

Age estimates for female eastern and whitebelly spinner dolphins (*Stenella longirostris*) incidentally killed in the eastern tropical Pacific tuna purse-seine fishery from 1973-82

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ABSTRACT

Age was estimated from teeth for 1,267 female eastern spinner dolphins (*Stenella longirostris orientalis*) and 1,071 female whitebelly spinner dolphins (*S. longirostris*) incidentally killed in the eastern tropical Pacific yellowfin tuna purse-seine fishery between 1973 and 1982. The final age assigned to each specimen was the mean of two readers' age estimates made independently and without knowledge of the corresponding biological data for each specimen. The oldest eastern spinner dolphin was estimated to be 24.5 years and the oldest whitebelly spinner dolphin was 26 years. Age bias plots revealed nonlinear systematic bias between readers while a measure of overall precision, coefficient of variation (CV), indicated equivalent difficulty in estimating age for each population. The age frequency distributions generated in this study document the age structure of dolphins sampled from the observed incidental kill, which will facilitate further assessments of the impact of the fishery on these dolphins.

KEYWORDS: SPINNER DOLPHIN; PACIFIC OCEAN; PURSE-SEINES; INCIDENTAL CATCHES; AGE DETERMINATION; AGE DISTRIBUTION

INTRODUCTION

Eastern spinner dolphins (*Stenella longirostris orientalis*) and whitebelly spinner dolphins, a hybrid form of spinner dolphin (*S. longirostris*), have been incidentally killed in the yellowfin tuna (*Thunnus albacares*) purse-seine fishery that operates in the eastern tropical Pacific (ETP) for more than four decades (Perrin, 1969). These two forms are managed as separate populations in the region. Using estimates of the incidental kill and population abundance, the eastern spinner dolphin population was estimated to be at approximately 44% of its pre-exploitation size of 1,100,000 to 1,956,000 dolphins in 1988 (Wade, 1993) and is listed as 'depleted' under the US Marine Mammal Protection Act¹. The whitebelly spinner dolphin population is incidentally killed less frequently and was estimated to be between 58% and 72% of its pre-exploitation size of 400,000 to 500,000 dolphins in 1979 (Smith, 1983). Recent evidence suggests that these two dolphin populations are not recovering as expected, despite greatly reduced mortality levels of <1,000 dolphins per year since 1993 (Gerrodette and Forcada, 2005; IATTC, 2004; Reilly *et al.*, 2005a; Reilly *et al.*, 2005b).

Since the 1970s, research on spinner dolphins and other ETP dolphin populations incidentally taken during purse-seine fishing activities has been conducted in order to better understand the dynamics of their populations and the impacts of the fishery on them. Included in that research were biological studies to characterise the age and sex selectivity of the fishery kill and to quantify vital rates for estimating the reproductive potential of the populations.

For this research, fishery observers working aboard purse-seine fishing vessels collected biological samples from more than 4,000 eastern and whitebelly spinner dolphins incidentally killed in the ETP tuna fishery since 1968. Two studies conducted in the late seventies and the mid-eighties estimated age for 250 female eastern spinner dolphin (Perrin and Henderson, 1984; Perrin *et al.*, 1977) and 232 female whitebelly spinner dolphin (Perrin and

Henderson, 1984) specimens collected through 1978 to study growth and reproductive patterns in these populations. In these studies, one reader counted tooth growth layer groups (GLGs) for each specimen and several models of GLG deposition rate were explored. Age frequency distributions were not presented in these studies because samples were selected to describe age-specific growth patterns and not to describe the age structure of the incidental kill (Perrin and Henderson, 1984).

Following these two studies and calibration of GLG deposition in captive Hawaiian spinner dolphins, *S. longirostris* (Myrick *et al.*, 1984), a study was conducted to document the age structure of the incidental kill of females for the two spinner dolphin populations by estimating age for a larger dataset collected over a longer time series. The results of this study are presented here. The analyses employed quantify the bias and precision in age estimation by two independent readers for the female eastern and whitebelly spinner dolphins and generate an age frequency distribution for the dolphins incidentally killed in the fishery between 1973 and 1982 for each population.

MATERIALS AND METHODS

Biological data collected

In 1968, the National Marine Fisheries Service (NMFS) began collecting mortality and biological data from dolphins incidentally killed during fishing operations (Perrin *et al.*, 1976). Beginning in October 1972, biological data collection procedures were standardised, and the sampling scheme that selectively collected large, female specimens was replaced by a less-selective sampling scheme that sampled the first available dead dolphins brought aboard. In 1979, the Inter-American Tropical Tuna Commission (IATTC) joined the NMFS in placing observers aboard US-registered vessels and collecting life history data from incidentally killed dolphins. Instructions and protocols for data collection were the same for NMFS and IATTC observers.

¹ Federal Register Vol. 58, No. 164, August 26, 1993 (58 FR 45066).

The biological data collected by observers included the species, stock, total body length and sex of all cetaceans incidentally killed and brought aboard the vessel along with the date, geographic location and a tally of the total number (examined and unexamined) of dolphins killed in the set (Myrick *et al.*, 1986; Perrin *et al.*, 1976; Perrin and Oliver, 1982). Reproductive organs and a section of the middle of the lower left jaw containing teeth were collected and preserved in formalin from as many specimens as possible.

Potential bias in the analyses was reduced by only using data from specimens collected after October 1972, which is when observers stopped selecting large female dolphins to sample and started collecting samples from dolphins in the order they were brought aboard. The data set includes 1,267 female eastern spinner dolphins and 1,071 female whitebelly spinner dolphins that were incidentally killed in 991 purse-seine sets between 1973 and 1982 (Table 1). Specimens were collected throughout the range of each form of spinner dolphin in the ETP (Fig. 1).

Age estimation

Multiple age estimates of a specimen permit the precision in interpreting GLGs to be quantified. Results from a prior ageing study of spotted dolphins (*S. attenuata*), which are closely related to spinner dolphins (LeDuc *et al.*, 1999), found inter-reader variation to be notably greater than intra-reader variation (Reilly *et al.*, 1983). Thus, the study design for this experiment specified that two readers would age each specimen once to minimise workload and to allow quantification of the more important contributor to ageing variation, inter-reader precision.

Samples were randomly selected from all female specimens incidentally killed between 1973 and 1982. A tooth was removed from the jaw section of each specimen, decalcified, thin sectioned, hematoxylin-stained and mounted on microscope slides for ageing (Hohn and Hankins, 1983; Myrick Jr *et al.*, 1983). Two readers (hereinafter referred to as readers A and B) with experience ageing *Stenella* spp. estimated age by counting GLGs in the dentine of prepared tooth sections without knowledge of the specimen's accompanying biological data (e.g. population, total body length, state of maturity) or any prior age estimates. Neither of these readers had estimated ages for the two prior eastern and whitebelly spinner studies. The GLGs identified in eastern and whitebelly spinner dolphin teeth were interpreted as annual events based on conclusions from a calibration experiment conducted with captive Hawaiian spinner dolphins exposed to the seasonal variability of the subtropics because they were kept in outdoor pens (Myrick *et al.*, 1984). For each specimen, readers independently scored the same tooth recording their best estimate of age to the nearest 0.1 year for the first three GLGs and to the nearest integer thereafter, their confidence in the estimate, and the quality of the tooth sections read. If a reader did not feel confident in their first reading because the quality of the preparation was poor, another tooth was prepared and used by both readers to estimate age of that specimen. When more than one age estimate was made by a

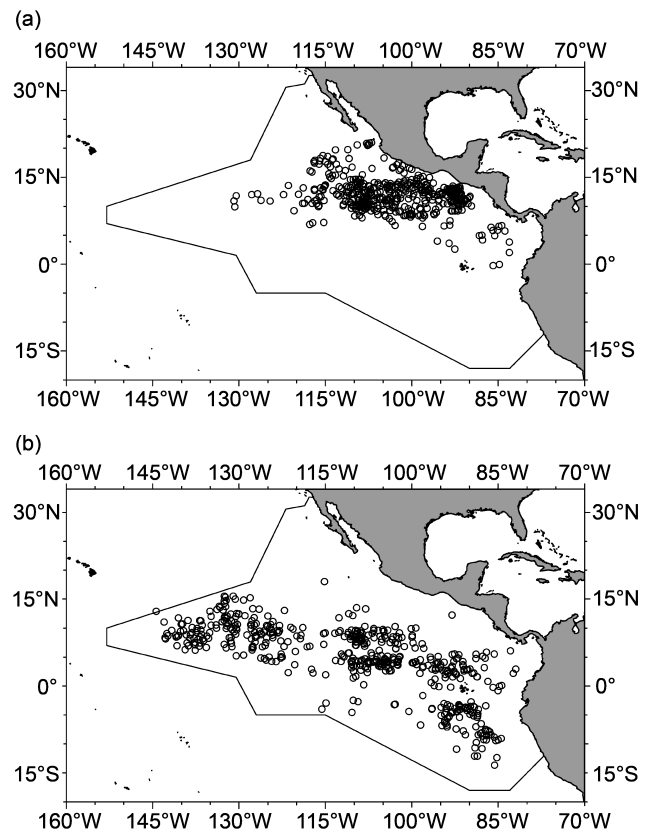


Fig. 1. Locations where each aged (a) female eastern spinner dolphin specimen ($n=1,267$) and (b) female whitebelly spinner dolphin specimen ($n=1,071$) were collected. The dolphins were sampled in the eastern tropical Pacific yellowfin tuna purse-seine fishery between 1973 and 1982. The boundary line shown marks the study area used to estimate species abundance for all *Stenella* sp. impacted by the purse-seine fishery (Wade and Gerrodette, 1993).

reader for a given specimen, the estimate with the highest confidence rating was chosen as the reader's best age estimate. The final age assigned to each specimen was the mean of the two readers' best estimates, which is referred to as the 'assigned' age. The interval between successive readings varied from days to months, and the age estimates were generated over a three year time period, from 1983 to 1985.

Age selectivity of the incidental kill

Dolphin schools may segregate by age or sex and certain age classes may have a higher probability of becoming entangled in a purse-seine net, which could result in non-random sampling and collection of data that is not representative of the population. Previous analyses of data on spotted dolphins incidentally killed in the ETP tuna purse-seine fishery have shown that the age structure of the kill was not independent of the total kill size (Barlow, 1985). Rather, low kill sets contained relatively higher numbers of young spotted dolphins than presumably less selective large kill sets. To test for age selectivity in the spinner dolphins data, the method of Barlow (1985) was followed and used a

Table 1

Number of aged female eastern spinner dolphin and whitebelly spinner dolphin specimens sampled in the eastern tropical Pacific yellowfin tuna purse-seine fishery by year collected.

	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	Total
Eastern	248	306	290	79	114	55	76	33	33	33	1,267
Whitebelly	74	36	168	264	195	94	54	39	69	78	1,071

contingency table to test the null hypothesis that age frequency (binned into 0-1, 1-2, and 2+ yr) was independent of the size of the total kill² (1-10, 11-20, 21-30, 30+ dolphins). Power was calculated by first calculating the effect size index, w , where

$$w = \sqrt{\frac{\chi^2}{N}}$$

and N is the total sample size (Cohen, 1988). Using the effect size index, total sample size, degrees of freedom, and significance level, power may be found in tables.

Bias and precision in age determinations

Systematic differences in inter-reader age estimates were assessed by interpreting age bias plots, which have been demonstrated to be more appropriate for detecting both linear and nonlinear bias patterns than other methods, including parametric and nonparametric matched-pair tests, regression analysis, analysis of variance, and age difference plots (Campana *et al.*, 1995). Age bias plots depict the ages estimated by one reader, grouped into categories, against the means of the other reader's estimates for the same specimens within a category. Bias between two readers is detected by visually comparing the observed line to a 1:1 equivalence line. A 1:1 expected correspondence in age estimates made by the readers would be expected when readers use the same model of GLG deposition and no reader bias exists. The reader chosen for the abscissa is arbitrary. Reproducibility of age determinations was evaluated by use of the coefficient of variation, CV (Campana *et al.*, 1995; Chang, 1982). CV can be expressed as

$$CV_j = 100 \times \frac{\sqrt{\sum_{i=1}^R (X_{ij} - X_j)^2}}{R - 1 X_j}$$

where R is the number of times each specimen is aged, X_{ij} is the i^{th} age determination of the j^{th} specimen, and X_j is the mean age of the j^{th} specimen. A mean CV was calculated for each age class as well as averaged over all specimens.

Age distributions

Given the potential sampling biases due to fishery activities and the removal of a large portion of both populations by the fishery in the more than ten years prior to and during the collection of specimens, one would not expect the populations to have stable age distributions. However, comparisons of age distributions generated in this study to stable age distributions provide a reference for characterising the age selectivity of the sampled incidental kill and comparing the populations. No empirical data are available to generate age distributions for the populations before they were exploited by the purse-seine fishery, but there is also no evidence that suggest the populations were previously exploited. Therefore, expected stable age distributions were compared to the observed age distributions. The stable age distributions were generated using an estimate of longevity derived from the results of this study together with age-specific fecundity and survival schedules based on published reproductive data (Perrin and Henderson, 1984) and methods for estimating survival rates (Barlow and Boveng, 1991). Kolmogorov-Smirnov (K-S)

tests comparing the observed and expected age distributions illustrate potential under- and over-representations of age classes.

Comparison to prior studies

In two prior studies that estimated age for eastern spinner dolphins, Perrin *et al.* (1977) analysed specimens collected from 1968 to 1975, and Perrin and Henderson (1984) analysed specimens collected from 1968 to 1978. All aged specimens that were common to these earlier studies and to this study were selected for comparison ($n=207$). Although both prior studies analysed several models of GLG deposition rates, their final GLG count for each specimen was interpreted as the best estimate of age for the specimen. An age bias plot and age frequency distribution was generated to compare estimates between the studies.

RESULTS

Age selectivity of the incidental kill

A count of the total number of dolphins killed in the purse-seine sets in which the dolphins aged in the study were collected was available for 99.8% of the eastern spinner specimens and 100% of the whitebelly spinner specimens. The total number of dolphins killed in a set ranged from 1-624 for sets containing eastern spinner dolphins and 1-738 for sets containing whitebelly spinner dolphins. The null hypothesis that kill size per set and specimen age were independent variables could not be rejected for either eastern spinner (chi-square, $P=0.17$, power=0.82) or whitebelly spinner (chi-square, $P=0.87$, power=0.70) dolphins, and therefore all available data were used in further analyses.

Bias and precision in age determinations

The maximum age estimated for eastern spinner dolphins by reader A and B was 25 and 28yr, respectively, while the maximum assigned age was 24.5yr. For whitebelly spinner dolphins, the maximum age estimated by readers A and B was 30yr and 26yr, respectively, with a maximum assigned age of 26yr. The mean age of the oldest 5% of specimens was 20.0yr (SE=0.2) for eastern spinner dolphins and 19.3yr (SE=0.2) for whitebelly spinner dolphins.

Age bias plots for both populations (Fig. 2) indicated nonlinear systematic differences between readers. Variance in age estimation increased with specimen age for both populations. CV tended to increase with age and mean values between populations were similar (Table 2). Imprecision for the 0-1 year old age class was substantially greater relative to other age groups; however, this is understandable because the complexity in estimating fractions of a year would cause small differences between readers that translated into large values for CV especially considering that the mean values for the age class were less than unity.

Age distributions

The observed age frequency distribution for eastern spinner dolphins was significantly different from a stable age distribution (K-S test, $P<0.001$) and contained notably fewer 0-1 year-olds and more 1-3 year-olds than a stable distribution (Fig. 3). The observed age frequency distribution for whitebelly spinner dolphins was also significantly different from a stable age distribution (K-S test, $P<0.001$) and contained fewer 0-4 and 6-7 year-olds and a greater number of 7-15 year-olds than a stable distribution (Fig. 3).

² Total kill refers to the number of all dolphin species killed in a set.

Table 2

Number of specimens and age estimation coefficients of variation (CV) by age class for female eastern spinner and whitebelly spinner dolphins. The mean CVs for all age classes are weighted by sample size.

Age class	<i>n</i>		CV	
	Eastern	Whitebelly	Eastern	Whitebelly
0	43	31	35.6	56.6
1	150	71	9.0	7.0
2	109	52	8.5	6.7
3	90	58	10.7	8.5
4	88	68	9.2	8.2
5	65	52	9.7	10.8
6	53	44	10.1	11.9
7	64	68	9.6	11.8
8	62	82	9.3	9.5
9	61	67	11.8	10.7
10	46	81	9.8	10.3
11	62	83	11.1	11.0
12	62	63	10.2	8.9
13	60	59	12.5	14.7
14	53	50	11.1	12.0
15	55	44	11.6	10.4
16	51	34	13.3	12.5
17	24	20	16.9	11.2
18	20	18	16.8	12.6
19	21	11	10.3	15.6
20	11	6	11.1	4.3
21	8	6	8.4	20.5
22	2	0	14.4	
23	5	1	11.1	6.1
24	2	1	2.9	0.0
25	0	0		
26	0	1		21.8
27		0		
\sum	1,267	1,071		
\bar{x}			11.3	11.7

Comparison to prior studies

There were 207 specimens of eastern spinner dolphins aged in this study that were also aged in previous studies (Perrin and Henderson, 1984; Perrin *et al.*, 1977). An age bias plot comparing age estimates indicated a systematic difference for the older specimens (Fig. 4). The age frequency distribution generated from eastern spinner dolphin specimens in the two previous studies was significantly different from this study's age distribution for the same specimens (K-S test, $P < 0.001$). Original data used by Perrin and Henderson (1984) could only be obtained for nine whitebelly spinner dolphin specimens and therefore a between study comparison was not possible for this population.

DISCUSSION

The results of this study characterise the age selectivity for female eastern and whitebelly spinner dolphins killed in the ETP tuna purse-seine fishery from 1973 to 1982. Dolphins from all age groups were sampled with the oldest eastern spinner dolphin specimen estimated to be 24.5 years old and the oldest whitebelly spinner dolphin to be 26 years. No significant reader bias was detected except for the oldest specimens, for which sample size was small, but because the 'true' age of specimens is unknown, the assigned age is considered the best estimate of age for each specimen. Precision was comparable between populations and calves were underrepresented relative to a stable age distribution in both populations.

Fishery bias

Analyses of age data for stocks of spotted dolphins incidentally killed in the fishery have shown that the total number of dolphins killed in a set affects the observed age structure of that set's kill (Barlow, 1985; Perrin and Oliver, 1982). Samples from small-kill sets (<40 dolphins) of spotted dolphins were found to have proportionately more calves than larger kill sets. Contrary to spotted dolphins, a significant effect of the kill-size of a set on the proportion of young (0-2 years old) spinner dolphins was not found.

Variation in the age and sex composition of dolphin schools, and those subsequently encircled during fishing operations, was another potential source of bias in the subset of dolphins sampled. Evidence of segregation by age or breeding condition has not been consistent between *Stenella* spp. studied. No evidence was found of school segregation for spotted dolphins in the ETP (Perrin *et al.*, 1976). Conversely, three types of striped dolphin (*S. coeruleoalba*) schools have been reported in the waters off Japan: juvenile; adult; and mixed (Miyazaki and Nishiwaki, 1978). More recently, length information from aerial photogrammetry of striped dolphins in the ETP indicated segregation based on size analogous to that found in the western Pacific (Perryman and Lynn, 1994). Earlier preliminary research of ETP spinner dolphins suggests schooling by age and sex, with small schools more likely to be composed of immature males, females or adult males (Perrin and Gilpatrick, 1994). However, it was not possible to determine how representative the sample of dolphins associated with tuna was compared to the whole population.

Age validation

The importance of validating the process, or model, used to estimate age has been well documented (Beamish and McFarlane, 1983; Campana, 2001; Campana *et al.*, 1995; Kimura and Lyons, 1991) and is only possible when mark-recapture studies can be conducted or known-age dolphins are available (Power *et al.*, 2006). Neither are possible or available for pelagic dolphins. The absence of a reference collection of known age samples, meant that it was not possible to measure reader accuracy or analyse the ageing process to identify reader drift over the three years during which ages were estimated.

The ageing model used was based on the results of a calibration experiment of captive Hawaiian spinner dolphins that concluded GLGs were deposited annually; however, annual GLG formation was not verified for the entire age range (Myrick *et al.*, 1984). The model chosen in this study for ageing spinner dolphins was considered the best available; the calibration study involved dolphins of the same species and available data suggest that the application of calibration study results from captive dolphins to wild populations is valid (Hohn, 1990; Myrick *et al.*, 1984).

For this study, age acceptance criteria were not implemented. That is, readers did not re-evaluate or discuss specimens whose estimated ages varied beyond some set limit. While this avoided the potential for choosing inappropriate acceptance criteria and subsequent bias in age estimates and derived parameters (Marriott and Mapstone, 2006), it resulted in several instances for which readers' estimates for a particular specimen varied by many years (Table 3a and 3b).

Reader bias and precision

Age bias plots indicated nonlinear systematic differences between readers for both eastern and whitebelly spinner dolphins. Except for the very oldest dolphins (with small

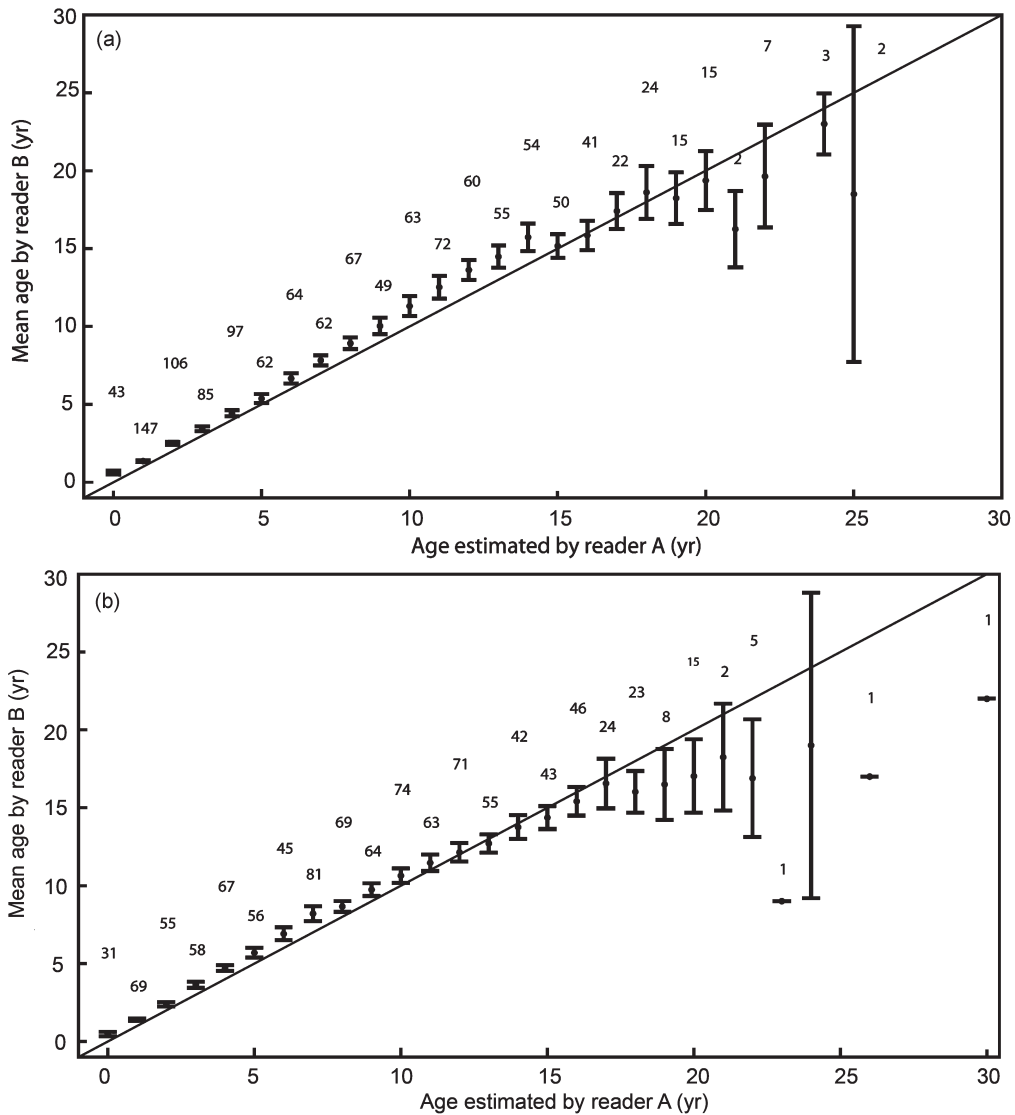


Fig. 2. Age bias plots for pairwise comparison between two readers of aged (a) female eastern spinner dolphin ($n=1,267$) and (b) female whitebelly spinner dolphin ($n=1,071$) specimens sampled in the eastern tropical Pacific yellowfin tuna purse-seine fishery between 1973 and 1982. Reader A estimates are grouped into one year age categories. Error bars are the 95% confidence interval of the means of reader B age estimates. Sample size for each age group is given above the error bar. The solid line is the expected 1:1 correspondence for both readers' age estimates assuming no bias.

sample sizes), these patterns showed a bias of no more than one year, suggesting that these results are not practically significant considering the lifespan of these dolphins. The offset from the 1:1 correspondence line for the younger dolphins might be partially explained by differences between readers in interpreting the first GLG, which can be particularly difficult. Hohn (1990) and Hohn *et al.* (1989) noted that the prominence of accessory layers produced during the first and second year in particular which may cause misidentification of GLGs and subsequently bias age estimates upwards. As a dolphin matures, GLGs tend to become compact, irregular and possibly indiscernible (Myrick Jr *et al.*, 1983) leading to increased inter-reader variation. In addition, the greater number of accessory layers may cause disparity as well.

The CV indicated that the level of difficulty in interpreting age structures is similar for the two populations. Although Akin (1988) reported differing tooth morphology with the average whitebelly spinner tooth being longer and wider than the average eastern spinner dolphin tooth, these

differences did not translate into more consistent identification of GLGs in whitebelly spinner dolphins compared to eastern spinner dolphins as the CV was not appreciably different between populations.

Values of overall CV for eastern and whitebelly spinner dolphins (~11%) were lower than those reported by Reilly *et al.* (1983) for incidentally killed ETP spotted dolphins (CV=16%). These differences in CV may reflect improved ageing techniques or variation in GLG deposition patterns and the ability to identify and interpret GLGs between the *Stenella* species. Additionally, the experimental design for the studies differed. In the spotted dolphin study, each tooth was read three times by two readers and overall CV was presumably calculated based on all estimates and therefore incorporated both inter- and intra-reader variability. They found inter-reader differences to be much larger than intra-reader differences. For this study of spinner dolphins, each reader estimated age for each specimen only once, therefore the estimates of CV only reflect inter-reader variation.

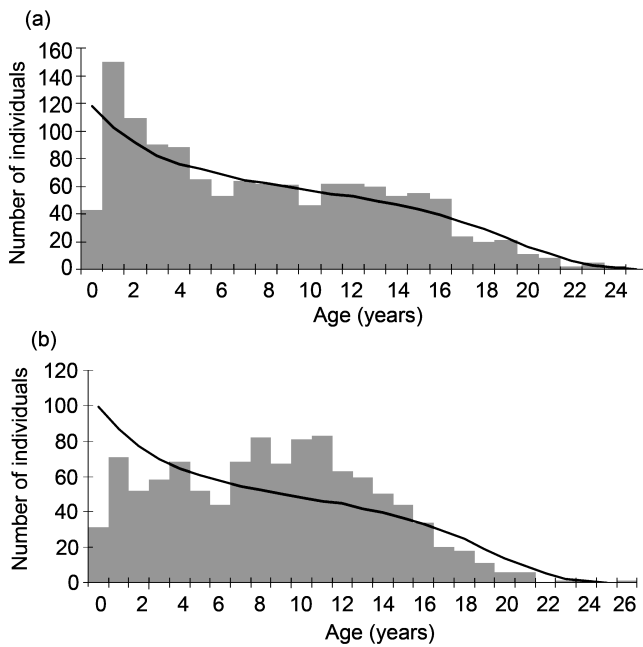


Fig. 3. Age frequency distribution of (a) female eastern spinner ($n=1,267$) and (b) female whitebelly spinner dolphins ($n=1,071$) sampled in the eastern tropical Pacific yellowfin tuna purse-seine fishery between 1973 and 1982. The solid line represents a stable age distribution for a population with a sample size equivalent to that studied here.

Age distributions

The observed age distributions for eastern and whitebelly spinner dolphins were found to be significantly different from stable age distributions. This comparison characterises the apparent age selectivity of the incidental kill of these dolphins in the yellowfin tuna purse-seine fishery. The age selectivity of the fishery kill in the years prior to sampling and its effect on the populations is unknown, and therefore whether the observed age distributions captures the underlying age distribution of the populations could not be determined.

In the observed age distributions for both eastern and whitebelly spinner dolphins, 0-1 yr olds were under-represented for all years combined as well as when the observed age distributions were examined by year, except for whitebelly spinner dolphins in 1977. The dearth of specimens in the first age class is observed every year for both populations and suggests there is bias in either sampling of the incidental kill or ageing methodology. Archer *et al.* (2001; 2004) proposed several hypotheses of how mothers and nursing calves may become separated during purse-seine fishing and are therefore less likely to be caught in the nets. For example, cows with calves may not be able to keep up with the portion of the school being chased and therefore, may not be set on, killed and sampled. The extent to which this may occur is unknown. This could explain the observed under-representation of calves in the age distributions of spinner dolphins.

Another contributing factor, more so for eastern spinner dolphins than whitebelly spinner dolphins, is the lesser extent to which teeth were collected from very young dolphins killed and brought aboard tuna vessels. Although teeth were not necessarily collected from every dolphin, total length was recorded. In this study length information in conjunction with estimates of average length at one year reported by Perrin and Henderson (1984) were used to partition the data into two length categories. The percentage of teeth collected from dolphins estimated to be in the ≤ 1 yr old age class was less than that collected from dolphins estimated to be in the >1 year old age class for both eastern spinner dolphins (70% and 84%, respectively) and whitebelly spinner dolphins (79% and 81%, respectively). However, even if teeth from calves were collected in the same proportions as dolphins in the older age classes, which translated to an additional 47 eastern spinner dolphin and 6 whitebelly spinner dolphin specimens being collected, the <1 yr old age class would still be under-represented. Therefore, it can be concluded that some of the mechanisms proposed by Archer *et al.* (2001; 2004) to be affecting spotted dolphin sampling from this fishery are likely to be acting for spinner dolphins.

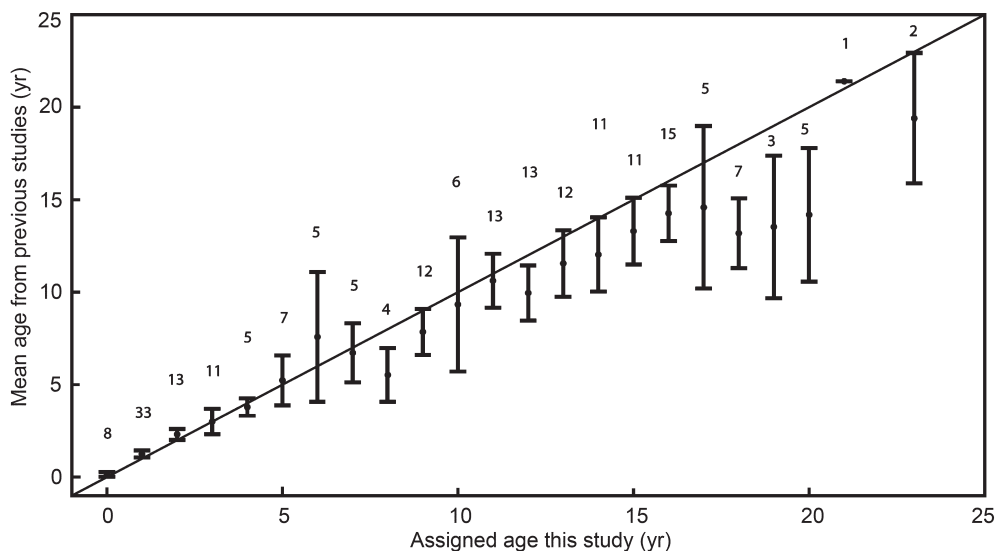


Fig. 4. Age bias plot for pair-wise comparison of female eastern spinner dolphins ($n=207$) from this study and previous studies (Perrin and Henderson, 1984; Perrin *et al.*, 1977). Estimates from this study are grouped into one year age categories. Error bars are the 95% confidence interval of the means of prior studies' age estimates. Sample size for each age group is given above the error bar. The solid line is the expected 1:1 correspondence for both readers' age estimates.

Comparison to prior studies

Refinement of tooth processing, ageing techniques and reader experience between previous studies and this study were most likely responsible for the different age estimates made for the same specimens. Ages estimated in this study followed procedures outlined by Myrick *et al.* (1986) who considered their methodology improved over earlier studies of *Stenella spp.* for two reasons: (1) new tooth preparation methods improved GLG resolution; and (2) a study of captive Hawaiian spinner dolphins (Myrick *et al.*, 1984) was used to calibrate a model of GLG deposition. Improvements in methodology and the calibration study occurred after the earlier studies and benefited this study by improving understanding of GLG deposition patterns.

Differences in age estimates for eastern spinner dolphins between this study and earlier studies by Perrin *et al.* (1977) and Perrin and Henderson (1984) were detected in both the age bias plot and by statistical tests. Bias patterns appeared to be close to linear and variance was relatively large, even for younger age groups. The differences in age estimation are probably due to the ageing model being improved and refined between the earlier studies and the one described here. The discrepancy in age estimates suggests that revision of the age-specific reproductive rate estimates reported in earlier studies (Perrin and Henderson, 1984; Perrin *et al.*, 1977) may be warranted using the age estimates generated in this study.

CONCLUSIONS

This study has improved on earlier ageing studies of spinner dolphins through the calibration of GLG deposition rates in the Hawaiian spinner dolphin, the use of a larger sample size and employing two readers to estimate age to capture inter-reader variation in age estimation. The age structure presented here is the best available for eastern and whitebelly spinner dolphins incidentally killed in the ETP yellowfin purse-seine fishery. This large data set documenting the age structure of the incidental kill includes specimens with additional biological data collected and will benefit future studies of these populations and assessing the impacts of the fishery on them.

ACKNOWLEDGEMENTS

We thank the staff and biological technicians of the Inter-American Tropical Tuna Commission and the National Marine Fisheries Service for collecting the biological specimens used in this study. Ages were estimated by A.C. Myrick Jr. and P. A. Akin. Laboratory processing and data editing were done by staff at the Southwest Fisheries Science Center, including R. Miller, A. Jackson, and D. Mattson. We thank F. Archer, K. Danil, T. Gerrodette, W. Perrin and W. Perryman for providing thoughtful comments for improving this manuscript.

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Date received: July 2008

Date accepted: December 2008