Natural markings and their use in determining calving intervals in right whales off South Africa

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Since 1979, 245 right whales (excluding calves) have been individually identified in aerial photographs taken annually on the South African coast, using variations in dorsal pigmentation and callosity patterns. White or grey blazes (or both) occurred dorsally in 16,7% of individuals, one form of which (partial albinism) occurred in 3,6% of the calves born but may be sex linked. In 19 animals carrying dorsal marks that were resighted two to seven years later, changes in the appearance of the callosities were noted in 95% of individuals, 58% showing pronounced changes. Definite matches between years were made for 139 cows with calves. The average per capita calving interval, adjusted for incomplete spatial and temporal coverage, was 3,183 ± 0,091 (SD) years, or a calf production rate of 0,314 ± 0,009 (SD) per adult female per year. From a simple model it is shown that rates of population increase as high as that observed (6–7%) can only be maintained with a calf production rate of this order if the age at first parturition is relatively low and/or the adult survival rate high.

Sedert 1979 is 245 suidelike noordkapers (kalwers uitgesluit) op grond van variasie in dorsale pigmentasie en velgroeiselpatrone afsonderlik geïdentifiseer op lugfoto's wat jaarliks aan die Suid-Afrikaanse kus geneem is. Dorsaalgelee wit of grys vlekke (of albei) kom op 16,7% van die indiwidue voor. Een vorm (gedeeltelike albinisme) wat op 3,6% van die kalwers voorgekom het, mag geslagsgekoppel wees. Van die 19 diere met dorsale merke wat na twee tot sewe jaar weer waargeneem is, het 95% veranderinge in die voorkoms van die veluitgroeisels getoon. Hiervan het 58% sterk verandering ondergaan. Positiewe identifikasie van 139 koei-en-kalfpare op 'n meerjarige grondslag is gemaak. Die gemiddelde kalfinterval per capita, aangepas by die onvolledige dekking m.b.t. ruimte en tyd was 3,183 ± 0,091 (standaardafwyking) jare of 'n kalfproduksietempo van 0,314 ± 0,009 (standaardafwyking) per volwasse koei per jaar. Met behulp van 'n eenvoudige model word aangetoon dat so 'n hoë aanwastempo (6–7%) in 'n populasie slegs met bogenoemde kalfproduksie-tempo volgehou kan word indien die ouderdom van die koeie by die geboorte van hul eerste kalf redelik laag is en/of die kans op oorlewing van die volwassenes hoog is.

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Right whales *Eubalaena australis* can be seen each spring close inshore along the southern coast of South Africa (Figure 1), tending to favour certain localities which can roughly be separated into 'mating' and 'calving' areas (Best 1970, 1981). Regular aerial surveys have shown that the component of the population that visits the coast increased from 1971 to 1987 at an exponential rate of 6,8% per year (Best in press).

In view of the relative rarity of demonstrable recovery in whale populations following depletion (IWC 1982), the demographic parameters of this population are of considerable interest to an understanding of how such an increase might be generated.

In this paper an attempt is made to measure one of the most important reproductive parameters, the calving interval, through resightings of individuals recognizable from natural markings.

Materials and methods

Near-vertical aerial photographs of right whales have been taken on the South African coastline each year since 1979 (Table 1). Photography has concentrated on cow–calf pairs to maximize the amount of information, although other individuals were photographed when they were associated with cows and calves, or when flights were for training purposes only.

Most (97%) of the animals were photographed on annual helicopter surveys in October. These started 2–25 (average 10,8) days after fixed-wing surveys of the entire coastline from Muizenberg to Woody Cape (the standard survey area) had been completed. For economy, the limits of these helicopter surveys were set according to the distribution of calves seen on the fixed-wing surveys, with the easternmost individuals normally being omitted for logistical reasons. In practice this meant that the annual helicopter flights covered the area where 95,2–100 (mean 97,5)% of calves had been seen on fixed-wing surveys. The entire coastline within the chosen survey limits was searched from an altitude of *ca* 305 m and at a speed of about 50 m/s. The flight path of the aircraft was about 0,61 km offshore, and one observer (besides the pilot) covered each side of the flight path. All groups seen were inspected for the presence of a calf before photography began.

Occasionally the limits of the annual helicopter flight were extended up the west coast or photographs were taken incidentally of animals outside the normal survey area; such animals constituted only 13 (or 3%) of the 387 non-calves photographed (Table 1).

Photography was through the open door of the aircraft at a scheduled altitude of 91 m (although this was sometimes unintentionally reduced during helicopter manoeuvres to obtain a better angle). All but four cow-calf pairs and four other individuals were photographed using a handheld 70 mm camera with motor-drive and 250 mm f5,6 lens, the remainder being photographed
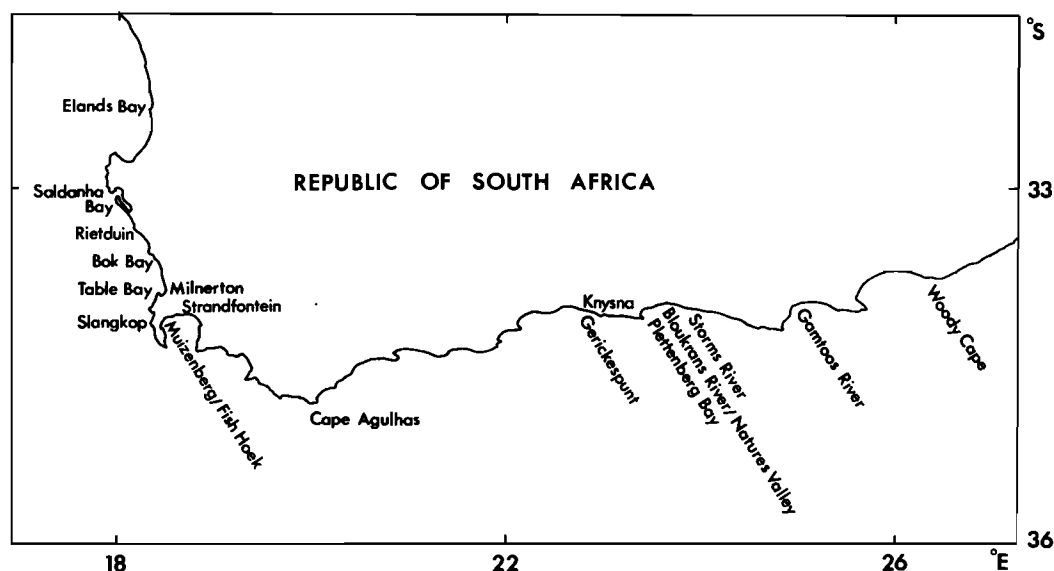
Figure 1 Southern coast of South Africa, showing location of place names mentioned in text.

Table 1 Details of aerial photography of right whales off South Africa

Dates of survey	Survey type	Aircraft	Survey limits	Whales photographed Cow-calf pairs	Others
12.10–13.10.79	Annual	Sikorsky S62A	Agulhas–Plettenberg Bay	27	0
21.10–23.10.80	Annual	Bell Jet-Ranger	Strandfontein–Gericke Point	34	2
6.10–7.10.81	Annual	Bell Jet-Ranger	Muizenberg–Bloukrans River	47	0
8.10.81	Extension	Bell Jet-Ranger	Slangkop–Saldanha Bay	3	0
15.10–16.10.82	Annual	Bell Jet-Ranger	Muizenberg–Storms River	40	2
14.10–16.10.83	Annual	Bell Jet-Ranger	Muizenberg–Gericke Point	41	4
19.10.83	Extension	Bell Jet-Ranger	Table Bay–Rietduin	2	0
8.10–11.10.84	Annual	Bell Jet-Ranger	Muizenberg–Natures Valley	66	6
28.9.85	Incidental	Partenavia P68C	Gamtoos River	1	0
16.10–18.10.85	Annual	Bell Jet-Ranger	Fish Hoek–Bloukrans River	49	3
22.10.85	Extension	Alouette	Milnerton–Elands Bay	3	0
16.9.86	Incidental	Puma	Bokbaai	0	4
7.10–10.10.86	Annual	Bell Jet-Ranger	Muizenberg–Knysna	45	8
Total				358	29

with a 35 mm camera plus motor-drive and 100–300 mm f5,6 lens. All pictures taken were colour slides (Ektachrome 200 ASA). Usually one film of the larger format (10–12 exposures) was taken of each group, so providing a number of frames of each animal and reducing possible confusions of identity between groupings. Three standard views of each animal were attempted; two near-vertical views of the head region, one just before the whale surfaced (to avoid confusing highlights and splashes) and one with the rostrum as 'dry' as possible (for maximum detail), and a view of the back of the animal above water to establish the presence or absence of grey or unpigmented markings. Films were individually numbered by the second observer as they were exposed, and notes taken of associated information on locality, group size and composition, and any conspicuous natural markings. These individual film numbers were maintained during processing. A total of about 5000 frames of 358 cow-calf pairs and 29 other individuals off South Africa is on file (Table 1).

Unless otherwise stated, all figures given in this paper as ± refer to one standard error of the mean. All chi-square values given for tests with one degree of freedom have incorporated Cochran's correction for continuity.

Authorization for this work was provided in terms of the provisions of the Sea Fisheries Act, 1973 by the Director of Sea Fisheries (permits issued to the author 3 March 1975 and 18 September 1984).

Results

Natural markings

Payne, Brazier, Dorsey, Perkins, Rowntree & Titus (1983) categorized the natural markings of southern right whales potentially useful for individual identification as

(1) skin mottling
(2) wounds
(3) white blazes
(4) partial albinism
(5) grey blazes
(6) callosity patterns
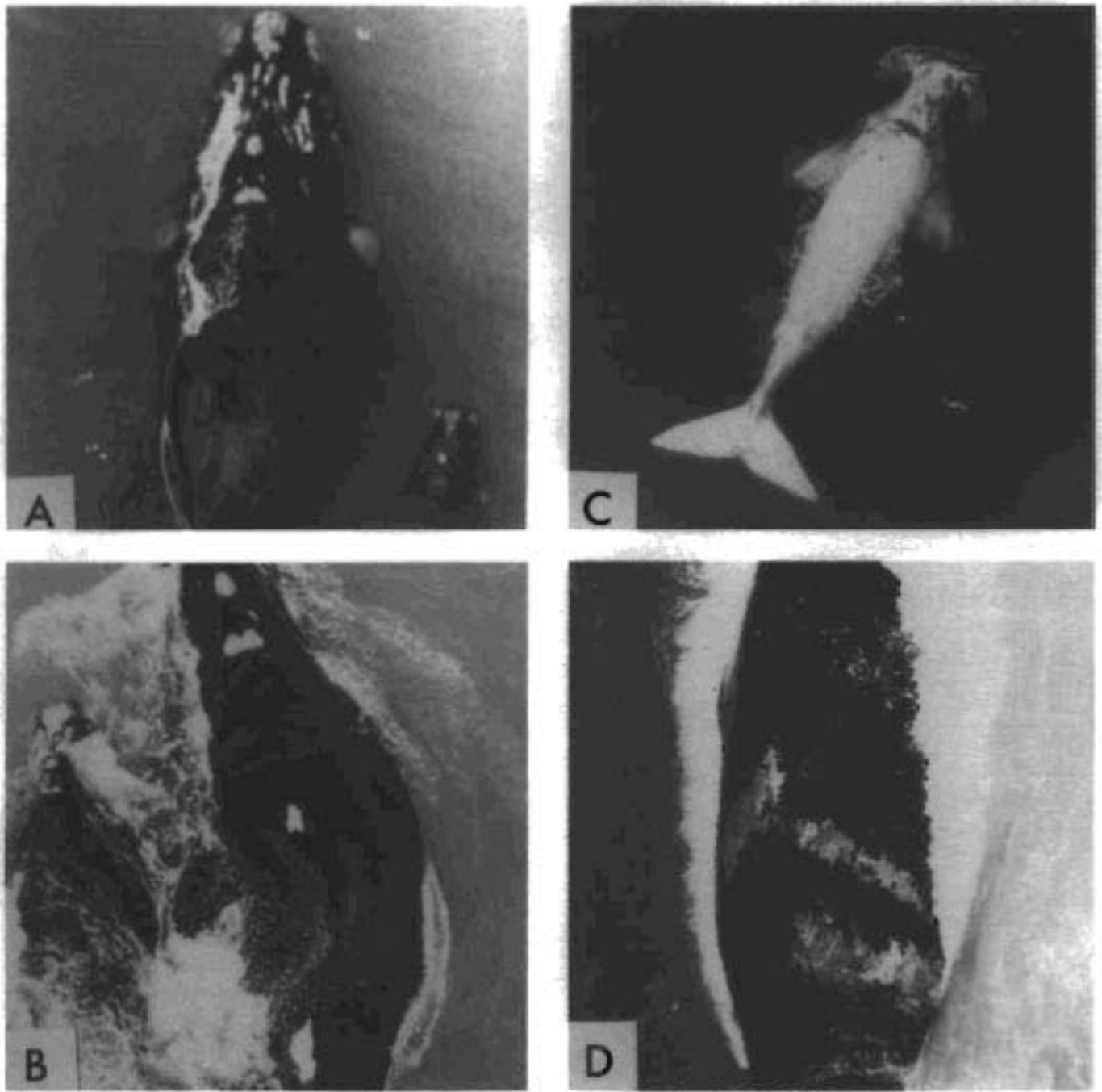
Figure 2 Dorsal markings of right whales off South Africa: (a) moult (b) white blazes (c) partial albinism (d) grey blazes.

Skin mottling

This clearly represents moulting of the outer layers of skin (Figure 2a), and although such mottling can be quite distinct, photographs even one day apart of the same individual show that the outline of the marks can change rapidly. Thus skin mottling is effectively excluded as a means of identification (except over extremely short periods). Such markings are important, however, because it is possible to confuse them with grey blazes.

Wounds

Payne *et al.* (1983) found dorsal markings attributable to wounds in 1,9% of Argentinian right whales (*n* = 484), with a further seven (1,4%) carrying white marks so small that it was not clear whether they were of natural origin or not.

Eleven adults (or 4,4% of all identified non-calves) photographed off South Africa carried marks that could have been scars. These were essentially either elongated scratch-like marks (3) or small white or pinkish spots (7); the exception was an animal with a blunt and scarred tip to the left tail fluke. In two animals these scratch-like marks were not present when the animal was first photographed, and one mark was not visible three years later, lending support to the belief that they are temporary features. Five (or 71,4%) of the white or pinkish marks occurred round the base of the tail, either on the peduncle or the leading edge of a fluke. Collisions

with vessels and entanglement in fishing gear have already been documented for right whales on the South African coast (Best 1984), and could provide the source for some of these 'scars'. Two of these animals carried such marks (with little apparent change) for six years, indicating that they may be more permanent than the scratch-like markings.

Kraus, Moore, Price, Crone, Watkins, Winn & Prescott (1986) found scars to be present in 57,9% of North Atlantic right whales ($n = 38$); this higher incidence than so far recorded for the southern hemisphere may at least partly be the result of the finer detail visible in shipboard photographs. Over periods of up to nine years 14% of the scars diminished in visibility, indicating that their use for individual identification may be limited. They have not been used here for primary matching of individuals.

In an earlier, smaller sample from South Africa, Payne et al. (1983) were unable to find any dorsal marks of this type.

White blazes

As described by Payne et al. (1983), these are strikingly unpigmented areas that have very distinct edges (Figure 2b). They are irregular in shape but not highly so (cf. grey blazes), and although most commonly found as large white patches usually centred around the umbilicus (Omura, Ohsumi, Nemoto, Nasu & Kasuya 1969), they do occur in a small proportion of animals as smaller spots or streaks mid-dorsally. Because of the relative rarity with which a right whale exposes its ventrum, it is only the dorsal blazes that have been used in this study to identify individuals.

White blazes dorsally have been seen in 17 (7,1%) of 239 non-calves, of which four also bore grey blazes. This incidence is higher than off Argentina (1,9%), even if seven animals are included that were reported by Payne et al. (1983) to have had white marks so small that it was impossible to tell whether they were blazes or small wounds ($\chi^2 = 5,177; p < 0,025; 1$ df). White blazes in non-calves do not seem to become progressively pigmented with time (cf. partial albinism), and do not seem to change in shape (Kraus, Moore et al. 1986; Payne et al. 1983).

Partial albinism

As described and illustrated by Best (1970, 1981) and Payne et al. (1983), a certain proportion of right whale calves are born with a nearly complete lack of pigmentation over (apparently) the entire body, apart from scattered black spots, particularly in the neck region (Figure 2c). Best (1981) estimated the incidence of such partial albinism among 251 calves off South Africa as 4,0%; in the photographs of 358 calves since 1979 there were 13 such animals (or 3,6%), with a further three animals predominantly white dorsally.

Both Best (1981) and Payne et al. (1983) commented that no adults with such widespread albinistic markings had been seen, and concluded that the partially albino calves must darken with age, a process actually observed

in one individual (Payne et al. 1983). Some adults are seen with a distribution of grey over the dorsal surface that closely resembles that of the non-pigmented areas of the partially albinistic calves: Best (1981) and Payne et al. (1983) concluded that these must originally have been partial albinos. Their incidence amongst sightings of non-calves off South Africa was estimated as 3,6%, identical to that of partially albinistic calves (Best 1981). However, in the photographic sample of 217 identified adult cows for which suitable photographs exist there is only one (0,5%) such animal; this is a significantly lower proportion than that of partially albinistic calves ($\chi^2 = 4,99; 1$ df; $p < 0,05$). A similar disparity can be seen in the earlier sample of sightings (Best 1981): only two of 35 (5,7%) light phase adults were seen with calves, compared with 251 of 946 (26,5%) dark phase adults ($\chi^2 = 7,59; 1$ df; $p < 0,01$). This suggests either that the lighter phase (= partially albinistic) animals are predominantly male, or that their female component is reproductively less successful than normally coloured females.

In order to compare the incidence of partial albinism between populations, therefore, it is essential to use samples of comparable components of the population. Payne et al. (1983) reported an incidence of 1,4% in their total sample of 484 identified animals. The most comparable data set available from South Africa is that of the 358 photographed calves; the proportion in this sample (3,6%) is not significantly greater than that in the sample from Argentina ($\chi^2 = 3,35; 1$ df; $0,10 > p > 0,05$). However, while both sexes are presumably equally represented in the calf sample, the same assumption cannot necessarily be made for the Argentinian whales.

Grey blazes

Right whales photographed off South Africa also carried distinctive bluish-grey markings, more purplish in colour than those attributed to moult (Figure 2d). Apart from those non-calves that were probably partially albinistic as calves and were predominantly grey in colour, other individuals bore smaller grey markings dorsally, often in the form of a rough V-shape with the apex pointing anteriorly. Although their edges were well defined, these marks differed from the white blazes in being far more irregular in outline, usually larger in size and sometimes with small inclusions of dark pigment. These grey blazes may all start out as white marks in the calf, and darken with age but never disappear (Payne et al. 1983).

Excluding four animals that are assumed to have been partially albinistic as calves, 23 (or 9,6%) of 239 known non-calves off South Africa (for which photographs of the back were available) had grey blazes, four of which also bore white blazes. Payne et al. (1983) reported that 1,4% of 484 animals identified off Argentina had grey markings, a significantly lower proportion than off South Africa ($\chi^2 = 24,9; 1$ df; $p < 0,001$).

In general, therefore, right whales off South Africa appear to have a higher incidence of dorsal marks of all kinds (except wounds) than those off Argentina. In
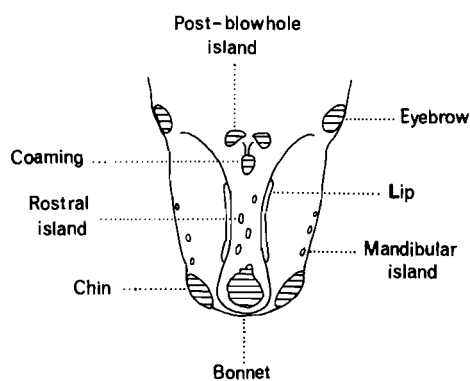
total, 16,7% of identified non-calves suitably photo-graphed off South Africa had white or grey dorsal marks or both, and this greatly assisted in the matching process.

Callosity patterns

Unlike any of the natural markings mentioned above, callosities are a universal feature of southern right whales. This makes their natural variation extremely useful for individual identification. The distribution of callosities in general is similar to that described by Payne *et al.* (1983), and his nomenclature has been followed (Figure 3).

As described by Payne *et al.* (1983), callosities appear in the newborn calf as smooth rounded protuberances, at least the larger ones of which split and crack with age as they grow in size. Their distribution appears to correspond to the position of facial hairs (Matthews 1938; Omura *et al.* 1969). Probably because of their effects on the rate of water flow these callosities are frequently associated with large numbers of cyamids, and (as originally suggested by Schevill, Moore & Watkins 1981) it is probably a combination of the colour of these ectoparasites and of the callosity tissue itself that provides the contrast with the (usually) black surrounding skin discernible in aerial photographs. As the cyamids are mobile, this contrast (and the resultant outline of the callosity) can and does change with time, a fact that is crucial to an interpretation of aerial photographs of callosity patterns.

In the only two fresh stranded right whales examined by the author that were not calves, the major callosities (e.g. chin, bonnet and eyebrow) were also inhabited by the burrowing barnacle *Tubicinella* sp. In one animal an estimated 110 *Tubicinella* were located in the chin callosity, 68 in the eyebrow and six in the bonnet, with two in the posterior blowhole islands and one in the first mandibular island. These two whales, both stranded in September, were respectively only 10,06 m and 9,25 m long, and thus probably juvenile; in adults the number of barnacles present could obviously be greater. If this is so, their presence could contribute substantially to the stability, conformation and even colour (the cirri and mantle being light yellow) of the callosities.

Table 2 Incidence of lip callosities in southern right whales

Number of lip callosities	Argentina (n = 188)	South Africa (n = 245)
None	38 (20,2)	64 (26,1)
One		
Right only	11 (5,9)	22 (9,0)
Left only	1 (0,5)	2 (0,8)
Two	138 (73,4)	157 (64,1)

Because of their greater visibility in aerial photographs (and perchance because it is these callosities that are the most variable), the principal features used to distinguish individual whales have been the rostral islands and lip callosities, as well as the shape of the posterior edge of the bonnet.

The variation in lip callosities can be compared with data from Argentina (Table 2). The proportions of animals with two, one or no lip callosities were similar in both localities ($\chi^2 = 4,42$; 2 *df*; $p > 0,10$). As described by Payne *et al.* (1983), there was a definite asymmetry in the distribution of lip callosities in the whales that carried only one, nearly all being found on the right hand side.

Matching individuals

As a first step in the matching procedure, the complete set of colour photographs available for any one individual was examined under 8× magnification and the animal placed in one of several alternate classes under four separate categories, namely dorsal body colour (all black, grey markings only, grey and white markings, white markings only, no data), incidence of lip callosities (none, on one lip only, on both lips, no data), size of lip callosities (length of larger less than half, about half or more than half distance from posterior edge of bonnet to anterior edge of coaming) and number of rostral callosities (minimum–maximum number).

These classifications were entered on a Paramount punch card (together with data on the area, photographer, behaviour, age and sex of the animal). A 7 × 8 cm black-and-white enlargement of the head region of the whale (and a similar size print of any coloration feature not visible on the head photograph) was also pasted on the card. Additional information (exact date and locality of all sightings) was entered on the back of the card.

The card for a newly photographed (and therefore unknown) whale could then be compared with all known animals on file and all those individuals that did not resemble the unknown animal in all four categories rapidly excluded. As an example, for the 72 individuals from the 1984 survey, this procedure resulted in from 72,9 to 100 % (mean 88,2%) of the total file being excluded for each unknown animal examined.

The remaining candidates for a match were compared visually with the unknown animal, using the black and white prints on the cards. If a possible match was found, a final comparison was made between all the original

Figure 3 Nomenclature of the callosities on the head of a southern right whale (hatched structures are universal, unhatched are highly variable features.)

colour slides available of the two animals. This included an examination of criteria not used in the original sorting procedure, e.g. shape of the bonnet, coaming and post-blowhole islands, positions of rostral islands, shape, number and position of chin patch and mandibular islands, etc. If there was consistent agreement between the unknown whale and the possible match in all observable criteria (allowing for the changes to be expected over time, see below), the unknown whale would be recorded as a 'synonym' of the known animal.

As a check on the initial sorting, the file of each year's photographs remaining after matching was compared against all other known individuals including those with which it had already been compared.

Constancy in callosity patterns with time

A crucial assumption in the use of any natural marking for long-term identification of individuals is that the marking either remains unchanged with time or that the changes are such that they do not interfere with the recognition of the individual.

As a principal contributor to the conspicuousness of the callosities may be their ectoparasite burden, changes in the distribution of these parasites (particularly the cyamids) could produce changes in the appearance of the callosities.

Payne et al. (1983) investigated the constancy of callosity patterns over time by examining photographs of 17 individuals that carried some other natural marking that could be considered permanent. A similar approach has been adopted here for 19 individuals carrying either

white or grey dorsal blazes that were photographed off South Africa and resighted 2–7 years later; all were non-calves (Table 3).

Changes with time were noted in all the features examined in at least some individuals. Comparisons have been scored as no observable change, slight change and pronounced change; the latter category is one that implies that the changes are such that the feature (by itself) could lead to misidentification of the animal as a new individual.

The incidence of change was highest in the shape of the lip callosities (66,7%), followed by both anterior and posterior edges of the bonnet, the intensity of rostral islands and the shape of the post-blowhole callosities (all about 46–48%). Change was least in the number of rostral callosities (5,3%) and the shape of the coaming (10,5%). Pronounced changes were most prevalent in the anterior edge of the bonnet, the size of lip callosities and the shape of the post-blowhole callosities (20–21%); no such changes were found in the number of rostral islands or in the shape of the coaming, while they occurred in less than 10% of cases in the posterior edge of the bonnet and in the shape of the lip callosities.

It is not clear from the photographs whether these changes were due to shifts in the cyamid infestation or alterations in the actual callosity tissue; however, as reversal in the intensity of contrast of some rostral islands did occur with time in one individual, shifts in cyamid distribution certainly seem to be a contributory factor.

Payne et al. (1983) noted change in the colour of

Table 3 Constancy of callosity patterns over time in double-marked right whales off South Africa, where 0 = feature absent, x = feature not visible in more than one year, − = no observable change, + = slight change, ++ = pronounced change

Whale no.	Years sighted	Bonnet shape		Rostral islands		Lip callosities		Coaming shape	Post-blowhole islands shape	Caused missed match?
		Ant. edge	Post. edge	No.	Inten-sity	Size	Shape			
79/01A	79, 84	−	+	−	−	−	−	−	−	No
79/06A	79, 85	×	+	−	++	−	+	−	+	No
79/07A	79, 82, 85	++	−	−	++	−	−	+	−	No
79/15A	79, 82	++	−	−	+	++	−	+	++	Yes
79/17A	79, 83, 86	−	−	−	+	−	−	−	+	No
79/21A	79, 82, 85	−	+	−	−	0	0	−	−	No
79/27A	79, 82, 85	+	−	−	−	−	+	−	−	Yes
80/05A	80, 83	×	−	−	−	0	0	−	−	No
80/12A	80, 83, 86	−	+	−	+	++	++	−	+	Yes
80/33A	80, 83	×	−	−	−	−	+	−	−	No
81/19A	81, 84	+	−	−	+	−	+	−	++	No
81/35A	81, 84	++	−	−	−	−	−	−	−	No
81/38A	81, 83, 86	+	+	−	−	0	0	−	++	No
81/39A	81, 84	+	+	−	++	0	0	−	+	No
81/43A	81, 84	−	−	−	−	++	+	−	−	Yes
81/45A	81, 84	−	++	+	+	+	+	−	+	Yes
82/03A	82, 85	×	−	−	+	−	+	−	−	No
83/02A	83, 85	−	+	−	−	−	+	−	++	No
83/23A	83, 86	−	+	−	−	−	+	−	−	No

callosities in at least 59% of their doubly-marked individuals; these mainly involved the posterior rostral islands and the lip callosities. Such changes were in some cases reversed later, and this was attributed to changes in the level of cyamid infestation. Only one possible instance of change in callosity tissue with time was found.

Kraus, Moore *et al.* (1986) analysed changes over time in identifying features of right whales in the North Atlantic. The situation is not entirely comparable with that for the southern hemisphere data, as the photographs were taken both from aircraft and ships (the latter allowing finer detail to be examined), and the arrangement of callosity tissue is somewhat different in this stock, nearly half the animals having callosities that are continuous from the anterior tip of the rostrum to the blowholes, and which display fewer variations useful for individual identification. In the 17 adult females examined, 65% displayed some changes over time in the configuration or topography of their callosities (*cf.* 95% in the present sample), but only 18% showed large (= pronounced) change (*cf.* 58% in the present sample), and these were confined to the lip callosities (three cases) and the bonnet (one case). These authors also concluded that large variations in the apparent patterns of some callosities may have been due to cyamid movements between callosities. Callosity tissue without cyamids in adult right whales can appear either black or grey, so that its detection in the absence of cyamids may be difficult. However, one cow was found in which clearly visible lip callosity tissue had nearly disappeared within three years.

Payne *et al.* (1983) concluded that the type of change in the appearance of callosities seen would not hinder recognition of individuals by callosity pattern alone. Kraus, Moore *et al.* (1986), however, felt that on rare occasions the same individual might not be recognized using callosity photographs taken several years apart, and they recommended photography of both callosity patterns and at least one other distinctive identifier for confirmation.

In the present data, the degree of change seen was certainly sufficient to cause the miscoding of some individuals so that they failed to be identified as potential matches until the final cross-checking was carried out. Of 14 such instances, 12 involved differences in the number or relative size of the lip callosities, one involved differences in the number of rostral callosities and one involved both. Misclassification was due to apparent expansion in size of the lip callosity in six cases, and to apparent shrinkage of the lip callosity in seven cases. Most of these involved either very small callosities ('spots'), whose appearance or disappearance caused the animal to be coded as having none, one, or two lip callosities on different occasions, or discontinuous lip callosities, in which one portion disappeared or shrank perceptibly so that the relative size of the callosity was miscoded. The two instances in which the number of rostral callosities apparently changed involved the incorporation of a rostral island in the posterior margin of the bonnet, probably by the movement of cyamids

(Kraus, Moore *et al.* 1986). Some of these problems could have been avoided by adopting a more flexible sorting procedure with less emphasis on lip callosities, but it is important to note that the overall effect of any possible change in callosity pattern with time will be to increase the likelihood of one animal being identified as two different ones, rather than vice versa. In the present context, therefore, this might result in the recognition of fewer calving intervals and (if the changes are reversed over time) ultimately in an increase in the number of longer intervals (i.e. multiples of the true calving interval) deduced.

Calving interval

Within the photographic sample of 358 non-calves there were 142 positive matches between years. The intervals between these resightings varied from 1–6 years (seven years being the maximum possible given the temporal range of the surveys), but most (82,4%) were three years.

Three matches are not considered to represent actual calving intervals, for reasons given below.

(i) In 1983 photographs were taken of a group of two adults with a calf, and during the period of photography the calf moved from one adult to the other. In 1984 the adult identified as the mother of the 1983 calf returned with another calf, while the other adult returned in 1986 with a second calf. It is possible therefore that the mother of the 1983 calf was incorrectly identified.

(ii) In 1985 a cow was photographed with a very small calf, and the next year it was photographed again with a very large calf. It was impossible to establish whether the two calves were the same individual because of the diminutive size (and poorly differentiated callosities) of the 1985 animal. The only part of the calf that could be measured in both years against the same part of the adult in the same frame was the length of the rostrum from the tip of the bonnet to a line intersecting the posterior margins of the blowholes. This increased from 0,321 of the adult's rostrum in 1985 to 0,654 in 1986, or just over double. This dimension exhibits allometric growth, and seems to increase from about 16% of body length in calves to 17,5% at one year of age (Figure 7 and equation (5) in Whitehead & Payne 1981).

Consequently if the two calves were the same individual, and the mother's rostrum did not grow in the interim, the relative increase in body length of the calf would have been $^{16}/_{17,5} \times 2,04$ or 1,865 times. According to Whitehead & Payne (1981), right whale calves measure 5,5 m at birth and are estimated to be 9,61 m long at one year of age (an increase of 1,747 times). The 1986 calf was therefore certainly large enough relative to the 1985 calf to have been the same animal one year later.

(iii) In 1984 two adults were photographed with a calf. The adult considered less likely to be the mother of the calf was rephotographed on a training flight in 1986 in a group of four adults, with no calves present.

These three records have therefore been excluded

from further calculations of the calving interval. The remaining 139 matches were from 2–6 years apart, with 84,2% at three years (Table 4).

Some of these longer intervals may represent animals that have given birth twice in the interim but which have only been rephotographed after the second birth. This could arise because the intermediate calf (a) was absent from the survey area, (b) was born after the survey, (c) died before the survey, or (d) failed to be detected during the survey.

There is some indication that factor (a) may be occurring. Table 4 shows that 56% of 'long' calving intervals (in excess of three years) involved females that were photographed either on one or both occasions with calves on the periphery of the survey area, compared to 31% of 'short' intervals (three years or less in duration). The relative frequencies of 'long' and 'short' calving intervals are significantly different in the centre of the survey area and on the periphery ($x^2 = 3,8661$; $p < 0,05$; 1 $df.$). This tendency towards longer calving intervals at the periphery of the survey area suggests that some intermediate calves are being missed because they are outside the limits of the area at the time of the survey. More accurate information would therefore be provided by the data from the central survey area, where calving intervals ranged from 2–5 years with 88% at three years.

These data must be adjusted to give equal weighting to animals on long and short calving intervals. This has been done by expressing the calving intervals on a *per capita* basis, and by applying temporal correction factors to allow for the unequal periods for which cows on different calving intervals have been available for photography.

If the population of adult females (N) consists of p_1, p_2, p_3, p_4, p_5 and p_6 individuals calving consistently at 1–6-year intervals, and if equal proportions of these

calve annually, then each year

$$p_1 + p_2/2 + p_3/3 + p_4/4 + p_5/5 + p_6/6$$

of these will calve. After seven years, the numbers of these that will have calved more than once will be

$$6p_1 + 5p_2/2 + 4p_3/3 + 3p_4/4 + 2p_5/5 + p_6/6.$$

If n_1.......n_6 corresponds to the number of matches made at 1–6-year intervals, then

$$n_1 = 6p_1 . N, \quad n_2 = 5p_2/2 . N .... n_6 = p_6/6 . N.$$

The mean calving interval

$$(\bar{t}) = p_1 + 2p_2 + 3p_3 + 4p_4 + 5p_5 + 6p_6$$

or

$$\bar{t} = \frac{n_1/6 + 4n_2/5 + 9n_3/4 + 16n_4/3 + 25n_5/2 + 36n_6}{N}$$

where

$$N = n_1/6 + 2n_2/5 + 3n_3/4 + 4n_4/3 + 5n_5/2 + 6n_6.$$

Given the values for n_1......n_6 in the fourth column of Table 4, and allocating animals on mean calving intervals of 2,5 and 3,5 years equally between adjacent intervals,

$\bar{t} = 193,858 / 60,908$ or 3,183 years,

with a jack-knife variance of 0,008 ($n = 76$).

This average calving interval is equivalent to a calf production rate per adult female per year of 0,314 ± 0,001.

Discussion

Similar observations of the frequency of calving of known individual right whales have been made off Argentina (Payne 1986), for a total of 89 intervals recorded for 74 individual cows. The relative frequencies of 2–3, 4–5 and 6–7 year-intervals are significantly different between South Africa and Argentina ($x^2 = 21,48$; 2 df; $p < 0,001$). There is a smaller proportion of three-year intervals off Argentina (65% *cf.* 84%) and a larger proportion of six-year intervals (18% *cf.* 3%). As Payne suggested, some of the six-year intervals off Argentina probably represent missed three-year intervals, owing to relatively poor survey coverage in one or two years. The overall average calving interval of 3,775 ± 0,134 years for Argentinian right whales is therefore probably biased upwards.

In the western North Atlantic, data are available for 17 calving intervals from the same number of individually identified females (Kraus, Prescott, Knowlton & Stone 1986). The proportion of three-year intervals (82,4%) is similar to that recorded off South Africa, and although the sample size is small the average calving interval of 3,12 ± 0,15 years is not significantly different from that off South Africa (Mann-Whitney U test, $z = 0,091$; $p > 0,50$).

As pointed out in the report of the IWC special meeting on right whales held in Boston in June 1983, the observation of a roughly three-year calving interval can only be reconciled with a 7% rate of population increase

Table 4 Frequency of calving intervals in right whales off South Africa, comparing the central survey area (20–22°E)[1] with the periphery (< 20°E, > 22°E)[2]

Calving interval (years)	Number of intervals			Number of cows		
	20–22°E	<20, >22°E	Total	20–22°E	<20, >22°E	Total
1						
2	4	2	6	2		2
2,5				2	2	4
3	81	36	117	65	21	86
3,5				1	1	2
4	5	2	7	5		5
5	2	3	5	1	4	5
6		4	4		4	4
Total	92	47	139	76	32	108
Ave.	3,054	3,383	3,165	3,059	3,609	3,222

[1] Animals photographed with successive calves between these longitudes.

[2] Animals photographed with successive calves (or only one of them) outside longitudes 20–22°E.

(as recorded off South Africa) if certain limiting conditions apply (Anon. 1986). This is illustrated further below.

Assuming that

(i)   the sex-ratio of newborn calves is 1:1, and

(ii) all females give birth to their first calf at the same age,

the average survival rate of juveniles from birth to first parturition that is needed to produce a given rate of increase in the adult female population can be calculated for a range of calf production rates, adult survival rates and ages at sexual maturity, using the equation

$$N_t \cdot p/2 \cdot \bar{S}^m_j = N_{t+m-1} \{(1 - S_a) + e^r - 1\}$$

where $N_{t+m} = N_t \cdot e^{rm}$

and

N_t = number of adult females at time t

p = calf production per adult female per year

$\bar{S}^m_j$ = mean annual survival rate of juveniles (from birth to age at first parturition

S_a = annual survival rate of adult females

r = exponential rate of increase of the population

m = age in years at first parturition.

Besides 'best estimates' for p of 0,314 and r of 0,068 (Best, in press), calculations have been made using the upper and lower 95% confidence limits of each. Adult survival rates of 0,95–0,98, and a minimum age at first parturition of three years, have been considered likely restraints for the other parameters.

The conclusions are fairly clear (Table 5). If it is accepted that, on average, the juvenile survival rate is unlikely to be higher than that of adults, rates of population increase as high as those observed are only compatible with a calf production rate of about 0,314 per female if the age at first parturition is relatively low compared to those reported for other large cetacea, and/ or the adult survival rate is high. Alternatively, of course, either the observed rate of increase or the mean calving interval might be overestimated, or both.

Priorities for further research should be (i) to narrow the confidence limits of the increase rate, (ii) to establish the age at first parturition, and (iii) to estimate adult survival rate. Improved precision of the increase rate can be achieved through continuation of the fixed-wing surveys. The return of animals photographed as calves with their own first calf will provide estimates of the age

Table 5 Juvenile survival rates needed to produce the observed rate of increase in adult right whales, given values for calf production, adult survival rate and age at first parturition (values in brackets indicate an average juvenile survival rate exceeding that of adults)

Age at first part-urition (years)	Calf production = 0,312 Adult survival rate				Calf production = 0,314 Adult survival rate				Calf production = 0,316 Adult survival rate			
	0,95	0,96	0,97	0,98	0,95	0,96	0,97	0,98	0,95	0,96	0,97	0,98
4,6% rate of increase												
3	0,867	0,836	0,803	0,766	0,865	0,834	0,801	0,765	0,863	0,833	0,799	0,763
4	0,909	O,885	0,858	0,829	0,908	0,883	0,857	0,827	0,906	0,882	0,855	0,826
5	0,935	0,915	0,893	0,868	0,934	0,914	0,891	0,867	0,932	0,912	0,890	0,866
6	(0,953)	0,936	0,917	0,896	(0,952)	0,935	0,916	0,895	(0,951)	0,934	0,915	0,894
7		0,951	0,934	0,916		0,950	0,934	0,915		0,949	0,933	0,914
8		(0,962)	0,948	0,932		(0,962)	0,947	0,931		(0,961)	0,946	0,930
9			0,958	0,944			0,958	0,943			0,957	0,942
10			0,967	0,954			0,966	0,953			0,966	0,952
11			(0,974)	0,962			(0,973)	0,961			(0,973)	0,961
12				0,969				0,967				0,968
13				0,974				0,974				0,973
14				0,979				0,979				0,979
15				(0,984)				(0,983)				(0,983)
6,8% rate of increase												
3	0,938	0,912	0,883	0,853	0,936	0,910	0,881	0,851	0,934	0,908	0,880	0,849
4	(0,970)	0,949	0,927	0,903	(0,968)	0,947	0,925	0,901	(0,967)	0,946	0,924	0,900
5		(0,972)	0,954	0,934		(0,971)	0,953	0,933		(0,970)	0,951	0,932
6			(0,972)	0,955			(0,971)	0,954			0,970	0,953 ,
7				0,971				0,970			(0,984)	0,969
8				(0,983)				(0,982)				(0,981)
9,2% rate of increase												
3		(0,980)	0,955	0,929		(0,978)	0,953	0,927		(0,976)	0,951	0,925
4			(0,988)	0,968			(0,987)	0,966			(0,985)	0,964
5				(0,992)				(0,990)				(0,989)

at first parturition. Calculations of adult survival rate should be possible either directly, from the rate of return of known individuals in successive surveys with constant effort, or indirectly from the output of mark-recapture models. All three actions require a commitment to continued long-term study of the population.

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