Long Term Behavioral Studies of the Southern Right Whale (*Eubalaena australis*)

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ABSTRACT

Since 1970, southern right whales have been studied on their winter/spring aggregation areas in protected waters near the coast of Peninsula Valdes, Argentina. These areas have been repeatedly surveyed from the air and from shore and over 580 individuals have been identified from aerial photographs of natural markings on their heads. Many individuals return to the area each year, but mature females tend to be seen only in years when they give birth (usually every third year). Seventy-four of the known females have had two or more calves, with a mean calving interval of 3.7 ± 1.25 years ($n = 89$ calving intervals). The age of first calving for two females was seven years. Mothers with young calves are usually positioned along the coast in water about 5 m deep. Right whales are found at Peninsula Valdes in three separate areas: one predominantly occupied by mothers and calves, a second predominantly occupied by males and mature females in non-calf years, and a third occupied by all categories of whales including subadults and mating groups.

INTRODUCTION

Right whales (genus *Eubalaena*) occupy two broad bands of ocean encircling the world between 20 and 60° latitude in Northern and Southern Hemispheres. The number of species in the genus is unresolved, but most authors consider there to be two species, *Eubalaena glacialis* in the Northern Hemisphere and *Eubalaena australis* in the Southern Hemisphere. This paper concerns the southern right whale which we have studied since 1970 during the Southern Hemisphere winter and spring in the waters surrounding Peninsula Valdes, Argentina (42.5 °S, 64°W).

Most major recent advances in behavioral studies of free-ranging populations of large mammals seem to have come from research in which two conditions were fulfilled: first, it was possible to recognize individuals, and second, it was possible to extend the study over several years.

We looked for a practical way to identify individual right whales and soon discovered that an excellent natural marker existed in the pattern of callosities – patches of raised, thickened epidermis on their heads (see Fig. 1). Some of the callosities are exposed every time a whale surfaces to blow. The number, position and shape is unique to each whale, and although minor changes occur with time, the overall pattern remains identifiable from birth and almost certainly throughout the life of the whale (Payne, Brazier, Dorsey, Perkins, Rowntree and Titus, 1983).

To make a long-term study at Peninsula Valdes feasible, we built a permanent field station in the southeast corner of Golfo San Jose overlooking an area frequented by right whales in winter and spring. This has been occupied since 1972 and data have been collected from this area every year since 1970, mostly between August and mid-November.

METHODS AND MATERIALS

Frequent air flights were made throughout the season in order for us to take photographs of the heads of right whales to identify individuals, mostly using a CESSNA 182, single engine, high wing aircraft. Our usual practice was to search for whales along the coast, flying at 200 m or less. When whales were sighted we would drop down to between 150 m and 65 m and circle them until we had taken a series of photographs which we felt was sufficient to identify the whales. We also made observations from cliffs, boats and occasionally from underwater (for a complete description of survey techniques see Payne *et al.* 1983). The study is in its sixteenth year (1985) and we plan to continue it indefinitely. Most data reported here were taken during the first 12 field seasons. Our most complete data were collected in 1973. The data base is extensive and includes, for example, over 40,000 still photographs.

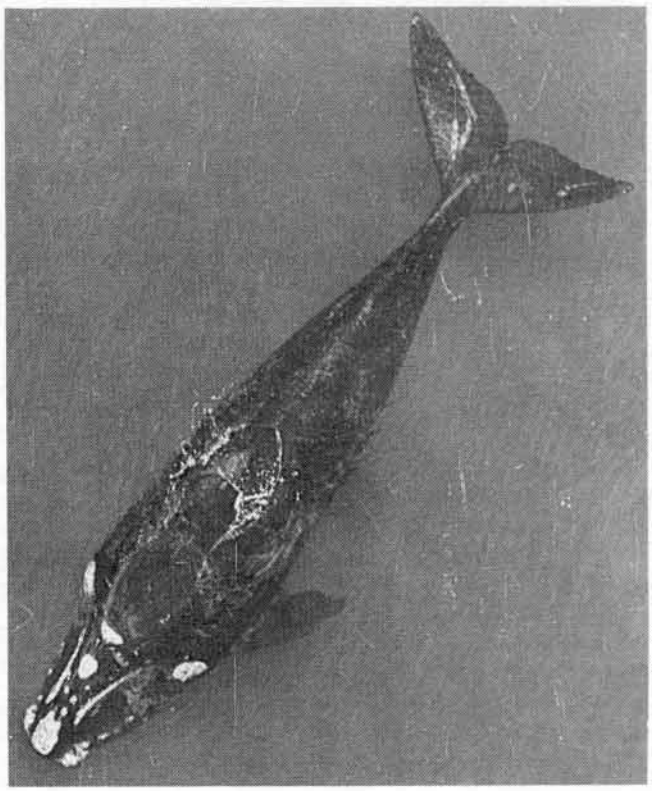

Fig. 1. Aerial photograph of a southern right whale showing atypical callosity pattern.

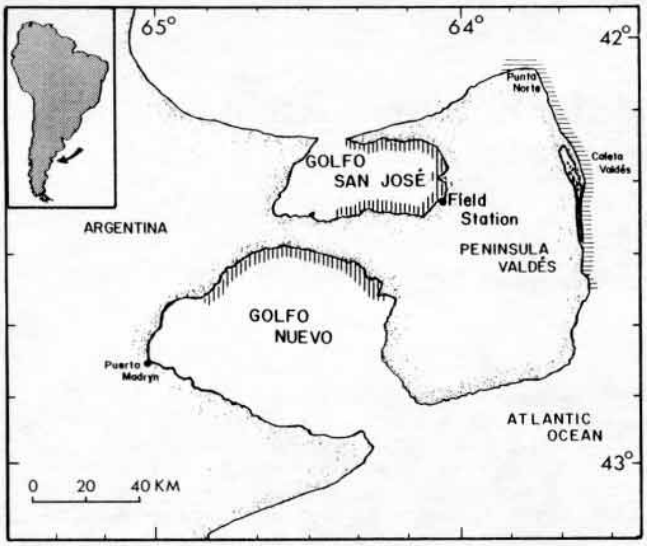

Fig. 2. Map of Peninsula Valdes. The hatched areas indicate regions of concentrations of right whales. (Taken from AAAS Selected Symposium Series Volume 76, *Communication and Behavior of Whales*, R. Payne (ed.) copyright 1983 by the American Association for the Advancement of Science)

Over 580 individuals have been identified and we have been able to determine the sex of many of them from anatomical and/or behavioral evidence (for a description of techniques used in sexing right whales see Payne and Dorsey, 1983).

The coastline of Peninsula Valdes is 495 km long (see Fig. 2). We repeatedly surveyed the coast, dividing it into five sections: Golfo San Jose, the Northern Outer Coast, the Eastern Outer Coast, the Southern Outer Coast, and Golfo Nuevo. Of these, three (Golfo San Jose, the Eastern Outer Coast and Golfo Nuevo) were 'aggregation areas' (areas where whales were frequently encountered). Within these aggregation areas were 'regions of concentration', stretches of coast along which right whales regularly congregated. A few flights across the two large bays and many observations from shore led us to the conclusion that the great majority of the right whales wintering at Peninsula Valdes are concentrated near the coast.

We had to develop several new techniques in order to study these whales. We sought to measure length of the whales at the surface to provide a clue to age. To do this we developed several techniques based on aerial photographs. For example, we took aerial photographs of whales next to a boat which was carrying a white disc one m. in diameter. In the resulting photographs of disc and whale, the longest apparent diameter of the disc can be used as a ruler with which to measure the whale. We also measured whales by noting the ratio of head length to body length, which we found to be an age-dependent variable, and by using whales of known length as rulers with which to measure whales of unknown length lying parallel to them. In these ways, we could distinguish subadults from adults, and in a few cases, even calculate growth rates of free-swimming right whales. Details of these techniques are given in Whitehead and Payne (1981).

When whales can be seen from shore, it is possible to track their movements with useful accuracy out to a distance of five or more kilometers by means of a surveyor's theodolite. The distance at which whales can be followed depends on the height of the observation

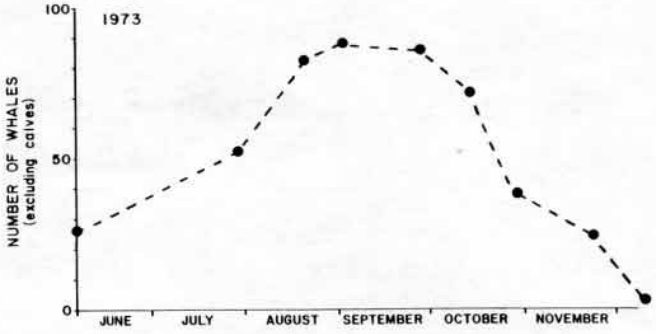

Fig. 3. Build-up and decline of right whales at Peninsula Valdes during 1973. Dots indicate the number of whales (excluding calves) identified, observed and extrapolated in each of nine flights along the coastline.

platform. Bearings to the whale are taken in the vertical and horizontal plane. The vertical bearing is used to compute the distance to the whale. That distance applied along the horizontal bearing gives the map position of the whale. This technique has since been used successfully by a number of researchers (see Würsig and Würsig, 1979 and Tyack, 1981).

RESULTS

The whales are present at Peninsula Valdes only during the winter and spring seasons, during which their normal food is in low abundance and they probably get little or nothing to eat. Data from 1973 (in which we had the broadest coverage) illustrates how the population at Valdes builds and declines within the year. Fig. 3 shows the number of whales seen in each of nine flights. (There were ten flights, but those for 22 and 24 November have been combined into a single flight since they covered different areas.) Three curves are shown giving the number of whales (excluding calves) identified, observed and 'extrapolated'. The last category merely corrects the three flights that covered only two of the three aggregation areas by adding a value for the missing area which was midway between the totals observed there during flights immediately before and after the missing date. The extrapolated curve is probably our best estimate of the lower limit to the number of whales actually present (lower because we undoubtedly failed to see whales that were present but out of sight underwater when the plane was overhead). Fig. 3 shows that the population builds slowly, remains at a high value for about eight weeks, and then declines more rapidly than it built up, suggesting that at the end of the long winter of semi-starvation the whales depart relatively rapidly for their summer feeding grounds.

Structure of the herds at Peninsula Valdes

The term 'herd' has many usages. It is used here to describe a very local grouping: all whales seen in and near a single aggregation area at Peninsula Valdes, e.g., the Golfo San Jose herd or the Eastern Outer Coast herd. The whales in a given region move together as a loosely knit group while staying roughly clustered about a focal group. Local land forms, like headlands and bays, delineate the different herds. In all three aggregation areas, the herd was usually found in the same general

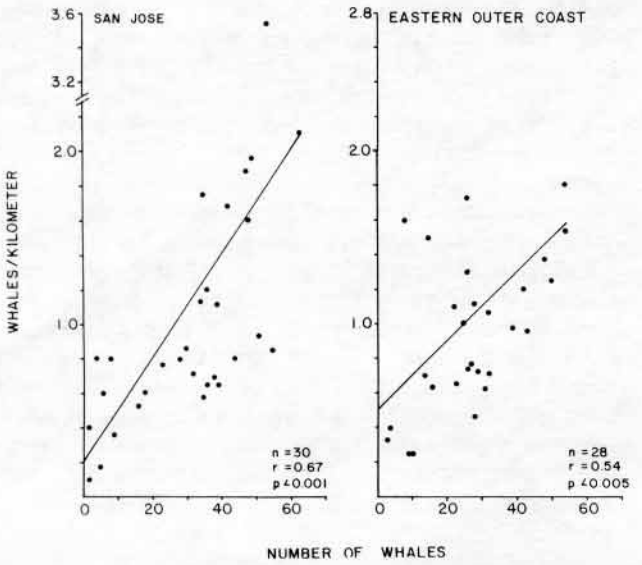

Fig. 4. The correlation between the number of whales observed and their density, in Golfo San Jose and along the Eastern Outer Coast. n = the number of flights with sufficient coverage to see the entire herd. In both areas there is a significant positive correlation.

area. The herd in Golfo Nuevo was much smaller than the others during most of our study and usually more spread out. Our usual experience was to fly for many kilometers of coastline without seeing whales and then to come upon a lone individual or pair. This signalled a buildup in the next 10–30 km to a central group of whales, usually more than 10. Having passed the densest concentration, the numbers fell off in much the same way that they had increased. We considered that we had reached the end of a herd, or at least sampled it adequately, once we had flown 10 km or more beyond the last whale sighted without seeing another whale.

We have made 6 complete surveys along the entire coast of Golfo San Jose and 19 surveys along the entire Eastern Outer Coast. In 23 of these 25 complete surveys, the herd was clustered together regardless of where we found it.

The overall mean herd width for all of Peninsula Valdes was about 37 km. The mean herd width for females with calves was 22 km. Females with calves were often located near the center of the herd, although it appears to be all females, and not just those lactating, that are the focus of the herd.

In both Golfo San Jose and the Eastern Outer Coast, there is a significant positive correlation between numbers of whales and density (Fig. 4), i.e. the whales do not spread out over a longer stretch of coast to maintain the same density as their numbers increase, which they might do if they were maintaining territories and which they could easily do because the available coastline is much longer than the width of the herd. Instead, they apparently incorporate additions to their group by crowding more tightly into a relatively small area. (We have found no evidence for territoriality in this species.)

In order to study the distribution of the herds in space, we counted the number of whales seen in every consecutive 5 km segment of coastline. We plotted the mean herd shape for Golfo San Jose by taking the distribution plots for each flight and sliding them so as to line up the 5 km strip with the greatest number of whales. We then calculated the mean number of whales

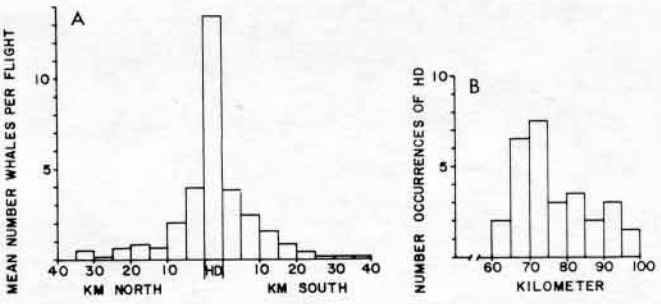

Fig. 5. Spatial distribution of the Golfo San Jose herd. A. The mean distribution of whales observed around the densest five km segment of coast (HD). B. The variation in location of the densest segment (HD) of the herd.

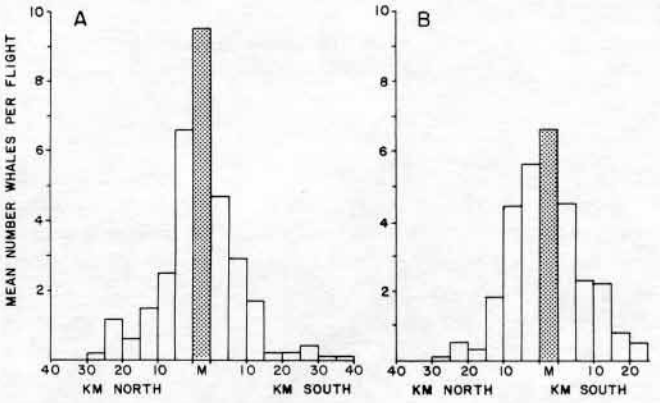

Fig. 6. The distribution of the herd around its mean position (M): Golfo San Jose vs the Eastern Outer Coast.

seen in each of the 5 km segments flanking the densest segment. The result (Figure 5A) is a sharp, symmetrical curve representing the mean shape of the herd in Golfo San Jose.

The herd does not stay fixed in space but moves back and forth along sections of the coast 30–40 km in length, apparently with no relation to such natural features as water temperature or food abundance. It therefore appears that at this season at least, whales are attracted to each other. Fig. 5B shows that the herd kept mostly to one end of a 40 km stretch of coast along the perimeter of Golfo San Jose.

In Fig. 6 we compare the shape of the herd at Golfo San Jose with the herd shape along the Eastern Outer Coast by the same means outlined above for Golfo San Jose. The Golfo San Jose herd tends to have a higher density of whales at the center than the Eastern Outer Coast herd and also tends to spread out a little further to the south of its mean position.

Depth Preference

To look at depth preferences, we used a surveyor's theodolite from three prominent cliff lookouts to locate the positions of all whales within the study area. We made censuses on 18 calm days in 1973 and 1974 and calculated 857 whale positions. The positions were mapped on a detailed chart of the bay, and the depths were corrected for the tide height at the time the whale was observed. In Fig. 7 the number of whales is plotted for each half meter interval of depth. The striking preference for shallow water, and particularly for a depth of 5 m, is apparent.

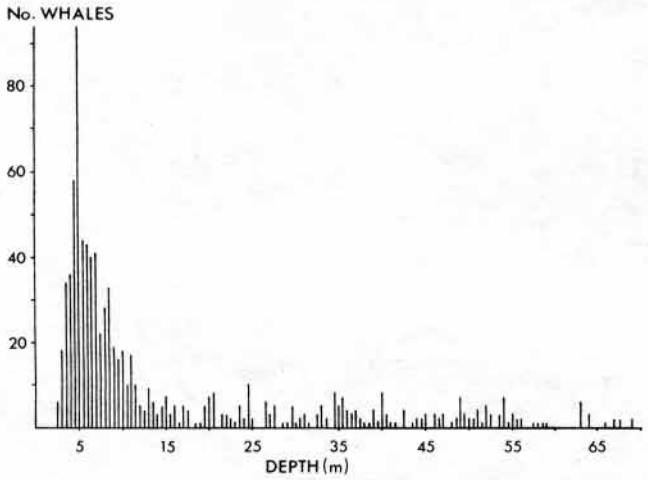

Fig. 7. Depth preference of all right whales visible from shore in the southeast corner of Golfo San Jose.

This preference was not an artifact of decrease in sightability with increase in depth. The three different lookouts from which we worked were at each end and in the middle of a long strip of coast. When working from either of the two end cliff lookouts we were noting whales 8–10 km away which were right in close to the shore at or near the other end of the strip of coast. From these end lookouts, all of the whales seen in deep water were closer to us than the most distant nearshore whales along the coast. In order to be sure that the result was not simply a consequence of the distribution of average water depths in our study area, we calculated the distribution of mean depths (Fig. 8). By comparing Figs 7 and 8, it is apparent that the whales are selecting specific depths. These results suggest that there may be important selective pressures on right whales for remaining in 5 m of water at Peninsula Valdes.

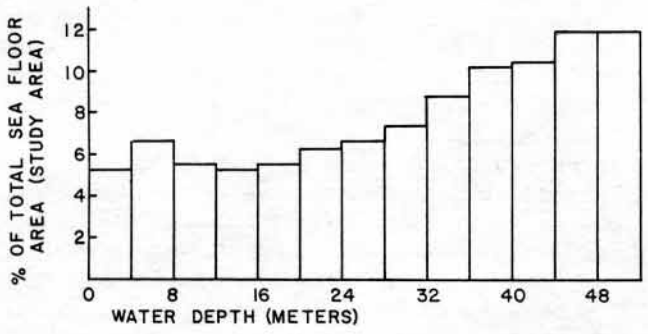

Fig. 8. Distribution of water depths during an average tidal cycle within the south east corner of Golfo San Jose. This is the same area for which the depth preferences of whales are given in Fig. 7 and 9.

The strong preference of right whales for a depth of 5 m caused us to start referring to the 5 m depth contour as the 'whale road'. Whales usually swam along this contour and carried out social interactions (sometimes lasting for hours) with the other individuals they encountered. Their trips kept to this contour even when a shortcut through deeper water would have brought them to their day's final destination much more quickly. For these reasons it appeared as though staying within or following the 5 m contour was a convenient way for right whales to encounter each other. We feel that different age/sex categories may gain different advantages from shallow water, but that the majority of individuals could benefit from using the 'whale road' as a means of meeting each other. Unlike rorquals, whose low, loud voices can travel in deep ocean for hundreds of kilometers under some circumstances before being lost in background noise (Payne and Webb, 1971), the right whale vocalizations are at significantly higher frequencies and are made in shallow water. Thus they do not appear to be well suited to long range communication. As a result, it seems likely that right whales need to have a meeting place, and the 'whale road' both within and between aggregation areas (particularly along sections of relatively unfrequented coast hundreds of kilometers long) may provide a region for rendezvous.

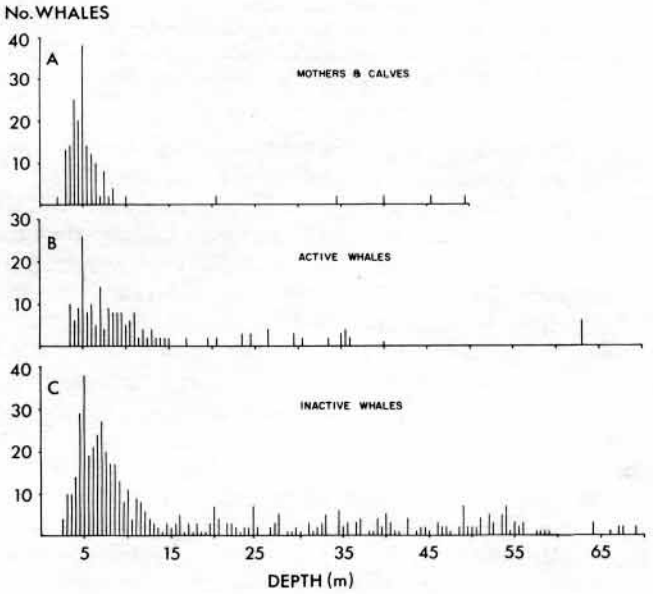

Fig. 9. Depth preferences of different categories of right whales in Golfo San Jose.

During most cliff surveys there was a second observer watching through a telescope to determine for each whale or group of whales the type of behavior. This behavior was put into one of five categories: active groups (obviously moving or white water present), breaching, lobtailing, flippering, and inactive animals (not moving). Our division into age/sex categories was limited to two groups, females with calves and all other whales. The results are given in Fig. 9, which again presents the number of whales by depth. They show that females with calves, Fig. 9A, are almost never seen in water over 10 m deep and that most activity, Fig. 9B, takes place within water less than 15 m deep. Most of the activity observed was group activity and the great majority of groups whose behavior could be determined were obviously involved in mating behavior (see below). Fig. 9 shows that most whales which were found in water deeper than 15 m were inactive. Because of the local restrictions on flying over water in single engine planes, we know very little about these deep water individuals.

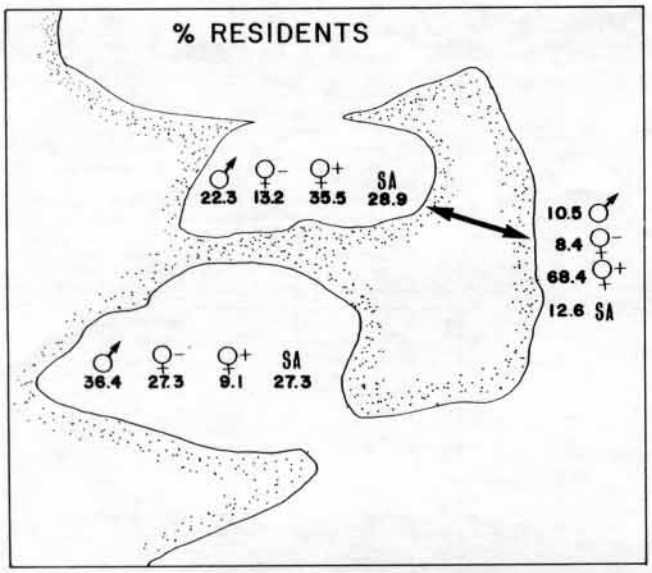

Fig. 10. Proportion of known age/sex categories in all identified residents for each area. ♂ = known males, ♀+ = known females with calves, ♀− = known females without calves, SA = subadults.

Table 1. Residence times (days) by age/sex category in the three aggregation areas at Peninsula Valdes. The flight dates and effort are the same in Golfo San Jose and along the Eastern Outer Coast, but different in Golfo Nuevo. Therefore direct comparisons are possible only between Golfo San Jose and the Eastern Outer Coast

	Males	Females in non-calf years	Females in calf years	Subadults	All known age/sex categories	
Golfo San Jose						
$\bar{x}$	29.5	28.1	38.1	35.8	34.0	Balanced flights
sd	16.17	15.68	20.39	23.38	20.28	
n	27	16	43	35	121	
Eastern Outer Coast						
$\bar{x}$	36.8	42.3	48.3	30.3	44.3	
sd	37.59	18.95	24.90	22.26	26.16	
n	10	8	65	12	95	
Golfo Nuevo						
$\bar{x}$	37.0	24.0	27.0	70.0	41.6	Principal flights
sd	34.80	9.85	-	5.20	27.63	
n	4	3	1	3	11	

Different uses of the aggregation areas

One of the most unexpected results that we found at Peninsula Valdes was that the three aggregation areas (Golfo Nuevo, Golfo San Jose, and the Eastern Outer Coast) have different functions. We have been studying the usage of the three different areas ever since 1971 when we first noticed that the three areas had different ratios of females with calves to mating groups. A possible separation of mating and calving areas has also been observed by Best (1981). The three aggregation areas are occupied for different lengths of time by different proportions of the various age/sex categories.

To explore these differences, we calculated the proportion of the known age/sex categories in all identified 'residents' in each area, that is, whales seen two or more times in that area in one year. Fig. 10 presents the results. The age/sex categories that were used were: known males, females with calves, females without calves and subadults. Because males are considerably harder to sex than females, we do not know the absolute sex ratios at Peninsula Valdes and these figures can only be used for comparisons between areas.

The area in which the proportion of females with calves is the greatest among identified residents is the Eastern Outer Coast, suggesting that this is principally a calf rearing area. We have seen eight unaccompanied females along that coast which were accompanied by calves later in the same year, so we suspect it is also a calving region.

The area in which the proportion of males to other known categories is largest is Golfo Nuevo. Golfo Nuevo also has a high percentage of females without calves, suggesting that it is principally a mating area. In the last four years, however, females with calves have been seen in increasing numbers in this area. We seem to be witnessing the founding of a calving/nursery area within a mating area.

Golfo San Jose appears to contain good samples of all categories, including the largest ratio, as well as the largest number, of subadults. Golfo San Jose and Golfo Nuevo appear to be important areas in which subadults can undergo their development. The former is also a major mating area, as indicated by the high ratios of males and females without calves and by the high incidence of mating activity observed there during census flights. We have therefore classified it as a 'general' area.

An examination of the mean periods of residency for differing age/sex categories in the different aggregation areas (Table 1) shows that females with calves have the longest residency times, both in Golfo San Jose and along the Eastern Outer Coast.

Also with respect to area use, we investigated the question of which area individual adult females prefer in their calving and non-calving years. The Eastern Outer Coast was found to be the preferred location in calving years and Golfo San Jose in non-calf years. It thus appears that individual females are switching from one area to another depending on whether they have a calf that year, which again supports the view that different areas at Peninsula Valdes have different functions.

Age at sexual maturity

Matthews (1938), working from dissected animals, noted that a male southern right whale of 13.5 m length and two females of 15.2 and 14.4 m were sexually mature. Collett (1909) showed that North Atlantic right whale females were sexually mature at 13 m. According to the growth curve for southern right whales of Whitehead and Payne (1981), these lengths correspond to ages between 3 and 5.7 years. This suggests that sexual maturity occurs quite early in life. We have not yet completed the analysis of all our data taken from 1980 onwards. However, a preliminary look at some of the females with calves from those years reveals two females first identified in their calf year which were seen with calves of their own 7 years later. If, as some believe, gestation is about 10–12 months (see review in Lockyer, 1984), these individuals were sexually mature at the latest by the age of 6 years. For North Pacific right whales Klumov (1962) gives lengths at sexual maturity of 14–14.5 m for females and 14–15 m for males, while Omura, Ohsumi, Nemoto, Nasu and Kasuya (1969) conclude that males reach sexual maturity at 14.5–15.5 m and females at 15–16 m. Although these data seem to support our belief that the onset of sexual maturity is at a greater length than indicated by Collett (1909) and Matthews (1938), this may not necessarily be true since North Pacific right whales apparently attain a greater size (17–21 m Klumov '1962') than Southern Hemisphere right whales.

Calving interval and questions of conception

By keeping track of the years in which we saw recognizable females with and without calves, we were able to determine the calving interval. The data for each female who had more than one calf are shown in Fig. 11 by year. Each year has been graded from A to D. This grade is a measure of the extent of analyzed aerial surveys for that year. A failure to see a given individual in the years with low grades (1974, 1978 and 1979) means less than a failure to see her in years with an A grade.

We found calving intervals from 2 to 7 years. The six year intervals have been pooled with the three year intervals in Fig. 11 and it is clear that the most common interval is three years. The observed mean calving interval was $3.7 \pm$SD 1.25 years ($n = 89$ observed calving intervals). This mean may however be subject to biases in both directions. Cases of early calf mortality as well as our failure to observe a calf that was born in a year with poor coverage (e.g. 1974) would produce upward biases on the mean (for example we have probably included several 6-year intervals where there actually were twice that number of 3-year intervals). On the other hand, since our data cover only nine years, there is a downward bias against multiple observations of long calving intervals.

There appear to be three different groups of adult females using the calving areas, such that it takes at least three years for a complete cycle of occupancy (still longer when females on longer calving intervals are taken into account). We call the three female groups 'year-classes'. The sizes of the three year-classes appear to be different. Fig. 11 shows that there were 13 females calving in a 3-year cycle in the year-class first seen in 1971 (the 'class of 1971') while 17 such females were seen in the class of 1972, and 23 in the class of 1973 (plus 4 new recruits which first joined this class in 1976). In the nine years presented in Fig. 11, the class of 1973 was always larger than the other two year-classes of females.

There really is not adequate evidence from which to deduce the length of the gestation period of right whales. In spite of this, as noted earlier, it is usually considered to last about one year – an assumption whose best support may simply be that most other mysticetes seem to have one-year gestation periods. If there is no delay in fertilization or fetal growth, and if gestation indeed lasts about one year, we would expect most females to appear at Valdes the year prior to giving birth if that is where they are impregnated. There can be no question that mating is taking place at Valdes; one of the commonest group behaviors we see during the winter/spring is mating (including numerous direct observations of intromission). However there is some question whether the observed mating results in the observed calves. Only 18 out of 91 females (19.8%) were seen at Valdes one year before their first calf (by first calf we mean the first calf seen by us). This statement includes females for which the year prior to the first calf was an A-grade survey year. It also includes females seen with only one calf and not included in Fig. 11. After the first calf, however, the tendency of females to return to Valdes one year prior to giving birth decreases dramatically. With females that have had more than one calf (those in Fig. 11), we could have seen 44 returns in A-grade survey years prior to the second or third calf but we saw only 3 (6.8%). If we combine the return rates for first calves and for subsequent calves, out of 135 possible returns one year before calving, females were observed at Valdes in only 21 cases (15.6%). Does this mean that almost 84% of conceptions are taking place outside of Valdes?

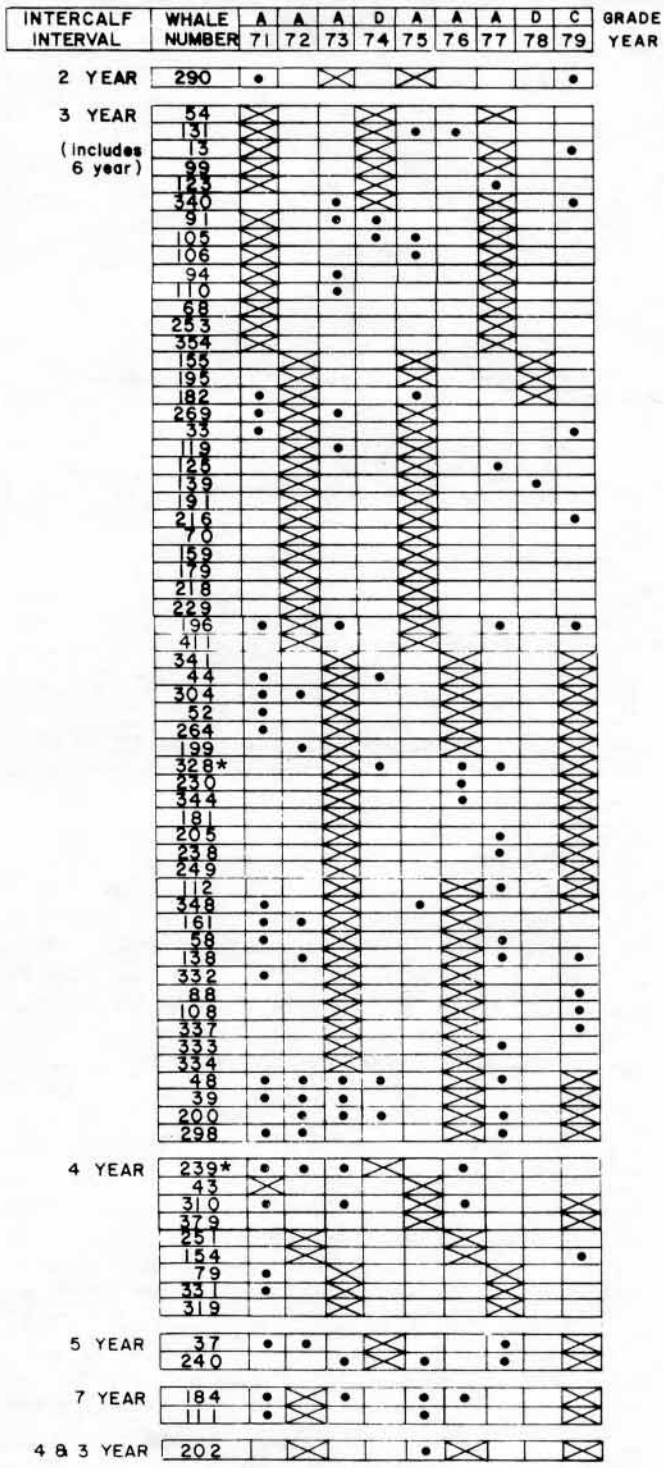

Fig. 11. Sightings of female right whales that have had two or more calves at Peninsula Valdes, 1971 through 1979. The whales are ordered according to length of intercalf interval and to the year in which we first observed them with a calf. Each line is an individual female; each column a year. Years marked with an X are years in which the female was seen with a calf; years with a dot are years in which the female was seen without a calf; and years with neither a dot nor an X – the blank spaces – are years when that whale was not seen. The years are graded A–D according to the number of representative flights made. Two females in this figure, No. 239 and No. 328, were also photographed with calves in 1970, a year which is not included here.

I see several possible alternative explanations to the above: (1) the gestation period may be up to two years (since we have one female who calved on a two-year interval, two years must be the upper limit); (2) delayed fertilization or implantation may occur as it does in several other mammals; or (3) during the year before calving, females may return only briefly to mate and thus could be missed in our aerial surveys. I favor the last alternative but have no firm evidence for it. The timing and location of conception in these right whales is an enigma that awaits explanation.

SUMMARY

(1) Southern right whales migrate annually to the coast of Peninsula Valdes, Argentina. They begin to appear in the area in May and June. Their numbers build to a peak in late September, then decline more rapidly than they built up so that only a few right whales remain in the area by early December.

(2) At Peninsula Valdes, right whales concentrate in three separate areas. The composition of groups within these areas varies – one area being predominantly mothers with calves, a second predominantly males and females without calves and a third composed of all categories of whales, including subadults and mating groups.

(3) Right whales at Peninsula Valdes show a preference for water 5 m deep, a preference exhibited particularly strongly by mothers with calves.

(4) Two females identified in their calf year have been seen with calves of their own at seven years of age. If gestation is about one year then the age of sexual maturity for these two animals was no more than six years.

(5) In females which calved more than once at Peninsula Valdes, calving intervals ranged from 2 to 7 years with a 3-year interval being by far the most common.

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