

**REPRODUCTION, GROWTH AND MIGRATIONS OF SEI WHALES
BALAENOPTERA BOREALIS OFF THE WEST COAST OF SOUTH AFRICA***P. B. BEST** and *C. H. LOCKYER†*

Results of the examination of 1 062 sei whales *Balaenoptera borealis* landed at the whaling station at Donkergat, Saldanha Bay, South Africa, in the 1962 and 1963 whaling seasons are presented. Sei whales were usually encountered off the edge of the continental shelf, with males being caught closer inshore than females and mature females furthest of all from the station. Females reached puberty at an average length of 46.1 ft (14.1 m) and an age of 8.2 (95% CI = 7.3, 9.0) years (assuming one growth layer group is formed in the ear plug per year). Males reached sexual maturity at an average length of 45.3 ft (13.8 m) and an age of 8.6 (95% CI = 7.8, 9.4) years. Mean lengths at which growth ceased were 52 ft (15.8 m) in females and 48.6 ft (14.8 m) in males. Most (~90%) conceptions occurred over a 70-day period with a peak in June, and primigravid females conceived six days later than multigravid females. Observed pregnancy rates were as high as 86.1%, but with ovulation rates averaging only 0.47 a year, the catch could not have been fully representative of the population. There was no significant decline in the observed pregnancy rate with age. During the northward migration (May–July), fewer whales were taken in water shallower than 2 000 m than in the southern migration, and the catch was largely composed of immatures. The few adult males taken at that time of year had significantly heavier testes than males of an equivalent size on the southern migration. The southward migration (August–October) was markedly structured, such that pregnant females and immatures of both sexes were in the vanguard, followed by mature males and lastly lactating females and calves. The availability of sei whales off Donkergat declined rapidly from 1965 to 1967, following an episode of massive catching by pelagic whalers in higher latitudes.

Key words: growth, migration, reproduction, sei whales, South Africa

Like most other rorquals in the southern hemisphere, sei whales *Balaenoptera borealis* migrate seasonally between summer feeding grounds in the Subantarctic and winter breeding grounds in warmer waters, including off the South African coast. Between 1910 and 1979 (when the species was classified as a Protected Stock by the International Whaling Commission), some 176 000 sei whales were reported as taken in commercial whaling in the southern hemisphere. Of all the whaling grounds for sei whales outside the Antarctic, that off the African west coast was by far the most productive. An estimated 9 480 sei whales were taken there between 1912 and 1967, almost twice that reported for the next most important wintering ground, i.e. Brazil (Horwood 1987). Despite this importance, little has been published on sei whales in the region (Matthews 1938, Best 1967a, Best and Gambell 1968), although Gambell (1968) produced a monograph on sei whale seasonal cycles and reproduction that included a large amount of information from Durban on the east coast of South Africa.

In this paper, the results of the examination of 1 062 sei whales landed at the Donkergat whaling station on the west coast of South Africa in the 1962

and 1963 whaling seasons are presented, concentrating on age, growth, reproduction and migratory characteristics. The study was opportune, because the total catch of southern sei whales increased dramatically from 3 629 in 1959 to a maximum of 22 207 in 1965 (Horwood 1987). The consequence was a collapse in the population from which the African animals may have originated. It has been estimated that the exploited population size of sei whales in Area III of the Antarctic (that due south of the African continent, between longitudes 0 and 70°E) declined from some 21 000 animals in 1960 to about 5% of that number in 1979 (International Whaling Commission 1980b). Catches at Donkergat declined accordingly, from 764 in 1965 to 152 in 1967, when the whaling station closed down. Subsequent opportunities to study sei whales off the west coast of South Africa (or to monitor their status) have been virtually non-existent.

A preliminary draft of this paper was submitted to the special meeting of the Scientific Committee of the International Whaling Commission on the assessment of southern sei whales, held in Tokyo, April 1977, and as such was referred to by Horwood (1987). Some of the results presented in the 1977 document have been substantially revised in this paper.

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MATERIAL AND METHODS

The availability of sei whales on the whaling grounds off Donkergat, Saldanha Bay, South Africa (33°S, 18°E), was expressed as the catch per 10² catcher-days (*cpue*) per month from May to October, for the seasons 1962–1967. Except for 1963, effort data were not available on a finer temporal basis than one month, so where it was necessary to look at finer detail (e.g. by 10-day period for the months of August–October), it was assumed that effort was distributed uniformly throughout the month. The abundance of each reproductive class in each month (or 10-day period) was then calculated by multiplying its proportion in the catch by the overall *cpue* value for that period. An exception was made for lactating females, which, because of their legal protection, featured only rarely in the catch. Their availability was calculated from sightings from the spotter aircraft working at Donkergat from 1963 to 1965, and expressed as the number seen per 10² spotting-hours flown (*spue*), on a monthly basis from March to July, and on a 10-day basis from August to October. While the use of *cpue* as a measure of relative abundance for whales has been criticized (De la Mare 1984, Cooke 1985), most of these criticisms refer to its use as an index of abundance over time. In this paper, *cpue* has been used to examine differences in sei whale abundance within a season, rather than between seasons. Similarly, while *spue* data may not be directly comparable with *cpue* data, they are used here to investigate trends in monthly abundance of one particular reproductive class, with no assumption about their comparability with *cpue* data for other reproductive classes.

Catch positions were recorded as bearings and distances from the whaling station, and these have been converted to latitude and longitude. All animals taken on the same day in one area by the same ship tended to be allocated an identical catch position. In recognition of this, and given the limited accuracy of position-fixing in the 1960s, catch positions were grouped by 12-minute cells of latitude and longitude for the purpose of analysis. These cells were allocated to one of eight depth strata, depending on which stratum was dominant within the cell: 0–100, 100–200, 200–500, 500–1 000, 1 000–2 000, 2 000–3 000, 3 000–4 000 and >4 000 m.

Between July 1962 and October 1963, 663 female and 399 male sei whales were examined at the land station at Donkergat. As the whales were brought onto the flensing platform, their length from tip of snout to notch in flukes was measured with a tape held at either end. Lengths were measured in feet and inches and expressed to the nearest foot (40 ft 6 in = 41 ft).

Because metric conversions of these length measurements might give a spurious impression of accuracy, the original measurements in feet have been retained and metric equivalents given in parenthesis.

Female sei whales were first examined for the presence of a vaginal band or tag (the cetacean equivalent of a hymen – Ommanney 1932). Instances were recorded as “intact” (where the band was still present as an antero-posterior strip), “present” (where anterior or posterior or both tags were present) or “absent” (where there was no trace of band or tags). After the belly blubber was removed, the mammary glands were examined for the presence of milk, their depth (to the nearest cm) measured at the widest point of the glands, and the maturity of the gland assessed. Immature glands were soft, pinkish in colour, and with a high proportion of connective tissue. Mature (non-lactating) glands were firmer, orange-brown, and with a lower proportion of connective tissue (Laws 1961).

Later during flensing the diameter of each uterine horn was measured with a ruler while the uterus lay flat on the deck, and if a corpus luteum was present in one of the ovaries, each horn was opened and searched for a foetus. If a foetus was found, it was removed from its foetal membranes, the umbilical cord severed close to the body and its length and sex determined. Lengths were normally measured from the tip of the upper jaw to the notch in the flukes, but in the smallest foetuses the measurement was essentially from the crown of the head to the midpoint of the trailing edge of the tail. All foetuses, apart from the largest, were weighed whole; the largest was cut into three sections for weighing. As obvious fluid loss was minimal, no correction was made to the recorded weight for that animal.

Because the penis was not always fully extruded when male sei whales were brought onto the flensing platform, its length was normally measured after the belly blubber had been removed.

Ovaries and testes were collected during both the 1962 and 1963 seasons, and examined for sexual maturity. Ovaries were fixed in 5% formalin, and later examined as described for sperm whale ovaries by Best (1967b). Each testis was weighed and measured after trimming off all epididymis.

Mature females were those in which at least one corpus luteum or corpus albicans was present in the ovaries. Females were classed as pregnant if (a) there was a foetus present or (b) if a corpus luteum was present, no foetus could be found but a set of empty foetal membranes or a patch of uterine mucosa that was conspicuously vascular was found. Primigravid females were those that were pregnant for the first time, because their mammary gland was still immature;

multigravid females were those that were pregnant for at least the second time, judging by the macroscopic appearance of the mammary gland. Females were classed as ovulating if there was a corpus luteum present but no foetus, despite a thorough search of both horns of the uterus (which was usually cut out of the whale for closer and more protracted examination, if a foetus could not be palpated from the outside). Other females with a corpus luteum present, but in which no evidence of a foetus could be found, were classed as a separate category – pregnant/ovulating? In this case, and in (b) above, the uterus had usually been ruptured before examination, either by a harpoon or a flensing knife, and any foetus present may have been lost. Females were classed as lactating if the mammary gland contained milk. Resting females were mature females with no foetus or corpus luteum present and no milk in the mammary gland.

The size of the corpus luteum was used as an arbitrary means of allocating “pregnant/ovulating” animals to either category. According to Gambell (1968), the mean diameter of sei whale corpora lutea of ovulation was 5.47 ± 0.27 cm, and that of corpora lutea of pregnancy for females with foetuses up to 10 cm in length, 7.62 ± 0.18 cm. Taking a median value (6.55 cm), all whales with a corpus luteum smaller than this have been assumed to be ovulating and all those with an equal or larger corpus luteum to be pregnant.

Applying this criterion to Gambell’s data would result in about 34% of corpora lutea of ovulation being incorrectly classified as corpora lutea of pregnancy. Whereas this might suggest that the size criterion is not very robust, in reality some of the apparently ovulating females with large corpora lutea may have been in early pregnancy with a very small, undetected blastocyst or embryo (given the inherent difficulty of searching the uterus comprehensively under field conditions). Consequently, the extent of misclassification resulting from application of the 6.55 cm criterion is probably less than indicated here.

From a histological study, Gambell (1968) concluded that sexual maturity in male sei whales occurred at a single testis weight of 1 500 g, above which all animals were either pubertal or mature. Separate weights of left and right testes were available for 301 males examined at Donkergat. In 21 instances the testes were equal in weight, in 210 the left testis was heavier than the right and in 70 the right was heavier than the left. The ratio of the last two frequencies is significantly different from parity ($\chi^2 = 70$, $df = 1$, $p < 0.001$). This indicates an asymmetry in testis development, with the left testis being generally heavier than the right (although in 148 of the animals in which the left testis was heavier, the difference was <100 g). Never-

Table I: Sample sizes of ear plug collections from sei whales at Donkergat

Season	Sex	Total catch	Ear plug sample (%)	Readable ear plugs	
				Catch (%)	Sample (%)
1962	Male	141	107 (76)	48	64
	Female	242	167 (69)	43	63
1963	Male	269	169 (63)	46	73
	Female	451	293 (65)	45	70
Total		1 103	736 (66.7)		

theless, Gambell (1968) stated that the testes sampled at Durban were selected at random, so simply doubling single testis weight should be an appropriate means of obtaining combined testis weight. On that basis, the criterion for sexual maturity in male sei whales has been taken to be a combined testis weight of 3 000 g. Applying the 1 500 g single-testis weight criterion to Gambell’s data for Durban would result in no immature, but about 3% of mature whales, being incorrectly classified. The weight criterion therefore seems reasonably robust.

Attempts were made from each whale landed to collect ear plugs for age determination (Lockyer 1974), but in some the plugs were too small, soft or fragmentary to be worth preserving. In total, 736 plugs were collected from 1 103 whales landed (66.7% of the catch; Table I). During processing, the plugs were cut down to the midline of the core and then examined under low-power magnification for growth layers. Darkly pigmented plugs were bleached in 20 volumes percent hydrogen peroxide. From one to three persons examined the plugs, and satisfactory counts of layers were made for between 63 and 73% of the ear plug sample. However, this represented only 43–48% of the total catch (Table I). Counts were expressed as the number of growth layer groups (GLGs), where a GLG consisted of at least one adjacent dark and light layer forming part of a cyclically repetitive pattern (International Whaling Commission 1980a). Good evidence has been presented that one GLG may be formed per year in southern sei whales (Lockyer 1974).

The physical maturity status of individual whales was assessed by chipping the corner off either a mid-caudal, mid-lumbar or anterior thoracic vertebra with a hand axe, thus exposing the region of fusion between the epiphysis and centrum. Epiphyses were recorded as fused if no cartilage (or line of fracture) could be detected between the epiphysis and centrum. Epiphyseal

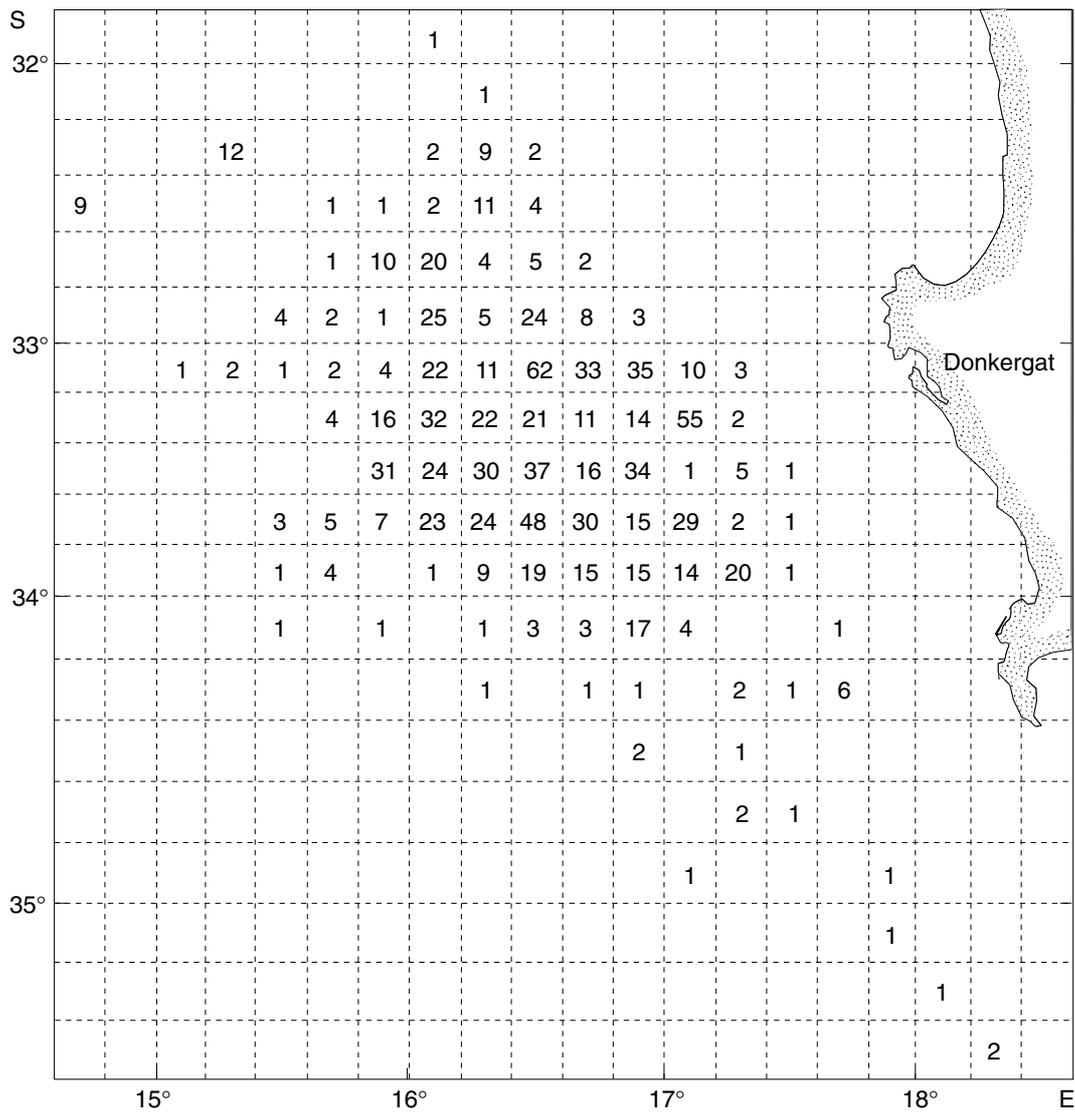


Fig. 1: Distribution of catch positions for sei whales examined at Donkergat, 1962–1963 (numbers in each grid are total whales caught)

fusion was assumed to progress from either end of the vertebral column, but more rapidly from the caudal end, so that the last vertebral epiphyses to fuse were in the anterior thoracic region, as in the fin whale (Wheeler 1931, Ohsumi *et al.* 1958). Thus, if a caudal vertebra was found unfused, it was assumed that both lumbar and anterior thoracic vertebrae would be un-

fused, whereas if a lumbar vertebra was fused, then the caudal vertebra would be fused. These have proved to be robust assumptions, following a number of mysticete and odontocete dissections (Aguilar and Lockyer 1987, PBB, pers. obs.). Physical maturation was studied this way in 155 female and 47 male sei whales at Donkergat in 1962 and 1963.

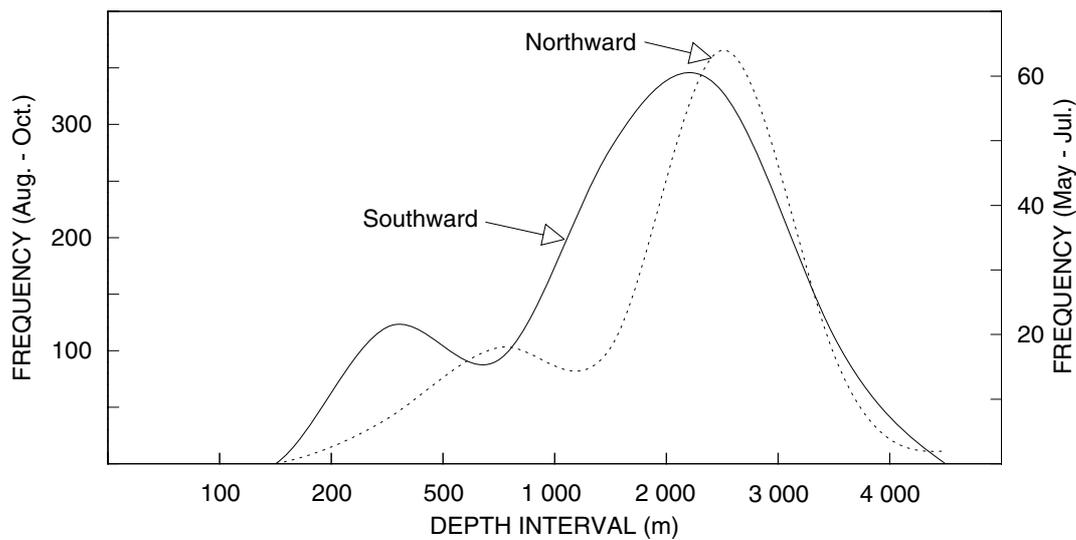


Fig. 2: Spline curves fitted to distribution of sei whale catches relative to water depth, for northward (May–July) and southward (August–October) migrations

RESULTS

Distribution

According to the evidence given by a whaling captain at Saldanha Bay in 1919, the season for sei whales was mostly in late September, and they were usually found far offshore, 50–60 miles (Best 1994). This distribution would have accounted for the scarcity of sei whales in the catch, because in the early years of whaling the catching grounds (mostly for humpback whales *Megaptera novaeangliae*) were centred much closer to the coast. For instance, sperm whales *Physeter macrocephalus* were rarely taken because the catchers only infrequently went as far as the edge of the continental shelf.

The distribution of sei whales examined at Donkergat during the 1962 and 1963 whaling season is shown by 12-minute square of latitude and longitude in Figure 1. It seems to agree with that described in 1919, in that very few whales were taken within 40 miles of the station, and the bulk of catches were made 60–100 miles from Donkergat. Similar distributions seem to prevail for each season from 1958 to 1963, judging by the average distances at which sei whales were caught from the station in those years (Table II).

This offshore distribution may be correlated with the

known preference of sei whales for water warmer than that preferred by fin whales *Balaenoptera physalus* or blue whales *B. musculus*, because the cold Benguela Current runs close inshore along the west coast of South Africa (Best 1967a).

The distribution of sei whale catches relative to water depth in 1962 and 1963 has been plotted separately for the periods May–July and August–October, because these are believed to correspond roughly to episodes of northern and southern migration respectively (Fig. 2). No sei whales were taken in water <200 m deep, and very few (two) in depths >4 000 m. The relative numbers of animals caught in each depth interval between 200 and 4 000 m were significantly different in the two periods ($\chi^2 = 24.81, p < 0.0001, df = 4$). Whereas there was little difference in the shape of the distribution

Table II: Distances of sei whale catches from Donkergat whaling station by year

Season	Number of records	Mean distance (miles)	Standard deviation
1958	401	67.7	15.2
1959	525	94.2	28.6
1960	489	89.7	20.6
1961	225	92.7	23.7
1962	382	89.1	21.8
1963	721	77.6	21.7

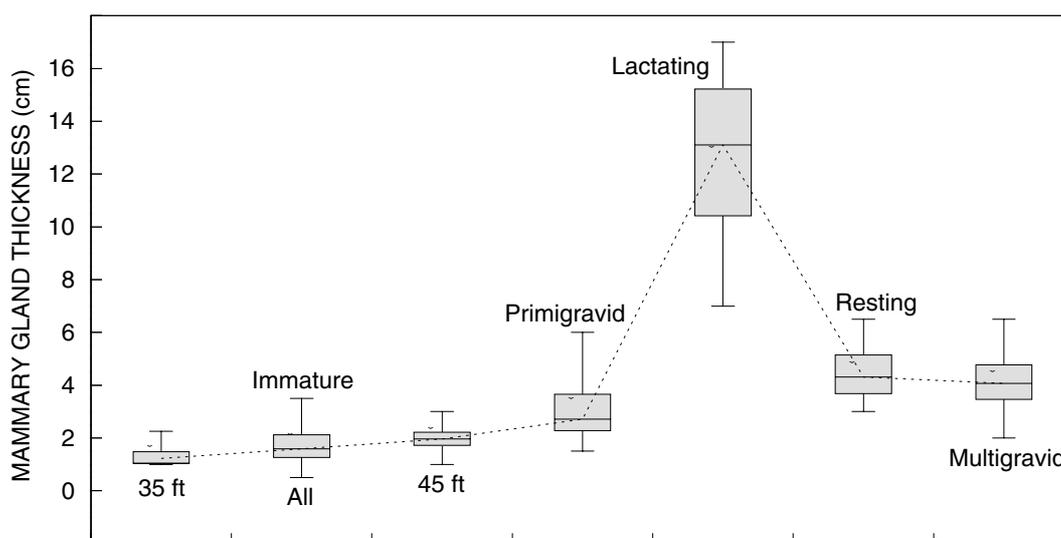


Fig. 3: Thicknesses of mammary glands in sei whales at Donkergat, 1962–1963 (range, mean and one standard deviation indicated)

with depth offshore (probably reflecting a common limit to the operational range of the catchers), a markedly lower proportion of sei whales was caught in water depths <2 000 m in May–July (34.1%) than in August–October (52.7%).

For the sei whales examined in 1962 and 1963, the average distance at which mature females were caught from the station (86.2 miles, $n = 381$) was greater than that for immature females (81.0 miles, $n = 280$; $t = -3.0614$, two-tailed $p = 0.0023$). There was no such difference between immature and mature males (mean distances = 77.3 miles [$n = 225$] and 78.1 miles [$n = 166$] respectively; $t = -0.3963$, two-tailed $p = 0.6921$). Males on average were caught closer to the station than either mature or immature females ($t = -5.4225$, two-tailed $p < 0.0001$, and $t = -1.9687$, two-tailed $p < 0.05$ respectively). The average distance at which lactating females were caught from the station (77 miles, $n = 13$) was less than that for other mature females (86.5 miles), but not significantly so ($t = -1.7629$, two-tailed $p = 0.1014$).

Reproduction

ATTAINMENT OF SEXUAL MATURITY IN FEMALES

An intact vaginal band was recorded in only 19 (3.7%) of 509 females examined, and the presence of tags (indicating a broken band) in another 22 (4.3%). Of

those with an intact band, all but two were immature females 35–45 ft (10.7–13.7 m) in length, the ages of six of which ranged from 2 to 11 GLGs. The two exceptions were primigravid females, 47 ft (14.3 m) and 51 ft (15.5 m) in length, each with a single corpus in the ovaries. Successful intromission is therefore possible without the band necessarily being broken (though clearly it would not survive the subsequent birth of a calf).

Mammary glands in immature, non-pregnant individuals ranged in depth from 0.5 to 3.5 cm, most being between 1 and 2 cm thick (Fig. 3). The glands enlarged as maturity approached, increasing from a mean depth of 1.2 cm at a length of 35 ft (10.7 m) to 2 cm at 45 ft (13.7 m). Animals early in their first pregnancy had slightly larger glands, ranging from 1.5 to 6 cm (mostly 2–3 cm) thick, with a mean of 2.7 ± 0.8 cm. During lactation, glands swelled to depths of 7–17 cm (mean 13.1 ± 2.6 cm). Following the first lactation, the mammary glands failed to regress to their former size, ranging from 2 to 6.5 cm (most 3–5 cm, mean 4.1 ± 0.8 cm) thick in multigravid animals (those in their second and later pregnancies).

Uterine cornua in immature and resting females were generally bilaterally symmetrical (Fig. 4). Their width in immature animals increased very little in individuals between 35 and 40 ft (10.7 and 12.2 m) long, on average ranging between 3 and 3.5 cm. Thereafter, the cornua enlarged rapidly to a mean diameter of 5.9 ± 1.4 cm in females 45 ft (13.7 m) long and $7.2 \pm$

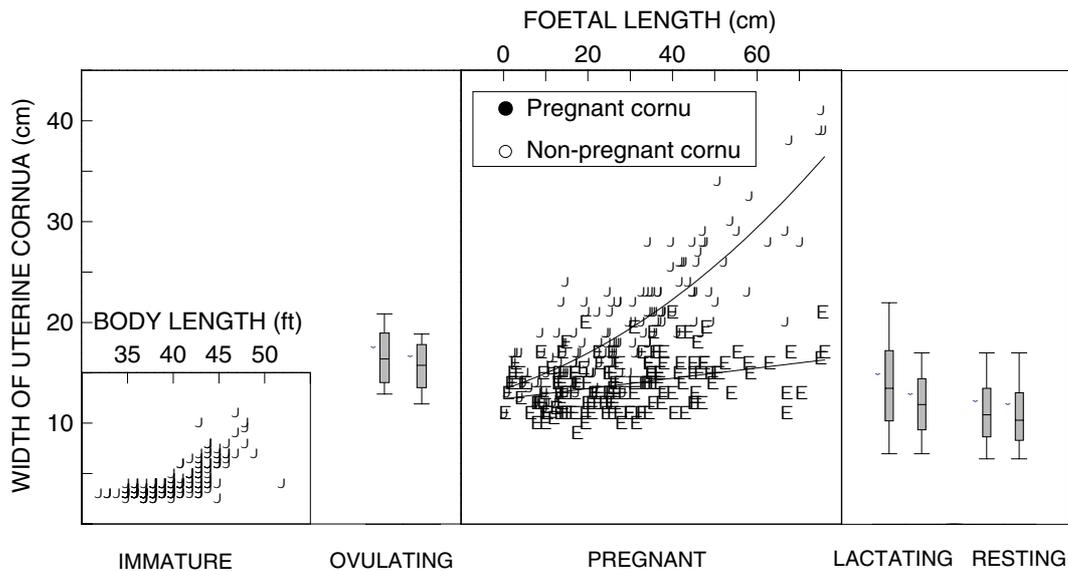


Fig. 4: Diameters of uterine cornua in sei whales at Donkergat, 1962–1963. For ovulating, lactating and resting females, the larger cornu is on the left, and ranges, means and one standard deviation are indicated. For immature and pregnant females, diameters are plotted against body length and foetal length respectively

2.8 cm in animals 46 ft (14 m) or more in length. The uterus presumably enlarged considerably at ovulation, because eight females classified as ovulating had cornua averaging 16.5 ± 2.6 cm (larger) and 15.9 ± 2.3 cm (smaller) in width. In pregnant females, however, a trend line fitted to cornua diameters plotted against foetal size predicted that, at conception, both cornua would be of similar width (12.4 cm for the non-pregnant and 12.9 cm for the pregnant horn). With the subsequent growth of the foetus, the pregnant horn expanded exponentially in width, whereas the width of the non-pregnant horn increased linearly. By the time the foetus reached a length of 70 cm, the pregnant horn is estimated to have measured 33 cm in width, compared to 16 cm for the non-pregnant horn. There were no data for females in late pregnancy. Regression of the uterus after birth must be rapid, because in 12 lactating females the diameters of the larger and smaller horns averaged 13.5 ± 3.6 and 11.9 ± 2.8 cm respectively, and in 18 resting females averaged 10.8 ± 3.0 and 10.3 ± 2.9 cm respectively.

The incidence of mature individuals among 661 females at each foot of body length is shown in Table III. The smallest mature individual was 43 ft (13.1 m) long and the largest (but one) immature individual 49 ft (14.9 m). One female 52 ft (15.9 m) long taken on 29 September 1963 was markedly underdeveloped, with an immature mammary gland 2 cm thick, uterine

cornua 4 cm in diameter and ovaries weighing 40 and 45 g each, with no ovarian corpora. Although no ear plug could be collected, the degree of scarring on the body surface did not indicate that this was a very young animal. The specimen was considered abnormal and was therefore excluded from further analyses. The average length at sexual maturity was calculated, using the method of DeMaster (1978) as 46.1 ft (14.1 m), with 95% confidence intervals of 45.8 and 46.4 ft (14.0 and 14.1 m).

ATTAINMENT OF SEXUAL MATURITY IN MALES

Penis length was measured in 123 males, and ranged from 33 to 178 cm. There was a marked increase in penis size at a body length of 44 ft (13.4 m), from an average of 67.5 ± 17.5 cm at 43 ft (13.1 m) to 106.8 ± 23.1 cm at 44 ft (13.4 m – Fig. 5). This increase is presumably correlated with sexual maturation.

Combined testes weights were available for 391 males (Fig. 6). Adopting a weight of 3 000 g as the criterion for sexual maturity, the incidence of mature individuals at each foot of body length is shown in Table III. The smallest mature male was 42 ft (12.8 m) long and the largest immature male 50 ft (15.2 m) long. The average length at sexual maturity was calculated, using the method of DeMaster (1978), as 45.3 ft (13.8 m), with 95% confidence intervals of 45.0 and

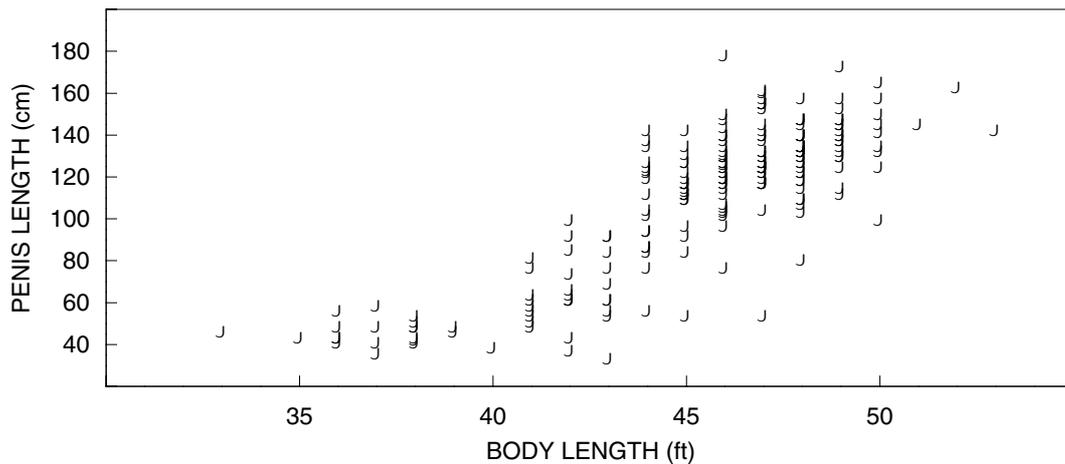


Fig. 5: Penis lengths in sei whales of different body lengths at Donkergat, 1962–1963

45.7 ft (13.7 and 13.9 m). A regression of the log of combined testis weight in g (y) against penis length in cm (x) indicated a close relationship ($r^2 = 0.7912$):

$$\text{Log } y = 2.2060 + 0.0122x$$

Using this equation, a recently matured male with a penis 106.8 cm long would have testes averaging 3 228 g in combined weight. This is close to the weight of 3 kg used as the criterion for sexual maturity, confirming that penis length may be a useful indicator of sexual maturity.

Pregnancy, foetal growth and seasonality of breeding

FOETAL SEX RATIO

A total of 245 foetuses from sei whales was sexed (Table IV). There was no significant difference between the sex ratio of foetuses from primigravid and from multigravid females ($\chi^2 = 0.166, p = 0.684, df = 1$), and the total sex ratio for all foetuses examined (51.4% male, 48.6% female) was not significantly different from parity ($\chi^2 = 0.2, p > 0.5, df = 1$).

OCCURRENCE OF MULTIPLETS

Only two of the pregnant females examined carried twins. One of these was an apparent example of functional polyovuly, involving 38 cm male and 39.5 cm female foetuses (Best and Bannister 1963); this had apparently occurred at the whale's first ovulation. The other record was of a pair of female foetuses, 29 and 30 cm long, from a whale with a total of 25 ovarian corpora; these were associated with two separate

corpora lutea in the same ovary. The overall incidence of multiplets in these data (0.67%) was somewhat less than that recorded from Donkergat in the succeeding

Table III: Body length and sexual maturity in sei whales at Donkergat, 1962–1963

Body length (ft)	Males		Females	
	Number examined	Mature (%)	Number examined	Mature %
32			1	0
33	2	0	2	0
34	3	0	1	0
35	15	0	13	0
36	18	0	22	0
37	24	0	26	0
38	29	0	26	0
39	25	0	15	0
40	16	0	30	0
41	23	0	25	0
42	23	4.3	22	0
43	15	0	33	3.0
44	20	30	25	8.0
45	27	74.1	26	38.5
46	40	77.5	36	75.0
47	34	100	42	81.0
48	39	94.9	57	87.7
49	22	95.5	52	98.1
50	11	90.9	63	100
51	1	100	64	100
52	3		41	97.6
53	1		20	100
54			12	100
55		6	100	
56		1	100	
Total	391		661	

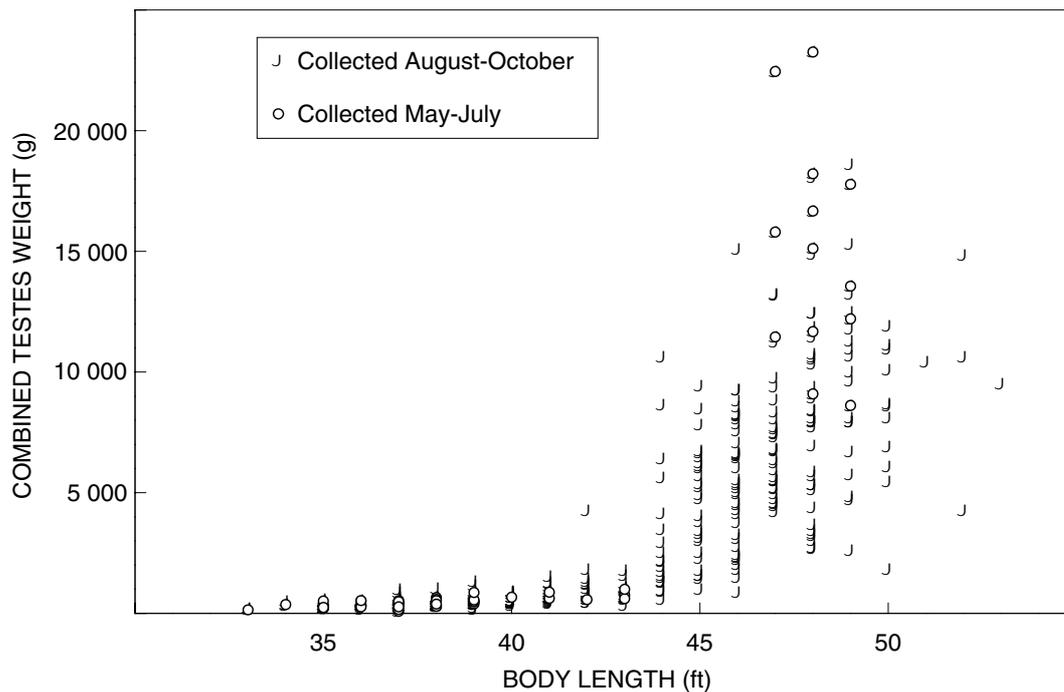


Fig. 6: Combined testes weights in sei whales of different body lengths at Donkergat, 1962–1963

seasons 1964–1967, where it averaged 1.25% ($n = 321$). Because of a tendency to record the unusual, commercial whaling data may tend to exaggerate the incidence of multiplets (Gambell 1968). There were an additional 75 females reported as doubtfully pregnant between 1964 and 1967. If these are included in the sample, the incidence of multiplets would fall to 1.01%. All cases recorded were twins.

INTRA-UTERINE MORTALITY

There were four instances of possible intra-uterine mortality recorded (Table V), representing 1.6% of all pregnancies. This is presumably an underestimate of actual foetal mortality because of the difficulty in detecting early embryonic mortality in these field conditions. Three of these involved females in their first pregnancy, and the fourth was a multigravid female (implying foetal mortality rates of 3.5 and 0.5% respectively). They have all been omitted from the analysis of foetal growth.

IPRESENTATION

The corpus luteum was found in the right ovary in 51.8% of 193 pregnancies, and the foetus in the right uterine cornu in 53.5% of 172 pregnancies. These

included three instances in which the foetus was found in the opposite cornu to the corpus luteum. In two of these instances, a vascular patch was detected on the wall of the same uterine cornu as the ovary with the corpus luteum, suggesting that the foetus and its membranes had been dislodged after death. Of 132 foetuses between 5.5 and 98 cm long examined, 84 (63.6%) were orientated in a head presentation; this proportion did not change significantly between foetuses 0–20, 21–40 and >40 cm long ($\chi^2 = 3.04$, $p = 0.218$, $df = 2$).

FOETAL LENGTH/WEIGHT RELATIONSHIP

For 250 sei whale foetuses, both body length and weight were measured. When plotted logarithmically, the relationship between these variables is generally linear, except for foetuses smaller than about 8 cm, in which the weights fall above the regression line. This probably reflects the changing shape of the foetus around a length of 8 cm, so that in larger foetuses, measurements of total length are taken from the snout to the tail, rather than from crown to tail. Separate length/weight relationships have therefore been estimated for foetuses above (W_l , $n = 236$) and below (W_s , $n = 14$) a length of 8 cm, as

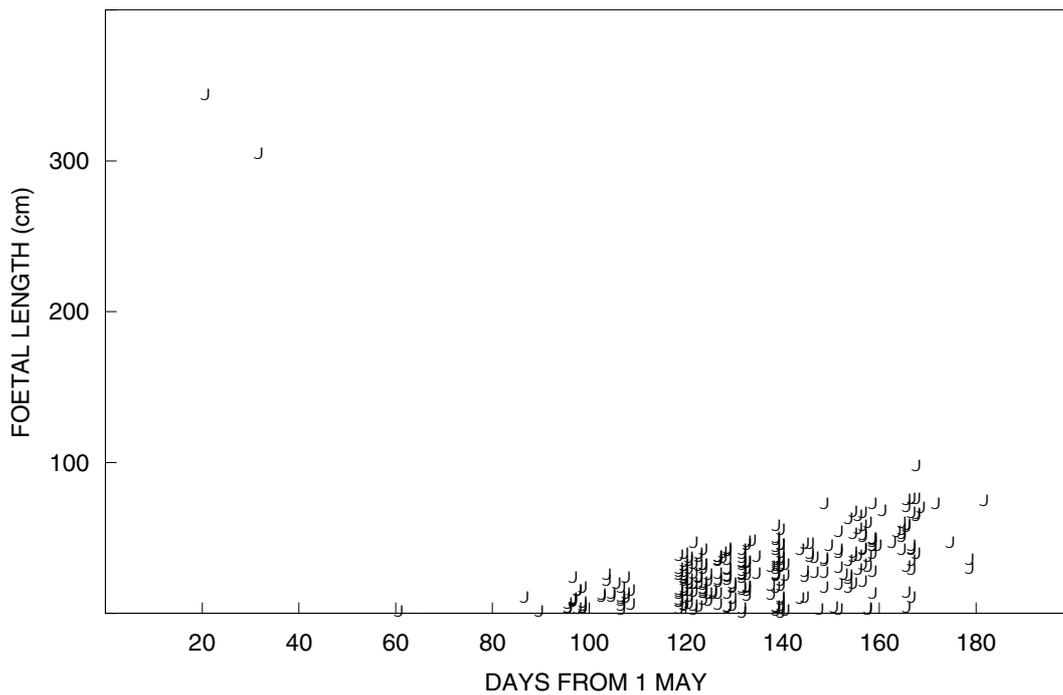


Fig. 7: Dates and lengths of sei whale foetuses examined at Donkergat, 1962–1963

$$W_i = 0.0445L^{2.6529}$$

and

$$W_s = L^{1.105}$$

where W_i is weight in g and L is length in cm ($r^2 = 0.9918$ and 0.6078 respectively). The correlation for W_s is poor, but this is probably a combination of small sample size and forcing the regression to go through the origin. Using the regression for W_i , the weight of the foetus at birth, assuming a length of 4.58 m, was calculated to be 509.8 kg.

FOETAL GROWTH AND SEASONALITY OF BREEDING

Laws (1959) described foetal growth in length in several balaenopterid species (including sei whales) as exponential after about the initial five months from conception. When the cube root of body weight instead of length is plotted against time since conception, the latter growth phase of the foetus is reasonably described by a straight line (Lockyer 1981). The gradient of this line gives a , the foetal growth velocity constant, and the point where this line cuts the x -axis, if produced backwards, gives the value of t_0 , the time in days since conception prior to the linear growth phase. As stated by Lockyer (1981), this method of determining a and t_0 is open to question, because doubt still exists as to which growth phase should be used to determine the growth constants.

The lengths of foetuses from 298 pregnant females examined are plotted against date in Figure 7. Two females killed in autumn were carrying a 344-cm female foetus (on 21 May) and a 305-cm female foetus (on 1 June) respectively; they were classed as in "late pregnancy". The remaining 296 females, taken in late winter and spring, were carrying foetuses 1–98 cm

Table IV: Foetal sex ratio of sei whales examined at Donkergat, 1962–1963

Class of female	Male foetuses	Female foetuses	Indeterminate sex	Total
Primigravid	33	35	17	85
Multigravid	83	75	28	186
Indeterminate	10	9	9	28
Total	126	119	54	299

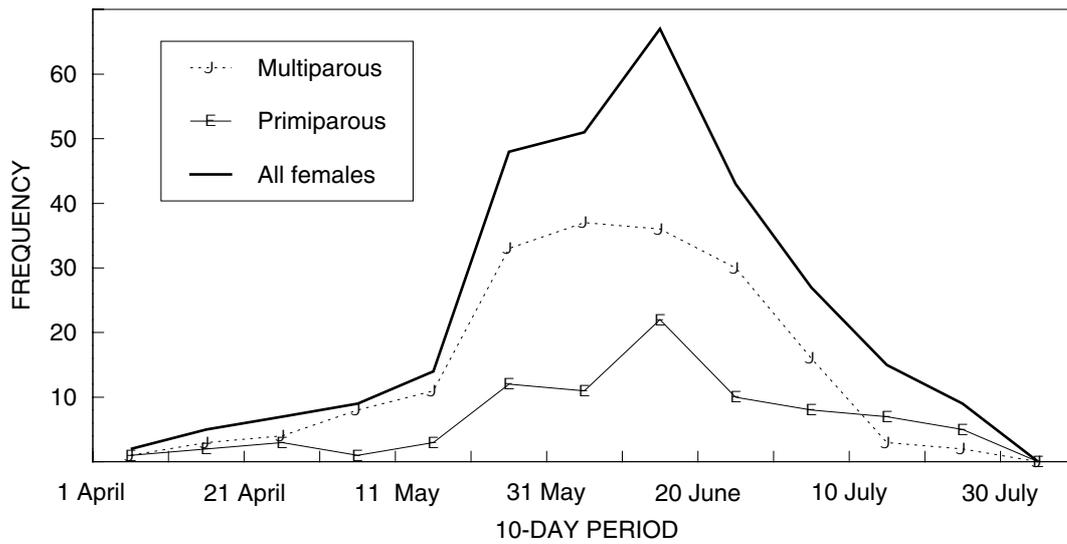


Fig. 8: Distribution of conceptions by 10-day period in primigravid, multigravid and all pregnant sei whales at Donkergat, 1962–1963

long and were considered as in “early pregnancy”. Only the latter have been used in the analysis below.

Fitting a trend line to the data for females in early pregnancy, from which foetal growth rate (and hence seasonality of reproduction) might be estimated, is problematic, because it is difficult to establish where the inflection between the two phases of foetal growth might occur. It is also clear from the size of the foetuses that some conceptions or implantations may still be occurring in winter and spring, so that trend

lines fitted to the observed foetuses may underestimate foetal growth at this stage of pregnancy. For those reasons, no estimation of foetal growth parameters has been attempted using these data. Lockyer (1981) estimated the rate of foetal growth in southern sei whales, using data mainly from the Antarctic in summer, thus (a) avoiding most of the seasonal bias in foetal size distribution and (b) allowing reasonable determination of the inflection point between the two phases of foetal growth. That author also employed

Table V: Possible instances of intra-uterine mortality of sei whale foetuses

Platform number	Date	Length of adult	Status	Foetus, length, sex	Remarks
73	7 Aug. 1962	45 ft (13.7 m)	Primigravid – corpora count one	5.5 cm, ?	Foetus trapped at distal end of cornu due to terminal vesicle of the chorion becoming entangled in narrow uterine lumen. Dark in colour, head and forelimbs deformed or decomposing – foetus filled whole amnion
333	13 Sep. 1962	48 ft (14.6 m)	Primigravid – corpora count two	?	Elongated vesicle 31.5 × 6.5 cm in pregnant horn – amnion-like sac free in vesicular lumen – sac contained free-floating object
1 776	3 Aug. 1963	46 ft (14 m)	Primigravid – corpora count one	CBL* 2.3 cm	Skull, pieces of vertebral column, placental remains in pregnant cornu
2 025	29 Aug. 1963	53 ft (16.2 m)	Multigravid – corpora count 10	6 cm, ?	Foetus odd – amnion very large and chorion very round for size of foetus – already dead?

* CBL = Condylar-basal length

Table VI: Numbers of immature and mature female sei whales examined each month at Donkergat in 1962 and 1963, combined, and the proportions of different reproductive classes among mature females (values in parenthesis refer to whales classified as pregnant?/ovulating? allocated to either pregnant or ovulating classes, depending on the size of their corpus luteum)

Month	Reproductive class					
	Number immature	Number mature	Proportion pregnant	Proportion ovulating	Proportion resting	Proportion lactating
May	23	3	0.333	0	0.667	0
June	21	8	0.25	0.375	0.375	0
July	8	4	0.50 (0.75)	0 (0.25)	0	0
August	69	114	0.781 (0.860)	0.07 (0.088)	0.053	0
September	74	163	0.89 (0.92)	0.012 (0.031)	0.025	0.025
October	81	88	0.83	0.011 (0.023)	0.057	0.091
Total	276	380				

foetal weights rather than length, allowing comparison with the foetal weight/gestation time relationship first proposed by Huggett and Widdas (1951). Consequently, in this paper, Lockyer's (1981) predicted growth in weight with time for sei whales has been adopted, i.e.

$$W = [0.35(t - 74)]^3$$

where W is weight in g and t is time from conception in days.

To estimate conception dates, foetal weights were entered into the above equation. Where foetal weights were not available (24 of <8 cm, 25 of >8 cm), they were estimated from one of the two length/weight relationships above, depending on the size of the foetus. The distribution of conception dates by 10-day period calculated in this manner indicates that most (89%) occurred over a 70-day period, between 11 May and 19 July, with a mean date of 11 June (Fig. 8).

Primigravid females appeared to conceive a few days later on average than multigravid females, with mean conception dates of 13 June and 7 June respectively ($t = -2.27$, $p = 0.024$).

As an independent assessment of the timing of the breeding season, the monthly proportion of mature females classified as ovulating is shown in Table VI. Despite very small samples of mature females in May, June and July, the proportion of ovulating animals is clearly highest in June (37.5%) and rapidly declines to <10% in August and only 2–3% in September and October. Although there are no data prior to May, and the observed proportions may be influenced by catch selection, especially against lactating females, the pattern is consistent with the distribution of conceptions estimated from foetal data.

As a further confirmation of the seasonality of reproduction, mature males taken between May and July had much heavier testes than males of a similar size

taken between August and October, whereas immature males had similar-sized testes in both periods (see Fig. 6). The average combined testes weight for the 13 males taken in the period May–July (all were between 47 and 49 ft [14.3 and 14.9 m] long) was $15\,069 \pm 1\,277$ g. This is significantly heavier than the average weight of $7\,968 \pm 384$ g for 81 males in the same size range taken in the period August–October ($t = 5.325$, two-tailed $p < 0.0001$). The average lengths of the males in the two samples were 48.1 ± 0.2 and 47.9 ± 0.1 ft (14.7 ± 0.06 m and 14.6 ± 0.03 m) respectively.

SIZE AT BIRTH

There are no records of neonatal animals in the dataset, and there appear to be none published for the southern hemisphere. The largest foetus in the current dataset measured 3.44 m, and was taken in May. In other sets collected by biologists, foetuses as large as 4.09 m have been measured in February, and in data from commercial sources, foetuses as large as 4.88 m in March (Matthews 1938) and 4.71 m in April (Risting 1928). In the northern hemisphere, a sei whale calf of 4.27 m has been recorded (Tomilin 1957); the record of a 4.4 m calf attributed to Mizue and Jimbo (1950) by Horwood (1987) and others seems to be an error because it is not in the original publication. Taking the average of the 4.27 m calf and the largest southern hemisphere foetus gives a value of 4.58 m for size at birth, close to the value of 4.5 m used by Matthews (1938), Gambell (1968) and Horwood (1987).

INCIDENCE OF REPRODUCTIVE CLASSES AMONG MATURE FEMALES

In all, 380 sexually mature female sei whales for which both ovaries were collected were examined (Table VI).

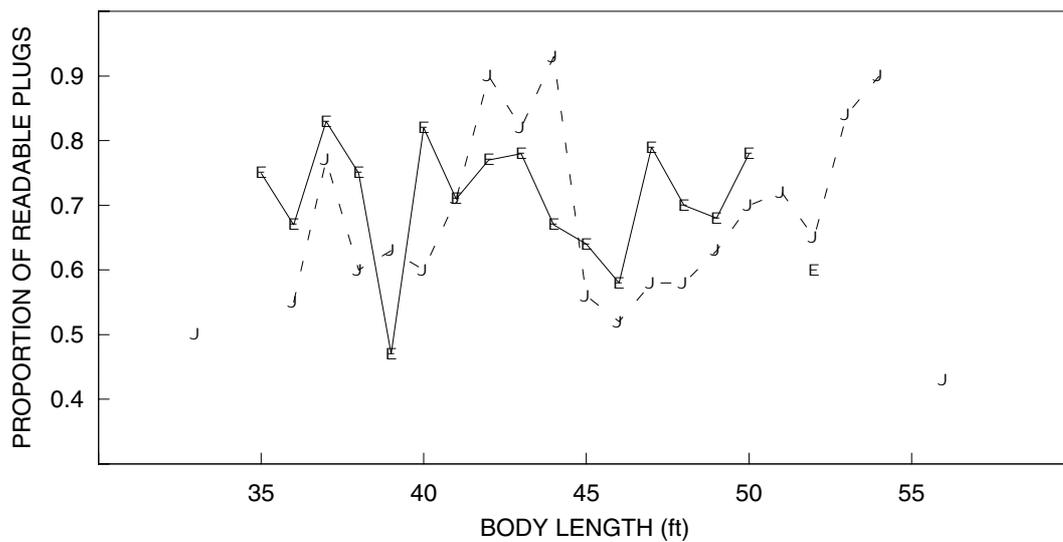


Fig. 9: Readability of ear plugs from male and female sei whales at Donkergat, 1962–1963. Straight lines indicate overall means for each sex

Of these, 312 (82.1%) were pregnant, 14 (3.7%) ovulating, 12 (3.2%) lactating, 20 (5.3%) resting, and a further 22 (5.8%) were classified as pregnant?/ovulating?. One pregnant individual (taken on 26 October 1963) was simultaneously lactating, although the left mammary gland only (14.5 cm thick) contained (little) milk. The right nipple of this individual was deformed (no external opening), and the corresponding mammary gland was 9 cm thick, non-lactating but with wide ducts and apparently pathological tissue. The foetus (female) measured 36 cm in length. It is not clear whether the abnormal mammary gland contributed to the persistence of lactation in this individual.

To estimate the pregnancy rate, only whales taken after July (i.e. on the southern migration) have been considered, because conceptions were probably still occurring during the northward migration. Of 365 mature females taken from 1 August to 31 October, 307 (84.1%) were pregnant, 11 (3.0%) were ovulating, 20 (5.5%) were pregnant?/ovulating?, 15 (4.1%) were resting and 12 (3.3%) were lactating. If all the females classified as pregnant?/ovulating? were actually pregnant, the overall pregnancy rate would become $(307 + 20)/365 = 89.6\%$. Assuming that only corpora lutea 6.55 cm or more in diameter represented corpora lutea of pregnancy (see Material and Methods), an adjusted overall pregnancy rate can be estimated as $(307 + 14)/365 = 87.9\%$ (and an adjusted proportion ovulating of $11 + 6 = 17/365$, or 4.7%). However, all of these rates are not true reproductive rates, principally because of the selection against lactating females.

Nevertheless, the small number of non-pregnant, non-lactating females examined indicates that actual pregnancy rates are likely to be high. An approximation to the true rate can be calculated, assuming that the ratio of adjusted pregnant to non-lactating, non-pregnant individuals is unbiased, and that there are likely to be as many lactating as pregnant females in the population. This produces a “true” pregnancy rate of $(307 + 14)/2(307 + 14) + 17 + 15 = 47.6\%$. Approximate 95% confidence intervals for this overall estimate (using the binomial distribution) would be 44.3 and 51.0%, but these do not take into account any of the uncertainties involved in estimating the component parts of the overall rate.

Age and growth

AGE/LENGTH KEYS

The whales for which a satisfactory ear plug growth layer count was obtained were used to construct age/length keys. The validity of using such keys in further analyses has been tested, by examining whether or not the information therein is likely to be representative of the total catch.

In Figure 9, the percentage of satisfactory layer counts at each body length is shown. The numbers of very small and very large animals are naturally low. However, between body lengths of 36 and 54 ft (11.0 and 16.5 m) in females and 36 and 50 ft (11.0 and

Table VII: Age-length key of male sei whales at Donkergat, 1962–1963

Age (GLGs)	Body length (ft)																		
	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
1																			
2																			
3	3	1	1	2	2	1	2			2	1								
4		2	4	3	1	1													
5		2	3	3	2	2													
6		1	1	2	2	2	3	1	1										
7					1	2	4	6	1										
8						2	1	1	1	1	2	1							
9					2			1	1	2	2								
10								1	1	1	1								
11									1	2	2								
12										1	2								
13										3	1								
14											2								
15											4								
16										1	2								
17											2								
18											1								
19											2								
20											1								
21											2								
22											1								
23											2								
24											1								
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31											1								
33											1								
34											1								
35											1								
36											1								
41																			
42																			
50																			
53																			
57																			
60																			1

15.2 m) in males, there appears to be no steady indication of variation in plug readability with body size.

The body length frequency distribution of the readable ear plug sample has been compared with that of the total catch, taking the latter information from International Whaling Statistics Volumes 51 and 53. The observed size frequency distributions of the readable ear plug samples were not significantly different from the expected distributions calculated from the total catch in each case (1962 males; $\chi^2 = 8.64, p > 0.95, df = 18$; 1963 males; $\chi^2 = 18.41, p > 0.25, df = 19$; 1962 females; $\chi^2 = 23.26, p > 0.25, df = 20$; 1963 females; $\chi^2 = 31.04, p > 0.10, df = 24$).

In conclusion, the ear plug samples for which satisfactory layer counts have been made are almost cer-

tainly representative of the whale catches in both seasons, for both males and females. Age/length keys for 191 males and 307 females are provided in Tables VII and VIII respectively. The oldest male had 60 GLGs and the oldest female 53 GLGs. The latter value compares with a maximum corpora count of 28, equivalent (at an annual ovulation rate of 0.47 and an age of 8.2 years at first ovulation – see below) to an estimated age of 67.8 years. However the ovarian sample size was much greater than that for readable ear plugs (656 v. 307).

SEXUAL MATURATION

The age of females at their first ovulation could be

Table VIII: Age-length key of female sei whales at Donkergat, 1962–1963

Age (GLGs)	Body length (ft)																				
	34	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
56																					
1			1																		
2	1	2	5	2	1	2			1	1											
3		3	3				3	2	1	2	1										
4				2	1	1	2	2	1	1	1	2									
5		1	1	1	1		4	2	1	3	1	1	1	1	1		1				
6				1	1	3		1		3	2	4	1					1			
7					1			1		1	1	1	1		1				1		
8										2	3	1	1		1						
9						1					1	2	2	2	6						
10							1	1		2	1	2	2	2	2	2	1			1	
11										1	1	3	3	3	4	2					
12											1				3		1		1	1	
13										1			2	3	1	6		1			
14													1	2	1	1	1				
15											1			1		1	1		2		1
16																2	2			1	1
17													2	1		1	1		1	3	1
18																3	5			2	2
19													2			2				2	1
20																2			1	2	
21														3			5				
22																1	3			4	
23														1	1	1	3				
24																2	4				
25																2	2				1
1																1	4				
26																					
27											1						3				
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29																	1	2			
30																1					
31																				1	2
32																	2				
33																1	2				1
34																	1			1	
35																					
37																				1	
38																					
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45																					
52																					
53																					

determined in 25 females, ranging from 3 to 15 GLGs, (average = 8.2 ± 3.2 GLGs). The first ovulation, of course, is not necessarily followed by conception (and intra-uterine foetal mortality seems to occur more commonly in the first pregnancy – see above). The age of primigravid females (i.e. in their first pregnancy, as determined from the appearance of the mammary gland) could be determined in 31 females, ranging from 3 to 17 GLGs (average = 8.1 ± 3.3 GLGs). Although the majority of primigravid females had ovulated only once (64/88, or 72.7%), 16 had two ovarian corpora, four had three ovarian corpora, and single females each had 4, 5, 6 and 8 ovarian corpora, giving

an average of 1.5 ± 1.1 ovulations to produce the first successful pregnancy. Data on age (in GLGs) and maturity (presence of ovarian corpora) are available for 273 females (Table IX). The average age at sexual maturity was calculated using the method developed by DeMaster (1978) as 8.2 (95% CI = 7.3, 9.0) years. All three methods for examining the mean age at female sexual maturation therefore gave essentially identical results, although the data were largely the same in each case.

Data on age (in GLGs) and maturity (combined testis weights) are available for 160 males, and the proportions judged to be sexually mature from their testis weights

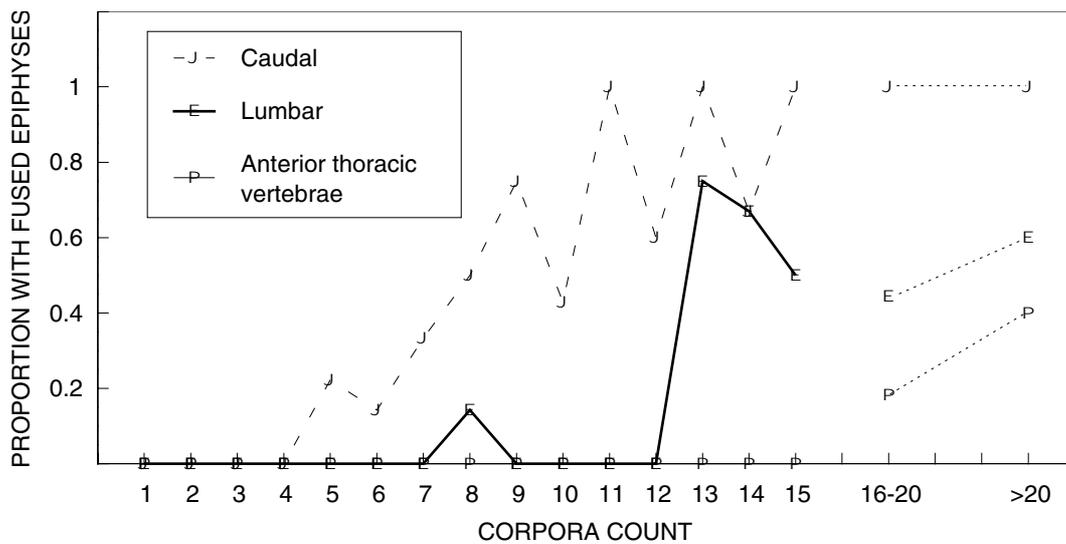


Fig. 10: Pattern of fusion of vertebral epiphyses in female sei whales at different reproductive ages at Donkergat, 1962-1963

are listed against age in GLGs in Table IX. The youngest mature male had 3 GLGs and the oldest immature 10 GLGs. The average age at sexual maturity was calculated using the method developed by DeMaster (1978) as 8.6 (95% CI = 7.8, 9.4) years.

PHYSICAL MATURATION

In female sei whales, epiphyseal fusion in caudal vertebrae commenced after sexual maturation, and 50% fusion was attained after about eight ovarian corpora had accumulated (Fig. 10), at a body length of 50-51 ft (15.2-15.5 m), and at around 22-24 GLGs. As predicted, epiphyseal fusion occurred later in lumbar vertebrae (50% were fused after between 13 and 14 corpora had accumulated), whereas in anterior thoracic vertebrae, the rate of fusion reached a maximum of only 40% in animals with more than 20 ovarian corpora. Trends in epiphyseal fusion against the number of GLGs in the ear plug are less clear, possibly because of the smaller sample size involved ($n = 96$ v. 155). However, although individual females had fused lumbar epiphyses at ages of 16-33 GLGs, and fused anterior thoracic vertebrae at ages of 45-52 GLGs, 50% fusion occurred in both lumbar and anterior thoracic vertebrae only after more than 45 GLGs had accumulated. Equivalent body lengths at which the incidence of fused lumbar and anterior thoracic epiphyses reached maxima were 52 and 53 ft (15.8 and 16.2 m) respectively, but both were well below 50%.

The pattern of epiphyseal fusion against age in male sei whales was more difficult to evaluate because the sample size was small ($n = 29$), and there were only two individuals with more than 28 GLGs, no individuals with fused anterior thoracic, and only two with fused lumbar vertebrae. In caudal vertebrae, 50% fusion

Table IX: Age and sexual maturity in sei whales at Donkergat 1962-1963

Age (GLGs)	Males		Females	
	Number examined	Mature (%)	Number examined	Mature (%)
1	2	0	2	0
2	17	0	13	0
3	12	8.3	14	7.1
4	8	0	14	14.3
5	16	6.3	20	30.0
6	10	20.0	17	58.8
7	9	44.4	6	33.3
8	9	33.3	11	45.5
9	7	57.1	15	66.7
10	7	71.4	12	75.0
11	3	100	11	72.7
12	4	100	8	100
13	7	100	12	91.7
14	2	100	6	100
15	1	100	8	87.5
16	2	100	4	100
17+	44	100	100*	100
Total	160		273	

* One female immature at 27 GLGs omitted as abnormal

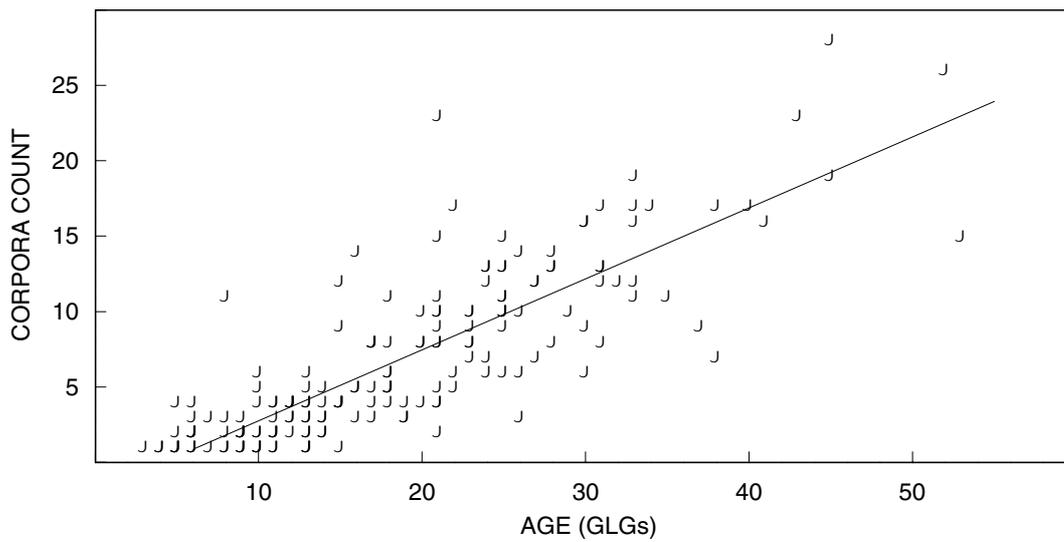


Fig. 11: Number of ovarian corpora in female sei whales of different ages at Donkergat 1962–1963 (regression line indicates Bartlett's best fit)

seemed to be reached at an age of 16–18 GLGs. The sample size for testis weight and body length was larger ($n = 47$), but also contained no individuals with fused anterior thoracic and only three with fused lumbar epi-

physes. Caudal epiphyses seemed to reach 50% fusion at a testis weight of 8 000–9 000 g and a body length of about 48 ft (14.6 m). The incidence of fused lumbar epiphyses reached a maximum of 33% at 49 ft (14.9 m).

Table X: Distribution of reproductive classes among mature female sei whales at Donkergat, 1962–1963, and their relationship with total corpora count (i.e. corpora lutea and albicantia)

Age (corpora count)	Number examined	Pregnant (doubtful) (%)	Ovulating (doubtful) (%)	Lactating (%)	Resting (%)
1	73	93.2 (4.1)	0	2.7	4.1
2	61	85.2 (11.5)	3.3 (1.6)	1.6	9.8
3	37	86.5 (5.4)	2.7	2.7	8.1
4	39	92.3 (5.1)	7.7 (5.1)	2.6	0
5	27	85.2	3.7 (3.7)	3.7	7.4
6	14	78.5 (7.1)	7.1 (7.1)	0	14.4
7	12	91.7	8.3 (8.3)	0	0
8	24	79.2 (4.2)	8.3 (8.3)	12.5	0
9	11	100 (9.1)	0	0	0
10	12	83.3	8.3	0	8.3
11	10	80.0 (10.0)	0	10.0	10.0
12	9	88.9	0	11.1	0
13	9	88.9*	11.1 (11.1)	0	0
14	5	80.0	0	0	20.0
15	6	100.0	0	0	0
16	4	75.0 (25.0)	0	25.0	0
17	7	100 (14.3)	0	0	0
18	3	100 (33.3)	0	0	0
19	4	75.0	25.0	0	0
20–24	6	83.3 (20.0)	0	0	16.7
25–28	4	75.0	0	0	25.0
Total	377	87.8 (5.8)	3.7 (2.4)	3.2	5.3

* One animal also lactating (but see text)

Table XI: Distribution of reproductive classes among mature female sei whales at Donkergat, 1962–1963, and their relationship with (chronological) age

Age (GLGs)	Number examined	Pregnant (doubtful) (%)	Ovulating (doubtful) (%)	Lactating (%)	Resting (%)
3–4	3	100	0	0	0
5–6	16	93.3	6.7	0	0
7–8	7	100	0	0	0
9–10	19	89.5 (5.3)	5.3	0	5.3
11–12	15	93.3 (6.7)	0	0	6.7
13–14	17	76.5 (5.9)	11.8 (11.8)	5.9	5.9
15–16	11	90.9 (9.1)	0	9.1	0
17–18	16	87.5	12.5 (12.5)	0	0
19–20	7	71.4	0	28.6	0
21–22	15	80.0	6.7	0	13.3
23–24	11	90.9	0	0	9.1
25–26	14	92.9	0	7.1	0
27–28	7	100	0	0	0
29–30	5	100 (20.0)	0	0	0
31–32	6	83.3* (16.7)	0	16.7	0
33–34	7	85.7 (14.3)	0	0	14.3
35+	12	83.3 (8.3)	0	8.3	8.3
Total	188	88.3 (3.7)	3.7 (2.1)	3.7	4.3

* One animal also lactating (but see text)

In order to obtain estimates of L_{∞} , or the length at physical maturity, sigmoidal Chapman's 3-parameter curves $Y = L_{\infty} (1 - e^{-bx})^c$ have been fitted to the data in Tables VII and VIII, where b is Brody's growth coefficient, x is age (in years) and c a sigmoidal shape parameter. The model fits to the data are quite good ($r^2 = 0.7048$ for females and 0.7058 for males). The curves indicate asymptotic lengths of 52.0 ± 0.49 ft (15.8 ± 0.15 m) for females and 48.6 ± 0.49 ft (14.8 ± 0.15 m) for males. Both lengths are similar to those at which the incidence of fused lumbar epiphyses reaches a maximum (52 and 49 ft, or 15.8 and 14.9 m respectively). Other theoretical growth curves could be fitted to these data, but there is likely to be substantial bias at younger ages, as a result of size selection (i.e. the larger individuals at younger ages have a greater chance of being sampled). Such bias is likely to be much reduced once growth slows down, so that estimation of L_{∞} is still valid from these data.

OVULATION RATE

There was an overall good correlation ($r^2 = 0.6857$) between the total number of ovarian corpora (corpus luteum plus corpora albicantia) and the number of GLGs in the ear plug in 185 mature females (Fig. 11). On the assumption that one GLG accumulated per year, the annual ovulation rate has been estimated from the regression of corpora count against age, using Bartlett's best-fit method (Simpson *et al.* 1960). If the result, 0.47 ovulations per year (95% $CL =$

0.418, 0.523), is compared with the estimate for the "true" pregnancy rate (47.6%), a very high rate of conception per ovulation is implied. However the estimate of "true" pregnancy rate is an approximation of unknown error.

PREGNANCY RATE V. AGE

Apparent pregnancy rates declined slightly with reproductive age, as measured by total corpora counts (Table X), but not significantly so ($b = -0.2277$ per corpus, $t = -0.8007$, $p = 0.4332$, $r^2 = 0.0326$). A similar slight decline is also seen with chronological age, as determined by GLGs (Table XI), but again not significantly so ($b = -0.2352$ per GLG, $t = -0.9762$, $p = 0.3373$, $r^2 = 0.0329$). Consequently, there was little indication of a real decline in reproductive rate with age.

Migrations

The seasonal appearance of sei whales off the west coast of South Africa was described by Best (1967a). The species showed an annual peak in abundance in early spring (between August and October) and, in some seasons, a second, much smaller peak in May or June. Recorded directions of travel (from the spotter aircraft) indicated that the first of these represented a wave of animals migrating south to higher latitudes for the summer feeding season, whereas the smaller peak

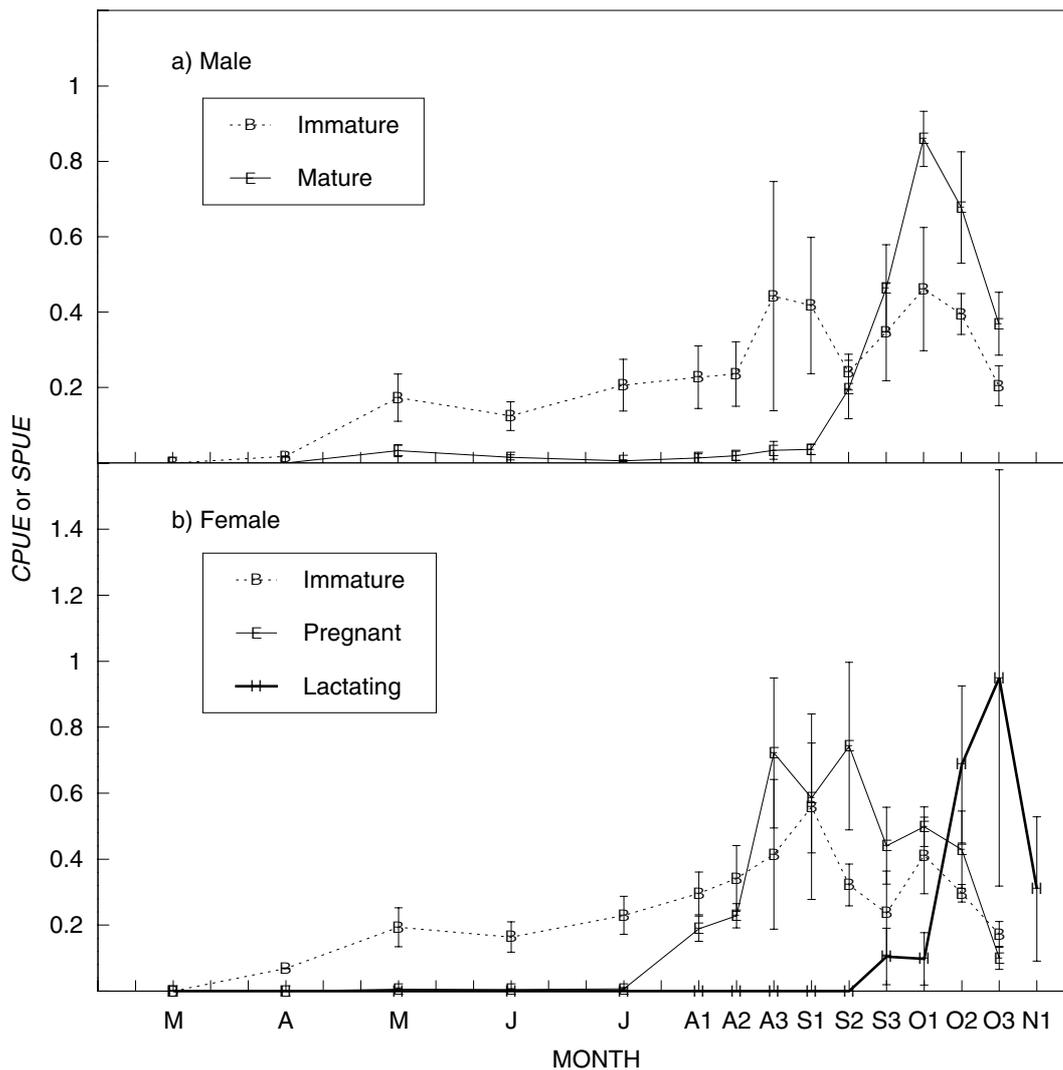


Fig 12: Seasonal trends in availability of different reproductive classes of (a) male and (b) female sei whales at Donkergat, 1962-1963 (mean \pm SE)

in autumn represented animals returning northwards from higher latitudes. However, these overall trends in abundance masked the fact that different components of the population passed through the whaling grounds at slightly different times. The animals did not migrate therefore in a random manner, but showed a considerable degree of segregation (here called "migration structure" to avoid confusion with animals that did not migrate at all).

This feature has been investigated using trends in

average *cpue* or *spue* values for immature and mature males, immature, pregnant and lactating females (Fig. 12). Immature animals of both sexes showed less seasonal fluctuation in availability than mature individuals. Although the *cpue* of immature males and females tended to be higher in spring than in autumn/winter, this was at most by a factor of two. From May to July immature animals predominated in the catch, to such an extent that mature animals could hardly have been involved in the purported northern

Table XII: Sex ratio in sei whales landed at Donkergat, 1962–1966

Month	Sexually immature				Sexually mature			
	Males	Females	z	p	Males	Females	z	p
May	94	105	0.636	0.525	17	18	-0.169	0.866
June	59	78	1.435	0.151	7	17	1.428	0.153
July	92	108	0.986	0.324	3	23	2.347	0.0189
August	137	159	1.160	0.246	10	212	9.454	<0.0001
September	167	184	0.799	0.424	115	350	9.616	<0.0001
October	195	158	1.852	0.064	353	270	3.215	0.0013
Total	744	792	1.171	0.242	505	890	9.881	<0.0001

migration in autumn (at least, as it passed through the whaling grounds). From the first 10 days of August onwards, however, pregnant females began to appear in the catch to an increasing extent, reaching a peak from the third 10 days of August to the second 10 days in September, before declining to winter levels of abundance by the last 10 days in October. Lactating females (as judged by the *spue* of cow-calf pairs) only appeared in the third 10 days of September and peaked in the last 10 days of October. Mature males arrived in the whaling grounds a month later than mature females, peaking in the first 10 days of October and still predominating in the catch in the last 10 days of October.

Within the spring migration (i.e. after 1 August), multigravid females ($n = 170$) appeared to travel later than primigravid females ($n = 88$), their median dates of capture being 16 and 9 September respectively (Mann-Whitney Rank Sum Test, $t = 10020.5$, $p = 0.015$). For 79 mature males in the same migration, however, a regression of age (in GLGs) against date of capture revealed no significant trend ($b = -0.0747$, $t = -0.82$, $p = 0.41476$, $r^2 = 0.0087$).

The structured nature of the migration is reflected in the monthly sex ratios in the catch between 1962 and 1966 (Table XII). For immature whales the ratio did not differ significantly from parity in any of the months between May and October, or in the overall catch. For mature whales, however, the sex ratio differed from parity in each month from July to October, being skewed in favour of females in July, August and September, and in favour of males in October. In the total mature catch the sex ratio was also significantly skewed in favour of females.

DISCUSSION

There has been considerable annual variation in the number of sei whales caught off the west coast of

South Africa, in particular in the period 1917–1930 (Best 1974). Matthews (1938) discussed this irregularity and indicated that it could be caused by changes in oceanographic conditions, by extending hunting from the coast, or simply by a shortage of other, more favoured species. In view of what has been said above, it is very probable that the apparent variability in abundance historically was because of the reduced availability of one or other of the more favoured species, which in turn caused the catchers to go farther afield to take sei whales.

The perception that sei whales are unpredictable in their annual migrations seems to have originated in the eastern North Atlantic. Extensive annual variations in the northward limit to the migration apparently occurred around Finmark (northern Norway) and the Faeroe Islands (Collett 1886, Ingebrigtsen 1929). Marked seasonal fluctuations in the timing of movements along western European shores and in the annual arrival times at the coast of Norway were also described (see review by Jonsgård and Darling 1977). The species was believed to have a “roving disposition” (Kellogg 1929), and “invasion years” were reported when phenomenal catches were made, only for the species to disappear the following year (Thompson 1928).

Some of these fluctuations seemed to be linked to changes in food supply related to shifts in oceanographic features (Ingebrigtsen 1929). Furthermore, these records all refer to waters north of 50°N, where it can be assumed that sei whales were principally engaged in foraging, so fluctuations in distribution from year to year might be expected.

In contrast, the whaling grounds on the east and west coasts of South Africa (at c. 30° and 33°S respectively) were presumably closer to the midpoint than to the extremes of the latitudinal range of sei whales. The timing of the whales' appearance in these localities, and the structured nature of their appearance in the catch, suggested that they were on migration between Subantarctic feeding grounds and breeding grounds

in warmer waters. Feeding behaviour, although it occurred, was clearly substantially less intensive than in the Subantarctic (Bannister and Baker 1967, Best 1967a), and correlations between distribution and indicators of local productivity were poor (Best 1967a). Therefore, although the distribution of sei whales in higher latitudes might be highly variable between years, migration to and from the breeding grounds seems considerably more consistent.

Because of the highly structured nature of the migration, it is difficult to establish how representative the catches were of the population. Hence, although the overall sex ratio in the catch of mature whales was skewed towards females, the patterns of *cpue* suggest that the migration of mature males was still incomplete by the time the whaling season closed (end of October). This may be one possible reason for the skewed sex ratio. On the other hand, selection against lactating females is likely to have reduced the relative contribution of females in the mature catch. Despite these uncertainties, there is no indication that the ratio would be significantly skewed towards males, as has been described for humpback whales migrating between breeding and feeding grounds (Brown *et al.* 1995).

The structure of the southward migration in sei whales is similar to that recorded for humpback whales in the southern hemisphere (Dawbin 1966), in that pregnant females and immature whales of both sexes are in the vanguard, followed by mature males and then lactating females. The apparent northward migration in May–July, however, contained very few mature animals, and so its composition cannot be compared with that of humpback whales. Mature animals could have passed before the season opened (on May 1), or after that date but outside the seaward range of the catchers. Sightings of “sei whales” had been made off Donkergat earlier than 1 May, and in 1963 a special scientific permit was issued by the South African Government to allow 50 sei or Bryde’s whales *Balaenoptera edeni* to be caught in March/April. However, only five of these proved to be sei whales, all immature and all taken after 25 April – the remainder were Bryde’s whales of the offshore population. Consequently, it is unlikely that the timing of the northern migration preceded the baleen whale season at Donkergat. It is more likely that the main body of the migration passed offshore from the whaling grounds; the fact that a smaller proportion of the catch was taken in water <2 000 m deep in May–July than in August–October would support that hypothesis. If the migration did pass farther offshore, then the tendency for mature females to be caught at greater distance from the station than any other class would further reduce their chances of being sampled during

the northward migration.

The finding that mature male sei whales on their northern migration had testes almost double the weight of those taken on the southern migration is the first indication of a male seasonal cycle for this species in the southern hemisphere. Comparisons made between the average testes weights of sei whales taken at Durban and in the Antarctic have failed to reveal any seasonal variation (Gambell 1968), but this may be because the Durban sample consisted mainly of animals on their southern migration. Matthews (1938) compared histological material from 20 mature males taken in the Antarctic between February and April with that from 4 mature males landed at Durban and Saldanha Bay between July and September. The results were inconclusive, possibly because of the small sample sizes and the restricted seasonal coverage. Mitchell and Kozicki (1974) argued for a seasonal cycle in both testis weight and spermatogenesis in sei whales from the Northwest Atlantic, with activity apparently increasing from June/July to September/October. Although they had no material between December and April, the trend they observed would agree in timing with that seen off South Africa, assuming a six-month difference in seasonality between the hemispheres. The pattern for southern sei whales appears similar to that described for gray whales *Eschrichtius robustus*, where males migrating to their breeding grounds had heavier testes and significantly enlarged semeniferous tubules compared to males migrating away from their breeding grounds (Rice and Wolman 1971).

Very little is known about the distribution of the southern balaenopterids in winter (Mackintosh 1942, 1966, Mackintosh and Wheeler 1929). It is believed that blue and fin whales mostly move out of the Antarctic in autumn, and some reach subtropical or tropical waters, but the northern extent of the migration is unknown, nor is it known whether their distribution outside the Antarctic is dispersed or concentrated. Because catches of blue and fin whales were usually seasonally bimodal at land stations in the Cape Province, but unimodal at Durban, Harmer (1931) concluded that both species migrated farther north than the latitude of Donkergat on the West Coast, but not much beyond the latitude of Durban on the East Coast. From the fact that 80–90% of the animals taken in warmer waters were immature, Mackintosh and Wheeler (1929) concluded that most mature blue and fin whales do not resort to coastal waters (i.e. within range of shore-based whaling). As a consequence, little is known about their migration structure. Differences in the timing of migration of immature and mature blue and fin whales past Durban have been described (Bannister and Gambell 1965). Mackintosh (1942) also refers to

a decline in the proportion of pregnant and an increase in the proportion of immature female blue and fin whales throughout summer in the Antarctic. These trends presumably reflected either an earlier departure of pregnant and older animals from, or a later arrival of resting and younger females on the feeding grounds, features that could be considered consistent with an ordered migration such as that seen for humpback whales (Lockyer 1981). However, none of these descriptions provides such convincing evidence for a structured migration to and from their breeding grounds as that demonstrated for sei whales by Bannister and Gambell (1965) and herein.

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