEP computer program was used to define modes in the length-frequency distributions for eastern calves. The program was written by Hasselblad (1966)

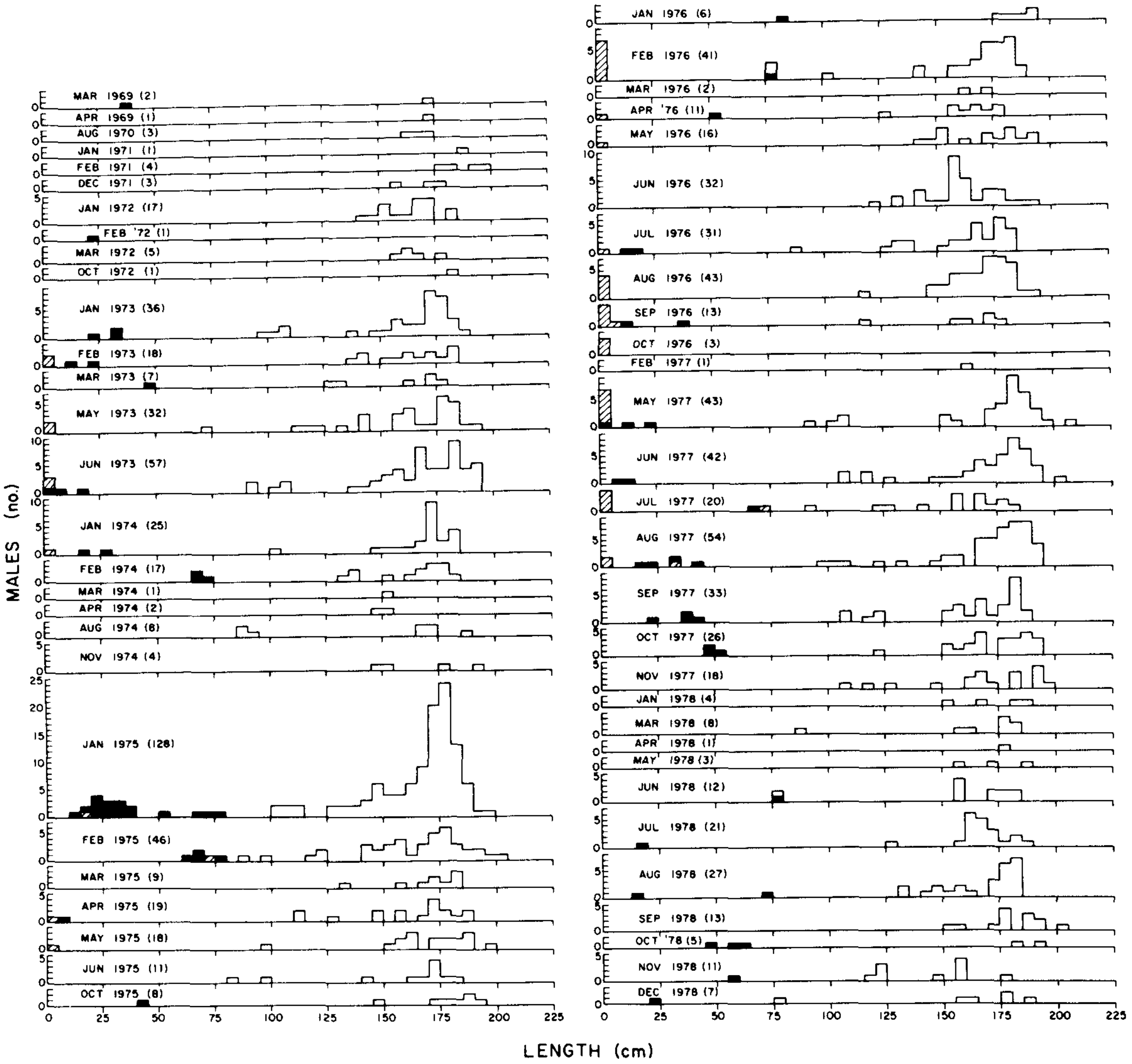

Fig. 2A. Length-frequency distributions by month and year of male northern whitebelly spinner dolphins collected 1969–78 and included in the present study. (Sample sizes in parentheses.)

and modified by Patrick K. Tomlinson, Inter-American Tropical Tuna Commission. The program separates a mixture of normal length distributions into its components, assuming that the length of individuals within age groups are normally distributed and that an unbiased sample of the length distribution was obtained that would allow estimation of growth rates in juveniles. The computer programs BMDPAR and BMDP3R (Dixon, 1981) were used in fitting nonlinear models.

RESULTS

Growth

Length at Birth

The average length at birth in the eastern spinner was estimated by Perrin *et al.* (1977) at 76.9 cm based on a sample of 101 foetuses and calves, including 23 specimens of the whitebelly spinner and 23 unidentified to race. We estimated average length at birth in the whitebelly spinner based on a sample of 51 foetuses and calves to be 75.9 cm, based on a fit to the logistic model (Fig. 3). We rounded the estimate off to 76 cm in analyses below. The estimate is subject to the same potential biases as that for the eastern spinner (elaborated in Perrin *et al.*, 1977).

Length of gestation and foetal growth rates

We assumed these parameters to be the same in both forms, i.e. 10.6 months and 8.37 cm/month (linear phase), as estimated for the eastern spinner (Perrin *et al.*, 1977).

Postnatal growth

Perrin *et al.* (1977) examined length frequency data for the eastern spinner (data from 1975 and earlier) and found no pattern of length mode progression over time. Growth rates were therefore estimated by more deductive

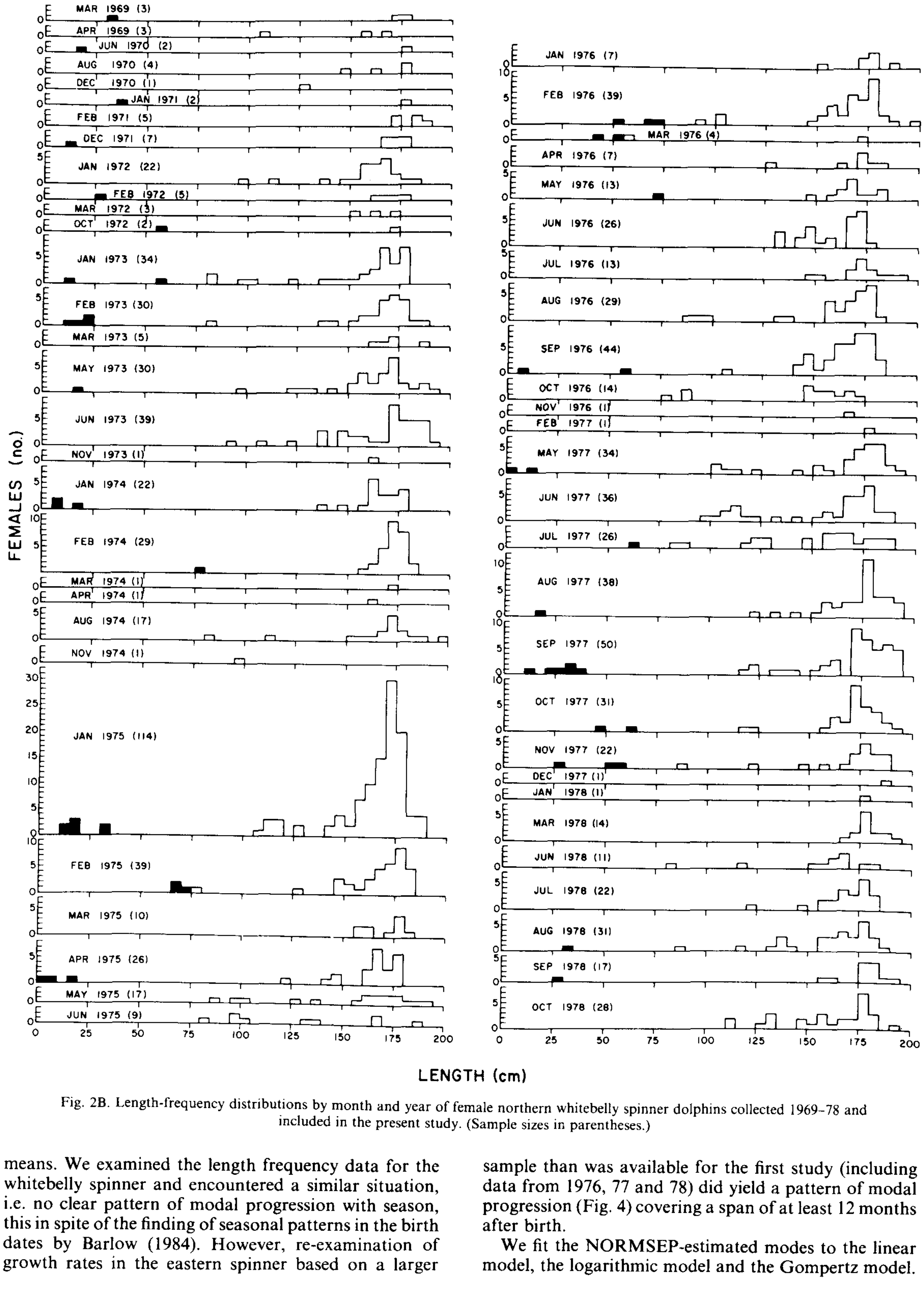

Fig. 2B. Length-frequency distributions by month and year of female northern whitebelly spinner dolphins collected 1969–78 and included in the present study. (Sample sizes in parentheses.)

means. We examined the length frequency data for the whitebelly spinner and encountered a similar situation, i.e. no clear pattern of modal progression with season, this in spite of the finding of seasonal patterns in the birth dates by Barlow (1984). However, re-examination of growth rates in the eastern spinner based on a larger sample than was available for the first study (including data from 1976, 77 and 78) did yield a pattern of modal progression (Fig. 4) covering a span of at least 12 months after birth.

We fit the NORMSEP-estimated modes to the linear model, the logarithmic model and the Gompertz model.

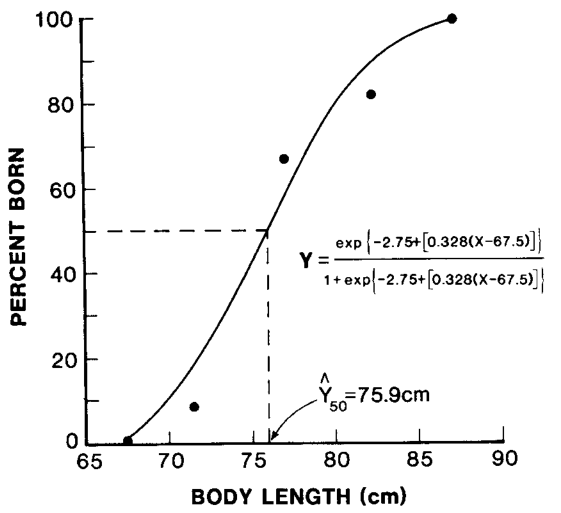

Fig. 3. Estimation of average length at birth, based on least-squares fit of per cent postnatal (percentage that are calves and not foetuses) on body length, in 5-cm increments, to the logistic model for 51 specimens of the northern whitebelly spinner dolphin (24 foetuses and 27 calves) between 65 and 89 cm long.

The Gompertz model provided the best fit (Fig. 3), yielding an estimated average growth rate for the first year of 4.3 cm/month and an average length at one year of 127.5 cm.

Length relative to tooth layering

Perrin *et al.* (1977) presented growth curves and equations for the eastern spinner in terms of length relative to number of postnatal dentinal growth layer groups (GLGs, terminology of Perrin and Myrick, 1980, = 'dentinal layers' in terminology of Perrin *et al.*, 1977). We examined relationships between GLGs and length for 170 male and 232 female northern whitebelly spinners (Fig. 6). The sub-samples for age determination were selected as for the eastern spinner (Perrin *et al.*, 1977).

We fitted curves to the single-GLG means using a two-cycle model[2] as was done for the eastern spinner (loc. cit.), with some differences. (1) The upper end of the second-phase curve (asymptotic length) estimated as it was for the eastern spinner, as the average length of the few very old (⩾ 13 GLGs) specimens in the samples for both sexes, was lower (by 16 mm in females) than the average length of adult animals, probably a statistical artifact. The procedure resulted in estimates of asymptotic length close to the average sizes of adults (for example 174.9 cm vs 175.2 cm in the females). (2) In the eastern-spinner analysis (Perrin *et al.*, 1977), animals with ⩾ 13 GLGs were pooled into a single class. Whitebelly spinners with ⩾ 15 GLGs were pooled in the final stratum because of a relatively larger number of older specimens – particularly in the male sample. (3) For the eastern spinner, male and female juveniles were considered jointly; the respective length and age means coincided almost exactly. For the northern whitebelly spinner, the

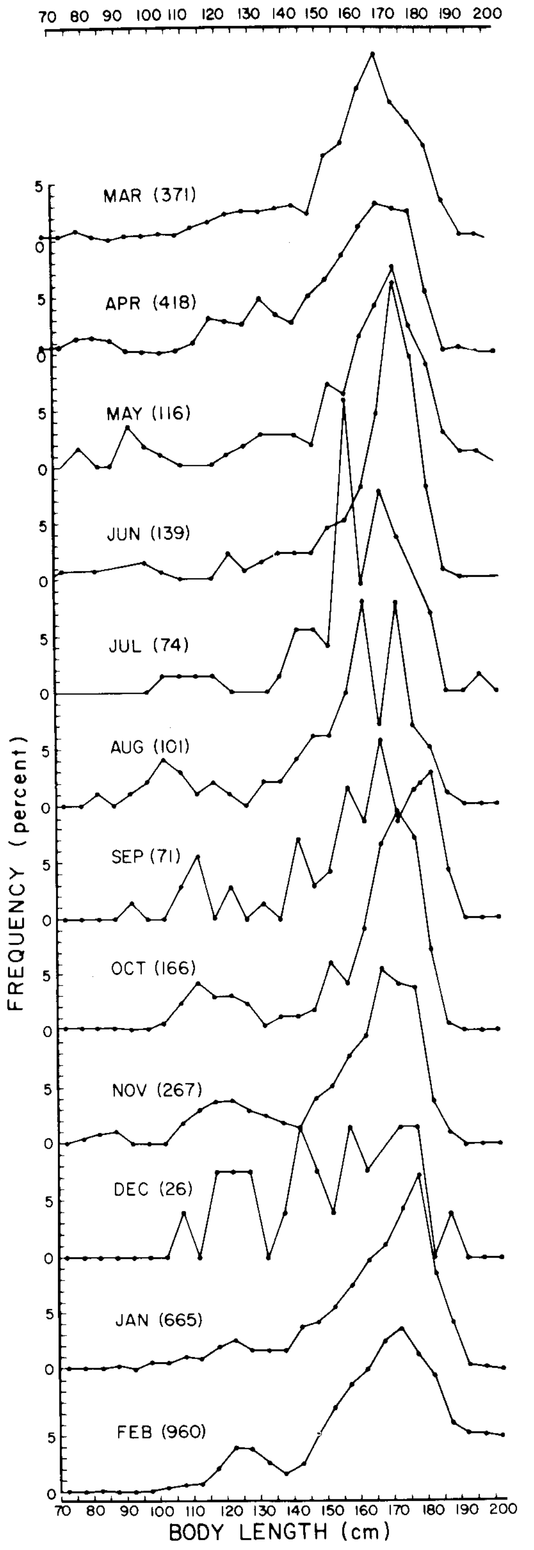

Fig. 4. Length-frequency distributions, by month for all years pooled, of body length in postnatal eastern spinner dolphins. (Sample sizes in parentheses.)

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[2] See Perrin *et al.* (1976) for discussion of the rationale for a two-cycle model.

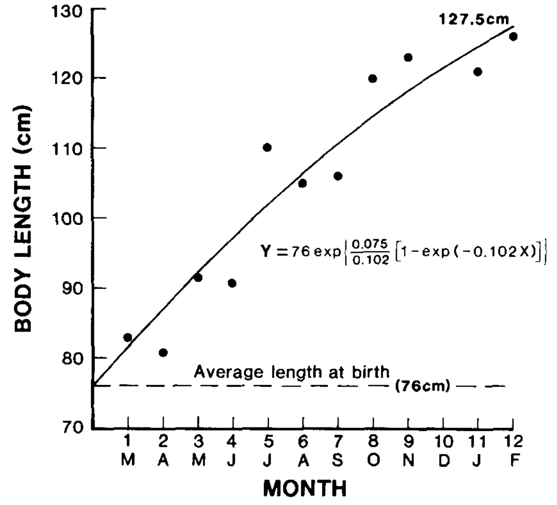

Fig. 5. Least-squares fit to the Gompertz model of mean body-length modes (NORMSEP-estimated from data in Fig. 4) on month of year. December was excluded because of small sample size.

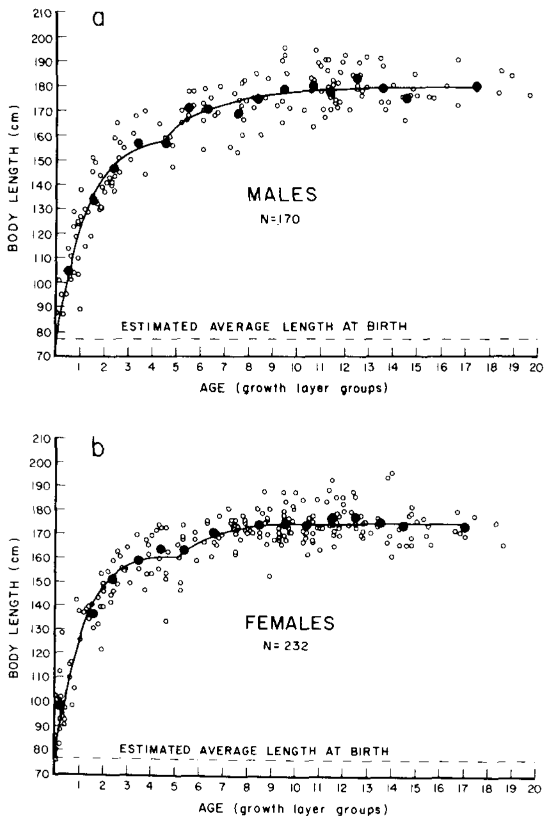

Fig. 6. Relationship between body length and age in northern whitebelly spinner dolphins. Lines are double-Laird-model fits to single-GLG means (solid symbols).

juvenile means differed between sexes, those for the females being higher than those for the males, and the data for juveniles of the two sexes were therefore fitted separately. Age at shift from the juvenile to 'adult' portions of the overall curve (age at onset of the adolescent growth spurt) differed between the sexes. It was 4.4 GLGs in males and 5.1 GLGs in females. Estimated lengths at these ages are 157.8 cm and 160.9 cm, respectively. The shift for the eastern spinner (sexes combined) came at 4.11 GLGs (rounded off to 4 GLGs).

The fitted growth equations for males are, for juveniles < 4.3 GLGs old,

$$L = 77\exp\{0.730[1-\exp(-0.946t)]\}$$

and, for $\geqslant 4.3$ GLGs,

$$L = 157.8\exp\{0.128[1-\exp(-0.480(t-4.339))]\}$$

where L = length in cm and t = age in GLGs.

For females the equations are, for juveniles with < 5.1 GLGs,

$$L = 77\exp\{0.740[1-\exp(-1.117t)]\}$$

and, for age $\geqslant 5.1$ GLGs,

$$L = 160.9\exp\{0.085[1-\exp(-0.775(t-5.145))]\}.$$

The equations rearranged and reduced for estimating age from length are:

♂ < 158 cm

$$t = -1.058\ln(6.954-1.371\ln L)$$

♂ $\geqslant 158$ cm

$$t = 4.339-2.082\ln(40.542-7.813\ln L)$$

♀ < 161 cm

$$t = -0.895\ln(6.874-1.352\ln L)$$

♀ $\geqslant 161$ cm

$$t = 5.145-1.292\ln(60.993-11.806\ln L).$$

Length at 1 year of age in the eastern spinner was estimated above at 127.5 cm, based on progression of a length mode. That length is achieved at 1.29 GLGs, from the growth equation in Perrin *et al.* (1977). The previously used estimate of 134 cm (loc. cit.) was deductively derived; corresponding age is 1.57 GLGs, rounded off to the nearest half-GLG to 1.5 GLGs. The new estimate is also close to 1.5 GLGs, and that value is used below for both the eastern and the northern whitebelly spinners. Estimated average length at one year from the growth equations are then 132.5 cm for the eastern spinner and 137.2 cm (average of estimates for males and females) for the northern whitebelly spinner. Lacking a basis for calibrating the growth curve beyond the first year, we provisionally use below three alternative hypotheses for the rate of GLG disposition:

I. One and one-half GLGs per year,

II. One and one-half GLGs in the first year and one per year thereafter, or

III. One and one-half GLGs per year until puberty and one per year thereafter.

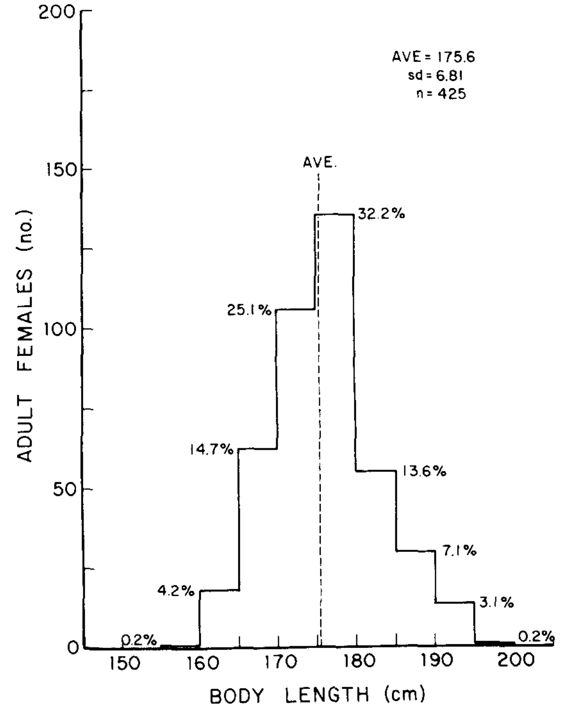

Fig. 7. Distributions of length of sexually adult female northern whitebelly spinner dolphins.

Table 1

Comparison of juvenile growth rates in female eastern and northern whitebelly spinner dolphins

	Average length at 4 GLGs	Average length of adults
Eastern spinner	156.6 cm[1]	171.2 cm ($n = 560$)
Northern whitebelly spinner	159.9 cm	175.6 cm ($n = 425$)
Difference between races	3.3 cm	4.5 cm

[1] From new growth equation based on females included in pooled juvenile sample in Perrin *et al.*, 1977:

$$L = 77\exp\left\{\frac{0.6521}{0.8984}[-\exp(-0.894)t]\right\}.$$

Adult female northern whitebelly spinners (those of which the ovaries contain at least one corpus of ovulation) average 175.6 cm in length (Fig. 7), compared to 171.2 cm for eastern spinners (Perrin *et al.*, 1977), a difference statistically significant at $P < 0.0001$ (t-test). Length of adult males is more difficult to assess comparatively because of the absence of a clear criterion for attainment of sexual maturity (discussed below in section on male maturation). The difference in length of adult females is reflected in a difference in juvenile growth rates. Size at birth is the same or very nearly the same in the two populations, but juvenile northern whitebelly spinners grow faster than do juvenile eastern spinners, the difference being most pronounced in females (Table 1).

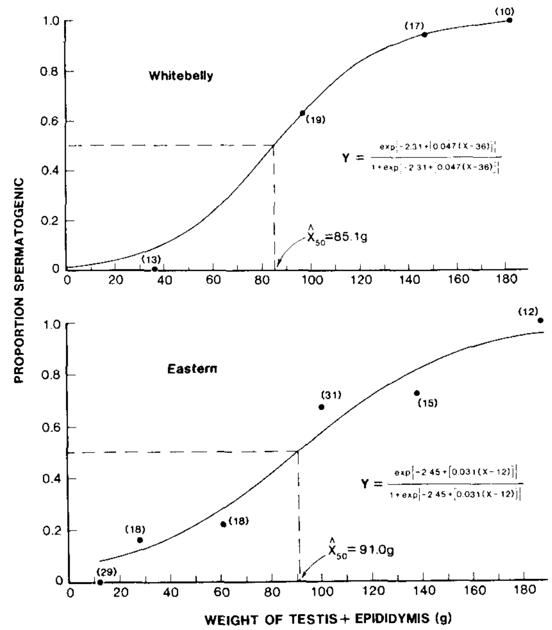

Fig. 8. Least-squares fit to the logistic model of testis-epididymis weight on proportion of males spermatogenic in the northern whitebelly and eastern spinner dolphins. Eastern data from Perrin *et al.*, 1977.

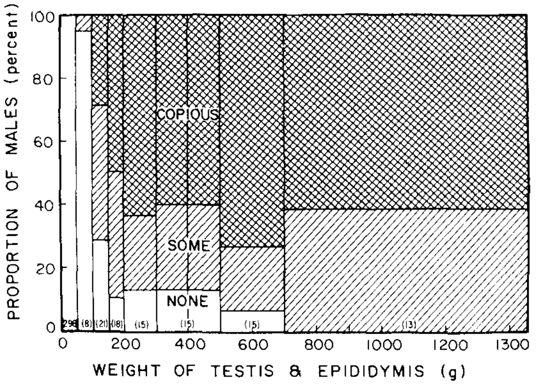

Fig. 9. Amount of sperm in epididymis in relation to combined testis-epididymis weight in northern whitebelly spinner dolphin. Terms defined in Perrin *et al.*, 1976. Sample sizes in parentheses. To be compared with Fig. 18 in Perrin *et al.*, 1977.

Reproduction

The male

There are marked differences between the two populations in morphological indices of reproductive maturity and function for males. Average weight of testis (with epididymis) at onset of spermatogenesis is 85.1 g, based on a logistic fit, in the whitebelly spinner. A similar fit of the data in Fig. 17 of Perrin *et al.*, 1977 for the eastern form yields a 50% value of 91.0 g (Fig. 8B). The two estimates of 91.0 g and 85.1 g are not statistically different from each other. The rounded-off average of 88 g is used below for both forms. The further course of average testicular development differs sharply between

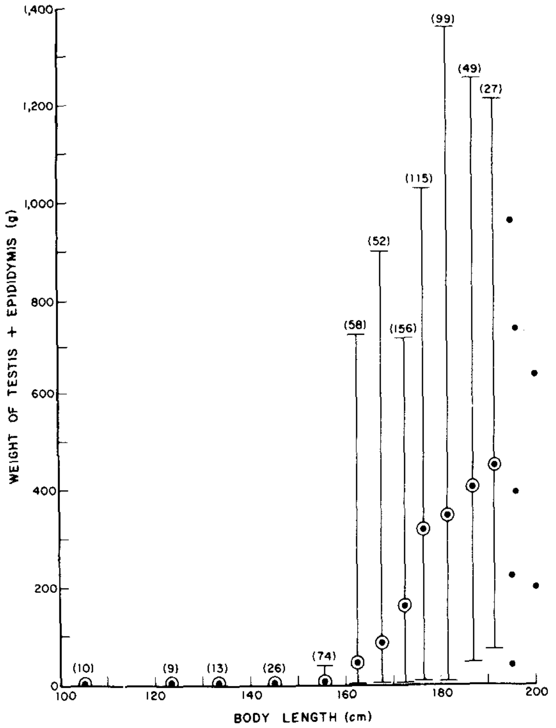

Fig. 10. Relationship between testis-epididymis weight and body length in the northern whitebelly spinner dolphin. Sample sizes in parentheses. Circled dots are sample means; vertical bars are ranges. Dashed circles are means for eastern spinner; sample sizes and ranges in Perrin *et al.* (1977).

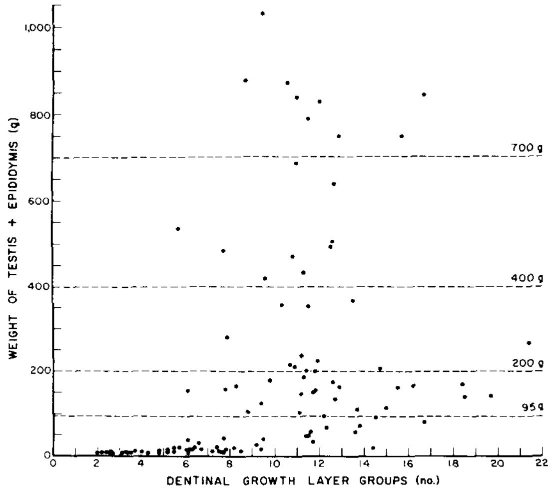

Fig. 11. Scatter plot of testis-epididymis weight on age (in GLGs) for 102 northern whitebelly spinner dolphins.

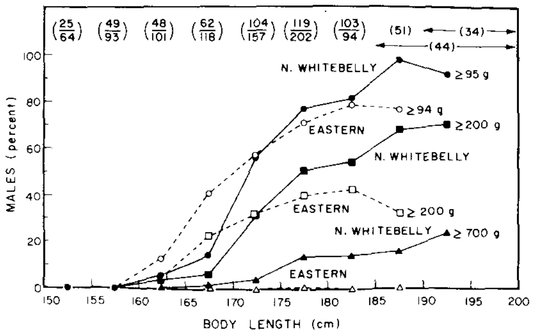

Fig. 12. Proportion of males of given length that have testis-epididymis weights ⩾ 95 g, ⩾ 200 g and ⩾ 700 g in two populations of spinner dolphin: northern whitebelly spinner (solid lines) and eastern spinner (dashed lines). Sample sizes in parentheses (northern – bottom, whitebelly – top).

the two forms. In the eastern spinner, proportion of animals with 'copious' sperm in the epididymis increases to about 50% at testis-epididymis weight of about 400 g (loc. cit.) and levels out, whereas in the northern whitebelly spinner it increases to about 35%, at about 200 g (Fig. 9). In the original eastern sample (Fig. 18 in loc. cit.), no testis weighed more than 700 g, and only a very few of that size (but weighing less than 900 g) have been collected since (unpublished data). However, a sizeable proportion (> 20% at the upper end of body-length size range) of northern whitebelly spinner testes weigh over 700 g (up to 1,354 g in the sample) and all of these examined histologically have had at least 'some' sperm in the epididymis. Amount of sperm in the epididymis would seem to be positively correlated with testis size, and adult eastern spinners have on the average smaller testes than do northern whitebelly spinners of the same length (Fig. 10) (even with a 5-cm adjustment for the racial difference in average length of adults) or age (compare Fig. 11 with Fig. 21 in loc. cit.). At any body length above about 170 cm for eastern spinners and 175 cm for whitebelly spinners, a greater proportion of northern whitebelly spinners attain any particular testis-weight criterion, even the criterion of average weight at first spermatogenesis, and very few eastern spinners attain the high testis weights (> 700 g) associated with 100% incidence of sperm in the epididymis (Fig. 12). At least four alternative explanations suggest themselves: (1) there is seasonal fluctuation in testis size and the differences reflect seasonal biases in sampling, (2) there are inherent differences between the two populations in male reproductive development and morphology, (3) there are differential sampling biases *vis a vis* reproductively active males for the two populations, or (4) testis size (and possibly, male fertility) is depressed in the eastern population, possibly due to some aspect of exploitation.

To address the first of the above possibilities, we examined testis-weight distribution by month for the two populations (Fig. 13). The sample sizes are relatively small for some months, but a clear picture of pronounced seasonality emerges nonetheless. In the northern whitebelly spinner, a mode of large-testis-weight animals appears in February, centered around 700–800 g. The mode persists through May (although possibly retreating slightly), appears in June centered around 400–500 g; moves out to 600–700 g again in July–August; and all but disappears in September through January. The months of peak testis weight (and, presumably, peak fertility and breeding) are February and July–August. The eastern

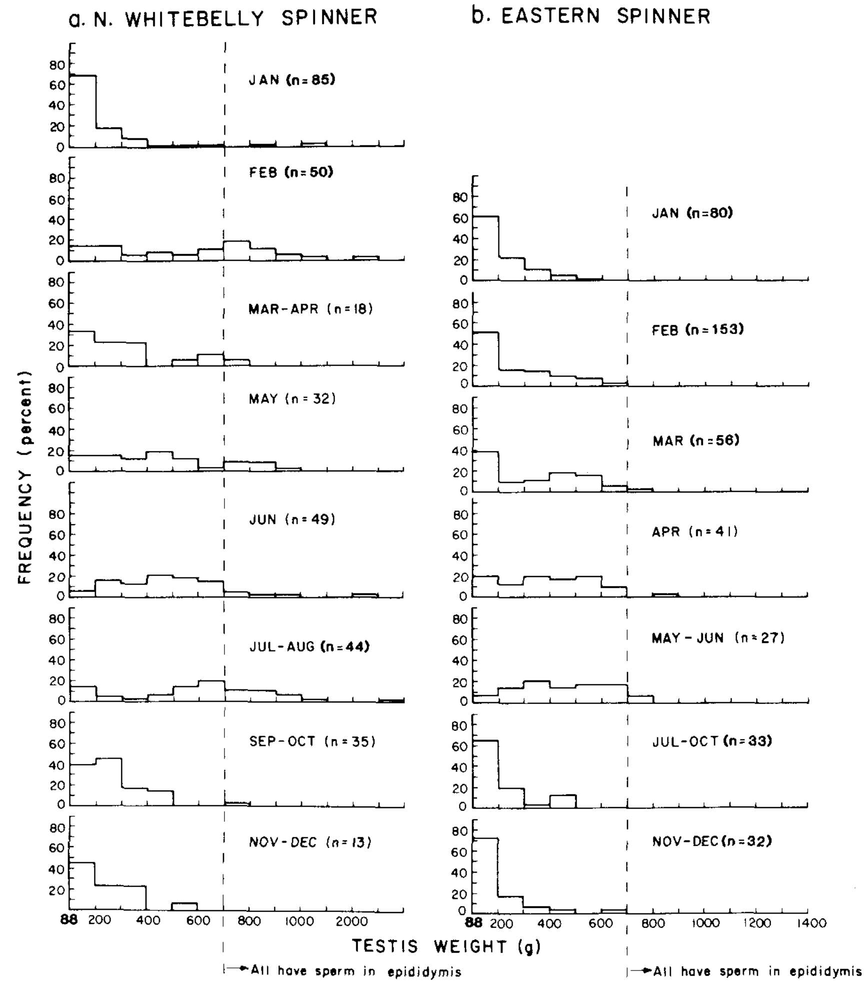

Fig. 13. Testis-epididymis weight distribution by month in two populations of spinner dolphins. Data from 1968–78 (most from 1973–78).

spinner also exhibits seasonality (Fig. 13b), but with important differences. A mode is present in March–June, centered around 400–500 g rather than around 700–800 g as in the northern whitebelly spinner. Only a very small proportion of the animals in the seasonally appearing mode in any month extend above the 700 g level, above which all individuals can be expected to have sperm in the epididymis. The apparent dearth of large-testis males, therefore, in the eastern samples is not an artifact of seasonally biased sampling.

The second alternative, that of inherent difference in testis weight, is unlikely because of the similar testis weight at first spermatogenesis and similar adult body length in the two populations.[3] The third alternative is also unlikely, because fishing practices do not differ with type of spinner dolphin involved. Of the four alternatives considered here, the most likely is that of depression of testis weight in the eastern spinner population, although inherent difference in testis size or differential sampling bias cannot be eliminated from consideration completely.

The female

Attainment of sexual maturity. The smallest sexually mature whitebelly spinner female (possessing at least one corpus of ovulation in the ovaries) encountered was 157 cm long, and the largest immature female was 188 cm long. This compares to 152 cm and 182 cm in the eastern spinner (Perrin *et al.*, 1977). The differences reflect the above-discussed approximately 5-cm difference in average length of adult females. Average length at attainment of

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[3] There is one other instance (based on adequate samples and comparable methods) of wide variation in maximum testis weight between populations of a single delphinid, that of *Delphinus delphis* in the Black Sea ($n = 2{,}138$, maximum weight = 1,000 g) and in the eastern North Pacific ($n = 31$, maximum weight = 1,672 g) (Perrin and Reilly, 1984). In this case also, the population with smaller testes is the more exploited one, in fact thought to have crashed because of over-exploitation (Smith, 1982). The difference between average lengths of adults in the two populations may be greater than for the two populations of *S. longirostris*, because the Black Sea form is relatively very small (Perrin, 1983).

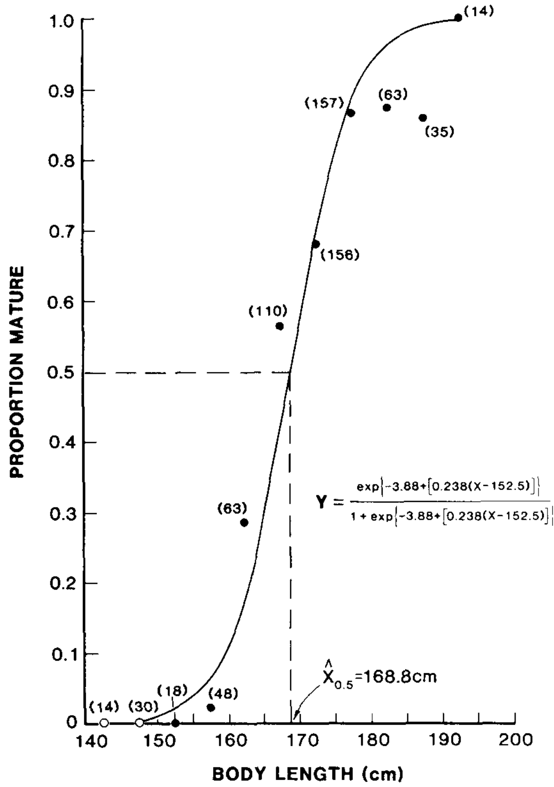

Fig. 14. Estimation of body length at which 50% of female northern spinner dolphins show ovarian evidence of sexual maturity, based on weighted least-squares fit to the logistic model. Sample sizes in parentheses. Open circles not included in regression.

sexual maturity differs between the two populations in the same direction (167.2 cm in the northern whitebelly spinner (Fig. 14) vs 164.1 cm in the eastern spinner (Fig. 22 in loc. cit.). The difference (4.7 cm) yields a younger predicted average maturation age (from the growth equations) in eastern spinners (5.2 GLGs) than in northern whitebelly spinners (7.1 GLGs).

Another estimate of average length at attainment of maturity is that length for which the number of longer immature animals is equal to the number of shorter mature animals. This point for the northern whitebelly spinner is 170 cm and for the eastern spinner is 165 cm, yielding estimates of age at maturation of 6.5 and 5.8 GLGs, respectively. These may be underestimates, because the method does not take mortality into account.

An estimate of length at first conception (not necessarily the same as age at first ovulation) can be made by calculating the average length of pregnant females with a corpus luteum only (indicating first pregnancy) and subtracting the growth that they can be assumed to have undergone during pregnancy. Sixteen primiparous northern whitebelly females averaged 171.6 cm in length. Predicted age at that length is 6.95 GLGs. The average length of their fetuses was 248 mm. This length is attained at about 4.3 months. Using the growth equations above to predict growth during 4.3 months for the various tooth-layering models and subtracting the growth increment from 171.6 cm yields estimates of length at first conception ranging from 169.7 cm (6.4 GLGs) to 170.4 cm (6.6 GLGs). The primiparous females in this sample, however, are only those that became pregnant at the first ovulation. This may cause the estimate to be an underestimate, because some females may ovulate several times, and presumably continue to grow, before becoming pregnant the first time. Also, this method

Table 2

Results of analyses of length and age at attainment of sexual maturity in two populations of spinner dolphins. Values calculated with the growth equations are in parentheses

	Length (cm)		GLGs (no.)		Age (years) under hypotheses					
					I		II		III	
Methods (and comments)	N.WB	EAST.	N.WB	EAST.	N.WB	EAST.	N.WB	EAST.	N.WB	EAST.
1. Length at which 50% have corpora (probable underestimate)	168.8	164.1[1]	(7.1)	(5.2)	4.7	3.5	6.6	4.7	5.3	3.8[5]
2. Length at which mature below equals immature above (possible underestimate)	170.0	160.0[2]	(6.5)	(5.8)	4.3	3.9	6.0	5.3	4.8	4.4
3. Number of GLGs at which 50% have corpora (interpolation, but small sample sizes)	(170.8)	(164.2)	6.7	5.3[1]	4.5	3.5	6.2	4.8	5.0	3.9
4. Length at first conception,[3] under hypothesis:										
I	(169.7)	(—)	(6.4)	(—)	4.3	(—)	—	—	—	—
II	(169.7)	(—)	(6.6)	(—)	—	—	6.1	(—)	—	—
III	(170.4)	(—)	(6.6)	(—)	—	—	—	—	4.9[4]	(—)

[1] From Perrin *et al.* (1977).

[2] Includes data through 1978.

[3] No estimates for the eastern spinner by this method; see text.

[4] Switch from 1.5 to 1.0 GLG/year assumed to occur at 161 cm (5.41 GLGs).

[5] Ditto, at 157 cm (4.13 GLGs).

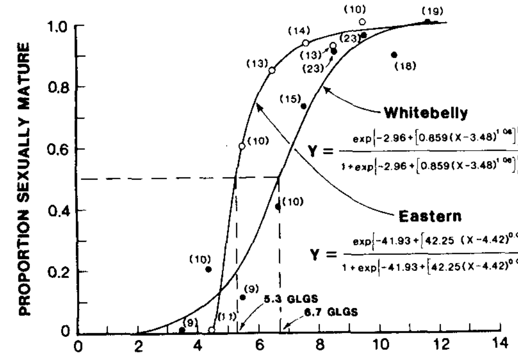

Fig. 15. Relationship between proportion of females sexually mature and age (in GLGs) in two populations of spinner dolphins, based on weighted least-squares fit to a generalized sigmoid model (described in text). Sample sizes in parentheses.

Table 3

Calculation of estimates of gross annual reproductive rates in two populations of spinner dolphins, based on pooled data for 1973–78. Approximate 95% confidence limits are ±2 S.E. Sample sizes in parentheses. From Henderson *et al.*, 1980

	Northern whitebelly spinner	Eastern spinner
A. Percent female	50.9±2.4 (1,778)	51.0±1.8 (2,938)
B. Percentage of females reproductive	52.2±3.6 (905)	43.2±2.8 (1,492)
C. Annual pregnancy rate (percent)	35.6±5.0 (366)	33.9±4.2 (521)
A×B×C. Gross annual reproductive rate (percent)	9.4±1.4 (1,631)	7.5±1.2 (2,624)

assumes no effect of pregnancy on growth rate. Average length of 16 primiparous eastern spinners (171.4 cm) slightly exceeded the estimate of asymptotic size (170.9 cm) used in the growth curve fit; an estimate from the growth equation, therefore, was not possible for the eastern spinner.

Estimates of age at sexual maturity were also derived directly from the smaller samples for which age determinations (GLGs in dentine) were made (Fig. 15), bases on a weighted (weight = inverse of variance estimated as $\mathrm{Var} = p(1-p)/n$) least-squares fit to a generalized sigmoid function:

$$Y = \frac{\exp(a+bX)^c}{1+\exp(a+bX)^c}$$

where a, b and c are fitted parameters. The estimates are 5.3 GLGs in the eastern spinner and 6.7 GLGs in the northern whitebelly spinner. The fitted curves, albeit based on few and small samples, are quite different in form.

The largely independent different estimates of age (in GLGs) at maturation are not widely disparate (Table 3). Averaging of the estimates for the northern whitebelly spinner by the various methods (using Option II in Table 3 of 1 GLG/year after the first year) yields a value of 6.7 GLGs, which value is used below. Averaging of the two relatively most reliable estimates available for the eastern spinner yields an estimate of 5.6 GLGs.

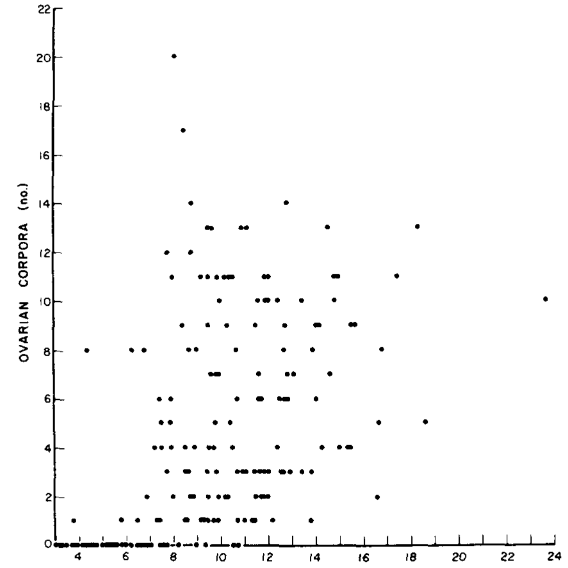

Fig. 16. Scatterplot of number of ovarian corpora on age in GLGs in the northern whitebelly spinner dolphin.

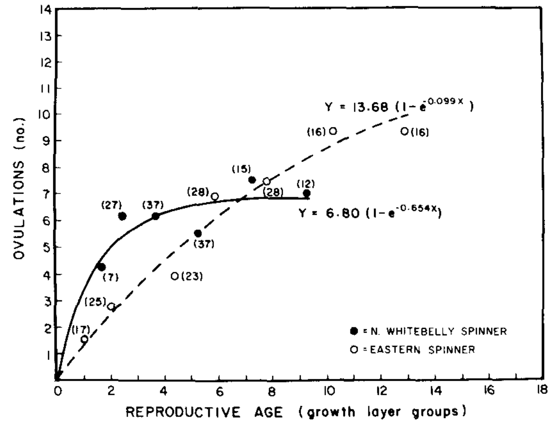

Fig. 17. Asymptotic fit of corpus count on average reproductive age in the northern whitebelly spinner dolphin. Dashed line is asymptotic fit to data for eastern spinner (Fig. 27 in Perrin *et al.*, 1977). Origin set at 0.001/0.001.

If it is assumed that one GLG is deposited after the first year (Hypothesis II in Table 3), female northern whitebelly spinners on the average mature at about 6 years of age and eastern spinners at about 5 years.

Ovulation Rate. Number of corpora in the ovaries (an index of reproductive history of the individual female dolphin) increases sharply at about 6–7 GLGs in the northern whitebelly spinner (Fig. 16) and at about 5–6 GLGs and more rapidly in the eastern spinner (Fig. 6 in Perrin *et al.*, 1977). To estimate ovulation rate, the required estimates of average reproductive ages for 2-GLG intervals were calculated as in Perrin *et al.* (1977).

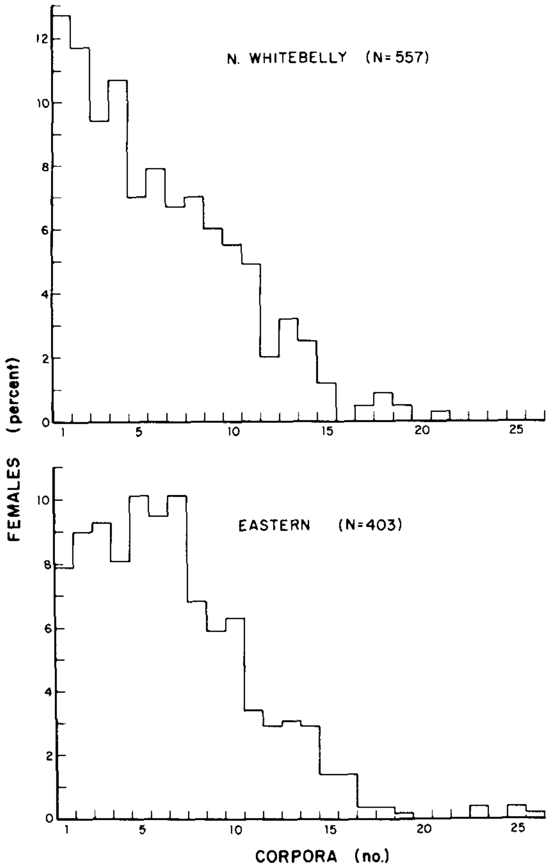

Fig. 18. Frequency distribution of corpus count in two populations of spinner dolphins. Includes samples from 1973–78.

Table 4

Percentage of females sexually immature in two populations of spinner dolphins, 1973–78. Sample sizes in parentheses. From Henderson *et al.*, 1980

Year	Northern whitebelly spinner	Eastern spinner
1973	48.9 (133)	54.4 (344)
1974	40.8 (49)	55.3 (396)
1975	45.5 (191)	57.0 (402)
1976	52.9 (191)	59.4 (106)
1977	48.2 (222)	59.7 (92)
1978	50.0 (118)	70 (92)

Table 5

Summary of parameters for two populations of *Stenella longirostris*. Sources in text and Tables 2–4

Parameters	Eastern spinner	Northern whitebelly spinner
1. Proportion of original population size	17–25%	58–72%
2. Length of gestation	10.6 months (0.88 year)	10.6 months (0.88 year)
3. Average length at birth	77 cm	76 cm
4. Average length at one year (1.5 GLGs, from growth curves)	132.5 cm	Ave. for M & F 137.2 cm
5. Average length of sexually mature female	171.2 cm	175.6 cm
6. Smallest adult female	152 cm	157 cm
7. Largest adult female	182 cm	188 cm
8. Average length of female at attainment of sexual maturity	164.1 cm	167.2 cm
9. Average age at attainment of sexual maturity in female (average of estimates by several methods)	5.6 GLGs (~ 5 years)	6.7 GLGs (~ 6 years)
10. Proportion of population female	0.510	0.509
11. Proportion of females reproductively adult	0.432	0.533
12. Annual pregnancy rate	0.339	0.356
13. Gross annual reproductive rate	0.075	0.094

Ovulation rates were estimated by fitting asymptotic curves to the 2-GLG-interval means of average reproductive age (Fig. 17) (assumes eventual cessation of ovulation in old females). Ovulation rate, as measured by these fits, in young females is higher in the northern whitebelly spinner than in the eastern spinner, but also levels off faster. The relative behavior of the two curves beyond about 8 GLGs of reproductive age may be greatly influenced by the small sample sizes involved at the higher ages, however, and all that can be said with some certainty is that during the first few years of reproductive life spinners in the eastern population ovulate less frequently than do those in the northern whitebelly population.

The shape of the corpora-count frequency distribution is an index of ovulation rate independent of the above fit to the corpora count on reproductive age. The distributions differ in the two populations (Fig. 18), most markedly so between 0 and about 7 corpora. The pattern of difference (higher frequency in the whitebelly population between one and four corpora and the reverse between four and seven corpora) can be explained by initial higher ovulation rate in the northern whitebelly population (although this does not take into account the possibility of differential mortality rates). The results of the two analyses agree quantitatively as well; the asymptotic fits (Fig. 17) estimate that about seven corpora represents about the same reproductive span in the two populations, about seven GLGs (about 7 years, if a one-GLG/year deposition rate is assumed).

Gross production. Gross annual reproductive rate, estimated as proportion of the population female times proportion of females sexually mature (and not post-productive) times annual pregnancy rate (proportion of reproductive females divided by length of gestation – 0.883 year), did not differ between the two populations for the period 1973–78 (Table 4). Overall sex ratio was virtually identical in the two (very large) samples, about 0.96:1. The age structure of females, however, was quite different. Fifty-two percent of the northern whitebelly females were sexually mature, whereas only 43% of the eastern females were mature. The difference is statistically significant at α 0.05 (*t* test). (A larger proportion of females were immature in the eastern than in the northern whitebelly samples for each year, 1973–78 (Table 5).) Pregnancy rate was about the same in the two populations, perhaps reflecting the above-discussed earlier age at maturity. The estimate of gross production was slightly higher for the northern whitebelly population than for the eastern population. The difference, however, is not statistically significant at $\alpha = 0.05$[3].[4]

DISCUSSION

Although differences exist between the northern whitebelly spinner and eastern spinner populations in several growth and reproductive parameters (summarized in Table 5), there is no clear basis for inferring that historically greater exploitation of the eastern spinner has resulted in a higher gross reproductive rate for the population. As would be expected, age at attainment of sexual maturity is lower in the eastern spinner population, but the major difference between the two populations in terms of gross production is in the proportion of females that are sexually mature. Although eastern specimens mature earlier, the mortality rate in this population may be sufficiently greater to effect a reproductively significant downward shift in age structure. In addition, the dearth of mature males hardly seems an adaptive population response and conceivably is an effect on male maturation structure (and perhaps age structure) by the purse-seining operation, through age- and maturity-selective fishing mortality, disruption of maturity-inducing social structure, or some other mechanism. In short, density-dependent population response in reproductive rates induced by the fishery may be counteracted by a more direct effect of the same fishery.

The various parameter estimates used here may be subject to sampling bias of various sorts. The bias in favor of calves in small-kill samples found in the case of the offshore spotted dolphin (Henderson *et al.*, 1980) was not found to be significant in the spinner-dolphin samples, although that does not eliminate the possibility of systematic bias in sampling from kills of all sizes. In any case, it can reasonably be assumed that whatever sampling biases exist are operating similarly for samples from the two populations. A possible exception to this is seasonal bias, as both reproduction and sampling are differentially seasonal (Barlow, 1984), but the effect, if any, can be presumed to be very small because of the length of gestation (almost a year) and the relatively diffuse nature of the reproductive seasonality.

As noted above, one alternative hypothesis to that of non-response (in reproductive rates) to exploitation in the eastern spinner population is that response has occurred in both populations, i.e. that the northern whitebelly spinner population even at 58–72% of its original size is substantially below its level of maximum productivity. In this context it would be useful to examine reproductive rates in a third population, the southern whitebelly spinner population, which has been more lightly exploited than the other two (Smith, 1979, 1983). Sample sizes to date have not been large enough to allow meaningful comparisons (Henderson *et al.*, 1980), although the trend in pregnancy rates with status for the three populations (higher rate with heavier exploitation) is consistent with the hypothesis that the northern whitebelly population has already responded to exploitation (Perrin and Reilly, 1984).

Although it has been assumed in assessment of the dolphin populations that there has been no effect of exploitation on survivorship (Smith, 1979, 1982), the possibility that such an effect exists cannot be ruled out. The possibility can be examined only through analysis of large representative samples of ages. The age analyses carried out in the study reported here were based on selected stratified samples that were aged to allow estimation of an age/growth curve; these aged samples were not adequate to allow estimation of populational age structure.

The results here point out the need for further research on the biology of the several populations, particularly on age structure and on male reproductive functional morphology and physiology.

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