Growth Patterns of the Pacific White-sided Dolphin in the Central North Pacific Ocean

by

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INTRODUCTION

The Pacific white-sided dolphin, *Lagenorhynchus obliquidens* Gill, is one of the most abundant, widely distributed, small cetacean species inhabiting the temperate waters of the North Pacific Ocean. In the eastern North Pacific they are reported from the continental shelf and slope waters extending from the lower Gulf of California, Mexico, (approximately lat. 23°N) north along the coasts of California, Oregon, Washington, British Columbia, and Alaska. In the western North Pacific this species has been reported to occur from Taiwan northward along the coasts of Japan to the Kurile and Commander Islands. Pacific white-sided dolphins have also been observed infrequently in the southern Bering Sea. Recent reports related to studies of the high-seas driftnet fisheries reveal the Pacific white-sided dolphin to have a continuous distribution across the temperate waters of the North Pacific between lat. 38° and 47°N.

Biological information on *L. obliquidens* in the coastal waters of the eastern North Pacific Ocean provide age and reproductive data on 142 animals collected primarily off the coasts of California and Mexico, but the sample likely contained a mixture of two populations and was not used to describe population parameters. For the western North Pacific Ocean, little biological information has been published on this species. Research on the Japanese high-seas driftnet fishery has recently provided a large number of biological samples from *L. obliquidens* in the oceanic portion of its distribution. Based on samples and data from this region, preliminary analyses have been presented of age (75 males and 73 females) and of reproductive parameters (25 males and 40 females) from animals taken in Japanese squid driftnets from 1988 to 1990. Preliminary analyses have been presented of similar data (38 males and 42 females) collected by U.S. and Canadian observers in the squid fishery during 1990.

During 1991, additional biological samples and data were collected by U.S. observers in the Japanese, Korean, and Taiwanese squid driftnet fisheries and the Taiwanese large mesh fishery. The combined 1990 and 1991 sample provided an opportunity to examine growth patterns for *L. obliquidens* in the oceanic waters of the North Pacific Ocean.

METHODS

Specimen Collection

Scientific observers collected biological data from all cetaceans caught in Japanese, Korean, and Taiwanese driftnet operations monitored. Soon after arrival on deck, each cetacean was identified, sexed, measured (total length to nearest 1.0 cm), photographed twice (left lateral and ventral), and given a unique specimen number.

When an animal was dissected, the left lower jaw was tagged and frozen intact. For males, the right testis and epididymis were collected whole, tagged, and preserved in 10% formalin. Females were checked for evidence of lactation by longitudinal incision through the left mammary gland. The ovaries and uteri for most females were collected intact. The left ovary and entire reproductive tract were tagged and preserved in 10% formalin. If the animal was pregnant with a large fetus or was recently postpartum, only the ovaries and a cross-section of the left uterine horn were collected. Fetuses were sexed, weighed to the nearest 1.0 g, and measured to the nearest 0.1 cm.

Examination of Reproductive Organs

Males

Right testes with epididymides were weighed to the nearest 0.01 g and measured to the nearest 0.1 cm. A 1-cm^3 block was removed from the center of each testis; a similar section of epididymis was removed at mid-length, and both were prepared histologically. Paraffin-embedded tissues were sectioned at 6 μm, stained with hematoxylin and eosin, and mounted on glass slides. Testes and epididymides were examined for evidence of spermatogenesis using a compound microscope at 100x with transmitted light.

Males were considered mature if sperm were present in testes tubules.

Females

Ovaries were weighed to the nearest 0.01 g. Maximum diameter of the left uterine horn was measured to the nearest millimeter. Each ovary was sliced transversely into serial sections (1 mm thick) with a scalpel and examined for the presence of corpora lutea and corpora albicantia. Two measurements of corpus diameter, taken at right angles, were recorded for well-regressed corpora; three diameters were recorded for larger corpora. Total corpus counts included corpora albicantia and corpora lutea from both the right and left ovaries. Females were classified as sexually mature if at least one corpus was present on either ovary.

Age Determination

Teeth were extracted from the center of the left lower jaw for age determination. Each tooth was decalcified and sectioned (24 m) longitudinally on a freezing microtome. The teeth were oriented on the microtome stage so that each cut section was parallel to the plane encompassing the crown apex and the approximate center of the root canal. The crown apex was oriented horizontally. Tooth section preparation and dentinal growth layer group (GLG) counting procedure guidelines developed for *Stenella* spp. were used. Eight to ten stained sections from the center of each tooth were mounted on a glass slide and examined under a compound microscope at 40x and 100x magnification with either transmitted or polarized light. One GLG was assumed to represent 1 year of growth.

Each tooth was read independently by two readers at least twice. Ages were estimated to the nearest 0.5 layer except for animals with less than one complete GLG. In these cases we estimated the fractional portion of the incomplete layer and recorded it as 0.1, 0.3, 0.5, or 0.7 GLG. Predetermined limits on reader variability were established following those utilized for *L. obliquidens* and for *Lissodelphis borealis*. Our procedure allowed for a 0.5-layer difference between readings for estimated ages 1 to 5 years (measured from the median reading), one layer for estimates between 5 and 10 years, then one additional layer for every 5-year interval thereafter. Within these limits, we averaged the two readers' estimates to obtain the final age. When readings differed by more than these limits the tooth was reread. For animals with less than one complete GLG, the independent readings were compared, and if different, both readers jointly re-read the tooth to arrive at a single best estimate.

The abundance of young animals in our sample, our corresponding interest in examining early postnatal growth, and the relative imprecision in ageing animals less than 1 year old by assessing presence of GLG components prompted us to measure postnatal dentine thickness as an index of age. This approach constituted an alternative method for estimating first year growth rates.

Postnatal dentine thickness measurements were taken perpendicular to the longitudinal axis of the tooth, from inner border of the prenatal dentine to the adjacent wall of the pulp cavity, as close as possible to where the neonatal line approached the outside of the tooth (Fig. 1). To provide the best consistency between measurements, only tooth sections taken at the center of the tooth were examined. In addition, noting lateral asymmetry in the postnatal dentine deposition, we always measured the same side of the tooth (i.e., the convex side with respect to the crown).

The measurements were obtained using digital imaging equipment. Our system for recording and analyzing tooth section images included a Sony digital RGB video camera (model XC-77) mounted in the camera tube of a Nikon Labphot-2 compound microscope linked to a 486-DX50 personal computer equipped with an Imaging Technology VISIONplus-AT Overlay Frame Grabber processing board, and Image-Pro Plus (version 1.2) image processing software. The images were viewed in black and white on a Sony Trinitron high resolution color video monitor (model PVM-1344Q) in both real time (as an aid to two reader examinations) and after image capture. The Image-Pro Plus linear measurement routines were used to calculate distances between endpoints we identified on screen at 40x or 100x. We calibrated the Image-Pro Plus linear measurement routines, converting pixels to microns, for each microscope magnification based on captured images of a stage micrometer.

RESULTS

The Sample

A total of 341 *L. obliquidens* (171 males and 170 females) sampled from the North Pacific Ocean were examined from June to September 1990 and 1991 (Fig. 2). Sex, total length, collection date, and catch

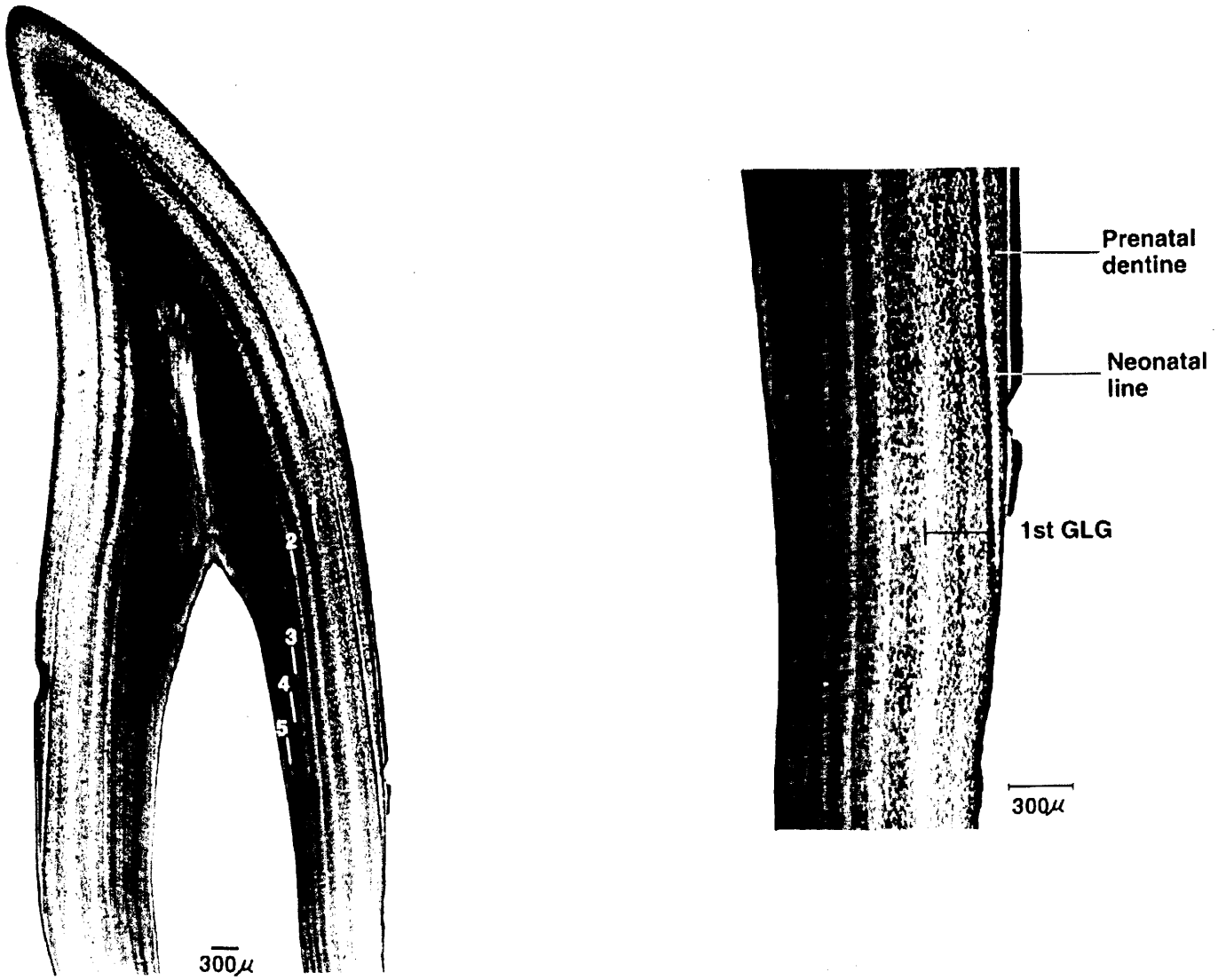


Figure 1. ***Lagenorhynchus obliquidens*** **tooth sections from a male showing approximately six GLGs and a female with less than one complete GLG. On the male, the boundaries between adjacent GLGs and the approximate location of the dentinal thickness measurement are marked. On the female, the location of the dentinal thickness measurement (μ) is indicated.**

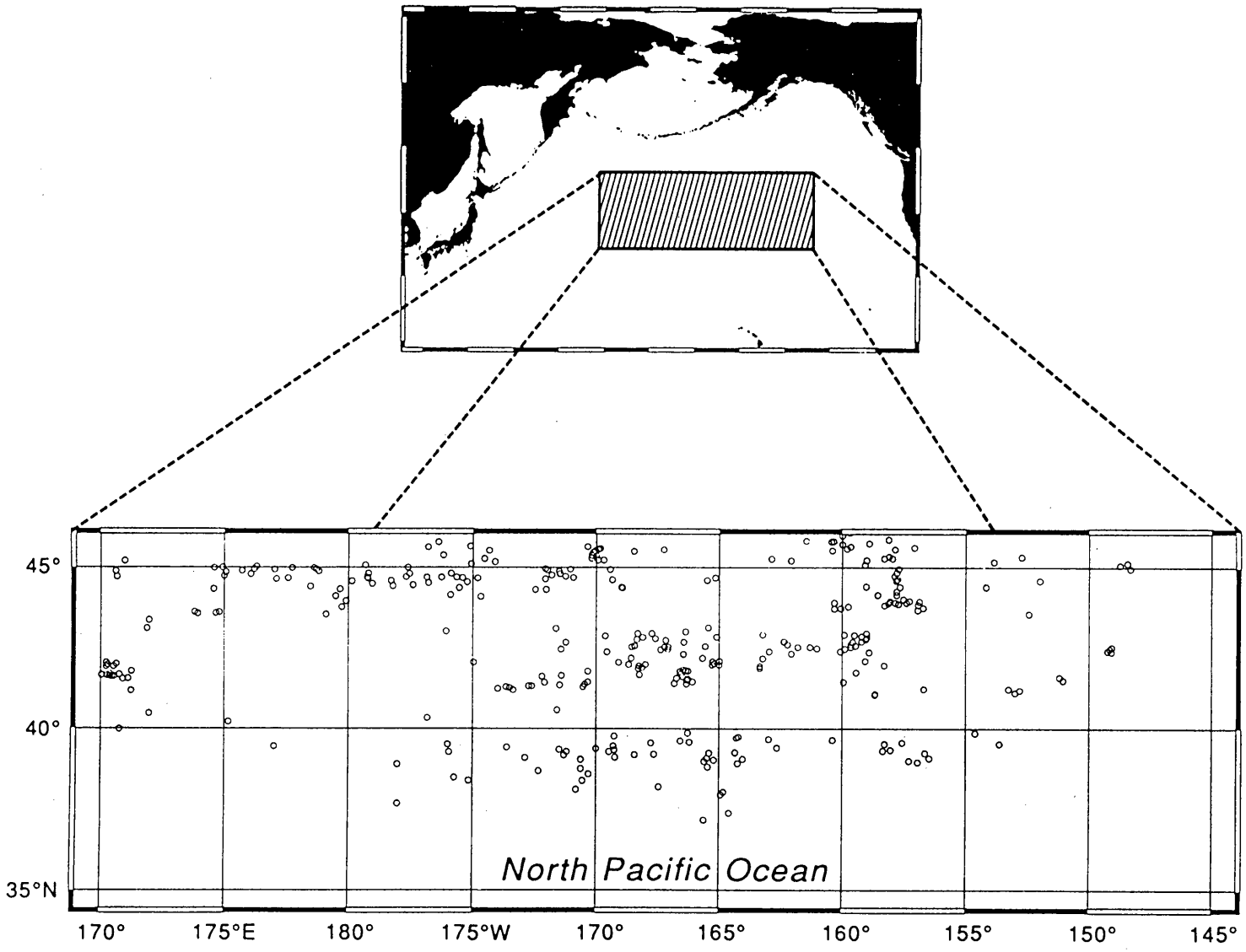


Figure 2. Sampling locations of 341 *L. obliquidens* (171 males and 170 females) taken in high seas driftnets during 1990 and 1991.

location were recorded for each specimen, while biological samples were collected from 149 of these dolphins (73 males and 76 females).

Postnatal growth, tooth ageing patterns, and the reproductive parameters average age and average length at sexual maturation were examined using the dissected sample, minus two males for which reproductive status could not be determined (i.e., leaving 71 males and 76 females). To assess potential subsampling biases we tested for differences in the length distributions of the total sample and the dissected sample for each sex; no significant differences were detected (Kolmogorov-Smirnov Test, males: D=0.0648, P>0.50, females: D=0.0999, P>0.50).

Male *L. obliquidens* ranged from 0 to 36 years in age (n=73); 1% were newborns (n=2), 34% were calves less than 1 year old (n=25), 19% were yearlings (n=14), and the remainder were greater than 2 years old. Female ages ranged from 0 to 40 years (n=76); 5% were newborns (n=4), 26% were calves less than 1 year old (n=20), and 12% were yearlings (n=9). The age distribution of non-neonates declined intrinsically for both sexes.

Length at Birth

No near full-term fetuses were collected; therefore, we could not calculate a length at birth using rigorous methods. Instead, we derived a preliminary estimate by averaging the lengths of newborns that met the following criteria: 1) no neonatal line or postnatal dentine could be detected in prepared tooth sections, and 2) external features indicating recent birth were present (e.g., unhealed umbilical scars, pronounced evidence of fetal folds, and curling of the fluke margins.

Of the six animals collected with no evidence of a neonatal line or postnatal dentine, only four also met the second criterion. The mean length of these four newborns, ranging from 91 cm to 93 cm, was 91.8 cm (SE=0.4787).

Postnatal Growth

Male and female growth curves were each fitted using a nonlinear least-squares method. The Laird/Gompertz formula was used as a base model for both sexes:

$$[1] \qquad L(t) = Lo \exp\{a\,[1-\exp(-\alpha\, t)]\},$$

where $L(t)$ is the length at age t, Lo is the length at birth, t is the age, a is the specific rate of exponential growth, and is the rate of decay of exponential growth.

Females

For females, we fitted a single Laird/Gompertz curve (Fig. 3) with Lo fixed at 92 cm, our preliminary estimate of length at birth. The distribution and magnitude of the residuals in the upper portion of the curve indicated a satisfactory fit; however, the residual distribution in the lower portion of the curve was strongly positive. The predicted length at age 1 was 128.8 cm. Asymptotic length was predicted to be 177.1 cm. For comparison, we also shifted the growth curve to optimize the fit in the lower region of the curve (ignoring the lack of fit above age 1) and obtained a predicted length at age 1 of 149.9 cm.

Males

For males we fitted two Laird-Gompertz curves, one for the sexually mature animals and the other for the sexually immature animals, in order to minimize the number of positive residuals in the upper curve segment (Fig. 4). For the lower curve Lo was fixed at 92 cm. Lacking samples around the age of sexual maturation, we could not iteratively fit the two curve segments and locate the intersection point. As in the case of females, we were able to satisfactorily fit the growth model to the data for animals over 1 year old, predicting an asymptotic length of 183.8 cm, but the residual distribution at ages less than 1 year were again strongly positive. The predicted length at age 1 was 133.4 cm. By shifting the growth curve to provide the best fit in the lower region (again, ignoring the lack of fit at ages above age 1), we obtained a predicted length at age 1 of 147.8 cm.

Alternative Approach to Predicting Length at Age 1

We reexamined first year growth patterns using length and postnatal dentine thickness in place of GLG estimates. This approach was considered less susceptible to potential ageing biases inherent in visual estimation of first GLG completeness. Measurements of postnatal dentine thickness were obtained from 47 teeth (25 males and 22 females) with incomplete first GLGs, and plotted against total length (Fig. 5).

We regressed length and postnatal dentine thickness for females less than age 1 (n=22) and obtained the equation:

$$[2] \qquad y = 98.4 + 0.1548x$$

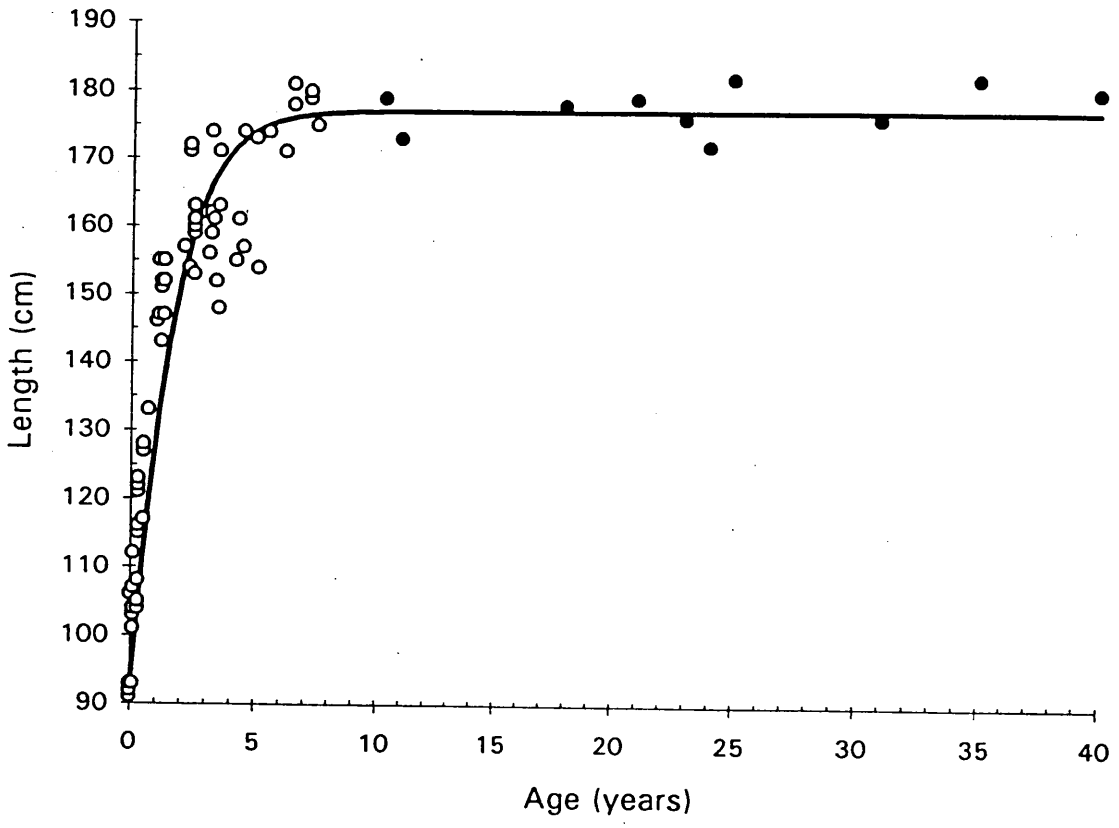


Figure 3. Age at length of female *L. obliquidens* with fitted growth curves (Laird-Gompertz (1969) model). The open circles represent sexually immature animals; the closed circles represent sexually mature animals.

where x equaled postnatal dentine thickness and y equaled total body length. The slope was significant ($P<0.001$).

Similarly, we regressed length and postnatal dentine thickness for all males less than 1 year old (n=25) and obtained the equation:

[3] $$y = 101.0 + 0.1419x$$

where x equaled postnatal dentine thickness and y equaled total body length. The slope was significant ($P<0.001$).

To convert postnatal dentine accumulation to age and use it to predict length at age 1, we measured 44 teeth (23 males and 21 females) from animals with one or more complete GLG showing clearly stained first GLG boundaries. We calculated the mean thickness of the first complete GLG (males: $\bar{x}$=308.0μ, SE=3.127, females: $\bar{x}$=312.1μ , SE= 3.239); no significant difference was detected between the male and female means (Student's t test, t=0.9193, $P>0.35$), so samples were combined and a new mean calculated ($\bar{x}$=309.9μ , SE=2.246).

Substituting the mean thickness of the first GLG (309.9) for x in regression Equation 2, we obtained a predicted length at age 1 of 146.4 cm for females. For males, we substituted the mean thickness of the first GLG (309.9) for x in regression Equation 3, and obtained a predicted length at age 1 of 145.0 cm. For both sexes, the predicted values were slightly less than the predicted lengths at age 1 derived by simply adjusting the growth curve to optimize the fit for young animals (i.e., 149.9 for females and 147.8 cm for males).

For use in subsequent analyses, we calculated monthly growth rates for each of the three methods. Using length and age (in GLGs), we subtracted the length at birth estimate (92 cm) from the predicted length at age 1 and divided the difference by 12. Using length and postnatal dentine thickness, subtracted 92 cm from the predicted lengths at age 1 from Equations 2 and 3 and divided the differences by 12 (Table 1.)

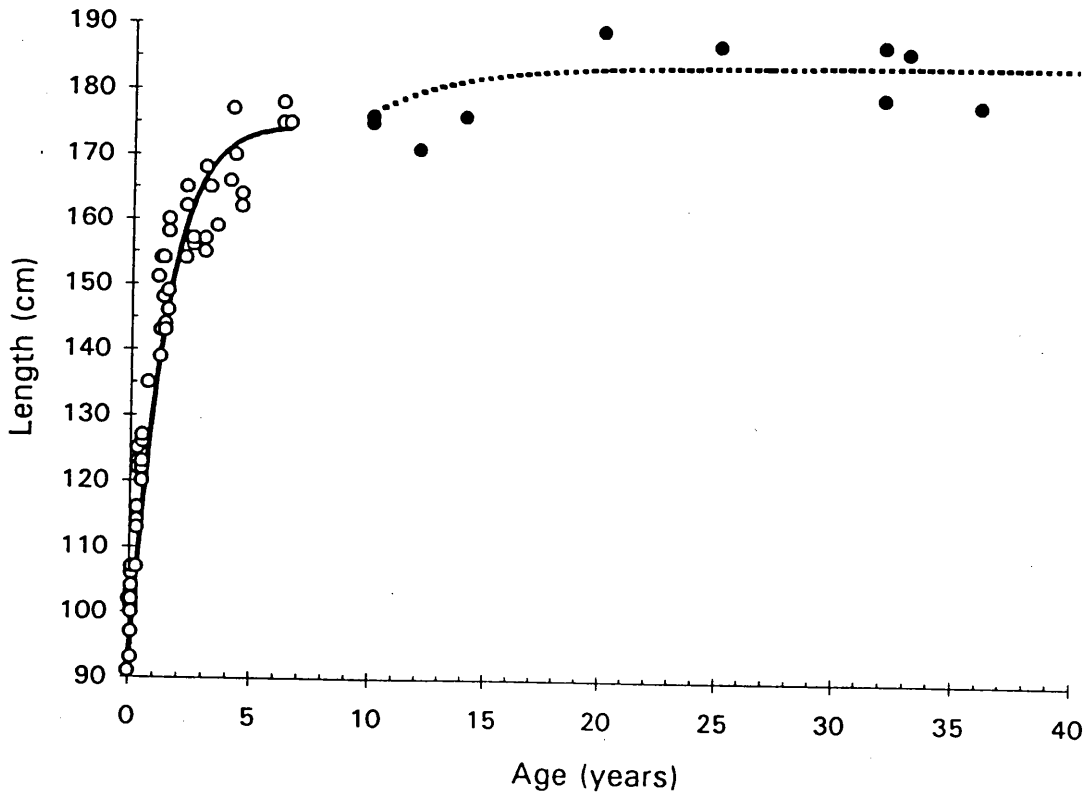


Figure 4. Age at length of male *L. obliquidens* with fitted growth curves (2-stage Laird-Gompertz (1969) model). The open circles represent sexually immature animals, the closed circles represent sexually mature animals.

Comparison of Predicted Asymptotic Lengths

The Laird-Gompertz growth model fits (Figs. 3 and 4) were used as the basis for comparing male and female asymptotic lengths. The mean length of males age 15 and older (i.e., the animals likely to have reached maximum size, based on predicted length at age 15 falling on the asymptotic portion of the upper growth curve) was 184.3 cm (n=6, SE=1.89). The mean length of females age 15 and older was 178.1 cm (n=8, SE=1.20). The difference in mean lengths between sexes was significant (Student's *t* test, two-tailed, P=0.02).

DISCUSSION

The *L. obliquidens* growth curves (Figs. 3 and 4) adequately reflected the growth rate of animals greater than 1 year old and provided useful asymptotic length estimates, but they appeared to understate growth in the observed portion of the first year. In our analyses of growth and attempts to fit the Laird-Gompertz model to the *L. obliquidens* length and age data, we considered two possible causes for failure to achieve a satisfactory fit for all regions of the curve.

First, we assumed that the age data for 1-year-olds or less were not biased and that other unrecognized biases in older age groups were affecting the curve fit. We then shifted the curve to fit the data below age 1 and examined the effect on the predicted length at age 1. The results (Table 1) were not consistent with our observed length frequency distributions. If the animals had grown to nearly 150 cm by age 1, most should have moved through the 135-150 cm size range prior to the start of sampling in June, yet this length class was well represented in the sample.

With very little data for animals between 6 months and 1 year old, the fit was largely driven by the observed lengths and ages from animals 0 to 6 months old. It is possible, therefore, that this rapid growth period was followed by a period of slower growth.

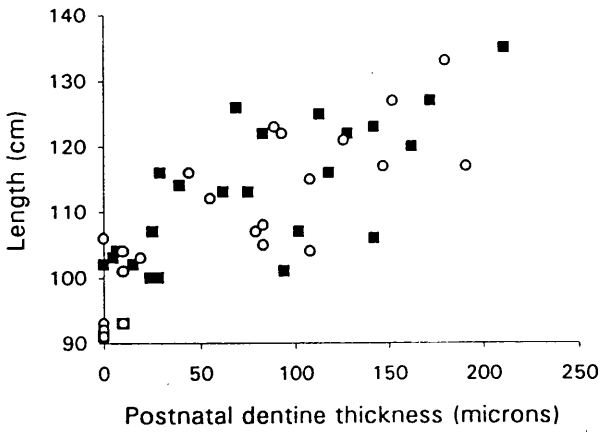
Table 1. - Monthly growth rates calculated for male and female *L. obliquidens* using three methods, the Laird-Gompertz growth curve, the Laird-Gompertz growth curve with optimal fit to the animals less than 1 year old (i.e., "shifted" curve fit) and the linear regression of postnatal dentine thickness and length.

	Laird-Gompertz Curve Fit		"Shifted" Curve Fit		Dentinal Thickness and Length Regression	
	Male	Female	Male	Female	Male	Female
Predicted Length at Age 1 (cm)	133.4	128.8	147.8	149.9	145.0	146.4
Monthly Growth Rate (cm/mo)	3.45	3.07	4.65	4.85	4.42	4.53

Second, we speculated that the less-than-1 GLG age estimates were biased, and that the lower region of the growth curve, despite the strongly positive residual distribution, actually reflected the growth rate. The GLG age parameter was replaced with the dentinal thickness measures. As with the first hypothesis, this approach did not provide an acceptable solution since the resulting predicted lengths at age 1 were only slightly lower than those obtained using the original age data. Again, the predicted length conflicted with the observed length frequency distribution.

We then considered one additional explanation for the lack of fit, related to the application of the growth model itself. The two-phase Laird-Gompertz model has been used in previous small cetacean growth studies to improve the fit of age/length data over the fits achieved using single curves. The two-phase model can accommodate a significant change in growth rate, presumably linked to a biological event. To date, the two-phase curve has been used to describe a secondary increase in growth occurring at about the onset of sexual maturity.

Figure 5. Scatterplot of postnatal dentine thickness (μ) and length (cm) for 47 (25 male and 22 female) *L. obliquidens* with incomplete first dentinal GLGs. Simple linear regressions of length on postnatal dentine thickness yielded the equations: y = 101.0 + 0.1419x, for males; y = 98.4 + 0.1548x, for females. Both slopes were significant (P<0.001).



The *L. obliquidens* sample suggested that a more complex growth model also may be necessary to adequately characterize changes in early postnatal growth. If the growth rate for *L. obliquidens* slows over the course of the first year, departing from a nearly linear form and becoming more curelinear, then a separate phase of the growth model may be warranted.

Weaning may be the biological event which triggers slower growth. Previous examination of *L. obliquidens* stomach contents from samples collected in 1990 support this hypothesis as they showed evidence of weaning during the latter half of the first year.

ACKNOWLEDGMENTS

This article is based on the article which appeared in the *Canadian Journal of Zoology*, Volume 74, Number 9, 1996, entitled "Age,growth, and reproductive patterns of the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) taken in high seas drift nets in the central North Pacific Ocean" by Richard Ferrero and William Walker of the National Marine Mammal Laboratory (NMML).