Abstract.—A total of 707 common dolphins, *Delphinus delphis* Linnaeus, (376 males and 331 females) taken in Japanese, Korean, and Taiwanese drift nets in the central North Pacific Ocean from February to November 1990 and 1991 were examined. Sex, total length, date, and location of capture were recorded. Biological samples were collected from 152 of the dolphins examined (93 males and 59 females). Ages were determined by counting dentinal layers. Female reproductive status was determined by macroscopic examination of ovaries (n=43). Eight females were mature, two were pregnant, three were resting, two were lactating, and one was of unknown condition. Testes and epididymes were examined for evidence of spermatogenesis (n=70); 21 males were mature. A preliminary estimate of gestation period was 11.1 months. The sex ratio appeared to favor males; segregation during the sampling period may be responsible for differences from 1.0. Male average age at sexual maturation was estimated to be 10.5 years. The largest sexually immature male was 179 cm; the smallest sexually mature was 182 cm. Mature testis weights ranged from 273.2 g to 1,190 g. Females reached sexual maturation at about 8.0 years; estimates of length at sexual maturation were 172.8 and 170.7 cm. Predicted asymptotic lengths for males and females were 188.1 cm and 179.4 cm, respectively. Calving appeared to peak in May and June. Sampling effort moved northward through September; infrequent sampling of parturient females and neonates during the projected calving mode suggests they were segregated outside the fishing area at that time.

Growth and reproduction of the common dolphin, *Delphinus delphis* Linnaeus, in the offshore waters of the North Pacific Ocean

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The common dolphin, *Delphinus delphis* Linnaeus, is an oceanic species widely distributed throughout the tropical and temperate seas of the world. In the western North Pacific Ocean, published accounts have dealt almost exclusively with taxonomy, distribution, and seasonal movements (Ogawa, 1937; Nishiwaki, 1967; Kasuya, 1971; Ohsumi, 1972). The common dolphin has been studied most extensively in the eastern North Pacific Ocean where research has focused primarily on species distribution, herd movements, reproductive seasonality, stock differences, and behavior (Norris and Prescott, 1961; Brownell, 1964; Hui, 1979; Evans, 1982; Perrin et al., 1985; Perryman and Lynn, 1993; Heyning and Perrin, 1994; Walker and Cowan[1]; Walker et al.[2]).

Two morphotypes of common dolphin, a short-beaked form and a long-beaked form, differing in rostral length, overall size, and color pattern, have been described from southern California waters (Banks and Brownell, 1969; Evans, 1975). Heyning and Perrin (1994) described two species of *Delphinus* from the eastern North Pacific Ocean, a short-beaked form which is referable to *D. delphis* Linnaeus and a long-beaked form assigned to the nominal species *D. bardaii* Dall,

1893. Recent studies of molecular genetics confirm the morphologic findings and support distinction of these two morphotypes of common dolphin as separate species (Rosel et al., 1994).

Despite the abundance of *D. delphis* in the eastern North Pacific Ocean, little biological information on age, growth, and reproductive condition exists in the literature. Ridgway and Green (1967) and Harrison et al. (1972) present gonadal data for a total of 30 male and 25 female specimens collected over a 16-year period from single strandings or live-capture. Correlations with age were not incorporated in either study. Hui (1979) correlated age, reproductive condition, and flipper bone development and summarized

[1] Walker, W. A., and D. F. Cowan. 1981. Air sinus parasitism and pathology in free-ranging common dolphins, *Delphinus delphis*, in the eastern tropical Pacific. Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 8604 La Jolla Shores Dr., La Jolla, CA 92038. Admin. Rep. LJ-81-23C, 19 p.

[2] Walker, W. A., F. G. Hochberg, and E. S. Hacker. 1984. The potential use of parasites *Crassicauda* (Nematoda) and *Nasitrema* (Platyhelminthes) as biological tags and their role in the natural mortality of common dolphins, *Delphinus delphis*, in the eastern North Pacific. Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 8604 La Jolla Shores Dr., La Jolla, CA 92038. Admin Rep. LJ-84-08C, 31 p.

data on age and gonadal condition for 35 male and 52 female specimens. Most of the dolphins examined in this study were collected during purse-seine research operations off the southern California coast (Hui, 1973).

In the late 1970's, Japan, Taiwan, and the Republic of Korea initiated high-seas driftnet fisheries for flying squid, *Ommastrephes bartrami*, and large-mesh fisheries for pelagic fish species including albacore tuna, *Thunnus alalunga*. The majority of squid driftnet fisheries operated from June to November in the central North Pacific Ocean between lat. 34°–46°N and long. 171°E–147°W, while large-mesh fisheries operated farther south and west between lat. 29°N–45°N and long. 147°E–150°W from February to November. *Delphinus delphis* was the most frequently killed cetacean in the large-mesh fisheries and was also found regularly entangled in the squid driftnet fisheries (Hobbs and Jones, 1993).

Beginning in 1990, under international cooperative agreements, biological samples were collected from marine mammals killed in the Japanese and Taiwanese squid and large-mesh fisheries and from marine mammals killed in the Korean squid fishery. Combining the 1990 and 1991 biological samples provided an opportunity to estimate growth and reproductive parameters for *D. delphis* from the offshore waters of the North Pacific Ocean.

Materials and methods

Specimen collection

Scientific observers collected biological data from all cetaceans caught in Japanese, Korean, and Taiwanese driftnet operations. 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 an individual 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 was 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 1.0 cm.

Frozen and preserved samples were shipped to the National Marine Mammal Laboratory in Seattle, Washington, for analyses.

Age determination

Teeth were extracted from the center of the left lower jaw for age determination. Each tooth was decalcified and sectioned (24 µm) longitudinally on a freezing microtome. Tooth-section preparation and dentinal growth-layer group (GLG) counting procedure followed guidelines developed by Myrick et al. (1983) for *Stenella* spp. Six to eight stained sections from the center of each tooth were mounted on a glass slide and examined under a compound microscope at 40× and 100× magnification with transmitted light. Dentinal GLG characteristics have been described for *Delphinus* (Perrin and Myrick, 1981). Annual deposition of dentinal GLG's has been established for tetracycline-marked common dolphins (Gurevitch et al., 1981). We followed these findings and assumed one GLG represented one year of growth.

Each tooth was read independently by two readers. Ages were recorded to the nearest 0.5 layer except for animals with less than one complete GLG. In these cases, we estimated the thickness of the incomplete layer to the nearest 0.2 GLG. Predetermined limits on reader variability were established following those used for *Lissodelphis borealis* in Ferrero and Walker (1993). This procedure allowed for a 0.5-layer difference between readings for estimated ages up to 5 years (measured from the median reading), one layer for estimates between 5 and 10 years, and 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.

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-cm³ block was removed from the center of each testis; a similar section of epididymis was removed at mid-length, and both were prepared for histological analysis. 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 by using a compound microscope at 100× 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 ($\approx$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.

Corpora were examined externally for indications of regression, including color change (i.e., darkening), reduced size and surface furrowing, and were classified by type following Perrin et al. (1976).

Results

The sample

From February to December 1990 and 1991, a total of 707 *D. delphis* (376 males and 331 females) were examined (see Fig. 1 for approximate collection locations). Sex, length, collection date, and location were recorded for each specimen, and biological samples were collected from 152 of these dolphins (93 males and 59 females).

Postnatal growth patterns and the reproductive parameters, average age and average length at sexual maturation, were measured by using the portion of the dissected sample for which both age and reproductive status were determined (70 males and 43 females). We tested for differences in the length distributions of the total sample and the reproductive sample; no significant differences were detected (Kolmogorov-Smirnov Test, D=0.18, P>0.05) The total sample (n=707) was used to examine sex ratios, gestation period, and reproductive seasonality. The spatial and temporal distribution of the total sample reflects the movement of the driftnet fisheries northward from February to August, then southward in the fall (Gong et al., 1993; Nakano et al., 1993; Yatsu et al., 1993; Yeh and Tung, 1993; Table 1).

Male *D. delphis* ranged from 0.4 to 27 years in age (n=93): 3% were calves <1 year old (n=3), 23% were yearlings (n=21), and the remainder were >2 years old. Female ages ranged from 0 to 26 years (n=59); one newborn was

sampled, 5% were calves <1 year old (n=3), and 32% were yearlings (n=19). The age distribution of both sexes (Fig. 2) declined intrinsically except between the two youngest age groupings.

Males ranged in length from 86 to 211 cm. Females ranged from 81 to 199 cm (Figs. 3 and 4).

Stock identification

The two recently described species of common dolphin in the North Pacific Ocean are separable on the basis of cranial morphometrics and color pattern (Heyning and Perrin, 1994). To date five cranial specimens are available from the driftnet fisheries and of these, one is from an adult animal. The rostral length to zygomatic width ratio for the single adult specimen (201 cm, male) was 1.36. The mean ratio for adult male short-beaked common dolphin presented in Heyning and Perrin (1994) was 1.37 (SE=0.046). Preliminary comparison of photographs of common dolphins taken in the driftnet fisheries (color pattern features are described in Heyning and Perrin [1994]) suggests that our sample more closely resembles the short-beaked common dolphin. Furthermore, the currently known distribution of both species of *Delphinus* presented in Heyning and Perrin (1994) indicates that only the short-beaked form of
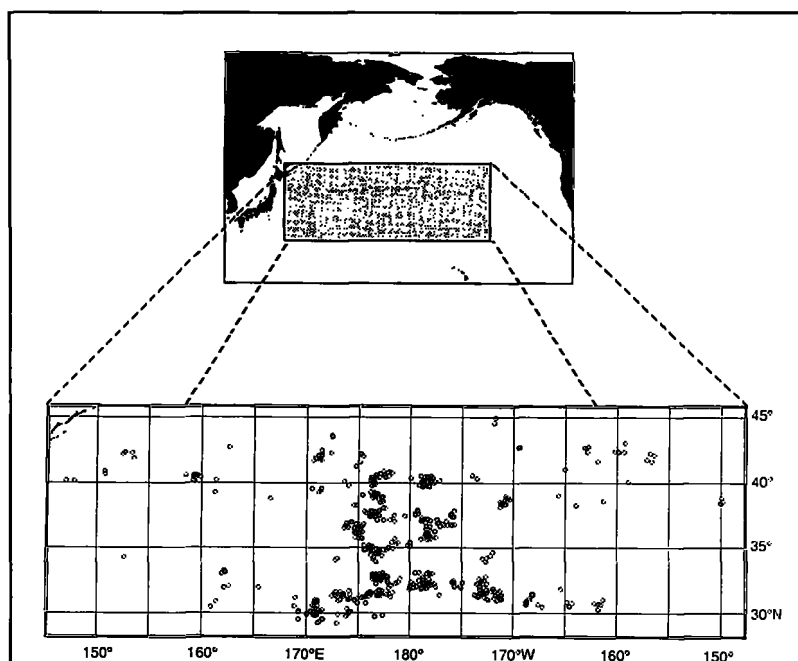
Figure 1

Approximate sampling locations of 376 male and 331 female common dolphin, *Delphinus delphis*, caught in Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991.

Table 1

Number of *Delphinus delphis* specimens examined from February to December, 1990 and 1991, from latitudes 29°N to 44°N in Japanese, Korean, and Taiwanese drift nets.

Month	Latitude (in degrees)

Month	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
February	1	9	8	0	0	0	0	0	0	0	0	0	0	0	0	0
March	15	41	92	15	0	0	0	0	0	0	0	0	0	0	0	0
April	0	4	10	103	10	0	0	0	0	0	0	0	0	0	0	0
May	0	0	0	0	0	53	24	0	0	4	0	0	0	0	0	0
June	0	0	0	0	0	0	15	46	59	33	6	8	0	0	0	0
July	0	0	0	0	0	0	0	0	0	2	21	37	2	13	0	0
August	0	0	0	0	0	0	0	0	0	0	1	11	0	5	2	2
September	0	0	0	0	0	0	0	0	0	0	0	0	2	6	0	0
October	0	0	0	0	0	0	0	0	0	0	0	21	12	4	0	0
November	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
December	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

common dolphin extends into the driftnet fisheries area of the central North Pacific Ocean. On the basis of these factors, we provisionally assign the *Delphinus* in our sample to the short-beaked common dolphin *D. delphis*.

Growth

Length at birth and gestation period
Only two fetuses (65.0 cm and 12.6 cm) and one age-0 neonate (82 cm) were collected; this small sample size limited our ability to calculate a length at birth with the method described by Hohn and Hammond (1985) or the modified DeMaster (1978) approach described by Ferrero and Walker (1993).

The small sample size of newborns and lack of near-term fetuses also limited estimation of the gestation period. However, if we assume that the length of the age-0 neonate approximates the size at birth (82.0 cm) and consider the collection dates and lengths of the two fetuses, then preliminary estimates can be determined. We explored the gestation period parameter in two ways: 1) by using the relationship between fetal length and time described by Hugget and Widdas (1951), and 2) by using the relationship between size at birth and gestation period described for several species of delphinids by Perrin et al. (1977).

Following Hugget and Widdas (1951), we regressed the lengths (y) of our two fetus specimens and the
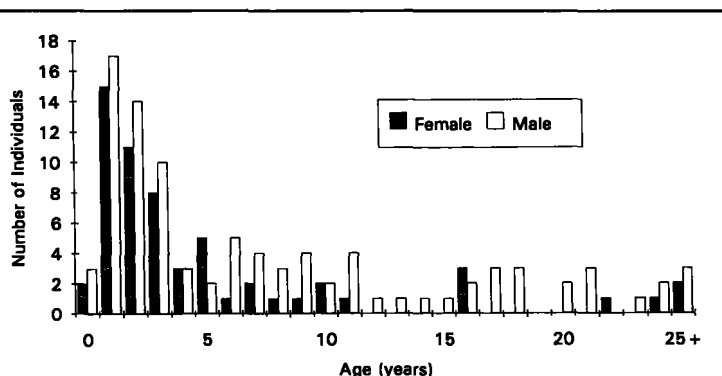
Figure 2

Age-frequency distribution of 93 male and 59 female common dolphin, *Delphinus delphis*, caught in Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

age-0 neonate (we assumed this animal was recently born given the complete absence of postnatal dentine) on time, indexed by day of the year of collection (x), in order to estimate the linear phase of growth ($t_g - t_o$), where t_g is the gestation period and t_o is the "nonlinear" phase of growth. The regression equation

$$y = -57.04 + 0.264x \qquad (1)$$

was significant ($r^2 = 0.996$, $P < 0.001$). The linear growth phase was estimated to be 10.5 months. We did not attempt to estimate the nonlinear phase be-

cause an empirical method for doing so is lacking (Perrin and Reilly, 1984).

We also used Perrin et al.'s (1977) regression equation:

$$Log(y) = 0.1659 + 0.4586 Log(x), \quad (2)$$

substituting x with the length of our age-0 neonate. The *D. delphis* length at birth estimate of 82.0 cm approximated the gestation period at 11.1 months.

Postnatal growth Growth curves were fitted separately for males and females by using a nonlinear least-squares method. The Laird/Gompertz formula (Laird, 1969) was used as a base model for both sexes:

$$L(t) = L_0 \exp\{a[1 - \exp(-\alpha t)]\}, \quad (3)$$

where $L(t)$ is the length at age t, L_0 is the length at birth, t is the age, a is the specific rate of exponential growth, and α is the rate of decay of exponential growth.

For both sexes, we fit two Laird/Gompertz curves, one for the sexually mature animals and the other for the sexually immature, in order to minimize the number of positive residuals in the upper curve segment. The low sample size prohibited attempts to iteratively fit the two curve segments and locate the intersection point.

Female growth through age 2 was rapid, with a predicted length at age of 146.4 cm. The predicted asymptotic length was 179.4 cm (Fig. 5).

The male growth curve through age 2 was slightly steeper than that portion of the female growth curve, reaching a predicted length at age of 149.8 cm. The predicted asymptotic length was 188.1 cm (Fig. 6).

The mean length of females age 16 and older (i.e. those animals likely to have reached maximum size based on the predicted length at age [16 yr] falling on the asymptotic portion of the upper growth curve) was 179.8 cm (n=5, SE=6.76). The mean length of males age 16 and older was 187.1 cm (n=15, SE=5.57). The difference in mean lengths between sexes was significant (t-test, one-tailed, P=0.04).

**Reproduction**

Sex ratio Sex ratios were estimated for four subsets of the aggregate sample of measured animals
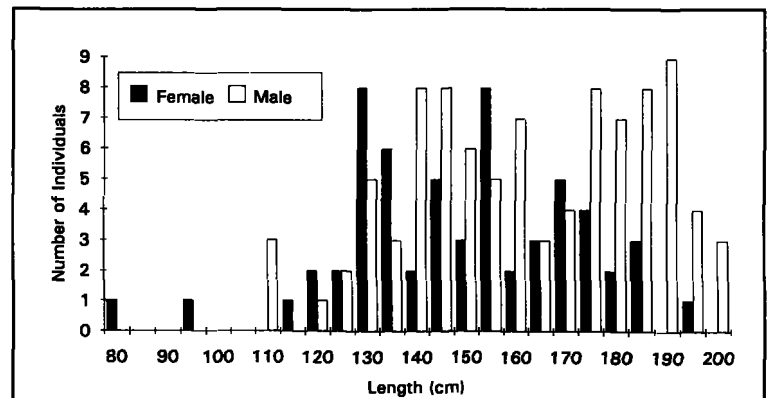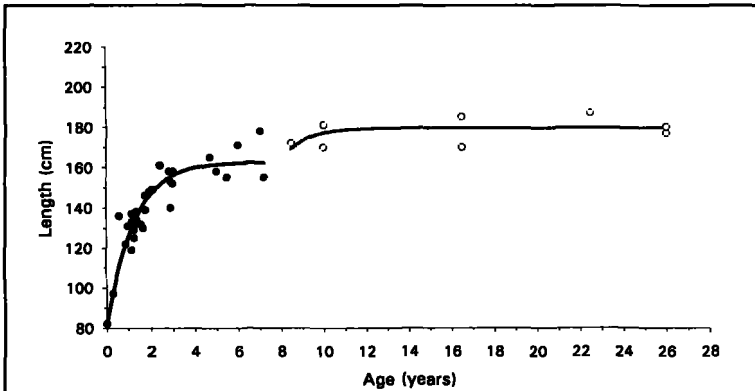

Figure 3

Length-frequency distribution of 93 male and 59 female common dolphin, *Delphinus delphis*, for which ages were determined. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.
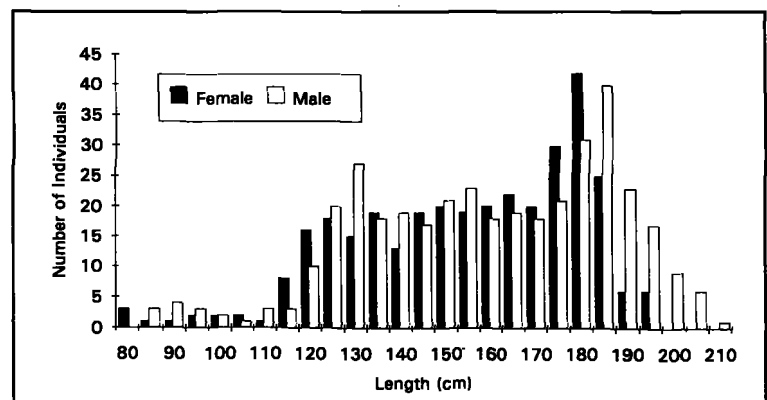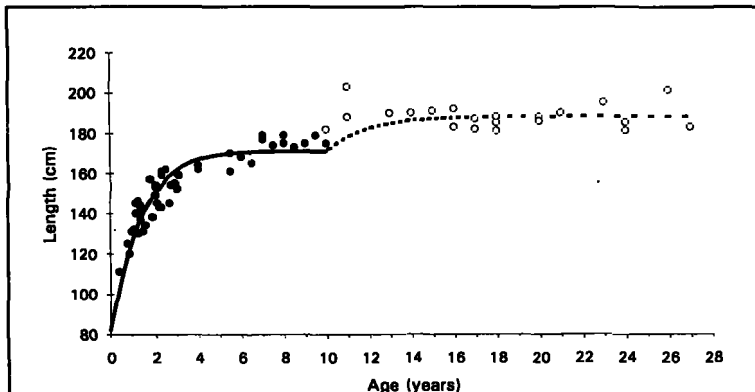

Figure 4

Length-frequency distribution of all common dolphins, *Delphinus delphis*, examined at sea February–November 1990–91 (376 males and 331 females). Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

(n=707) to represent progressively older age groups. The predicted length at age from our postnatal growth models (Figs. 5 and 6) were used to separate the sample into four approximate age groups ($\leq$1 year, 1 to 10 years, 10 to 15 years, and >15 years) on the basis of length. In addition, we calculated separate sex ratios for the portions of the sample collected north and south of 34°N latitude. The latitudinal break corresponded to a break in the timing of collections, splitting February, March, and April sampling from the remainder of the year (Table 1). We used the empirical logistic transform method (Cox and Snell, 1989) to estimate sex ratio as

Figure 5

Age at length of female common dolphin, *Delphinus delphis*, with fitted growth curves (Laird/Gompertz model). The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

Figure 6

Age at length of male common dolphin, *Delphinus delphis*, with fitted growth curves (Laird/Gompertz model). The open circles are mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

$$r = \frac{m+0.5}{f+0.5}, \qquad (4)$$

where r is the ratio of males to females, m is the number of males, and f is the number of females. The natural logarithm of r is normally distributed with variance,

$$\mathrm{var}[\ln(r)] = \frac{(n+1)(n+2)}{n(m+1)(f+1)}, \qquad (5)$$

where n is the total number of males and females, m is the number of males, and f is the number of fe-

males. Of the sex ratios calculated by using the sample collected from all areas, only the 10 to 15 year-old group ratio (1.792) was significantly different from 1.0 (Exact Binomial Test, $P<0.01$). When only the portion of the sample collected south of 34°N was considered, none of the ratios was significantly different from 1.0 (P-values were all >0.2). The sample collected north of 34°N yielded a sex ratio significantly different from 1.0 (Exact Binomial Test, $P<0.01$) in the 10 to 15 year-old group (2.641) (Table 2).

Average age at sexual maturation Only preliminary estimates of average age at sexual maturation (ASM) could be calculated owing to the insufficient number of indeterminant age classes represented in the sample. No indeterminant age classes were represented in the female sample. For males we used the DeMaster (1978) method which computes the mean age as

$$ASM = \sum_{a=j}^{k} a(f_a - f_{a-1}), \qquad (6)$$

where f_a is the fraction of mature animals in the sample aged a, j is the age of the youngest mature animal in the sample, and k is the age of the oldest immature animal in the sample.

Maturity status overlapped one age class in the male sample, where we estimated the variance as

$$\mathrm{var}(ASM) = \sum_{a=j}^{k} \frac{f_a(1-f_a)}{(N_a-1)}, \qquad (7)$$

where N_a is the total number of animals aged a.

Males The preliminary estimate of average age at onset of sexual maturation for males was 10.5 years (SE=0.50). Only at age 10 did both sexually mature and immature specimens appear in the sample.

There was a significant linear correlation between testis weight and age among the immature animals ($r^2=0.83$, $P<0.01$), but the overall increase in testis weight was small (<50 g over 10 years). A linear relationship between age and testis weight was not apparent among mature animals ($r^2=0.15$). Testis weight dramatically increased after age 10 (Fig. 7A).

The sample contained 21 sexually mature and 50 sexually immature males. The testis weight of the

youngest sexually mature male (10 years) was 370 g; the testis weight of the oldest immature (10 years) was 34.6 g. Weights of mature testes ranged from 273.2 to 1,190 g.

Females Only a rough approximation of female average age at sexual maturation was determined. The oldest sexually immature female was age 7.2 years, and the youngest sexually mature was 8.5 years. Of the forty-three female reproductive tracts collected, 8 were from mature animals. The youngest sexually mature female had three corpora (Fig. 8A). Of the mature females, three were resting, two were pregnant, two were lactating and had stage-2 corpora, and one was of unknown status (Table 3).

Average length at sexual maturation Calculation of average length at sexual maturation was limited for the male sample because no indeterminant length classes were represented. The female sample was adequate to estimate the parameter. Two methods were used: the DeMaster (1978) method, modified to estimate the average length instead of average age, and a logistic regression method.

The modification of DeMaster's method, applied to females, used lengths grouped into even intervals as

$$LSM = \sum_{i=i_{min}}^{i_{max}} l_i (f_i - f_{i-1}), \qquad (8)$$

where i_{min} is the index of the size class with the smallest mature animal, i_{max} is the index of the size class with the largest immature animal, l_i is the lower limit of the ith size class, and f_i is the fraction mature in the ith size class.

The variance estimate on female LSM was obtained by modifying the formula of DeMaster (1978) to account for the interval width (w) so that
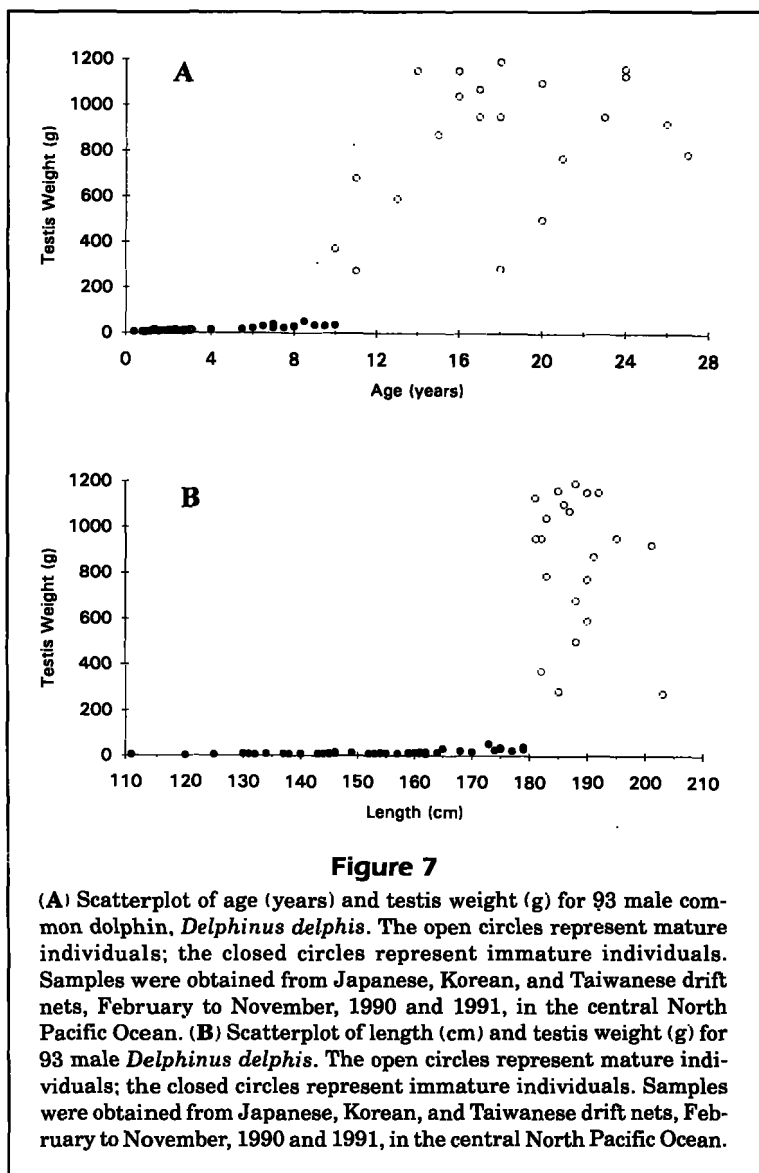
Table 2

Sex ratios for four age groups of *Delphinus delphis*. Predicted lengths at age from the Laird/Gompertz growth model were used to determine the upper limits for each group (i.e. 125 cm, both sexes ≤1 year; 171 cm for males and 169 cm for females aged 1 to 10 years; 187 cm for males and 179 cm for females aged 10–15 years). Sex ratios significantly different from 1.0 (α=0.05) are marked with an asterisk. SE = Standard error.

Area and age groups	No. of individuals			
	Male	Female	Sex ratio	SE
All areas				
≤1	32	41	0.7831	0.2342
1–10	182	161	1.1362	0.1079
10–15	90	50	1.7921*	0.1756
>15	71	79	0.8994	0.1630
South of 34°N latitude				
≤1	11	18	0.6216	0.3750
1–10	78	72	1.0828	0.1629
10–15	39	31	1.2540	0.2388
>15	24	35	0.6901	0.2625
North of 34°N latitude				
≤1	21	23	0.9149	0.2985
1–10	105	89	1.1788	0.1437
10–15	51	19	2.6410*	0.2649
>15	47	44	1.0674	0.2086

$$\text{var}(LSM) = w^2 \sum_{i-i_{min}}^{i_{max}} \frac{f_i(1-f_i)}{N_i - 1}, \qquad (9)$$

where N_i is number of individuals in the ith size class and the interval width (w) was constant.

The logistic regression (Cox and Snell, 1989) fits a logistic curve, ($\mu(a)$), the probability that a dolphin

Table 3

Age, length, corpus count, and reproductive condition for eight mature female *Delphinus delphis* taken in Japanese, Korean, and Taiwanese drift nets in the central North Pacific Ocean from February to December, 1990 and 1991.

Specimen number	Collection date		Length (cm)	Age (years)	Corpus count	Reproductive condition
RAT 036	23 Sep	90	170	10	1	Pregnant
EJW 037	25 Sep	90	172	8.5	3	Unknown
RAT 050	3 Oct	90	180	26	8	Resting
JAS 045	28 Mar	91	185	16.5	3	Pregnant
JAS 062	4 Jun	91	187	22.5	5	Resting
JAS 071	7 Jun	91	181	10	7	Lactating
JAS 109	26 Jun	91	177	26	6	Lactating
JAS 121	17 Jul	91	170	16.5	2	Resting

Figure 7

(A) Scatterplot of age (years) and testis weight (g) for 93 male common dolphin, *Delphinus delphis*. The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean. (B) Scatterplot of length (cm) and testis weight (g) for 93 male *Delphinus delphis*. The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

Males Length at sexual maturation could only be suggested by the largest immature male, 179 cm, and the smallest mature male, 182 cm. There was a significant linear correlation between length and individual testis weight among immature animals (r^2=0.61, P<0.0001). Testis weights changed little with length up to the onset of sexual maturity when weights increased greatly (Fig. 7B). No correlation between length of mature animals and testis weights was detected (P>0.4).

Females Female average length at sexual maturation based on the DeMaster (1978) method was 172.8 cm (SE=0.56). With the logistic method, female LSM was 170.7 cm (SE=2.74). The smallest sexually mature female measured 170 cm; two corpora were present on the left ovary. The largest sexually immature female was 178 cm (Fig. 8B).

Ovulation rate Calculation of ovulation rate followed methods used for *Stenella attenuata* in Perrin et al. (1976). The average reproductive age ($\overline{A}$) in interval p was calculated as

$$\overline{A}_p = \frac{\left(\sum_i^p a_i b_i\right)}{c}, \tag{11}$$

where a is the percent maturing in the ith interval, b is the average reproductive age in interval p of females which matured in i, and c is the percent mature in interval p. The average corpus count in each age interval was calculated by dividing the sum of corpora counted in interval i by the number of mature females in interval i. We then regressed the average corpus count on the average reproductive age.

Ovarian scars numbered from 1 to 8 corpora among mature females. A linear model provided the best fit to the corpus count and average reproductive age data (r^2=0.61, P<0.1).

Seasonality Evidence of reproductive seasonality was detected by correlating age and length on collection date. From the aged portion of the sample we regressed ages of specimens ≤0.5 years (n=5) and the day of the year of collection using a linear model that resulted in the equation

$$y = 158.76 + 265.14x, \tag{12}$$

of length l is mature, to the distribution of mature and immature animals by age:

$$\mu = \frac{e^{lb+c}}{1+e^{lb+c}}, \tag{10}$$

where, l is the length of the dolphin and b and c are the slope and intercept of the regression. Average length at sexual maturation is then estimated as the age where $\mu(a) = 0.50$ so that LSM = $-c/b$.

The regression was done by using a maximum likelihood and iteratively reweighted least-squares algorithm (Chambers and Hastie, 1992). The standard error for μ was obtained by transforming the standard error of the linear fit.

where x is age and y is the day of the year of collection. At age 0.0, the intercept corresponds to a date in early June, suggesting the calving mode. Both the slope and the intercepts were significant ($P<0.001$ and $P<0.05$, respectively).

We also regressed the lengths of specimens ≤ 115 cm from the overall sample ($n=30$) with day of the year. The 115-cm length corresponded to ages slightly older than 0.5 year for both sexes according to the predicted length-at-age relationship from the Laird/Gompertz growth model. We obtained the equation

$$y = -133.44 + 3.435x, \qquad (13)$$

where x is the length and y is the day of the year. Substituting 82 cm, our provisional length at birth, for x, the line intercepts a date in mid-May. Both the age- and length-based regressions suggest a seasonal peak in mid-May or early June. The lengths and dates of collection for the two fetuses also support this modal peak. The 65-cm fetus collected 28 March 1991 and the 12.6-cm fetus collected 23 September 1990 were projected to reach full-term in late May to early June.

Discussion

The structure of the *D. delphis* sample suggested that it was suitable for preliminary estimation of several basic growth and reproduction parameters, although our values would be improved with larger sample sizes. With uncertain prospects for collecting additional *D. delphis* samples, owing to the discontinuation of the high seas squid driftnet fisheries and thus any associated sampling programs, we attempted to provide as much quantitative analysis as possible; however, we must regard many of our estimates as provisional. In particular, more reliable estimates of ASM and LSM will require more samples in the indeterminant age and length classes. Strong evidence of seasonality in calving made this sample unsuitable for calculation of calving interval, length of lactation, age of weaning, length of resting period, or reproductive rates.

Our application of the double Laird/Gompertz growth model is consistent with methods applied in previous growth studies on small cetaceans (Perrin et al., 1976, 1977), although our sample was not large enough to iteratively fit an intersection point between
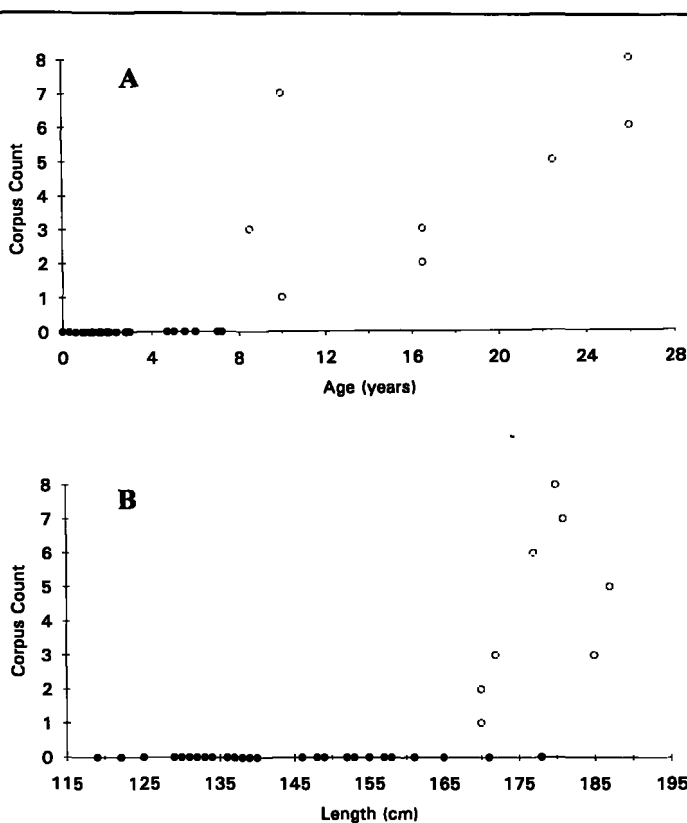
Figure 8

(A) Scatterplot of age (years) and total corpus count for 59 female, common dolphin, *Delphinus delphis*. The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean. (B) Scatterplot of length (cm) and total corpus count for 59 female *Delphinus delphis*. The open circles represent mature individuals; the closed circles represent immature individuals. Samples were obtained from Japanese, Korean, and Taiwanese drift nets, February to November, 1990 and 1991, in the central North Pacific Ocean.

the upper and lower curves. While our application of the two-stage model suggests a secondary growth surge near the onset of sexual maturation, the magnitude and timing of that event should not be considered reliable without further sampling.

We attempted to fit a single Laird/Gompertz model to both the male and female data sets, but in both cases we encountered a preponderance of positive residuals at predicted lengths at age >10 years. Using the single curve, we predicted asymptotic lengths for both sexes at least 10 cm lower than any of the observed lengths for mature specimens. Our results from the double Laird/Gompertz model provide predicted length-at-age relationships with comparatively smaller residuals, distributed both positively and negatively at older ages.

Very few neonates, pregnant females with near-term fetuses, or lactating females, were collected even though we found strong evidence for a calving mode during the sampling period. We considered three possible factors to explain the inconsistency: 1) differing entanglement rates by various age and sex strata, 2) temporal disproportion in sampling effort, especially during the projected peak of the calving season, and 3) population segregation.

Following the same rationale developed for sampling *L. borealis* in Ferrero and Walker (1993), we did not consider the potential for bias as a result of the sampling method (i.e. incidental take in drift nets) to be a major factor. *Delphinus delphis* entanglements were scattered randomly along the length of the nets. Multiple entanglements were rare. The entanglements, therefore, appear to arise as individual events rather than as whole school encounters. Consequently, the sample likely reflects the composition of the population in the area rather than the composition of an individual school. There is also no evidence to assume that neonates or pregnant females avoid entanglement more than other age or sex strata.

Regarding the second possibility, the temporal distribution of the sample does not reflect low sampling effort during the late spring and early summer months. The peak in sampling effort occurred in June, and over 75% of that effort was accomplished in March–June. Thus, the absence of neonates and parturient females in the sample did not result from inadequate collection effort at that time.

Population segregation appears to be a likely factor in contributing to the small number of neonates and parturient females in our samples, and its effect is reflected in our sampling where collection locations tracked the northerly progress of the fishery. Our only advanced-term fetus was collected at the southern end of the study area in March. As the sampling effort moved northward, the parturient or lactating females and calves probably remained to the south and were unavailable for sampling. The remaining part of the female population appeared to have been represented in the sample.

The age and length distributions also reflect the likelihood that a significant portion of the female population was missing from the sample. The sex ratios calculated for specimens collected in areas south of lat. 34°N were not significantly different from 1.0; however, north of 34°N the ratio significantly differed from 1.0, favoring males in the 10 to 15 year-old age group. Furthermore, in the 15+ age group the sex ratio was not significantly different from 1.0 which is inconsistent with data for other delphinid species characterized by a greater propor-

tion of mature females in the population (see Table 8 in Perrin and Reilly, 1984). Our age and length distributions, which suggest a male-dominated ratio, better describe only the part of the *D. delphis* population inhabiting the northern portion of the study area during the fishing season. These distributions and the sex ratio, therefore, should not be considered indicative of the overall population structure.

Schooling segregation by age, sex, and reproductive status has been demonstrated for numerous species of delphinid cetaceans (Perrin and Reilly, 1984); *Delphinus delphis* is among this group. Schooling segregation of *D. delphis* has been documented in the Black Sea where during calving and early lactation, females occur predominantly in offshore waters (Kleinenberg, 1956; Tomlin, 1957).

Our preliminary estimate of 11.1 months for gestation is similar to published accounts for the common dolphin. Gestation periods ranging from 10 to 11 months have been reported for *D. delphis* (Kleinenberg, 1956; Tomlin, 1957; Harrison, 1969).

Growth curves for North Pacific *D. delphis* have not been published and little definitive information on age and length at the onset of sexual maturation is available. Gurevitch and Stewart[3] reported that male *D. delphis* in the eastern tropical Pacific Ocean (central tropical population) reach sexual maturity around 6–7 GLG's, at a mean length of 200 cm. Hui (1979) presented data on *Delphinus* from southern California where females were reported to attain sexual maturity around 7–14 GLG's, and males between 8 and 12 GLG's. Length at onset of sexual maturation was 165–182 cm for females and 175–190 cm for males. Our preliminary estimates of age and length at sexual maturation for both sexes fall within the ranges presented in Hui (1979).

However, comparisons of our findings on the short-beaked *D. delphis* from the North Pacific transition zone with those from the southern California sample of Hui (1979) are potentially misleading, given recent evidence for the occurrence of two sympatric species of common dolphin in the southern California area (Heyning and Perrin, 1994). These two species, *D. bairdii* and *D. delphis*, are documented to differ markedly in overall size, and it is possible that Hui's (1979) sample contained members of both these species, accounting for the wide ranges in lengths at sexual maturation. In addition, differences in ages at onset of sexual maturation between our sample

[3] Gurevitch, V. S., and B. S. Stewart. 1978. Structure of kill of the common dolphin, *Delphinus delphis*, from the eastern tropical Pacific in 1977. Final Rep. for Contract 03-78-M02-0101, Southwest Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 8604 La Jolla Shores Dr., La Jolla, CA 92038, 19 p.

and those presented in Hui (1979) and Gurevitch and Stewart[3] may be due to ageing methods. Both these studies employed an early technique of reading undecalcified, thin sections of formic-acid-etched teeth. This method is now considered imprecise for ageing small cetacean teeth (Perrin and Myrick, 1981).

Perryman and Lynn (1993) documented reproductive seasonality differences between three morphologically distinct common dolphin populations from adjacent but differing habitats in the eastern North Pacific Ocean. Calving season in the tropical region was year-round. In the temperate regions, which are characterized by a wider range of oceanographic conditions, strong evidence of reproductive seasonality was evident.

Our sample suggests evidence for a May–June calving peak as well as for schooling segregation of parturient females in the southern regions of the transition zone, closer to the subtropical domain. Evidence for pronounced reproductive seasonality should be anticipated in this region because the North Pacific transition zone is characterized by extreme oceanographic conditions, particularly in the northern regions adjacent to the subarctic frontal zone (Roden, 1991).

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