NEW TECHNIQUES FOR ASSESSING POPULATIONS OF RIGHT WHALES WITHOUT KILLING THEM

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Abstract

Aerial photographs of the population of southern right whales (*Eubalaena* sp.) off Peninsula Valdez, Argentina, were used to recognize and measure individual whales. Individuals could be recognized by examination of photographs showing the unique pattern of light-coloured head markings, or callosities. Between 1971 and 1976, 1 648 identifications of 484 different whales were made. The lengths of whales were measured directly by comparing the image of the whale on film with a disk of known diameter carried on a fast boat next to the whale when it surfaced for breath; 29 animals were measured in this way. The lengths of 4 whales were found by comparing them to whales of known length swimming parallel to them. Similarly, ratios of the lengths of mothers and their calves were used to estimate the initial growth rate of calves and provide evidence for birth dates and lengths at birth. Results indicated that most calves seen at Peninsula Valdez are born in or near August, are about 5.5 m at birth and grow about 35 mm each day, for the first few weeks of life. A ratio of snout-to-blowhole length to overall length was found for 202 known whales photographed clearly but without the disk being present for size comparison. Formulae relating this ratio to length and describing changes in them over time, were used to estimate the growth rate of older animals and produce an approximate age-length key. Based on these results, it was estimated that females in this population become sexually mature at about 3 to 4 years of age. These new techniques provide estimates of parameters used in population models of large whales without killing them and, in some cases, do so in a more direct way than do traditional methods dependent on a fishery. Some of them can probably be applied to other species of large whales.

Résumé

Des photographies aériennes de populations de baleines franches australes (*Eubalaena* sp.), se trouvant au large de la péninsule Valdez, en Argentine, ont été utilisées pour reconnaître et mesurer les individus. Les sujets ont pu être reconnus par l'examen de photographies montrant la disposition unique de marques claires, ou callosités, de la tête. De 1971 à 1976, on a effectué 1 648 identifications de 484 baleines différentes. La longueur des baleines a été mesurée directement en comparant l'image de la baleine avec un disque de diamètre connu porté par un bateau rapide proche de la baleine quand elle émergeait pour respirer. On a mesuré 29 animaux de cette façon. On a trouvé la longueur de 4 baleines en les comparant à des sujets de longueur connue qui leur étaient parallèles. De même, le rapport entre la longueur des mères et de leurs petits a été employé pour estimer le taux de croissance initial des jeunes; il donne des indications sur la date des naissances et la longueur à la naissance. Les résultats ont indiqué que la plupart des jeunes observés à la péninsule Valdez sont nés en août ou à une date voisine, mesurent environ 5,5 m à la naissance et grandissent d'environ 35 mm chaque jour pendant les premières semaines de leur vie. Le rapport entre la distance museau-trou d'évent et la longueur totale a été déterminé pour 202 baleines connues, photographiées clairement mais sans le disque permettant de comparer la taille. Des formules établissant une liaison entre cette distance et la longueur, et décrivant les changements qui les affectent avec le temps, ont été utilisées pour estimer le taux de croissance des animaux plus âgés et établir un tableau approximatif âge-longueur. Sur la base de ces résultats, on a estimé que les femelles de cette population atteignent la maturité sexuelle vers 3 ou 4 ans. Ces nouvelles techniques ont fourni des estimations de paramètres employés dans les modèles de populations de grands cétacés sans qu'il soit nécessaire de les tuer et, dans certains cas, elles le font de façon plus directe que les méthodes traditionnelles, dépendant de la pêche. Certaines peuvent être probablement appliquées à d'autres espèces de grandes baleines.

Extracto

Gracias a fotografías aéreas de la población de ballena franca austral (*Eubalaena* sp.) que se encuentra frente a la Peninsula Valdés (Argentina) ha sido posible reconocer y medir algunos individuos. El reconocimiento de los individuos se consiguió con fotografías que mostraban las marcas características (o callosidades) de coloración clara que presentan esas ballenas. Entre 1971 y 1976 se hicieron 1 648 identificaciones de 484 ballenas distintas. La longitud de las ballenas se midió directamente, comparando la imagen de la ballena en la película con un disco de diámetro conocido que se desplazaba en una lancha rápida cerca de la ballena cuando ésta salía a la superficie para respirar; con este sistema se midieron 29 animales. La longitud de cuatro ballenas se halló comparándolas con ballenas de longitud conocida que nadaban paralelas a ellas. De igual forma, se utilizó la relación entre la longitud de la madre y los ballenatos para estimar el índice inicial de crecimiento de éstos y obtener datos sobre las fechas de nacimiento y su longitud en ese momento. Los resultados indican que la mayoría de los ballenatos observados en la Península Valdés habían nacido en agosto o poco antes o después de ese mes, tenían en el momento de nacer 5,5 m de longitud y crecían unos 35 mm al día durante las primeras semanas de vida. En 202 ballenas que se habían fotografiado con claridad, pero sin la presencia del disco necesario para determinar su talla, se halló la relación entre la distancia desde el hocico al orificio nasal y la longitud total. Mediante fórmulas que relacionan esa proporción con la longitud y describen los cambios que se producen con el pasar del tiempo, se estimó el índice de crecimiento de los animales adultos y se obtuvo una clave aproximada de la relación edad-longitud. Sobre la base de esos resultados se estimó que las hembras de esta población alcanzan la madurez sexual entre los 3 y los 4 años de edad. Estas nuevas técnicas permiten estimar algunos parámetros utilizados en los modelos de población de grandes ballenas sin necesidad de matarlas y, en algunos casos, permiten hacerlo en forma más directa que los métodos tradicionales, que dependen de la pesquería. Probablemente algunas de estas técnicas podrán aplicarse también a otras especies de ballenas de gran talla.

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Introduction

In 1975 the International Whaling Commission adopted what was called the New Management Procedure (NMP). The NMP requires full protection for any stock which falls below 10 % of the maximum sustainable yield level.

However, once a stock is severely enough depleted to require full protection, it is difficult to monitor its recovery. This is because, with the exception of aerial and shipboard censuses (which are often ambiguous), the data used in traditional techniques for estimating whale populations have come from corpses provided by the whaling industry. It is frequently argued that without these corpses one cannot calculate ages (by counting growth layers in teeth, baleen or plugs of wax filling the ear canal), determine sex, or find out calving rates (by examining ovaries).

Migration studies, as well, will suffer because they have traditionally been based on finding numbered steel darts in the cooker after a whale is melted down for oil: these darts were fired into the same individual at some other time and place.

It is clear that if we are to monitor the recovery of depleted stocks, we must develop new methods for determining such parameters as length, age, individual identity, sex, reproductive history, and migration routes that do not rely on killing the whales. In this paper we introduce several new techniques for determining these parameters which we have developed over the last 8 years while studying a small population of right whales (*Eubalaena* sp.) off the coast of Argentina in the protected waters of Peninsula Valdez. As will be explained, these techniques should be applicable, with minor modifications, to most if not all other species of baleen whales.

We also give length frequencies within the Peninsula Valdez herds, calculate length at birth, and determine the growth rates for newborn calves and later stages.

Methods

Between 1970 and 1974 one of the authors, working from the coast of Peninsula Valdez in southern Argentina, censused and photographed right whales from a single engine plane[1]. We attempted to obtain several photos of every whale using a 35-mm single lens reflex camera and 300-mm f/2.8 lens, hand-held, shooting from the window of the plane. In all, we had 52 flights of an average duration of 3.2 h, which repeatedly covered the waters in the vicinity of the peninsula. Between 1971 and 1976 we obtained a total of 19 590 photographs of whales from which we have been able to make 1 648 identifications of our total group of 484 recognizable individuals. Sometimes there are several identified whales per picture (though this is infrequent) and sometimes several pictures per whale (the usual case). The technique of identifying individuals from aerial photographs is described in another paper (Payne *et al.*, in prep.) but, briefly, is as follows: the head of every right whale is naturally adorned on top and sides with a series of raised thickened patches of cornified epidermis called callosities. The pattern of these callosities is different in every whale. Changes after birth are insignificant and do not interfere with individual recognition. Because most callosities appear to be lighter then the surrounding normal skin, they show prominently and their pattern can be used to distinguish individuals (we currently recognize 454 adult right whales in the Peninsula Valdez population). The callosity pattern on top of the head is best seen from above and can be photographed from a plane circling overhead whenever a whale surfaces to breath. Most right whales can be photographed well enough for identification in less than 6 minu-

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[1] These flights were kindly continued by B. Würsig (1975) and Clark (1976-77).

tes. Their identity is determined by comparison of the resulting photographs with a "head catalogue" which contains clear pictures of every head we have seen since the project started. A "known" whale as referred to below is a whale we can see well enough in our photographs to identify.

From 1971 to 1973, 2 or 3 flights were made each year to explore a new technique (see Appendix 1) for measuring whales by photogrammetry, using an object of known size, a 1-m disc, next to the whale. This is accomplished by photographing both whale and object in the same frame from a plane circling overhead. The photographer is in radio contact with the driver of the boat and tells him where to steer so as to be next to the selected whale when it surfaces for air. In the resulting photographs the whale is measured by using the maximum diameter of the disc to represent 1 m. The reason one uses the maximum diameter is that no matter what angle one is at in relation to a circle, his line of sight to the centre of the circle will always be perpendicular to at least one diameter of the circle, and that diameter will always appear to be the maximum diameter. Thus, by choosing the maximum diameter of the circle shown in the photograph, one has a scale with which to measure with useful precision any dimension of the whale that is perpendicular to the observer's line of sight and which lies in approximately the same plane as the circle.

In an improved version of this technique, the circle is held level, allowing any dimension of a whale to be measured, provided that the whale is lying parallel to the water's surface. The scale chosen is that diameter of the 1-m disc which is parallel to the desired dimension on the whale. As long as a disc is held level, each diameter in the resulting photograph will be correctly foreshortened for use in measuring any line in the plane of the disc that lies at the same orientation to the observer's line of sight as the diameter selected.

When the whale was not beside the disc, we applied a correction (see Appendix 1 for measurement techniques). The standard error in measurements of the same whale, measured from different photographs taken during the same year, is 0.32 m (using 23 pairs of measurements). This error includes all qualities of data, for much of which the end points of the whale were not clearly visible. For measurements where these points were distinct, the errors approximated 0.216 m. An error of 0.32 m for a 12-m whale would be 2.7 % (1.8 % for clear pictures). However, only 2 pairs of measurements of total length were used in the calculation of the standard error (the other 21 were of shorter dimensions such as snout-to-blowhole) and thus the actual errors in measuring length may have been somewhat greater.

Results

With the 1-m disc we obtained length measurements of 18 known whales, and 16 unidentified whales. We also made measurements of total and of snout-to-blowhole lengths in 202 known whales which we expressed only as a ratio (no scale being available in these photos). In 4 additional cases we used whales as rulers to measure each other, in photographs in which a whale of unknown length was parallel to one of known length. We built up a catalogue of these absolute and comparative measurements, on known and unknown whales. In some cases measurements not actually made could be inferred (e.g., the length, L, of a whale could be calculated even when the only measurement made by comparison with the circular disc was α, snout-to-blowhole, as long as there was another frame of the same individual taken in the same year from which the ratio α/L could be estimated).

Each measurement was graded from 1 to 6 (good to bad) depending on how accurately the measurement was judged to have been made (for a discussion of grading, see Appendix 1). A summary of the notations used is given before the appendixes.

LENGTH FREQUENCIES

Fig. 1 gives histograms for frequencies of 3 different measurements on the Peninsular Valdez right whales. It shows, at 1-m increments, frequencies of measured absolute length, L. It gives frequencies of snout-to-blowhole length, α, for every 0.25 m. Fig. 1 also shows the most accurate determinations (grades 1 to 4, with the whale perpendicular to camera) of z (z is α as a percentage of L) for each 1 %.

Fig. 1 indicates that known mothers are the longest whales in our population, followed by whales whose sex was undetermined (we suspect here a high percentage of males), which are in turn larger than calves accompanied by mothers.

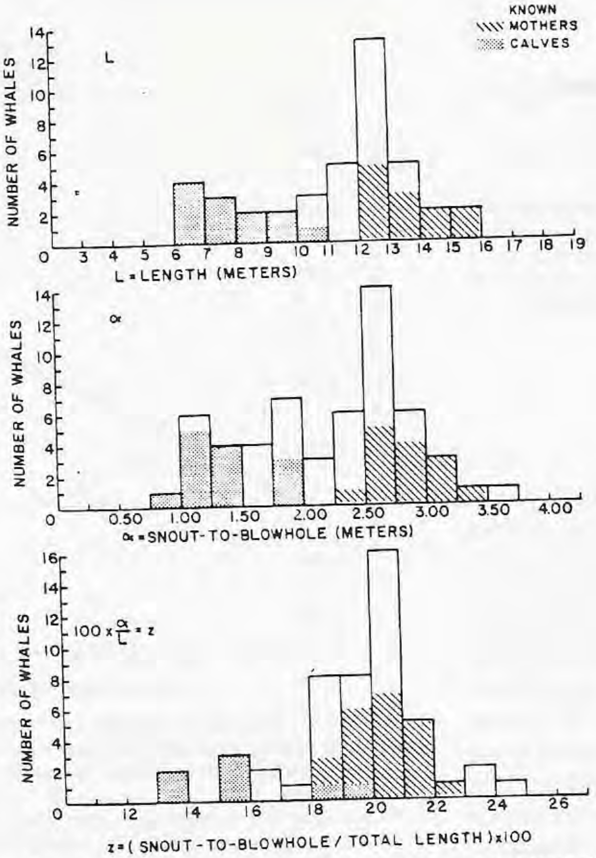

FIG. 1. - Histograms of length (L) and snout-to-blowhole length (α) for the measured whales, and of z (α as a percentage of L) for the most accurate determinations (Grades 1-4). The similarity of the histograms for z and L should be noted.

The shape of the histogram for z and its similarity to that for L suggest that z might be an indicator for L. Thus we would be able to determine length of a whale from any photograph in which the ratio of α (snout-to-blowhole distance) to overall length could be calculated without the necessity of having a reference object in the picture.

We made most of our direct measuring flights in November (a few were made in October) which is almost certainly an important factor in the relative abundance of different lengths and sexes that we observed. There are 2 reasons for this: (i) more males than females had left the area by this time; (ii) most small calves are seen earlier in the season.

GROWTH IN CALVES

There were photographs of 87 calves swimming parallel and right next to their mothers. Using these pictures we could compare the calf's dimensions with those of its mother's, and we could calculate ratios such as L_c/L_m (length of calf/length of mother).

Growth by month

Fig. 2 is a series of histograms L_c/L_m for each calendar month in which aerial census flights were made. It is apparent that from September through November the calves are growing. The best data, grades 1 to 4, are shaded. They seem representative of the rest of the data but not noticeably better grouped than it.

In order to quantify this growth we have plotted in Fig. 3 the mean value of L_c/L_m for each month together with approximate 95 % confidence limits. The growth of the calves is shown clearly in Fig. 3.

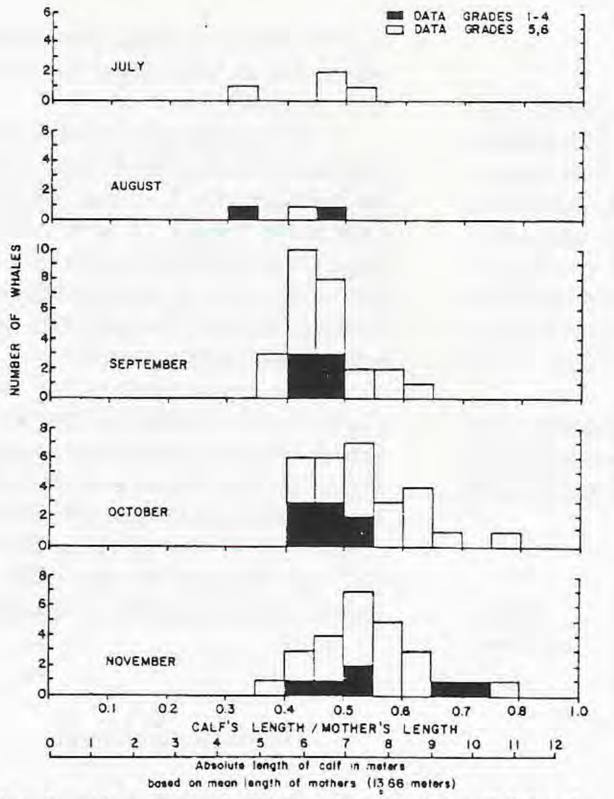

FIG. 2. – Histograms of calf's length/mother's length for each month. The best data (Grades 1-4) are blackened. A scale is included to show the absolute length of the calf if it had a mother of "mean length" (13.66 m). The calves appear to be growing and a length at birth of 5 to 5.5 m is suggested.

Growth for individuals

For 20 known mother and calf pairs, L_c/L_m could be estimated from photographs taken on 2 or more days in the same year. In Fig. 4 the change in L_c/L_m is plotted against the interval (in days) between measurements. There is much scatter in the plots, due mainly to measurement inaccuracies, but significant growth is shown (significant at a 5 % level). This growth was numerically estimated by a regression line (see Appendix 2), which gives a rate of growth for the calf of .00253 of mother's length/day. Our mean of length measurements for 12 known mothers was 13.66 m. If calves are growing at .00253 of this length per

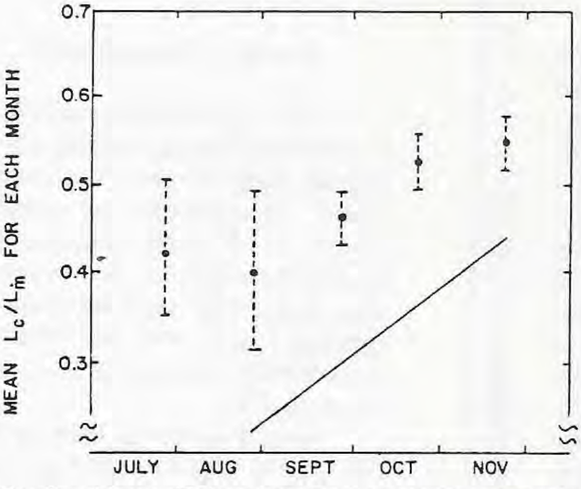

FIG. 3. – Mean calf's length/mother's length for each month, together with 95 % confidence limits. The slope of the line at the bottom right-hand corner gives the ratio of growth of individually known calves that were seen more than once in the same season (from Fig. 4).

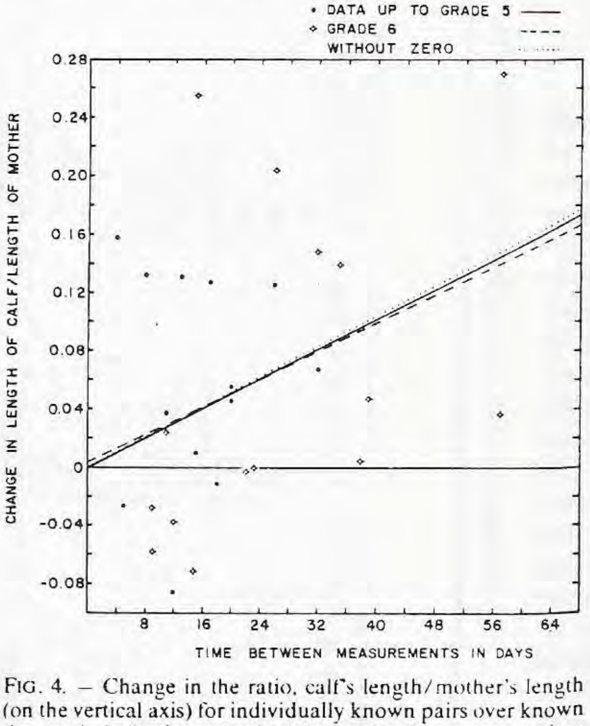

FIG. 4. – Change in the ratio, calf's length/mother's length (on the vertical axis) for individually known pairs over known time periods (horizontal axis). The solid points represent data up to Grade 5, the open ones Grade 6 data, the solid line is a regression line through the origin using data up to Grade 5, the dotted line a regression line through the origin using all the data. The dashed line a regression line, not artificially made to pass through the origin, using all the data. The slopes of these lines give the approximate initial rate of growth of calves.

day, it would mean that the initial growth rate of right whale calves is 34.6 mm/day. This figure is in remarkably close agreement with Klumov (1962) who found the rate of growth of the North Pacific right whale foetus just prior to birth to be 30-33 mm/day.

To compare the rates of growth from the monthly histograms and from the known mother and calf pairs seen more than once, a line with slope corresponding to .00253 mother's length/day is drawn in Fig. 3. The slope of this line seems in good agreement with the placing of the points for August, September and October, but in November the rate at which the overall length of the calf is increasing seems to have slowed.

Date of birth

The agreement in the rates of growth for August through October indicates that only a small proportion of the observed calves were born in the latter part of this period. For if many new small calves were being added to the population, the rate of growth of the mean of the population would be slower than the average rate of growth of known individuals, and it is about the same.

Young calves are usually close to their mothers, but sometimes either the mother or the calf is photographed alone (with the other being just out of the frame). In order to determine when calves are born, we have analysed pictures containing known mothers noting what months they were seen with their calves. We have then calculated the percentage of known mothers with calves to known mothers without calves for each month June through December (see Table 1).

This indicates that few mothers are photographed before their calves are born. There are several plausible explanations for this: (i) mothers rarely come to Valdez before their calves are born; (ii) they do come but are hard to photograph; (iii) most of the calves are born before September when the bulk of our photographing begins. It seems likely that the figures above reflect a combination of these 3 explanations. However, the impression given by the evidence in Table 1 and by the growth of calves is that the majority of calves are born before the beginning of September. Since some small calves are seen in October (e.g., 6.35 m) and they are growing at approximately 1.00 m per month, these calves cannot have been born long before.

Table 1. Numbers and proportions of known mothers seen each month

No. known mothers seen	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
No. known mothers seen	3	13	20	102	73	30	6
No. known mothers seen with calves	0	12	15	93	67	28	6
% known mothers seen with calves	0	92	75	91	92	93	100

We are aware of measurements for only a few, small, southern right whale calves and foetuses in the literature. These are given in Table 2.

It seems from the table that the majority

Table 2. Small southern right whale calves and foetuses

Source	Date of Measurement	Length Ft	Length M	Calf/ Foetus
Committee for International Whaling Statistics, 1938	12 July 1937	19'4"	5.89	Foetus
	22 July 1937	19'9"	6.02	Foetus
	28 July 1937	17'2"	5.23	Foetus
	21 Sep. 1937	1'0"	0.30	Foetus
Matthews, 1938	26 Aug. 1926	–	6.5	Calf
Lonneborg, 1906	12 May 1905	–	4.19	Foetus
D'Oyly, 1968	23 June 1832	20'0"	6.10	Foetus
Our data[1]	20 Sep. 1972	13'6"	4.11	Calf

[1] Local residents reported it had beached "in August". The corpse was in good condition indicating a relatively short time in the water.

of calves are born in or near August. This can be compared with Klumov (1962) who gives the birth date of North Pacific right whales to be December or January.

Length at birth

The minimum lengths of calves, and the data on foetuses in Table 2, indicate that there seems to be considerable variation in length at birth. The dead calf we found on a beach in Argentina and measured in September may have been premature. Other very small dead calves were seen beached in Argentina. The 2 foetuses greater than 6 m could be distorted – 1 comes from the caption to a picture in the sketchbook of a travelling artist which was drawn in 1832. As the measurement given is as an even 20 ft it raises doubts as to how carefully it was made. It also seems possible that this measurement of length might have been taken from the hind margin of the flukes rather than the fluke notch as is usual. (The calf from Lonneborg, 1906, was measured incorrectly – to the hind margin – thus exaggerating the length of the whale.)

In Fig. 2 we have noted on the abcissa the lengths the calves would have had, had they all had average sized mothers (13.66 m). The result is very few calves smaller than 5.5 m, approximately 17 % of the calves between 5.5 and 6.0 m, and all the other calves greater than 6.0 m, all of which suggests a possible length at birth of 5.5 m.

As further evidence for a length at birth of approximately 5.5 m we have 3 calves whose mothers were photographed alone early in the season and with their calves later that same season (see Table 3).

It must be borne in mind that the calf could have hidden on the date that the mother was seen "alone" and so the ages when calves were measured are estimates. However, using the mean value of L_c/L_m for these whales (0.427) and the mean length of mothers (13.66 m) we have an estimated average length for the calves when first photographed of 5.83 m.

Table 3. Mothers seen alone and then with calves [1]

Date measured	L_c/L_m	Date mother seen alone	Date calf first seen	Age of calf when measured (days)	
				Min	Max
20 Oct.	.432	8 Sep.	26 Sep.	24	42
21 Oct.	.478	15 Oct.	21 Oct.	0	6
4 Oct.	.372	29 Sep.	4 Oct.	0	5

[1] Calves could have been born on the days when mothers were seen "alone".

We therefore conclude that while the length at birth is variable for individuals, its mean value is approximately 5.5 m, and almost certainly lies between 4 and 6.2 m. This is in agreement with Klumov (1962) who put the length at birth between 5.0 and 6.0 m for the North Pacific right whale.

Initial growth curve

Using a length at birth of 5.5 m, and the calculated growth rates, an initial growth curve was constructed and is shown in Fig. 5. It is divided into 2 parts, the division occurring at an age of 2 months. If we assume that southern right whales are born in August, it can be seen from Fig. 3 that at an age of about 2 months (October) the growth slows down. The actual initial growth curve is probably more like the smooth dashed line in Fig. 5. As a check, the mean length of the 9 calves measured in November is also shown in Fig. 5 when they would be around 3 months old (again assuming an August birth date). We have also indicated the 95 % confidence limits for this mean and it can be seen that the growth curve lies well within them.

GROWTH DURING LATER STAGES

Unfortunately, this growth curve cannot at present be continued in the same fashion for

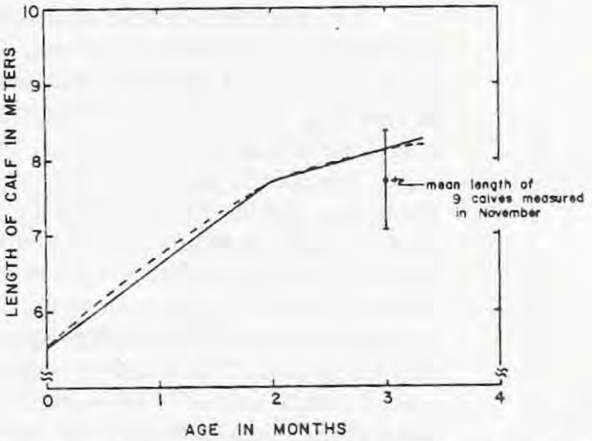

FIG. 5. — Initial growth of calves using data summarized in Figs. 3 and 4. The dashed line is a smoothed version of the 2 straight line portions. The mean length of 9 calves measured in November together with 95 % confidence limits for this mean is marked at 3 months of age (assuming calves born in August).

older whales, as this would require measurements of known whales over several years. Because our measuring flights were primarily intended to determine the feasibility of our new measuring technique, we could not afford specifically to seek out individuals measured in previous years for remeasurement. As a result, we have only one known whale (No. 156), a male, which was measured directly in more than 1 year (we now plan to extend our measuring programme, concentrating on remeasuring previously measured individuals). However, we have been able, using a less direct method, to estimate the later growth stages.

From Fig. 1 it appears that z (snout-to-blowhole distance, α, as a percentage of length L) is related to length. By using the regression of Log α on Log L, the following relationship is obtained:

$$z = 7.36 \times L^{.3768} \qquad (1)$$

(see Appendix 3 for details)

Because z is a ratio, its determination does not require having an object of known size in the same frame with the whale, thus we are able to measure z from any clear, full-length photograph of a whale. Using this method, we were able to measure 46 known whales in 2 or more years. Using the most accurate sets of measurements, we have expressed z as a function of the growth in z per year ($\delta z/\delta t$):

$$z = -4.138\,(\delta z/\delta t) + 21.66$$

(see Appendix 1 for details) .... (2)

On integration this gives a growth curve for z:

$$z = 21.66\,(1 - e^{-0.2417(t-t_k)}) \quad .... \quad (3)$$

(where t is the age in years and t_k a constant of integration).

Combining equations (1) and (3) we can create a growth curve for L:

$$L = 17.04\,(1 - e^{-0.2417(t-t_k)})^{2.66} \quad .... \quad (4)$$

To fix t_k, one further piece of information was used: the measured lengths of whale No. 156 (7.77 m on 17 November 1972 and 9.9 m on 21 November 1973). Using the initial growth curve (Fig. 5) this would make No. 156 2-3 months old on 17 November 1972, with a birth date in the first half of August of that year. He was first seen by us on 8 September 1972 (fortunately after his theoretical birth date!). On 24 November 1973 he would be 1.2 years old. Putting $t = 1.2$, $L = 9.9$ in equation (4) we find $t_k = -5.79$ years and the formulae for growth in z and L become:

$$z = 21.66\,(1 - e^{-0.2417(t+5.79)}) \quad ...... \quad (5)$$

$$L = 17.04\,(1 - e^{-0.2417(t+5.79)})^{2.66} \quad ... \quad (6)$$

Fig. 6 shows the growth curve given by equation (6) added to the curve of initial growth from Fig. 5. It is gratifying that the curves appear to join smoothly.

In Fig. 7, the growth curve for z is plotted for whales older than 1 year, using formula (5). Also plotted are the 8 smallest whales for which we have measured L (age, t, was estimated from Fig. 6). There seems to be rapid

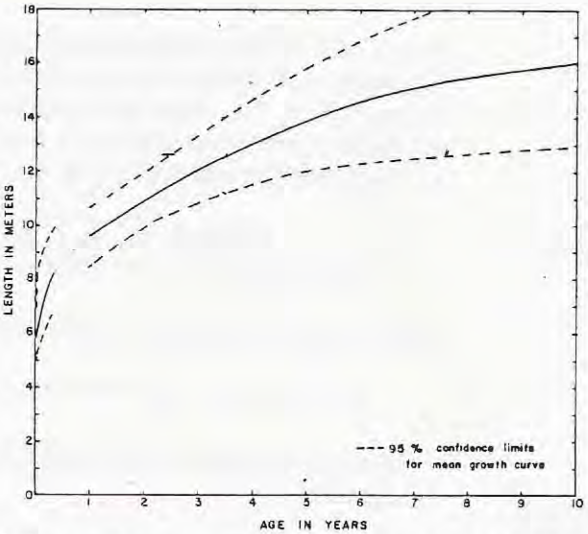

FIG. 6. – Approximate mean growth curve for the southern right whale. Dashed line indicates 95 % confidence limits for this mean (see Appendix 4).

variation in the growth of z in the first year of life and we feel there is not sufficient data currently available to estimate this growth.

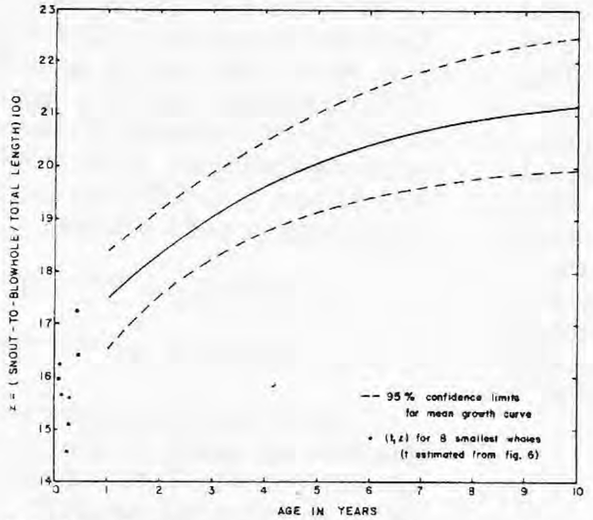

FIG. 7. – Approximate mean growth curve for z (snout-to-blowhole) as a percentage of total length. Dashed line indicates 95 % confidence limits for this mean curve (see Appendix 4). Points are plotted for the eight smallest whales measured, their ages being estimated from Fig. 6.

SEXUAL MATURITY OF FEMALES

The smallest mother accompanied by a calf that we have measured was 12.44 m (we have measured 5 mothers between 12 and 13 m (see Fig. 1). It seems reasonable to assume, therefore, that an average female becomes sexually mature at between 12.5 and 13 m or, using our age-length key (Fig. 6), between 2.5 and 6 years (average 3 or 4 years). We now have 15 calves of unknown sex seen at age 4 or older, of which 9 were seen at age 5 or older. In no case has one of these calves appeared with a calf of its own. This strongly suggests that the age of sexual maturity for females is considerably older than indicated by our age-length key.

Further applications or our methods

With the amount of data analysed to date our age-length key can be no more than tentative but as more information becomes available the accuracy can be increased and perhaps someday we will be able to draw separate curves for each sex. Even with our present confidence limits it may be possible to use the curves, in conjunction with the measured lengths and z's to obtain estimates of mortality.

In the traditional methods of constructing age-length keys, an intermediate indicator of age (such as dentinal layers or ear plug laminae) is used. The validity of these indicators has been questioned particularly with baleen whales. Because our method of measuring whales does not require a dead whale, whales can be measured (by L or z) several times in their life, and growth can be determined directly.

Some of the ideas presented here can probably be applied to other large whale species: comparisons between measurements on mothers and calves, when photographed swimming parallel to one another, should be possible; the estimation of length and thus age from z could be particularly important in estimating gross length or age frequencies of other species. All that is needed is one aerial photograph per whale, preferably with the whale's long axis approximately perpendicular to the photographer's line of sight, showing the snout, blowhole and flukes. The position of the dorsal fin might also be an important point to measure. The important factor in the success of this method is the slope of the regression line in the plot of Log α against Log L. The further it is from unity the better the method works, indicating that head and body grow at quite distinct rates. Shown below are some values of this slope for different species in the adult (defined as post-weaning) growth stages, based on measurements reported in the literature.

Southern right whale	– this paper –	1.320
Balaenoptera	– Ohsumi, 1960	1.41
Megaptera	– Ohsumi, 1960	∾ 1.41

These figures indicate that our technique should have broad applicability within the mysticetes.

It is frequently said that some form of fishery is essential to obtain valid population data on whales. Our work in analysing measurements from aerial photographs provided estimates of some of the parameters (such as age at sexual maturity) on which population models are based. The time span between calvings of known females is being obtained from direct observation, and stock estimates are being made by noting the ratio of known to unknown whales in successive airflights over the same population. Because this technique uses natural patterns of individual whales (of which we currently recognize 484) we can also study migration paths and destinations by searching for known right whales elsewhere in their range. This work shows, we think, that it is feasible to determine parameters for population models of large endangered whale species without killing them, and that, at the very least, the approach is worth investigating further.

We intend to improve on our data on eight whales to increase the validity and applicability of our conclusions, but we already feel that other scientists should consider these methods before they sanction further reduction of endangered whale species on grounds that no other technique can be used to estimate stocks.

Summary

(1) A new technique is described for measuring whales by photogrammetry to an accuracy of approximately 3 %. It employs a disc of known diameter driven by a boat into the camera's field of view when a surfacing whale is being photographed by a hand-held camera from a light plane.

(2) The results indicate that:

- the initial growth rate of the southern right whale is approximately 35 mm/day, for the first few weeks of life;
- the majority of calves seen at Peninsula Valdez are born in or near August;
- southern right whales are approximately 5.5 m at birth.

(3) We have constructed an age-length key for the southern right whale, together with confidence limits for it.

(4) We have given a curve of z (snout-to-blowhole length as a percentage of total length) against time. It is pointed out that measurements of z from single photographs of other baleen whales could very probably be used successfully as an indication of age.

Acknowledgements

The authors acknowledge with gratitude the many contributions of others to this study, particularly Oliver Brazier, Nancy Davis, Lydia Leon, Judith Perkins and Victoria Rowntree who did most of the work of identifying individual whales from aerial photographs. We are also grateful to Hugo Callejas who served as pilot during most flights, to Nancy Davis for typing the many versions of the manuscript, to Judith Perkins for analysing and collating data on known mothers with calves, to Victoria Rowntree and Katharine Payne for drawing the figures, and to Cheng-yuan Shao of the Smithsonian Astrophysical Observatory who made measuring equipment available to us for calibrating our camera lenses.

Appendix 1

Measurement Techniques

Live whales were measured by photogrammetry using an object of known size next to the whale photographed by a 35-mm, single-lens reflex, hand-held, motor-drive camera, through an f/2.8 300 mm lens. On most occasions the object photographed was a white disc, 1 m in diameter, painted on a flat board; it was carried next to the whale on the bow of an outboard motor boat, which was in radio contact with an aeroplane circling overhead.

Pictures containing the disc, in which the whale was lying perpendicular to a line joining the whale and the camera, were analysed. The judgement that the whale was perpendicular was made by eye, with a probable error of less than 5°. Usually a sequence of frames was taken with a motor drive camera from an aircraft circling close to the whale so that there was at least 1 frame in which the whale appeared perpendicular to the line joining it to the camera.

The length and other dimensions of the whale were calculated by comparing their measured lengths on the negative with the maximum diameter of the disc. A correction was applied in cases where the distances camera-to-whale and camera-to-disc were different so that the length of the whale (L) was given by:

$$L = \frac{l}{u}\left[1 \pm \frac{h}{v}\sqrt{\left(\frac{u}{s}\right)^2 - 1}\right] \text{ metres}$$

This was done using a + (plus) sign if the whale was further from the camera than the disc and a − (minus) sign if the whale was closer to the camera than the disc.

l mm = measured length of whale on negative
u mm = measured maximum diameter of disc on negative
h mm = measured distance from centre of whale to centre of disc on negative
s mm = measured diameter of disc which when extended passes through centre of whale
v mm = "image distance" of camera lens. This was calculated by photographing a series of objects of known size at known distances and measuring their image lengths on the resulting negatives using a photogrammetry measuring stage accurate to 1 micron. The resulting measurements were used to calculate image distances for our camera lenses according to the formula:

$$v = \text{image distance} = \frac{\text{object distance x image size}}{\text{object size}}$$

In our final year (1974) we developed a new technique – holding the disc horizontal during measurement. When a whale was parallel with the surface (e.g., while breathing) any dimension of the whale could

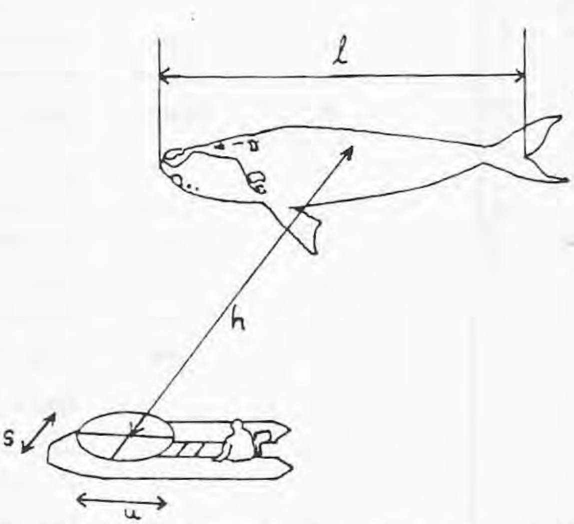

FIG. 8. – Right whale and disc, showing measurements made from each negative and used in calculations of length.

Notation

Letter	*Units*	*Definition*
α	m	Snout tip to centre of blowholes
a		Constant used in allometry formula
β	degrees	Angle of yaw of whale (between midline of whale and a line lying on the water's surface which is perpendicular to the line-of-sight from camera to whale)
b		Constant used in allometry formula
d	m	Depth of whale
e_1	m or %	Errors in growth curve due to errors in regression of $\bar{z}$ on $\delta z/\delta t$
e_2	m or %	Errors in growth curve due to errors in regression of Log α on Log L
e_3	m or %	Errors in growth curve due to errors in estimation of t_k
h	mm	Measured distance from centre of whale to centre of disc on negative
l	mm	Measured length of whale on negative
L	m	Length of whale – fluke notch to snout tip
L_c	m	Length of calf
L_m	m	Length of mother
L^{1}_{m}	m	True length of whale (see Appendix 1)
μ		Refractive index of water
m	m	Height of camera above water surface
n		Number of data points when applying regression error formulae
$\Phi(k)$	%	Indicator of how accurately measurement (k) is made – defined in Appendix 1
$\Psi(k)$		Indicator of how much measurement (k) is related to length – defined in Appendix 1
ρ		Standard error in height of regression line
r		Correlation coefficient
s	mm	Measured diameter of disc which, when extended, passes through centre of whale
τ	degrees	Inclination angle (pitch), between midline of whale and water's surface
θ	degrees	Angle between camera-to-disc line of sight and line parallel to water surface passing through centre of disc and centre of whale
t	years	Age of whale
t_1	years	Time when z_1 is measured
t_2	years	Time when z_2 is measured
t_k	years	Constant of integration
u	mm	Measured maximum diameter of disc on negative
v	mm	Image distance of camera lens
(x, y) (x_i, y_i)		Used in allometry and regression error formulae
$(\bar{x}, \bar{y})$		Mean values of x_i, y_i
z	%	$\alpha/L \times 100$
z_1	%	Value of z at time t_1
z_2	%	Value of z at time t_2
$\bar{z}$	%	$(z_1 + z_2)/2$
$\delta z/\delta t$	% yr^{-1}	$(z_1 - z_2)/t$

be measured by comparing it with whatever diameter of the horizontal disc was parallel to the dimension in question. Regardless of the point of view from which a circle is observed, the circle always shows a correctly foreshortened diameter for measuring any line parallel to that diameter in the same plane as the circle.

For each identified whale we recorded (i) all absolute length measurements made either (a) directly from the disc, or (b) through an intermediate whale or whales; (ii) all comparative ratios made between the identified whale and other whales, known or unknown, that were photographed parallel to it; (iii) all ratios of measurements of the identified whale (e.g., z).

Each measurement or ratio was graded from 1 to 6 (good to bad) depending on how accurately we thought the measurement was determined. Factors influencing the choice of grade included: (a) the clarity of the endpoints of the measurements, (b) certainty of identity of the whale (any uncertainty automatically gave the measurement grade 6), (c) the straightness of the whale, (d) how parallel 2 whales being compared really were, and (e) how many steps were involved in calculations of lengths from parallel whales. The orientation of the whale to the line between camera and whale was also recorded when recording ratios such as z.

As an example of grading: a measurement made from a well identified whale with its body held straight and perpendicular to the camera-whale line whose endpoints were clearly visible would be graded 1; one which had a small failing in any of these categories might be graded 3, while one which required visual extrapolation to find the endpoints would be graded 6.

Theoretical errors in our method of measuring photographs taken from the air

We considered 5 different sources of errors: (i) errors due to the whale not being beside the disc, (ii) errors due to the long axis of the whale failing to perpendicular to the line joining whale and camera, (iii) errors due to inclination of the whale, (iv) distortion of dimensions of whale due to refraction of light by water, (v) measurement errors. We will consider these in order.

Errors due to whale not being beside the disc

$$\operatorname{co\,sec}\theta = \frac{u}{s} \quad \text{and} \quad \sqrt{\left(\frac{u}{s}\right)^2 - 1} = \cot\theta$$

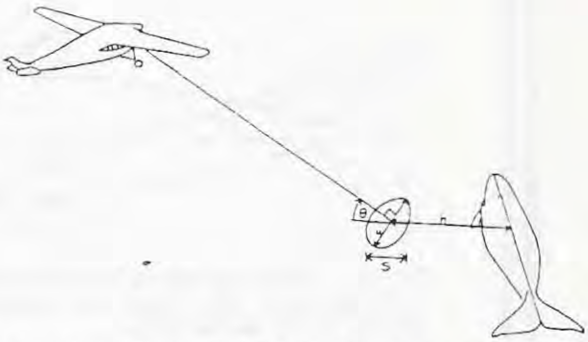

FIG. 9. – Diagram of a plane through camera, disc and whale. The angle between the camera-to-disc line and the water surface is θ.

In our photography $\theta > 30^\circ$, $h < 20$ mm (as 35-mm film was used and the camera was held with the long axis of the frame horizontal) and $v = 300$ mm.

Therefore the correction due to the whale not being beside the disc,

$$\left(\pm \frac{h}{v} \sqrt{\left(\frac{u}{s}\right)^2 - 1}\right),$$

was less than

$$\frac{24}{300} \times \sqrt{3} = .139$$

The errors in this correction were principally due to the whale not lying in the plane of the disc. For often either the disc was tilted when the boat rode over waves, or the whale would be lying beneath the surface. These errors were, we feel, less than 5°. Using $\theta = 35^\circ$ and 25° we have corections of .114 and .172. Thus in the extreme case the error in the calculated length of the whale would be less than about .03 (.172 – .139 = .033) of the true length, or 3 %.

Errors due to yaw of whale

If the whale is yawed in the horizontal plane, and not perpendicular to the line joining the whale and the camera, the true length of the whale (L^1) is given by:

$$L^1 = L\sqrt{\cos^2\beta + \sin^2\beta\,\sin^2\theta} \text{ metres}$$

Where L metres is the calculated length of the whale by the formula in the text, β° is the yaw of the whale in the horizontal plane.

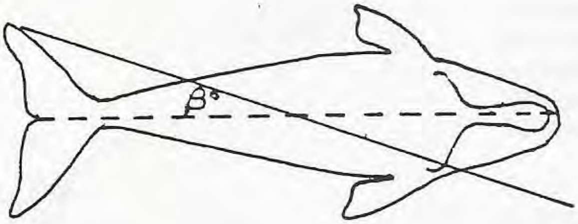

FIG. 10. – Bird's eye view of whale showing angle of yaw. Solid line lies on water surface and is perpendicular to line between camera and the whale.

From this we find that to produce a given error δ % in the calculated whale length, the yaw (β°) needed is given by:

$$\beta = \cos^{-1}\left(\sqrt{\frac{(1 - \delta/100)^2 - \sin^2\theta)}{\cos\theta}}\right)$$

Table 4. Critical angles for α

	$\theta = 80°$	$\theta = 60°$	$\theta = 45°$	$\theta = 30°$	$\theta = 0°$
$\delta = 1.0\%$	$\beta = 54°$	$\beta = 16.0°$	$\beta = 11.5°$	$\beta = 9.4°$	$\beta = 8.1°$
$\delta = 0.5\%$	$\beta = 35°$	$\beta = 11.5°$	$\beta = 8.1°$	$\beta = 6.6°$	$\beta = 5.7°$

Thus, if $\theta = 60°$ and 6 pictures are taken regularly as the aeroplane flies in a semicircle around the surfacing whale, the error due to the whale not being perpendicular to the line between the whale and the camera in the final result, calculated from the "best" photograph, is less than 1 % (the change in β between pictures is

$$\frac{180°}{6} = 30°$$

and so for the "best" picture β is less than

$$\frac{30°}{2} = 15°.$$

Errors due to inclination of whale

Exactly the same theory can be used to calculate the errors due to the inclination of the whale to the water surface in the vertical plane τ, but θ must be replaced by 90 – θ.

Table 5. Inclinations of whales needed to produce given errors in length measurements

	$\theta = 90°$	$\theta = 60°$	$\theta = 45°$	$\theta = 30°$
$\delta = 1.0\%$	$\tau = 8.1°$	$\tau = 9.4°$	$\tau = 11.5°$	$\tau = 16.0°$
$\delta = 0.5\%$	$\tau = 5.7°$	$\tau = 6.6°$	$\tau = 8.1°$	$\tau = 11.5°$

The inclinations (τ) ne[illegible] to produce given errors (δ) are shown in Table 5.

Errors due to refraction

Finally we studied the errors due to refraction, as often the extremities of the whale, between which the measurements are made, will be beneath the water as the photograph is taken.

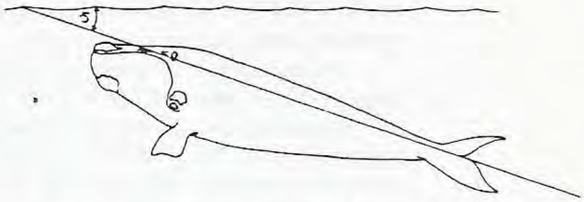

FIG. 11. – Inclination angle of whale to water surface.

The error (δL) due to refraction, in the calculated length of the whale, δ metres below the surface, photographed from m metres above the surface, is given by:

$$\delta L \approx \frac{L\delta}{m}\left(1 - \sqrt{\frac{\sin\theta}{\mu^2 - \cos^2\theta}}\right) \text{ metres,}$$

where μ is the refractive index of water.

The percentage error in the final length of the whale

$$\frac{\delta L}{L} \times 100$$

is given by:

$$\frac{\delta L}{L} \times 100 \approx 100 \, \frac{}{m}\left(1 - \sqrt{\frac{\sin\theta}{\mu^2 - \cos^2\theta}}\right)\%$$

Table 6. Relation of angle of view (θ) to errors in calculated length due to refraction by sea water

% error	$\theta = 90^\circ$	$\theta = 60^\circ$	$\theta = 45^\circ$	$\theta = 30$
$(\frac{\delta L}{L} \times 100)$	0.25 %	0.30 %	0.37 %	0.50 %

Using $\delta = 1.0$ metres, $m = 100$ metres, $\mu = 1.332$, we get the values indicated in Table 6.

This formula is linear in δ and m, so the percent error for the above values of θ can be calculated with different depths (d) and camera heights (m). For instance, if $\theta = 45^\circ$, $d = 2$ metres, $m = 50$ metres, the error in the final length of the whale is approximately

$$.37 \times \frac{2}{1} \times \frac{100}{50} \approx 1.5 \%.$$

In our situation $\theta > 30^\circ$ $d < 2$ metres, $m \approx 100$ metres, and the errors due to refraction are less than 1 %.

Errors in longitudinal aerial measurements of southern right whales

Measurement (our notation) (k)	$\Phi(k)$	$\Psi(k)$
[1]	0.2 %	–
[4]	0.99 %	0.102
[5]	0.82 %	0.091
[6]	2.72 %	0.125
[7]	1.14 %	0.085
[8]	0.85 %	0.094
[9]	20.40 %	0.520

Twenty different whales were used ($i = 1 \ldots 20$). Six different head measurements were considered ($k = 4, 5, 6, 7, 8, 9$) plus the total length of the whale. Each measurement was made 3 times ($j = 1, 2, 3$) for each whale, x_{ij}^k is the jth time the kth measurement was made on whale i:

$$\Phi(k) = \sum_{i=1}^{20} \sqrt{\sum_{j=1}^{3} (x_{ij}^k)^2 - \left(\sum_{j=1}^{3} (x_{ij}^k)\right)^{2/3}} / 20 \operatorname{Sup}_i \left[\sum_{j=1}^{3} (x_{ij}^k)/3\right]$$

Where $\operatorname{Sup}_i \left[\sum_{j=1}^{3} (x_{ij}^k)/3\right]$ is the greatest value of $\left[\sum_{j=1}^{3} (x_{ij}^k)/3\right]$

Let $y_i^k = \sum_{j=1}^{3} x_{ij}^k / \sum_{j=1}^{3} x_{ij}'$

(x_{ij}' is j'th measurement of length-snout tip to fluke notch) (Fig. 12). Then:

$$\Psi(k) = \left[\sqrt{\sum_{i=1}^{20} (y_i^k)^2 - \left(\sum_{i=1}^{20} (y_i^k)\right)^{2/20}}\right] / \sum_{j=1}^{20} y_i^k$$

Φ (k) gives an indication of how accurately the measurements are made. For instance, when making measurement 7 we can expect a measurement error of the order of 1.14 % in each measurement from the true value. A high value of Φ (k) means that the measurement is hard to make, a low value that it is easy. Ψ (k) gives an indication of how closely related a particular measurement is to length. High values of Φ (k) indicate poor correlation, low values a good correlation.

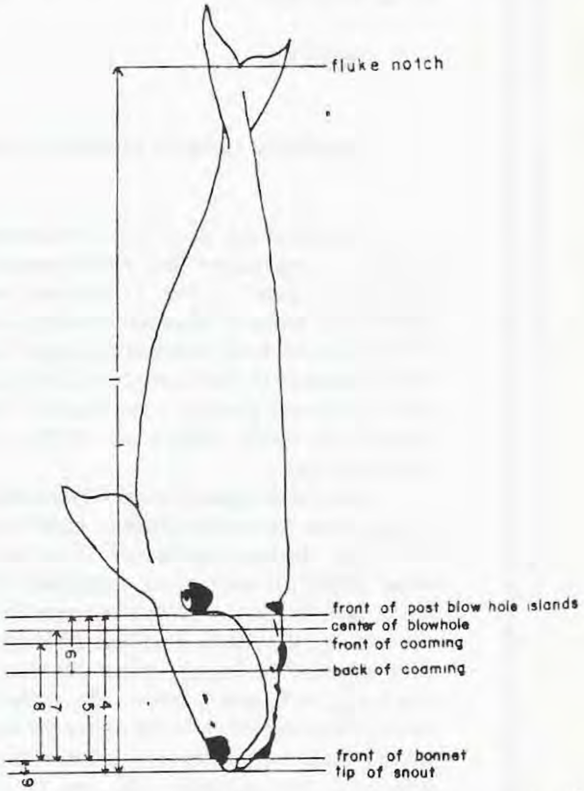

FIG. 12. – Measurements made on aerial photographs of southern right whales.

The α (3 in "Discovery" notation) we use is measurement [7] + measurement [9] and while not directly measured in this survey probably would have Φ and Ψ values close to those of measurement [7], with perhaps Φ a little higher, and Ψ a little lower.

Summary

In the normal case where a circling aeroplane is taking pictures almost continuously, the total error, if $\theta = 30°$, due to errors in correction for the whale not being beside the disc ($< 3\ \%$), the yaw of the whale ($< 1\ \%$), the inclination of the whale ($< 0.5\ \%$) and refraction ($< 1\ \%$) is less than 5.5 % (3 + 1 + 0.5 + 1) and probably around 3 % as these effects will rarely all produce their maximum errors in the same direction at the same time (errors decrease, in general, as θ increases).

Errors due to mismeasurement were reduced by making 3 separate attempts at each measurement and using their mean.

Appendix 2

Regression Lines for Individual Growth Rates

The initial rate of growth of calves was estimated by fitting a regression line which passed through the origin to the points in Fig. 4 (as no calf would grow an appreciable amount instantaneously). Lines using the best data (with both endpoints Grade 5 or better), the worst data (one or both endpoints Grade 6), and all the data, agree very closely – the slopes of these lines are respectively .00255, .00253 and .00253 of the mothers' length per day.

As a check against bias a regression line was fitted to the points but not artificially made to pass through the origin. The intercept was .0033 on the y axis and the slope .00242, a very close agreement with the lines which were made to pass through zero (see Fig. 4).

In Fig. 4 it can be seen that 20 whales appear to be growing and 9 shrinking; that is 20 points lie above the line $L_c/L_m = 0$, and 9 below. The probability of 20 or more points, out of 29, being above the line if they were equally likely to fall above or below it (a situation of no growth) is approximately .02, i.e., the probability of obtaining this or more significant data when the whales were not growing is about .02. We therefore conclude that significant growth is shown (at the 5 % level).

Appendix 3

Methods Used in Obtaining Growth Curve

Huxley (1932) determined experimentally that 2 different dimensions of animals (x and y) tend to be related as:

$$y = bx^a \tag{7}$$

Ohsumi (1960) found that for balaenopterids the constants a and b are, in general, different for the different growth stages (such as birth to weaning, or weaning to physical maturity). Plotting Log x against Log y, Huxley's formula [7] is a straight line, of slope a, and an intercept Log b. This relationship is called by Ohsumi the "allometry formula".

We considered the allometry formula of α and L for those whales where both α and L had been measured. Where just one of them was present we combined it with a calculation of z from another frame taken in the same year. In this category we had a total of 17 known whales and 24 unknown whales (one whale, No. 156, is plotted in 2 different years).

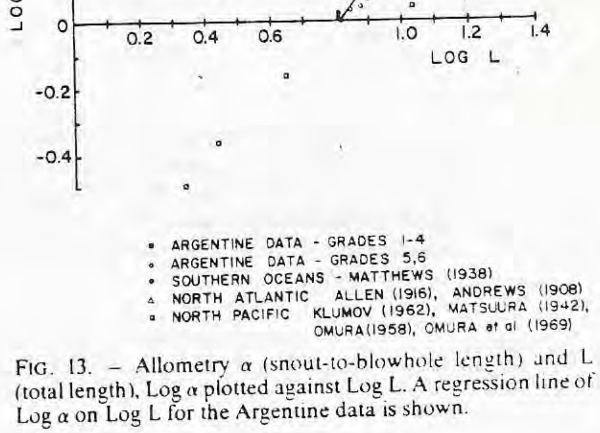

FIG. 13. – Allometry α (snout-to-blowhole length) and L (total length), Log α plotted against Log L. A regression line of Log α on Log L for the Argentine data is shown.

In Fig. 13 we have plotted Log α against Log L as Ohsumi (1960) did for fin whales. Also plotted are measurements of right whales given in the literature. There seem to be only 5 measurements of α and L for the southern right whale in the literature (all are from Matthews, 1938). We have, therefore, added in values for North Pacific right whales, of which we know of 27, and North Atlantic right whales, of which we know of 2. There seems to be little variation in the value of L for any given α between the different species (or subspecies as some would have it), or the sexes. We feel that the validity of our technique of determining α and L from photographs is strongly supported by the good agreement between our values and those from the literature.

One pair of measurements from Klumov (1962) ($L = 10.75$ m, $\alpha = 1.1$ m) appear to be mismeasured.

The points for non-foetal whales appear to lie on a straight line, which, for the Argentine data, we have estimated to be (using linear regression):

$$\text{Log } \alpha = 1.376, \text{ Log L} = -1.127$$

Which gives:

$$z = 7.46 \times L^{0.376} \,\% \; (z = \alpha / L \times 100 \,\%)$$

Correlation coefficients (r) were calculated for different sets of data, as shown in Table 7:

Table 7. Correlation coefficient (r) for different sets of data, for Log α and Log L

	No. points	r
Argentine data (all grades)	40	.970
Argentine data (grades 1-4)	18	.973
Argentine data (grades 5-6)	22	.962
Southern Oceans (literature)	5	.987
All literature[1]	28	.964

[1] Note including data on foetuses or Klumov's doubtful measurement.

α Snout-to-blowhole length.

L Total length.

The best measurements (grades 1-4) are only slightly better correlated than the worst measurements (grades 5-6) indicating that the deviation from the regression line is mainly due to variation between individuals and not to measurement errors.

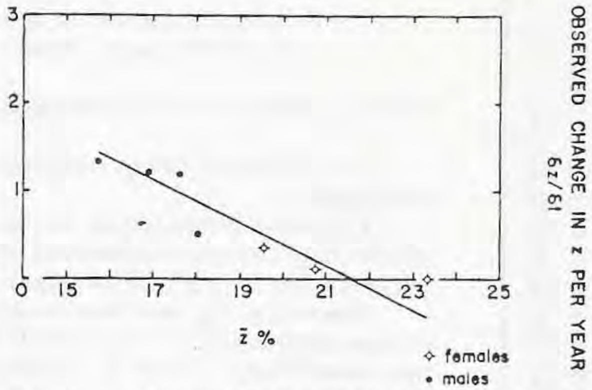

FIG. 14. – Changes in z for A quality data. From a known whale two estimates of z are made, z_1 % in year t_1 and z_2 % in year t_2 and then

$$\bar{z} = \frac{z_1 + z_2}{2}, \quad \frac{\delta z}{\delta t} = \frac{z_1 - z_2}{t_1 - t_2}$$

Points representing $\bar{z}$ and $\delta z / \delta t$ for 7 pairs of measurements are given and a regression line is drawn through the points.

In Fig. 14 we have plotted the change in z per year

$$\left(\frac{\delta z}{\delta t}\right)$$

against the mean value of z in the intervening period ($\bar{z}$)

$$\bar{z} = \frac{z_1 + z_2}{2}$$

Where a whale was measured as z_1 at time t_1 and as z_2 at time t_2 then:

$$\frac{\delta z}{\delta t} = \frac{z_2 - z_1}{t_2 - t_1} \; \% \text{ per year.}$$

The points entered in Fig. 14 were graded as follows:

Grade A –	both measurements of z better than grade 5 and made with the whale perpendicular to a line between the camera and the whale
Grade B –	each measurement of z either better than grade 5 and within 15° of being perpendicular to the line between camera and whale (angle estimated by eye) or grade 5

or 6 and perpendicular to the line between the camera and the whale

Grade C – other pairs of measurements.

Plots of Grade C are so widely scattered as to be meaningless.

Regression techniques are not theoretically applicable since errors in measurement of either z_1 or z_2 will produce an error in both $\bar{z}$ and $\delta z/\delta t$.

However, in Fig. 14 we have attempted to fit a line to these points as follows: we used only the most accurate measurements – Grade A – to minimize the effect of measurement errors.

The variation of the plots due to individual differences between whales can be looked at in 2 ways:

Case 1 – different whales with the same value of z may have this ratio (z) growing at different rates;

Case 2 – different whales with the same rate of growth in z ($\delta z/\delta t$) may have different values of z.

If we interpret Fig. 14 as Case 1 we would have to use regression of $\delta z/\delta t$ on $\bar{z}$, while if we interpret it as Case 2 we would use the regression of $\bar{z}$ on $\delta z/\delta t$.

Included in data of Grade A there is a whale with $\bar{z}$ = 23.23 %, a value which most whales probably never attain and so it seems more reasonable to use Case 2, i.e., the regression of $\bar{z}$ on $\delta z/\delta t$.

Table 8. Selecting between Case 1 and Case 2

Case	Slope	($\delta z/\delta t = 0$)	($\delta z/\delta t = 1$)	r
Case 1 ($\delta z/\delta t$) on $\bar{z}$	-0.1980	22.28	17.23	0.905
Case 2 $\bar{z}$ on ($\delta z/\delta t$)	-4.138	21.66	17.53	0.905

The maximum value of $\bar{z}$ is when $\delta z/\delta t$ = 0 and is given in the table above. We can convert these into maximum theoretical lengths using the regression line obtained from our data in Fig. 13:

$$z = 7.46 \times L^{.376} \,\% \qquad (1)$$

In the case of the regression line for $\bar{z}$ on $\delta z/\delta t$ the maximum length ($\delta z/\delta t$ = 0) would be 18.36 m while for the regression of $\bar{z}$ on $\delta z/\delta t$ the maximum length would be 17.04 m. This latter seems more reasonable on the basis of the greatest lengths of southern right whales given in Table 9, and the line for Case 2 gives equation (2).

Unfortunately at present there is not enough data to draw separate regression lines that are meaningful for each sex.

Table 9. A summary of maximum and minimum lengths of right whales (m)

Source	Total whales measured	Known whales measured	Maximum male length	Known females measured	Maximum female length	Calves measured	Min. calf. length measured	No. of foetuses measured	Largest foetus measured
SOUTHERN OCEANS									
Our data - alive	41	3	12.37	12	15.56	12	6.35		
Our data - dead						1	4.11		
Lonneborg, 1906	3	2	15.21					1	4.19
Committee for Whaling Statistics, 1938				4	15.55			4	6.02
Matthews, 1938	5	2	13.54	2	15.23	1	6.54	2	15.23
NORTH ATLANTIC									
Various sources summarized in Omura, 1958	12	2	12.93	8	16.46	2	8.48		
NORTH PACIFIC									
Omura, 1958	4	2	13.60	2	17.80				
Omura *et al.*, 1969	13	6	17.10	5	16.10			2	2.70
Klumov, 1962	10	5	17.06	5	18.30			1	4.40

Appendix 4

Confidence Limits for Growth Curves

For early growth (0-0.5 year) there are 2 possible sources of error: (1) our estimates of the length at birth and (2) the estimate of the initial rate of growth. We have estimated 95 % confidence limits for the length at birth to be 5.0-6.0 m or ± 0.5 m. 95 % confidence limits for the initial growth rate can be found from the data in Fig. 4 and the standard formulae for the confidence limits in the slope of a regression line which is made to pass through the origin:

$$\pm\, t_{n-1}\,(0.05)\sqrt{\frac{\sum_{1}^{n} y_i^2 - (\sum_{1}^{n} x_i y_i)^2 / \Sigma x_i^2}{\sum_{1}^{n} x_i^2\,(n-1)}}$$

Where n is the number of data points.

(x_i, y_i) are the data points

t_{n-1} (0.05) is the 2-sided, 0.05 significance point of the student's t distribution with $n - 1$ degrees of freedom.

These limits were ± 8.19 m/year in this case. So our confidence limits for the initial growth curve become:

$$\pm \sqrt{(0.5)^2 + (8.19\,t)^2}\ \text{metres,}$$

where t is the age in years. These are the confidence limits shown in Fig. 6 for the initial growth.

As there are checks for the calculated initial growth curve (the growth by month, and the mean length of calves measured in November), which were not taken into account in these calculations, the confidence limits are almost certainly conservative.

For the later growth stages, the errors in the formula for growth in L and z (equations (5) and (6)) were broken down into 3 possible sources: errors in the regression of z on $\delta z/\delta t$, errors in the regression of Log α on Log L, and errors in the estimation of the constant t_k.

The standard error, ρ, in the height of the regression line of y on x at x is given by:

$$\rho = \sqrt{\frac{\left[\sum_{1}^{n} (y_i - \bar{y})^2 - \left(\sum_{1}^{n} (y_i - \bar{y})\ (x_i - \bar{x})\right)^2 / \left(\sum_{1}^{n} (x_i - \bar{x})^2\right)\right]}{n - 2}\left(\frac{1}{n} + \frac{(x - \bar{x})^2}{\sum_{1}^{n} (x_i - \bar{x})^2}\right)}$$

Where n is the number of data points,

(x_i, y_i) are the data points,

x and y are the means of x_i and y_i.

For the regression of z on $\delta z/\delta t$, the maximum value of ρ in the range $\delta z/\delta t$ we are considering, was 0.743.

Thus $\bar{z} = -4.138\ \delta z/\delta t + 21.66 \pm .743$ (from (2)) for 1 standard error in this regression. For these limits new growth formulae for z and L were constructed and the errors in z and L for different values of t found. These errors are shown in Table 10.

Similarly we found the errors in the regression of Log α on Log. L.

t_k was fixed by the measurement of whale No. 156 at 9.9 m on 21 November 1973, when he was assumed to be 1.2 years old. This procedure introduces 3 sources of error:

(1) errors due to whale No. 156 not being of average size;

(2) errors in measuring whale No. 156 on 21 November 1973;

(3) errors due to whale No. 156 not being 1.2 years old on 21 November 1973.

The standard errors from these 3 sources were estimated at (1) 0.5 m (at a length L of 9.9 m), (2) 0.22 m (L = 9.9 m) and (3) 0.1 years (when t = 1.2 years). The errors in length can be converted into errors in time from equation (4) and the 3 errors can be combined to make a total standard error in t_k of ± .39 years.

The corresponding errors in L were calculated and are shown in Table 10.

If the standard errors in the regression of $\bar{z}$ on $\delta z/\delta t$, Log α on Log L, and the estimation of t_k are denoted by e_1, e_2, and e_3 respectively, 95 % confidence limits for the errors in the growth curves (equations (5) and (6)) were approximated by:

$$\pm\, 1.96\sqrt{e_1^2 + e_2^2 + e_3^2}$$

These values are shown in Table 10 and also as the confidence limits in Figs. 6 and 7.

Table 10. Summary of errors in growth curves

Age (years)	Error arising from: Regression of $\bar{z}$ on $(\delta z/\delta t)$ (e_1)	Regression of Log α on Log L (e_2)	Estimation of t_k (e_3)	95 % confidence limits for errors $1.96\sqrt{e_1^2 + e_2^2 + e_3^2}$
		In length curve (Fig. 6)		
	± (m)	± (m)	± (m)	± (m)
1	.05	.04	.57	1.12
2	.22	.06	.49	1.06
3	.45	.15	.41	1.23
4	.66	.28	.34	1.55
5	.84	.45	.27	1.94
7	1.10	.71	.17	2.59
8	1.31	.99	.09	3.29
		In z curve (Fig. 7)		
	± %	± %	±	± %
1	.04	.28	.39	.94
2	.14	.22	.31	.79
3	.27	.17	.24	.78
4	.36	.13	.18	.83
5	.45	.11	.15	.95
7	.55	.06	.09	1.10
10	.66	.03	.05	1.30

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