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INTERPRETING SPOTTED DOLPHIN AGE DISTRIBUTIONS

Jay Barlow

Aleta Hohn

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U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Center

NOAA Technical Memorandum NMFS

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Jay Barlow

Aleta Hohn

Southwest Fisheries Center

National Marine Fisheries Service, NOAA

La Jolla, California 92038

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U.S. DEPARTMENT OF COMMERCE

Malcolm Baldrige, Secretary

National Oceanic and Atmospheric Administration

John V. Byrne, Administrator

National Marine Fisheries Service

William G. Gordon, Assistant Administrator for Fisheries

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INTERPRETING SPOTTED DOLPHIN AGE DISTRIBUTIONS

by Jay Barlow and Aleta A. Hohn

ABSTRACT

Previous work has determined the age distribution from a sample of spotted dolphins (Stenella attenuata) killed in the eastern Pacific tuna purse-seine fishery. In this paper we examine the usefulness of this age distribution for estimating natural mortality rates. The observed age distribution has a deficiency of individuals from 5-15 years and cannot represent a stable age distribution. Sampling bias and errors in age interpretation are examined as possible causes of the "dip" in the observed age structure. Natural mortality rates are estimated for the 15+ age classes based on the assumption that these are sampled representatively. The resulting annual survival rate (0.82) is too low to allow population growth, given what is known about dolphin reproductive rates.

INTRODUCTION

A research program began in 1979 at the Southwest Fisheries Center to determine the ages of dolphins that are killed in the eastern Pacific tuna purse-seine fishery. The initial goal was to develop age estimation methods and to determine ages of individual animals from a large, random sample of male and female spotted dolphins, Stenella attenuata. Age-specific birth and death rates were to be estimated from this information. The ultimate goal was to refine estimates of population growth rates.

The purpose of this report is to interpret some of the results of this age determination study. Methodology for age determination has been previously reported by Myrick, Hohn, Sloan, Kimura, and Stanley (1983). Studies of age-specific reproductive rates have been presented by Myrick, Hohn, Barlow and Sloan¹ and Hohn, Chivers and Barlow². This paper will consider the estimation of mortality rates from the age distribution data. There are, however, peculiarities in the spotted dolphin age distribution that preclude a straightforward estimation of mortality rates. Possible causes of these peculiarities are discussed in Section 1. Estimates of spotted dolphin mortality rates based on a number of simplifying assumptions are given in Section 2.

¹Myrick, A. C., A. A. Hohn, J. Barlow, and P. A. Sloan. 1984. Reproduction in female spotted dolphins, Stenella attenuata, from the eastern tropical Pacific. (manuscript).

²Hohn, A. A., S. J. Chivers and J. Barlow. 1984. Reproductive maturity and seasonality in male spotted dolphins, Stenella attenuata, in the eastern tropical Pacific. (manuscript).

Section 1. UNDERSTANDING THE AGE DISTRIBUTIONS

Aging Methods and Sample Selection

Ages were determined by counting growth layer groups (GLGs) in the dentine and cementum of teeth (Myrick et al. 1983). Teeth were sectioned and stained to make the layers more distinct. GLGs are defined as repeating series of growth layers which can be defined and counted, but which have no implied deposition time (Perrin and Myrick, 1980). However, GLGs in spotted dolphins were assumed to be annual, based on analogy to Hawaiian spinner dolphins, *S. longirostris*, (Myrick, Shallenberger, Kang and MacKay, in press).

Ages were estimated for a random subset of spotted dolphins in the dolphin life-history data base at the Southwest Fisheries Center (SWFC). These data are from a sample of the dolphins that were killed in the yellowfin tuna purse-seine fishery (see Perrin, Coe and Zweifel (1976) and Perrin, Miller and Sloan (1977) for life history sampling criteria). In practice, the random subsampling of specimens to be aged was confounded because teeth were not collected at sea from all individuals (due to exigencies of the commercial fishing operation). The initial procedure for selecting teeth in the laboratory was to proceed down a randomized list of all specimens until teeth were found for 800 males and 800 females collected during the period 1973-78. Ages were estimated independently by two tooth readers, with each reader making multiple estimates. All these estimates were combined to yield a composite or "pooled mean" age for each specimen (Reilly, Hohn, and Myrick 1983); however, the estimates made by the two readers differed significantly. Subsequently, ages were estimated for all females which were collected in 1981 and for which teeth were available (n=321). Only one age estimate was made by each reader for the 1981 sample, and these 2 estimates were averaged to obtain an age estimate for each specimen. For the 1981 sample, between reader differences were small (Reilly et al. 1983). Ages given in this report refer to the composite or average estimate for each specimen (unless otherwise noted). This report only considers aged specimens (1088 females and 793 males) from the northern offshore stock (Perrin, Sloan and Henderson 1979) of spotted dolphins.

Very young individuals (those with neonatal color patterns) are underrepresented in the aged subsample relative to the life-history sample³. Despite instructions to sample randomly at sea, teeth were apparently less likely to be collected from very small specimens.

The Problem

Age frequency distributions for the random samples of male and female

³Hohn, A. A. and A. C. Myrick. In prep. Age distribution of the kill of spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific.

spotted dolphins are shown in Fig. 1. Superimposed on these figures is an age distribution characteristic of a population in stable age distribution and which has a stereotypic mammalian pattern of age-specific mortality⁴. There is a notable dearth of specimens in age classes 5 to 15. This "dip" in apparent frequencies cannot occur in populations that have any conceivable stable age structure.

Three hypotheses could explain this aberrant age structure:

Hypothesis (1): (Non-stable age structure) The observed age distributions reflect the actual population age structure, which has been subject to a large perturbation and is not in stable age distribution;

Hypothesis (2): (Sampling bias) The observed age distributions are a biased sample of the true population age structure;

Hypothesis (3): (Variable rate of tooth layer deposition) The rate of tooth-layer deposition is not constant at 1 GLG per year, so that frequency distributions of GLGs are not the same as age frequency distributions.

All are examined in some detail below.

Non-Stable Age Distribution

If the paucity of specimens in age classes 5-15 were due to a large perturbation in the underlying age structure, we would expect to see the perturbation propagate through the age structure with time. For instance, if a minima in age class abundance in 1973 occurred at 8 years of age, we would expect that minima to occur at 16 years in 1981. Comparing the 1973 and 1981 age structures (Fig. 2), a minima occurs near 8 years for both, and in 1981 a maxima in age class abundances occurs near 16 years. The cumulative age frequency distributions were tested pairwise for individual years (1973 to 1981 for females, 1973 to 1978 for males). In only 2 of these 36 pairwise comparisons were the between year differences significant (Kolmogorov/Smirnov test, $p < 0.05$). This number of significant results would be expected given random variation (alpha error). On the basis on these observations, the first hypothesis is regarded as untenable.

Sampling Bias

Juveniles (age classes 5-15) may be underrepresented in tuna purse-seine samples relative to the underlying population. This could occur if juvenile dolphins segregate from other dolphins, and if schools of juvenile dolphins were less likely to be captured by tuna fishermen. Hohn and Scott⁵ presented evidence for such segregation. Furthermore, they found "juvenile schools" to have a smaller characteristic school size, which might make them

⁴Barlow, J. 1984. Variability, trends and biases in reproductive rates of spotted dolphins (*Stenella attenuata*). (manuscript).

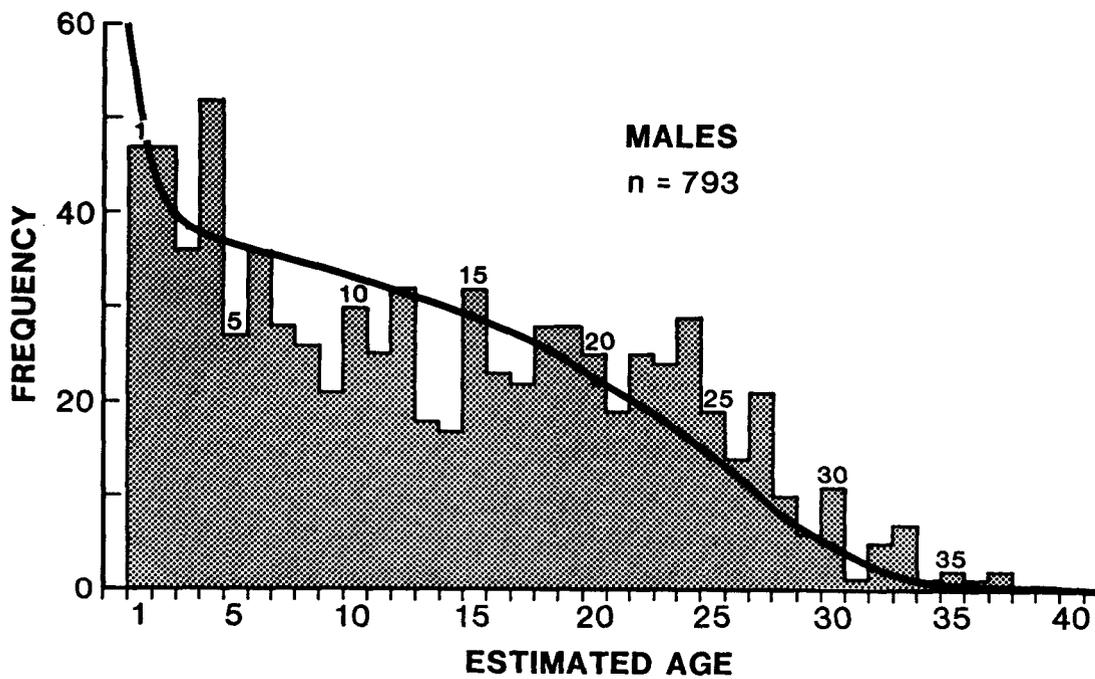
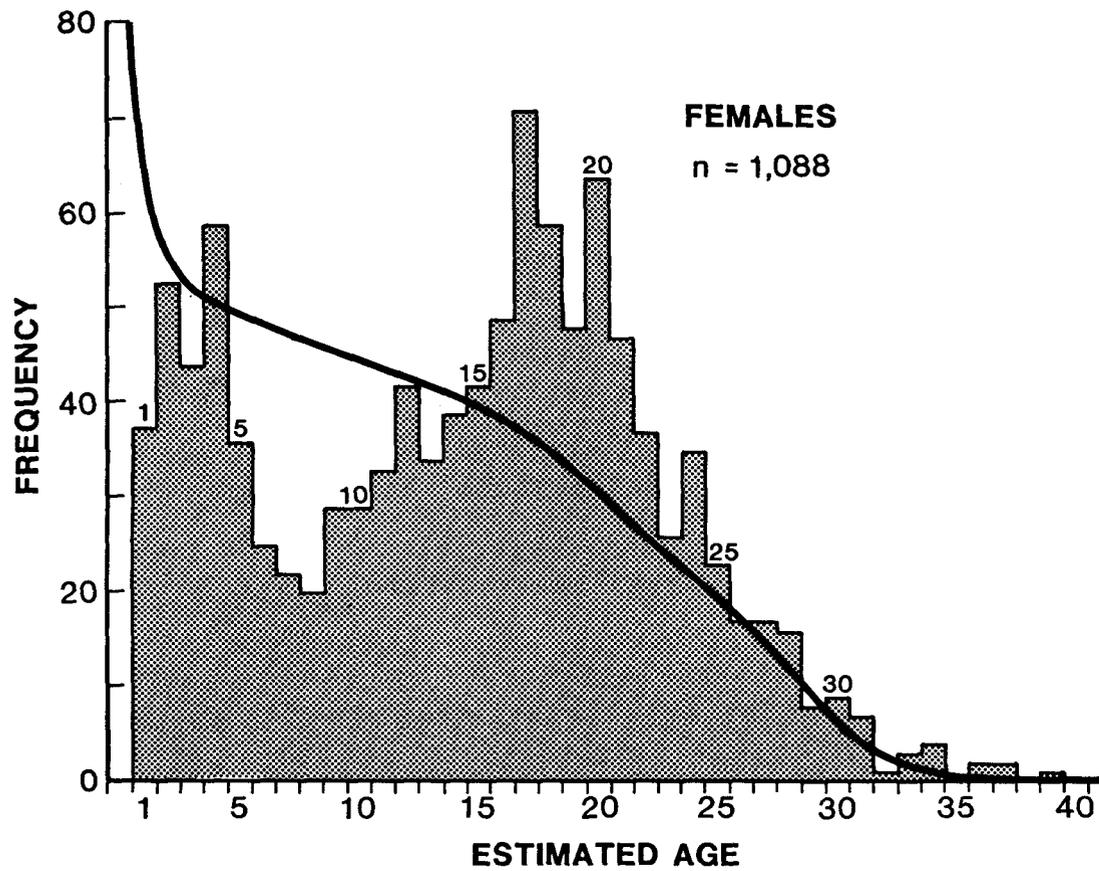


Figure 1. Observed age frequency distributions for female and male spotted dolphins based on tooth aging samples (1973-81)(figures from Hohn and Myrick. Age distribution of the kill of spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific, in prep.). Solid curves represent typical stable age distributions for the given sample sizes based on a generalized mammalian pattern of age specific mortality⁴.

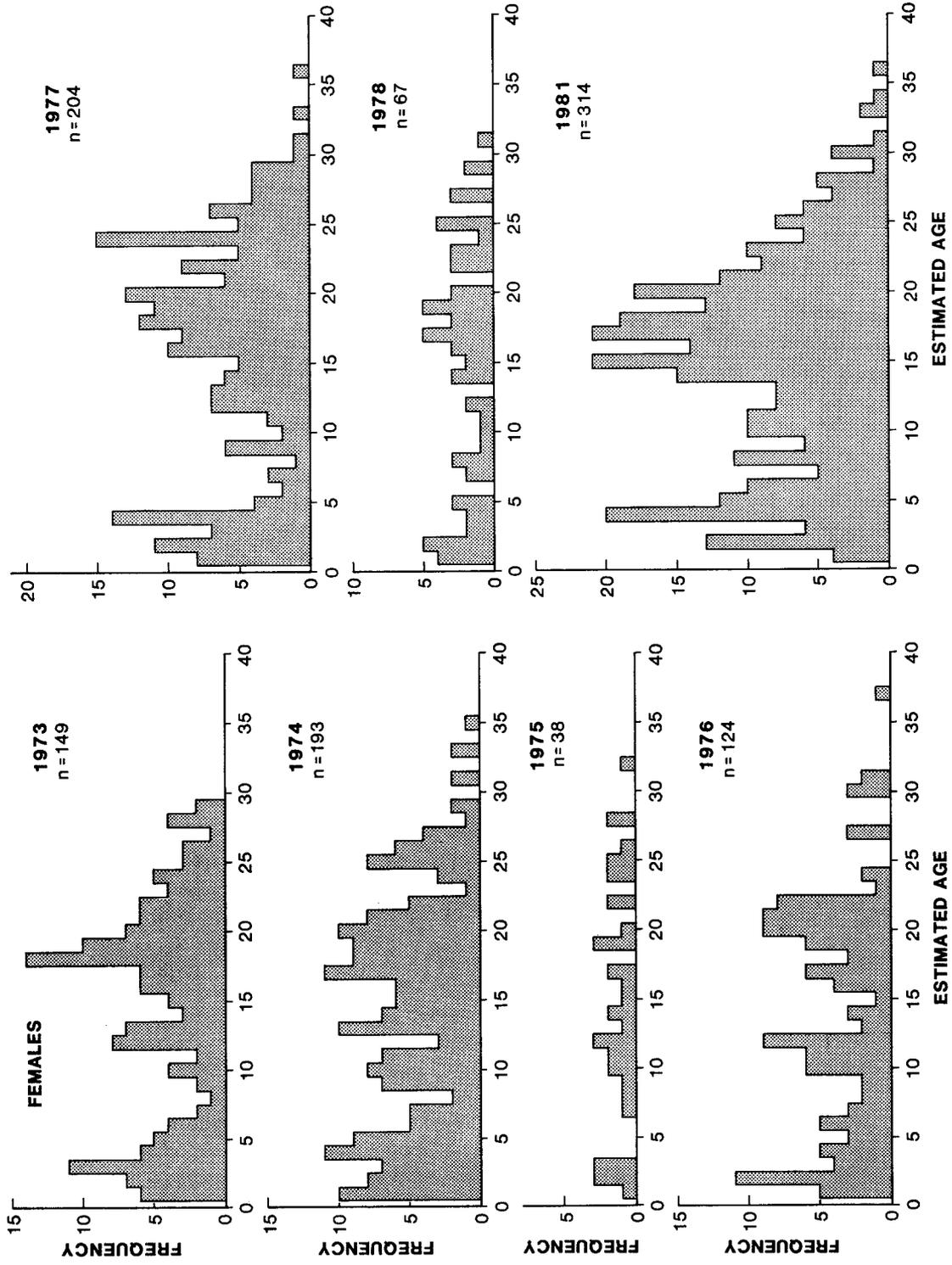


Figure 2. Observed age frequency distributions for female spotted dolphins based on tooth aging samples from 1973-81 (figures from Hohn and Myrick. Age distribution of the kill of spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific, in prep.).

less attractive to tuna fishermen. These observations support Hypothesis (2) above. It is not known if the magnitude of this effect is sufficient to account for the apparent bias in age distributions.

Variable Rate of Tooth-layer Deposition

There is no direct evidence for variable deposition rate in dolphin tooth layers. By analogy, however, we compare results from spotted dolphin age analyses with those from other dolphin species to help evaluate whether GLGs represent annual increments.

Growth Curve Comparisons

It is sometimes possible to verify aging methods by comparing growth curves based on estimated ages of wild animals to growth curves of known-age captive animals (Laws 1966). The mean lengths of male and female spotted dolphins are plotted in Fig. 3 as a function of age. We compare these spotted dolphin growth curves to growth in captive-born and known-aged wild bottlenose dolphins (Tursiops truncatus).

Individual growth curves for known-age bottlenose dolphins are shown in Fig. 4 (data from Myrick and Cornell⁶ (captive dolphins); Ridgway, pers comm. (captive); Harrison, Brownell and Boice 1972 (captive); Irvine, Scott, Wells, Kaufmann, and Evans 1979 (wild); and Wells, Irvine, and Scott 1980 (wild)). Published growth curves based on tooth aging are also shown for two wild populations of bottlenose dolphins (Sergeant, Caldwell and Caldwell 1973; Hohn 1980) and one western Pacific population of spotted dolphins (Kasuya 1976). The average length at a given age for female spotted dolphins in this study (Fig. 3) is repeated in Fig. 4. All the growth curves based on tooth-layers tend to underestimate the rate at which captive dolphins can grow. Within species, growth is relatively determinate in mammals (Case 1978), hence this degree of growth enhancement due to captivity does not seem likely. Typically, if growth is increased by improved diet, asymptotic lengths also change. Captive dolphins are not growing to greater asymptotic lengths than wild specimens (Ridgway and Fenner 1982). Also, the length of known-age wild specimens are similar to captive dolphins of the same age (Fig. 4).

Spotted dolphins apparently grow more slowly than known-age bottlenose dolphins. True growth rates would be faster if young spotted dolphins laid down more than one GLG per year (Hypothesis 3).

⁵Hohn, A. A. and M. D. Scott. 1983. Segregation by age in schools of spotted dolphins in the eastern tropical Pacific. Abstract, Fifth Biennial Conference on the Biology of Marine Mammals, Boston.

⁶Myrick, A. C. and L. H. Cornell. In prep. Calibration of dental layers in captive bottlenose dolphins, Tursiops truncatus, using tetracycline labels and tooth extractions.

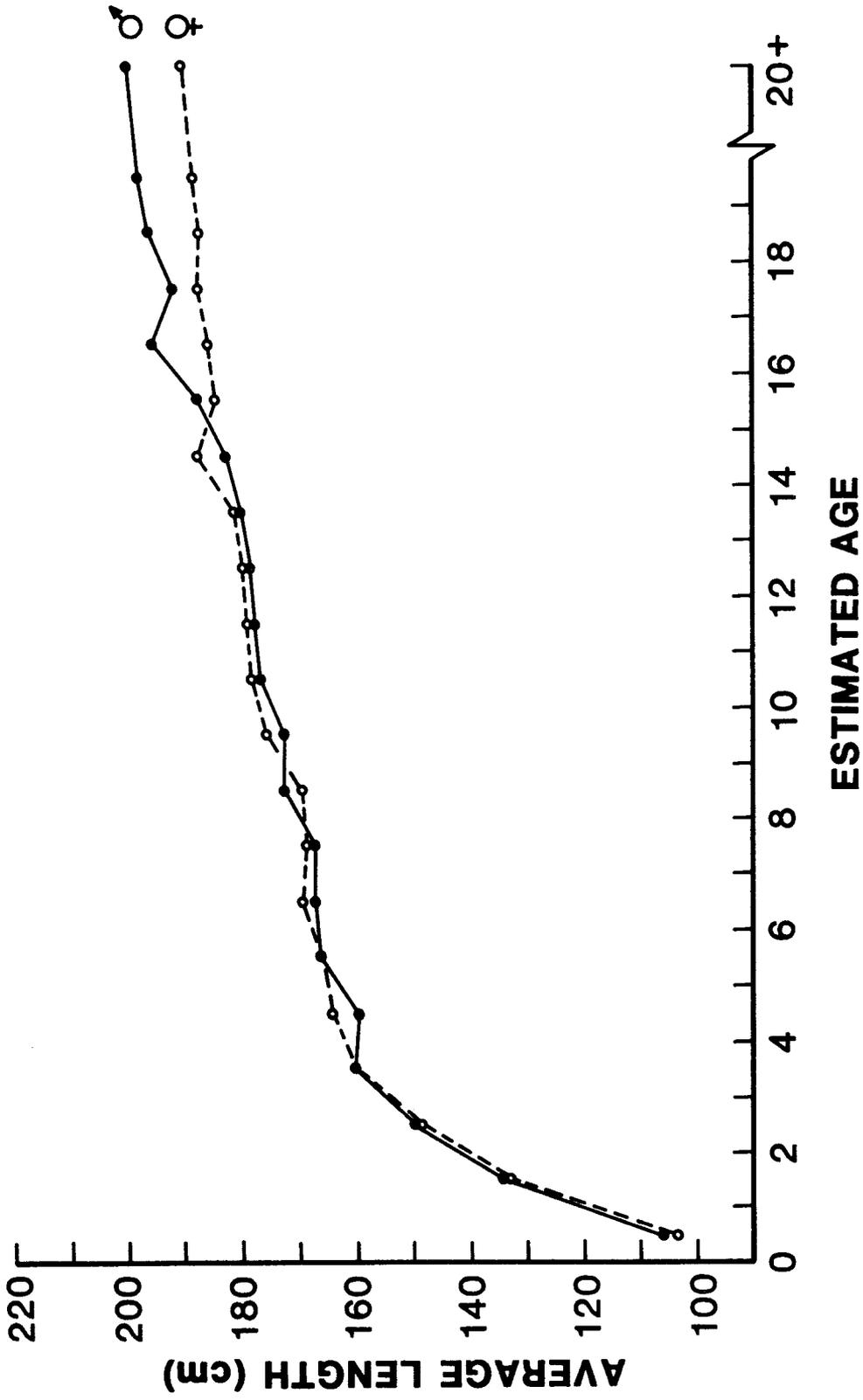


Figure 3. Mean growth curves for female and male spotted dolphins in the eastern Pacific, based on tooth aging. Points represent mean values for each age class.

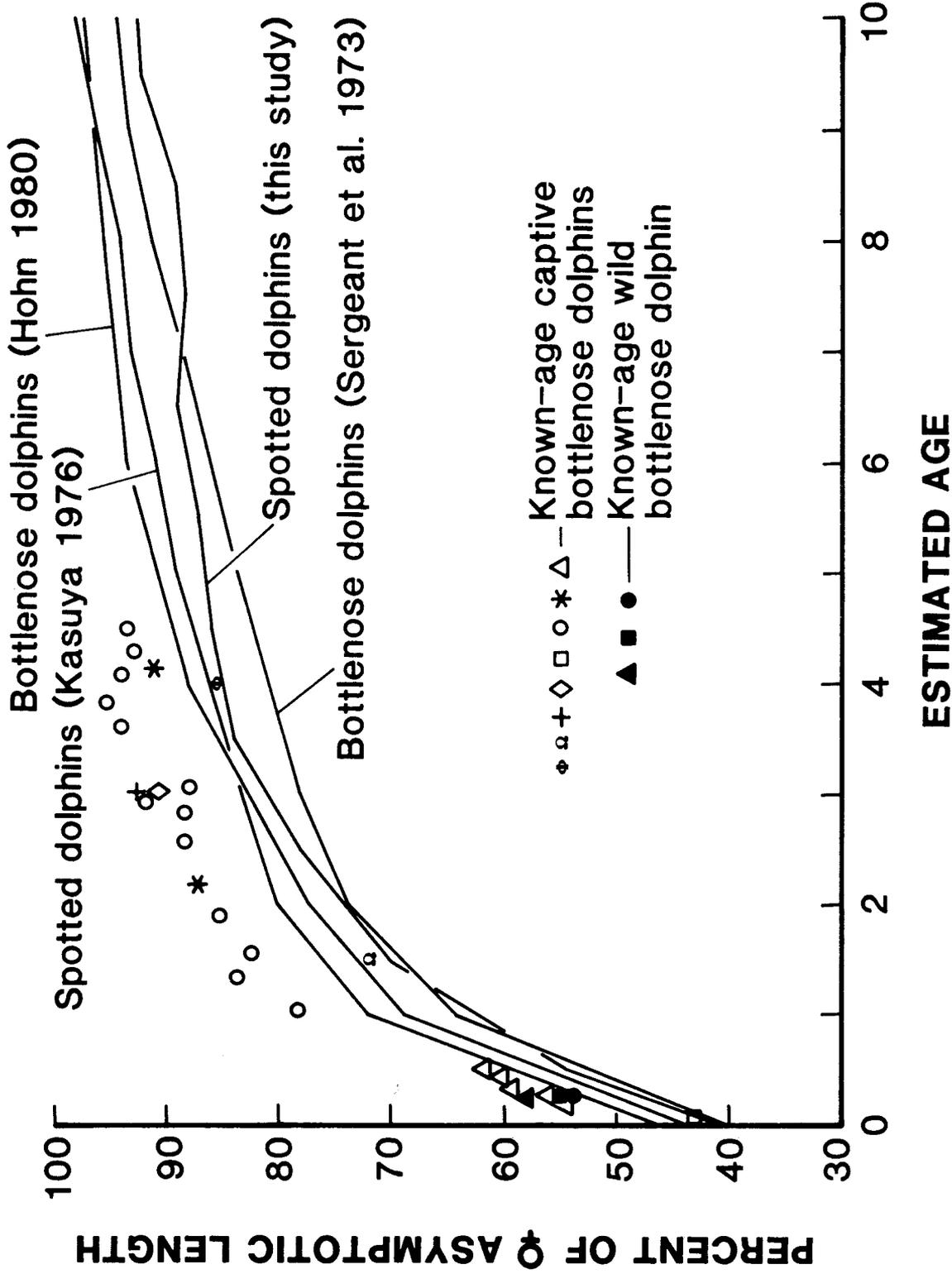


Figure 4. Age-length relationships for a variety of dolphins. Length is scaled as percentage of asymptotic length of females (250 cm for bottlenose dolphins, 190 cm for spotted dolphins). Solid lines represent growth curves based on mean lengths at ages determined by tooth aging. Each symbol represent age-length relationship from a different known-age individuals (note: more than one measurement for some individuals).

Age at Sexual Maturation

The age of sexual maturation in spotted dolphins as estimated from tooth layer data is higher than that of bottlenose dolphins for which ages are known directly. The mean age of sexual maturity in spotted dolphins was determined from tooth layer counts to be 11.3 years for females (range of 10.6 to 12.0 for the two readers)¹ and 15.1 for males (range of 13.6 to 16.6 for the two readers)². For the two readers, the youngest sexually mature females were 9.0 and 9.8 years.

For known-age captive bottlenose dolphins the youngest to give birth was 7 years old (Ridgway and Benirschke 1977), implying sexual maturity at age 6. Captive dolphins may mature at an earlier age if they have a greater fat reserve than wild dolphins (Frisch and Revelle 1970); however, a known-age bottlenose dolphin in a wild population gave birth at age 8 (Wells and Scott, pers. comm.), implying sexual maturity at age 7.

Spotted dolphins are smaller than bottlenose dolphins and thus might be expected to mature at a younger age. Based on tooth-layer ages for spotted dolphins and on a small sample of known ages for bottlenose dolphins, spotted dolphins appear to mature at an older age than bottlenose dolphins. If expectations were true, and spotted dolphins mature earlier than bottlenose dolphins, then more than one GLG (as defined in the spotted dolphin age study) must be deposited per year in young spotted dolphins.

Age Distribution Comparisons

Age distributions have been determined for several other dolphin populations using the tooth layer method. Western Pacific spotted dolphins were sampled from the Japanese drive fishery for dolphins (Kasuya 1976). The age distribution of these spotted dolphins is similar to those of the eastern Pacific, with a dearth of individuals in age classes 4-13 (Fig. 5) (Kasuya 1976, his Figs. 16 & 17). He also found that the "dip" in the age distribution was more pronounced for females.

Age distributions of bottlenose dolphins in the western Atlantic show a similar pattern. Samples were obtained from a shore-based net fishery in 1927-28 on the outer banks of North Carolina (Mead 1975). Although sample size is small, age distributions from these samples appear to show a dearth of specimens from 8 to 16 years (Fig. 6) (A. A. Hohn and J. G. Mead, unpubl. data).

Samples from three different dolphin populations all show similar patterns in their age distributions. This may be evidence of a common social structure whereby juveniles segregate from adults and their dependent calves (Hypothesis 2). To be consistent with observations, the juvenile schools would always have to be under-sampled. Alternatively, consistent errors in interpreting GLGs as annual layers for young dolphins could also explain the consistency in these patterns (Hypothesis 3).

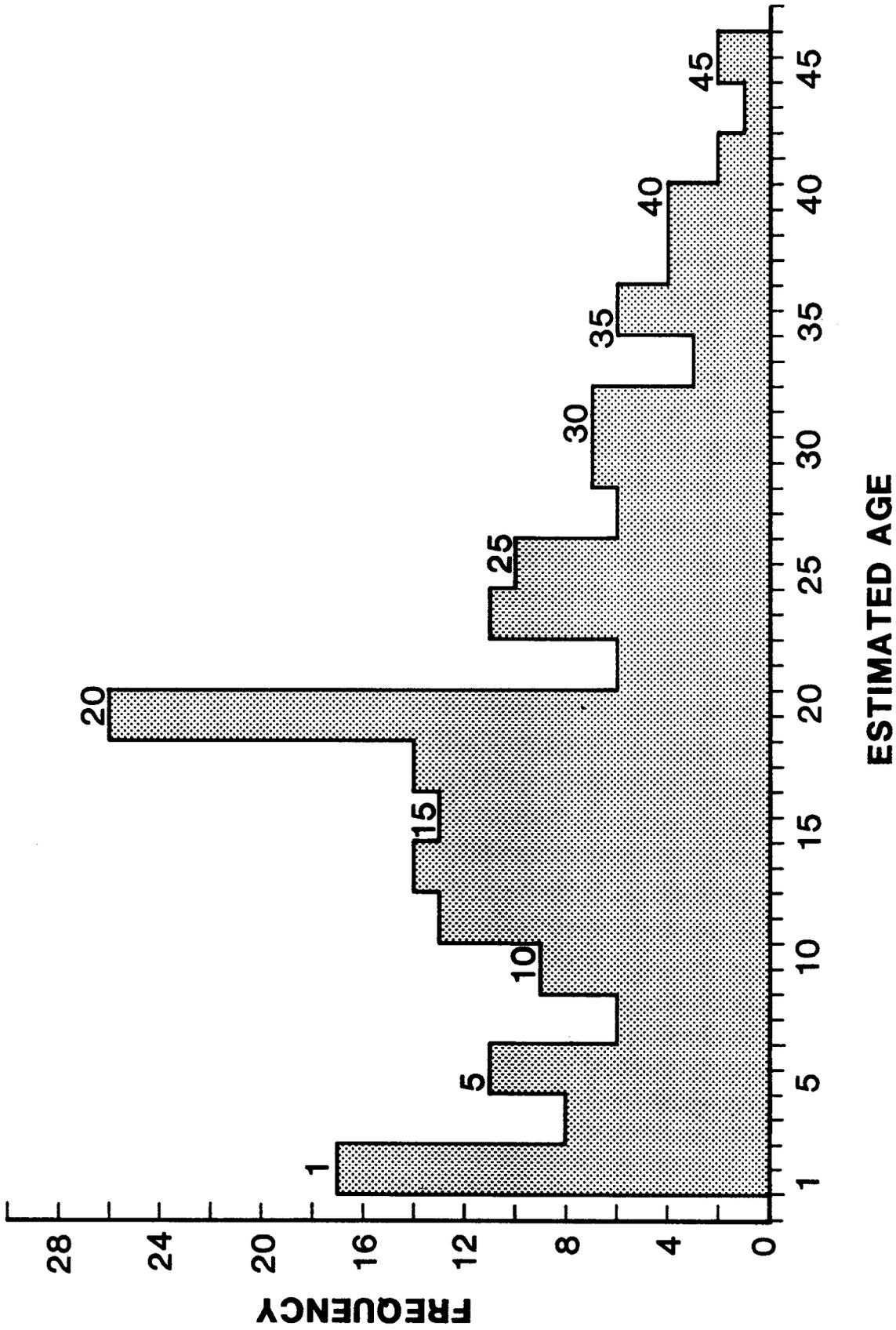


Figure 5. Observed age frequency distribution for females in a Japanese population of spotted dolphins based on tooth aging (Fig. 16 from Kasuya 1976).

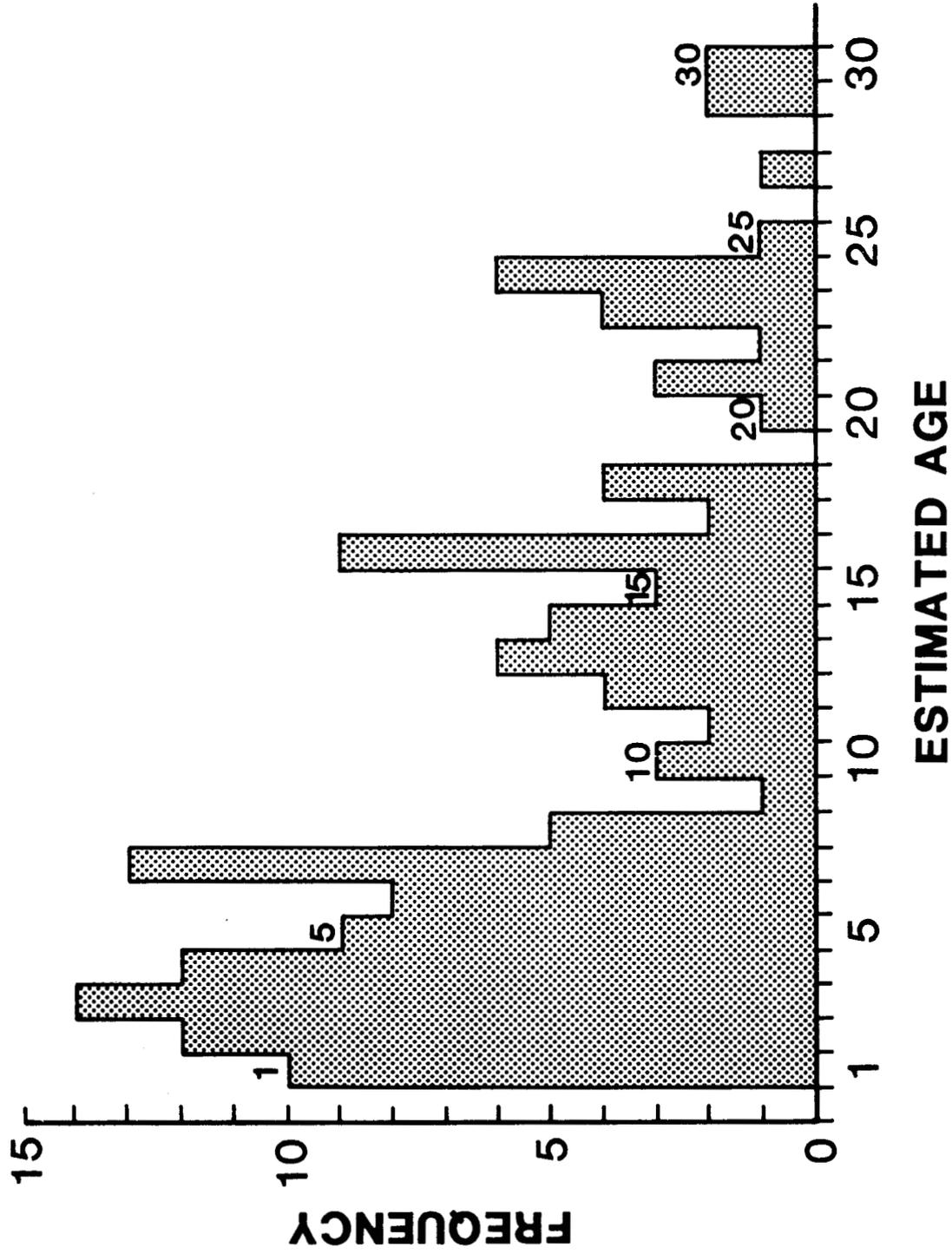


Figure 6. Observed age frequency distribution for a western Atlantic population of bottlenose dolphins based on tooth aging (Hohn and Mead, unpubl. data). Males and females are pooled.

Calibration of Aging Methods

The most direct verification of aging methods uses known-age individuals. Using 4 captive bottlenose dolphins (2 born in captivity), Sergeant (1959) concluded that GLGs (as defined by him) are deposited annually. Sergeant, Caldwell and Caldwell (1973) reported on 13 more captive bottlenose dolphins (one born in captivity and 21 yrs old), again concluding that their GLGs are annual. Additional studies on captive bottlenose dolphins (Hui 1980) reported the same conclusion. Myrick et al. (in press) examined teeth from one captive-born Hawaiian spinner dolphin (*S. longirostris*); again the number of GLGs matched the age of the specimen.

Additional evidence for the annual deposition of GLGs is from tetracycline-marked dolphins. This approach has been used on *Lagenorhynchus obscurus* (n=3, Best 1976), *Delphinus delphis* (n=3, Gurevich, Stewart, and Cornell 1980), and *S. longirostris* (n=6, Myrick et al. in press). In each case, the GLGs were interpreted to be annual.

Annual growth layers have also been verified in teeth of tropical, terrestrial species based on known-age specimens. Spinage (1976) found one layer per year in three species (waterbuck, lion, and giraffe) and 2 annual layers in another species (black rhinoceros). In the latter case, the two layers could be distinguished, and thus both layers fit into the current concept of a growth layer group (GLG). Spinage (1976) suggests that differences in deposition patterns are influenced by environmental factors, specifically annual vs. biannual rainfall patterns.

GLGs in teeth have been found to be annual in most species for which this has been examined. Some of these studies can be faulted, however, for their lack of blind tests. Blind GLG counts by experienced readers can differ markedly when approximate age is not known (Kimura, 1980). Between reader differences may result from subjectivity in defining GLGs. This subjectivity can result in defining GLGs that do not represent annual patterns. Regardless, previous calibration studies of dolphin age determination tend to discount Hypothesis (3).

Summary

In examining causes for the observed "dip" in the age structure of female spotted dolphins, we have found that non-stable age structure cannot be the cause of this peculiarity, but that sampling bias or age determination errors could be. Evidence of social segregation is strong⁵, but this alone cannot cause a bias unless sampling is also selective. Additional work on sampling bias is needed. In spotted dolphins, GLGs in teeth have not been proven to correspond to age in years. Based on comparing patterns of age-specific growth and maturation to known-age bottlenose dolphins, age estimates for spotted dolphins may be too high (ie. more than 1 GLG may be deposited annually, at least for young dolphins). Comparisons to GLG patterns in other dolphins suggest that 1 GLG per year would be expected. Resolution of this apparent conflict will require additional information.

Section 2. ESTIMATING NATURAL MORTALITY RATES

This section deals with the estimation of survival rates from the above age frequency distributions. The first section raised doubts about the suitability of the data for this exercise, specifically whether sampling or age determination are biased. This section simply examines some of the possibilities for mortality estimation if Hypothesis 2 is true and Hypothesis 3 is false (ie. ages are known, but frequency distributions are biased for younger age classes).

Survival or mortality rates can be estimated from the age frequency distribution of a population provided that 1) the population is in "stable age distribution" and 2) the population growth rate is known (Caughley 1977). The first of these conditions would be met if age-specific birth and death rates had remained constant for a sufficient period of time prior to sampling the age distributions (Lopez 1961). The second would be met if population growth rates were measured by direct observation (Barlow 1982) or if a stationary population were assumed (hence zero growth, Caughley 1966).

For spotted dolphins, problems exist with both assumptions. Given varying levels of fishery-related mortality since 1959, we know that age-specific mortality rates have not remained constant. We do not know the population growth rates of the spotted dolphin populations (although an attempt has been made to define likely ranges⁷).

It is, however, possible to address the more limited problem of estimating pre-1959 mortality rates. If we assume that dolphin stocks were in equilibrium prior to 1959, we can then assume that age-specific birth and death rates were constant prior to that time and that the population growth rate was zero. Historical rates of natural mortality can be estimated from current age distributions (Ohsumi 1978). Although teeth were not collected for age determination until the 1970s, details of the 1959 age distribution can be derived from what is known of the 1973-81 age distributions. These pre-1959 mortality rates are important because they correspond to natural mortality rates, or the mortality rates prior to incidental fishing mortality.

Two additional assumptions are necessary to estimate natural mortality by these means. First, there must be no compensatory changes in adult mortality rates with population density. Eberhardt (1977) and Fowler (1981) suggest that adult mortality is less likely than other vital rates to show density dependent changes in marine mammals. Second, fishery-related dolphin mortality must not be selective with respect to age, or the age-specific selectivity must be known. If the first assumption is true and if fishery-related mortality has not been selective, the age distribution of individuals over 14 years of age would be the same in 1973 as it was in 1959.

⁷Reilly, S. B. and J. Barlow. 1984. Rates of increase in delphinid cetaceans. (manuscript).

Effects of Selective Harvest

If dolphin harvests between 1959 and 1973 were not distributed evenly over all ages, estimation of mortality rates becomes more difficult. No data exist from which 1959-72 selectivities could be estimated; however, as was discussed in Section 1, considerable age selectivity may have existed in the 1973-81 harvests (Fig. 1). A simulation model is used to examine the effect of selective harvests on the estimation of annual mortality rates.

A population is assumed to be in stable age distribution with an equilibrium population size of 6 million in the year 1959. Assume a 13-year age of first reproduction for females, a fecundity of 0.15, and a constant survival rate of 0.95. The population is projected to the year 1974 using a Leslie matrix model. Each year, harvests are applied to each age class based on the age-specific selectivities given in Table 1. Density dependent changes are allowed in age of maturation and fecundity, but not in survival rates. This example was patterned after spotted dolphins, and the actual estimates of dolphin mortality (Smith 1983, Table 4) were used for harvest numbers. Details of the density dependence are not relevant so long as adult mortality does not change through time.

Results of the simulation model show that selective harvests can affect the estimation of natural mortality rates. The initial age distribution in 1959 (Fig. 7, upper line) show a constant slope which corresponds to the stationary age distribution of a population with a constant mortality rate of 0.95. The projected age distribution in 1974 (Fig. 7, lower line) has a variable slope due to the effects of a density dependence and a time varying age-selective harvest. If the harvest had not been age-selective, the portion of the 1973 age distribution over 15 years would have had the same slope as in 1959. Using the 15+ age classes, the Chapman and Robson (1960) mortality estimator give a value of 0.932 rather than the true value of 0.95. In this case, non-selective harvests resulted in a slight under-estimate of pre-1959 natural mortality rates.

Pooling Age Distributions

Age distributions for individual years (Fig. 2) do not contain sufficient numbers of older individuals to estimate mortality reliably for each year. The problem is how to pool the years so as to obtain a single natural mortality estimate. Ages less than 17 years were not used, in order to avoid the potential bias in age frequency distributions (above). The method used here was to sum the frequency of individuals in age class 17 in the 1973 sample, plus the frequency in age class 18 in 1974, plus the frequency in age class 19 in 1975, etc., to get a first age class. The second and subsequent age classes were summed in the same way, using successively higher starting ages in 1973. Since this method can introduce errors if mortality rates change appreciably with age, sums were pooled over a span of only 5 years (1973-77), as well as over the entire data set (1973-81). The effect of age-varying mortality rates has not been investigated.

Table 1. Relative age-specific harvest selectivities used in the simulation model for population projection.

Age Class	Relative Selectivity
1	1.0
2	1.0
3	1.0
4	0.9
5	0.8
6	0.7
7	0.6
8	0.5
9	0.5
10	0.6
11	0.7
12	0.8
13	0.9
14	1.0
.	.
.	.
.	.
15+	1.0

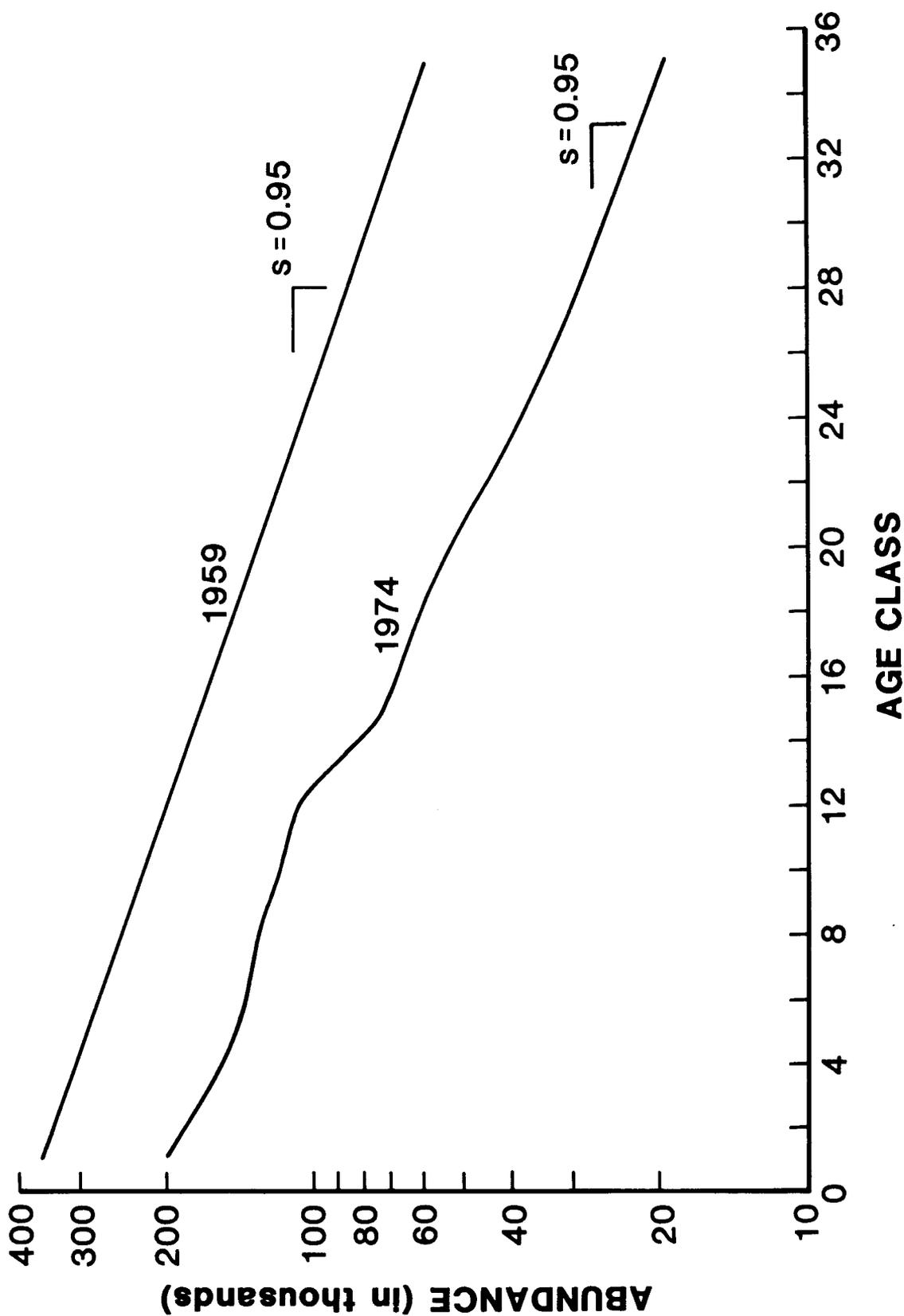


Figure 7. Age frequency distributions of a hypothetical population of spotted dolphins in 1959 and 1974 (see text). Differences represent effects of age-selective time-varying harvests, population reduction, and density compensatory increases in fecundity.

Results

The synthesized age distributions from 1973-77 and 1973-81 are given in Table 2. If all of the above assumptions were met, these should approximate the age distribution in 1959 for individuals of 17 years or older. The Chapman-Robson model was used to estimate a constant survival rate from these age frequency distributions (Chapman and Robson 1960). Annual survival rates were 0.829 (s.e.=0.012) for 1973-77 data and 0.818 (s.e.=0.012) for 1973-81 data. Attempts were made to estimate age-specific survival rates from these data by fitting non-linear functions to this age frequency data (Barlow 1982). The non-linear functions gave better fits to the data, but these improvements were not statistically significant. Expected age frequencies predicted by the geometric (Chapman-Robson) model were not significantly different from the observed age frequencies (chi-square test). Since we are not able to discern age-specific changes in survival rates, pooling the entire 1973-81 data set is justified.

Discussion

The estimation of natural survival rates for spotted dolphins is dependent on many assumptions. Some of these assumptions (e.g. non-selective harvesting) are undoubtedly not met. Additional simulations may be useful to determine the sensitivity of this method to violations in the assumptions. First, however, attempts should be made to resolve the questions of age estimation raised in Section 1. Without accurate age estimates, mortality rates simply cannot be estimated by these means.

The survival rate estimated above (0.82) is less than expected for an adult survival rate for spotted dolphins. The simulation model indicated that selective harvests could cause this value to be 2 percentage points low. However, even assuming survival rates of 0.85 and high estimates for fecundity (age-at-first-birth = 7 yrs, calving interval = 2 years), this adult survival would result in a population declining at more than 5% per year⁷. This is obviously not an equilibrium survival rate. This low estimate may be an artifact of the difficulty in aging older individuals. Alternatively, the estimate may be accurate as a composite estimate for older age classes, though younger age classes may have much higher survival rates. The latter might be expected given the mortality patterns seen in other mammals (Caughley 1966).

CONCLUSION

Current age distributions provide little direct information which will allow us to refine estimates of dolphin population growth rates. Until uncertainty in age estimation and sampling bias can be resolved, analysis of age distributions will be of little value. However, several of the approaches used here may be useful in resolving these uncertainties.

Potential exists to use growth curves of known-age dolphins to verify age estimation procedures. Given our limited samples, we do not know the inter-specific range of variability in dolphin growth. Growth curves are needed for a variety of dolphin species. Also, we do not know the possible

Table 2. Synthesized age frequency distributions for spotted dolphins. Included are distributions taken female spotted dolphin age distributions from 1973-77 and from 1973-81 (see text for methods).

Age Class	Age Class Abundance (1973-77)	Age Class Abundance (1973-81)
a	33	44
b	42	51
c	33	38
d	33	42
e	18	19
f	16	23
g	13	14
h	21	23
i	13	15
j	10	12
k	6	6
l	8	9
m	3	3
n	3	3
o	0	0
p	3	3
q	0	0
r	2	2
Total	257	307

range of intra-specific growth in dolphins and whether captivity can appreciable alter growth rates. Unpublished data of this sort may exist at a number of marine aquariums throughout the world. Additional data on captive animals can certainly be gathered, and the possibility exists for gathering more data from certain wild populations (M. D. Scott, pers. comm.).

Additional data on age at sexual maturation in captive dolphins may also help verify age estimation procedures. Estimates for species other than bottlenose dolphins would be especially useful. Data on marked, wild populations would be of great value also.

In addition to uncertainty in age estimation, uncertainty exists in the degree of sampling bias. Even if social segregation is extreme, a large bias would require that the fishing operations be selective, either consciously or unconsciously. Work is underway to determine whether known levels of selectivity are sufficient to explain the apparent level of sampling bias (A. A. Hohn and M. D. Scott, pers. comm.).

Much work has yet to be done before questions of sampling bias and age estimation in spotted dolphins can be completely resolved. In this paper we have raised more questions than we have answered. We hope that by bringing these questions to light, we can ensure that they will be answered. The answers may be broadly applicable and useful in other dolphin population studies.

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