

## Population Size, Trends and Reproductive Parameters of Right Whales (*Eubalaena australis*) off Peninsula Valdes, Argentina

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### ABSTRACT

Photo-identification of individual whales, based on natural markings, has been used to study a population of southern right whales, *Eubalaena australis*, on their winter assembly grounds around Peninsula Valdes, Argentina. Right whales have raised patches of roughened skin (callosities) on their heads. The pattern of callosities differs between individuals. This enables known individuals to be monitored over time. Photographs of individual whales have been obtained from aerial surveys conducted each year between June and December from 1971 through 1986. A total of 909 distinct individuals were identified over the period, of which 481 were identified in more than one season. These data have been used to estimate various population parameters. The mean calving interval is estimated to be 3.6 years (95% confidence interval 3.3 to 4.1 years). It is estimated that there were 99 (SE 18) calvings in the population in 1986, which implies a total population of about 1,200 in that year. The population is estimated to be increasing at a rate of 7.6% p.a. (SE 1.7%). These estimates should be treated with caution until the validity of the underlying assumptions has been verified.

### INTRODUCTION

Individual southern right whales (*Eubalaena australis*) can be identified by raised patches of roughened skin (callosities) on the dorsal surface of their heads. The number, size, shape and position of callosities differs among individuals and appears to undergo only minor changes over time; furthermore the variability in the patterns is sufficient in principle to uniquely identify each individual in a population of billions (Payne, Brazier, Dorsey, Perkins, Rowntree and Titus, 1983). Fig. 1 shows an example of a whale photographed in 1971 and again in 1986.

Natural markings such as these have a number of advantages over artificial marking of individuals as a means of studying populations, including: (i) they do not have to be installed (which saves both animals and biologists considerable stress); (ii) they are easily visible in the field at reasonably large distances, making collection of data feasible from aircraft, etc; (iii) since identification of the tag does not involve killing the animal as is the case for some artificial marks, e.g. Discovery marks, the same individual can be resighted many times during its life; (iv) they do not interfere with locomotion or behaviour; (v) they appear to be retained throughout life; (vi) they provide plenty of redundancy in confirming the identity of an individual; (vii) last but not least, they leave little doubt over the number of individuals effectively marked. The latter point is especially important with respect to population estimation, where a common problem with 'Discovery' tagging is to know how many animals have been effectively tagged (e.g. see Buckland and Duff, 1989). The 'tagging' of a naturally marked animal involves the taking of a photograph. For the purpose of a given piece of analysis, the effective number of tags placed is

simply the number of photographs of adequate quality received; the date and location of each photograph are the only additional information required. Thus it is feasible to perform an analysis on data gathered from a variety of sources even when the field data have not been collected in carefully controlled circumstances.

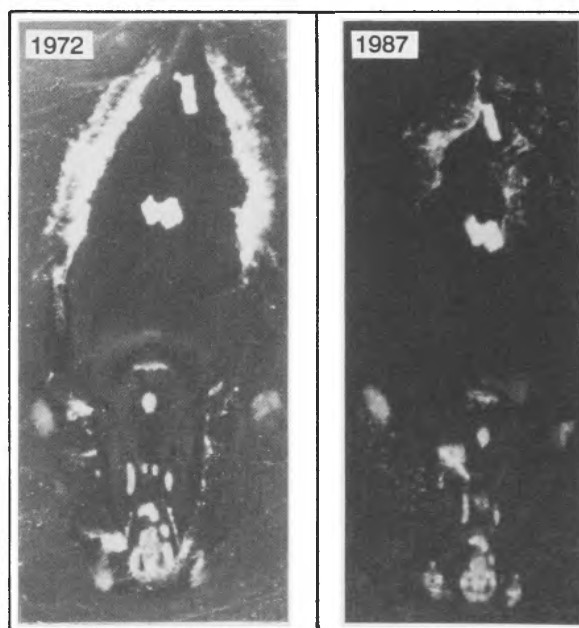


Fig. 1. Photographs of an individual taken in 1971, and the same individual photographed in 1986, showing the features used to identify the individual.

In the 18 years of this study, 909 individual whales have been identified and 481 have been identified in more than one season. In this paper, the data on identification and resightings of individuals are used to obtain preliminary estimates of some demographic parameters.

## MATERIALS AND METHODS

### Study site

The study site is the area surrounding Peninsula Valdes, Argentina (Fig. 2), where right whales are found between June and December every year. Calves are born there during this period. At the Peninsula, the whales concentrate along three different regions of the shoreline (Payne, 1986). We have collected data here every year since 1970 and the study is continuing. Between 1971–86, 87 aerial surveys were conducted during which individuals were photographed for identification. The number of flights per year has decreased during the course of the study, owing to the increasing cost of flying time. Fig. 3 shows the dates when flights were made. There was a minimum of two flights per year. The three regions in which the whales are most highly concentrated were surveyed at least once each year. There has been a tendency in recent years to focus survey effort on those areas where mother-calf pairs are common.

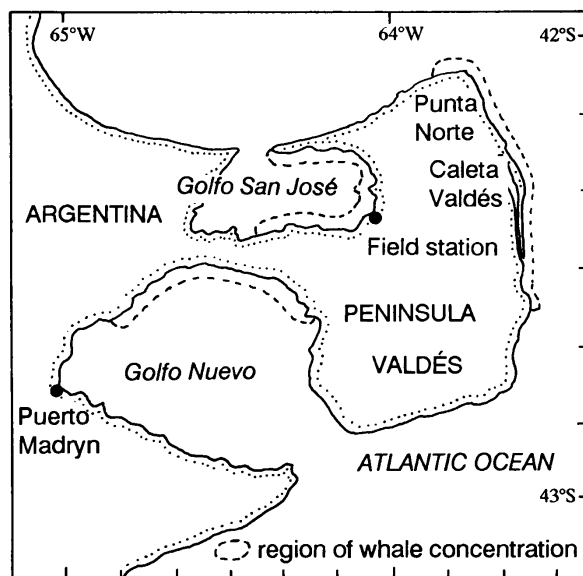


Fig. 2. Peninsula Valdes, Argentina showing, by hatching, the principal areas of right whale concentration from mid-June to mid-November. The New York Zoological Society field station from which studies are carried out is also indicated. (Taken from Payne *et al.*, 1983).

### Aerial procedure and photography

Most flights were made in a Cessna 182 single engine, high-wing aircraft. Most of the whales are found along the 5m depth contour (Payne, 1986), so that flights are usually within 2km of the tide line. There are a few whales in the middle of the bays, but flights over open water in a single engine plane are prohibited. The procedure is to fly at an altitude of 100–200m along the coast of the peninsula while searching for whales. When whales are sighted their location is recorded, the plane circles at 100m,

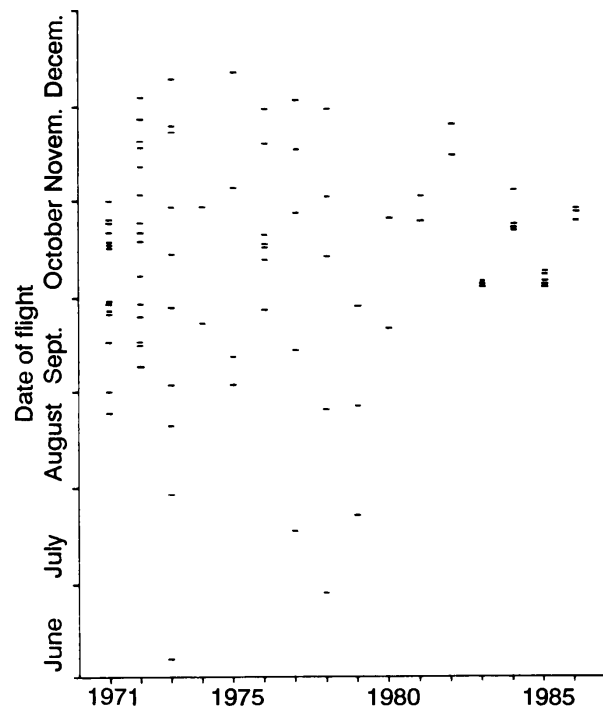


Fig. 3. Dates of each flight 1971–86.

photographs are taken and the number of whales seen determined and recorded. Usually most of the whales encountered are photographed. Some whales surface only briefly (those making a transit) or stay underwater for long periods of time. If, after 4 or 5 circles, we have been unable to obtain photographs, we abandon the whale.

Most photographs are taken at a shutter-speed of 1/500th of a second or faster, using 300mm lenses on motor driven 35mm single-lens reflex cameras. There is an unavoidable trade-off between the speed of the film (to compensate for vibrations in the airplane and occasional low light levels) and the fineness of its grain (to ensure as much detail as possible in the outline of the callosity-pattern). We have used both black and white film (Kodak Plus-X) and colour film (Kodachrome 64 and Ektachrome 200). Callosities can more easily be distinguished from white-water splashes in colour images than in black and white, so in recent years we have used colour films exclusively. Some photographs were taken with a gyrostabilising unit attached to the base of the camera, but they were not of significantly higher quality than those taken with a hand-held camera.

The photographer sits behind the pilot so that they both look out of the same window; thus when the pilot maximises his view of the whales he does the same for the photographer. Whenever possible the closest approach is made such that the whale is head-on to the plane and the plane is between the sun and the whale. It is important to photograph the whales from in front because much of the callosity variability occurs at the anterior end of the rostrum and is less visible in a rear view. The best pictures are taken when the dorsal surface of the whale's head is above the water as the whale surfaces to breathe. Where possible we take several pictures of each individual, striving particularly for motor drive sequences in which the shutter release is depressed for several frames. This removes the inevitable motion of the camera when pressing and releasing the shutter and makes those pictures in the

middle of the motor drive sequences steadier than the first and last frames of the same sequence. Furthermore, the callosity pattern is often obscured partly or wholly by foam and/or specular reflections of sunlight. The pattern is also subject to distortion by refraction from overlying waves when seen through the water. By taking a series of photographs of the whale as it surfaces, identifications can be based on those features present in two or more photographs from different angles. After every sequence of photographs, a 'blank' is taken of some identifiable object to avoid ambiguity in later analysis.

#### Analysis of aerial photographs

The sequence of photographs of a whale's head is analysed to determine the pattern of its callosities. Once the pattern is determined, it is compared to the current collection of known whales, which is organised into a catalogue containing the best single photograph of the callosity pattern of each individual. In making a match it is often necessary to compare other photographs from files of the whale in the catalogue to the sequence of photographs of the individual in the film being analysed. In the initial film analysis, each whale photographed is recorded as being either (1) a match with a whale found in the catalogue, (2) a new whale not existing in the catalogue or (3) unidentifiable. All new whales in a year are compared with each other to determine that there are no duplicates. An identification as a match or a new whale is confirmed by another researcher experienced with right whale identification, and any conflicting opinions are resolved before an identification is accepted. New whales are then added to the catalogue. Each identification is graded on a scale of A (excellent) to D (marginal) for certainty of identity and the best photograph in each sequence of photographs of each whale is graded for quality of the photograph using the same scale.

One record is kept for each whale that has been identified. The record contains the whale's identification number from the catalogue, and, for each year in the study, the number of times the whale was identified, and whether it was accompanied by a calf. Occasionally the calf itself can be identified; these are recorded and provide a valuable, if small, sample of known-age individuals. However calves are usually difficult to identify in their first three months of life because the callosity area on the head is often obscured by a species of cyamid that is not confined to the callosity tissue. As a result only a minority of calves

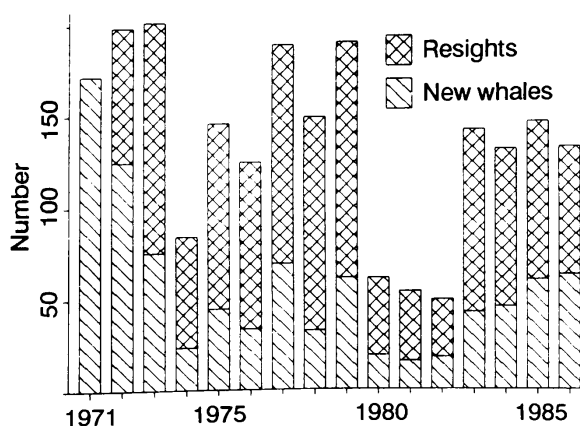


Fig. 4. Number of whales identified each year, divided into 'new' whales, and whales resighted from previous years.

can be entered into the catalogue in their year of birth. Fig. 4 shows the number of whales identified in each year, divided into 'new' whales and resightings of whales identified in previous years.

Each record also contains an indication of whether the animal is known to be male, female or if, as in about half the animals, the sex is unknown. The sexing method is described by Payne *et al.* (1983). As currently compiled, the data base does not indicate in which year the animal was sexed. Since the probability of sexing an animal is a function of the number of times it is seen, stratification of analyses by sex, where known, would result in an extremely complex problem of inference. Therefore, the sex information was not used in the analyses that follow.

## ANALYSES AND RESULTS

### Calving interval

Fig. 5 shows the distribution of observed apparent intervals between calvings. By far the most common inter-calf interval is three years; intervals less than this are rare. However, whales may not always be seen each year they have a calf and thus it is not clear how many of the longer intervals are 'real' and how many are the result of missed calvings. Furthermore, the large variation in annual sample sizes and the fact that we observe only a window in time, means that the apparent frequencies in Fig. 5 will be distorted by the unequal numbers of opportunities to observe different lengths of interval.

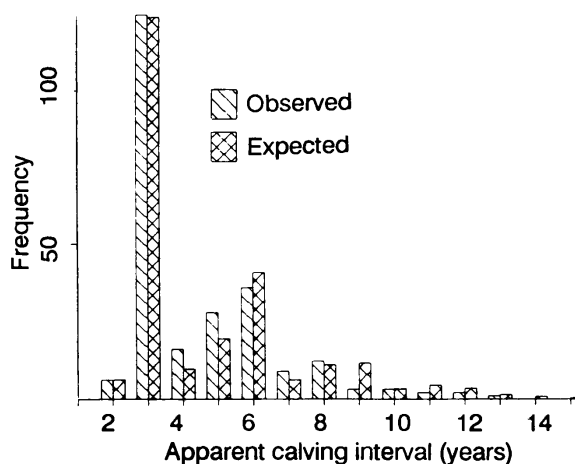


Fig. 5. The distribution of observed intervals between known calvings of individual whales. See Appendix for an explanation of the 'expected' distribution.

Barlow (1990) presents a method for estimating the frequency of different birth intervals in a population from photo-identification data. The method makes use of data on the years in which each identified whale was seen with a calf, and the years in which it was seen without a calf. It depends on the assumption that a given whale in a given year is equally likely to be seen whether or not it has a calf and that if it is seen in a year in which it has a calf, then it is also recorded as having a calf.

There are two major problems with using Barlow's method with these data: (1) as noted by Payne (1986), the breeding females in this population appear in the study area mainly in years when they have calves and less so in intervening years; and (2) it cannot be proved that calves

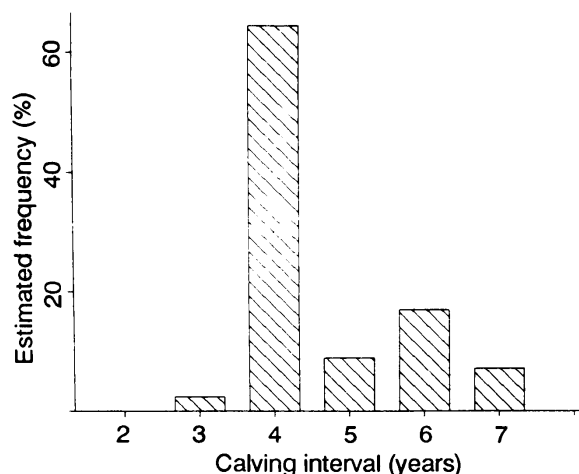


Fig. 6. Estimated relative probabilities of different inter-birth intervals for breeding females.

are always recorded even if the mother is seen. The event 'a calving is recorded' means that the mother is identified and is seen to be accompanied by a calf.

We therefore developed our own model for interpreting these data. This is described in the Appendix, it makes use only of identifications of whales with calves. The main assumptions of the model are that: (i) the probability that a random calving in a given year will be recorded is independent of whether that whale's previous calving was recorded; (ii) the probability that a whale will calve in a given year is a function only of the time elapsed since its preceding calving, if any, and not the time elapsed since calvings previous to the immediately preceding calving (i.e. successive calvings of an individual form a Markov chain). Further, less critical assumptions about survival rates are detailed in the Appendix.

Fig. 6 gives the resulting estimates of the relative frequency of different birth intervals. The mean calving interval is estimated at 3.63 years with a 95% confidence interval of 3.27 to 4.09.

Fig. 7 shows the observed ratio of calves to other whales sighted each year. There is a considerable increase in the proportion of calves over the period. While this may suggest an increase in the calving rate, it may also simply reflect a tendency to concentrate the sampling effort on the

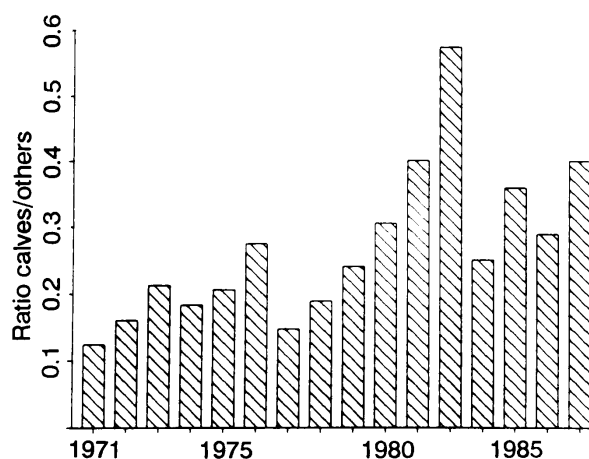


Fig. 7. Observed ratio of calves to identified non-calves by year.

areas or periods in which mother-calf pairs predominate in the later years. If the observation is due to a real increase in the calving rate, then this would imply a decrease in the mean calving interval. Since the bulk of calving intervals are in the range 3–5 years, one would expect a decrease in mean calving interval to be reflected in a tendency for 4- and 5-year intervals to become relatively less common with time compared with the 3-year intervals.

The analysis of the data for possible trends in these frequencies detailed in the Appendix reveals no significant trends. There is even a non-significant increasing trend in the relative frequency of 4- and 5-year intervals and hence in the mean calving interval. It can therefore be concluded that the apparent increase in calving rate is not real.

#### Age at first calving

As noted earlier, a small number of calves could be entered into the catalogue in their year of birth. This provides a sample of known age individuals from which information on the year of first calving can be obtained. Because new calves are being added to this sample every year there are relatively more observations of known age animals in younger than in older age classes. Surveys began in 1971 and thus the maximum known age in 1986 was 15 years.

Fig. 8 shows the distribution of age at first known calvings of known age individuals that have calved. The minimum age at first calving is 7 years. Because inter-calf intervals less than three years are rare, it can be assumed that the apparent first calvings at ages 8 and 9 are also genuine first calvings. Given that we estimate that about half the calvings in the later years have been missed (Fig. 10), some or possibly all of the remainder of apparent first calvings will be second or subsequent calvings.

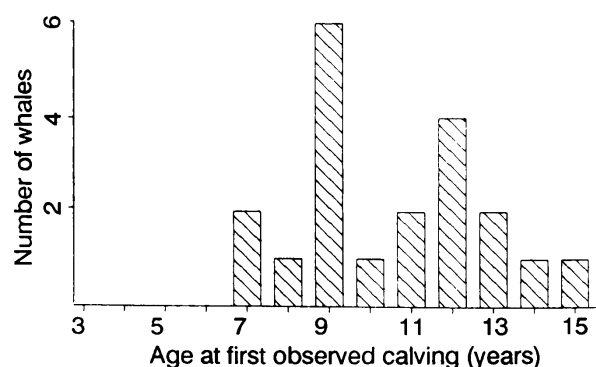


Fig. 8. Distribution of age at first known calving of known-age individuals.

The data suggest that the majority of first calvings may occur at 9 years of age, while the subsidiary peak at age 12 represents second calvings, but sample sizes are too small to draw any definitive conclusions. In principle a model could be developed to estimate the proportions of apparent first calvings at each age that are genuine, but in view of the small numbers it does not seem worth doing so at present.

Provided that the study is continued, sample sizes of known age animals in the key age classes will accumulate rapidly over the next few years, enabling more precise estimation of the mean age at first calving.

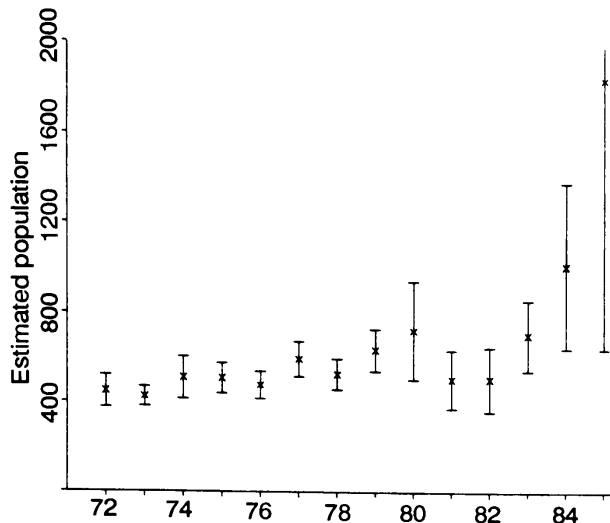


Fig. 9. Estimates of population size by year 1972–85 using the Jolly-Seber 3-sample method. Error bars are two estimated standard errors each side of the estimate (actual 95% confidence intervals would be asymmetric).

#### Population size and trends

Estimates of the total population size and the numbers of known females by year were obtained in an earlier paper from the first six years of this data set (Whitehead, Payne and Payne, 1986), using the Jolly-Seber three-sample method (Seber, 1982).

Updated estimates of the total population (excluding calves) using the same method are shown in Fig. 9. However, these estimates should be treated with caution, because some of the assumptions of the method are known to be violated. A key assumption of the method is that the probability that a random individual is sampled in a given year is independent of whether it was sampled in previous years.

Because the raw apparent calving rate of the population (Fig. 7) is greater than the calving rate implied by the estimated mean calving intervals in the preceding section, we know that the samples are biased towards calving females. Furthermore, this bias increases in the later years, so that estimates of trends in population size as well as estimates of absolute population size from the Jolly-Seber method will both be biased.

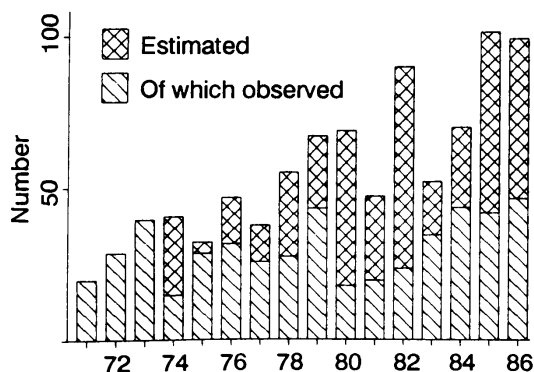


Fig. 10. Estimates of numbers of calvings occurring in the population by year 1974–86, using the method described in the Appendix. The portion of the estimated number that was actually observed in each year is also shown. No estimates are available for 1971–73: observed numbers only shown.

The reason why the estimates for the final two years are so much higher than the estimates for all other years is that the samples in the later years consist mainly of calving females which tend not to be resighted in the two years following a sighting. Since the population estimates are inversely related to the return rates, estimates of population size one or two years before the end of the data series will be biased upwards relative to previous estimates. This effect biases the trend in all other years to some extent, albeit less dramatically.

The tendency of females to return at 3-year intervals can also be viewed as a violation of the assumption of the Jolly-Seber method that animals do not emigrate from the population to return later.

If we restrict attention to the calving population, the method described in the Appendix, with its somewhat weaker assumptions, can be used. The estimated number of animals calving in each year using that method are shown in Table 1 and Fig. 10. Because the estimates are based on records of repeat calvings of females previously observed to calve, the method does not provide estimates for the first three years of the study.

Calculation of standard errors of these estimates is laborious and has only been done for the final (1986) estimate. Since the estimates in different years have considerable covariances, a simple regression of these estimates against time would not necessarily provide a valid estimate of the rate of change. The annual rate of change is estimated by the method described in the Appendix to be 7.6% (SE 1.7%).

Table 1

Observed and estimated number of calvings in the population.

| Year | Obs. | Est. | SE | Year | Obs. | Est. | SE |
|------|------|------|----|------|------|------|----|
| 1971 | 20   | —    | —  | 1979 | 44   | 66   | —  |
| 1972 | 29   | —    | —  | 1980 | 18   | 69   | —  |
| 1973 | 40   | —    | —  | 1981 | 20   | 48   | —  |
| 1974 | 15   | 41   | —  | 1982 | 24   | 90   | —  |
| 1975 | 29   | 33   | —  | 1983 | 35   | 52   | —  |
| 1976 | 32   | 48   | —  | 1984 | 44   | 70   | —  |
| 1977 | 26   | 38   | —  | 1985 | 42   | 101  | —  |
| 1978 | 28   | 56   | —  | 1986 | 47   | 99   | 18 |

#### DISCUSSION

Assumption (i) of the method may be violated in several ways. Firstly, the classification of photographs or photo-sequences of whales into 'match', 'new' and 'unidentifiable' is done in the following way: an attempt is made to match the photograph with one in the catalogue; if no match can be found, it is either entered into the catalogue as a new whale or discarded as unidentifiable. This procedure does not guarantee that whales that in reality match a whale in the catalogue are equally likely to be considered identifiable as are those which in reality are 'new' whales. Hence the assumption that the probability that a calving whale is identified in a given year is independent of whether it was identified in a previous year may not be justified. Secondly, some whales may be intrinsically more likely to be identified than others, due to their behaviour, calving date or migrational habits. To some extent this can be ascertained from the data themselves.

A further implicit assumption of the method is that all classifications of whale sightings into 'matches' and 'new' whales are correct. We have some evidence that some matching whales have been incorrectly classified as new, and it cannot be ruled out at this stage that some new whales have been incorrectly classified as matches. While the frequency of errors is thought to be low, a final judgement on this must await an appropriate analysis. Furthermore, the probability of errors of either type may be a function of catalogue size, since each new photograph or photo-sequence has to be compared with every whale in the catalogue. This could bias any apparent trends with time, such as the trend in population size.

The assumptions of the model are likely to be more seriously violated for the 'non-calving' segment of the population, because of its inhomogeneous composition. It comprises subadults of either sex, adult males, and adult females which have not yet been observed to calve. It would not be safe to assume *a priori* that the frequency of returns of subadults to the study area are independent of age. Hence no attempt has been made here to analyse these components of the population directly. It might be possible after recompilation of the data to perform analyses on subsets of the population of known status such as adult males. Otherwise, it may be necessary to wait until a larger sample of known age animals has accumulated.

If the mean age at first calving is 8.5 years then, assuming a stable age structure and a 50:50 sex ratio, we would expect 27% of the population to have had a calf if there is no mortality, and a lower proportion if there is mortality occurring. The estimate of 99 calvings in 1986 corresponds to an estimated population of females who have calved by 1986 of 320 assuming the estimated mean calving interval of 3.63 to be correct. (It is not a simple product of the numbers calving in 1986 and the mean calving interval, because of the effect of the increasing trend in the calving population.) This corresponds to a total population of 1,190 (more if mortality is occurring).

The calf production rate estimated from the mean inter-calf interval could generate an annual population growth rate of 7.6%, in the absence of immigration, only if the mortality rate is low enough. If mortality occurs equally at all ages, the annual rate would have to be less than 0.6%. If mortality occurs in the first year of life only, a value of up to 9.5% would be consistent with the observed rate of increase. A total of 12 dead calves have been observed during the period 1981–85, which places a lower bound on calf mortality of about 3%.

A low mortality rate does not necessarily imply an unreasonably long life span if the population is increasing. For example, even if no animal lived beyond 35 years of age, the annual mortality rate in a population with a stable age structure growing at an annual rate of 7.6% would be only 0.6% provided there was no mortality before this age. If it is growing as fast as it appears to be, the current population is too young to provide much information on lifespan.

The apparent rate of increase in the population could be exaggerated if there is net immigration from other calving areas in the southwest Atlantic, or if the interchange with other calving areas has been increasing even if there has been no net immigration. Furthermore, the possible biases

mentioned above relating to the identification process may also bias the apparent rate of increase especially if they are related to catalogue size. Thus the estimate should be regarded as provisional until these factors have been further investigated.

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# Appendix

## A MODEL FOR ESTIMATING CALVING INTERVALS AND RELATED PARAMETERS

Let  $p_j$  be the probability that a calving in year  $j$  is recorded and  $h_j$  be the probability that a female that calved in year  $m$  will have its next calf in year  $m+j$ , conditional on its survival to year  $m+j$ . Let  $j_{\max}$  be the maximum calving interval, so that:

$$\sum_{j=1}^{j_{\max}} h_j = 1$$

Let  $q_j$  be the probability that a whale which calved in year  $m$  also calves in year  $m+j$ , conditional on its survival to year  $m+j$ . The  $q_j$  are related to the  $h_j$  by the relations:

$$q_j = \sum_{i=1}^j h_i q_{j-i}$$

where  $q_0 = 1$ .

Conditional on  $n_i$ , the number of calvings recorded in year  $i$ , the expectation of  $n_{ij}$ , the number of whales recorded to calve both in year  $i$  and in year  $j$ , is:

$$E(n_{ij}) = n_i p_j q_{j-i} s_{j-i} \quad (j > i) \quad (1)$$

where  $s_k$  is the probability that a whale calving in year  $m$  survives to year  $m+k$ .

To simplify the calculations, the model can be fitted as if the  $n_{ij}$  had a Poisson distribution about their expectation, even though this leads in theory to some overestimation of variance compared with the more realistic binomial model (Sandland and Cormack, 1984).

The following assumptions are implicit in the model:

- the probability that a calving of a randomly selected individual in a given year will be recorded is independent of whether that individual's previous calving was recorded;
- the probability that the interval between a given calving of a given individual and the next calving of that individual, if any, will be of a given length is independent of the length of the interval between the given calving and the previous calving, if any;
- the relative probabilities of calving intervals of each length do not change with time;
- survival probabilities of females are not affected by calvings and do not change with time.

Table 2

Estimated probability distributions of calving intervals for different assumptions about the maximum calving interval.

| Interval<br>(years)   | Assumed maximum interval (years) |        |        |        |
|-----------------------|----------------------------------|--------|--------|--------|
|                       | 4                                | 5      | 6      | 7      |
| 1                     | 0.00                             | 0.00   | 0.00   | 0.00   |
| 2                     | 0.13                             | 0.03   | 0.02   | 0.02   |
| 3                     | 0.80                             | 0.73   | 0.65   | 0.65   |
| 4                     | 0.07                             | 0.08   | 0.08   | 0.08   |
| 5                     | —                                | 0.16   | 0.17   | 0.17   |
| 6                     | —                                | —      | 0.08   | 0.08   |
| 7                     | —                                | —      | —      | 0.00   |
| Mean calving interval | 2.94                             | 3.39   | 3.63   | 3.63   |
| Relative likelihood   | 0.00001                          | 0.70   | 1.00   | 1.00   |
| Verdict               | reject                           | accept | accept | accept |

The above formulation yields a series of nested models according to the value chosen for  $j_{\max}$ , the maximum calving interval. Calculations were conducted for  $j_{\max} = 4, 5, 6$  and  $7$ . Table 2 shows the estimated  $h_j$  for each of the four models, on the assumption that survival rates are all unity.

While the relative likelihoods of such models should not be interpreted too literally, it is clear that the model with  $j_{\max} = 4$  is rejected. This is largely because there are too few 2-year intervals to adequately explain the relatively higher number of 5-year intervals in terms of sequences of 2 and 3-year intervals with a missed calving. The model with  $j_{\max} = 5$  is not rejected. The model with  $j_{\max} = 7$  led to exactly the same estimates of the  $h_j$  as the model with  $j_{\max} = 6$ , because in the former model the estimate of  $h_7$  was zero.

Fig. 5 shows the expected distribution of apparent inter-calf intervals from the models with  $j_{\max} = 6$  or  $7$ . The model seems to have some trouble fitting the large number of 4 and 5-year intervals and the relative paucity of 9-year intervals.

Due to the non-linear nature of the model and the complex covariance structure of the estimates of the  $h_i$ , individual standard error estimates for each of the  $h_i$  would not be particularly meaningful and have not been calculated. The mean calving interval is given by:

$$\sum_{j=1}^{j_{\max}} j \cdot h_j s_j / \sum_{j=1}^{j_{\max}} s_j$$

For the model with  $j_{\max} = 6$ , the estimate of the mean calving interval is 3.63. The 95% confidence interval based on the likelihood ratio criterion is 3.77 to 4.09.

In principle, the survival rate can be estimated along with the  $h_i$ . The best estimate of the annual mortality rate using the model with  $j_{\max} = 6$  is approximately 0.01, but a zero value is not rejected at the 95% level. The upper 95% confidence limit is approximately 0.05. It can be concluded that such data are not sufficient for the estimation of the natural mortality rate. Natural mortality is reflected in such data as a tendency for the resighting rate to decay with time elapsed since the previous sighting. In this case, any apparent decay is confounded with the pattern of calf interval probabilities and is therefore difficult to detect.

There is a positive correlation between the value assumed for the natural mortality rate and the estimated mean calving interval. Hence the above estimate obtained with the assumption that the mortality rate is zero is in that respect a minimum estimate. Using the estimated value of  $M$  (0.01) changes the estimate of mean calving interval to 3.65 years, while using the upper confidence limit for  $M$  (0.05) increases the estimated mean calving interval to 3.77 years.

### Numbers of calvings by year and trends over time

As a by-product, the fitted model (1) provides estimates of the  $p_j$ , the probability of recording a calving occurring in year  $j$ . These yield the estimators of the numbers of calvings in each year,  $N_j$ , given overleaf:

$$\hat{N}_j = n_j / \hat{p}_j$$

$$\text{where } \hat{p}_j = \frac{\sum_{i=0}^{j-1} n_{ij}}{\sum_{i=0}^{j-1} q_{j-i} s_{j-i}}$$

The method yields no estimate of  $N_0$ , the number of calvings in the first year of the study. Since there are no observed 1-year calving intervals in this data set, the method yields no estimate of  $N_1$  either. Because there are so few two-year calving intervals, no meaningful estimate of  $N_2$  is obtained. The remaining estimates are listed in Table 1. Because the estimates have considerable covariance, the simple procedure of regressing these estimates against time would not necessarily provide a valid estimate of the trend in the calving population size. A trend in the calving population size can be estimated with the following model:

Let  $N_j = N_0 \cdot \exp(\delta \cdot j)$ , where  $\delta$  is the annual rate of increase expressed as an instantaneous rate. We can then fit the model:

$$E(n_{ij}) = n_i n_j \exp(-\delta \cdot j) q_{j-i} s_{j-i} / N_0 \quad (j > i)$$

Provided that we require only an estimate of  $\delta$  and not of  $N_0$ , we can fit this model directly, treating the  $q_j$  as nuisance parameters, without having to go via the  $h_j$ . The  $s_j$  and  $N_0$  can be absorbed into the  $q_j$  parameters without changing the structure of the model. Thus for the purpose of estimating  $\delta$  we do not need to assume a value for the natural mortality rate nor do we need to assume a value for

the maximum calving interval. The model is in the standard log-linear form, for the fitting of which various algorithms such as GLIM (Nelder and Wedderburn, 1972) are available. The estimate of  $\delta$  is 0.073 (SE 0.017). This corresponds to an annual rate of increase of 7.6% p.a. (SE 1.7%).

#### Detection of trends in the mean calving interval

We note that since the  $h_1$  and  $h_2$  probabilities are zero or small, probabilities  $q_1$  through  $q_5$  are very close to the corresponding  $h$  values. Furthermore, the bulk of calving intervals are five years or less. Thus any trend in the mean calving interval will be reflected in terms of a trend in the relative values of the  $q_3$ ,  $q_4$  or  $q_5$  over time. We restrict attention to intervals of 3, 4 and 5 years inclusive and fit the model:

$$E(n_{i,j}) = n_i q_{j-i} p_j$$

where  $q_{ij} = q_{i0} \exp(j \cdot \delta_i)$  ( $i = 3, 4, 5$ )

Again, we can work with the  $q_j$ 's alone without invoking the  $h_j$  and so without needing to assume a value for the natural mortality rate.

$\delta_i$  is the time trend in the frequency of calving intervals of length  $i$ . Because of the relative smaller size of the sample of 4 and 5 year intervals, we estimated a common value for  $\delta_4$  and  $\delta_5$ . Since there is one degree of redundancy between the  $\delta_i$  and the  $p_j$ , one of the  $\delta_i$  (say  $\delta_{4,5}$ ) can be set to zero without loss of generality. This leaves only  $\delta_3$  to estimate. The estimate was -0.018 (SE 0.052). The negative sign implies a tendency for 3-year intervals to get less common relative to 4- and 5-year intervals with time, i.e. for calving intervals to get longer, but the trend is not significant.