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12. External Features in Southern Right Whales (*Eubalaena australis*) and Their Use in Identifying Individuals

Abstract

Individual southern right whales (*Eubalaena australis*) can be recognized on the basis of several external features, the most important of which is the pattern of callosities (raised and thickened patches of skin) on the head. An analysis of these external features has been made, primarily from 16,000 aerial and shore-based photographs taken off Peninsula Valdés, Argentina, from 1971 through 1976. The callosities and several types of pigmentation patterns are described and are shown to be different for each individual and constant enough over time for individual recognition. A total of 484 individuals were identified at Peninsula Valdés between 1971 and 1976 (mortality rates are not known). Both similarities and differences are found between right whales in the western South Atlantic, the eastern South Atlantic, the North Atlantic, and the North Pacific. A technique is presented for calculating the chance that there exists in a population animals too similar to be distinguishable. It is argued that natural markings are better than visual tags as a means of identifying large populations of some wild animals.

Introduction

One of the distinguishing features of black right whales (genus *Eubalaena* Gray 1864) is the presence of unique structures called callosities, which are patches of thickened, cornified epidermis on the tops and sides of their heads. The function of these callosities has been the subject of speculation for years. During a study of southern black right whales, we noticed that the distribution, size, and

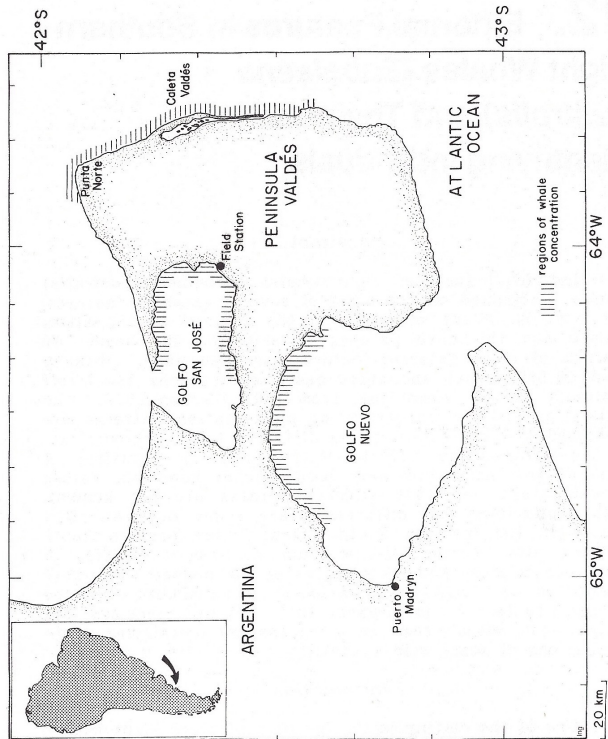


Figure 1. Map of Peninsula Valdés, Argentina showing principal areas frequented by right whales and the field station established for this study.

the callosities vary from whale to whale, as do some other external features. We guessed that these differences would allow us to identify individuals and would thus lay the foundation for modern behavioral studies of these whales.

Methods and Materials

Species Studied

The taxonomic status of right whales is not settled. It is accepted that the Greenland right whales or bowhead whales (*Balaena mysticetus* Linnaeus 1758), which are restricted to cold waters of the northern hemisphere, are a separate species from the black right whales (genus *Eubalaena* Gray 1864), which are found in temperate waters of both northern and southern hemispheres. Some authors place black right whales in the genus *Balaena* as one or more species (e.g., Eschricht and Reinhardt 1866; Rice 1977). More authors place them with the genus *Eubalaena*, with two to five species (e.g., Allen 1908; Lönnberg 1923).

The whales we have studied are black right whales from the southern hemisphere. We call them *Eubalaena australis*, in spite of the unsettled state of the taxonomy, because currently it is the most unambiguous reference to the black right whale that lives in the South Atlantic. We will refer to them as southern right whales in the remainder of the paper.

Study Areas

The main region of our study was the waters surrounding Peninsula Valdés, Argentina, a large cape which encloses two bays, Golfo San José and Golfo Nuevo. On the south shore of Golfo San José, the New York Zoological Society has built and maintained a field station from which our research is based (Figure 1). We have studied southern right whales in this region between June and December, the months when they are abundant there, from 1970 through 1981, but in this report we include the results only through 1976. These results are mostly from 52 airlights along the coast of Peninsula Valdés, from which we have analyzed nearly 16,000 photographs. Table 1 shows the monthly distribution of analyzed airlights for each year in Argentina.

In addition, one of us (R.P.) spent 10 days, in September 1974, in Cape Province, South Africa doing a brief survey of the southern right whales there for comparison with the Argentine whales. The survey consisted of two airlights, covering most of the coast of Cape Province from 13 miles north of Capetown to 25 miles east of Port Beaufort. Our techniques of collecting and analyzing aerial photographs were essentially the same as those described below for the work in Argentina.

Aerial Techniques

In Argentina, we used a Cessna 180 airplane for observations from the air. We soon realized that the whales are concentrated near shore in three quite specific areas, so we focused our efforts in these areas (Figure 1). We almost always followed the coastline of the peninsula, staying less than two km out from the tide line, and flying at altitudes less than 200 m when searching for whales. When taking photographs for individual identification, we dropped down to between 65 m and 150 m (usually 100 m) while circling over each whale or group of whales. We found that it was important to take several pictures of each individual, striving particularly for motor drive sequences in which the shutter release was depressed for several frames. This removed the inevitable motion of the camera when pressing and releasing the shutter and made those pictures in the middle of the motor drive sequences steadier than the first and last frames of the same sequence.

We used a 300 mm f2.8 Topcon lens on a hand-held 35 mm, motor-driven Nikon camera, usually with a shutter speed of 1/500th of a second. In 1971-73, most photographs were made on black and white film (Kodak Plus-X), and in 1974-76 most were taken in color (Kodachrome or Ektachrome). Although color film is more difficult to work with when analyzing the data, we found that it made it easier to distinguish between apparent and real callosities (see below). Some photographs were taken with a gyrostabilizing unit (Kenyon Stabilizer, Model KS-6) attached to the base of the camera, but they were not of significantly better quality than those taken with a hand-held camera.

We directed the pilot to guide his approach to each whale so that the plane was closest to the whale when its head was closest to the plane, and when the plane was between the sun and the whale. We found it to be important to take photographs of the heads of whales from in front of them, not from behind, because much useful variability which occurs near the anterior end of the rostrum (the bonnet) is lost in a rear view. After every sequence of photographs, the photographer recorded the location, number, and behavior of the whales photographed and put a "blank" on the film to avoid ambiguity in later analysis. Usually, an additional observer counted the total number of whales seen in each group. The average flight time was 3.6 hours (range 1.5-6.5).

Analysis of Aerial Photographs

The process of identifying a whale was primarily based on the careful analysis of photographs of its head to

Table 1. Monthly distribution of analysed airflights at Peninsula Valdés, 1971-1976.

Year	June	July	Aug	Sept	Oct	Nov	Dec	Total for Year
1971	0	0	3	5	7	0	0	15
1972	0	0	0	5	4	5	0	14
1973	1	1	1	2	2	2	1	10
1974	0	0	0	1	1	0	0	2
1975	0	0	0	2	0	1	1	4
1976	0	0	0	1	4	2	0	7
Total for Month	1	1	4	16	18	10	2	52

José and used a 1000 mm Century Precision Optics lens to photograph whales, which sometimes swam directly underneath the observation point.

We often used one or more Avon or Zodiac inflatable boats to approach whales closely on the water. By working from boats, we were able to obtain excellent above and below water close-up photographs of callosities and, in several cases, to collect by hand bits of loose callosity tissue, skin, and ectoparasites from whales that came within touching distance of boats or swimmers. We have had the opportunity of closely examining three right whale corpses that stranded at Peninsula Valdés: two male calves, probably stillborn (by their short length), that stranded in Golfo San José in August and October 1972, and one adult lactating female that stranded in Golfo Nuevo in October 1972.

Results

Reactions of Whales to Planes and Boats

We found the response of right whales to our airplane to be somewhat varied. Most whales, especially those in groups, demonstrated no obvious changes in their behavior. Calves playing with their mothers continued to play, courting groups continued their courtship, breaching or lobtailing whales continued those behaviors, and whales apparently asleep (motionless at the surface with infrequent shallow breaths and often a dry back) were usually not aroused by the plane. Whales that were traveling or "making-a-passage" were, however, usually very difficult to photograph; they would appear at the surface to breathe for only a few seconds after especially long periods underwater. They gave no indication, however, that they were avoiding the plane but rather were simply involved in a behavior that kept them below the surface most of the time.

Isolated individuals that were milling or still, in contrast, often appeared actively to avoid the plane, breathing only when the plane was not over them. Their avoidance seemed calm and deliberate as though they simply chose to be below water when a disturbance was nearby. There were also a very few individuals (probably less than 2%) that exhibited pronounced fright reactions: rapid swimming or diving as the plane came overhead and, very rarely, rapid swimming accompanied by defecation. Their behavior, as reported by observers on the shore, appeared soon to return to normal as the plane left the area. With the exception of these animals, we felt that small planes circling 100 m or more above the whales caused only minor interruptions of normal behavior, when they interrupted it at

Table 2. Sighting frequency of 484 identified right whales at Peninsula Valdés, 1971-1976. Repeated sightings are not necessarily in consecutive years.

# years photographed at Peninsula Valdés	1	2	3	4	5	6
# identified whales	216	135	81	38	13	1

all. For this reason we feel that our technique allows identification of right whale populations with a minimum of disturbance.

The reactions of individual whales to closely approaching boats powered by outboard motors was varied. Some stayed in the vicinity of the boat for several seconds or minutes after a slow approach to within touching distance; others made one or two passes on a stationary boat before leaving, and still others avoided boats altogether. We found that close encounters only followed slow approaches by the boat. On several occasions the whales made what we learned to be threat displays from later observations of interactions of individual right whales with their own and other species. However, in no instance was any threat carried as far as physical violence to the boat.

Identification of Individuals

From the 52 airflights in Argentina and nearly 16,000 photographs, we have recognized 484 different whales, that is, we got at least one photograph of each one with enough information to distinguish it from any other well-photographed whale. The number of whales identified per airflight ranged from 6 to 111. Table 2 shows the sighting frequency at Peninsula Valdés for the 484 identified whales, 268 of which we have seen in more than one year. In South Africa, from the two airflights and just over 400 photographs taken in 1974, we identified 30 different individuals. No whales were seen in both locations, suggesting that these are separate populations with little or no mixing.

During the airflights, we were able to distinguish two age categories of right whales: calves -- very small whales (clearly animals in their first year) accompanied by very large whales; and non-calves -- all other right whales. Within the category of non-calves, we could sometimes distinguish subadults from adults, a technique which required a boat or an obviously larger whale with which to compare lengths. Using airflight photographs we were often able to

Table 3. Number of southern right whales identified by year (Argentina airlights only).

	1971	1972	1973	1974	1975	1976	Total	Annual Mean
All whales	184	202	205	86	146	129	952	158.7
Mothers with calves	19	27	37	14	30	31	158	26.3
% of non-calves identified for the first time	100%	56%	34%	23%	27%	21%	-	-

calculate the ages of whales by measuring photographic negatives (Whitehead and Payne 1981).

Non-calves were much easier to identify than calves. In Argentina, we have encountered non-calves from the air a total of 1992 times and have been able to identify the whale in 1715 (86%) of these encounters. Many of these are, of course, the second, third...up to sixteenth identification of the same whale on different days. Calves, on the other hand, have been photographed on 568 occasions and identified in only 158 (28%) of these times. The reasons for the difficulty with calves are that the heads of young calves are small and are often covered with ectoparasites (cyamids) that obscure the callosity pattern by inhabiting bare skin as well as callosity tissue. Both problems disappear within the first few months of life.

We have also considered the accuracy with which we made our identifications. During the years 1971-75, we identified non-calves 1299 times. Of this total, we gave 81% of our identifications an A rating for reliability. Twelve percent were B rated, six percent C, and one percent D. Taken together with our previous data showing that we could identify 86% of all of the non-calf whales photographed, this indicates that we can identify with confidence (with an A rating for reliability) 70% of all the adults and subadult whales (i.e., non-calves) we photograph.

We have summarized the number of whales identified each year from airlights at Peninsula Valdés in Table 3. We identified a mean of 158.7 whales per year. Of these, an annual mean of 26.3 were identified mothers with calves. Since each mother had one calf, the total number of identified mothers, 158, is also a minimum figure for the number of calves born during these six years. We have also calculated the percent of non-calves identified each year which were seen that year for the first time. In 1971, of course, 100% of the non-calves were seen for the first time. That figure decreases with time and appears to be stabilizing somewhere between 20% and 30% in the last three years analyzed. In a later paper we will present the conclusions we can draw from our individual identification data about the population biology of these whales.

Catalog of Individuals

Our work on individual identification has resulted in a catalog of individual whales photographed at Peninsula Valdés. The main section of this catalog contains the best single photograph of each whale's head showing the distinctive features, the callosity patterns (see below). A second and much smaller section contains photographs of

distinctive features on the backs of right whales -- pigment patterns and wounds (see below).

Callosities

Appropriateness of the term "callosity". Since the work of Matthews (1938), the term "callosity" has been used to describe the patches of thickened skin on the heads of right whales. However, prior to his work, several terms were used, with "excrecence" being the most common (Van Beneden 1868, Ridewood 1901, Lönnberg 1906, Allen 1916). We feel the term "excrecence" is inappropriate, inasmuch as in its primary meaning it indicates "an abnormal growth", whereas the growths on the heads of black right whales are normal. "Callus", on the other hand, refers to a host of tissue types which have in common that they are thickened, though not necessarily from wear. For example, the thickened pads of skin on the rumps of primates are called callosities, and in botany, "callus" refers to thickened formations on sieve areas and at the base of cuttings or below wounds. As Esau (1953, p. 271) explained, "These two unrelated formations bear the same name because both constitute thickened masses, a concept implied by the word 'callus'." Thus, adhering to the general biological meaning, we will call the normal, thickened patches of skin on the heads of *Eubalaena* callosities.

General description. Callosities of southern right whales vary from mostly smooth in fetuses with a molded or wrinkled appearance (Lönnberg 1906, Matthews 1938) to very rough in adults with tall, irregular projections and deep clefts. Some time after birth, they become roughened and pitted and almost completely covered with colonies of amphipod crustaceans of the family Cyamidae (whale lice). It is not known whether the nature of the whale-cyamid relationship is commensal, parasitic, or symbiotic, but the cyamids contribute significantly to the appearance of the callosities. We will discuss in some detail what causes callosities to appear light or dark because contrast with the darker skin is part of the way one detects the callosity outline in aerial photographs.

Color. When viewed from a distance, callosities appear to be principally white (Figure 2). However, as first suggested to us by W.E. Schevill, this could be due to the almost continuous layer of white cyamids covering each callosity. Our observations support his suggestion. Later we became aware of an article by Roussel de Vauzème (1834) who said that the chalk white cyamids occur in such prodigious quantities on the heads of right whales that one sees them a long way off at sea. On at least 20 occasions,

we have had close looks at the callosities of whales that surfaced within less than two meters of our boat. In all cases, the callosity tissue visible in spaces devoid of cyamids was not white, but some shade of gray. We also have over 50 close-up color photographs of the heads of free-swimming right whales, and they indicate the same thing (see Payne 1972, 1976 for close-up color photographs). And once when we were able to dislodge a callosity projection from a live whale, the color of the tissue was dark gray.

We have dissected and examined callosities from all three right whale corpses described above. The callosity tissue from the two calves was very light gray (though skin near it was black), with several patches on the mandibles ("mandibular islands", see below) being white. On the adult corpse, one callosity had black tissue, but this color may have been a consequence of exposure after death. In all callosities that we dissected, the surface was darker than the underlying tissue, with the darker outer layer being no more than a few millimeters thick. Struthers (1887), who examined the corpse of a humpback whale, noted that "when the epidermis is off the *cutis vera* is at first white or cream colored ... then under exposure for some time to the air it becomes bluish, and on being scraped the cream color is restored." Our observations indicate that with the exception of white blazes (see below), all right whale skin, including callosities, darkens with time. We have several examples of this: 1) peeling skin is darker than the underlying layers it exposes; 2) when small calves are first seen, they are lighter gray than their mothers and they darken with age; 3) the rare calves that are white become gray as adults, although their ventral white blazes do not; and 4) scrapes on skin are lighter than surrounding skin. The dark surface color of callosities seems to be just another example of this phenomenon.

In all observations of living whales including partial albinos, we found callosity tissue to be lighter than the whales' living skin.

The color of callosities that one usually sees on live whales is a combination of the colors of the ectoparasites and of the callosity tissue itself. On adult southern right whales, cyamids of a white color are by far the most predominant ectoparasite on the callosities. There are often patches of yellow and of orange on the whales' heads as well. In the best of our photographs, these appear to be clusters of cyamids also, but we have not sampled from these colored patches.

Our observations fit exactly with those of Roussel de Vauzème (1834) who examined cyamids on freshly killed right whales from the South Atlantic which were floating alongside the whaling ship. That allowed him to observe what was

presumably a more normal distribution of cyamids than would be found on the fully stranded specimens others have worked with. He noted three species of cyamids and described them as follows: 1) *Cyamus ovalis* - chalk white, living in great quantities on the callosities; 2) *C. erraticus* - wine-red, found at the base of callosities, on smooth skin between callosities, in the axes of flippers, in genital-anal grooves, and in wounds; and 3) *C. gracilis* - light yellow, like *C. ovalis* restricted to the callosities, but found there in jumbled masses ("pêle mêle"), not maintaining an orderly distribution as was true of *C. ovalis*.

The yellow, orange, and white organisms that we have seen are consistently located in different areas. White cyamids may completely cover a callosity and are most densely clustered on the sides and in shallow depressions. They are seldom found on very high projections. The orange color usually occurs separately from the white, either in isolated disc-shaped clusters on the smooth skin between callosities or in narrow bands (sometimes just a single row of animals) outlining the white cyamid concentrations. Orange is also seen in wounds and in other depressions on the body. An organism of this same orange color heavily infests the heads of most calves in their first few months of life, covering not just callosities, but usually the whole rostrum and sometimes most of the sides of the head as well. The yellow-colored organisms are often in distinct clusters, and are concentrated near the middle of the largest callosities and thus surrounded by white cyamids. Seen from a few meters away, callosities look somewhat like miniature snow-capped mountain ranges, studded with jagged black projections which, on closer inspection, turn out to be the bare peaks of callosity tissue projecting from out of the cyamid "snow" (like mountain peaks from which the snow has been blown). Occupying the snow basins like glaciers are the yellow cyamids, while fringing the mountains at their base are the orange cyamids.

A number of species of cyamids are reported to occur on right whales -- *Cyamus ovalis*, *C. gracilis*, *C. erraticus* (Roussel de Vauzème 1834, Leung 1965), *C. catodontis* (Best 1970), and *C. ceti* (Omura 1958). No color differentiation between these species is mentioned by Leung (1967) in his key to cyamids. Omura, Ohsumi, Nemoto, Nasu, and Kasuya (1969), however, noticed color variation in cyamids found on North Pacific black right whales. They report cyamids of a yellow-white color on the callosities and a yellow-brown color on "other body surfaces", without being clear about the species composition of these two colors.

On the beached right whales we have seen, cyamids were crawling all over the body. Other authors have erroneously assumed this indicates that cyamids are broadly

distributed over the live right whales' bodies (Matthews 1938; Omura 1958). However, in our underwater observations of live right whales, only a few cyamids are seen anywhere on the body of a non-calf except for callosities, creases in the skin, wounds, or scars. (On calves, we find them on the sides of the head and elsewhere where skin is temporarily rough).

Distribution of callosities. The overall distribution of the callosities on a right whale's head is very similar to the overall distribution of facial hair on a human being -- we assume that the parallel is meaningless biologically. Callosities are distributed along the mandible, along the upper margin of the lower lip, along the narrow dorsal surface of the rostrum and over the eyes (Figures 2 and 3). The number, shape, size, and distribution of these callosities varies from whale to whale and is usually asymmetrical on the same individual. From our sample of 484 Argentine right whales and 30 South African right whales, we find that the areas in which callosities are likely to grow are limited (Figures 3 and 10). Within callosity growth regions many different callosity structures and placements are possible. In some regions all individuals have callosities, while in other regions callosities occur in only some individuals.

The following is a list of the callosities always present in the southern right whales we have seen (see Figure 3 for illustration):

- 1) Bonnet: a large callosity (usually the largest on the whale) at the tip of the rostrum. "Bonnet" was a term first used by early whalers who fancied it resembled a lady's bonnet. Although the term seems inappropriate, it is probably too fixed in common usage to be abandoned.
- 2) Coaming: a single, large callosity directly in front of the blowholes. This callosity, which is analogous to the bulge of tissue situated directly in front of the nostrils in most other mysticetes, appears to prevent water that is running along the head when the whale is at the surface from entering the nostrils, by deflecting it to each side. We call this callosity the coaming after its functional resemblance to coamings on boats (baffles placed on the decks to prevent water that is running along the deck from entering the cockpit and hatches).
- 3) Post-blowhole islands: one or two (rarely more) callosities directly caudal to the nostrils. (We have called all small isolated callosities "islands").
- 4) Chin callosities: callosities positioned anteriorly on each lateral surface of the lower jaw. They are thus roughly in the position of the beard in man.

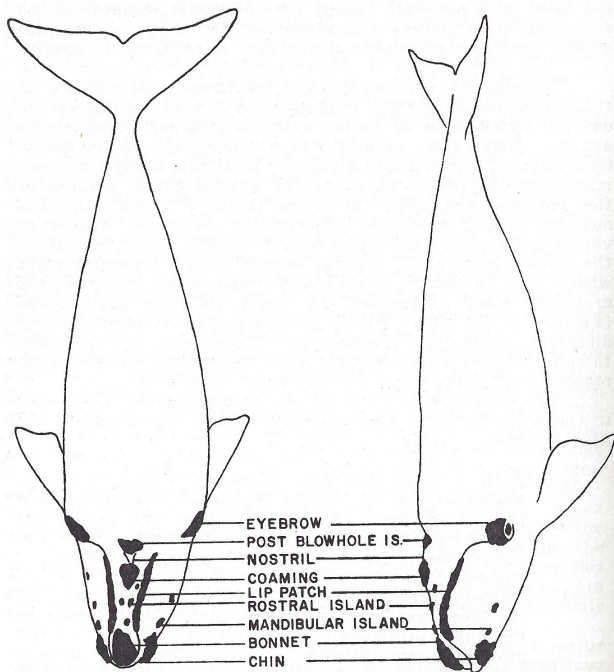


Figure 3. Diagrammatic view of a right whale showing the position and form of typical callosities. This is the same whale shown in Figure 2.

These are usually the largest callosities after the bonnet. In hundreds of opportunities we have never seen even the slightest indication of a callosity located medially on the lower jaw, such as was described by Clarke (1965) from a southern right whale off Chile.

- 5) Eyebrow callosities: large callosities lying directly over each eye. Our underwater photos of right whales showing the form of these callosities indicate that they are the callosities with the least variation in outline.

The following is a list of the callosities sometimes present in the southern right whales we have seen (Figure 3):

- 1) Mandibular and rostral islands: variable numbers of small callosities usually present in two areas: along the rami of the mandibles and on the rostrum between the bonnet and the coaming. Only in rare cases are they missing entirely. The rostral islands, along with the bonnet and the coaming, all occur between the nostrils and the tip of the snout. Collectively, these callosities comprise the whale's "moustache" -- a term first given to them by Van Beneden (1868), but not widely used since. We have never seen a continuous coverage of the rostrum in southern right whales (as is common in the northern right whale).
- 2) Nostril islands: small callosities lateral to the blowholes on either or both sides of the head. They are posterior to the anterior margin of the blowholes.
- 3) Lip callosities: callosities along the upper margin of the lower lips, ranging from a small spot to a long, broad strip covering almost the entire length of the upper margin of the lower lip.

A sampling of aerial photographs of Argentine right whale heads enables one to survey the individual variation in callosity patterns (Figure 4). The most obvious differences are in the extent of development of the lip callosities, in the number and arrangement of rostral islands, and in the size and shape of the bonnet. These callosities are all usually visible from the air when the whale blows. The post-blowhole islands, nostril islands, and coaming, though usually visible, are less variable from one whale to another and thus less useful for individual identification. Although there is much individual variation in the shape of the chin callosities and the number and arrangement of mandibular islands, these callosities are normally underwater and therefore obscured except in photographs taken on very calm days. Eyebrows

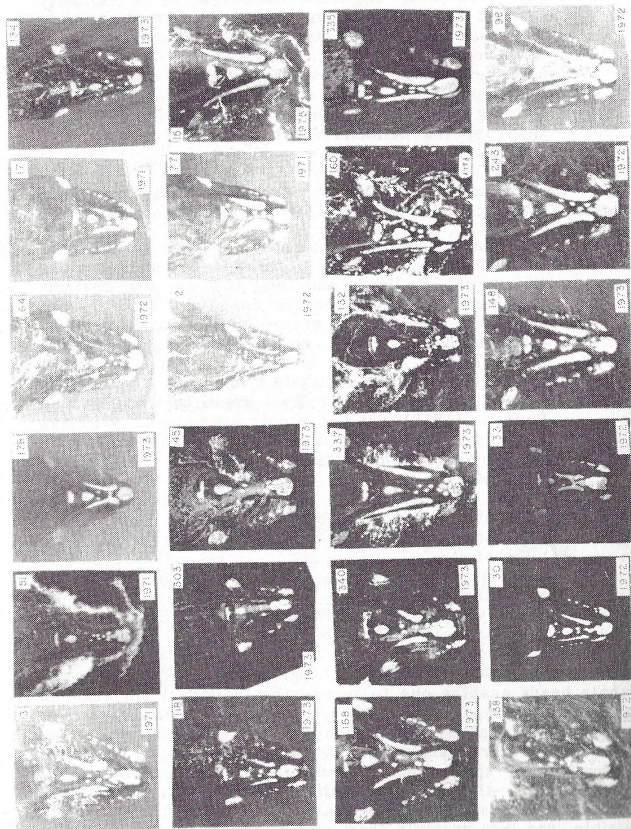


Figure 4. A sampling of Argentine right whale heads showing the individual variation in callosity patterns.

are never more than indistinct blurs through the water and are of no use in identifying individuals. Thus the principle features on which we have based our technique for distinguishing individual whales are the bonnet, the rostral islands, and the lip callosities.

In both populations of southern right whales which we studied, one of the features that is most obviously subject to individual variation is lip callosities. To study closely the individual variation of lip callosities, we selected for examination whales with good enough photographs of the lip area to be able to judge not only the presence or absence of lip callosities, but also the relative lengths of the callosities on each lower lip. The results are given in Table 4.

Two important conclusions can be drawn from these results. First, there is no significant difference between the Argentine and South African populations in the incidence of lip callosities: a chi-square test of independence between the three major categories of lip callosity distribution (no lip callosity, one lip callosity, and both lip callosities) and location resulted in $\chi^2 = 0.73$, $df = 2$, $p > 0.50$. Second, there is a pronounced and quite surprising lateral asymmetry in the distribution of lip callosities in both populations. When only one lip callosity was present, 13 out of 14 whales had that callosity on the right lower lip. And when both lip callosities were present and unequal in length, 90 out of 91 whales had the longer callosity on the right side.

When lip callosities are unequal in length, the longer is rarely more than 50% longer, and when just one lip callosity is present, it is always relatively short. Short lip callosities are usually found about midway between the snout tip and the posterior margin of the post-blowhole callosities. Thus, the tendency to form lip callosities seems to be greatest in the center of the right lower lip and least at the anterior and posterior ends of the left lower lip.

Another interesting aspect of lip callosities that we have noticed from sea-level observations in Argentina is that lip callosities always have a relatively low profile, and lack, in older whales, the tall projections that most other callosities appear to acquire.

A second feature of the callosity pattern which is especially subject to individual variation is the rostral islands. Rostral islands exhibit a gradation in size along the rostrum, with the largest being nearest the anterior end and the smallest nearest the nostrils. To demonstrate this gradation, we selected good aerial photographs of 27 whales and measured the length of each rostral island along the longitudinal axis of the head and expressed that length as a percent of the length of the longest rostral island for each whale. We did a regression of these relative lengths against the position of each rostral island ($n=142$) along the rostrum

Table 4. Distribution of lip callosities in two populations of southern right whales. Only whales with good photographs of the lip callosity area were included in the survey.

Number of lip callosities	ARGENTINA		SOUTH AFRICA	
	# of whales surveyed	% of whales surveyed	# of whales surveyed	% of whales surveyed
None	38	20%	5	25%
One				
right only	11	6%	2	10%
left only	1	1%	0	0
Two				
right longer	83	44%	7	35%
left longer	0	0	1	5%
equal	55	29%	5	25%
Total whales surveyed	188	100%	20	100%

(Figure 5) and calculated a correlation coefficient of $r=0.61$. This is significantly different from $r=0$ at $p<0.0001$. So, although there is a lot of scatter around the regression line, the rostral islands do tend to be smaller posteriorly.

When we had the opportunity to see right whales close-up at sea level, we noticed that the posterior-most rostral islands were not only smaller in area, they were also less developed in height than the more anterior islands on the same animal. Furthermore, we sometimes noticed smooth swellings on the skin which lay on a caudal extension of the same arc on which the rostral islands occurred and at about their same average spacing. Although they lacked a thickened callus covering entirely, in many cases these had a single hair in their center. Such bumps in the skin thus appear to be incipient callosities. Every gradation existed between these bumps without roughened skin and fully developed callosities. Only bumps with roughened surfaces supported white cyamids.

We suppose that the very smallest callosities provide very little area suitable for attachment of cyamids. We expect that such islands are inferior habitat and will only be colonized when the infestation of cyamids is heavy. This would mean that fluctuations in the cyamid population could cause posterior rostral islands to appear and disappear or to vary between white and gray in aerial photographs of the same whale taken at different times. This is in fact just what we see, and we have learned to take into account this kind of variation in the visibility of small islands when identifying whales.

Growth and development. A right whale's callosities enlarge as the head grows, thus maintaining essentially the same relative size to the head throughout a whale's life, and their surfaces, which are smooth at birth, split and crack with age to form numerous clefts. This gives adult callosities an appearance reminiscent of deeply checked and furrowed tree bark, which develops in a similar fashion. The splits are sometimes several centimeters deep, thus penetrating the callosity tissue at least ten times deeper than the gray surface pigmentation penetrates the underlying white tissue in the corpses we have examined. Yet, all exposed surfaces of the callosities, including the faces of the deep cleft, are gray, suggesting that the tissue surface on the walls of the clefts became darker after the split exposed them.

In southern right whales, we have frequently seen long projections of the callosity tissue sticking several centimeters above the general level of the surrounding surface (misidentified as "barnacles" in Payne 1976, p. 335). Some projections are only slightly higher than the longest

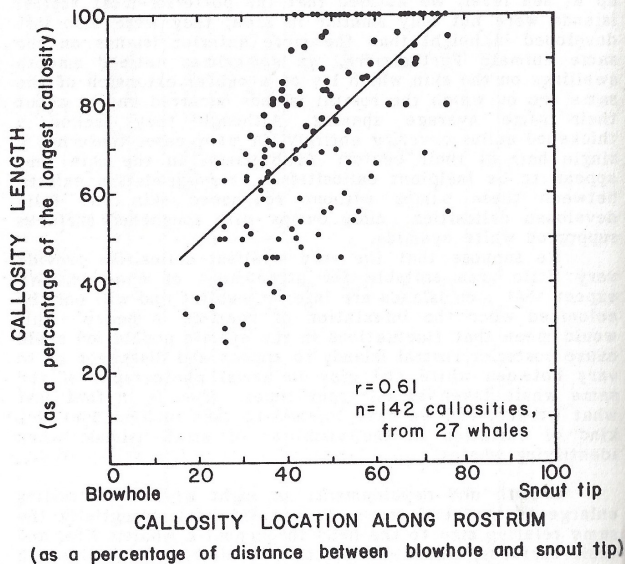


Figure 5. Length of rostral islands plotted against their position on the head. The correlation coefficient (r) is significantly different from zero ($p < 0.0001$).

diameters of their base, but others are very tall, have narrow bases, and project so far beyond the callosity surface that they seem almost like thickened hair. A common feature of all such projections is that they are seen only on large adults, never on calves or young juveniles, and are most pronounced on whales which by their size, wrinkled skin, general inactivity, and overall appearance appear to be old. These projections are also free of cyamids which may be a clue to how they are formed.

Several authors have assumed that the cyamids cause the pitting of the callosity tissue in adults. Frederick Martens who was the first to describe cyamids, claimed that cyamids "bite out entire portions of the skin, giving an appearance to the skin, as if birds were picking at it." (Martens 1675 cited by Lütken 1873). Roussel de Vauzème (1834) concluded that the digestive anatomy of cyamids showed that they ate whale skin listing toothed mandibles, jaws armed with hooked claws, chewing apparatus of the stomach, and intestines without convolutions as circumstantial evidence. He observed that the skin underneath cyamids was denuded of epidermis and corroded. Matthews (1938, p. 177) notes that myriads of cyamids "burrowed" in the callosities "... so that the deeper individuals were almost completely buried." Leung (1976) speculates that cyamids eat the cutaneous tissue of their hosts but offers no evidence in support. We have noted a high incidence of cyamids on the roughened skin, which was not itself callosity tissue of young calves, but we do not know whether the cyamids cause the roughness or only take advantage of pitting caused by another agent.

Our own examination of callosities leads us to believe that the smaller pits and depressions are probably excavated by cyamids. Part of the evidence concerns the projections of callosity tissue described above, which we propose are a consequence of simple fluid dynamic effects.

The places on the head in which cyamids concentrate demonstrate their preference for areas where water flowing past them is reduced in velocity. Thus they are likely to be concentrated in any depression as well as behind and between any obstacles, e.g., behind isolated callosities. Even when they cover callosity tissue densely, they rarely occupy the highest projections (Payne 1976, p. 334). However, when cyamids are attached to smooth skin surrounding a callosity, they are usually in dense clusters, which means only the animals on the perimeter are exposed to the full flow of water passing the whale. Furthermore, these clusters are only one layer deep (the cyamids are not clinging to each other; each is attached directly to the whale's surface). This must keep them well within the slower moving fluid boundary layers enveloping the whale.

Because flow rate past the whale will increase exponentially the further one gets from the surface (true of any submerged, moving object), callosity projections may extend into water layers that are moving too fast to be suitable habitat for cyamids. If cyamids are destroying callosity tissue, they could be expected to keep broad areas grazed flat as long as they kept up with callosity growth, but once a projection extended even a short distance above the surface, it might escape cropping by having its tip extend into fast-moving water. Such an escape into faster-moving layers of water would place the projection in a positive feedback situation in which any increase in length would improve the chances of it becoming still longer until it became long enough to be entirely exempt from cropping. In such a system, one would expect to get highly elongated projections of callosity tissue growing out of a level, grazed surface -- the condition we observe in older animals. These comments on cyamids eating callosity tissue do not presuppose any mechanism by which cyamids feed. In fact, the method of feeding in cyamids is a matter of considerable speculation.

Omura et al. (1969) suggest that callosities probably form around the bases of facial hairs. Callosities are not present in all areas where hairs are found, and hairs are not found on all callosity surfaces. However, in all right whale corpses we examined, hairs were widely scattered over the surface of the largest callosities, and the smallest callosities each had a single short, stiff hair located in a central depression.

The callosities on the calves also exhibit a peculiar feature visible in many photographs. A major part of the posterior portion of the bonnet is often found to consist of a bunch of discrete smaller callosities, each a roughly circular swelling touching the small callosities flanking it. In the center of each one of these circular swellings of "islands" there is a shallow depression (like a crater in a volcanic island) which is often darker than the surrounding tissue. From the center of this depression, a single hair emerges. In very young calves each discrete circular island in the bonnet appears to be almost entirely isolated. As the calf grows, the isolated regions also grow and make contact with each other on all sides until they fuse and form the single structure called the bonnet. The fusion does not disturb the outline of the bonnet enough to prevent recognition of the calf in future years.

Figure 6 shows the head of a calf (#191-72)¹ in which complete fusion of the bonnet has not yet taken place. The

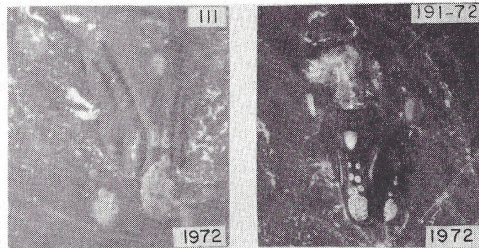


Figure 6. Two examples of bonnets showing fusion of small islands. The identification number of each whale is given in the upper right hand corner. A hyphenated number denotes a calf, the first digits being its mother's number, followed by two digits indicating its year of birth.

¹ We designate a calf by giving it its mother's number followed by a hyphen and the year of its birth.

fact that it is formed of separate callosity islands can be distinctly seen. Figure 6 also shows an adult whale (#111) whose bonnet is fully developed. Even here one can still discern the outline of the individual islands composing the bonnet. Note the dark center of each of these islands. This dark color appears to reflect that cyamids prefer a different habitat. They are aggregated around the borders and sides of isolated small callosities, the central peaks vacant. The natural gray color of the callosity tissue, therefore, shows through on the peaks, with the result that in aerial photographs each small callosity looks like a white disc with a dark center. Where several small callosities fuse to form a larger one (such as the bonnet), there are sometimes a series of dark spots that indicate the placement of the original elements or islands which fused to form the larger callosity.

Constancy of callosities over time. In order to use patterns of callosities to recognize whales over time, we must know that the patterns are essentially unchanging with time. Our evidence demonstrates that this is the case.

A small percent of the population of right whales in Argentina has white or gray pigment patterns on the dorsal surface that are usually visible when the callosities on the head are exposed during breathing. These whales are thus doubly marked, and each of the two types of marks serves as a check on the constancy of the other. Figure 7 shows two such whales photographed on two different occasions three and four years apart. Both the distinctive white blazes and the patterns of callosities have clearly remained the same over time, and there can be no doubt that it is the same individual whale photographed twice in each case.

A careful survey of 17 doubly marked whales (Table 5) bears out the constancy of callosities demonstrated in Figure 7. To make Table 5, we took all of the doubly marked whales for which we have photographs showing both the callosity pattern and the dorsal mark well in at least two different years. We examined both types of distinctive marks for changes over time. The double marking assures that we are looking at the same individual and that a significant change in one mark could be detected. Table 5 lists the years in which each whale was seen and the results of the survey. (The dorsal marks themselves are discussed in a later section of this paper).

In surveying the callosities, we found it necessary to make a distinction between changes in the distribution of callosities and changes in their color. In more than half of the whales, we noted variations in color between white and gray in one or two callosities, variations of a sort already described for posterior rostral islands and probably due to changes in the level of infestation by cyamids. These color changes were in some cases reversed later and in no case

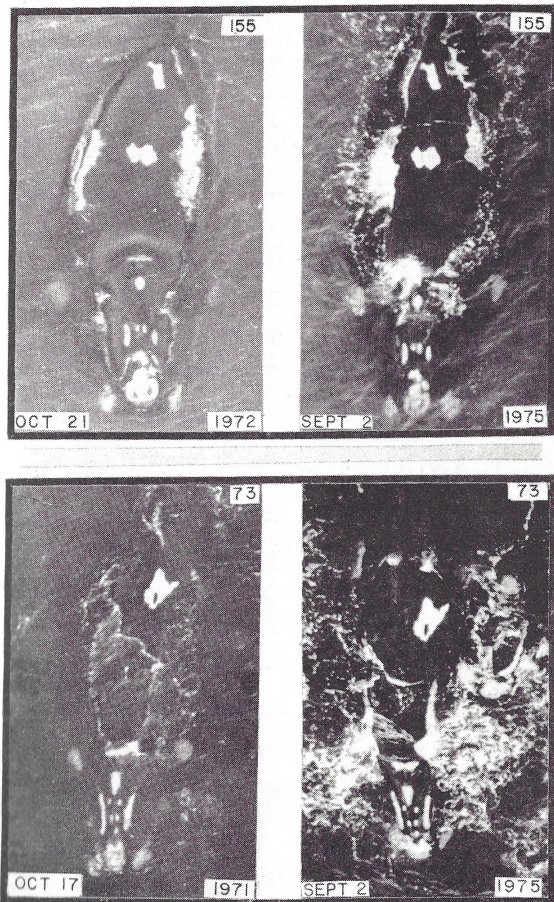


Figure 7. Photographs over time of two doubly marked whales. Neither the callosity pattern nor the blaze has changed in either whale.

Table 5. Constancy of distinctive features over time in doubly marked whales.

Type of dorsal marking	Whale I.D. #	Year					call. change	call. color change	dorsal mark change
		1971	1972	1973	1974	1975			
white blaze	54	CD			CD		-	-	
	73	CD					1x	-	
	79	CD		CD			-	-	
	155		CD		CD	D	-	2, 3x	
	162	CD	CD	CD	CD	CD	-	1x, 3, 4x	
278		CD	CD	CD			-	-	
304	D		CD			CD	-	-	
small white mark	19	CD	CD			C	-	1x	
	44	CD	CD	CD	C		-	1x	
94	CD		CD				-	-	
gray blaze	48	CD	CD	CD	CD		-	1x	
	154		CD	CD		CD	-	-	
wound	81	CD	CD	CD	D		-	5x	
	111	CD	CD	CD		CD	-	7x	
	125		CD	CD		CD	-	-	
partial albino	355	CD		CD	CD	CD	8?	8?	
	154-72		CD	CD	D	CD	9-	9-	

KEY: C callosities photographed well
D dorsal mark photographed well

- no detectable change
? questionable change
x definite change

¹posterior rostral island

²peninsula island

³lip callosity

⁴rostral island

⁵bonnet

⁶absent in 1971 and '72, white in 1973 and '74, gray in 1976.

⁷edges of wound blurred in 1972 only

⁸left lip callosity a long gray strip in 1971 and a short white spot in 1974 -- could represent a decrease in callosity tissue or in gray sloughing skin.

⁹Because this whale's skin color was mostly white when a calf and then gray, rather than black, when older, its callosities were more difficult to distinguish. All callosity features that we could see, however, showed no change over time.

¹⁰white as a calf, gray in later years.

rendered the whale unrecognizable by its callosities alone. This is partly because there was enough information in the remaining callosities and partly because the callosity that was changing color could still be recognized as callosity tissue distinct from black skin.

We found no definite changes in distribution of callosity tissue over time, just one questionable change where the pictures were not good enough to tell whether an increase in grayness represented an increase in callosity tissue or in gray skin exposed by peeling.² This examination of doubly marked whales indicates that the distribution of the callosities of most or all whales is constant over at least six years and that while minor changes in appearance do occur, these do not hinder recognition of individuals by callosity pattern alone.

Figure 8 demonstrates the minor variations that occur in the appearance of whales' callosities due to three factors: (1) changes in the angles between the camera, the whale, and the sun; (2) the obscuring and distorting effect of overlying water with foam and waves; and (3) actual changes in the color of callosities. It also demonstrates that these minor variations do not interfere with individual identification.

In Figure 8, whale #119 is pictured on four different days in 1972. While the bonnet, the rostral, and the lip callosities are visible each time, all three mandibular islands on the whale's right side show up on only two of the four days. Whale #81 is pictured in four different years. The bonnet has two anterior projections which are obvious in the last year, 1976, but which show the effect of different angles of view in pictures taken during 1973 and 1972. In 1971, the left projection appears to be missing. Close examination of very good photographs in that year reveals a gray color where it is white in subsequent years, indicating that the callosity tissue itself has not changed. What is missing is the cyanid cover over that part of the bonnet. Whale #120 is similarly represented by photographs in four different years and again shows a consistent callosity pattern over time with one minor change: the rostral island nearest the coaming is gray instead of white in 1976 and in a poor photograph would appear to be missing altogether (which stresses the importance of good photographs to this technique). However, there is enough

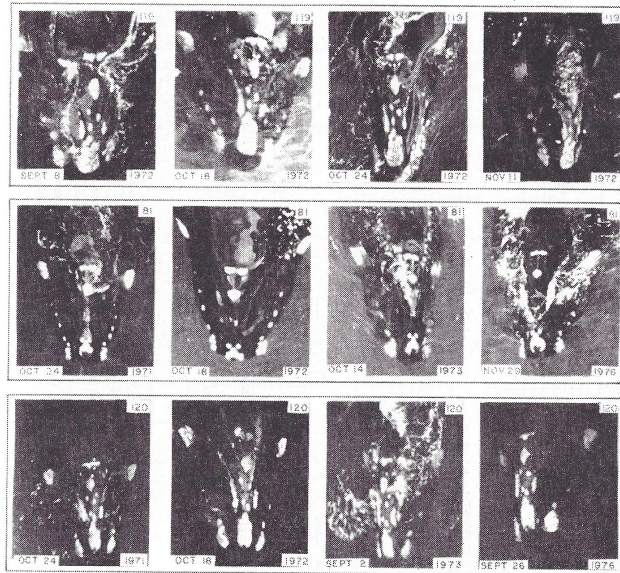
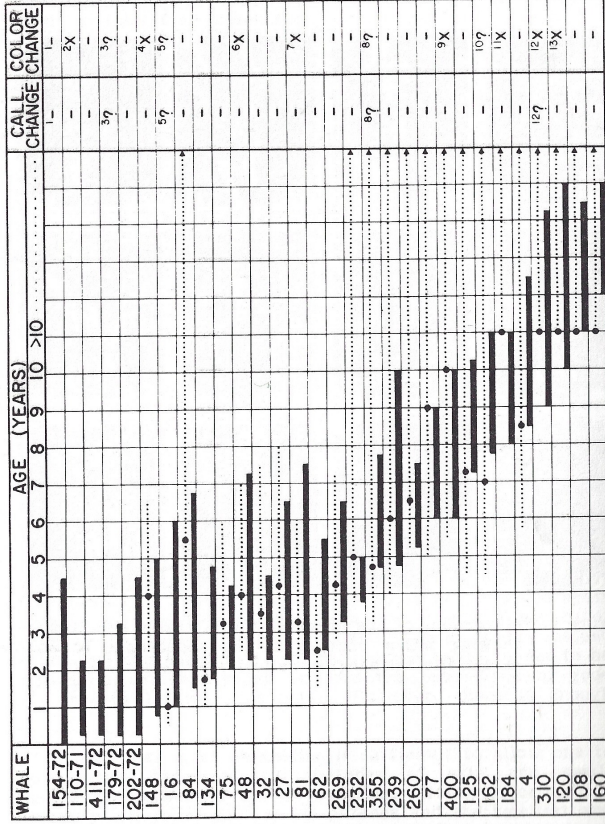


Figure 8. Photographs of the heads of three whales over time showing minor changes in the appearance of an essentially unchanging callosity pattern.

²The height of most callosities is sufficient to allow one to distinguish between gray patches of skin and small callosities without a cyanid covering. However, callosities of very low relief such as lip patches and the smallest and most caudal of rostral islands may sometimes be confused with gray skin in poor photographs. In practice this seldom presents problems in identification since there is usually enough other information to confirm identity.



■ AGE SPANNED BY GOOD CALLOSITY PHOTOGRAPHS
 ● MEAN AGE WHEN MEASURED
 95% CONFIDENCE INTERVAL FOR MEASUREMENT

- NO DETECTABLE CHANGE
 ? QUESTIONABLE CHANGE
 X DEFINITE CHANGE

Figure 9. Survey of callosity changes with age in southern right whales. The first seven whales were seen as calves, so we know their year of birth unambiguously (hence the lack of dotted lines and mean age dots for them).

- 1 See Table 5, footnote 9.
- 2 Nostril islands whiter in one year.
- 3 Nostril islands darker or absent in the last year.
- 4 Much of bonnet darkens.
- 5 Anterior notch in bonnet may have grown and lip callosity may have whitened in last year.
- 6 Small lip callosity alternates between white and gray.
- 7 Part of bonnet whitens (see Figure 7).
- 8 See Table 5, footnote 8.
- 9 Most of bonnet whitens.
- 10 Part of bonnet and of one lip callosity may be less fused in one year.
- 11 Rostral islands darken.
- 12 Anterior notch in bonnet becomes more distinct and also coaming acquires a gray patch.
- 13 Posterior rostral island darkens (see Figure 7).

information in the rest of the callosities to identify the whale in spite of the apparent change.

Having established that major changes in callosities over time do not occur as far as we can tell, we looked to see whether minor changes are concentrated in any period in a whale's life. We have developed methods to estimate the age of whales from photographs (Whitehead and Payne 1981). This technique, briefly, is to drive a boat that is carrying a circular disc of known diameter alongside a whale and to take an aerial photograph of the boat and whale next to each other. The length of the whale is then measured from the photograph using the maximum diameter of the disc as a scale. Since right whales are growing during the first 10 years of their lives, by knowing their length we can make an estimate of their age.

In order to get some idea of how callosity changes are distributed throughout a whale's life, we have selected individuals of different ages for which we also had good callosity photographs over time. Figure 9 lists these whales with the ages, when they were seen, estimated by photographic measurements or, for calves, by assuming that they were born on July first of their calf year (birth also occurs in months other than July). We have samples of whales of all ages up to and beyond ten years, where our ability to discriminate age stops. Out of 30 whales, 4 showed only questionable changes in distribution of callosity tissue (all of which could have been changes in cyamid cover), and 14 whales had possible or definite changes in color of callosities. There seems to be no age-related concentration of either type of change.

Our failure to find any age class within which major changes in the callosity pattern occurs strongly suggests that the callosity pattern remains well enough fixed throughout life to make individual recognition by this means a practical technique.

Number of theoretically possible callosity patterns.

Another requirement that must be met if we are to be able to use callosity patterns to distinguish individuals is that we must be sure that there are at least as many patterns possible as there are whales to be identified. For this purpose, we have tried to estimate the numbers of different patterns that could exist at the fineness of detail we are using to make our determinations of identity. That fineness of detail is quite coarse, and when identifying whales, we ignore much of the detail visible in the callosities. It is difficult to estimate just how much detail we do use, and it probably varies from whale to whale. However, we can approach the problem from a different angle. We can determine the "grain size" at which we can no longer tell heads apart and then assume that we must be examining patterns in somewhat more detail (i.e.,

at finer grain). If we base our calculations of the number of possible callosity patterns on grain size that is too coarse to distinguish between heads, we will get a conservative estimate of possible patterns.

In order to determine grain size, we took good quality aerial photographs of right whale heads and degraded them to a point where three observers, all experienced in identifying right whales' callosity patterns from photographs, were unable to identify them from among a sample of 450 heads. The degradation process consisted of projecting the photograph on a grid and fully blackening in every square of the grid that was touched by any portion of any callosity (Figure 10). The grid degrades the information in the head not only by eliminating details of outlines, but also by eliminating information on relief provided by shadows. We found that the experienced observers could no longer consistently identify whale heads that were degraded to a grain size of 50 squares by 50 squares. (The length of the side of each square was fixed at 1/50 the distance between the post-blowhole callosities and the tip of the snout).

To calculate the amount of information in a callosity pattern degraded to this degree, we first eliminated areas on the head which are never covered with callosities. The blackened areas in Figure 11 (arrived at by inspection of all the heads) constitute all points on which we have ever seen callosities. We next eliminated the areas on the head that always appear to support callosities (small areas at the location of the bonnet, chin, coaming, and post-blowhole callosity). When the resulting picture is superimposed on a 50 by 50 grid, the total number of squares occupied by optimal callosity growth areas is about 1,000. If each square can be either black or white, then there are about 2^{1000} (or 10^{301}) possible combinations of patterns -- a number fixing the upper limit to the number of different degraded callosity patterns that could be recognized from close analysis of good photographs.

Number of observed kinds of callosity patterns that can be distinguished in practice. In the above argument, we have assumed that every square area of callosity growth can be covered with callosity tissue or not, independently of every other area. In fact, however, we have never observed many sorts of theoretically possible callosity arrangements, and it is very likely that many of them do not occur. In addition, we have assumed that we are using only the best photographs, with each head photographed from a certain angle, without tilt. But often we wish to work from less good photographs or from photographs showing the head tilted at a greater or lesser angle to the film plane. When working with heads at an angle, we have to make mental transformations to overcome perspective distortions, and these transformations

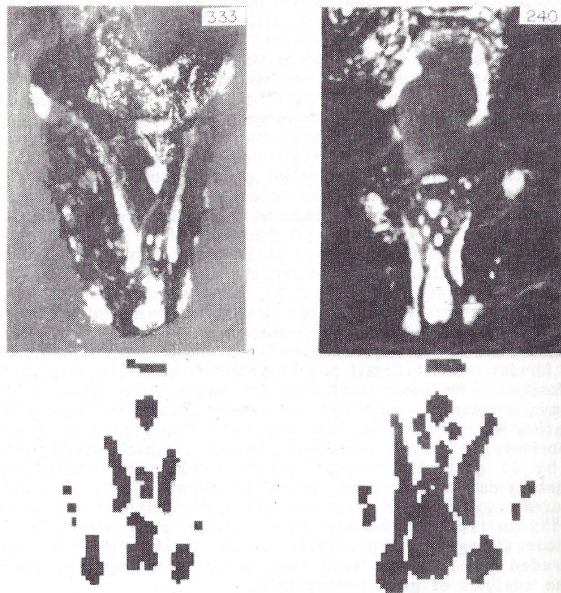


Figure 10. Photographs of two heads compared with their informationally degraded diagrams.

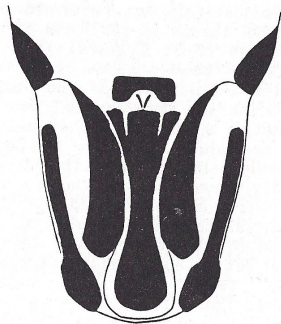


Figure 11. Diagram of the head of a right whale showing in black areas where we have observed callosities.

introduce uncertainties. As a result, although a very large number of patterns exist at the grain size required to identify individuals, we will be unable in practice to detect many of them. To get a more realistic estimate of the amount of variability available to us, therefore, we tried to calculate the number of patterns that could occur, based on the variation we have observed in Argentina and South Africa, and the number of those that we could expect to detect given the limitations to the data under the conditions that we normally face.

To make this calculation, we examined our catalog of head photographs from Argentina and from South Africa for the number of distinct forms (values) that each kind of callosity (character) has been observed to take. It was at once apparent that some portions of the callosity pattern show more useful variability than others. For instance, the outline of the bonnet is a character that can have a great variety of shapes or values, whereas the outline of the coaming is relatively simple. We therefore took each callosity or callosity group and estimated its variability independently. We were only concerned with the number of values for each character which could be recognized in practice, so we tried to pick values that were unambiguous.

As an example, let us consider lip callosities. Judging conservatively, we felt that we could distinguish unambiguously between four different lengths of lip callosity, in addition to absent lip callosities and to those consisting of a single spot. Each of the four lengths could be either continuous or broken in increasing number of distinguishable places according to length (2, 3, 4, and 5 places for short, medium, long, and very long lip callosities, respectively). This gives the following number of distinguishable configurations for each length: absent (1), spot (1), short (4), medium (8), long (16), and very long (32). Finally, each configuration of the latter four lengths could be two distinguishable widths, giving a total of 122 distinguishable types of lip callosity. Each whale has two sites for lip callosity placement (left side and right side), so that if all lengths could co-occur, the number of recognizable lip callosity patterns would be 122×122 or 14,884.

This may be an overestimate for three reasons. First, we have never observed dramatically unequal lip callosities, like a spot on one side and a long or very long callosity on the other. Second, we have never observed more than three breaks in a single lip callosity. Third, we have almost never observed lip callosities of unequal length where the left lip callosity is the longer (Table 4). To be conservative, then, we have subtracted the combinations and configurations we have never or almost never seen to get a corrected number of expected and recognizable patterns equal to 7,215.

We performed similar calculations on the observed variations in the other five callosity areas, with the following number of recognizable configurations for each: bonnet (208), rostral islands (14,810), coaming (12), blowhole islands (11), and post-blowhole islands (37). If we assume that the six characters sort independently and that they occur with equal frequency, then the number of possible overall head patterns is the product of the number of recognizable variations in all six areas multiplied together, which equals 1.09×10^{14} . It is likely that neither independent assortment nor equal frequency holds throughout. However, it seems unlikely that adjusting for these assumptions would force us to change our conclusion that the variability is vastly more than is needed to allow recognition of every whale that has ever existed at one time. Even the most optimistic estimate of the present world population of right whales falls short of 10^4 .

Look-Alike Whales

We have now calculated 1) how many different callosity patterns could exist at the level of detail we need to make our determinations and 2) how many different patterns we could recognize in practice with our technique. We still do not know the distribution of different recognizable patterns in the population. The reason we would like to know this is to be sure that there is not one pattern (or even several patterns) that is repeated.

Pennyquick (1978) offers a powerful technique based on information theory by which the reliability of identification can be calculated in terms of the probability that a pattern of natural markings will be duplicated in a population of given size. However, it might be wise to include a warning about applying his technique to field data. His technique involves determination of the frequency of occurrence of the values of all characters used to identify individuals of the species. When making this determination on animals in the wild, one is forced to assume that if an animal with a specific pattern is seen twice, that it is the same animal both times. But n sightings of the same identifying marks could represent anything between 1 and n animals of identical appearance. And inasmuch as Pennyquick's technique is employed in order to avoid confusing one's conclusions with animals of identical appearance, his technique seems to contain a circular fallacy. However, the fallacy can be avoided and Pennyquick's technique used if one marks some of the animals in the population and calculates the frequencies of characters only from them. When this is impossible, one is probably restricted to using corpses for calculating character frequencies.

We have developed a different approach to this problem. We offer a technique to estimate how many pairs of identical animals are likely to exist in a given population. Though applied here to right whales, this technique should be useful in research on many other animal species.

Let us assume that we have in a population several pairs of whales so identical in appearance that they cannot be distinguished by any means. We might think of these whales as perfect 'copies' or identical twins (though of course they need not necessarily be related). If such copies should exist, there are at least two types of events which could demonstrate their existence. One such event would be the photographing of a set of identical whales in the same photographic frame. A second such event would be the photographing of one whale in one place and its 'copy' in a different place, separated by a distance too great for a right whale to swim during the time between the photographs. One could also compare photographs taken simultaneously by different observers working in different areas, but in the case of right whales, this would require two planes, which has been a prohibitive expense for us.

If we assume that we have seen about 90% of the adult population visiting Peninsula Valdés, then there are about 550 right whales that pass through Peninsula Valdés waters. Following the usual form of statistical argument, we assume further, as a null hypothesis, that 25 sets of identical twins exist in this population. Assuming random distributions of whales, we have calculated the probability of *not* finding even one set of these twins by either of the first two methods mentioned above in all the aerial photographic data we have gathered and examined over six years. This probability turns out to lie between 0.03 and 0.04 (see Appendix 1 for derivation). Since the probability we obtained is less than the traditional level of 0.05, we shall reject the null hypothesis. In fact, in spite of two more years of census photographs beyond the data on which the above calculation was based, no identical twins have been detected.

If we accept random distribution of whales and independence of airmights, the conclusion from the above argument can be stated in another way. We can say that, even if sets of identical twins do exist in the population, we are at least 96% certain that there are fewer than 25 sets of twins in our population of 550 animals. Since 25 twins (50 whales) would constitute 9% of 550, we can feel confident that any conclusions we draw about the overall population based on our technique of recognizing whales will apply to at least 91% of the population. This is not as high a value as we would like, but as time passes, we will deal with a higher percentage of repeat sightings, meaning that as long as we do not detect any whales that look alike, the number of identical

pairs of whales that could exist in our population will keep decreasing (the confidence we can have in our conclusions will increase).

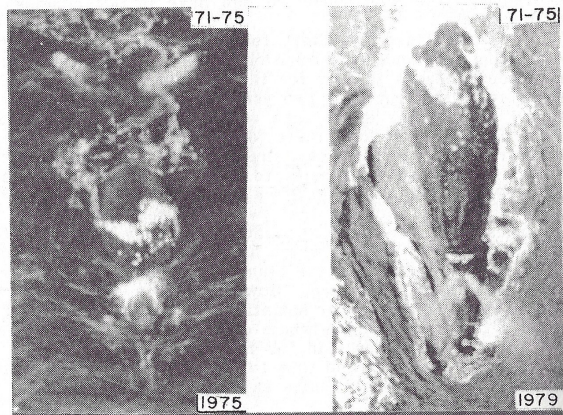
We developed the above technique long after we began collecting data and, not surprisingly, found we had overlooked numerous chances to test for the occurrence of twins. For example, during our first two years of taking data, we often failed to note the exact time we photographed each group, meaning that we lost those data for use in intergroup comparisons in the same bay, since we could not calculate the time available to the whales to swim the distance between the groups. The census path we chose to fly could also have been improved had we the twin argument in mind. On censuses that are simple counts, one tries to cover the territory so that animals which have already been seen won't have time to move into the plane's path again as it returns from searching elsewhere. However, since we census by identifying individuals, we sometimes flew back over areas in efforts to improve photographic coverage of a whale we felt we might have missed. In the future, we should be able to avoid these problems and thus to reduce our estimate of the likelihood of identical whales existing in our population.

Other Distinctive Features

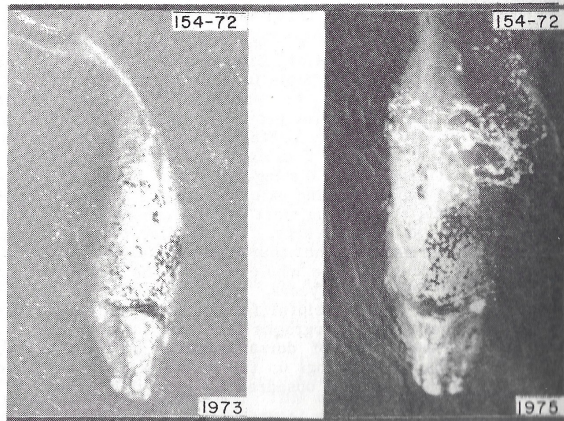
Dorsal Marks

A small percentage of our identified whales have, in addition to their callosities, distinctive markings on their dorsal surfaces that are visible in some photographs when the heads are also in view from above. As discussed earlier, these doubly marked whales provide a valuable check on the constancy of the callosity pattern over time, and two have been illustrated in Figure 7 as examples of the permanence of callosity patterns. We distinguish five kinds of marks. Although two types, peeling skin and partial albinism, affect the whole body, the back is most easily examined, hence their inclusion here as dorsal marks. Of the five types, three are essentially permanent and therefore useful for individual recognition throughout the whale's life. The fourth, wounds, may be useful over a few years. The fifth type, peeling skin, changes rapidly and is helpful for following individuals only within a sequence of photographs taken on the same day. We will discuss each type of dorsal marking in turn, omitting from consideration markings on the dorsal side of the flukes, because they are usually obscured by overlying water.

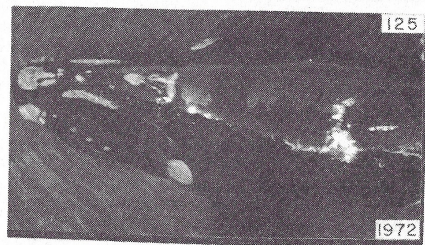
White blaze. The two dorsal markings illustrated in Figure 7 are examples of what we call white blazes. These are areas where the epidermis is presumably devoid of dark



a. GRAY BLAZE



b. PARTIAL ALBINISM



c. WOUND

Figure 12. Other distinctive features. a) Gray blaze. b) Partial albinism. c) Wound.

pigmentation. The skin is smooth and without special contour in the region of these white blazes, and the edges of the blazes are very distinct. Table 5 shows that we have found no evidence for any change in the shapes of white blazes over time. This kind of blaze appears not to darken with age but does appear to grow with a whale. We have measured the length of the blaze as a proportion of the total body length on one whale, #304-76, both as a two-to-three-month-old calf and 13 months later, and we found the proportions to be identical.

Out of the 484 identified whales in the Argentine population, nine, or 1.9%, have white dorsal marks that are clearly the white type of blaze. Another seven whales have white marks so small that we can't tell from our photographs whether they are blazes or small wounds (discussed below), so the rate of occurrence of white dorsal blazes at Peninsula Valdés is probably somewhere near 2%.

Gray blaze. A second kind of blaze occurs in these right whales, one which, unlike white blazes, darkens with age. It is also different from the white blazes in outline and in size. It is a brownish-gray color in adults and is not as easily visible as a white blaze (in poor photographs it may resemble peeling skin but the constancy of the pattern over time confirms its identity as a gray blaze). The outline of a gray blaze is much more complex than that of a white blaze: there are many more indentations and projections and small separate islands of gray and of black, so the ratio of perimeter area would be much higher in gray blazes than in white blazes. Compare the example of a gray blaze in Figure 12a with the white blazes in Figure 7. The smallest gray blaze we have seen is as large as the largest dorsal white blaze (the white blazes in Figure 7 are among the largest), while the largest gray blaze covers perhaps half of the dorsal surface.

We suspect that all of these gray blazes started out as white marks in the calf year. Four calves with white dorsal marks of the size and complexity of gray blazes have been photographed both as calves and as juveniles one or two years later. In three of these four, the dorsal mark was clearly brownish-gray after the first year. The marks of the fourth appeared still white, but it has only been seen as a yearling, and we expect that the marks will darken in the next year or two. Because we know that one gray-blazed whale is a full adult (#154, a female who has had at least two calves), we believe that the darkening of these blazes with age stops before they become as black as normal skin.

Aside from darkening from white to gray with age, the gray blazes do not change over time. The shape is constant (Table 5), and, as with white blazes, the size relative to the whale's length (measured in one calf, #403-75, at one to two

months of age and again 13 months later) appears to remain unchanged as well.

In the Argentine population, we have seen seven whales, 1.4% of our identified individuals, with this type of dorsal mark, although two of these have been seen only as calves and thus with a white rather than with a gray color to the blaze. We have also seen this type of blaze on the ventral side of two Argentine whales, both of which have gray blazes on the dorsum as well.

Partial albinism. A third type of body marking consists of a nearly complete lack of black pigmentation over the entire body. In the first months of life, such whales appear to be pure white with scattered black markings on their bodies (Figure 12b). In older whales, the background is no longer white, but is instead a gray or brownish-gray color similar to the color of gray blazes. We have never seen adults whose entire bodies were as white as the bodies of the partial albino calves and we have watched one partial albino calf (#154-72) gradually darken as it matured, to the same brownish-gray color we find in adults. It was quite gray by its second year, 1973, and has become darker since then. We conclude that partial albinos are born a white color that darkens with age. In the Argentine population, we have seen seven partial albinos, 1.4% of our identified individuals.

These whales stand out, even underwater, as noticeably paler than other whales. Their black pigmentation is restricted to a complex pattern scattered sparsely in the white or gray background. This pattern varies from individual to individual and does not change over time (Table 5). There seems always to be a rather dense accumulation of black pigment in a narrow transverse band, posterior to the blowholes and extending partly down the sides of the head, but in no case as far as the eyes. Best (1970) described three partial albino calves from South Africa, noting that in all three cases there was a black area on the posterior part of the rostrum or rostrum base. From the photographs he includes, it is clear that in all three cases the black pigmentation lies in the same region in which it is found in the Argentine partial albinos.

Wounds. The fourth type of distinctive dorsal mark that is useful for individual identification over time is a wound. We saw no apparent wounds in the South African whales, but in the Argentine population, nine whales or 1.9% of the population have what are clearly wounds, though the occurrence may be somewhat higher because there are seven whales with white marks so small that we can't tell whether they are blazes or wounds. Wounds usually consist of raised or depressed areas of skin and are colored white or orange.

The colors appear to be due to cyamids, though the white could also be exposed blubber. The outlines of wounds are often more blurred than those of unpigmented blazes, and the cyamid-infested part is often surrounded by the gray color exposed by sloughing skin (see below). Figure 12c shows an example of a wound.

In three cases the wound is a single narrow scratch running longitudinally along the back, in a different position on each whale. In the one instance in which we can see surface contours as well, the scratch occurs within a shallow groove. The scratches are usually white and may be surrounded by gray-colored skin. We have watched a scratch over time in just one whale, #81. In 1971 and 1972, the whale was photographed with no distinctive dorsal mark. The scratch appeared in 1973 and was quite distinctly white. In 1974 and 1976, #81 was photographed again, and the scratch, although still visible, had become grayer and less distinctive. It is possible that with time a small wound, like a scratch, will heal to invisibility and will thus be of no further use as an identifying mark.

Skin mottling. Another kind of marking is usually distinctive from one individual to another but is constantly changing with time. This is the pattern of gray mottling on the black skin that is apparently caused by widespread irregular shedding of the outer layer of skin. Figure 13 shows two extreme conditions of gray mottling in the same individual 15 days apart -- almost all black and almost all gray. All stages in between occur as well. The gray appears to be the new light gray skin revealed when old black skin sloughs off. It is a bluish-gray that is distinguishable from the brownish-gray of permanent gray blazes and of partial albino non-calves. The rate of change in the mottling varies: individuals photographed on consecutive days may have almost exactly the same pattern of mottling down to very fine detail or may have changed completely with no trace of the earlier pattern. Where we have seen rapid change in consecutive days, the change has been an increase of gray areas rather than loss of gray. Because of the possibility of rapid change, the pattern of gray skin can be useful for individual recognition only within a single airlight by helping to follow a whale in frames where its callosity pattern is not discernible. Best (1970) has published two photographs which show skin mottling in South African whales very clearly.

Ventral Blazes

There is one other feature, located on the ventral surface, that is useful for individual identification of southern right whales. Most southern right whales have one

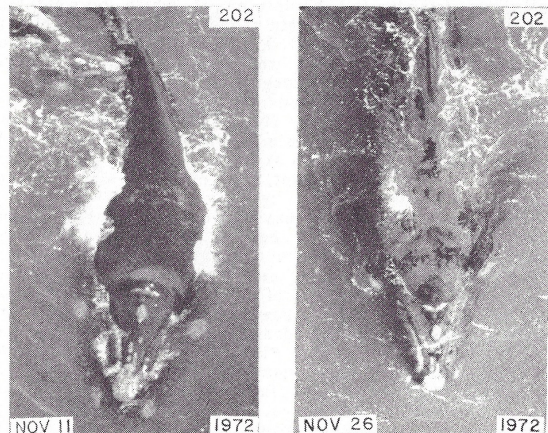


Figure 13. The change in the pattern of skin mottling due to sloughing skin on a whale photographed twice, 15 days apart.

or more white ventral blazes that range in size from small spots the size of larger rostral islands to enormous blazes covering a third or more of the ventral surface. Small single blazes invariably surround the umbilical scar and are usually elongated longitudinally. Larger blazes include the umbilical area as well as more extensive portions of the belly, throat, and/or lower flanks. They may be grossly asymmetrical and often have islands and peninsulas of white pigmentation trailing from them (particularly from the rear margins). In one peculiar case (Figure 14), a whale with a medium-sized ventral blaze has within the white pigmentation a strange, black zig-zag line surrounding the umbilical scar at a distance and in a form that looks just like the perimeter of a typical small ventral blaze. It suggests that at least two different underlying biochemical processes control development of white pigmentation skin cells and that where these processes overlap and interact, the end result is somehow normal black pigmentation.

Even small blazes may have a wealth of configurational information in the outline, as we observed in close-up examinations of nearby whales and of a corpse of a mature (lactating) female. In our aerial photographs of small, ventral blazes, however, most of the useful detail is too small to be seen. Larger blazes, however, are very complex and distinctive, making positive identifications possible from just a part of the ventral blaze. Figure 13 presents an example of a medium-sized ventral blaze and also demonstrates the constancy of the pattern over time. There is only a one year time span covered in this figure, but we have seen spans up to seven years with no visible change in pattern. This and the fact that even small calves have ventral blazes with distinct outlines leads us to believe that there is no change in these blazes over time. We have not yet, however, followed the ventral blaze of a calf as it matured.

We also believe that ventral blazes are unique to each individual, based on their variety and on the amount of information in even the smaller blazes. We cannot do a rigorous test of this, however, because the ventral blaze is almost always the only visible distinctive feature in a ventral view of a whale. In fact, more often than not, we cannot connect a ventral view to a dorsal view, showing the callosity pattern and thus the major source of information about each whale. In order to estimate the incidence of ventral blazes in the Argentine population, we examined photographs taken in 1971 alone and scored for presence or absence of a blaze only those ventral photographs of whales showing the area around the umbilicus. Out of 31 ventral surfaces that fit this criterion, 29 or 93.5% had a white blaze.

It is interesting to compare this figure with the rate of occurrence of white blazes on the dorsum which is only about 1.9%. While the latter type of blaze could be an aberration

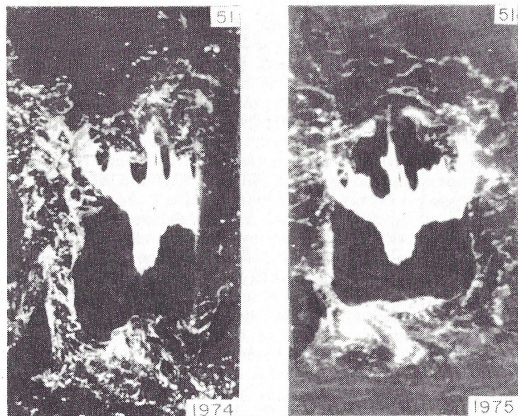


Figure 14. Example of a white ventral blaze showing constancy in the outline over a year. This whale has not been identified by any other distinctive features.

Table 6. Geographical variation in the incidence of external features of right whales. N is the number of whales that could be scored for presence or absence of each feature.

Feature	SOUTH AFRICA		ARGENTINA		NORTH PACIFIC	
	Best (1970)	Our data	Our data	Our data	Omura (1958) Omura et al (1969) Rowntree et al (1980)	
Lip callosities	86% N=7	75% N=20	80% N=188		18% N=12	
Post-blowhole callosities	100% N=5	100% N=30	100% N=475		69% N=13	
Dorsal markings (blazes and partial albinism)	11% N=75	23% N=30	5% N=484		7% N=14	
Ventral blazes	100% N=2	100% N=2	94% N=31		86% N=14	

of no adaptive significance, it would seem that blazes on the belly have been selected for and serve some function. Yablokov (1969) discusses coloration of this sort in several species of whales and suggests its possible use in species recognition. We suggest that it could also be useful to the whale in the same way it is to humans, for individual recognition when only the belly is visible.

Geographical Variation in the Incidence of External Features

We have compared our observations of callosities and other distinguishing features in the Argentine right whales with observations from other populations of right whales. Between the eastern and western South Atlantic and the North Pacific, we can make quantitative comparisons (Table 6), but only qualitative comparisons are possible with the North Atlantic because of the paucity of published data.

The data in Table 6 about the eastern South Atlantic right whales was collected off South Africa by us and by Best (1970). Our observed frequencies agree very closely with those of Best for most external features considered, but Best did not distinguish between individual whales. As a result, there may be overlap between individuals in his sample and in ours, or even overlap between individuals within his own data. For example, it is likely that some of the whales in his 1968 and 1969 census flights were the same individuals. For statistical comparisons with other areas, we have used only our own data from South Africa. In the North Pacific, we have data from three sources: Omura (1958), Omura et al. (1969), and Rowntree, Darling, Silber, and Ferrari (1980).

We found no differences in the incidence of any callosities between the South African right whales and those off Argentina. We therefore combined our data from both places and compared the South Atlantic to the North Pacific. In two features we found significant differences between the two oceans. The incidence of lip callosities in the North Pacific is only about one-fifth the incidence in the South Atlantic, a highly significant difference (t-test for comparing two percentages: $t=4.5688$, $df=218$, $p<0.001$). (Best noted a similar difference in incidence of lip callosities between these two areas). The incidence of post-blowhole callosities is also significantly lower in the North Pacific (t-test for comparing percentages: $t=4.1864$, $df=516$, $p<0.001$).

In the North Atlantic an unusual callosity configuration occurs. Andrews (1909) describes a whale from Long Island, New York and notes that there were callosities covering the head continuously from the snout to the blowhole. A similar configuration can be seen in photographs of three right whales, two from Florida and a third from Cape Cod published by Leatherwood, Caldwell and Winn (1976). In all these cases, the bonnet, maxillary islands, and coaming are fused

into one continuous callosity. We have never seen this sort of continuous callosity coverage in Argentine or South African whales in spite of our large sample. Other published photographs (Sergeant, Mansfield, and Beck 1970; Anonymous 1976) show callosity patterns on western North Atlantic right whales which are basically the same as those from the South Atlantic. There is a photograph in Watkins and Schevill (1976) which shows a callosity pattern from New England waters intermediate between these two types (wherein the bonnet, although elongated, is not in fact continuous with the coaming). We have a single Argentine right whale with a bonnet extending caudally about as far as the bonnet in the Watkins and Schevill photograph, but it seems to be an unusual pattern.

The incidence of dorsal markings varies geographically in a different way from the incidence of callosities. As noted earlier, we have seen five kinds of dorsal marks: white blazes, gray blazes, wounds, partial albinos, and marks that are too small to identify as either wounds or blazes. Of the 39 whales in the Argentine population that had dorsal markings visible from the air, 7 were partial albinos, 9 had white blazes, 7 had gray blazes, 9 had wounds, and 7 had unidentifiable white marks. Of the 30 whales we photographed in South African waters, 2 were partial albinos, 3 had white blazes, and 2 had gray blazes. There were none in the other two categories. Neither Best (1970) nor Omura et al. (1969) break down dorsal markings into these categories, so we have combined pigmented dorsal markings in Table 6. However, Omura et al. (1969) discuss wounds separately, and Best (1970) describes partial albino calves.

Using only our own data from Argentina and South Africa, we have compared the two populations in the incidence of all pigmented back markings. South Africa has a significantly higher incidence (t -test for comparing percentages: $t=3.0358$, $df=517$, $0.001 < p < 0.01$). Even if we consider the unidentifiable white marks in the Argentine whales to be blazes, the result is similar ($t=2.6984$, $df=517$, $0.001 < p < 0.01$). Although Best reported a lower frequency of these markings in South Africa than we did, the difference is not significant statistically. It may be due to his overlooking gray blazes, which can look like sloughing skin. Another possible difference between the eastern and western South Atlantic populations is the incidence of wounds. The difference is not significant statistically, but it may be of biological significance, as discussed below.

In the North Pacific, there is a single report of a white dorsal blaze (Rowntree et al. 1980) and none of a gray blaze or a partial albino. The incidence of these dorsal marks in the North Pacific is not significantly different from that in Argentina.

Ventral blazes are also examples of white pigmentation, and we found that there was no significant difference between the percentage of whales that have them in the Argentine and North Pacific populations. We have not, as yet, measured possible differences in the average size of blazes in these populations. Samples from South Africa and from the North Atlantic are too small to test statistically.

Discussion

Geographic Variation

As noted at the outset, the taxonomic status of right whales is unresolved. Our results show that, with the exception of continuous callosity coverage on the heads of some North Atlantic right whales, the differences which exist between populations are not unique to any population but are statistically significant.

To review our results: there is a highly significant difference between North Pacific and South Atlantic populations in the incidence of lip and post-blowhole callosities. There is no significant difference between these populations in the incidence of dorsal markings. The sites for callosity growth in North Atlantic right whales include areas of skin on which we never saw callosity development in the South Atlantic, and for which it has not been reported in the North Pacific.

Right whales living in the North Pacific tend to have the fewest head regions supporting callosity growth while those living in the North Atlantic have the most. (This latter point has yet to be investigated with samples from the North Atlantic large enough to make statistical comparison possible). The degree of isolation of right whales in the North Atlantic would appear to be greatest inasmuch as some North Atlantic individuals have a feature in their callosity patterns (continuous coverage between snout tip and blowholes) that appears to be found nowhere else. Until more data from the North Atlantic becomes available, it cannot be argued that the missing post-blowhole callosities in some North Pacific right whales is a unique condition.

What these differences may indicate regarding the taxonomic status of right whales is for others to decide.

The difference in the incidence of dorsal pigmentation and partial albinism between eastern and western South Atlantic right whales and the fact that we have not seen the same individual in both areas, combined with the otherwise complete correspondence of callosity growth sites on the head, seems to indicate that although the whales in these two areas are closely related, they constitute distinct stocks with little or no interchange. If theory is correct, then the two

stocks probably have different feeding destinations. This might explain why Argentine right whales have harpoon wounds whereas South African whales do not.

Of course it is not sure that the large wounds that we have observed in Argentina are caused by harpoons. They might with equal likelihood be the result of collisions with boats -- the white line directed towards the central portion of the wound being made by the keel near the bow rather than by the shaft, barb, or rope of a harpoon. But how then can we explain the fact that there are not such wounds in the South African population; and that in all cases where they do occur, the wounds are found in the same place on the back and in the same orientation to the whale's body?

It is well known (Clarke 1965) that right whales feed near South Georgia and we know of one example of what is almost certainly an Argentine right whale that was seen feeding there. There is still whaling going on in the area.

The occurrence of "harpoon" wounds only in the Argentine population also raises the intriguing possibility that the Argentine right whales, along with those seen off the coast of Tristan da Cunha (Best and Roscoe 1974) constitute a single stock, separate from the South African stock. We have made this speculation because there has been at least twice in the recent past, illegal hunting of right whales near Tristan da Cunha. One eyewitness to this was Mr. P.A. Day, then Administrator of Tristan da Cunha. His personal diary for 4 November 1963 includes this comment:

"A fine day, only marred by violation of territorial waters by Russian whalers whom we saw killing whales within half a mile of the settlement. From reports while the island was unoccupied, (during a period of volcanic eruptions), they pretty well killed all the whale around here, and obviously are unaware anyone is here."

On the following day Mr. Day writes:

"A beautiful day, whalers still active, steaming close in shore, towing whales out to a factory ship on the horizon. I have asked the Colonial Office to make diplomatic representations to the Russians."

Although the whales were not identified in his diary, Mr. Day has confirmed (pers. comm.) that they were right whales.

A second incident occurred 4 years later and was witnessed by Mr. Glen Norton, at the time Factory Manager for Tristan Investment (Pty.) Limited. He reports it as follows (pers. comm.):

"In March 1967, in Tristan da Cunha, an islander reported to the administrator, Mr. Brian Watkins, that he had seen a whale catcher operating off the southeast sector of the island. The Administrator requested me to take a boat around the island and if possible photograph any activity. We set out at 0900 in an easterly direction, keeping close inshore, and about noon, on rounding Sandy Point, sighted a Russian catcher operating off Lyon Point. We approached at low speed, taking photos from time to time. When we were about a half mile off, were sighted by the catcher, which immediately proceeded to the open sea. In doing so, all lines attached to the whale pulled out. We approached the whale as close as we dared, and photographed gaping wounds on its back, to which sea birds were paying attention. The whale was spouting pink frothy water to a height of about a foot, whilst moving very slowly in a westerly direction. By this time my film was used up, so we returned to the settlement.

The following day a Norwegian catcher (Capt. Carlsen) arrives off the settlement to drop mail. I discussed the incident with him, describing the whale, which he identified as a southern right. (Further evidence that it was this species which is often seen very close to shore comes from Mr. Norton's map showing that the catcher boat was 300 meters from the shore when he first saw it). He passed on the information to their factory ship, which was lying about ten miles n/w of the Island...

Months later we were advised; and I quote, "that the Russians apologize for accidentally straying in Tristan waters".

Reports such as these could explain the harpoon wounds on Argentine right whales. If the Argentine and Tristan da Cunha right whales are one stock, they may have the same behavior demonstrated by Darling and Jurasz (1983) and Payne and Guinee (1983) of visiting more than one breeding ground. It is a point we plan to investigate further.

Recognition by Natural Markings

In recent years the use of natural markings as a means to distinguish between individual baleen whales has been successfully employed with at least two other species. Hatler and Darling (1974) showed that the oddly shaped patches of pigmentation covering the bodies of gray whales (*Eschrichtius*

robustus) remained constant over at least three years. Katona et al. (1979) demonstrated the same for color patterns on the undersurfaces of humpback whale (*Megaptera novaeangliae*) flukes (about 900 have been identified by this means in the North Atlantic and about 400 in the North Pacific). In spite of these successes as well as our own with right whales (as this goes to press we can recognize 557), one repeatedly sees statements on recognition by natural markings such as the following by Kear (1978):

"The method is particularly useful for intensive studies involving relatively small populations and a few thoroughly trained observers, but it breaks down when...populations (are) large...(natural markings) cannot substitute for conventional marking when every individual of a sizable population must be distinguishable with a high level of certainty. Nor is the method convenient when many observers are involved, as in zoos and in extensive schemes of marking and recovery."

This objection is simply not true. Natural markings have been very successfully used to study large populations of whales with many different observers, often untrained, providing the data. The study of humpback whales in the North Atlantic in which 900 animals are currently recognized is a particularly clear example. The study is a cooperative effort by dozens of observers, many of them tourists, who have contributed photographs of whale flukes accompanied by the date and location of the photograph.

Probably the single most important factor in the success of this cooperative project is the fact that a photograph is required to identify the whale, so one is not relying on the ability of inexperienced observers to interpret their own observations. A layman who takes a useful photograph of a natural marking contributes solid, enduring evidence which the researcher can interpret for himself, referring to it as often as necessary for confirmation. A person reporting the number seen on a tag, on the other hand, is not really providing evidence but only his interpretation of the evidence. There is no way to confirm his interpretation. A study relying on reports by others is fated to generate spurious sightings, which may take as much time or more time to investigate as it would have taken to make identifications from photographs in the first place.

A few examples may help to set this in perspective. 1) When, in the late 60's, one of us was installing acoustic tags on whales, he received in one week three sightings of a single successful implant from other people. One sighting was physically too far away for the whale to have swum the

distance; the others were reported at the same time many miles apart. 2) P. Beamish (pers. comm.) had a similar experience with one of his early streamer tags deployed on a humpback whale. 3) B. Würsig (pers. comm.) spent several days following up a report that an orange tag he had put on the dorsal fin had been sighted near a distant island. When he finally located the eyewitness, he discovered that the orange object sighted was not on the dorsal fin but on the porpoise's head. A less careful observer might have used the report before verifying it, particularly since it indicated a plausible extension of range for Würsig's porpoises.

Another common objection to the use of natural markings for identifying animals is noted by Pennyquick (1978):

"It is important to realise from the outset that there is no way to be absolutely certain that an individual with particular markings is the only one so marked in the population. To be certain of this, artificial markings must be used, and the user must be able to ensure that no two are the same."

Strictly speaking this is, of course, true. But it pertains to a degree of accuracy which may be entirely unnecessary for many studies and which, if it is ever attained, may be lost in the noise of the other kinds of observational errors likely to affect biological field studies. For the vast majority of studies, a 99% probability that a pattern of natural markings has no duplicate in the population will be better than necessary, for it is almost certainly better than the accuracy with which most field studies record the behavior of the species in question.

Furthermore, it must be realized that visual tags cannot be trusted absolutely either. Humans misread and misrecord numbers, and tags may be ambiguous if animals naturally produce marks which resemble symbols on the tag. For example, there was a report of a southern right whale with a number 10 on its flukes, when apparently no one was placing any such marks (P. Best pers. comm.). The number seems to have been a pattern of shedding skin that chanced to take the form of the number 10. Similarly, several right whales in the Argentine population have white blazes like alphanumeric symbols ("Dot J" and "Y Spot", for example) which look virtually identical to the white markings that have been produced by freeze branding the skin of toothed whales. Field biologists must live with uncertainties whether identification is based on tags or natural markings.

The natural markings found in right whales and other whales have several major practical advantages which may prove difficult, if not impossible, to duplicate with artificial

tags. 1) They require no installation. 2) They are present at birth, in most cases. 3) They almost certainly last throughout the whale's life. 4) They don't interfere with locomotion or other natural behaviors. 5) They provide exceptional redundancy in confirming the identity of an individual. 6) They are rarely obscured from fouling marine growth. 8) They are much larger than any practical tag bearing the same information is ever likely to be and therefore can be read at a greater distance.

This last point needs to be stressed. The area over which the identifying marks of a right, gray, or humpback whale are spread is usually several square meters, but visual tags are limited to a much smaller size by the need to propel them for attachment to the animal. The smaller the size of a mark, the closer one must be to read it, the longer it will take on the average to obtain a satisfactory photograph or reading, and the smaller will be the proportion of successful identifications to sightings. The difficulty in reading artificial tags will increase as the number of animals tagged increases, for more information will be necessary on each tag to distinguish it from all others. If populations of whales comparable in number to those currently handled by natural markings are ever tagged, researchers who study them will have to deal with many of the same ambiguities of tag reading currently faced by researchers relying on natural markings.

Even when one considers smaller whales which have subtler natural markings, there are surprises in store when one considers the differences in the distances at which tags and natural marks can be read. There is an interesting example of this in Leatherwood, Caldwell, and Winn (1976). They have published a photograph of a free-swimming North Atlantic *Tursiops* with a spaghetti tag in place, as an example of what such a tag looks like in use. If we assume that they chose one of the better photographs available to them, then it is also a nice demonstration of just how difficult it is, under field conditions, to get a useful picture of something as small as a spaghetti tag. Were there not an arrow in the photo pointing out the tag, one might easily mistake it for turbulent water. This same photograph also shows several nicks on the trailing edge of the animal's dorsal fin. Though they too are somewhat blurred, the shapes and positions of the nicks can be clearly seen. It is from just such photographs (including some that were a lot worse) of just such nicks that individuals of this same species were identified in two excellent studies (Würsig and Würsig 1977; Shane 1977).

A final disadvantage of artificial tags concerns the way conspecifics may respond to them. It has been found in several species of terrestrial animals that the response of untagged animals to tagged conspecifics affects the social

position and/or reproductive success of the wearer (Ramakka 1972; Burley 1981). If whales have similar reactions to their tagged fellows, it might be difficult to detect, but it would affect the behavior under study.

We have pursued the argument on the usefulness of natural markings to counteract the opinion that natural markings cannot specify an individual adequately for serious scientific studies. It should be apparent that this opinion is indefensible. Clearly, the degree of detail in callosity patterns is enough to distinguish between far more individual right whales than will ever exist at one time and with a reliability that may affect the final conclusions of a study less than would the disruption caused by installation of artificial tags. There are also practical ways to estimate reliability of identification and to measure empirically the maximum number of identical animals that exist in one's study population.

We realize that there are some species in which adequate natural markings amenable to practical use probably do not occur. However, it is also true that many apparently simple natural markings are found upon close examination to be sufficiently rich in information to specify individuals reliably. It is only when this does not hold that we would advocate applying some kind of artificial mark.

We do not wish to be misunderstood as opposing radiotelemetry or any other kinds of active tags. There are certainly many things that can be learned only through radio tags, and if tags that can be read electronically from distances of a kilometer or more (such as radio transponders giving back a pattern unique to each tag) ever become a reality, then major advances will be possible. We are in opposition, however, to shooting numbers onto animals that are already more than adequately marked by nature. We feel that, although natural marks take longer to read, it is a relatively minor price to pay for the major advantages offered by them.

Summary

- 1) Individual southern right whales, *Eubalaena australis*, were identified based on the pattern of callosities on the head and of other distinctive features on the body. 484 individuals were recognized in the vicinity of Peninsula Valdés, Argentina, from an analysis of 16,000 photographs taken on 52 airlights from 1971 through 1976 during the months of June through December. 30 individuals were recognized off Cape Province, South Africa from two airlights in 1974. No individuals were seen in both locations. Calves were identified at a lower rate than non-calves.

- 2) Callosities are described along with the covering of cyamid amphipods. Lip callosities are highly variable and show a distinct lateral asymmetry.
- 3) Although minor variations in appearance occur, the callosity patterns are unchanging with time.
- 4) The number of distinguishable callosity patterns possible, and the number of callosity patterns recognizable in practice are both estimated to be far in excess of the world population of right whales.
- 5) A technique is presented to calculate the likelihood that identical whales exist in a population.
- 6) Five types of distinctive dorsal marks are described, of which at least three are essentially unchanging with time. Distinctive ventral blazes are described as well.
- 7) North Pacific right whales have fewer lip callosities and post-blowhole callosities than South Atlantic right whales, but the same incidence of dorsal markings as the Argentine whales. North Atlantic right whales have a callosity configuration -- continuous rostrum coverage -- that does not occur in the South Atlantic and has not been reported from the North Pacific.
- 8) Argentine and South African right whales show no difference in callosity frequency, but differ significantly in incidence of pigmented dorsal marks (greater in South Africa). They thus appear to constitute separate stocks in the South Atlantic. The existence of harpoon wounds on the Argentine right whales alone, coupled with illegal hunting of right whales in Tristan da Cunha (of which eyewitness accounts are presented), suggest that the Argentine and Tristan da Cunha whales may constitute a single stock.
- 9) Arguments are presented for the advantages of using naturally occurring markings over visual tags for studying large populations of animals in the wild when persistent markings are present.

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APPENDIX I

Derivation of the Probability
of Finding Identical Twins

The following calculations of the probability of detecting identical twins are based on several assumptions. We assume a population of 550 right whales, based on 484 identifications over 6 years, with no estimate of mortality. A larger population would reduce the likelihood of detecting twins, while a smaller population would increase it. We also assume the existence of 25 pairs of twins within the 550 whales, a number chosen arbitrarily. More twin pairs would increase the likelihood of detecting some, and fewer twin pairs would decrease that likelihood. If the variation in callosity patterns tended to cluster around a few common forms so that more than two animals had a given identical appearance, this would increase the likelihood of detecting at least one pair of them. The fact that we have not yet detected any twins suggests a lack of favored norms in callosity patterns.

We further assume random distribution of whales for the calculations below. We do not believe that their distribution is actually random, but we have no better model of distribution to use. We have no estimate of how the actual distribution of right whales would affect the probability of detecting identical twins, but we feel that our method provides a check against either of two extreme departures from randomness in the relative distribution of members of a twin set. If the two members of a twin set tended strongly to avoid each other, they would be more likely to occur in different bays at the same time, and the probability of their being thereby detected would increase. If, on the other hand, the two members tended strongly to seek each other's company, they would be more likely to be photographed in the same frame, and the probability of their being detected in that way would also increase.

Identical Twins in Different Bays

The first type of event which could demonstrate the existence of "identical twins" is the photographing on the same airflight of one whale in one bay and its twin in another bay. At Peninsula Valdés, there are three areas where right whales occur, each separated from one another by a greater distance than could be swum by a right whale during the

duration of an airflight. For simplicity we will call these areas bays (although one is in fact a semi-protected lagoon behind fringing shoals). Some census flights included photographs of whales in all bays while others included only two bays. We shall deal with the two situations separately.

A. Whales in two different bays. We shall consider an airflight with photographs of "a" identified whales in one bay and "b" identified whales in another bay. We wish to determine the number of distinct events in which a twin set could be photographed, one in each bay, given the above conditions. We will represent this number by α . A first approximation to α is given by:

$$25 \times 2 \times \binom{548}{a-1} \times \binom{549-a}{b-1} \quad (1)$$

The usual notation $\binom{n}{r}$ means "the number of combinations of n objects taken r at a time," which is given by the formula

$$\frac{n!}{r!(n-r)!}$$

The first factor is simply the number of twin sets we have postulated. The second factor, 2, is included because the first member of the twin set could be in either bay. Once we have specified the existence of one twin in the first bay, there remain $(a-1)$ unspecified whales that can be selected from the population of 550 whales diminished by the two specified twins. Thus, the third factor is $\binom{548}{a-1}$. The

fourth factor is the number of ways in which the $(b-1)$ unspecified whales in the second bay could be selected from the population of 550 whales diminished by the "a" whales already selected for the first bay and also diminished by the specified twin in the second bay.

The expression, (1), shown above was called a first approximation because it gives too large a number. It does this because it counts twice each event when twins from two sets, one from each set, appear in each bay. The number of such events is approximated by:

$$\binom{25}{2} \times 4 \times \binom{546}{a-2} \times \binom{548-a}{b-2} \quad (2)$$

The first factor is the number of ways that 2 sets of twins could be selected. The second factor, 4, is included because there are 4 ways in which the 2 sets of twins could be arranged such that one member of each set is in each bay.

The third factor is the number of ways of selecting the (a - 2) unspecified whales for the first bay from the 546 available whales. The fourth factor is the number of ways of selecting the (b - 2) unspecified whales for the second bay from the (548 - a) available whales. Therefore, our second order approximation to α is (1) - (2).

Let us consider now the events in which any given three sets of twins (labelled, for example, R, S, and T) are split between the two bays such that one twin from each set appears in each bay. These events will each be counted three times in (1), once with respect to twin set R, once for S, and once for T. Moreover, these events will each be counted three times also in (2), once with respect to the pairs of twin sets R and S, once for R and T, and once for S and T. Hence our second order approximation to α , namely (1) - (2), will not count any of the events when trios of twin sets are split between the two bays. An approximation to the number of such events is given by:

$$\binom{25}{3} \times 8 \times \binom{544}{a-3} \times \binom{547-a}{b-3} \quad (3)$$

following a logic very similar to that used to derive (2) above. Thus our third order of approximation to α is (1) - (2) + (3).

Continuing, let us consider the events in which any given four sets of twins are split between two bays such that one twin from each set appears in each bay. These events will each be counted four times in (1), $\binom{4}{2}$ times in (2) and $\binom{4}{2}$ times in (3). Therefore, these events will be counted twice in our third order approximation to α . The usual logic will show that such events are approximated by:

$$\binom{25}{4} \times 16 \times \binom{542}{a-4} \times \binom{546-a}{b-4} \quad (4)$$

This yields, as a fourth order approximation to α , the expression: (1) - (2) + (3) - (4).

This series could be developed further to obtain the 25th "approximation" which would, in fact, be the exact formula for α . However, in practice, the terms of the series decrease rapidly. Before showing this fact, let us recall that we are on the way to calculating a probability of observing a twin set in the two bays. To obtain this probability (or, to be strictly correct, a close approximation to it), we divide the fourth order approximation to α by $\binom{550}{a} \times \binom{550-b}{b}$ which is simply the total number of possible events of "a" whales being photographed in one bay and "b" whales in another. It can easily be shown by applying the usual formula for combinations, that when each of the four

expressions in our approximation is divided by the above denominator the resulting four terms are:

$$1.65 \times 10^{-4} \times ab \quad (5)$$

$$1.33 \times 10^{-8} \times ab(a-1)(b-1) \quad (6)$$

$$6.83 \times 10^{-13} \times ab(a-1)(b-1)(a-2)(b-2) \quad (7)$$

$$2.54 \times 10^{-17} \times ab(a-1)(b-1)(a-2)(b-2)(a-3)(b-3) \quad (8)$$

In order to make the most stringent test of the accuracy of successive approximations we choose actual values of a and b such that the ratio of each term in the series to the term following it is at a minimum. Empirically, we find these values are 48 and 40. For these values the expressions (5), (6), (7), and (8) take on the following values, respectively:

$$3.17 \times 10^{-1}$$

$$4.68 \times 10^{-2}$$

$$4.20 \times 10^{-3}$$

$$2.60 \times 10^{-4}$$

Clearly, the successive terms are diminishing by approximately an order of magnitude. For all other empirical values of a and b, successive terms will diminish even more rapidly. Therefore, the second order approximation, (5) - (6), to the probability of photographing a set of twins in the two bays, will be very close to the exact value. Moreover, since the third term is positive, this second order approximation will always yield a slight underestimate of the correct probability. Thus, the value obtained for the probability of not photographing twins in the two bays will be a very small overestimate. In other words, any slight inaccuracy in the second order approximation would tend to lead, if anything, to not rejecting our null hypothesis, that 25 sets of identified twins exist in the population.

Therefore, for each airlight with photographs from two bays, the second order approximation, (5) - (6), was subtracted from unity to obtain the probability of not photographing a set of twins in the two bays. We assumed each airlight to be an independent event and therefore multiplied these probabilities together, producing a value of 0.18347. This, then, is the probability, given the null hypothesis that 25 sets of twins exist in a population of 550 whales and, assuming random association between whales and independence of airlights, that none of the airlights, over six years, which covered two bays would have produced a photograph of a twin in one bay and its counterpart in the second bay.¹

¹ Since writing this appendix, it has been pointed out to us that there exists an exact formula for α for the two bay case, which is the following:
$$\sum_{j=1}^n (-1)^{j+1} 2^j \binom{n}{j} \binom{n-2j}{a-j} \binom{n-a-j}{b-j}$$

B. Whales in three different bays. We shall now consider an airlight with photographs of "a" whales in one bay, "b" whales in a second bay, and "c" whales in a third bay. The argument will follow similar lines to the two bay situation above but with somewhat more complicated formulae. We wish to determine β , the number of distinct events in which one member of a twin set could be photographed in a different bay. A first approximation to β is given by:

$$25 \times \left\{ \left[2 \times \binom{548}{a-1} \times \binom{549-a}{b-1} \times \binom{550-a-b}{c} \right] + \left[2 \times \binom{548}{a-1} \times \binom{549-a}{c-1} \times \binom{550-a-c}{b} \right] + \left[2 \times \binom{548}{b-1} \times \binom{549-b}{c-1} \times \binom{550-b-c}{a} \right] \right\} \quad (9)$$

The first factor is simply the number of twin sets postulated in the null hypothesis. The first term inside square brackets represents the number of events where one twin could be photographed in the first bay and its counterpart in the second bay. The logic behind the first term is the same as that used for expression (1), except for the inclusion of the final factor which denotes the number of ways of selecting the "c" whales for the third bay from the population of 550 diminished by the "a" and "b" whales already selected for the first two bays. The second and third terms inside square brackets represent the events when twins are in the first and third, and second and third bays, respectively.

As before, expression (9) is only a first approximation to β since it will count twice each event when two sets of twins are photographed and each set is divided between any two of the three bays. For any given pair of twin sets, M and N, there are nine possible arrangements as shown by the following array:

M in bays 1 & 2	M in bays 1 & 2	M in bays 1 & 2
N in bays 1 & 2	N in bays 1 & 3	N in bays 2 & 3
M in bays 1 & 3	M in bays 1 & 3	M in bays 1 & 3
N in bays 1 & 2	N in bays 1 & 3	N in bays 2 & 3
M in bays 2 & 3	M in bays 2 & 3	M in bays 2 & 3
N in bays 1 & 2	N in bays 1 & 3	N in bays 2 & 3

The number of possible events represented by this array is given by expression (10). The first term in square brackets corresponds to row 1, column 1 in the array. The second

$$\left[4 \times \binom{546}{a-2} \times \binom{548-a}{b-2} \times \binom{550-a-b}{c} \right] + 2 \times \left[4 \times \binom{546}{a-2} \times \binom{548-a}{b-1} \times \binom{549-a-b}{c-1} \right] + 2 \times \left[4 \times \binom{546}{a-1} \times \binom{548-a}{b-2} \times \binom{549-a-b}{c-1} \right] + \left[4 \times \binom{546}{a-1} \times \binom{547-a}{b-1} \times \binom{548-a-b}{c-2} \right] + \left[4 \times \binom{546}{a} \times \binom{548-a}{b-2} \times \binom{548-a-b}{c-2} \right] \quad (10)$$

term corresponds to row 1, column 2 and also to row 2, column 1: hence, the factor, 2, outside the square brackets. The second term will be used as an example to show the logic behind the formulae. We will use the situation depicted in row 1, column 2. The first factor, 4, is included because there are 4 possible configurations of the two sets of twins in the designated bays. In the next factor, only 546 whales are available for assignment to the first bay since the location or two sets of twins has already been specified. Likewise, there are only $(a - 2)$ free places in bay 1 since 2 places are filled by one member of twin set M and one member of twin set N. In the next factor, the "b" places in bay 2 are diminished by 1, since one twin in set M is specified for bay 2. The population available for assignment to bay 2 is 550 whales diminished by the "a" whales already selected for bay 1 and further by the two twins not selected for bay 1. The final factor depicts the number of ways of selecting "c" whales less the single twin set N from the population of 550 whales diminished by the "a" and "b" whales already selected and further by the single twin designated for the third bay.

In order to determine the number of events when two sets of twins are each divided between two of three bays, we must multiply expression (10) by $\binom{25}{2}$, the number of possible

combinations of pairs of twin sets. We shall define expression (11) in exactly this way.

Now we have, as a second order approximation to β , (9) - (11). In order to calculate the second order approximation to the probability of twins being photographed in different bays, we must divide this expression by:

$$\binom{550}{a} \times \binom{550 - a}{b} \times \binom{550 - a - b}{c}$$

This is the total number of ways of photographing "a", "b", and "c" whales in the three bays with no restrictions regarding twins. Algebraic manipulation will show that the first and second order terms of this probability are, respectively:

$$1.65 \times 10^{-4} \times (ab+ac+bc) \quad (12)$$

$$\text{and } 1.33 \times 10^{-8} \times [a(a-1)b(b-1) + a(a-1)c(c-1) + b(b-1)c(c-1) + 2abc(a+b+c-3)] \quad (13)$$

A third order term, analogous to that developed in the two bay case, has been derived, although the details of that derivation are too lengthy to be described here.

It can be shown that this third order term is given by:

$$\begin{aligned} & 6.83 \times 10^{-13} \times \{ (a)(a-1)(a-2)(b)(b-1)(b-2) \\ & + (a)(a-1)(a-2)(c)(c-1)(c-2) \\ & + (b)(b-1)(b-2)(c)(c-1)(c-2) \\ & + 3(a)(b)(c) \times [(a-1)(a-2)(b-1) \\ & + (a-1)(a-2)(c-1) + (b-1)(b-2)(c-1) \\ & + (a-1)(b-1)(b-2) + (b-1)(c-1)(c-2) \\ & + (a-1)(c-1)(c-2) + 2(a-1)(b-1)(c-1)] \} \quad (14) \end{aligned}$$

Selecting actual values such that the ratio of the second order to the first order term is at a maximum, we find expressions (12), (13), and (14) take on the following values, respectively:

$$\begin{aligned} & 2.60 \times 10^{-1} \\ & 3.12 \times 10^{-2} \\ & 2.24 \times 10^{-3} \end{aligned}$$

As in the two bay case, we find that the terms are diminishing by approximately an order of magnitude. Thus, we are again sure that the second order approximation not only is very close to the actual probability but also tends, if anything, to exert a force against rejecting the null hypothesis that 25 twin sets exist in the population.

Accordingly, for each airlight with photographs from three bays, the second order approximation, (12) - (13), was subtracted from unity to obtain the probability of not photographing a set of twins in two of the three bays. Taking each airlight to be an independent event, we multiply these probabilities together, yielding a probability of 0.20304. Finally, since the two bay situation and the three bay situation are independent events, we multiply the probability of one with the other and obtain a probability of not detecting a set of twins in different bays of 0.03725.

Identical Twins in the Same Photograph

The third type of event in which identical twins could be detected is the appearance of twins in the same photograph. Since the data include photographs with two, three, four, five, and six identified whales in the same photograph, separate probabilities were calculated for each situation.

A. Two whales in the same photograph. The number of such photographs is simply 25, that is, the number of twin sets postulated. The number of possible photographs of pairs of whales is simply $\binom{550}{2}$. There were 323 photographs of

pairs of whales. Therefore the probability that none of these included a twin set is given by:

$$\left[1 - 25 / \binom{550}{2} \right]^{323}$$

B. *Three whales in the same photograph.* The number of such photographs which include a set of twins is 25×548 , there being 548 ways of filling the third "slot", once it is stipulated that a twin set must fill two of the "slots". Since there are $\binom{550}{3}$ possible photographs of three whales and since

there were in fact 57 such photographs, the probability that none of these included a twin set is given by:

$$\left[1 - \frac{25 \times 548}{\binom{550}{3}} \right]^{57}$$

C. *Four whales in the same photograph.* The first approximation to the number of such photographs which include a set of twins is $25 \times \binom{548}{2}$. This number is a

little too large, since it counts twice the events in which two sets of twins are in a photograph. The number of such events is simply $\binom{25}{2}$. Following the usual procedure, then,

we find that the probability that none of the 10 photographs of 4 whales included a twin set is:

$$\left[1 - \frac{25 \times \binom{548}{2} - \binom{25}{2}}{\binom{550}{4}} \right]^{10}$$

D. *Five whales in the same photograph.* The number of this type of photograph containing a least one set of twins is given by $25 \times \binom{548}{3} - \binom{25}{2} \times 546$, the second term being the

correction for the events where two sets of twins appear together. Following the usual logic, the probability of not finding any sets of twins in these photographs (of which there are 3) is given by:

$$\left\{ 1 - \frac{\left[25 \times \binom{548}{3} \right] - \left[\binom{25}{2} \times 546 \right]}{\binom{550}{5}} \right\}^3$$

E. *Six whales in the same photograph.* The number of this type of photograph containing at least one set of twins is given by:

$$\left[25 \times \binom{548}{4} \right] - \left[\binom{25}{2} \times \binom{546}{2} \right] + \left[\binom{25}{3} \right]$$

The first and second terms are derived by the same logic as was used above. The third term is the final correction for the events when three sets of twins appear in one photograph. The probability, then, of not finding a set of twins in the two photographs of six whales is given by:

$$\left\{ 1 - \frac{\left[25 \times \binom{548}{4} \right] - \left[\binom{25}{2} \times \binom{546}{2} \right] + \left[\binom{25}{3} \right]}{\binom{550}{6}} \right\}^2$$

These five probabilities were all calculated and then multiplied together since they refer to independent events. The final probability of not finding any sets of twins in the same photographic frame, given the conditions of the null hypothesis, and given random associations between whales, works out to be 0.90331.

If the photographing of twins in the same frame were completely independent of photographing them in separate bays, we could multiply the probability of each together and obtain the overall probability of not detecting twins by these methods (given the null hypothesis and our other assumptions) of 0.03365.

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