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EXTERNAL CHARACTERS OF SOUTHERN MINKE WHALES AND THE EXISTENCE OF A DIMINUTIVE FORM

PETER B. BEST*

ABSTRACT

Two colour phases were found amongst minke whales examined at the Durban whaling station. The majority of the animals had asymmetrically-coloured baleen, with the right series having a larger number of white plates anteriorly than the left, and with the remaining plates having a black outer border whose width amongst the longest plates averaged about 31–34% of the width of the plate. These animals also had plain or two-tone flippers (Type 1 or 2) on which white patches were never found, and dark pigment on the neck did not descend below the level of the eye. Whales of the second colour phase were much rarer (~3 to 4% of the minke whales taken). They had all-white baleen or baleen with an unusually large proportion of white plates (with little or no asymmetry), in which the largest plates were either completely white or with a narrow black outer border less than 10% of the width of the plate. The flippers carried a striking white patch connected to a roughly circular white blaze on the shoulder (Type 3), and dark pigment in the neck region extended onto the ventral grooves.

Type 3 whales appear to be born smaller and attain a smaller size at sexual maturity than Type 1 or 2 whales. Off Durban they were found closer inshore and earlier in the year than Type 1 or 2 whales, and were not killed from the same groups. Whales with similar coloration to Type 3 animals have also been recorded from Brazil, New Zealand and Australia, but probably do not occur in higher latitudes of the Antarctic.

INTRODUCTION

Minke whales in the Southern Hemisphere are reported to have either no white flipper bands (Ohsumi, Masaki and Kawamura, 1970; Van Utrecht and Van der Spoel, 1962; Williamson, 1959, 1961; Zemsky and Tormosov, 1964) or flippers with "light" (Taylor, 1957) or white bands (Aguayo, 1974). The existence of two Southern Hemisphere forms, one with and one without white flipper bands is suggested by data provided by Baker (1983), Gaskin (1972) and Kasuya and Ichihara (1965). The baleen coloration of southern

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minke whales has been usually reported as consisting of some anterior all-white plates and the rest white with dark borders externally, with considerable individual variation in the proportion of all-white plates, and with asymmetry in their distribution between left and right sides of the head (Kasuya and Ichihara, 1965; Ohsumi *et al.*, 1970; Williamson, 1959, 1961). Some individuals have been reported with no all-white plates (Ohsumi *et al.*, 1970), even on both sides of the head (Van Utrecht and Van der Spoel, 1962). Gaskin (1972), Guiler (1978) and Baker (1983) are the only authors so far who have described southern minke whales as simply having "yellow or pale ochre", "yellowish" or "yellow-grey" baleen with no mention of dark edges.

It is clearly of some interest to establish whether different colour phases of minke whales do occur in the Southern Hemisphere, and particularly to investigate whether these might vary geographically as potential indicators of stock identity. Systematic observations were therefore made of the coloration of the baleen and flippers (and certain other parts of the body) of minke whales landed at Durban (ca 30°S, 31°E) and on the factory ship *Nisshin Maru no.3* in the Antarctic. This paper presents analyses of these observations together with some morphometric data, and includes information from animals stranded on the South African coast and elsewhere.

MATERIAL AND METHODS

As part of their routine examination of minke whales on the flensing platform, the whaling inspectors at Durban were instructed to record variations in coloration.

The most convenient way of recording flipper patterns was by photography. Photographs of one or both flippers of each minke whale landed were taken with an Instamatic camera (using flash for night shots). In order to distinguish between individual whales, a slate bearing the platform number of the whale was included in each frame.

Photographs were taken in three seasons (1970, 1971 and 1973) for a total of 299 whales.

Baleen coloration was recorded in several ways. Initially (1969) separate counts were made of the number of all-white plates and the number with black edges for at least one series of each whale. The plates counted included all those defined as hairs by Williamson (1973). Because this was so laborious, a more rapid method of assessing the relative proportions of the two types of baleen was used subsequently (1970, 1971 and 1973). One entire side of baleen was carefully removed and laid straight and flat (fringe downwards) on the deck. Its total length and the length of the series of all-white plates were then measured with a steel or fibreglass tape in a straight line between the anterior and posterior extremities of the series. The relative length of the all-white section could then be used as a measure of the proportion of white plates in the series. The coloration of baleen was recorded in these two ways for a total of 488 animals.

In addition, one of the longest baleen plates from one side of each whale was collected in 1970, 1971, 1973, 1974 and 1975, and fixed in formalin. These could be recognised as being from the left or right series depending on their shape, and were used to confirm on which side the measurements or counts of different-coloured baleen had been made. They were also used to provide measurements of the relative width of the black border to the outer edge of the plate.

The length and width of the plate were measured as described by Omura and Fujino (1954), while the width of the black border was measured with vernier calipers at the same level as the width of the plate. Baleen plates from 504 whales were so measured, to the nearest mm.

From 20 January to 17 February 1979, 161 minke whales were examined aboard the Japanese factory ship *Nisshin Maru no.3* while it operated along the ice edge between the longitudes of 62° and 107°E. The procedures followed were almost identical to those described above; the proportions of black and white baleen plates were obtained by measurement rather than counting, while a ruler rather than vernier calipers was used to measure the thickness of the black border.

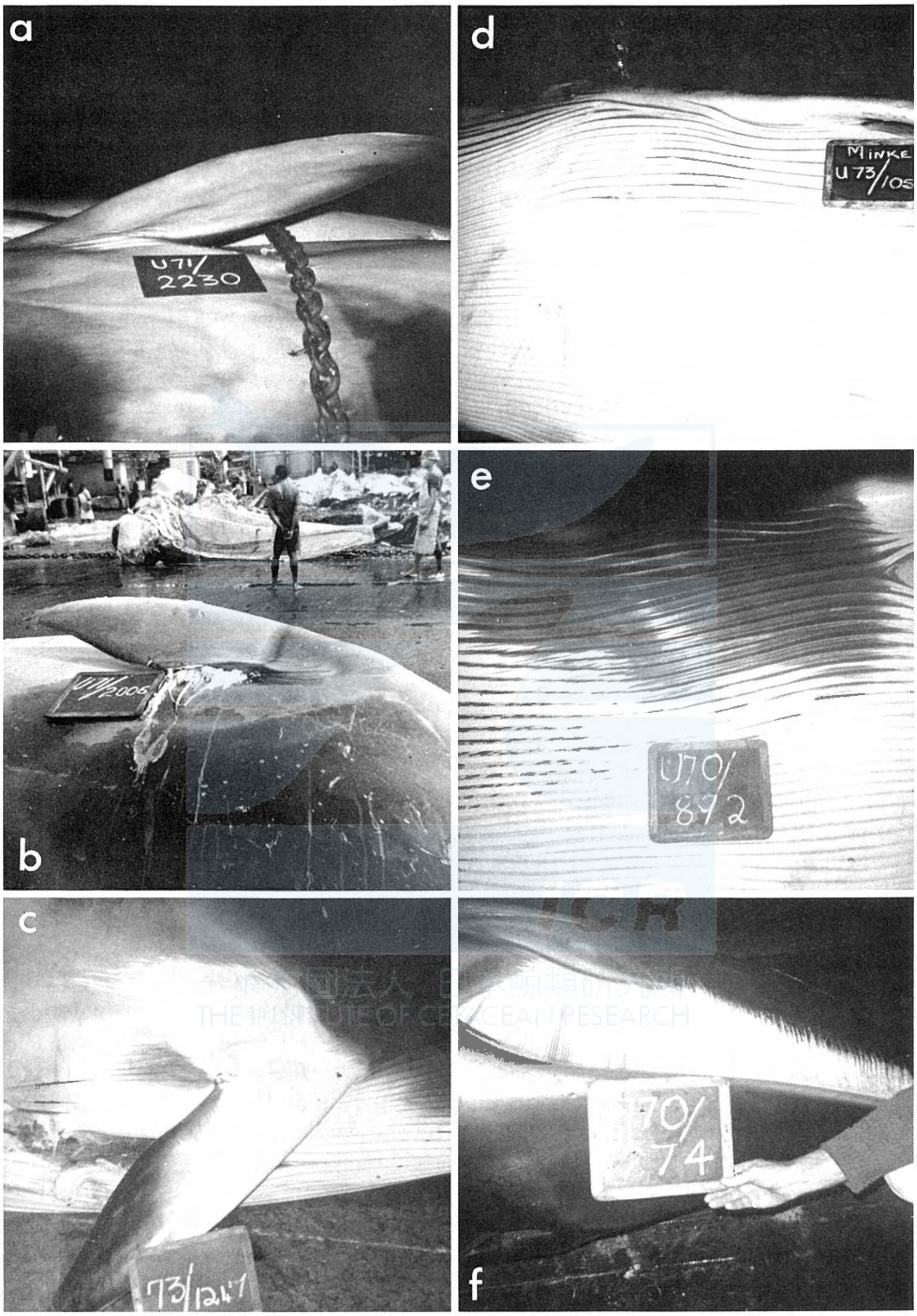
Throughout this paper a '±' figure following an estimate refers to one standard error.

COLORATION

Flipper and associated body coloration

From an examination of the photographs, the flipper coloration of minke whales landed at Durban and in the Antarctic could be classified into three types.

1. *Plain* – The outer surface of the flipper was a steely-grey (or slightly darker) colour, darkening on the trailing edge of the flipper but lightening to almost white on the leading edge. Such changes in coloration were not sharply differentiated but were diffuse in nature (Fig. 1a). This seemed to be equivalent to the Type 1 flipper coloration as illustrated by Doroshenko (1979) and Wada and Numachi (1979).
2. *Two-tone* – The outer surface of the flipper was of two tones of grey separated by a distinct line running perpendicularly across the width of the flipper approximately level with the axilla. This line varied from being roughly straight to being strongly backet-shaped in conformation, and separated the lighter colour of the distal part of the flipper from the darker proximal part (Fig. 1b). The clarity of this distinction into two tones varied considerably, depending on the degree of contrast between the colours of the proximal and distal parts of the flipper: the lighter in


a
U71/
2230
d
MINKE
U73/105
b
U71/2006
e
U70/
872
c
73/1247
f
70/
74

tone the distal part, the greater the distinction. Although animals could be classified as having weakly, moderately or strongly two-toned flippers, there actually appeared to be a continuous range in variation, with some flippers having such a faint line dividing the two tones that it was difficult to distinguish them from plain flippers, while at the other extreme the distal portion of the flipper was a bright grey colour (but never white). In all flippers there was a gradual darkening at the extreme trailing edge and a lightening at the leading edge, as described for plain flippers.

This seemed to be equivalent to the Type 2 flipper coloration as illustrated by Doroshenko (1979), and possibly to Types II and III coloration as illustrated by Wada and Numachi (1979).

3. *White* – The outer surface of the flipper was glossy white anteriorly and light grey rapidly deepening to glossy black posteriorly. The dividing line between the two was irregular in outline but clearly differentiated, and ran from the axilla to the leading edge of the flipper at about one-third of its length from the tip (Fig. 1c). The white proximal area of the flipper was connected (via the entire width of the flipper from anterior insertion to axilla) with a roughly circular white blaze on the shoulder immediately above the flipper. This blaze was highly irregular in outline but well-differentiated from the surrounding pigmented area. While there was some individual variation in these flipper patterns, and particularly the size and shape of the shoulder blaze, the basic coloration of the flipper remained proximally white and distally black. This has been termed "Type 3" flipper coloration in this paper.

   Although Wada and Numachi (1979) illustrate a flipper with a white transverse band as Type IV, it is not clear whether this is similar to the Type 3 coloration described here, or is simply a representation of the band commonly see in minke whales from the Northern Hemisphere.

Classification of flipper patterns into these three types (particularly the first two) could be affected by prolonged post-mortem times, which tended to darken lightly-pigmented areas, and by skin damage (particularly to the flipper that lay beneath the whale's body as it was transported from the water to the flensing platform), which tended to obliterate pigmentation patterns. Some photographs at Durban were also taken from an inappropriate angle so that the outer surface of the flipper could not be seen. Some of these photo-

Fig. 1. Minke whale coloration patterns
a. Plain (Type 1) flipper
b. Two-tone (Type 2) flipper
c. White (Type 3) flipper
d. Throat region of a Type 1 or 2 whale
e. Throat region of a Type 3 whale
f. Baleen coloration of a Type 3 whale

graphs could be used, however, to make gross classifications of coloration type because of a difference between the pigmentation pattern in the neck region of minke whales with flipper Types 1 and 2 and those with Type 3. In the former, the dark pigment of the back did not extend ventrally farther than a line roughly between the eye and flipper insertion, so that the ventral grooves appeared almost entirely white in the throat region (Fig. 1d). In whales with Type 3 flippers, however, this dark pigment extended much farther ventrally (as much as 15 ventral grooves down from the level of the eye to flipper insertion), so that there was a distinct tongue of black extending onto the throat (Fig. 1e). This feature could be seen clearly in photographs of the flippers taken from the ventral side of the whale, when details of the actual outer surface of the flipper were obscured. Consequently it was possible to deduce from such photographs whether the whale had a flipper belonging to Type 1 or 2 or to Type 3, though it was impossible to discriminate between Types 1 and 2 from this angle. Similarly the slate was sometimes placed over the area where the dividing line of Type 2 flippers occurred, so that it was impossible to be certain whether the flipper was Type 1 or 2. Under both these circumstances if it was clear that the animal was not a Type 3 whale it was recorded as "Type 1 or 2".

TABLE 1. FLIPPER COLORATION OF MINKE WHALES AT DURBAN FOR WHICH BOTH FLIPPERS WERE EXAMINED

Colour type	Frequency (number of whales)
Both Type 1	26
One Type 1, one Type 2	17
Both Type 2	18
Both Type 3	3
Total	64

Photographs were taken of both flippers of 64 whales at Durban (Table 1). In 17 of these animals one flipper was judged to be Type 1 and the other Type 2. This indicates that there is no phenotypic distinction between the two flipper patterns, and that Type 1 is actually one extreme of a range of variation including Type 2. Of these 17 animals, 14 had a Type 2 left flipper and three a Type 1 left flipper. These proportions are significantly different from parity (chi-square test, Yates' correction, $P < 0.02$, $df = 1$), indicating that there may be asymmetry of pigmentation in the flippers of the southern minke whale, as in its baleen. This is confirmed by differences in the intensity of pigmentation between right and left flippers of whales in which both flippers were classified as Type 2. Out of the 18 whales so classified, 11 had both flippers of the same intensity while seven had the left flipper with a brighter band of pigmentation (*i.e.* a more striking two-tone coloration) than the right. None had the reverse condition.

TABLE 2. COLORATION OF LEFT AND RIGHT FLIPPERS OF MINKE WHALES

Colour type	Durban				Antarctic			
	Left		Right		Left		Right	
	No.	%	No.	%	No.	%	No.	%
Type 1	51	27.6	81	43.8	12	17.4	36	45.0
Type 2a	31	16.8	36	19.5	28	40.6	28	35.0
Type 2b	44	23.8	16	8.6	23	33.3	16	20.0
Type 2c	8	4.3	1	0.5	6	8.7	0	0
Type 1 or 2	46	24.9	44	23.8	–	–	–	–
Type 3	5	2.7	7	3.8	0	0	0	0
Total	185		185		69		80	

Because of this asymmetry in pigmentation, any analysis of the variation in flipper coloration for southern minke whales must separate data for left and right sides of the animal. In Table 2 data have been presented separately for whales whose left or right flippers only were examined, and including relevant data from those whales for which both flippers were examined. Flippers of the two-tone type have been further classified into weak(2a), moderate (2b) or strong (2c), based on the intensity of the contrast in pigmentation. As might be expected from the asymmetry of coloration, whales whose left flippers were examined had a greater ratio of Type 2 to Type 1 coloration than whales whose right flippers were examined, both at Durban (chi-square $= 13.44$, $p < 0.001$) and in the Antarctic (chi-square $= 12.93$, $p < 0.001$).

Furthermore, in both areas there was a higher proportion of Types 2b and 2c relative to Type 2a coloration in the left flippers than the right, though this was only statistically significant in the Durban data (chi-square $= 12.10$, $p < 0.001$, Durban; chi-square $= 2.12$, $p > 0.10$, Antarctic). The two areas studied, however, seemed to differ in the intensity of flipper coloration. The proportion of Type 2 relative to Type 1 flippers was higher in the Antarctic than Durban, both for left (chi-square $= 9.09$, $p < 0.005$) and right flippers (chi-square $= 4.82$, $p < 0.05$). This may reflect the shorter post-mortem times in the Antarctic (producing less darkening of pigmentation after death), or it may represent a real difference between the two populations. There was no significant difference, however, between the proportion of Type 2a relative to Types 2b and c coloration in the Antarctic and Durban (chi-square $= 1.92$, $p > 0.10$, left flippers; chi-square $= 0.20$, $p > 0.50$, right flippers).

No asymmetry of pigmentation could be detected in whales whose flippers were classified as Type 3, and no whale was found with a Type 3 flipper on one side and a different type on the other. This group seemed to form a relatively uncommon but distinct phenotype (see below), and was not encountered in the Antarctic sample.

Data presented by Doroshenko (1979) indicate significant differences in

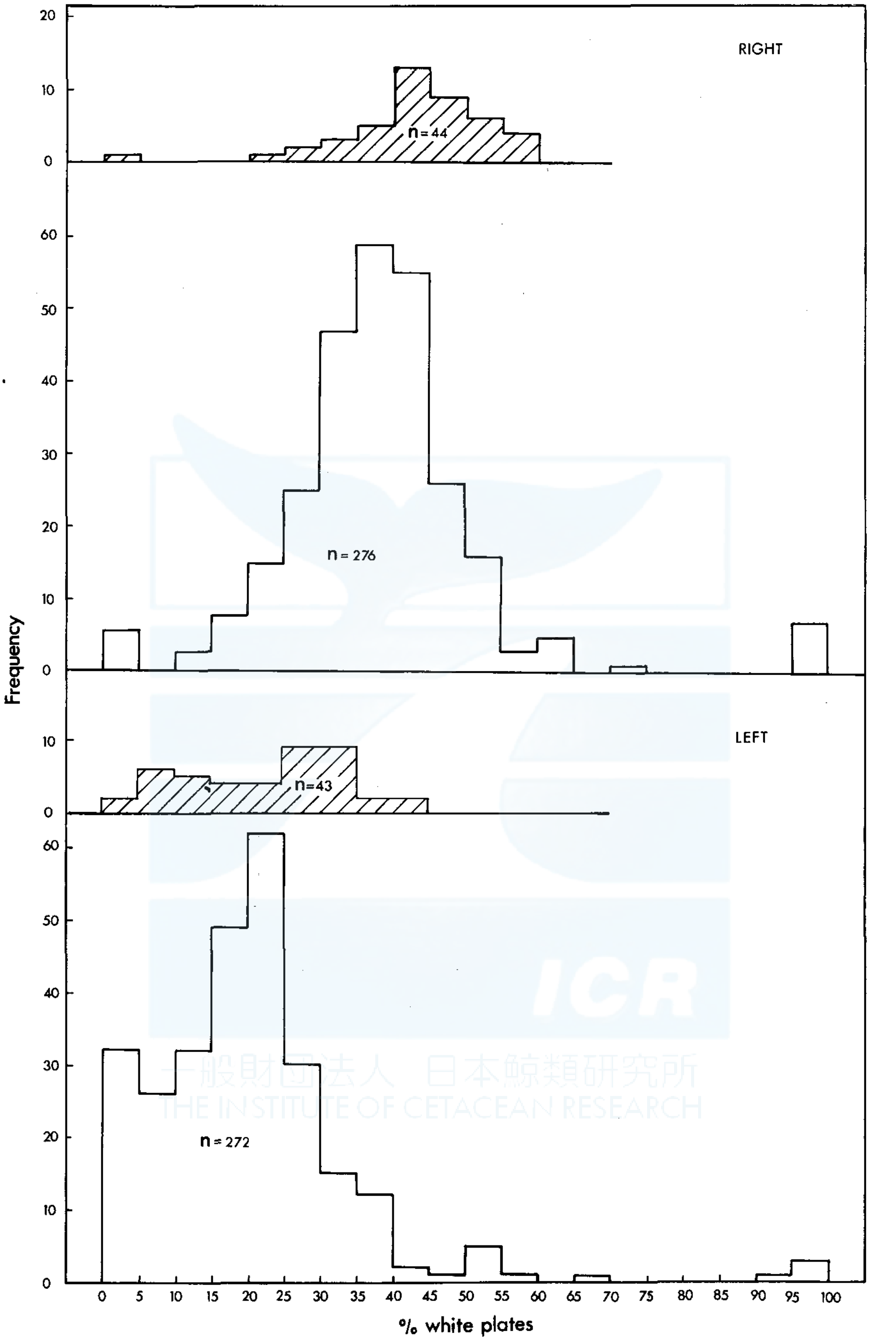


Fig. 2. Proportion of all-white baleen plates in each series, from plate counts (hatched) and proportional measurements (open).

the proportions of whales with Type 1 and Type 2 flippers between different areas of the Antarctic (Van Beek and Van Biezen, 1982), supporting the possibility that there may be population differences in this character. In presenting similar data (but for four flipper types), however, Wada and Numachi (1979) conclude that the data ".... include some bias arising from variation in the classification criterion among the observers, and that they are inadequate for stock identification or that the external characters of minke whales do not reflect stock units. Before this can be determined it is essential to unify the criterion classification technique of each observer." The apparent presence of whales with white bands on the flippers (their Type IV) in a small proportion of their data (0.9%) must therefore be viewed with caution.

Baleen coloration

The two methods of assessing the proportion of all-white plates in the baleen series did not give consistent results. Counts of individual baleen plates

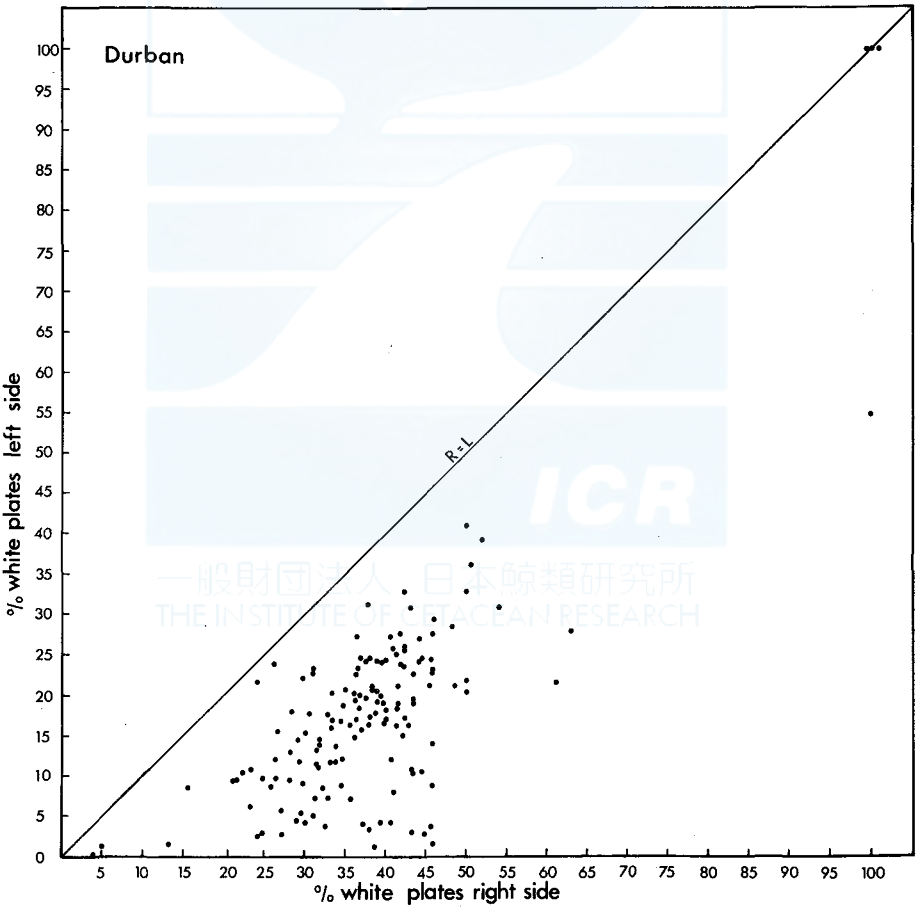


Fig. 3a. Comparison between proportions of all-white baleen plates on right and left sides of same whale at Durban.

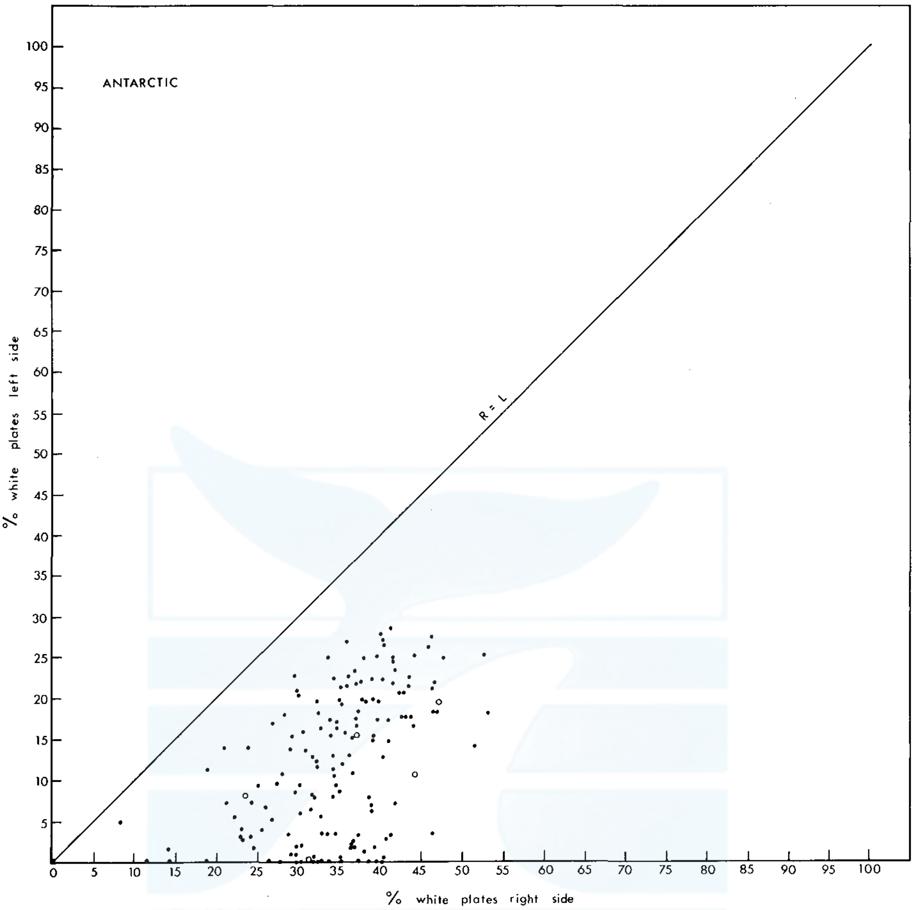


Fig. 3b. Comparison between proportions of all-white baleen plates on right and left sides of same whale in the Antarctic.

produced on average a higher proportion of all-white plates in the series than did relative measurements (Fig. 2). This is almost certainly due to the fact that a high proportion of the anterior, all-white section of the series consists of the small, closely-spaced structures termed "hairs" by Williamson (1973), and their relative contribution will therefore appear greater in counts than in measurements. However, the difference between the two methods is relatively small (the modes in the frequency data differing by 5 to 10%), and for further analysis the greater quantity of data (from measurements) has been used.

The proportion of all-white plates was measured for both right and left baleen series of the same animal in 148 whales from Durban (Fig. 3a) and 157 whales from the Antarctic (Fig. 3b). The asymmetry of the coloration in the majority of animals is clear. Four animals at Durban, however, seemed exceptional in the pattern of their coloration. Three of these were recorded as having (on both sides of the head) all-white baleen or white baleen interspersed with a few black plates having a very thin black outer border, estimated at 0.3 cm wide (see Fig. 1f). The latter animals were considered in effect to have all-white baleen. The fourth whale was recorded as having all-white baleen on the right-hand side and an unusually high proportion of white plates on the left-hand side. It is possible that this animal also had white baleen interspersed with a few plates very thinly edged with black, but that the measurement of the white baleen on the left side was taken to the first black-edged plate (as was done with subsequent whales but with an explanatory note in the records).

The remaining 144 whales at Durban with asymmetrically-coloured baleen ranged from individuals with almost no white plates on either side (as recorded by Van Utrecht and Van der Spoel, 1962), to individuals where as much as 41% of the left side and 50% of the right side were white, and included animals with only 2 or 3% white plates on the left side but up to 46% white plates on the right. Despite this variation, there was no obvious separation of these animals into different groups, and there is clearly a positive correlation between the proportion of white plates on either side of the head of these animals ($r = 0.5612$, $p < 0.001$). The average proportion of white plates was 16.6 ± 1.6% for the left series and 36.7 ± 3.2% for the right series.

All but one of the animals in the Antarctic sample had asymmetrically-coloured baleen. The exception was an animal in which all plates on both sides of the head had black or "dusky" outer edges, though those towards the anterior end of the righthand series were lighter in colour. There was a positive correlation between the proportion of white plates on either side of the head in the whole sample ($r = 0.4966$, $p < 0.001$), and the mean proportion of white plates was 12.0 ± 1.2% for the left series and 34.4 ± 2.8% for the right series. There were no animals in the sample with all-white baleen or white baleen interspersed with a few black-edged plates.

The mean proportions of white plates on both the left and right sides of the head differed significantly between Durban and the Antarctic ($t = 4.57$, $p < 0.001$, left; $t = 2.33$, $p < 0.025$, right), suggesting either a difference between populations or a difference in interpretation of what constitutes a black-edged or a white plate between the two areas (the data being collected by a technician at Durban but by the author in the Antarctic).

The existence of two groups of whales differing in their baleen coloration is also suggested by the larger body of data from Durban given in Fig. 2. One large group has a modal proportion of all-white plates on the right side of the head of 35 to 40% and on the left side of the head of 20 to 25%, while a second, much smaller group has from 90 or 95 to 100% white plates on either side of the head.

On the left side there also appears to be an intermediate group of animals with a higher-than-normal proportion (mode 50 – 55%) of white plates. Some of these may be animals with white baleen irregularly streaked with some black plates with narrow borders as described above, and in which the contribution of black-edged plates has been exaggerated because of the method of recording used (see above). It is impossible, however, to be sure on this point, consequently it is considered safest to ignore the data shown in Fig. 2 when calculating the relative proportions of the two groups of whales in the catch.

Correlation between flipper and baleen coloration

There was no significant correlation between increasing flipper pigmentation and the proportion of all-white baleen plates for animals with Types 1 and 2 flippers at Durban. Because of the asymmetry of pigmentation, data were analysed separately for left and right sides of each animal (Fig. 4). The correlation coefficients so calculated were −0.01212 (n = 92, $p > 0.9$) for the left and 0.07337 (n = 90, $p > 0.4$) for the right. This lack of correlation

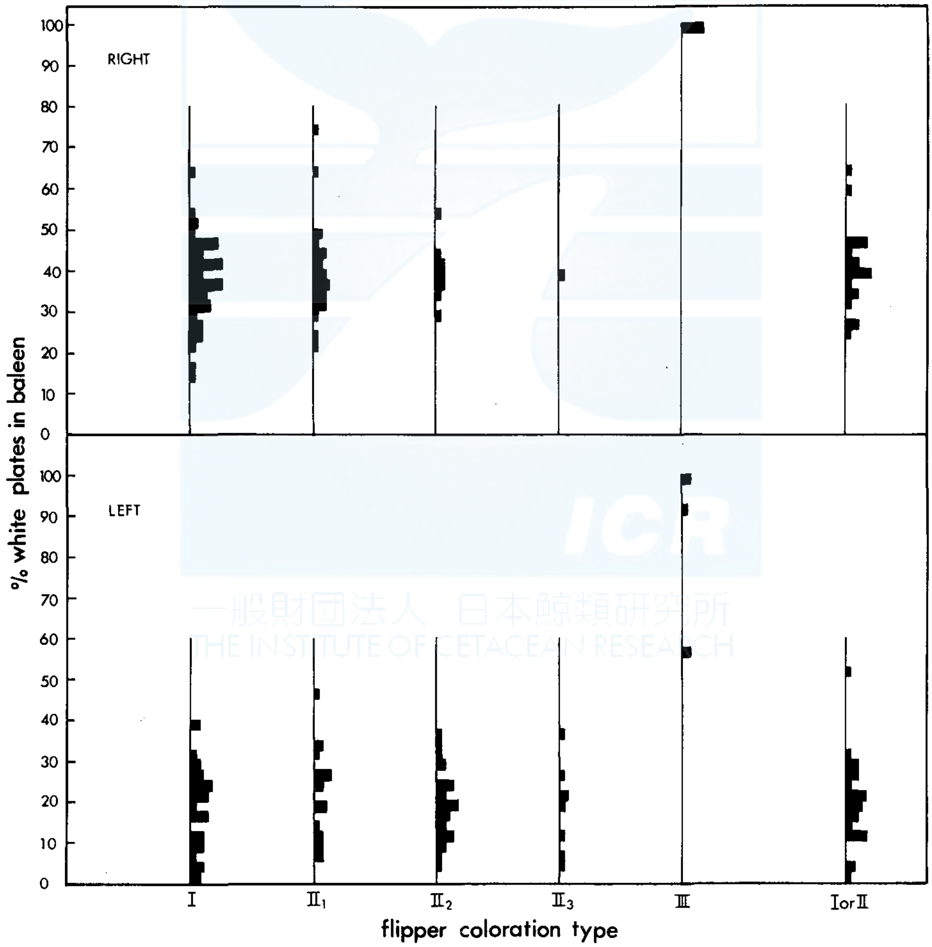


Fig. 4. Relationship between baleen and flipper coloration of same whale.

further suggests that whales with Types 1 and 2 flippers and asymmetrically coloured baleen are one homogeneous group. Whales with Type 3 flippers, however, differed from Types 1 or 2 in having all-white baleen or baleen with an unusually high proportion of white plates. These whales may therefore form an uncommon but distinct phenotype from the "normal" southern minke whale.

Width of black outer border of baleen

The width of the black outer edge (or border) of one of the longest plates of the baleen series was measured as a percentage of the total width of the plate. Some plates had a secondary black stripe on the lingual side of the black border: such plates were omitted from subsequent analysis. At Durban the frequency distribution of the relative width of the black border on the

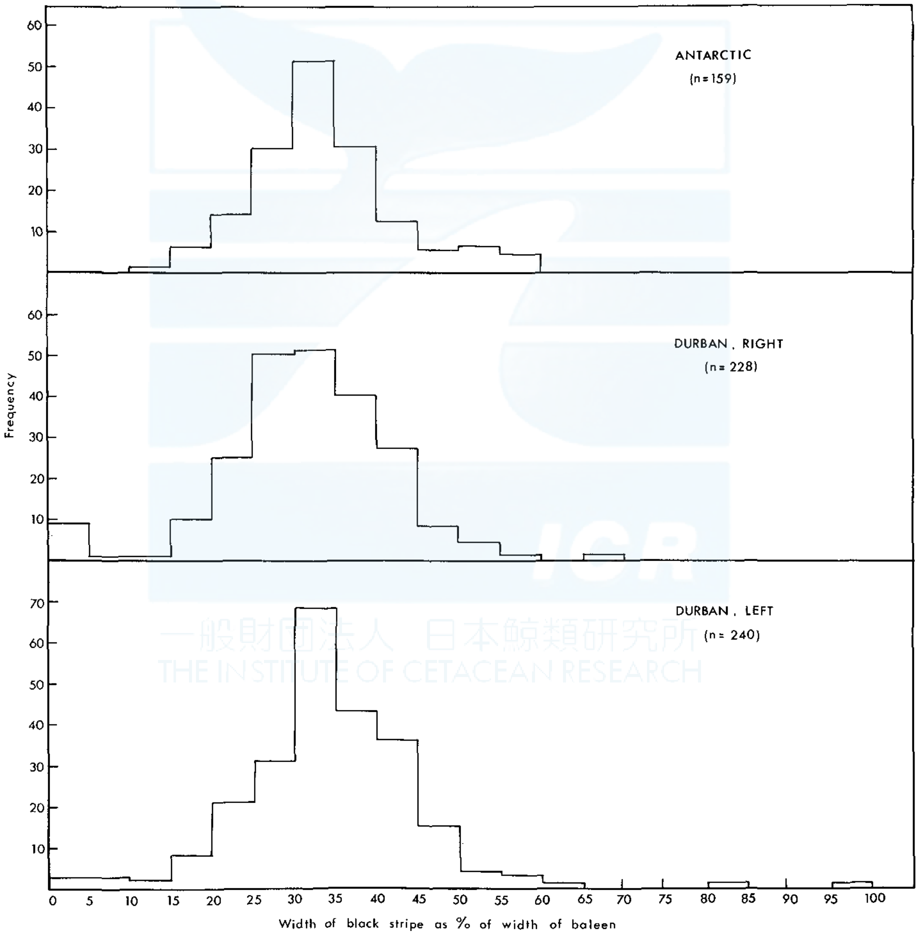


Fig. 5. Width of black border on one of longest baleen plates as a proportion of the total width of the plate at Durban, and in the Antarctic.

right side of the head shows a bimodality, with one group of animals having a mode around 25 – 35% and a second, much smaller, group having a mode of less than 5%; on the left side there is not such a pronounced bimodality but animals were still encountered with a black border less than 10% of the width of the plate (Fig. 5). Amongst such animals eight (or 50%) in fact had no black border at all. All whales with Type 3 flippers fell into this group, i.e. they either had all-white baleen or baleen with some plates having a very thin black outer border (less than 10% of the width of the plate). If only animals with a stripe 10% or more of the plate width (i.e. presumably Type 1 and 2 animals) are considered, the relative width of the border was greater on the left (34.9 ± 0.7%) than on the right (32.7 ± 0.6%) side of the whale ($t = 2.47$, $p < 0.02$, 450 df, the samples being independent as the left and right plates examined were from different animals). This difference in the coloration of the largest plates of the baleen series probably reflects the asymmetry of baleen pigmentation as a whole. Williamson (1961) has pointed out that the width of the border increases towards the back of the mouth, so that presumably the more anterior white plates in a series there are, the thinner the border will be on the largest plates. As there are (in asymmetrically-coloured animals) invariably more white plates on the right side of the head, it is to be expected that the width of the black border will be somewhat less in the largest plates of the right side.

In 159 animals examined in the Antarctic, the black border ranged from 14.7% to 58.5% of the width of the plate (right and left sides combined), with a mean of 33.4 ± 0.7% (Fig. 5).

Wada and Numachi (1979) classified baleen plates into six Types, depending on the width of the black border, with Type 0 representing plates with no black stripe and Type 5 representing all-black plates. The majority of animals (78%) were Types 2 and 3 (stripe one-third to one-half width of plate), which would be similar to the results obtained above for the Antarctic, but all six Types were recorded, although Types 0 and 5 only infrequently (0.1% and 0.2% respectively). However, Wada and Numachi (1979) express reservations about the reliability of this data (as described for flipper coloration – see above), and the inferred presence of minke whales in the Antarctic with no black border to the largest baleen plate must be viewed with caution.

Body coloration

Certain other features of body coloration were noted systematically in a limited number of animals examined at Durban, and in a larger sample of animals from the Antarctic in 1978/79.

(i) *Tongue of dark pigment extending onto the ventral grooves between the eye and the flipper insertion*

In 58 whales examined at Durban or in the Antarctic for which photo-

TABLE 3. DETAILS OF STRANDED (OR ENTRAPPED) MINKE WHALES WITH TYPE 3 PIGMENTATION

Field no.	Length (m)	Sex	Date stranded	Locality	Flipper colour	Pigment on grooves?	% white baleen	Source
72/8	1.92	M	15.5.72	Kommetjie, S.A. (34°07′S 18°21′E)	(L) Type 3 (R) Type 3	Yes Yes	100 100	SFRI files
N438	3.49	F	5.8.74	Nahoon Beach, S.A. (32°59′S 27°57′E)	(R) Type 3	Yes	–	G.J.B. Ross (pers. commn)
80/14	2.54	M	21.7.80	Gordons Bay, S.A. (34°09′S 18°51′E)	(L) Type 3 (R) Type 3	Yes Yes	100 100	SFRI files
–	–	–	26.6.76	N. of Rio Grande, Brazil (~32°S 52°W)	(L) –	Yes	–	G.R. Williamson (pers. commn)
–	–	–	–.6.54	Plimmerton, NZ (~41°05′S 174°52′E)	(R) Type 3	Yes	100	Gaskin (1968) Baker (1983)
–	3.85	M	17.8.80	Dargaville, NZ (~36°S 173°47′E)	(R) Type 3	Yes	100	M.W. Cawthorn (pers. commn)
–	4.04	F	27.8.82	Wonga Beach, Aus. (16°28′S 145°23′E)	(L) Type 3	Yes	100?	H. Marsh (pers. commn)
–	–	F	18.9.82*	Hook Reef, Aus. (19°50′S 149°13′E)	(L) Type 3 (R) Type 3	Yes Yes	– –	H. Marsh (pers. commn)

* Entrapped in coral reef.

graphs exist showing simultaneously both the pigmentation of the flipper and the region between the eye and the flipper insertion, all 53 with no such tongue had Type 1 or 2 flippers, while the remaining five animals with a tongue of dark pigmentation all had Type 3 flippers. Some of the animals with Type 1 or 2 flippers had dark pigment in the folds between the ventral grooves in this region, but this was only conspicuous when the throat region was relaxed, and none had the continuous dark pigmentation characteristic of Type 3 animals. This tongue of dark pigmentation was also present in eight stranded minke whales with Type 3 pigmentation (Table 3). When present this feature seemed to be symmetrical in extent between left and right sides of the same animal.

(ii) *Blowhole streaks*

A typical feature of the minke whales examined was a pair of grey streaks extending posteriorly for about 0.6 m from the blowholes, one from each opening (Fig. 6a). These streaks were irregular in course but both tended to veer towards the left side of the body posteriorly. They were present in all animals examined for this feature (12 at Durban and 149 in the Antarctic), all of which had Type 1 or 2 flippers. A similar marking was seen in a juvenile stranded minke whale from the South African coast that had Type 3 flippers (80/14), so it is possibly a universal feature of all southern minke whales. It can be seen in some of the photographs of ice-trapped animals published by Kellogg (1940) and Taylor (1957), and in a photograph of a calf stranded in New Zealand (Lillie, 1915). Photographs sent to me by M.W. Cawthorn of another animal stranded in New Zealand also show this charac-

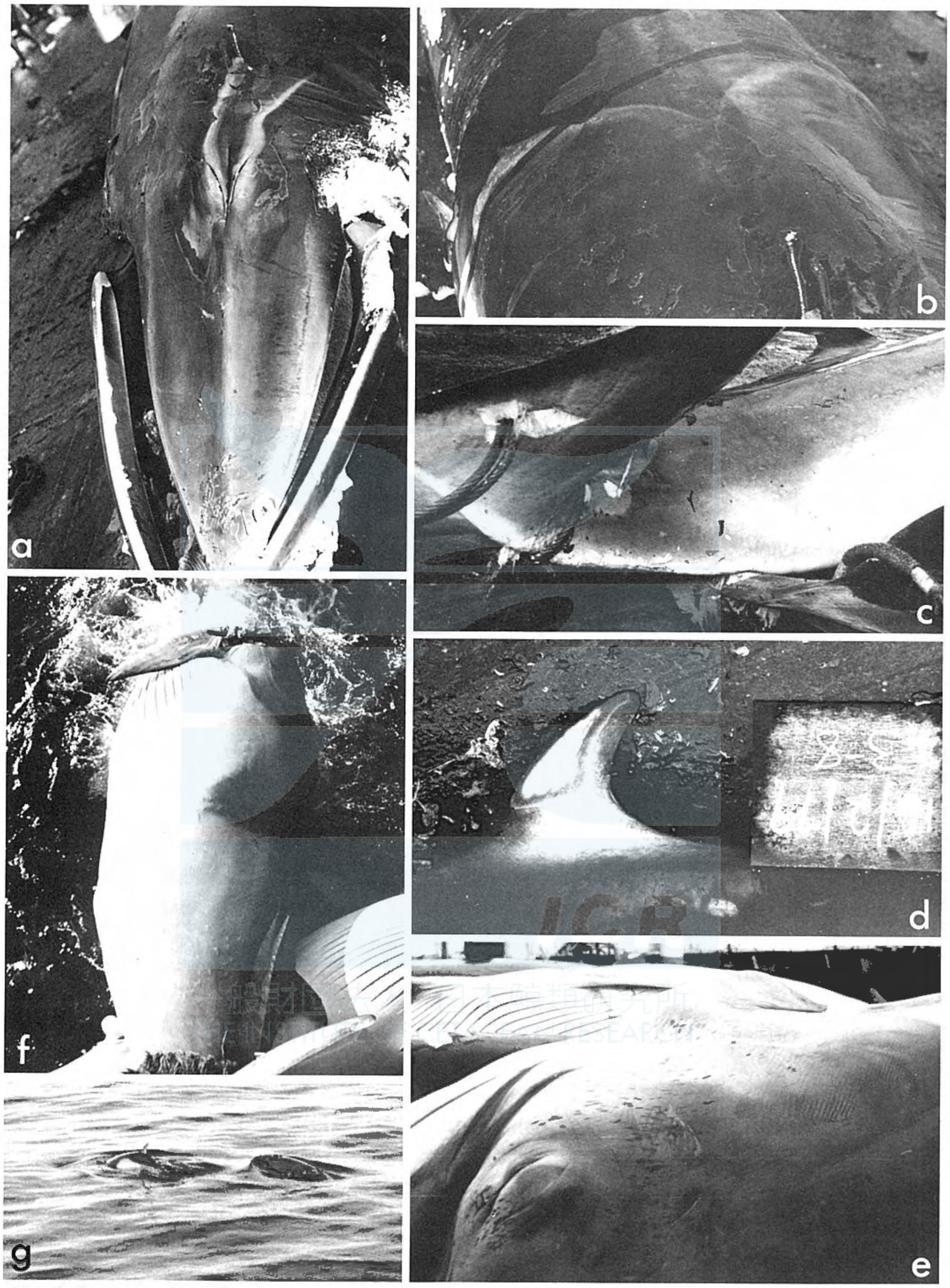


Fig. 6. Features of minke whale body coloration
a. streaks from blowhole
b. crescent-shaped streaks meeting mid-dorsally
c. chevron marks
d. dorsal fin flare
e. speckling
f. thorax blaze and flank patch
g. flank patch visible at sea

ter. However, it was not mentioned by Williamson (1959, 1961), Van Utrecht and Van der Spoel (1962), or Kasuya and Ichihara (1965).

(iii) *Grey streak up side*

In nearly all the animals examined, a crescent-shaped grey streak extended up each side of the whale above the flipper insertion towards the dorsal midline, where the streaks from either side met (Fig. 6b). This streak appears to be homologous to the pale streak originating near the anterior insertion of the flipper and extending towards the shoulder which was described and figured by Kasuya and Ichihara (1965), although the continuation of the streak as far as the mid-dorsum was not figured by those authors. This feature was seen in all 11 whales inspected at Durban, and in 96.3% of 134 whales examined in the Antarctic. It should be pointed out that this marking (as (ii) above) is most conspicuous in the living or freshly-dead animal, and rapidly fades after death, particularly when the animal is exposed to direct sunlight. Thus although it was not mentioned by Williamson (1959, 1961) or Van Utrecht and Van der Spoel (1962), the lack of previous descriptions of such features may in part represent an unfamiliarity with fresh material. Alternatively the markings may have been overlooked or considered unimportant: photographs of Williamson's (1959) whale no. 2 taken by the present author at the time the whale was flensed clearly show both the blowhole streaks and the crescent-shaped streaks meeting mid-dorsally. No minke whale with Type 3 flippers was examined for this feature at Durban. However a juvenile whale with Type 3 coloration stranded on the South African coast (80/14) shows a similar (but somewhat broader) crescent-shaped mark running from above the flipper towards the mid-dorsum, and there are indications of a similar marking in a whale with Type 3 body coloration stranded in New Zealand (Baker 1983). Consequently it is possible that this feature is common to all or nearly all southern minke whales.

(iv) *Caudal chevrons*

On most minke whales examined, the dark dorsal pigmentation extended ventrally as a pair of curved "chevrons" (pointing anteriorly), situated either side of the base of the tail on the caudal peduncle (Fig. 6c). Such markings were present in 80.3% of the 142 whales examined in the Antarctic for this character, all of which had Type 1 or 2 flipper coloration. No whales were inspected for this character at Durban. There were indications of possible chevron markings in a stranded minke whale from the South African coast that had Type 3 flippers (80/14), but the skin in the peduncle region was badly damaged.

(v) *Dorsal fin flare*

Some southern minke whales had a grey flare on the posterior half of the dorsal fin (Fig. 6d), as seen in some *Lagenorhynchus* species (see Fraser, 1966). This was very variable in intensity, and could be detected in only 55.4% of 74 minke whales examined in the Antarctic for this feature. It could not be detected in the only three whales with Type 3 flipper coloration that were examined, all of which were juveniles stranded on the South African coast, but because of the variability in this feature it is impossible to say whether such flares are only found in whales with Types 1 and 2 coloration.

(vi) *Speckling*

In some minke whales examined, small dark, irregularly-shaped speckles were present mid-laterally, usually at the border between the dark grey dorsal and the white ventral coloration (Fig. 6e). They were very variable in number, most often occurring in the region between the eye and the flipper insertion, but sometimes extending past the tip of the flipper and as far back as the level of the anus. Such speckling was seen in 63.6% of 11 whales landed at Durban but in only 30.7% of 114 whales examined in the Antarctic: all the whales examined in both localities had Type 1 or 2 flipper coloration. Such a character was not seen in two Type 3 coloration minke whales examined that stranded on the South African coast (72/8, 80/14), but because of its great variability in Type 1 and 2 animals it is impossible from this small sample size to determine whether Type 3 animals do or do not exhibit this feature.

Although it was not the subject of systematic recording, a conspicuous feature of the body pigmentation of most southern minke whales with Type 1 and 2 coloration at Durban and in the Antarctic was a light grey flank patch. Starting at the angle of the gape and progressing posteriorly, the border between the dark pigmentation of the back and the white of the belly initially ran between the angle of the gape and the anterior insertion of the flipper. Between the axillary region of the flipper and the caudal peduncle, however, this border extended dorsally twice (Fig. 6f). The first extension (or "thorax blaze") ran diagonally up from the axilla and then diagonally back again to about the same level, forming a roughly triangular invasion of light grey pigment dorsally. The second dorsal extension commenced only a short distance posterior to the completion of the first. The anterior border of this extension was nearly vertical and continued much farther dorsally than the "thorax blaze". Its posterior border sloped down gradually towards the midline, where it merged with the white of the ventral surface of the caudal peduncle.

Both Williamson (1959; 1975) and Kasuya and Ichihara (1965) have sketched these two dorsal extensions of light pigment on the side of southern minke whales (and Ohsumi *et al.* 1970 referred to "slight waves" in the transitional zone between dorsal and ventral pigmentation along the side of the body), but only in the illustration provided by Williamson (1975) was the prominence of the more posterior (flank) patch sufficiently stressed. This patch can be clearly seen at sea if the whale rounds its back before submerging (Fig. 6g): a photograph in Kellogg (1940) shows the flank patch and thorax blaze in the living animals particularly well. Presumably it was also the flank patch that was referred to in Lillie (1915) as "a characteristic triangular patch of lighter colour... on either side of the back, in the region of the dorsal fin." A sketch accompanying this description shows the patches in dorsal view. The flank patches can in fact be most conspicuous from the air (pers. obs.), when in dorsal view they are seen extending up either side in front of the dorsal fin, which is therefore situated in a comparatively narrow strip of dark pigment extending along the middle of the back of the posterior half of the whale.

The thorax and flank patches seemed to be present in the majority of minke whales landed at Durban and in all minke whales examined in the Antarctic. In the three stranded animals with Type 3 flipper coloration examined on the South African coast, both thorax and flank patches could be discerned, although the latter was faint. Their position also appeared further anterior than in minke whales with Type 1 or 2 coloration, the thorax blaze terminating just posterior to the tip of the flipper and the flank patch about the level of the dorsal fin. A third, tongue-like dorsal extension of lighter pigment could be detected in all three animals between the dorsal fin and the fluke insertion, here termed the peduncle patch. This was not noted in animals with Type 1 or 2 flipper coloration, and may be typical of Type 3 animals. Baker (1983) refers to two or three deep scallops of pale pigment along the flanks in minke whales with Type 3 body coloration, whereas a photograph of a minke whale stranded at Dargaville, New Zealand, with Type 3 body coloration and all-white baleen clearly shows a third, peduncle patch (photograph supplied by M.W. Cawthorn).

MORPHOMETRICS

Total Length

Southern minke whales in general are estimated to reach sexual maturity at 7.19 m (23.6 ft) or 7.59 m (24.9 ft) in males (Ohsumi and Masaki, 1975; Best, 1982), and 8.0 to 8.1 m (26.2 to 26.6 ft) in females (Best, 1982; da Rocha, 1980; Doroshenko, Kuzmin, Nikolsky and Patsenko, 1974; Ohsumi and Masaki, 1975). Asymptotic lengths are 8.5 to 8.6 m (27.9 to 28.2 ft) in males and 8.93 to 8.99 m (29.3 to 29.5 ft) in females (Best, 1982; Ohsumi and Masaki, 1975).

In Table 4 details of length, sex and maturity are provided for 13 minke whales landed at Durban between 1970 and 1973 which are considered (on the basis of exhibiting at least two of the pigmentation characteristics) to be Type 3 animals. Four males, ranging from 6.71 to 6.83 m in total length, were classified as sexually mature based on a histological examination of their testes, and the weight of their larger testis was from 0.64 to 1.10 kg (mean 0.875 ± 0.114 kg), about four times heavier than the average for their size (Best, 1982). The largest male examined was 7.62 m long, but this animal was

TABLE 4. PIGMENTATION, AGE AND REPRODUCTIVE DETAILS OF MINKE WHALES LANDED AT DURBAN WITH TYPE 3 CHARACTERS

Plat-form no.	Length (m)	Sex	Date killed	Flipper colour	Pigment on grooves?	% white baleen	Width of black stripe % plate width	Age (=GLGs)	Testes		Ovaries			Uterus diameter (cm)	Remarks
									Wt (g)	Maturity	Wt (g)	Diameter c. luteum (cm)	Diameter c. albicans (cm)		
837	6.96	F	25 May 1970	(L) Type 3 (R) Type 3	–	(L) 54.9 (R) 100	–	14 ?	–		–	–	–	7,8	
874	6.68	M	26 May 1970	(L) Type 3 (R) Type 3	Yes	(L) 100 (R) 100	–	17 ?	450, 435	–					
891	7.77	F	28 May 1970	(L) Type 3 (R) Type 3	Yes	(L) 100 (R) 100	–	30 ?			–	–	–	7,8	
1634	6.40	F	10 Aug. 1970	(R) Type 3	–	(L) 100 (R) 100	0	–			55, 40	4.0 0	0 2.2	3,4	
1214	6.15	F	26 May 1971	–	–	(R) 100	0	–			–	–	–	–	
981	7.62*	M	19 May 1973	(L) Type 3	Yes	(L) 55.7	0	10 ?	–	–					
1037	6.81	M	23 May 1973	(R) Type 3	–	(?) 68.2	–	21	1040, 880	Mature					
1245	7.37	F	19 June 1973	–	–	(R) 100	0	27 ? +			105, 95	0 0	2.5,1.45,1.05 0	6.25,5	Lactating
1246	6.71	M	19 June 1973	–	–	(L) 54.2	6	13 ?	720, 540	Mature					
1247	6.40	F	19 June 1973	(R) Type 3	Yes	(R) 70.5	4.3	–			45	0	0	5,3.75	One ovary lost
1248	6.83	M	19 June 1973	(R) Type 3	Yes	(R) 100	2.6	13	1100, 880	Mature					
1295	7.32	F	26 June 1973	–	–	(L) 68.2	7	–			70, 55	2.03 0	2.6 0.95	2,2.25	
1319	6.76	M	28 June 1973	(L) Type 3	–	(L) 91.7	2.4	19	640, 580	Mature					

* Measured to nearest foot (0.3 m)

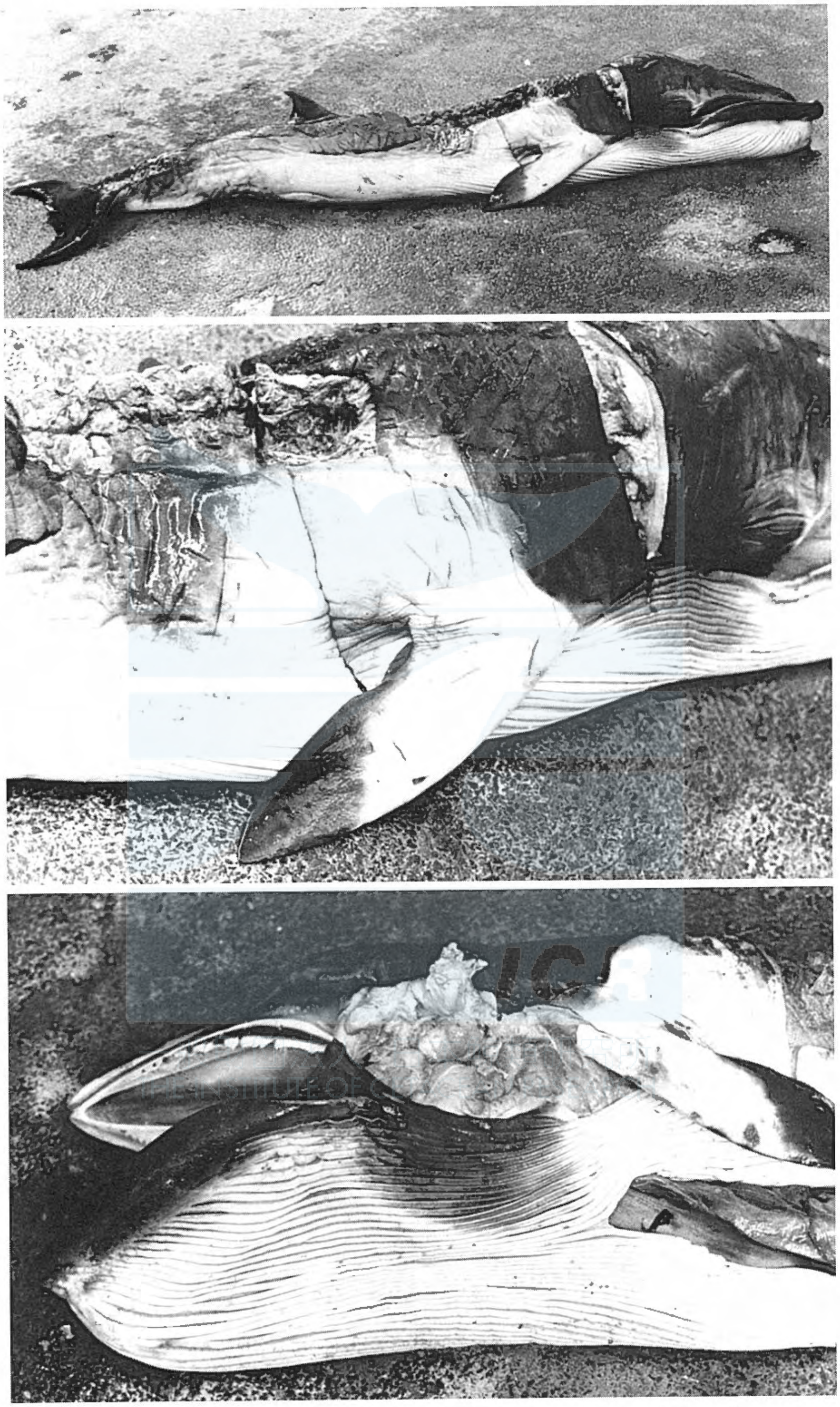


Fig. 7. Stranded newborn minke whale at Kommetjie, Cape Peninsula (PBB 72/8)

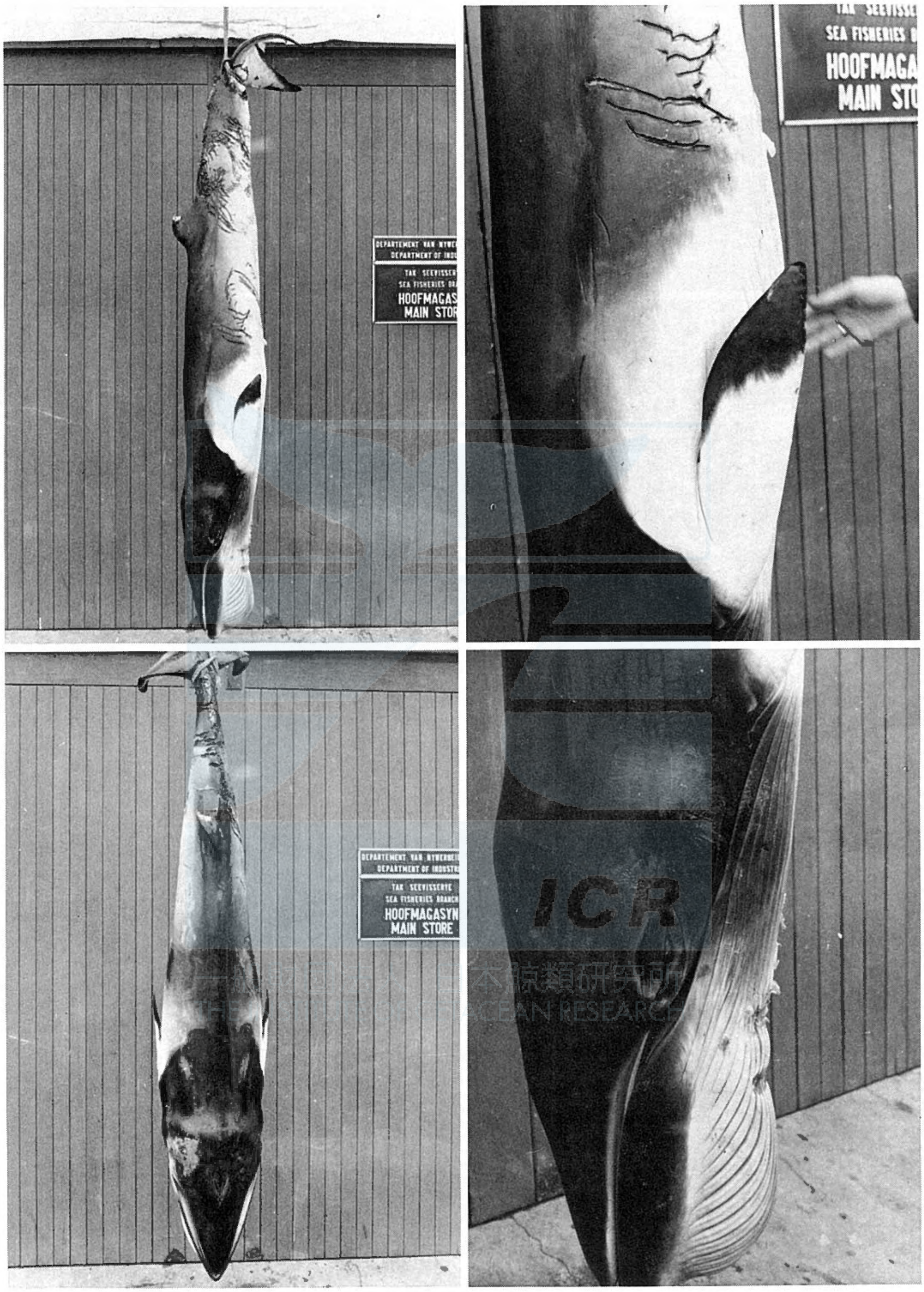


Fig. 8. Stranded juvenile minke whale at Gordons Bay, South Africa (PBB 80/14).

not measured as accurately as the others; the largest reliably-measured male was 6.83 m. Three females, ranging from 6.40 to 7.37 m in length, were classified as mature based on the presence of one or more corpora lutea or albicantia in the ovaries. The largest of these had three ovarian corpora, but was 0.5 m smaller than the smallest mature female with Type 1 or 2 coloration examined at Durban. The largest female examined was 7.77 m long.

The three whales with a 'white spot' on the flipper from Brazil mentioned by da Rocha and Braga (1982) also matured at an unusually small size. Two males 6.92 and 7.13 m in length were mature, each with a larger (?) testis weighing 1000 g, while a female 7.62 m long had eight ovarian corpora.

It seems clear that whales of this colour phase are significantly smaller than normally-pigmented southern minke whales, but with the small sample size available it is impossible to say how much smaller.

Further evidence of their diminutive nature comes from two juveniles stranded on the South African coast. A male minke whale 1.92 m long found dead on the beach at Kommetjie (Table 3) had a raw and completely unhealed umbilicus, while the lungs were air-filled, indicating a very recent live birth. The typical Type 3 flipper and associated body coloration was visible (Fig. 7). A male minke whale 2.54 m long seen swimming very slowly in Gordons Bay harbour, where it died later the same day (Table 3), had some severe lacerations to the posterior half of the body that were attributed to sharks. Its umbilicus was completely healed, both baleen series were fully erupted and there was heavy lungworm infestation in all bronchi, indicating an animal that had been alive for some time. The typical Type 3 flipper and associated body coloration was also visible on this animal (Fig. 8), and the baleen plates were all white.

The normal length at birth for southern minke whales is not well established, but most estimates lie in the range 2.7 to 2.9 m (Best, 1982; Ivashin and Mikhalev, 1978; Ohsumi and Masaki, 1975). While there may be considerable variation in this parameter, and strandlings may not be typical of normal newborn calves, the Kommetjie animal was only 68.5% of the estimated mean birth length, while the Gordons Bay animal was 74.1% of the length of the next smallest calf recorded with a healed umbilicus (Best, 1982). These examples suggest that whales of the Type 3 colour phase are born at a significantly smaller size than normally pigmented southern minke whales.

Body Proportions

Body measurements other than total length are available for only two whales with Type 3 coloration, the stranded juveniles 72/8 and 80/14. These, expressed as proportions of total length, are compared in Table 5 with similar measurements for six other juvenile minke whales (< 4 m long) stranded on the South African coast, and with measurements of 12 adult Antarctic minke whales (from Ohsumi *et al.*, 1970). In only two measurements did the values for both Type 3 animals fail to fall within the range for the six other juveniles,

TABLE 5. BODY PROPORTIONS (AS % TOTAL LENGTH) FOR SOUTHERN MINKE WHALES

Measurement	Type 3		Field no. & sex Type 1 or 2							
	72/8 (M)	80/14 (M)	73/12 (F)	80/28 (M)	76/26 (F)	81/15 (F)	78/23 (M)	75/11 (F)	Ohsumi et al. (1970) Range	Mean
Total length (cm)	192	254	301	341	343	345	353	377	710 – 930	
Tip of snout to centre of anus (%)	72.5	72.8	70.4	72.7	73.8	71.3	72.2	70.7	68.7 – 76.4	73.0
Tip of snout to centre of genital aperture	64.9	65.6	68.1	64.5	70.6	68.4	62.9	67.6	64.4 – 70.9	66.5
Tip of snout to tip of dorsal fin	71.5	71.3	76.1	73.6	72.9	74.8	74.8	73.1	(70.0 – 74.0	71.5)[2]
Tip of snout to ant. insertion dorsal fin	63.6	64.6	68.1	66.9	66.5	67.8	67.4	67.1	–	
Tip of snout to centre of umbilicus	54.3	52.4	52.8	51.9	52.5	53.0	49.9	51.5	47.5 – 62.4	53.7
Tip of snout to post. extremity ventral grooves	51.5	48.6	49.5	49.3	51.3	48.4	46.7	48.0	43.5 – 54.8	48.0
Tip of snout to ant. insertion flipper	31.5	28.9	30.2	30.5	30.0	28.7	28.9	27.7	24.0 – 32.0	29.3[4]
Tip of snout to external auditory meatus	25.2	24.2	27.2	24.9	25.1	24.6	–	23.6	23.4 – 27.0	25.1[3]
Tip of snout to angle of gape	18.2	17.9	20.6	18.0	21.6	18.3	20.1	17.2	17.1 – 20.5	18.7
Tip of snout to centre of eye	19.2	18.3	20.6	18.6	17.8	18.8	19.3	18.2	18.3 – 22.0	20.0
Tip of snout to centre of blowhole	13.2	14.0	15.0	14.5	13.4	13.9	13.0	13.3	12.2 – 16.0	14.3
Girth, at axilla	–	46.5	53.2[1]	47.5[1]	44.9[1]	52.2[1]	44.8	46.7[1]	–	
Girth, maximum	–	47.4	53.2[1]	47.5[1]	–	52.2[1]	44.8	49.3[1]	–	
Girth, at anus	28.5	27.0	–	29.9[1]	28.6[1]	29.3	28.6	31.0[1]	–	
Girth, midway anus to notch in flukes	–	17.7	–	20.5[1]	–	19.6	19.8	–	–	
Height of body at same locality	–	7.3	–	8.7	–	8.4	9.6	–	–	
Projection of lower jaw beyond upper	1.0	1.0	~0.8	0.9	0.4	0.4	1.3	0.7	–	
Centre of eye to external auditory meatus	–	6.1	6.6	6.5	5.8	5.8	–	5.8	4.7 – 5.7	5.1
Centre of eye to blowhole	–	10.8	12.0	11.1	11.4	10.4	9.9	10.5	–	
Blowhole length	4.0	3.9	3.5	4.0	3.1,3.4	4.5	3.1	3.1	–	
Blowhole width	2.3	2.2	2.2	2.8	–	1.9	1.4	1.6	–	
Eye length	1.5	1.4	1.5	1.3	1.2	1.7	2.0	1.3	–	
Eye height	–	0.3	0.4	–	–	0.5	0.6	0.2	–	
Length of genital slit	4.6	4.8	5.3	4.7	–	9.3	3.4	6.1	–	
Length of anal opening	1.3	1.4	0.2	1.8	–	0.7	0.7	0.5	–	
Flipper, length, ant. insertion to tip	19.2	16.5	19.9	17.6	16.9	18.0	15.6	16.2	12.5 – 17.5	15.8
Flipper, length, axilla to tip	12.6	11.7	12.1	12.3	11.1	12.8	12.0	10.6	–	
Flipper, maximum width	5.3	4.0	4.2	4.1	4.1	3.5	3.7	3.4	2.8 – 4.1	3.7
Dorsal fin, height	5.6	4.8	5.1	5.0	3.4	3.6	3.3	3.6	3.0 – 4.2	3.7
Dorsal fin, length of fin base	8.3	8.9	11.3	8.8	6.1	6.5	8.5	6.1	3.7 – 7.7	5.5
Flukes, width tip to tip	24.2	23.0	23.3[1]	24.3	19.5	24.6	20.1	24.1	25.1 – 35.8	29.0
Flukes, nearest point on ant. margin to notch	8.3	7.5	8.0	6.7	7.3	7.5	4.5	8.0	–	
Flukes, depth of notch	1.7	1.2	0.8	1.5	1.3	0.9	1.1	0.9	–	

[1] Measured half-way and then doubled

[2] To posterior emargination of dorsal fin, not tip

[3] Obtained by adding two measurements

[4] Obtained by subtracting two measurements

these being measurements concerning the position of the dorsal fin, which was apparently situated further forward in the Type 3 animals. Unfortunately the relevant measurements for the Antarctic minke whales are not comparable, being recorded to the posterior emargination of the dorsal fin rather than its tip or anterior insertion. Furthermore, Doroshenko (1979) reported small differences in the relative position of the dorsal fin between populations of southern minke whales, so the significance of the present finding remains uncertain until larger samples of Type 3 animals from different localities have been compared.

Both Type 3 animals measured differed from the sample of Antarctic adults in measurements concerning the size of the dorsal fin and the width of the tail flukes. The height of the dorsal fin was greater and the width of the tail flukes less in the Type 3 animals, but as the other juveniles examined appeared to be closer to the Type 3 animals in these measurements the differences may simply represent ontogenetic change. The length of the dorsal fin base is a particularly subjective measurement, and the differences shown here may arise mainly from differences in interpretation between Japanese and South African researchers.

Number of Ventral Grooves

These were normally counted (as recommended by Williamson, 1973) in the region between the eye and the flipper insertion, starting with the most dorsal (and smallest) groove and continuing to the mid-ventral groove (identified by tracing its path from the tip of the lower jaw). The counts are therefore essentially half-counts of the maximum number of grooves.

In the two stranded Type 3 animals these numbered 38 (72/8) and 27 (80/14) respectively, while in another five juveniles examined with Type 1 or 2 coloration the counts ranged from 22 to 38 with a mean of 32.8. Ohsumi *et al.* (1970) gave a range of 26 to 30 grooves in three animals with a mean of 28, and Williamson (1961) a single count of 30. These are all in reasonable agreement, indicating no significant difference in this character between Type 3 and other southern minke whales. In much larger samples, however, Doroshenko (1979) gave mean values (presumably for total counts) of 46 for two different populations ("Indian" and "New Zealand"), while for the Brazilian population da Rocha (1980) found a range of 15-35 with a mean of 22 in half-counts of grooves and Singarajah (1984) a mean of 47 in whole counts for both sexes. These results seem rather low compared to the present data, and may either represent population differences or (more likely) differences in interpretation. Da Rocha and Braga (1982) also give ventral groove counts of 19 to 29 (mean 23.7) for three minke whales landed in Brazil with (apparently) Type 3 flipper coloration, and state that the number and position of ventral grooves were "normal".

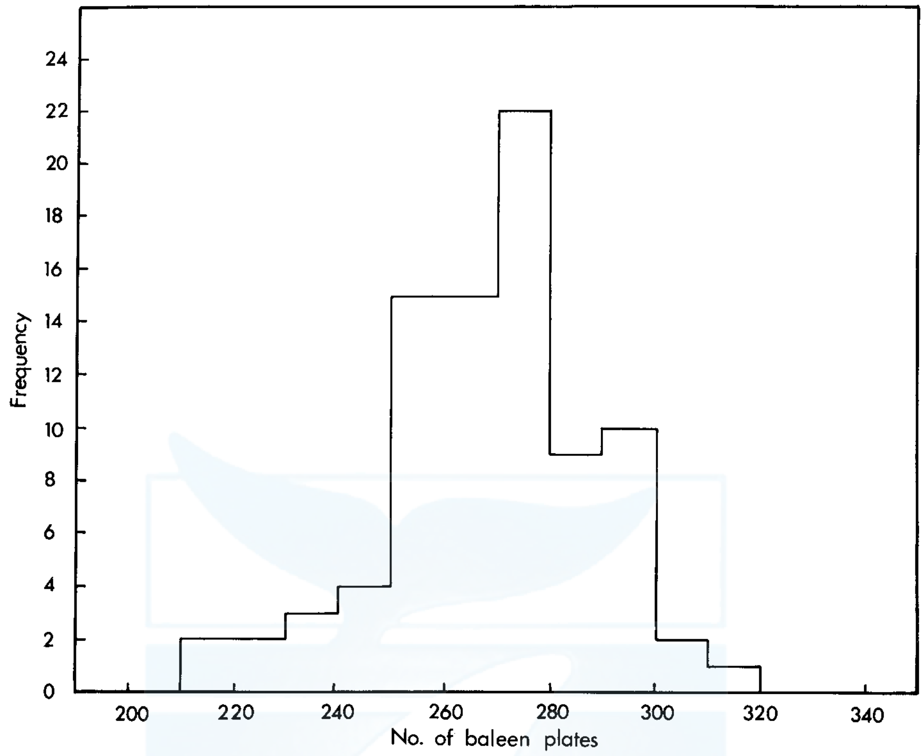


Fig. 9. Counts of baleen plates in minke whales at Durban.

Number of Baleen Plates

During the 1969 season at Durban, the whaling inspectors counted the number of baleen plates on one side of the mouth in 88 whales landed. These counts ranged from 215 to 310, but with three outlying counts of 135, 151 and 154. The latter are considered to be probable errors in recording, and have been omitted from the subsequent analysis.

The means of counts of left and right series were not significantly different (t-test, $p > 0.2$, $df = 83$), the samples being independent as they were from right and left sides of different animals, and so the data have been combined (Fig. 9). The distribution of counts approximates to a normal distribution, for which the mean was calculated as 268.3 ± 2.1.

Previous counts of baleen plates in southern minke whales are in general agreement with these values (270 either side-Van Utrecht and Van der Spoel, 1962; 247 on left side and 264 on right – Williamson, 1961), though Ohsumi *et al.* (1970) listed one animal in the four they examined with 359 plates on one side, more than in any animal examined at Durban. The remaining four series of baleen they counted ranged from 261 to 302. Doroshenko (1979) gives the mean number of baleen plates in the "Indian" population of minke whales as 242 and in the "New Zealand" population 274. Da Rocha (1980)

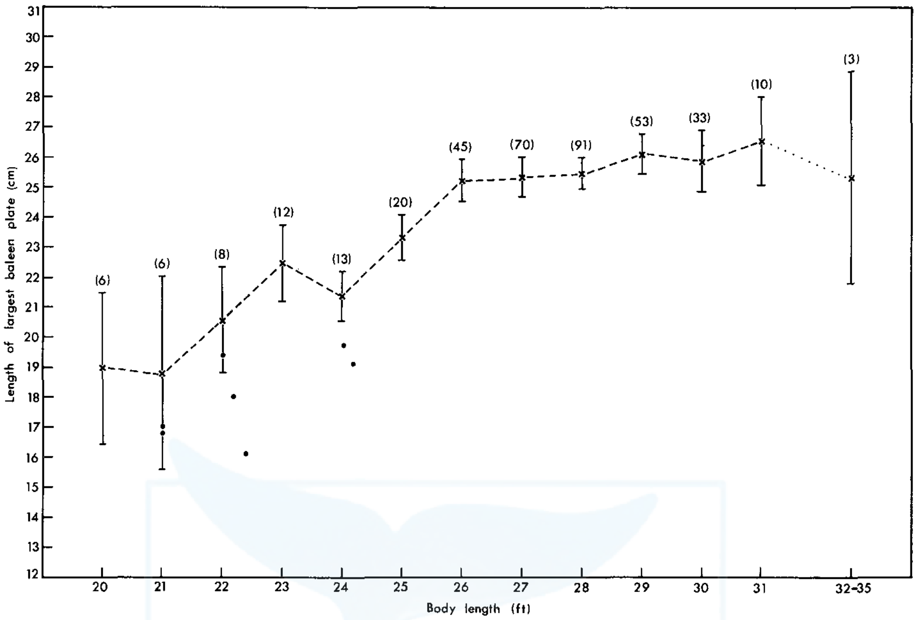


Fig. 10. Length of largest baleen plate against body length in minke whales at Durban (cross and vertical line = mean ± two standard errors for Type 1 and 2 whales, sample size in brackets; solid dot = individual data for Type 3 whales).

found a median value of 273 (range 155 to 415) in 246 minke whales from Brazil, while Singarajah (1984) gives an average count of 237 excluding hairs. There is no indication from these data of polymorphic variation.

The juvenile stranded at Kommetjie had 200 baleen plates on the left and 205 on the right, outside the range for Durban animals, but both series were incompletely erupted. The Gordons Bay juvenile had 251 plates on the left and 244 on the right, well within the range recorded at Durban. From this small sample, therefore, there does not seem to be any evidence of a significantly different number of baleen plates in minke whales with Type 3 coloration.

Dimensions of Baleen Plates

The largest baleen plates in minke whales with Type 1 and 2 coloration reached an average length of 25 to 27 cm in adult animals from Durban (Fig. 10). Other minke whales with this coloration have had baleen plates measured at 28 and 29 cm (Williamson, 1961), 30 cm (Van Utrecht and Van der Spoel 1962) or 22 – 26.1 cm (Ohsumi et al., 1970) in length. The largest baleen plates in the seven whales with Type 3 coloration examined did not exceed 20 cm and averaged 18 cm in length (Fig. 10). Even when whales in the same size range are compared, the values for the Type 3 animals all fall below the averages for Types 1 and 2, indicating that in relative terms also Type 3 whales seem to have shorter baleen plates for their size.

The shape of the longest baleen plates (as portrayed by the proportion breadth/length) did not differ significantly between Type 3 whales (average 0.43 ± 0.02, $n = 5$) and Types 1 and 2 whales (average 0.48 ± 0.01, $n = 34$), when the comparison was restricted to animals of the size range 21 to 24 ft ($t = 1.64$, $p > 0.10$). Overall, the proportion for minke whales with Type 1 and 2 coloration at Durban ranged from 0.37 to 0.78, with a mean of 0.51 ± 0.04 ($n = 331$): this compares with published values elsewhere of 0.42 to 0.64, with a mean of 0.52 (Ohsumi *et al.*, 1970).

DISCUSSION

In summary, two colour phases were found amongst the minke whales landed at the Durban whaling station. The majority of animals had asymmetrically-coloured baleen, in which the right side bore a larger number of anterior white plates than the left, and in which the remaining plates had a black outer border whose width amongst the largest plates averaged about 31 or 34% of the width of the plate, depending on which series was examined. These animals also had flippers whose pigmentation could be described as either plain or two-tone (Type 1 or 2) but on which white patches were never found. There also appeared to be asymmetry in the pigmentation of their flippers, the left flipper generally being brighter in contrast than the right, but there was no correlation between flipper and baleen coloration. The transitional zone between the dark dorsal and light ventral pigments on the neck was on a level with the eye and the flipper insertion. These animals seemed closest to the southern minke whales described by Williamson (1959, 1961), Van Utrecht and Van der Spoel (1962) and Ohsumi *et al.* (1970), although the occurrence of two-tone flippers was not mentioned by these authors. However, the apparent continual range in variation of flipper coloration within this colour phase suggests that the animals with two-tone flippers may have been overlooked. Following Williamson (1959), and taking into account the baleen coloration of the type specimens of *B. bonaerensis* (Burmeister, 1867) and *B. huttoni* (Gray, 1874; Williamson, 1959), Type 1 or 2 whales could be referred to as "*bonaerensis*"-type.

Whales of the second colour phase had all-white baleen or baleen with an unusually large proportion of white plates. The largest baleen plates of these animals were either completely white or carried a narrow black outer border less than 10% of the width of the plate. The flippers carried a striking white patch connected to a roughly circular white blaze on the shoulder (Type 3). There was no asymmetry of coloration in the flippers and little (if any) in baleen coloration. The transitional zone between the dark dorsal and light ventral pigmentation on the neck extended down onto the ventral grooves as a tongue of black pigmentation between the eye and flipper insertion on both sides of the head, to a roughly equal extent. These animals appeared to be born and to reach sexual maturity at a significantly smaller size than normal southern minke whales, with a dorsal fin possibly situated somewhat farther forward. The largest baleen plates in adults of this colour phase were less than 20 cm in length, compared to an average of 25 to 27 cm in adults of the normal colour phase.

Whales of the latter phase have been described previously only by Baker (1983) and possibly da Rocha and Braga (1982), though neither account makes clear the distinction in baleen coloration between these and normal southern minke whales nor the difference in size. Although there have been other references to southern minke whales with "light" flippers or flippers with white patches (see Introduction), the majority of these have been sightings; it is possible that some of these records may have been of minke whales with Type 2 flippers, which, when seen in the living animal through the water, stand out clearly in contrast to the darker dorsal pigmentation (personal experience of the author).

The incidence of this second colour phase off Durban is low. There is no significant difference between the incidence of Type 3 flippers on right and left sides of the whales (chi-square test, $p > 0.8$, $df = 1$), and their incidence if the data are combined is 3.24% ($n = 370$). The incidence of whales with a black border to the baleen plate less than 10% of the baleen in width also did not differ significantly between left and right sides of the whales (chi-square test, $p > 0.25$, df 1), and their incidence if the data are combined is 3.41% ($n = 469$). The incidence in the catch is therefore estimated to be 3 to 4% of all minke whales landed.

Singarajah (1984) states initially that no minke whales with white stripes on their flippers were found amongst 1745 animals examined in Brazil between 1979 and 1981, but later that on rare occasions (e.g. in 1980 and 1981 about 0.2% of the catch) a second type with a white stripe was recorded. It is not clear whether the latter include the three animals in a sample of 902 minke whales examined in Brazil in 1980, which were described as having a 'white spot' on the flippers, distinct from the 'all-black' flippers normally found (da Rocha and Braga, 1982). If the latter are true Type 3 animals, their incidence off Brazil is apparently even lower than off Durban. However it should be pointed out that in both areas the data originates from whaling operations, where commercial incentives may have resulted in selection for the larger form.

No whales resembling this second colour phase were seen amongst the 161 animals examined in the Antarctic in 1978/79. Photographs and/or sketches of this colour phase were shown to flensing plant foremen and other personnel aboard the *Nisshin Maru no. 3*, and subsequently to Japanese scientists with first-hand experience of Antarctic minke whales. None claimed to have ever seen a whale resembling it, and it must be concluded that this colour phase does not normally migrate to higher latitudes of the Antarctic.

Against this must be balanced the data presented by Wada and Numachi (1979), which seems to show that minke whales with white-banded flippers, and some with no black outer margin to their largest baleen plate, are found in the Antarctic. Given the authors' own reservations about their data, however, this conclusion must be treated with caution.

Besides Durban (ca 30°S, 31°E) and Costinha, Brazil (ca 7°S, 34°W), whales corresponding to this colour phase have been recorded from several other localities in the Southern Hemisphere (Table 3). These records indicate a latitudinal distribution from 7° to 41°S, and a presence in all three major oceans. Nowhere apart from the whaling grounds off Durban and Brazil is there a measure of its relative abundance, although Baker (1983) refers to it as "rare" compared to the "common" colour form. Apart from its probable exclusion from the higher latitudes of the Antarctic, the form appears to have the same overall distribution as the Type 1 or 2 animals. Patterns of schooling behaviour, onshore-offshore distribution and seasonality, however, may serve to segregate the animals to some extent.

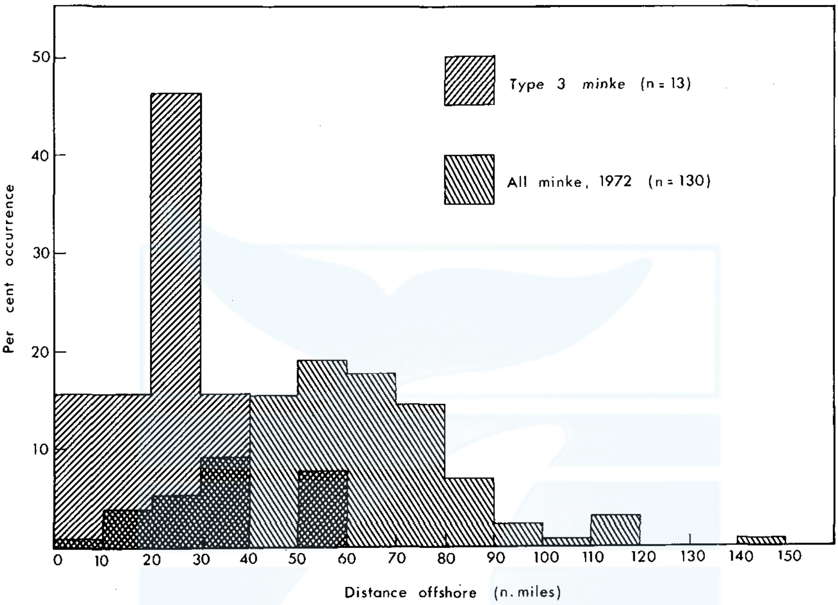


Fig. 11. Distribution of minke whale catches from coast, Durban whaling ground.

Inspection of catch positions and times for the 13 Type 3 animals examined at Durban (Table 4) reveals that they were all captured singly, so that there is no evidence of schooling together with Type 1 or 2 animals. The onshore-offshore distribution of catch positions for the same 13 animals has been compared with that for 130 minke whales (coloration type unknown) landed at Durban in 1972 (as extracted from Best and Surmon, 1974, Fig. 1), the data being grouped in 10 n. mile intervals (Fig. 11). The animals with Type 3 coloration were distributed closer inshore than minke whales as a whole, 77% of them being killed within 30 n. miles of the coast compared to only 10% of all minke whales. The mean distances offshore (27.0 ± 7.5 and 60.0 ± 5.6 n. miles respectively) were significantly different ($t=5.62$, $p<0.001$). (The dissimilarity in distribution might have been greater if it had been possible to identify and thus exclude any Type 3 animals killed in 1972). Of the 13 Type 3 animals examined at Durban, 12 (or 92%) were killed in the first half of the season (April to June) whereas in the same years (1970, 1971 and 1973) only 33% of the 530 other minke whales were killed in the same period. These proportions are significantly different (chi-square = 17.4, $p < 0.001$), suggesting a difference in seasonality of occurrence of Type 3 relative to Type 1 and 2 minke whales off Durban. (The alternative hypothesis, that more searching effort was spent inshore in the first half of the season, is considered very unlikely, as it was the last half of the season in which weather usually deteriorated).

Thus, at least for the Durban whaling area, there are indications of some spatial and temporal segregation of minke whales with Type 3 coloration from other minke whales. This segregation was not complete, however, and more information is needed on the seasonal movements and reproductive behaviour of Type 3 minke whales before any conclusions can be reached on the degree of reproductive isolation of this colour form from other minke whales. A decision on the taxonomic status of these animals is therefore premature.

It can be pointed out, however, that the differences in size, body and baleen coloration found between Type 3 and Type 1 and 2 (or "*bonaerensis*"-type) animals are at least as great as those between *B. acutorostrata* from the Northern Hemisphere and "*bonaerensis*"-type animals from the Southern Hemisphere (and the same seems to be true for skull characters – paper in preparation).

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OBSERVATIONS ON THE OVARIES OF AN ISOLATED MINKE WHALE: EVIDENCE FOR SPONTANEOUS STERILE OVULATION AND STRUCTURE OF THE RESULTANT CORPUS

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ABSTRACT

Examination of the reproductive organs of a parous "dwarf" minke whale who spent the last three months of her life alone in a Great Barrier Reef lagoon indicated that this animal ovulated spontaneously during this period despite illness. The structure of the resultant ovarian corpus provides further evidence that corpora lutea of "ovulation" cannot be distinguished from those of pregnancy in this species.

INTRODUCTION

Information from the reproductive organs of a minke whale*, *Balaenoptera acutorostrata*, which spent the last three months of its life in isolation in a small lagoon on the Great Barrier Reef, is relevant to two controversial topics in cetacean reproduction: (1) whether corpora derived from sterile ovulations can be distinguished from those of pregnancy and (2) whether ovulation can be spontaneous in wild cetaceans.

MATERIALS AND METHODS

The minke whale, first sighted in a small (approximately 250m × 150m × 10m deep) lagoon on Hook Reef (19°50′S, 149°13′E) on August 31, 1983, remained there until immediately before her death. Her carcass was found on the adjacent reef flat within four hours of death on November 28, 1983. While in the lagoon, the whale was checked several times each day by the pilots of light aircraft ferrying tourists to nearby reefs, the pilots reporting their observations to the Great Barrier Reef Marine Park Authority. No other whales were observed in the area during this time.

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The colouration of the flippers, shoulder regions and baleen of this minke resembled those of the diminutive form reported by Best 1985; this volume pp. 1-33 off Durban. This colour form is not included in the photographic records of 1200 minkes from the Antarctic which are held by Mr S. Wada, Far Seas Fisheries Research Laboratory, Shimizu, Japan and which he kindly allowed me to check.

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Necropsy commenced about 48hr after death. The whale was measured according to the standards of Norris (1961). The ovaries were excised and formalin-fixed for subsequent macroscopical and histological examination using methods similar to those outlined in Marsh and Kasuya (1984). The uterus was measured using a flexible tape, examined carefully for the presence of an embryo, and sampled for histology at the midlength of each cornu. The right mammary gland was likewise measured and sampled; in addition the depth of the gland was measured using vernier calipers. All histological samples were processed as outlined in Marsh and Kasuya (1984). The earplugs were not collected as they had disintegrated.

RESULTS

Details of the reproductive organs are summarized in Table 1. I had no difficulty interpreting their histology despite the interval between death and necropsy. Conspicuous stretch marks in the uterine serosa (see Benirschke, Johnson and Benirschke, 1980) and the histology of the mammary gland (see Mackintosh and Wheeler, 1929) indicated that the 7.1m long whale was parous and that she was not lactating. This agrees with Best's (Best, 1982) observations that whales of this colour form reach puberty at a smaller size than typical southern minke whales.

TABLE 1. DETAILS OF THE REPRODUCTIVE ORGANS OF THE MINKE WHALE ALL TERMINOLOGY AS IN MARSH AND KASUYA (1984)

Component	Left	Right	Histological details
Ovary weight (g)	100.6	92.0	
Mean diameters of ovarian structures (mm)			
Corpus luteum/albicans		33.3	As in Marsh & Kasuya (1984) Fig. 19a.
Old corpora albicantia	13.5,12.5,11.0	13.5,10.9	
Corpus atreticum *a*	18.4		As in Appendix B to Workshop Report Fig. 2c, d (Perrin *et al.*, 1984)
Corpus atreticum *b*	6.0		
Largest follicle	3.0	3.5	
Diameter of each uterine cornu (cm)	8.8	8.8	Endometrial glands well developed and crowded; some hyalinzation of stroma beneath surface epithelium; as in Benirschke *et al.* (1980) Figs 21 & 22
Depth of mammary gland at midlength (cm)		1.8	Completely involuted as in Mackintosh and Wheeler (1929) Fig. 138

The right ovary contained what appeared to be a well-established yellow corpus luteum with a fibrin-filled centre (Fig. 1). The corpus was 33.3mm in mean diameter. Histologically, this corpus showed signs of early degeneration into a corpus albicans (see Table 1). The whale showed no indications of recent pregnancy. The uterine cornua were equal in size and the endometrial histology was similar to that of specimens of *Stenella longirostris* and *Stenella attenuata* with an advanced corpus luteum of "ovulation" as described by Benirschke *et al.*, (1980). It thus seems certain that the corpus illustrated in Fig. 1 resulted from a sterile ovulation. The suggestion of Robins (1954) that only corpora lutea of pregnancy have fibrin-filled centres is thus untenable in the minke whale, and we conclude that corpora lutea of "ovulation" cannot be distinguished structurally from those of pregnancy. Many other cetologists have also come to this conclusion (for references see Marsh and Kasuya, 1984).

DISCUSSION

Despite our knowledge of the whale's activities in the three months prior to her death, it is impossible to be certain of the age of the corpus illustrated in Fig. 1, especially as the only comparable material is from seasonally limited catches of typical southern minke whales. The corpus falls within the size range of corpora lutea measured in 14 lactating minkes by Best (1982). Best classified these animals as "recently ovulated" and concluded that ovulations can occur during autumn and winter, but are most frequent in spring (the season when the minke was isolated in the lagoon).

C. Lockyer (pers. comm.) recorded a "post-ovulation, sterile, regressing" corpus luteum in the ovaries of three non-lactating typical southern minke whales, all of which were killed in January. The corpus illustrated in Fig. 1 was smaller than any of the three measured by Lockyer (which ranged from 3.78cm to 4.5cm in mean diameter), possibly reflecting the tendency for the size of the corpus luteum to be positively correlated with body size. However, Lockyer advises that two of the corpora she measured definitely appeared older (more regressed) than the one in Fig. 1.

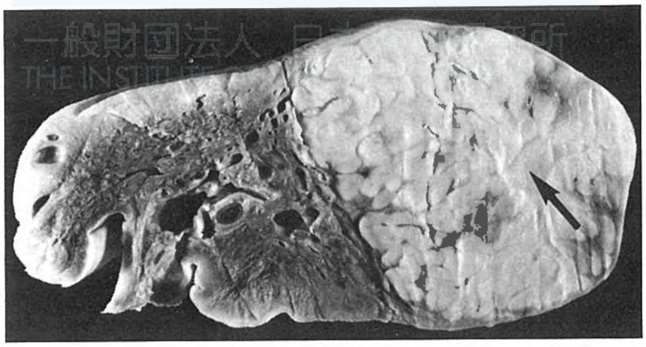

Fig. 1. Cross-section through the right ovary showing the corpus luteum/albicans of "ovulation" with its fibrin-filled centre (arrowed). The scale bar represents 1 cm.

Kirby and Ridgway (1984) concluded on the basis of hormonal monitoring of captive dolphins, that *Tursiops truncatus* and *Delphinus delphis* can ovulate spontaneously. If the minke ovulated spontaneously while alone in the lagoon she did so despite the fact that she was ill during this period. The pathologist present at the necropsy (Dr R. Speare, Graduate School of Tropical Veterinary Science, James Cook University) could not determine the cause of death but reported that (1) the whale had suffered (and recovered) from chronic peritonitis at least one month before death (2) a chronic gastric ulcer and two acute gastric haemorrhages were present in the second stomach (3) the blubber especially in the neck region was oedematous indicating starvation. This last symptom was consistent with the progressive encaving of the neck region which was photographically documented during the whale's tenure in the lagoon. Ridgway (1972) cites this as a sign of severe weight loss in porpoises.

If the whale last ovulated before entering the lagoon, the corpus in Fig. 1 must have been at least three months old. This seems unlikely in view of the observations of Sawyer-Steffan, Kirby and Gilmartin (1983) who monitored five, assumed ovulations in captive *T. truncatus*. The assumed ovulations were assessed by elevated serum progesterone levels which dropped markedly within one month, suggeting the corpus luteum of each of these animals was active for only a few weeks. I conclude that the minke whale ovulated spontaneously while alone in the lagoon despite her illness.

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The Great Barrier Reef Marine Park Authority funded several trips to monitor the whale during its tenure in the lagoon as well as the necropsy. I gratefully acknowledge their support, the field assistance of numerous volunteers, and Christina Lockyer for a stimulating correspondence on the subject of minke whale ovaries, and Toshio Kasuya and Peter Best for their comments on an earlier draft of this manuscript.

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VOCALIZATION AND COORDINATED FEEDING BEHAVIOR OF THE HUMPBACK WHALE IN SOUTHEASTERN ALASKA

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ABSTRACT

Coordinated feeding behavior of the humpback whale (*Megaptera novaeangliae*) was observed over a 3-day period in southeastern Alaska. Using distinctive pigmentation markings on the flipper, we verified that each whale maintained a constant physical orientation and spatial relationship within the group during vertical lunge-feeding maneuvers. A uniform vocalization, with a fundamental frequency of approximately 500 Hz, was closely associated with the initiation of the cooperative feeding behavior. A final, linearly ascending vocalization preceded simultaneous surfacing in the vertical lunge-feeding maneuver.

INTRODUCTION

At the southwest tip of Admiralty Island in southeastern Alaska (57°27′N, 133°51′W) an 80-m shoal separates two deep bodies of water, Chatham Strait and Frederick Sound. The strong upwelling currents created by this shoaling results in productive surface layer due to the increased nutrient supply. In this productive area we observed eight humpback whales (*Megaptera novaeangliae*) feeding on euphausiid crustaceans (*Euphausia pacifica*) and herring (*Clupea harengus*) in a coordinated manner over a three-day period.

When first sighted, on 9 August 1983, several members of the POD were swimming at the surface, with mouths agape and ventral pleats extended engaged in lateral lunge feeding (Jurasz and Jurasz, 1979; Watkins and Shevill, 1979; Hain *et al.*, 1982). We followed the pod for over an hour to photograph the ventral surface of their flukes for individual identification purposes (Katona *et al.*, 1979). The whales remained in a group during this period, independently lateral lunge-feeding on euphausiids with no apparent synchronization or cooperation within the pod. Recordings of vocalizations were made with a Nakamichi 681 ZX tape recorder, with an Ithaco 257AM preamplifier and a Clevite CH-17U hydrophone with a combined frequency response ±3 decibles (db) from 20 hertz (Hz) to 22 kilohertz (kHz). Aside

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from "grunts", very little vocalization was evident while the whales were surface swimming or lateral lunge-feeding. The limited vocalizations of humpback whales on feeding grounds have been reported by other researchers (Perkins and Whitehead, 1977; Thompson *et al.*, 1977).

A different feeding strategy was then initiated by the pod; all of the whales submerged, a single ring of bubbles 20-m in diameter appeared on the surface, and seven of the eight whales surfaced simultaneously within the ring of bubbles in a vertical lunge-feeding manner. The bubbles continued to emerge for about 15 s, until the remaining member of the pod surfaced after apparently completing the bubble "net." Whether the bubble net was used to concentrate the prey or simply enclose naturally occurring concentrations of prey is uncertain; however, curtains of bubbles can form an effective barrier to schooling fish (Bates and VanDerwalder, 1964).

After about 1 h of coordinated feeding on euphausiids, the whales began to feed on a large school of herring (approximately 200-m in diameter) which had moved into the area. The whales continued to utilize the vertical lunge-feeding strategy, but blowing a bubble net was not part of the repertoire. Humpback whales have been observed employing bubble nets for herring, and Jurasz and Jurasz (1979) reported that the net diameter is larger than that used for euphausiids.

The duration between surfacings varied from 5 to 15 m, and feeding bouts lasted up to 6 h. Over the 3-day observation period, feeding was interspersed with apparent resting periods during which time no surface feeding was observed.

The synchronized feeding on euphausiids within the bubble net and on herring without a bubble net seemed to be cooperative and structured. In the 130 vertical lunge-feeding maneuvers which we recorded with still and motion picture cameras, the feeding group of humpback whales always surfaced simultaneously in an identical formation (Fig. 1). By using distinctive pigmentation markings on the pectoral fins, we were able to verify that each whale maintained a constant physical orientation and spatial relationship within the group during vertical lunge-feeding maneuvers (Figs 2 and 3).

We recorded a uniform vocalization (Fig. 4) when the humpback whales initiated their cooperative vertical lunge-feeding behavior. The vocalization, heard only while the entire group was submerged, was 45 to 58 s in duration and began about 90 s prior to their surfacing. These phonations consisted of a distinct series of narrow bandwidth tones which were mostly constant in amplitude and slightly ascending and modulated in frequency. The vocalization ended with a drop and then upward sweep in frequency. The fundamental frequency was approximately 500 Hz, with multiple associated harmonics perceptible until they disappeared in the background noise above 8 kHz. The drop reached 400 Hz with an upward sweep to 800 Hz. These tonal segments were each 3 long. After this initial series of tonal segments, and an 11- to 14-pause, a final vocalization of about 6 preceded the vertical lunge-feeding maneuver. This last vocalization differed from the previous tonal segments in that it ascended linearly from 450 Hz to 600 Hz. In one instance the final vocalization was omitted and the whales surfaced without an devious group structure.

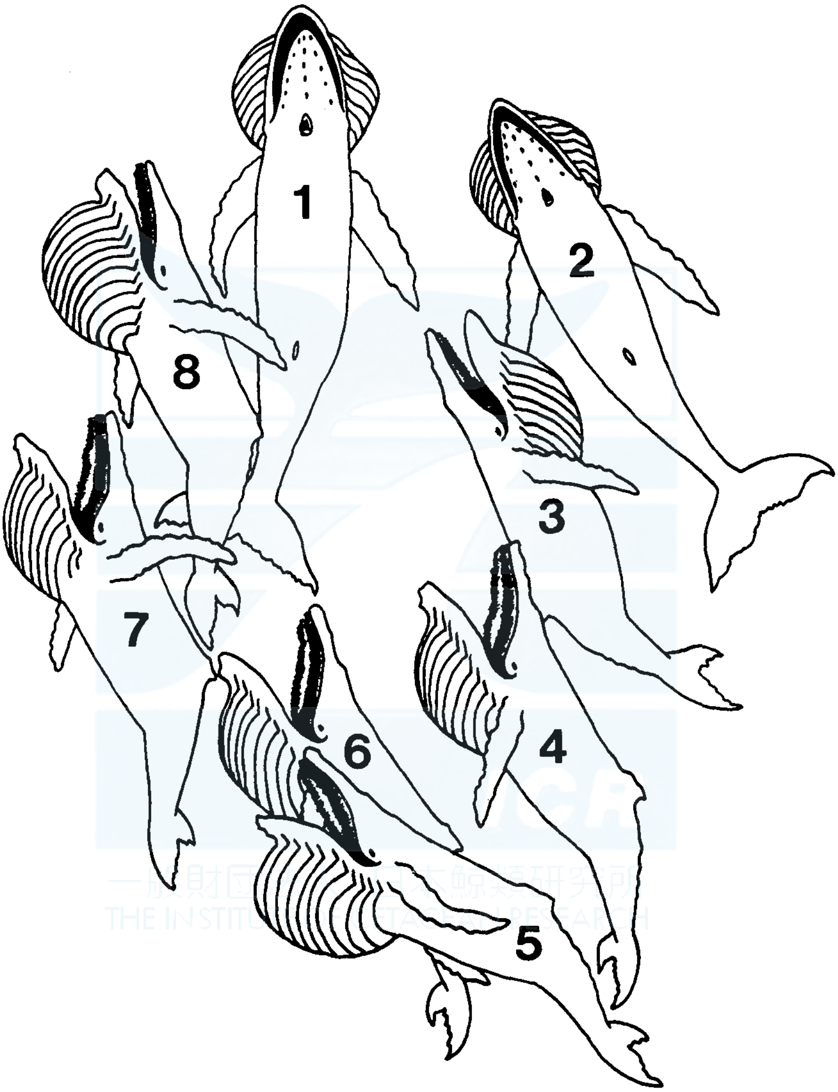

Fig. 1. The physical orientation of the group of eight humpback whales (*Megaptera novaeangliae*) feeding on herring. Whales #1 and #2 maintained a vertical position throughout the lunge-feed, with Whale #1 rising higher than #2. Whale #1 was the largest of the group. (Illustration by Robert J. Western.)

Fig. 2. The group of eight humpback whales lunge-feeding, 9 August, 1983.

Fig. 3. The group of eight humpback whales lunge-feeding, 11 August, 1983.

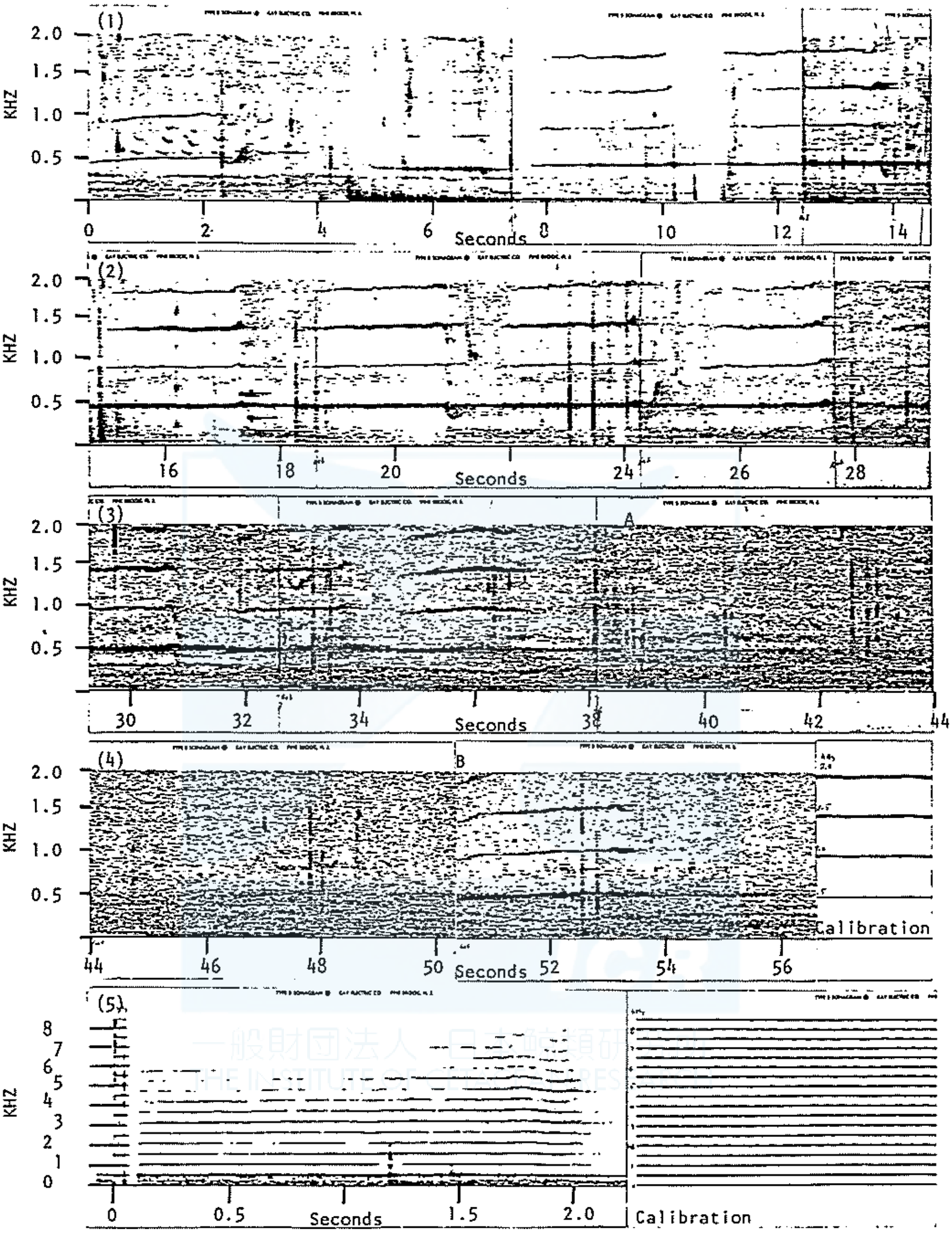

Fig. 4. Spectrographic representation of humpback whale vocalizations. Graphic representation of the vocalizations was obtained by playing the sounds through a Kay sonograph spectrum analyzer (model 7029A). Graphs 1 through 4 represent total sequence recorded prior to each vertical lunge-feeding maneuver, filter bandwidth 11.2 Hz. Graph 5 represents a portion of the final vocalization which begins at B on graph 4 (B) showing harmonics up to 8 kHz, filter bandwidth 45 Hz. Extraneous vocalizations most clearly represented are Steller's sea lions (A) (*Eumetopias jubatus*).

Apparent cooperative feeding behaviors associated with vocalizations have been reported for killer whales (*Orcinus orca*) preying on schooling fish (Steiner *et al.*, 1979). Jurasz and Jurasz (1979) observed apparent cooperative feeding in humpback whales in which breathing and surfacing were coordinated. They also recorded a uniform vocalization during feeding behaviors involving more than one whale, but only when the prey species was herring. This vocalization began with a "buzzing pattern" which was not present in our recordings. Annual changes in humpback whale vocalizations on the breeding grounds have been demonstrated (Winn and Winn, 1978; Winn *et al.*, 1981), and vocalizations on the feeding grounds may also vary from year to year. Our observations of the humpback whale feeding behavior closely corroborate those of others (Jurasz and Jurasz, 1979; Watkins and Schevill, 1979; Hain et al., 1982), but we document for the first time the spatial orientation of individual whales and demonstrate the cooperative nature of the feeding behavior.

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ANATOMICAL OBSERVATIONS ON THE LOWER BRAIN STEM OF THE RIGHT WHALE

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ABSTRACT

The lower brain stem of the right whale (*Eubalaena glacialis* Bonnaterre) was observed anatomically. Macroscopical findings were noted briefly, followed by the microscopical investigations and comments.

Nerve roots and their central nuclei of the cranial nerves were observed seemingly nothing particular in their positions and sizes, except sensory trigeminal nuclei. The most conspicuous finding was the extreme largeness of the sensory trigeminal structures in this whale, in this connection the sensory apparatuses on the head portion were discussed.

The inferior olivary nuclei, the nuclei of the posterior funiculi and the medical lemniscus were found in usual positions and sizes.

Pyramidal tract was specific in that making a wedge shaped unpaired tract at the lower medulla, and then changed in spindle shape in the depth of the anterior median fissure at the lowest medulla.

INTRODUCTION, MATERIAL AND METHODS

As far as we are able to know, very few studies have been done covering anatomical field of the central nervous system of the right whale, much more so regarding the microscopical observations. This fact must be related, at least in part, to the severe prohibition of whaling on to this whale.

In 1956, two right whales were captured in the coastal waters to Japan, with the special permission of the Japanese Government for the scientific investigations. These two whales were examined their external as well as internal characters by the staff of the Whales Research Institute, Tokyo, and the results were reported by Nishiwaki (1957) and Omura (1958). In one of these whales, Ayukawa specimen, which was young female and 38 feet 4 inches in body length, the brain and the spinal cord were removed two days after the capture by the staff of the Medical School, University of Tokyo, and fixed in formalin. Results of the anatomical observations on the spinal cord were reported previously by the present author (1958). Unfortunately, because chiefly of the prolonged post-mortem time, the deep parts of the cerebral hemispheres and cerebellum seemed not very well fixed by the for-

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malin, accordingly only the brain stem lower than the midbrain was separated from other parts of the brain and proceeded to make the microscopical preparates at the Brain Research Institute, University of Tokyo. The material was cut in to three blocks (anterior, middle and posterior)* and refixed in the Müller's solution at 37°C for three weeks and mounted in celloidin through the usual manner. Serial sections of 45 μm (anterior block) and 40 μm (middle and posterior blocks) in thickness, along the transverse plane, were made. Each fifth sections (with the last order of each figure being 0 and 5 or 1 and 6 etc.) were treated by the Weigert-Pal carmine or Kultschitzky's method for myelin staining. In this study, much efforts were made to obtain more precise findings on the internal structure of the brain stem, and many of remaining sections, which had been stored in the brain Research Institute, University of Tokyo, were stained by the Klüver-Barrera's method or the P-T method according to needs.

RESULTS AND COMMENTS

FEATURES OF THE BRAIN AS A WHOLE

Size of the brain (Figs 1 and 2) measured was ca. 200 mm in antero-posterior direction, ca. 196 mm in width and ca. 125 mm in height and the brain weight was 2640 g. The brain as a whole and the cerebral hemisphere appeared fore-shortened and widened transversely, though the height was not so prominent compared with the length. Pilleri (1964) reported the brain weighed 2750 g in a case of southern right whale of 43 feet in body length. He also measured as 205 mm in total length, 180 mm in width and 140 mm in height of the brain. According to Omura *et al.* (1969), brain weight ranges from 2.4 to 3.1 kg or from 0.0038 to 0.0050 of the body weight after investigation in 4 cases of black right whale caught in the Bering Sea during 1962 to 1963 season. Referring previous observations, the low brain weight seems conspicuous in this whale among the various species of big whales (Kojima, 1951; Breathnach, 1960; Morgane *et al.*, 1972 usw.).

The cerebral hemisphere was large and moderately convoluted, with the convolutions on the lateral surface arranged in upside-down U form along an almost vertical lateral sulcus of Sylvius. The large temporal lobe was prominent on the ventral aspect of the brain and contrasted to the occipital lobe which was not delimited distinctly. The olfactory bulb and tract were observed entirely absent in each side, but the lobule désert of Broca was recognized clearly as a transverse rising at the posterior aspect of the orbital gyri. In the Pilleri's report (1964), on the other hand, the olfactory trigone and stump of the trimmed olfactory tract are clearly visible on both sides in his Abb. 4 and 5. In general, the olfactory bulb and tract are extremely regressed in the ceta-

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* *A, M and P, preceding the serial section number of Figures, mean these blocks respectively. Serial section numbers were put on from caudal end to rostral one in each blocks. (Refer to Explanation of Figures).*

Fig.1

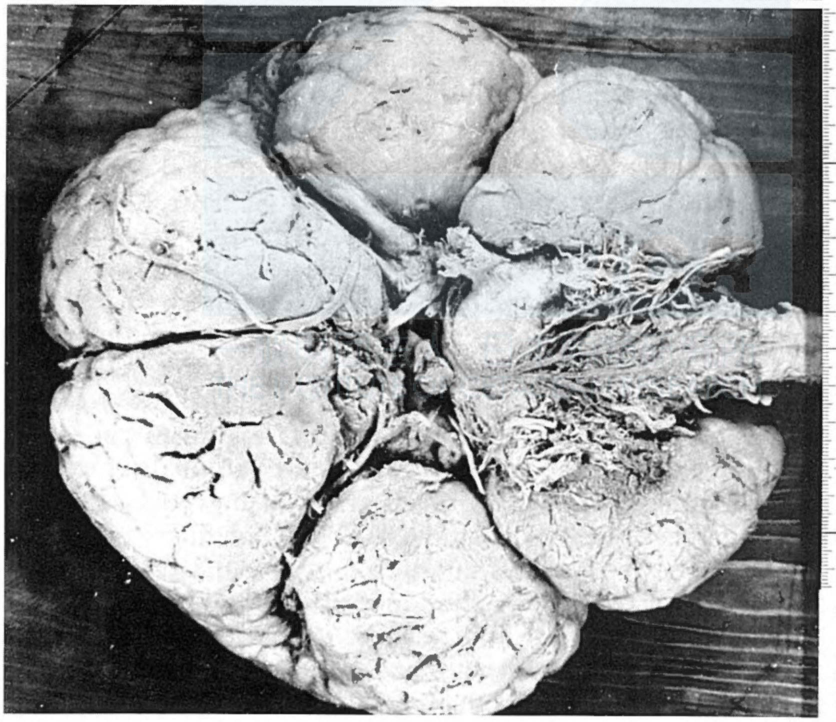

Fig.2

Figs 1 and 2. The dorsal (Fig. 1) and ventral (Fig. 2) views of the brain. Refer to text for details (Features of the brain as a whole).

cean brain, and especially in some Odontoceti, entirely absent of them had been reported (Langworthy, 1932; Ries and Langworthy, 1937; Kojima, 1951 etc.). In some Mysticeti, presence of the olfactory bulb or tract was reported including fetal specimen (Guldberg, 1885; Riese, 1928, 1936; Langworthy, 1935; Friant, 1957, etc.).

The cerebral peduncle and the large pons were short and wide. The inferior colliculus was protruded strikingly to the dorsal direction and exceeded than the superior colliculus in size. The flat and not so distinct eminence on the ventral surface of the medulla oblongata was made by the medullary pyramid and inside the eminence, on the cross sections, large olivary nucleus i.e. the medial nucleus of the inferior olive could be seen. Extremely large fifth nerve root on both sides proceeded towards the frontal direction from the lateral border of the pontine eminence. The eighth nerve was fairly big, though destroyed a little. According to the descriptions of previous investigators, generally the fifth nerve is the largest of all the cranial nerves in the whalebone whales, while the eighth nerve is the largest one in the toothed whales (Langworthy, 1932; Wilson, 1933; Breathnach, 1960 etc.).

The cerebellum was very large and consisted of narrow vermis and large hemispheres. Pilleri (1964) measured the weight of the cerebellum of the southern right whale and it was 600 g and corresponded to 22% of the total brain weight.

THE THIRD, FOURTH AND SIXTH CRANIAL NERVES

The motor nerve roots of the oculomotor, trochlear and abducens nerves are observed in ordinary position and size in appearance. The caudal end of the oculomotor nucleus is recognized as a single cell mass being surrounded its ventral side by the medial longitudinal fascicle (Figs 18 and 19) and some of the root fibers seemingly originating from these cells are visible at just ventral to the nucleus (Fig. 18). Unfortunately the major part of the oculomotor nucleus escaped from the material in both sides. Wilson (1933) noted that the nucleus of the third cranial nerve in the *Balaenoptera sulfurea* (*B. musculus*) consisted of two clusters of cells; the lateral nucleus lying in the medial longitudinal fascicle and the medial nucleus occupying the space between the raphe and the fascicle. Langworthy (1932) described the third nerve nucleus in the *Tursiops truncatus* as compact and composed of single cell mass.

The trochlear nucleus is found at a little caudal level, some distance apart from the oculomotor nucleus, as a single cell group being enclosed in the medial longitudinal fascicle (Figs 17 L and 20). The root fibers originating from the nucleus are traceable towards the dorsolateral and caudal direction, along the periphery of the central gray substance of the midbrain, and reaching to the crossing of the nerve root at the caudalmost level of the midbrain.

The abducens nerve roots are observed at the uppermost medullary level and passing through the lateral part of the medial lemniscus which is locating at the medial aspect to the superior olive (Figs 12L and 22). The abducens nucleus is recognized as fairly dispersed cell collection locating at the ventral aspect to the internal genu and just below the emerging bundle of the facial nerve root (Fig. 22). Wilson (1933) distinguished no definite abducens nucleus in the *Balaenoptera*; the only suggestion of it was a few scattered large motor type polygonal cells lying just ventral to the descending facial nerve root.

THE XIITH CRANIAL NERVE

Reduced development of the hypoglossal nucleus in the cetacea has generally been accepted, and this fact is commonly explained in relation with the lesser development of muscularization and motility of the tongue, especially so in the Mysticeti (Langworthy, 1932; Breathnach, 1960 etc.).

In the medulla oblongata of the right whale, on the other hand, there observed no suggestion of such regression of the hypoglossal nerve root and its origin nucleus; moderately large collection of big polygonal cells and many fiber bundles of the nerve root are recognized at usual position (Figs 5 - 8 and 27). Four cell groups can be divided in the main hypoglossal nucleus; dorsomedial, ventromedial, ventrolateral and dorsolateral, though each cell groups are observed continuing each other in some levels (Figs 7 and 27). The dorsomedial group is seen in strong development at the levels approximately lower two thirds of the entire length of the main nucleus and reduces its size gradually at the upper levels. The ventromedial group shows clear tendency to fuse with the dorsomedial one at the lower levels, and to separates from that and then fuses with the ventrolateral group at the upper levels. The dorsolateral group is observed in good development at the levels upper two thirds of the main nucleus.

Roller's nucleus consisting of smaller cells is distinguished on each side at the ventral aspect to the ventromedial cell group of the main nucleus (Fig. 27), except the uppermost and lowermost levels of it. The intercalatus nucleus consisting of very small cells is found at the lateral aspect of the dorsolateral group at the levels upper half of the main nucleus (Figs 8 and 9), increasing its size as the dorsolateral cell group diminishes towards the upper levels, and finally the nucleus changes with no abrupt transition into a prepositus nucleus at the uppermost medullar level. The interfascicular and the eminentiae teretis nuclei are unable to identify in the right whale.

THE VTH NERVE

The trigeminal nerve root is observed extremely large, the minor portion of it being located rostro-medial to the major portion. The nuclei of the trigeminal nerve are very well developed, except the mesencephalic nucleus which is seen as just ordinary size and position (Figs 16 L, 17 and 20).

The poor development of the posterior horn of the spinal cord in the cetacea had previously been described by many authors (Guldberg, 1885; Hatschek, 1896; Sano, 1909 usw.) and the situation is also the same in the right whale (Seki, 1958). At the first cervical level, however, the posterior horn is fairly big, as nearly the same size as the anterior horn at the same level. More rostrally, spinal tract and its nucleus of the trigeminal nerve are found of quite large size in the medulla oblongata (Figs 3 - 11). The rate of the dimension of the spinal trigeminal complex exists almost 30% of the cross sectional area at the lower medulla. Incidentally, the rate shows approximately 20% in the Sei whale (*Balaenoptera borealis*) and about 8% in the human at the same level. In the levels upper than the rostral medulla, the spinal trigeminal complex diminishes its size slightly but the rate of the dimension to the cross sectional area shows approximately 15% at the uppermost level of the medulla. Considering increase of the dimension of the surrounding structures in this level, this percent of the rate is thought to be still fairly big, while the rate is about 8% in the Sei whale and 4.5% in the human at the corresponding level. At levels upper than the middle of the inferior olive, the spinal trigeminal complex decreases gradually its nuclear mass and contrally increases fiber amount of the tract (Figs 9 - 12). At the level of the caudal limit of the superior olive, the principal nucleus and fiber mass surrounding it appear at the dorsal aspect of the spinal trigeminal complex. The principal trigeminal area expands its dimension rapidly towards the upper levels and makes its maximum extent at the level of the motor trigeminal nucleus, showing almost as nearly the same size as the motor trigeminal nucleus at the same level (Figs 12 - 14). Transition of the spinal trigeminal complex to the principal trigeminal nucleus seems not clear and the spinal tract can be traced upwards to the level of the motor trigeminal nucleus. Upper part of the principal trigeminal nucleus lies at the ventromedial aspect to the superior cerebellar peduncle and decreases suddenly its size at the uppermost pontine level.

Olszewski (1950) divided the spinal trigeminal nucleus into three portions in man and monkey in oral, interpolar and caudal. According to his criteria, these three portions are hardly divisible in the spinal trigeminal complex in the right whale because of lesser development of the gelatious substance in the caudal levels and difficulty of looking for large cells similar to those of the external cuneate nucleus in the middle levels of it. Marginal and intrafascicular cell groups of the spinal trigeminal tract, corresponding to the gray substances described by Fuse (1940) in *Delphinus delphis* and *Balaenoptera borealis,* are fairly well developed also at the upper medulla in the right whale.

Rather small sensory trigeminal nuclei had been reported by Langworthy (1932) in *Tursiops truncatus* and Jelgersma (1934) in *Phocaena communis.* Checking illustrations of studies of Hatschek and Schlesinger (1902) in *Delphinus delphis* and Hosokawa *et al.* (1969) in *Stenella coeruleoalba,* rather small sensory trigeminal nuclei could be assumed as in nearly the same extent as those of the figures of former two author's works. Referring these and other more works (Rawitz, 1909, *Phocaena communis;* Mc Farland *et al.*, 1969 and Morgane *et al.*, 1972, *Tursiops truncatus* usw.), it is highly probable that in these small Odontoceti have relatively less developed sensory trigeminal structures than those of the right whale.

Breathnach (1960) pointed out the importance of the tactile sensibility in the snout and oral regions in the cetacea in view of the poor development or absence of the olfactory sense, the alleged poverty of vision and lack of a sense of taste. Nakai and Shida (1948) described scanty but regularly arranged sinus hairs on the upper and lower lips of the Sei whale (*Balaenoptera borealis*). They thought that the hairs encounter pressure and resistance and emphasized the importance of these hairs not merely as a tactile organ in searching for tiny foods but more probably as the organ to feel the stream of water upon the head. While Ogawa and Shida (1950) noted widespread occurrence of sensory tubercles richly supplied with nerve fibers on the lips and oral cavity of Sei whale (*Balaenoptera borealis*) and Fin whale (*Balaenoptera physalus*) and concluded that they certainly represent highly sensitive tactile organs. These two authors confirmed also the existence of structures, which seem to be sensitive apparatuses having rich nerve endings in the lips, tongue, palate and basis of the mouth cavity of the right whale (Seki, 1958).

On the other hand, in Odontoceti, sinus hairs, though appears in the fetal period, are absent in the adult, and none of the description has been known on the sensory tubercles in the areas of trigeminal innervation. Attention must be paid on the fact that in these Odontoceti having rather small sensory trigeminal nuclei, perhaps without exception, conspicuously large hearing structures can be seen in their nervous system.

Reffering these previous findings and present investigation, there exist probably the whale species which are highly dependent upon the trigeminal sensitivity in their everyday life, like a typical case in the right whale, while other species are much more dependent on the hearing ability than the trigeminal sense, like such instances in *Tursiops* and *Stenella* etc. Further investigations must be needed for solution of problems on the sensory apparatuses of the head portion, including the bonnet and callosities of the right whale, and correlations to the sensory trigeminal structures in the brain of the cetacea.

The motor trigeminal nucleus is quite large mass situating at the lateral part of the pontine reticular formation and consists of big polygonal cells. It seems three cell groups could be indentified in the motor trigeminal nucleus; caudal, ventromedial and lateral. All of these cell groups can be observed at the level of the upper part of the facial nucleus. The caudal cell group is seen just above the facial nucleus (Fig. 12 R), while the dorsal subnucleus of the facial nucleus is separated caudally by a little distance from it. The caudal cell group diminishes its size at the level of the rostral end of the facial nucleus. The lateral cell group develops gradually towards the levels upper than the facial nucleus, and makes quite large cell mass at the upper pontine level. The ventromedial cell group is seen at the ventromedial aspect to the lateral cell group and diminishes its size at the upper pontine level.

THE VIITH NERVE

Facial nerve root and internal genu make a moderately thick bundle. The main facial nucleus is large enough and situating at the bottom of the reticular formation at the transitional level of the medulla and the pons. Differentiation of cells into groups is remarkable only in the dorsal subnucleus which is located at the dorsal aspect to the main facial nucleus with some distance from it and just medial to the outgoing facial nerve root (Fig. 22). The nerve cell collection of the main facial nucleus seems not so differentiated, in particular its ventral part is found as a large simple cell mass, while the dorsal part looks divided in some but indefinite groups.

On the other hand, Hatschek and Schlesinger 1902, in *Delphinus delphis;* Wilson, 1933, in *Balaenoptera sulfurea;* Jelgersma, 1934, in *Phocaena communis,* De Graaf, 1967, in *Balaenoptera physalus, Balaenoptera acutorostrata, Hyperoodon ampullatus* and *Orcinus orca,* described well marked cell groups in the facial nucleus.

Though the opinion, that there is a lack of sense of taste and questionable existence of the salivary glands in the cetacea, has been commonly accepted, Yamada (1953) described and illustrated the chorda tympani nerve in *Globicephalus* and *Balaenoptera,* and recently Yamasaki *et al.* (1978) reported taste buds in the tongue of the *Stenella coeruleoalba.* In this connection, none of noteworthy finding could be obtained in this investigation.

THE IXTH, XTH AND XITH NERVES

The glossopharyngeal nerve is observed rather small and its root fibers pass through inbetween the inferior cerebellar peduncle and the spinal trigeminal tract at the uppermost medulla and seems to connect chiefly with the rostral part of the solitary tract, which is small in this level (Figs 9 R and 10 L). At the medial aspect to the spinal trigeminal complex of the medulla oblongata, except the lower levels of it, a series of nerve rootlet, seemingly concerned as the vagus nerve, is seen. The accessory nerve root is observed fairly well developed in the lower medulla though its spinal root is found only in the first cervical level.

The dorsal motor nucleus is seen from the emerging level of the glossopharyngeal nerve to the lower medulla in good development and consists of large group of medium sized polygonal cells (Fig. 27). The solitary tract is moderately big in the upper half of the medullary level (Figs 7 and 8) and reduce its size slowly to the lower levels. The nucleus ambiguus is seen clearly but not so big throughout the medulla, in particular it is less developed in levels lower than the obex (Figs 5 - 10). Hosokawa (1950) noticed the conspicuously big nucleus ambiguus in Sei whale (*Balaenoptera borealis*) in connection with the muscular laryngeal sac of this whale. Small size of the spinal root of the accessory nerve was noted by some authors (Hepburn and Waterston, 1904, in *phocaena;* Ries and Langworthy, 1937, in *physeter;* Jansen, 1953, in *Balaenoptera physalus,* Breathnach, 1955, in *Megaptera novaeangliae;* Seki, 1958, in *Eubalaena glacialis* etc.) against Hatschek's description (1896, in *Delphinus delphis*) that was observable as "Respirationsbündel" of Krause until the level of the cervical enlargement.

THE VIIITH NERVE

The acoustic system in the cetacean brain had been mentioned by many previous investigators (Spitzka, 1886; Hatschek and Schlesinger, 1902; Hofmann, 1908; Valeton, 1908; Langworthy, 1932; Ogawa and Arifuku, 1948 usw.) in view of its exstremely high stage of development than that of the other common mammals.

Cochlear nucleus in the right whale, a little protruded to the ventral surface of the brain stem at the transitional level of the pons and the medulla, seems big but not so surprising size and situates outside the inferior cerebellar peduncle (Figs 10 and 11). Dorsal nucleus or the so called tuberculum acusticum is not clearly identified as mentioned by Ogawa and Arifuku (1948). Stria acustica of Monakow starts from dorsal part of the cochlear nucleus and passing through the dorsal periphery of the Deiters's nucleus towards the medical side up to the dorsolateral part of the reticular formation (Figs 9 - 11), though farther course is not traceable. In the right whale, the Held's tract is seen clearly as somewhat dispersed thin bundles, starting from the dorsomedial part of the cochlear nucleus and proceeds to dorsal and then to medial along the dorsal periphery of the inferior cerebellar peduncle, and farther penetrates the dorsal part of the spinal trigeminal complex and the facial nucleus (Fig. 11 L), afterwards it can not be followed up. The trapezoid body is quite well developed at the ventral part of the brain stem from the uppermost medulla to the lower pontine level. The superior olivary nucleus seems not so big, composed of two parts; medial and lateral, the lateral part being smaller in size than that of the medial part, and located dorsal to the trapezoid body and medial to the facial nucleus (Fig. 12). In the territory inbetween the medial lemniscus and the medial part of the superior olivary nucleus, disseminated cell mass can be seen, which is considered as the nucleus of the trapezoid body. Preolivary nucleus of Cajal is difficult to identify. A great deal of fibers accumulated chiefly at the ventral side of the superior olivary nuclei represents the lateral lemniscus, as it goes upper levels, reaching finally to the ventral side of the inferior colliculus (Figs 13 - 17). The lateral lemniscus contains a disinct nuclear mass in it, the nucleus of the lateral lemnisus (Figs 14 - 16). The inferior colliculus is very large and protruded to the dorsal direction, and receives the lateral lemniscus in its ventral side. Brachium of the inferior colliculus is scarsely seen at the lateral border of the inferior colliculus as it is destroyed superficially (Figs 16 L and 17 L).

The vestibular nuclei are found rather small, except the Deiters's nucleus, which occupies fairly large territory of the dorsolateral part of the uppermost medullary level (Figs 11 and 23). Hatschek and Schlesinger, 1902, in *Delphinus delphis,* and Wilson, 1933, in *Balaenoptera sulfurea,* obtained the similar results as mentioned above.

THE INFERIOR OLIVE

The cetacean inferior olive had been studied and described by many authors (Hatschek and Schlesinger, 1902; Rawitz, 1909; Kankeleit, 1913; Kooy, 1917; Brunner, 1919; Kooy, 1920; Langworthy, 1932; Wilson, 1933; Jelgersma, 1934 usw.), and characteristics of the cetacean inferior olivary nucleus are the extraordinarily big size of the rostral part of the medial accessory nucleus and lesser development of the dorsal accessory and principal nuclei.

In the right whale, the oral part of the medial accessory olivary nucleus is developed in a quite large size and triangle in shape, locating closely to the midline of the upper half level of the medulla, while the dorsal accessory olivary and the principal olivary nuclei are observed in far less developed and not clearly delimited from the surrounding structures (Figs 7 - 10 and 25). Beside this, though there existed some different opinions among previous investigators as to the homology on the caudal part of the medial accessory nucleus, which is found in moderately size upwards from the level of the obex to the middle medullary levels in the right whale (Figs 6, 7 and 26).

POSTERIOR FUNICULUS AND MEDIAL LEMNISCUS

In the right whale, the posterior funiculus is not so large, missing the posterior median septum to make a small Bischoff's nucleus on the midline at the lowest medulla (Fig. 4). Wilson (1933) mentioned poor development of the gracile and cuneate nuclei in *Balaenoptera sulfurea* and presumed the median triangular nucleus to be identical with the Bischoff's nucleus. At the levels below the obex, fused Goll's nuclei of the both sides can be seen because of the disappearance of the posterior median septum and fibers running beside it (Fig. 5). In levels upper than the obex, border of the Goll's and Burdach's nuclei becomes not clear, and Monakow's external cuneate nucleus appears in the lateral part of the posterior funiculus (Fig. 27).

The medial lemniscus is found in levels upper than the obex, surrounding the inferior olivary nuclei in lower levels and locating dorsal to the pyramidal tract in upper medullary and pontine levels. In the midbrain, the medial lemniscus of both sides lies beneath the superior cerebellar peduncle and moves gradually to the lateral direction (Fig. 17).

CRUS CEREBRI AND PYRAMIDAL TRACT

In the brain stem of the cetacea, pyramidal tract and associated fiber tracts had been mentioned by many authors. Hatschek and Schlesinger (1902) pointed out the small size of the pyramid at medullary levels in *Delphinus delphis.* Langworthy (1932) distinguished a temporopontine tract in the lateral part of the cerebral peduncle and identified the medial part of it as the corticospinal and frontopontine fibers in *Tursiops truncatus,* while Kojima (1951) in *physeter catodon,* noted two different parts in the cerebral peduncle according to the fiber direction.

In the right whale, the cerebral peduncle is made of considerable amount of fibers though upper part of it being out from the matrial. The big amount of these fibers diminishes very much during its course passing through the pontine nucleus, and reaches to the bulbar pyramid which is the flat assembly of bundles of thin fibers locating ventral to the inferior olivary nucleus (Figs 8 - 12). At the pontine level, the pontine longitudinal fasciculi including the corticospinal fibers, are observed lying near the tegmentum and showing transversely flat oval in shape, and closely approaching each other on both sides of the raphe (Figs 14 and 15).

As previously described by Seki (1958), in the lower medulla, pyramid on both sides comes to fuse together and changes gradually into a wedge shaped unpaired bundle between the anterior funiculi on both sides (Figs 4 - 6). More caudalward, the pyramid, decreasing its amount of fibers, changes into a spindle shaped tract and shifts its location slowly to the depth of the anterior median fissure (Fig. 3). The pyramidal tract fibers are not traceable below the second cervical level. Pyramidal decussation can not be confirmed as the most fibers of the tract are traced in longitudinal course and it is quite hard to ascertain the crossing is really exitsts or not. Rawitz (1909) and Gans (1916) in *phocaena,* Matsumoto (1953) in *Kogia breviceps* and *Berardius bairdii,* described the pyramidal decussation, but some authors could not confirm it (Hatschek and Schlesinger, 1902, in *Delphinus delphis;* Wilson, 1933, in *Balaenoptera sulfurea;* Jelgersma, 1934, in *phocaena communis* usw.).

SUMMARY

Anatomical observations on the lower brain stem of the right whale summarised as follows, accompanied brief note on the superficial findings of the brain as a whole.

Relatively low weight of the brain is thought to be conspicuous among that of the other big whales. Complete lack of the olfactory bulb and tract were noted. The trigeminal nerve root was observed as the largest in all of the cranial nerves.

Nerve roots and their central structures of the cranial nerves were noted and discussed briefly. Nerves and nuclei of the extraocular muscles were

found as nothing particular. None of regressive finding was obtained on the hypoglossal nerve and its nucleus. The extreme largeness of the sensory trigeminal nuclei was noticed and discussed in relation to the sensory apparatuses on the head portion of the Mysticeti. The motor trigeminal nucleus was observed as quite large size and differentiated into three cell groups. The facial nerve was moderately thick and its nucleus were large enough but differentiation into cell groups was remarkable only in the dorsal subnucleus. The glossopharyngeal, vagal and accessory nerves and related nuclei were observed in usual position and size. Acoustic nerve and related nuclei were found in considerable development though they were exceeded by the sensory trigeminal structures in size. Monkow's stria acustica and Held's tract were seen clearly. Among the vestibular nuclei, the Deiters's nucleus only was strongly developed.

Oral part of the medial accessory nucleus of the inferior olivary nuclei was conspicuously developed as commonly seen in other cetacea. Bischoff's nucleus was found on the midline at the lowest medulla. Goll's and Burdach's nuclei were seen in lesser development. Fused Goll's nucleus of both sides was observed at the level below the obex.

Pyramidal tract was specific in that making wedge shaped unpaired bundle between the anterior funiculi on both sides at the lower medulla. This tract proceeded farther caudalwards into the spindle shape and moved into the depth of the anterior median fissure, decreasing its fiber amount to disappearance at the second cervical level.

ACKNOWLEDGEMENT

The author is very sad that Dr Teizo Ogawa, formerly professor of Department of Anatomy and director of the Brain Research Institute, University of Tokyo, deceased at April 29, 1984. Sincerely gratitude is due to him for his constant direction and kind advices throughout this study. The author is very sorry that the completion of this work has become so much delayed that missed his revision, and no more. The author would like forgiveness for offering this poor study to the memory of the late professor, Dr T. Ogawa.

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EXPLANATION OF FIGURES

Figs 3–18. A little enlarged (× 4.5) photographs of selected sections stained by the Weigert-Pal carmine (Figs 3–12) or the Kultschitzky's method (Figs 13–18).

Serial section number of each section is as follows:

Fig. 3 : P–85
Fig. 4 : P–170
Fig. 5 : P–245
Fig. 6 : P–305
Fig. 7 : P–375
Fig. 8 : M–120
Fig. 9 : M–230
Fig. 10 : M–300
Fig. 11 : M–390
Fig. 12 : M–480
Fig. 13 : A–112
Fig. 14 : A–182
Fig. 15 : A–282
Fig. 16 : A–402
Fig. 17 : A–462
Fig. 18 : A–562

Figs 19–27. Photographs showing internal structures of selected sections (showing left side in each, except the Fig. 27) stained by the P-T method, a little magnified (× 10 or × 15). Serial section number, level and magnification of each section are indicated as follows:

Fig. 19 : A–544, level of the oculomotor nucleus, × 10.
Fig. 20 : A–464, level of the trochlear nucleus, × 10.
Fig. 21 : A–74, upper pontine level, × 10.
Fig. 22 : M–464, level of the facial nerve root, × 15.
Fig. 23 : M–344, level of the Deiters's nucleus, × 15.
Fig. 24 : Same section, same side as Fig. 23, spinal trigeminal complex and facial nucleus, × 15.
Fig. 25 : M–174, ventral part of the middle medullary level, × 10.
Fig. 26 : P–414, ventral part of the lower medullary level, × 15.
Fig. 27 : P–384, dorsal part of the lower medullary level, right side, × 10.

LIST OF ABBREVIATIONS IN FIGURES

Aqd	Aqueduct of the midbrain
CA	Anterior horn
CI	Inferior colliculus
CrC	Crus cerebri
FA	Anterior funiculus
FL	Lateral funiculus
FLM	Medial longitudinal fascicle
FLo	Pontine longitudinal fasciculi
FP	Posterior funiculus
FR	Reticular formation
FS	Solitary tract
IOLm	Medial nucleus of the inferior olive
LL	Lateral lemniscus
LM	Medial lemniscus
Nam	Nucleus ambiguus
NB	Nucleus of Bischoff
NCE	Nucleus cuneatus externus
NCo	Nucleus of the cochlear nerve
ND	Nucleus of Deiters
NDX	Dorsal motor nucleus of the vagus nerve
NFP	Nuclei of the posterior funiculi
NI	Nucleus intercalatus
NLL	Nucleus of the lateral lemniscus
NMeV	Mesencephalic nucleus of the trigeminal nerve
NMoV	Motor nucleus of the trigeminal nerve
NPo	Nuclei pontis
NPV	Principal nucleus of the trigeminal nerve
NRL	Lateral reticular nucleus
NRm	Nucleus ruber magnocellularis
NSpV	Spinal nucleus of the trigeminal nerve
NTr	Nucleus of the trapezoid body
NVeI	Nucleus inferior of the vestibular nerve
NVeM	Nucleus medialis of the vestibular nerve
NIII	Oculomotor nucleus
NIV	Trochlear nucleus
NVI	Abducens nucleus
NVII	Facial nucleus
NVIId	Dorsal subnucleus of the facial nucleus
NXII	Hypoglossal nucleus
PCI	Inferior cerebellar peduncle
PCM	Middle cerebellar peduncle
PCS	Superior cerebellar peduncle
Py	Bulbar pyramid
Ra	Raphe
RIII	Oculomotor nerve
RIV	Trochlear nerve
RV	Trigeminal nerve
RVI	Abducens nerve
RVII	Facial nerve
RIX	Glossopharyngeal nerve
RX	Vagus nerve
RXIc	Cranial root of the accessory nerve
RXII	Hypoglossal nerve
SHe	Tract of Held
SMo	Stria of Monakow
SN	Substantia nigra
SOLl	Lateral nucleus of the superior olive
SOLm	Medial nucleus of the superior olive
TMeV	Mesencephalic root of the trigeminal nerve
TSpV	Spinal root of the trigeminal nerve
VQ	Fourth ventricle

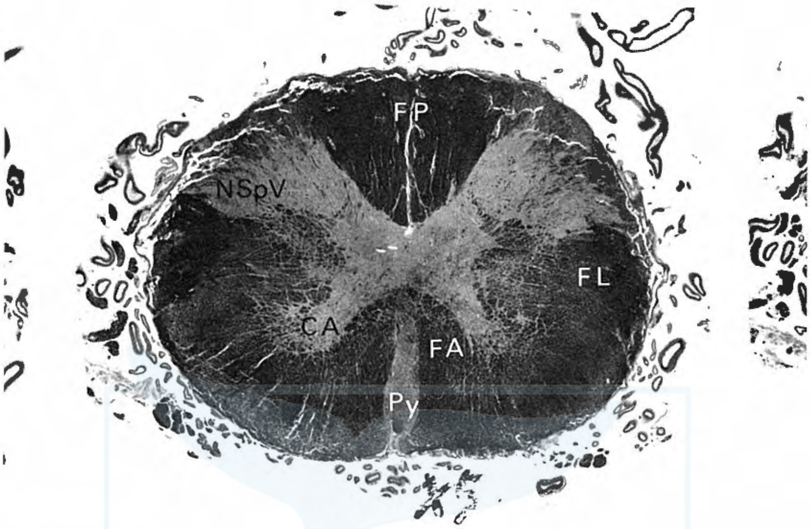


Fig. 3

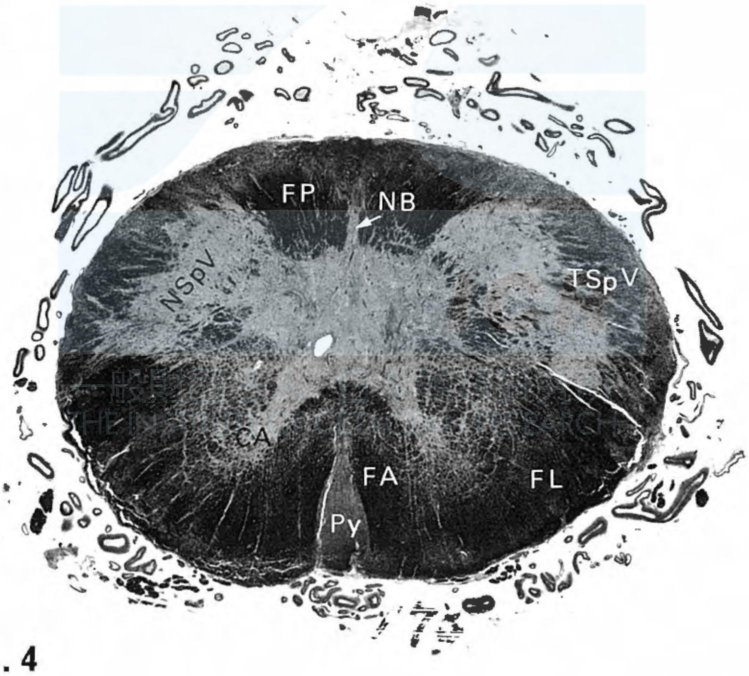


Fig. 4

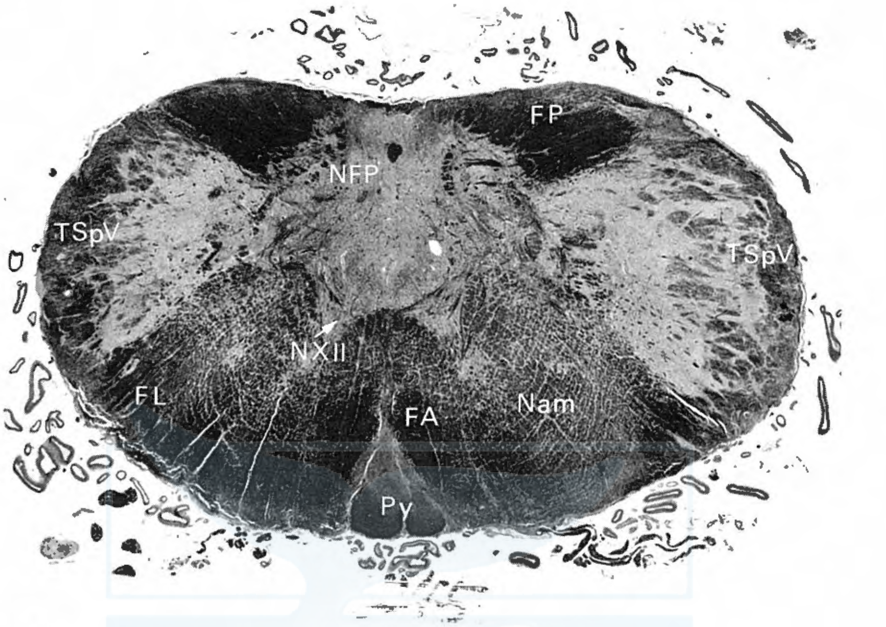

FP
NFP
TSpV
TSpV
NXII
FL
Nam
FA
Py

Fig. 5

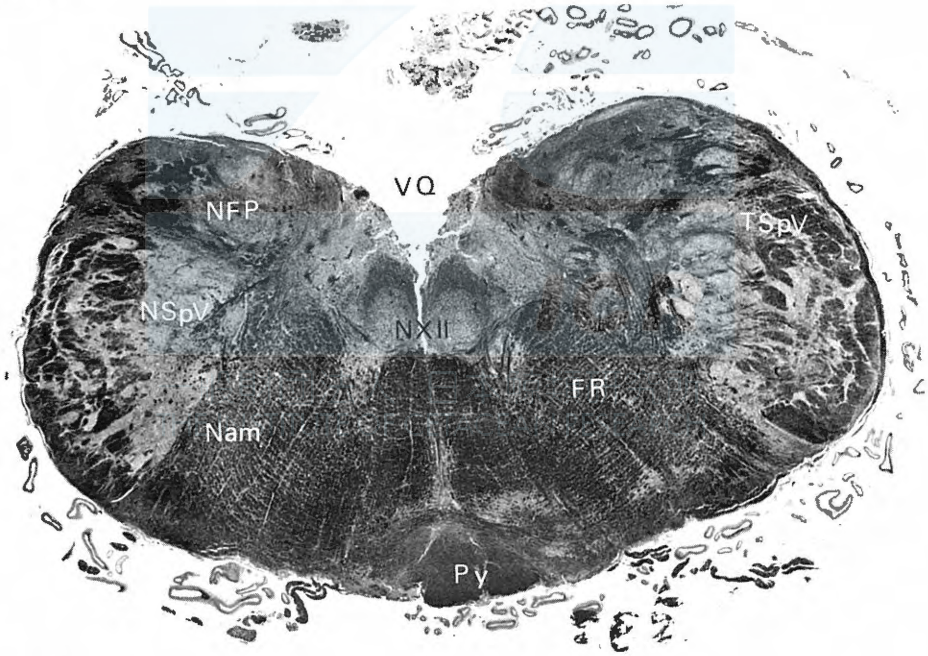

VQ
NFP
TSpV
NSpV
NXII
FR
Nam
Py

Fig. 6

Fig. 7

Fig. 8

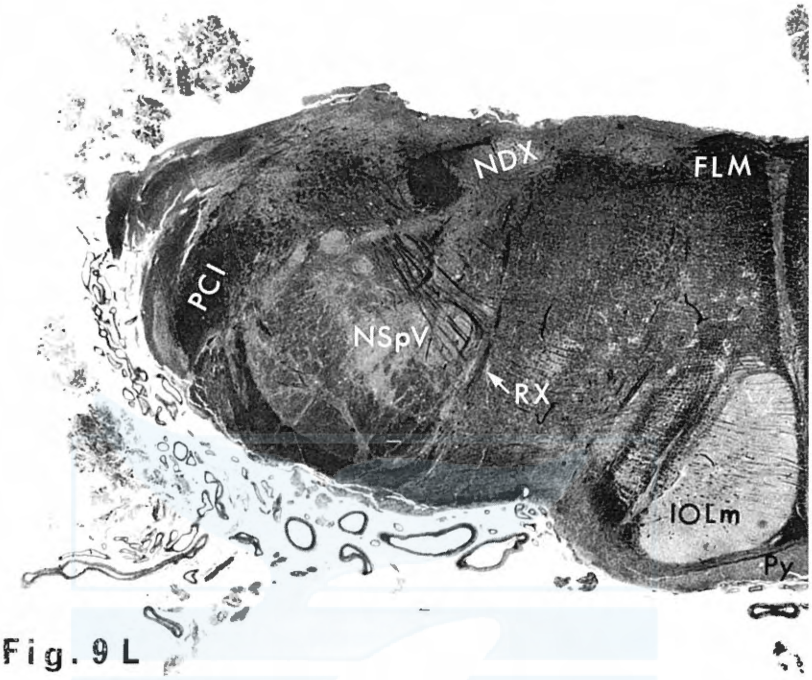


Fig. 9 L

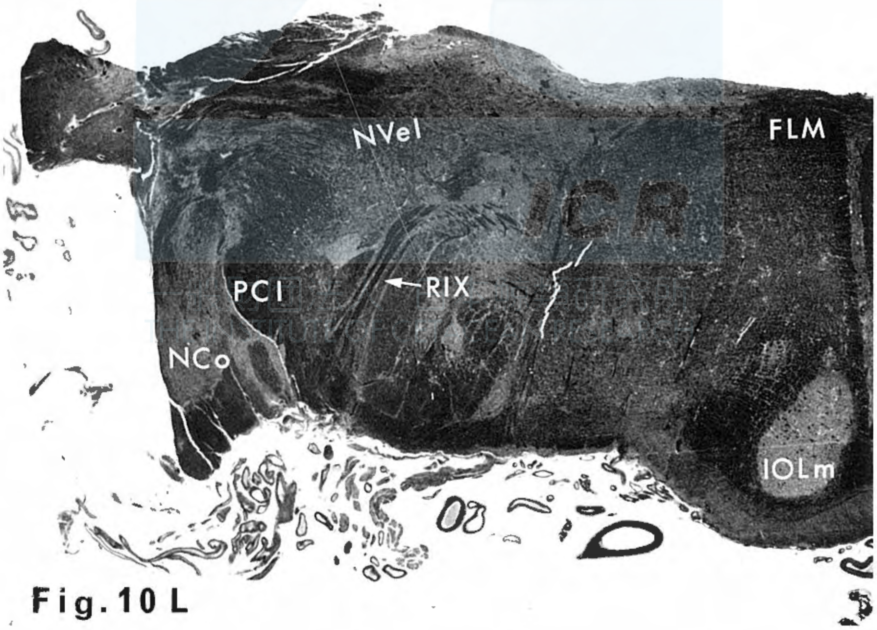


Fig. 10 L

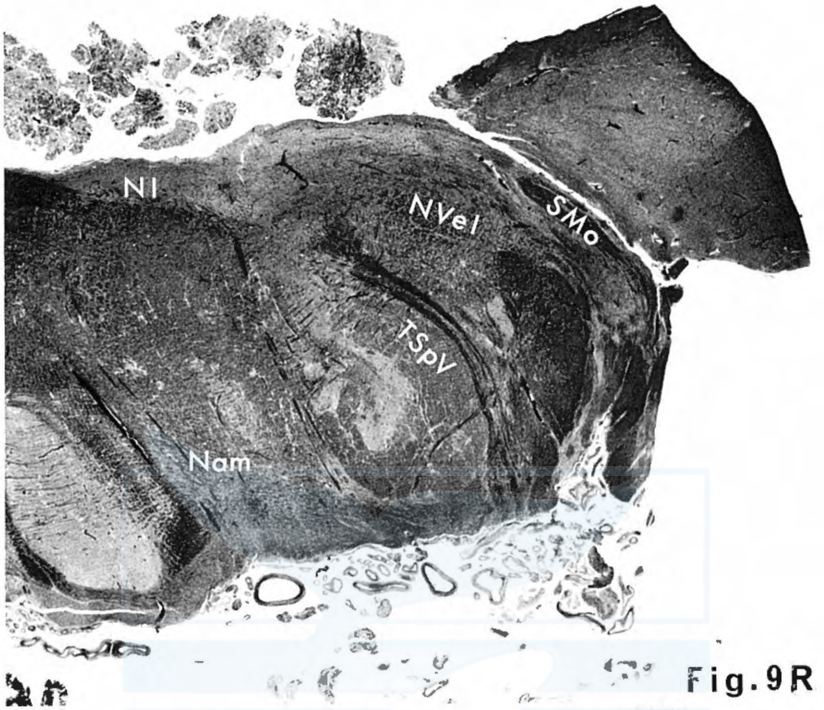


Fig. 9R

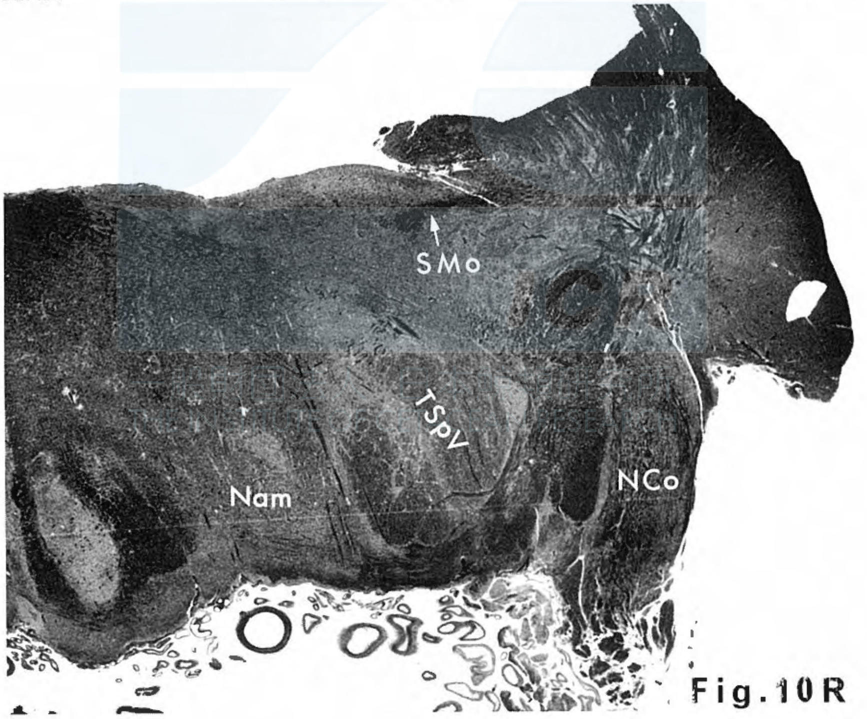


Fig. 10R

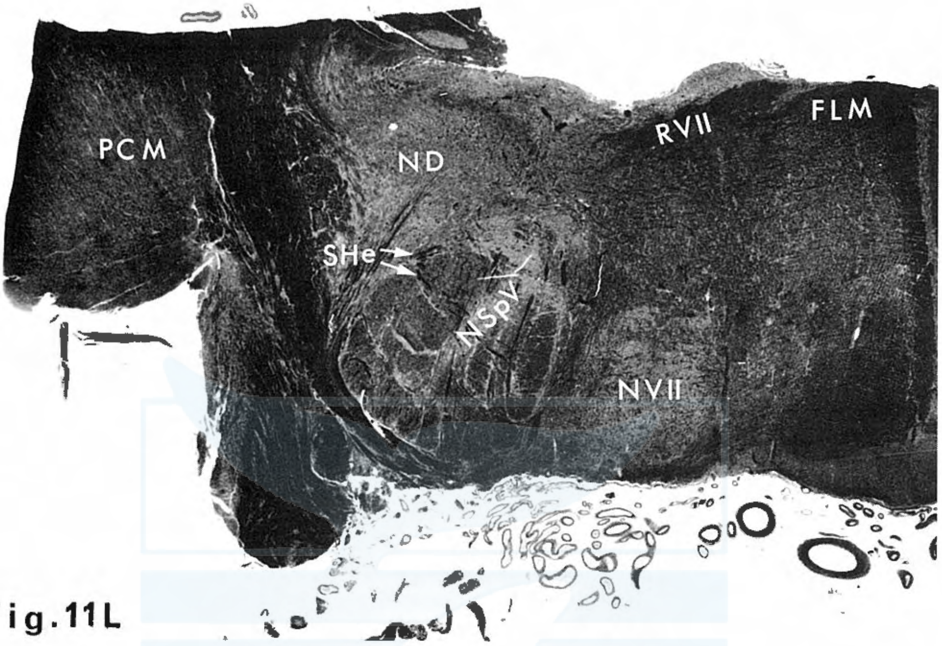
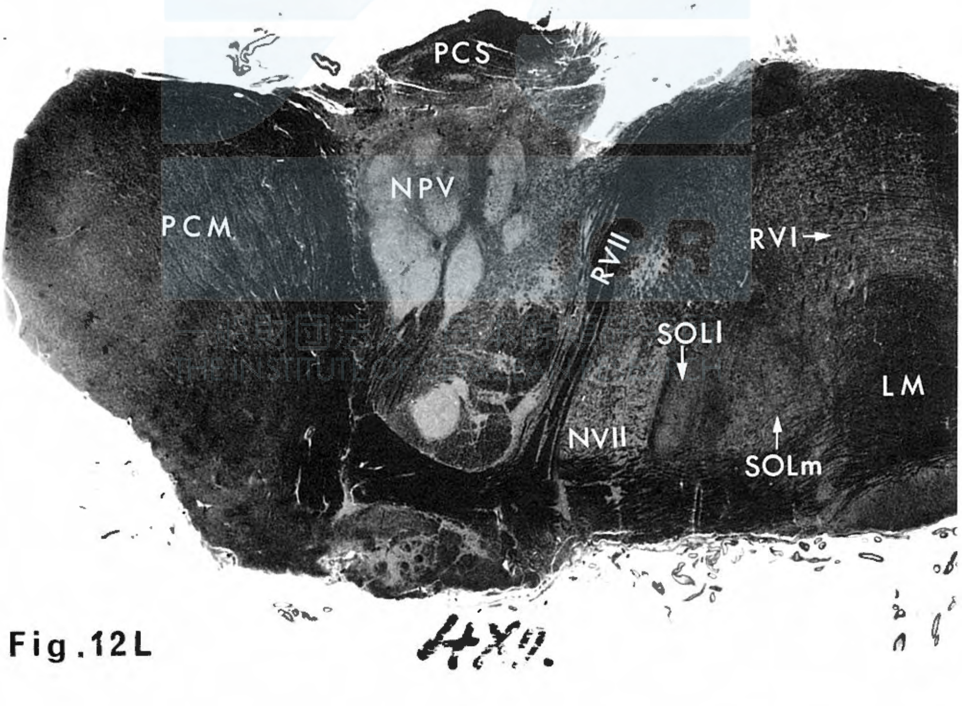


Fig.11L



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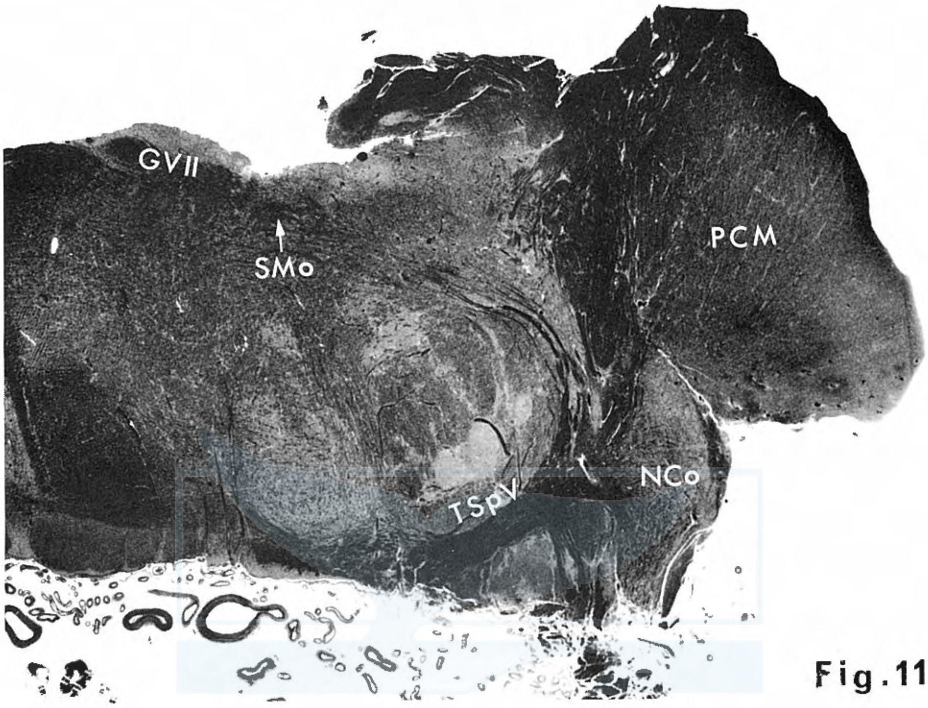


Fig. 11R

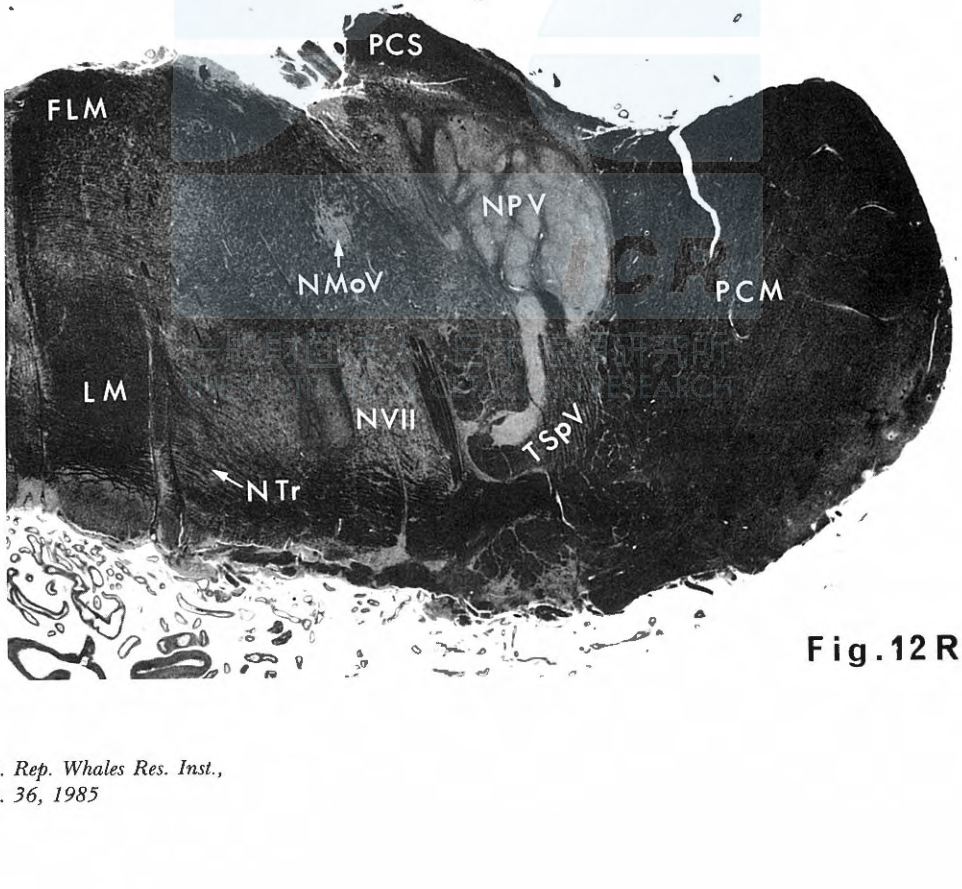


Fig. 12R

Fig.13L

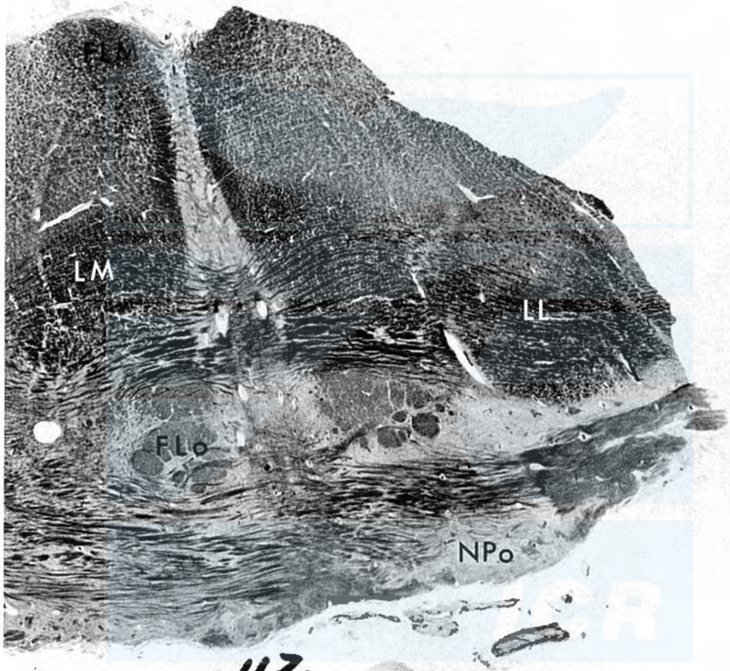


Fig. 13 R

1X2.

Fig.14L

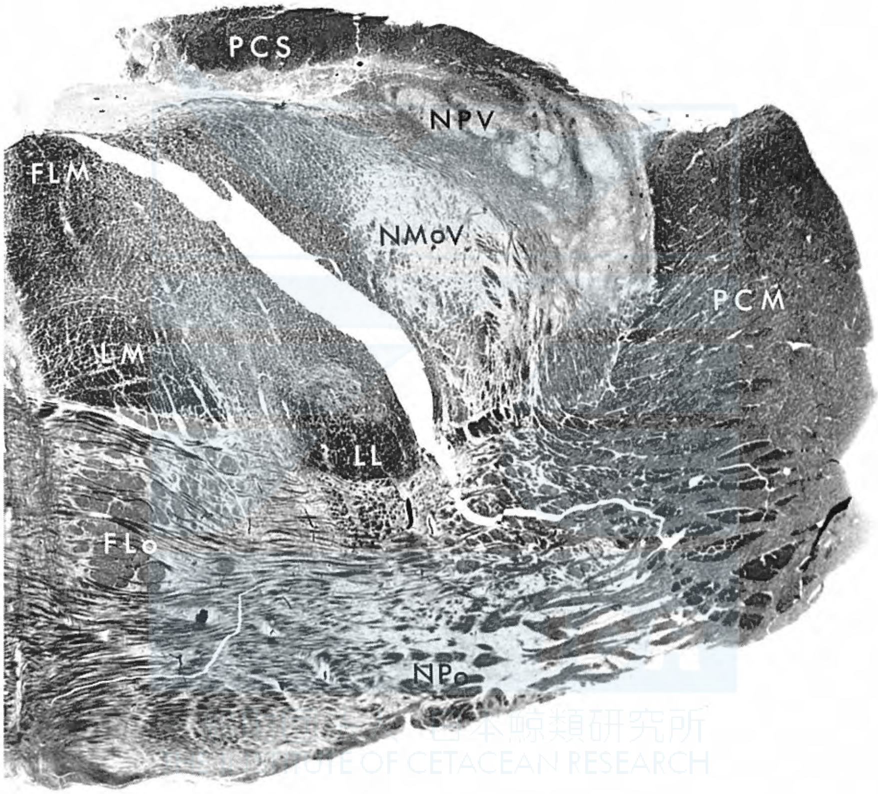


Fig. 14 R

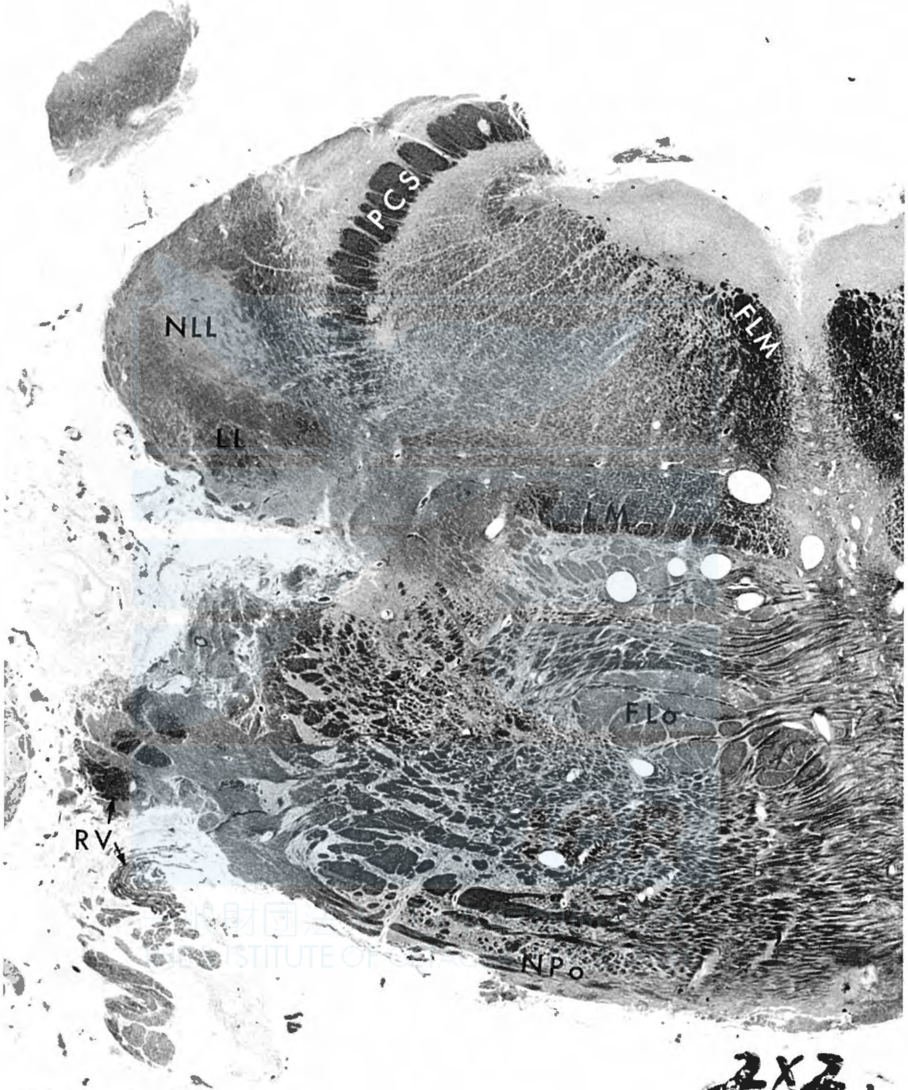
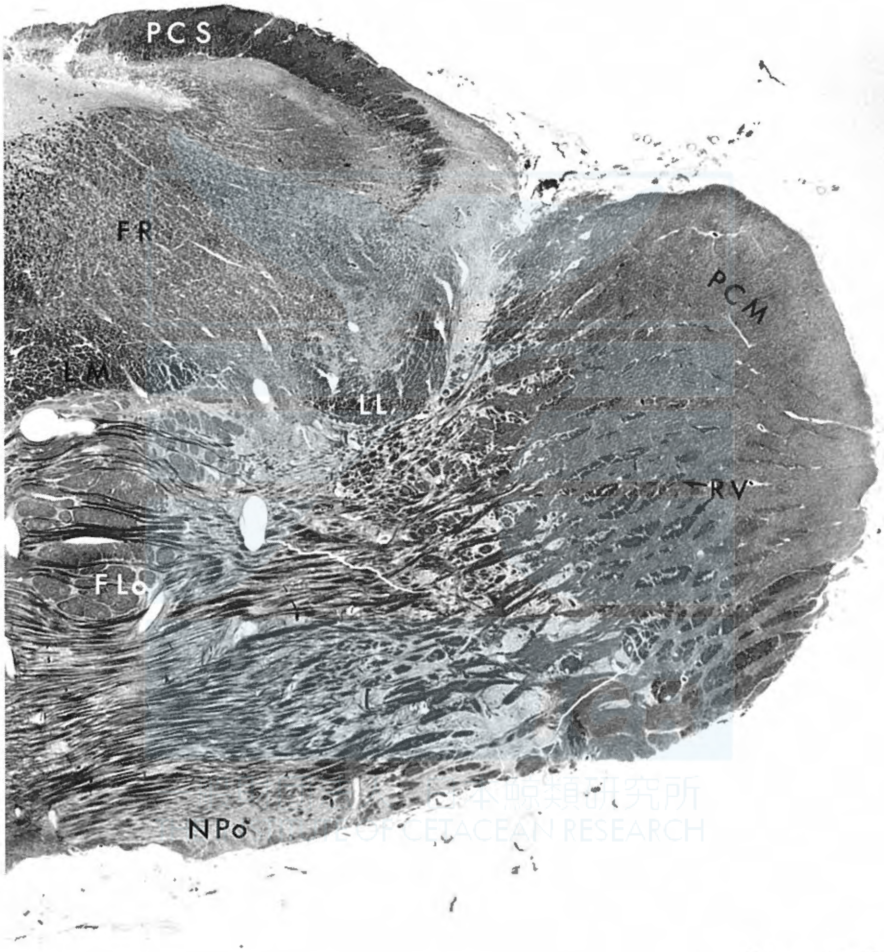


Fig. 15 L

2X2.



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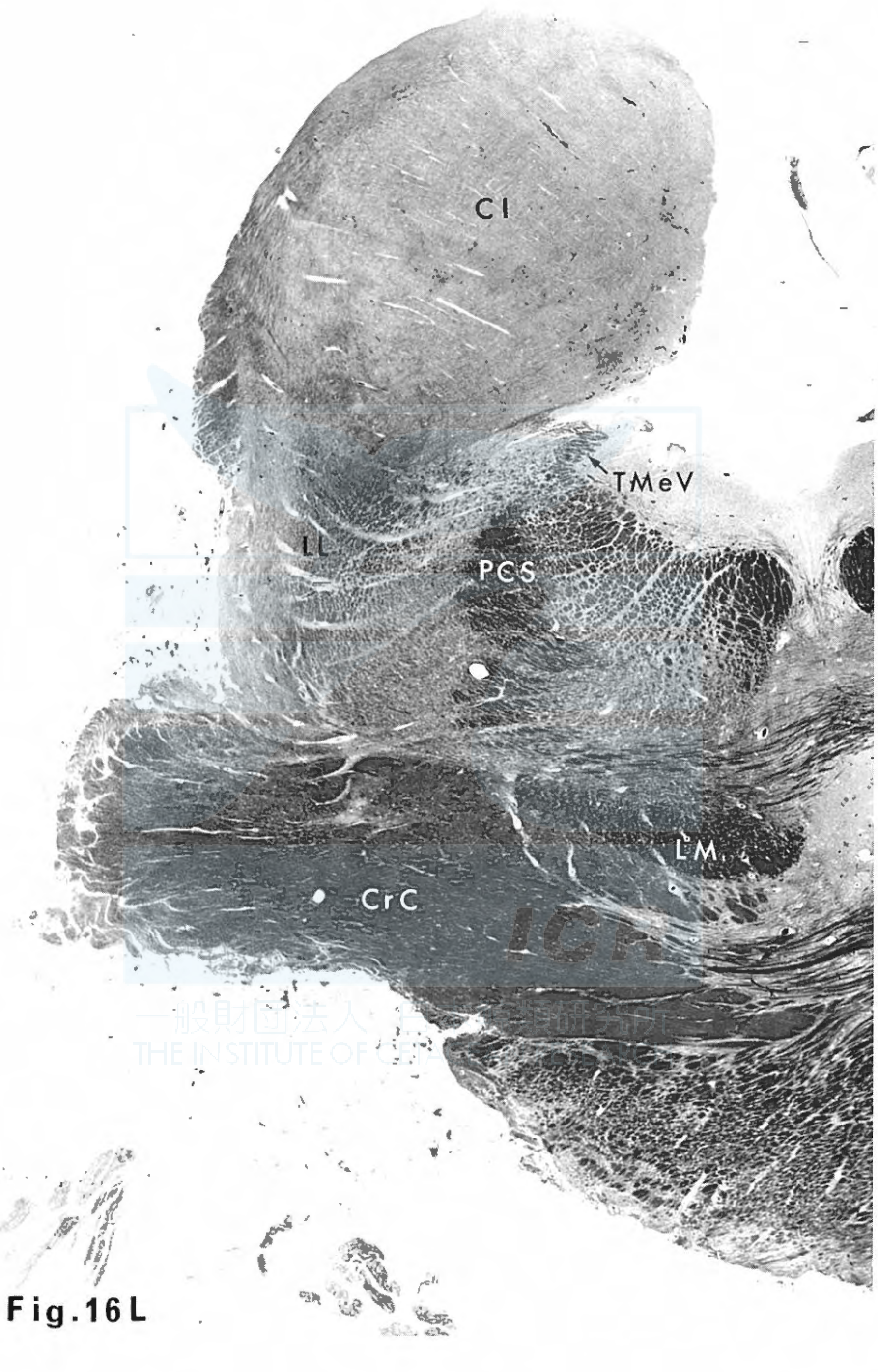

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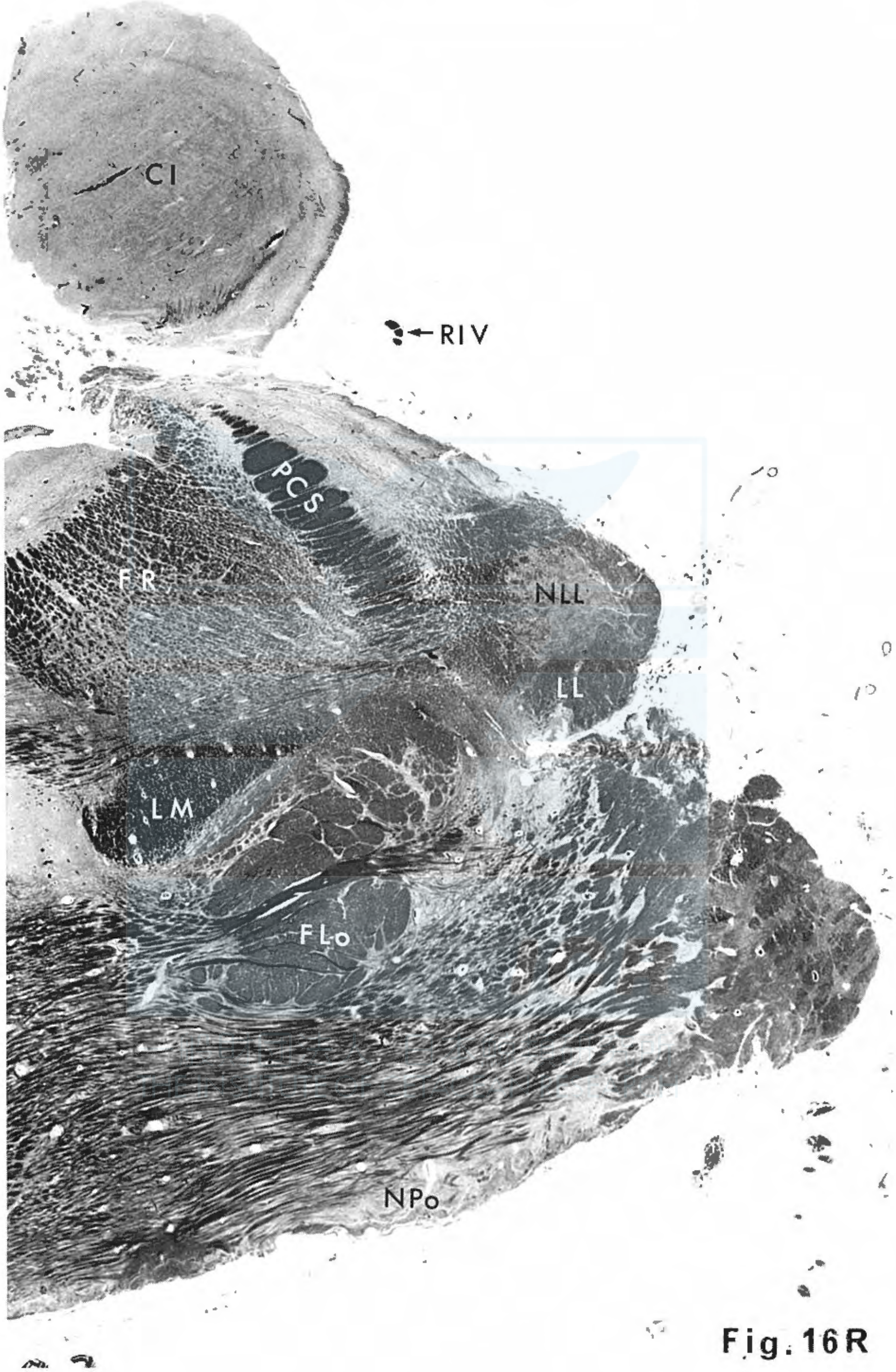


Fig. 16R

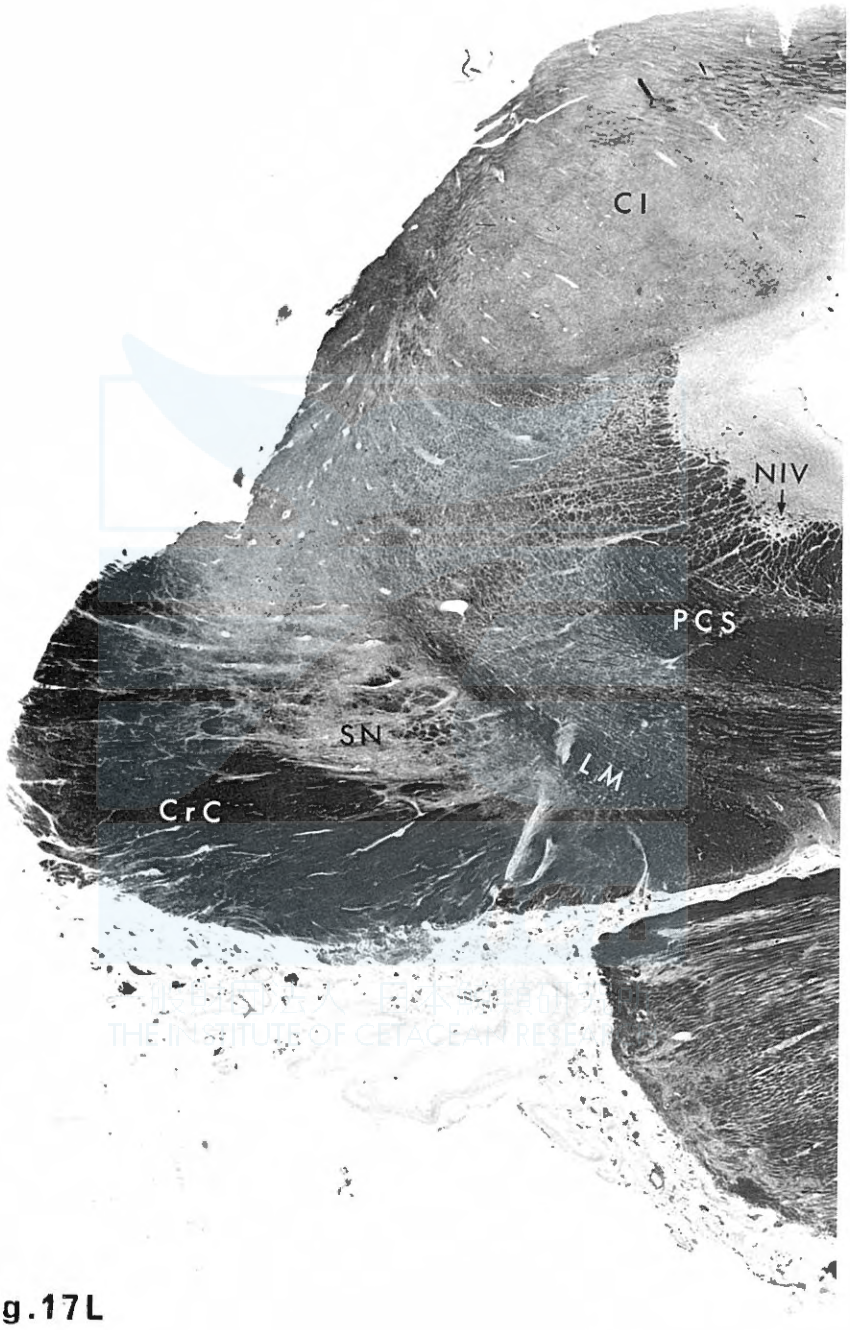


Fig.17L

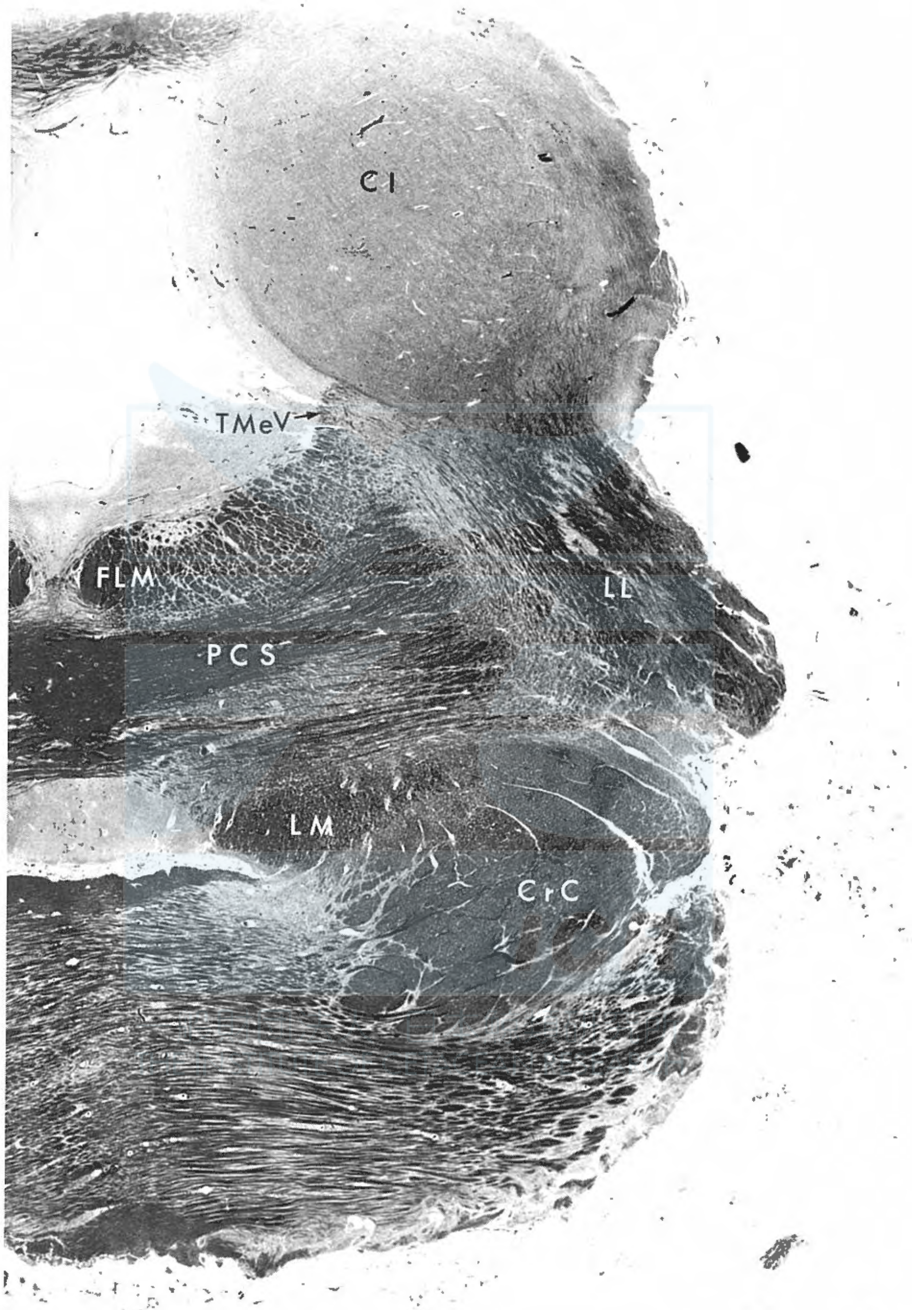


Fig.17R

Fig. 18

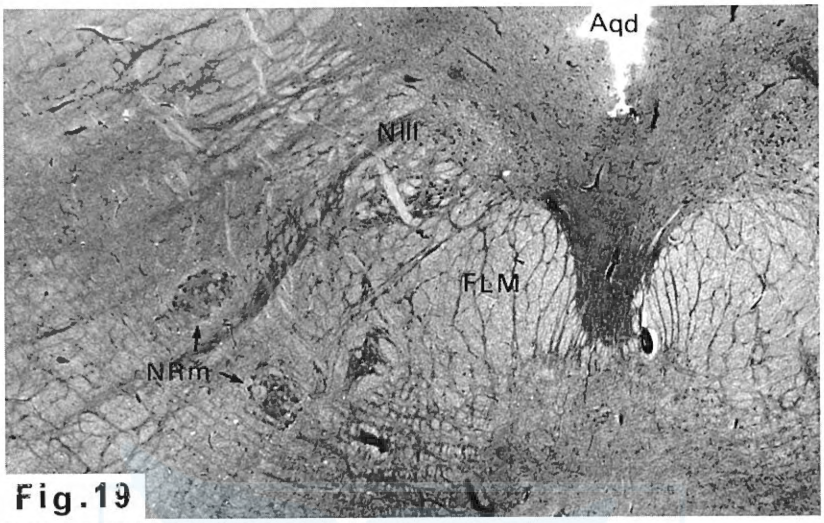
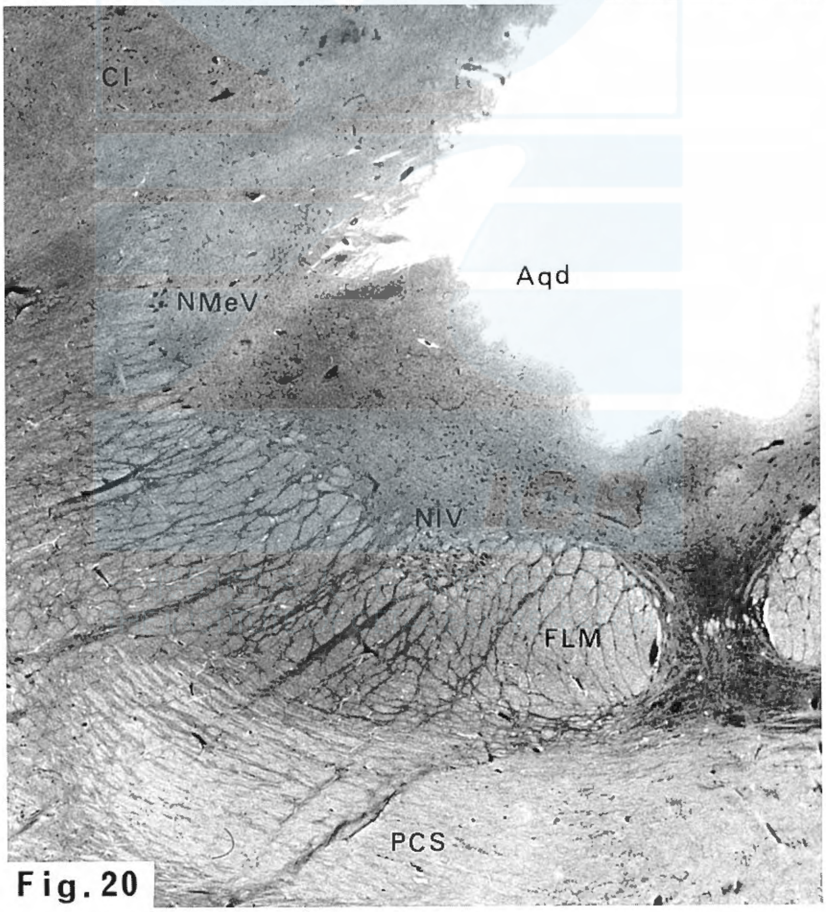


Fig. 19



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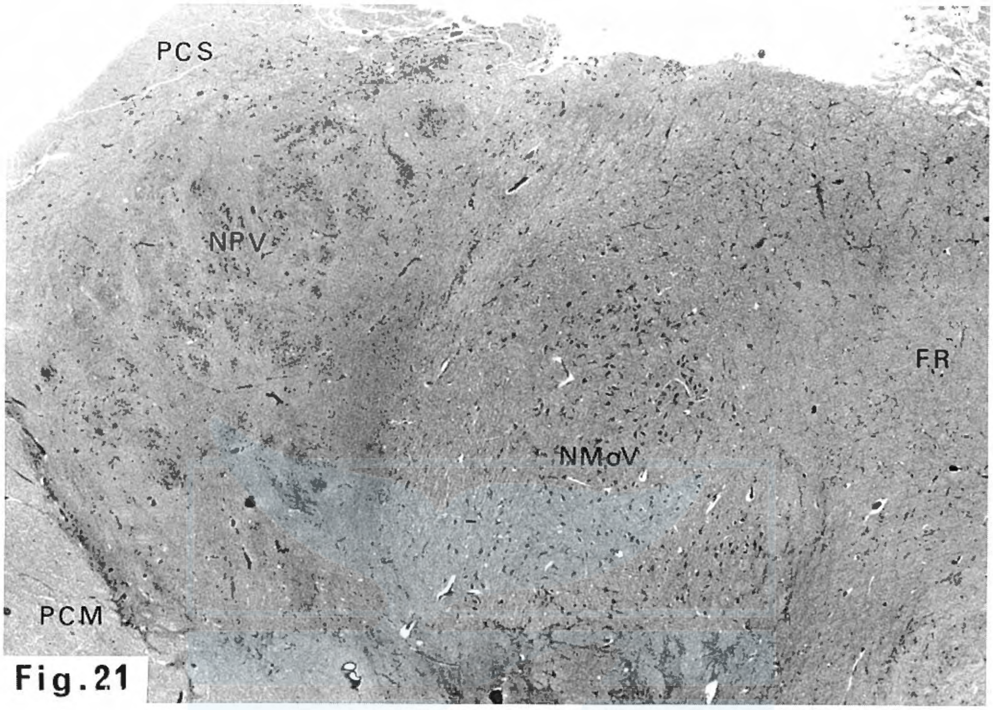

Fig.21

Fig.22

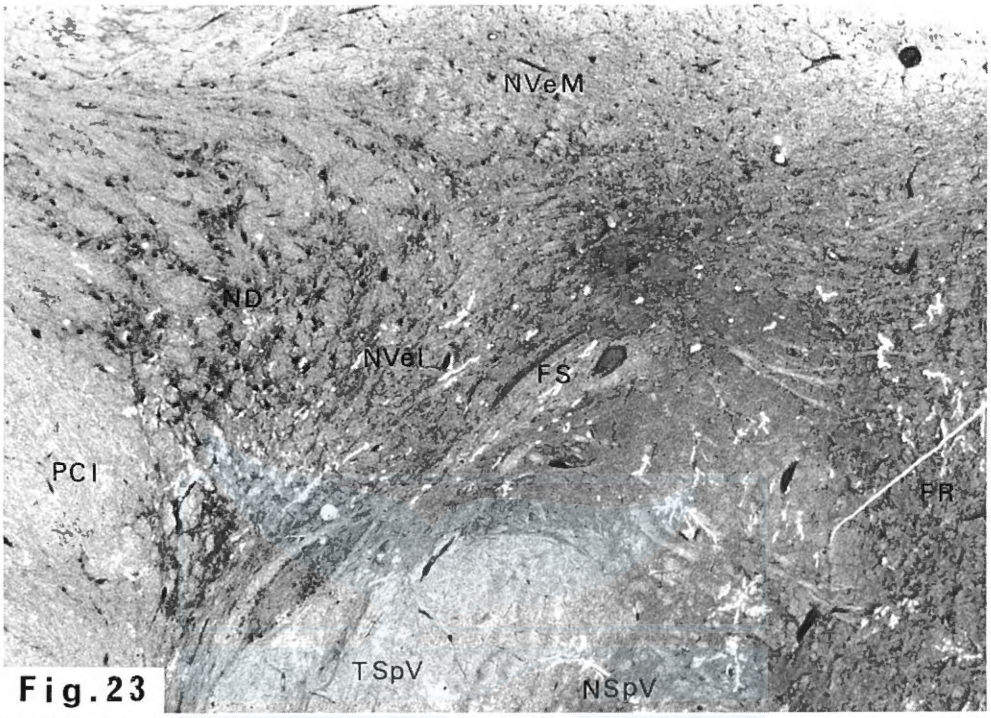

Fig. 23

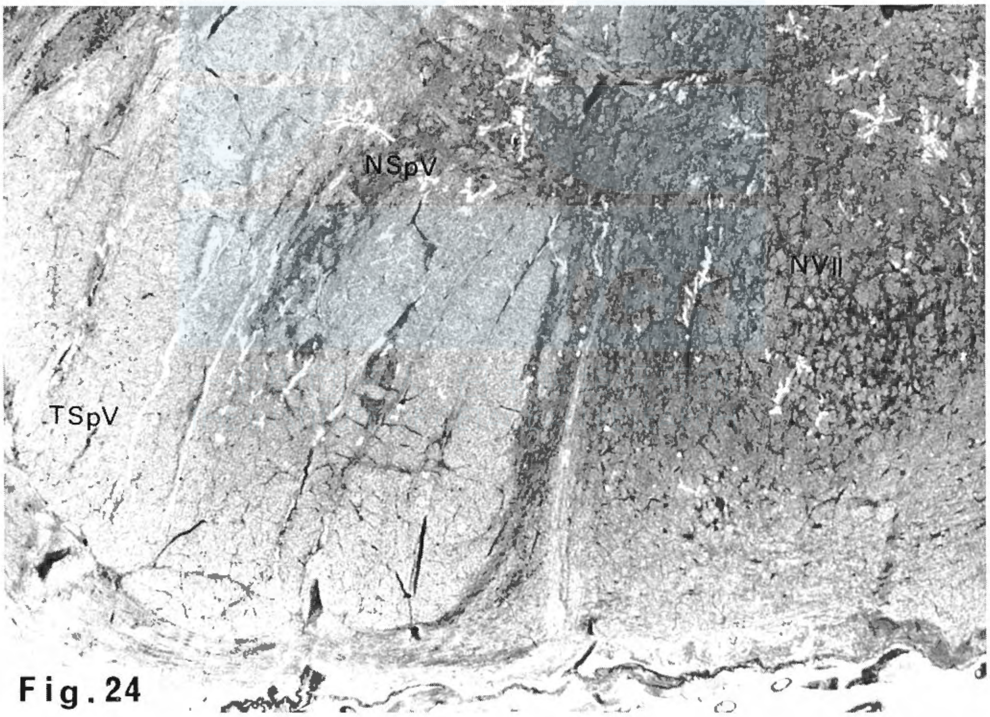

Fig. 24

Fig. 25

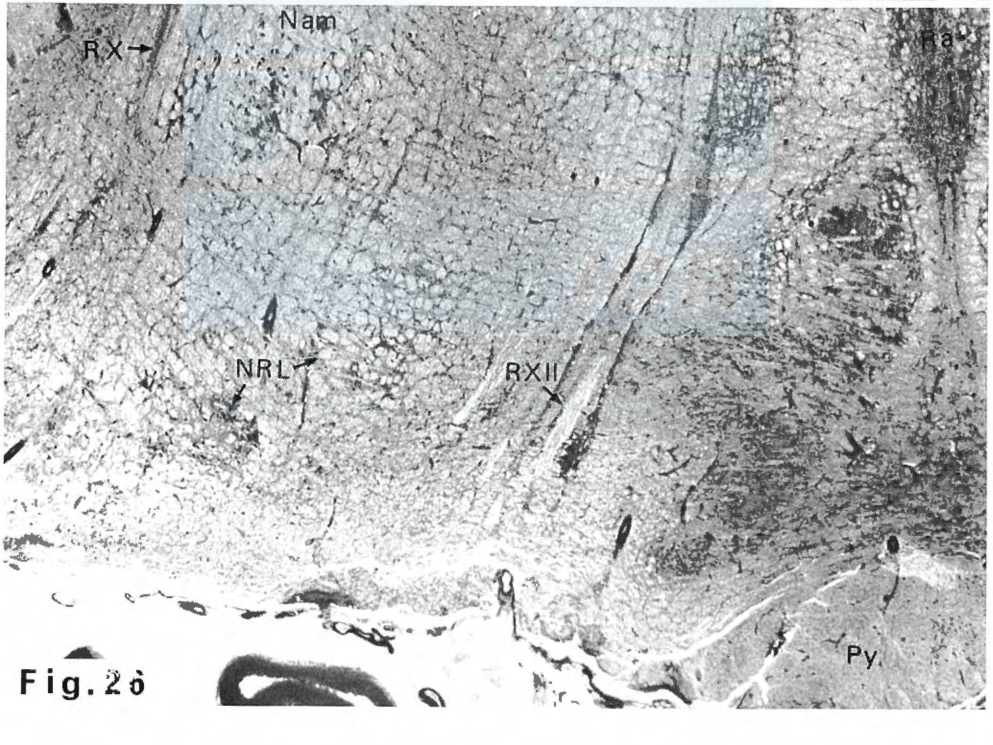

Fig. 26

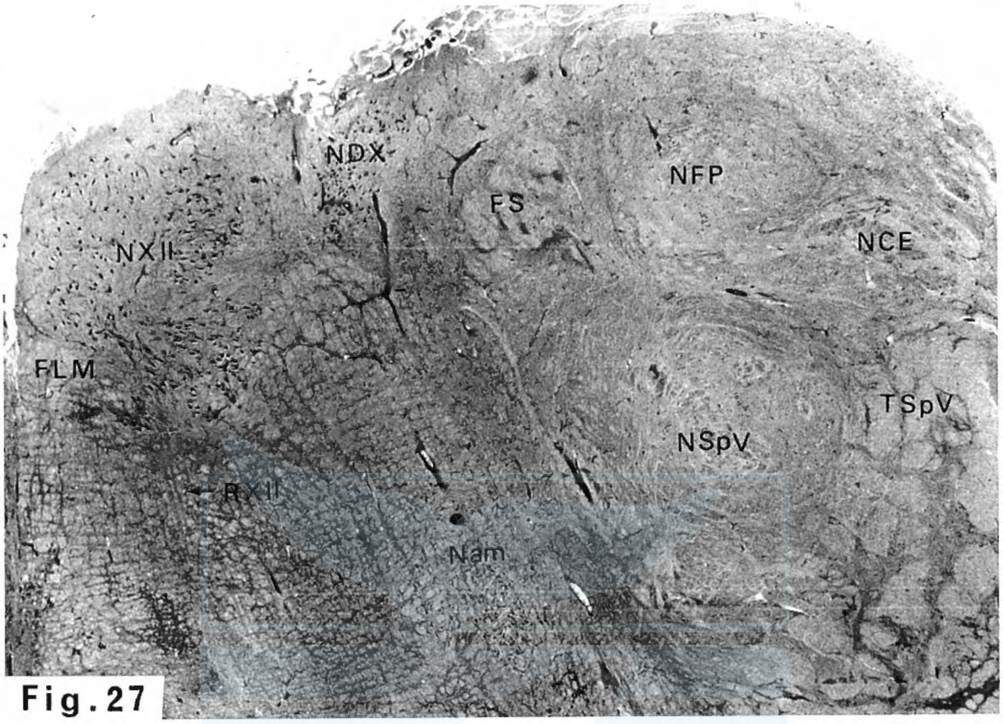

Fig. 27


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DUODENAL PORTION OF THE HEPATO-PANCREATIC DUCT OF THE BOUTU, *INIA GEOFFRENSIS*

KENJI KITO AND FUSAO YAMASAKI*

ABSTRACT

The duodenal portion of the hepato-pancreatic duct of the Boutu, *Inia geoffrensis* (body length 204 cm, female), was examined macroscopically and light microscopically. Passing through the muscle layer of the duodenum, the hepato-pancreatic duct ran intramurally, and formed the duodenal pouch, and opened into the lumen of the duodenum proper. The intramural cystic gland, mucous in nature, was located in the relatively thick submucosa of the duodenum, in which scattered bundles of muscle fibers were arranged in a layered appearance. A tentative comparison for some features of the duodenal portion of the hepato-pancreatic duct suggests that the fresh water dolphins may be a phylogenetically peculiar group in toothed whales.

INTRODUCTION

The hepato-pancreatic duct of the cetacean bile-passage generally dilates and forms a well-developed glandular structure in the duodenal wall (Kamiya, 1962; Yablokov, Bel'kovich and Borisov, 1972). This glandular structure, termed as the intramural cystic gland, supposedly plays a role in the storage and excretion of the gall, compensating to some extent for the absence of the gallbladder (Kamiya, 1962). According to the above two works, the intramural cystic gland is located in the submucosa of the duodenum in whalebone whales and the sperm whale, and in the muscle layer of the duodenum in toothed whales except in the case of the sperm whale. It is, therefore, suggested that the location of the intramural cystic gland in the duodenal wall is an important character to consider the phylogeny of the cetaceans.

Some studies on the fresh water dolphins also have mentioned the hepato-pancreatic duct passing through the duodenal wall: Takahashi and Yamasaki (1972) and Yamasaki, Takahashi and Kamiya (1972) on *Platanista gangetica*; Yamasaki, Takahashi and Kamiya (1975) and Takahashi, Yamasaki and Kamiya (1976) on *Pontoporia blainvillei*; Zhou and Li (1981) on *Lipotes vexillifer*; Zhou, Li and Pilleri (1982) on *Inia boliviensis*; and Yamasaki and Kito (1984) on *Inia geoffrensis*. In order to discuss the fresh water dolphins, regarding the features of the bile-passage, it is necessary that these features of the

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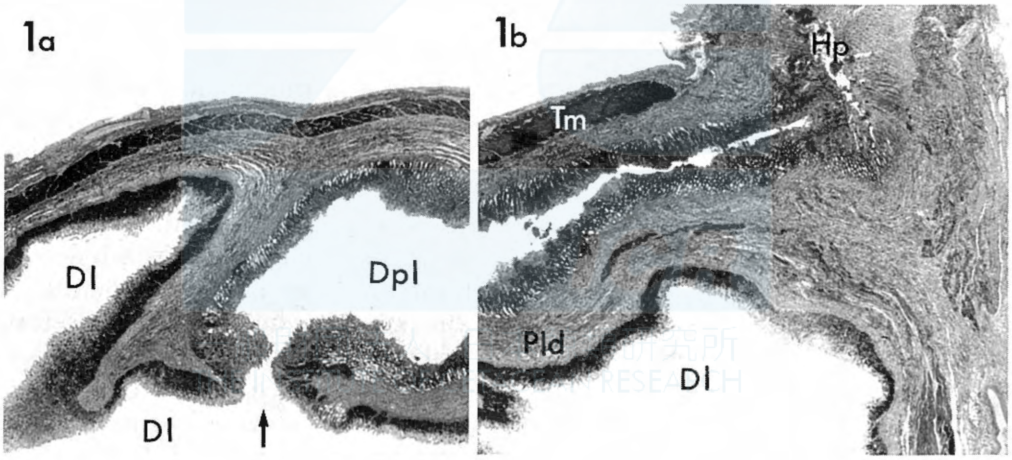
Inia and *Lipotes* be described at least as detailedly as that of the *Platanista* and *Pontoporia.* The present paper, as the third report on the morphological study of the digestive tract of *Inia geoffrensis,* describes detailedly the hepato-pancreatic duct in the duodenum and provides some fundamental knowledge to consider the phylogenetic relationship of the fresh water dolphins in the cetaceans.

MATERIAL AND METHODS

A specimen of the Boutu (Amazonian dolphin), *Inia geoffrensis* (body length 204 cm, female) was provided for this study by Kamogawa Sea World, Chiba, Japan, after death from an unidentified disease. The duodenum with the hepato-pancreatic duct taken from the abdominal cavity was preserved in 10% formalin solution and transported to our laboratory. The bile-passage outside of the duodenum has been excluded from the material transported, so that the present observation is restricted to only the hepato-pancreatic duct located in the duodenum. After macroscopical observation, the material was embedded in celloidin, sectioned, and stained with hematoxylin-eosin for light microscopy.



Figs 1a and 1b. Photomicrographs of the longitudinal section of the duodenal portion of the hepato-pancreatic duct which is located in the duodenal wall of the *Inia geoffrensis.* The midpart of the duct was sectioned transversely and shown in Fig. 2. Figs la and lb show the final one-fourth and the initial part of the duodenal pouch, respectively. The pouch exsists submucosally in the duodenal wall. Dl-duodenal lumen; Dpl-lumen of duodenal pouch; Tm-tunica muscularis of the duodenum; Hp-hepato-pancreatic duct; Pld-plica longitudinalis duodeni; an arrow shows the orifice of the duodenal pouch. H-E stain. × 8.

OBSERVATION

The hepato-pancreatic duct entered the wall of the duodenum proper at a rather steep angle and ran analwards intramurally (Figs la and lb). The distal three-fourths of the duct in the duodenal wall enlarged its lumen and formed the so-called duodenal pouch; the plica longitudinalis duodeni, which could be distinctly seen, is about 1.5 cm long and 0.6 cm wide, on the inner surface of the duodenum proper. The hepato-pancreatic duct opened into the

Fig. 2. A photomicrograph of the transverse section of the midpart of the duodenal pouch. The muscle layer of the duodenum consists of the thick inner and thin outer ones. The duodenal pouch is located in the thick tela submucosa in which some smooth muscle fibers can be seen (arrow). The mucosa of the pouch is thicker than that of the duodenal lumen and glands of the former are mucous and the lattert's are serous in nature. Dl-duodenal lumen; Dpl-lumen of duodenal pouch; Tm-tunica muscularis of the duodenum; Ts-tela submucosa; *-artificial structure. H-E stain. × 16.

duodenal lumen through the slit-like orifice with 2 mm in length (Fig. la), which was located about 9 cm away from the commencement of the duodenum proper. The duodenal papilla was indistinct and no peculiar structure was found around the orifice.

Microscopically, the hepato-pancreatic duct ran in the submucosa of the duodenum after passing through the muscle layer of the duodenum (Fig. lb). There were no longitudinal or transverse folds and also no villi on the inner surface of the duodenal pouch; luminal epithelium was seen to be worn-off. As shown in Figs 1 and 2, the lamina propria mucosae of the hepato-pancreatic duct was 0.3-1.2 mm thick, and was occupied with well-developed tubulo-alveolar glands. This glandular structure, the intramural cystic gland, was mucous in nature and apparently differed from that of the duodenum proper, mostly consisting of serous glands. Goblet cells were not found among the epithelial cells of the intramural cystic glands and lymphatic nodules were also absent in the lamina propria mucosae of the hepato-pancreatic duct. No sphincteric smooth muscles could be seen either at the proximal or distal portion of the duodenal pouch, though the outer longitudinal muscles of the duodenal wall irregularly and intermittently extended to the submucosa around the proximal portion of the intramural cystic gland. Scattered bundles of smooth muscle fibers gave a layered appearance near the middle of the submucosa between both the mucosa of the duodenum and the hepato-pancreatic duct.

DISCUSSION

Table 1 summarizes the macro- and microscopical features on the duodenal portion of the hepato-pancreatic duct of the fresh water dolphins, based upon the following studies, Takahashi and Yamasaki (1972) and Yamasaki *et al.* (1972) on *Platanista gangetica*; Yamasaki *et. al.* (1975) and Takahashi *et al.* (1976) on *Pontoporia blainvillei*; Zhou and Li (1981) on *Lipotes vexillifer*; and Zhou *et al.* (1982) on *Inia boliviensis*; Yamasaki and Kito (1984) and the present study on *Inia geoffrensis.* This table is unfortunately incomplete because all information on the features are not given from the above studies. Therefore, it is presently possible to compare the fresh water dolphins in only a few characters which are clearly described.

The hepato-pancreatic duct of *Inia* is similar to that of *Pontoporia* and *Platanista* in running analwards within the submucosa of the duodenum and in entering the lumen of the duodenum proper through the orifice not surrounded by any peculiar prominences. While, the hepato-pancreatic duct of *Lipotes* runs within the circular muscle layer of the duodenum and enters the lumen of the duodenal ampulla through the orifice surrounded by a lip-like prominence (Zhou and Li, 1981). The intramural cystic gland of *I. geoffrensis* is mucous in nature as that of *Pontoporia,* and it also clearly forms the duodenal pouch as that of *Platanista.* The duodenal pouch of *Platanista* is

TABLE 1. COMPARISON OF THE DUODENAL PORTION OF THE HEPATO-PANCREATIC DUCT IN THE FRESH WATER DOLPHINS

Character	*Inia geoffrensis*1)	*Inia boliviensis*2)	*Lipotes vexillifer*3)	*Pontoporia blainvillei*4)	*Platanista gangetica*5)
Location of the hepato-pancreatic duct in the duodenal wall	submucosa	submucosa*	muscle layer	submucosa	submucosa
Duodenal pouch	present	absent*	absent*	absent	present
Nature of the intramural cystic gland	mucous	mucous*	mucous*	mucous	serous, partially mucous
Thickness of the mucosa	0.3-1.2 mm	0.4-0.6 mm	1.3 mm	0.6-1.3 mm	0.5-2.4 mm
Lymphatic nodules	not found	–	abundant	present	abundant
Musculature around the hepato-pancreatic duct	scattered bundles of muscle fibers	–	circular muscle layer of the duodenal wall	well-developed longitudinal muscle layer	thin circular layer, many muscle fibers scattered
Location of opening of the hepato-pancreatic duct	duodenum proper	duodenum proper	duodenal ampulla	duodenum proper	duodenum proper
Duodenal papilla	indistinct	indistinct	lip-like prominence around the orifice	indistinct	indistinct
Size of plica longitudinalis duodeni**	1.5 × 0.6 cm	–	2.0 × 1.0 cm	1.5 × 0.9 cm	1.5 × 0.7 cm

References: 1) Yamasaki and Kito (1984) and the present study, 2) Zhou *et al.* (1982), 3) Zhou and Li (1981), 4) Yamasaki *et al.* (1975) and Takahashi *et al.* (1976), 5) Takahashi and Yamasaki (1972) and Yamasaki *et al.* (1972).

– Data not given. * Data suggested from photomicrographs of the hepato-pancreatic duct. ** Length × width.

more developed than that of *I. geoffrensis* and is especially characterized by the presence of many circular folds on its inner surface and the presence of villi of the mucosa; *Pontoporia* has no pouch in the duodenal wall*. There is no mention of the nature of the intramural cystic gland in *Lipotes* and *I. boliviensis,* though the photomicrographs of the hepato-pancreatic duct in the duodenal wall in *Lipotes* (Fig. 2-2, Zhou and Li, 1981) and *I. boliviensis* (Plate 4A, Zhou *et al.,* 1982) suggest that both their glandular structures are mucous in nature and they have no distinct duodenal pouch. If the duodenal pouch is really missing in the bile-passage of *I. boliviensis* but present in that of *I. geoffrensis,* the feature of the duodenal pouch appears to be one of the important characters in which to classify these two closely related dolphins of the genus *Inia.*

According to Kamiya (1962), the intramural cystic gland is located in the submucosa of the duodenum in whalebone whales and it is located in the circular muscle layer of the duodenum in toothed whales except in the case of the sperm whale, whose gland is located in the submucosa, the same as in whalebone whales. Yablokov *et al.* (1972) added to Kamiya's view, based upon their investigation on the duodenum of the white whale, *Delphinapterus,* that the intramural cystic gland has its own musculature in toothed whales (except the sperm whale) and is not found in whalebone whales and the sperm whale. Among the fresh water dolphins, *Lipotes* has the intramural cystic gland in the muscle layer of the duodenum as do most toothed whales, though it is not mentioned whether the gland of *Lipotes* has its own musculature or not. The *Pontoporia, Platanista,* and *Inia* have the intramural cystic gland in the submucosa as do whalebone whales and the sperm whale. The three differ, however, from whalebone whales and the sperm whale in regards to the distributional feature of the musculature in the submucosa. The intramural cystic gland of *Pontoporia* is surrounded by a very thin submucosa and a remarkably developed muscle layer, mainly consisting of longitudinal muscles, of the hepato-pancreatic duct; so that it appears to be located in the muscle layer of the duodenum. The intramural cystic gland of *Platanista* is also surrounded by a thin submucosa and a relatively thin muscle layer, and many muscle fibers are distributed within the submucosa and lamina propria of the duct. The intramural cystic gland of *Inia* is characterized by the scattered bundles of muscle fibers intermittently running near the middle of the thick submucosa between both the mucosa of the duodenum and the hepato-pancreatic duct. Thus, in toothed whales, the fresh water dolphins seem to be a peculiar group consisting of dolphins having the intramural cystic gland with its own musculature in the submucosa of the duodenum and those dolphins having the intramural cystic gland in the muscle layer of the duodenum.

The duodenal portion of the hepato-pancreatic duct of the fresh water

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* The glandular structure of the hepato-pancreatic duct having no distinct duodenal pouch is thought to be a kind of the intramural cystic gland.

dolphins have some important and useful characters as do other structures, such as the skelton, brain, the other digestive and respiratory organs, in order to clarify the phylogenetic relationship among the fresh water dolphins and cetaceans. For example, the location of the opening of the hepato-pancreatic duct into the duodenal lumen is already considered as a plesiomorphous character (located at duodenum proper) or an apomorphous character (located at duodenal ampulla) in discussing the phylogeny of the fresh water dolphins (Zhou, 1982). We will continue the discussion about the fresh water dolphins when more details and new findings are gathered in the future which will be sufficient to consider their phylogenetic relationship.

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STRUCTURE OF A LONG-FINNED PILOT WHALE SCHOOL STRANDED IN PATAGONIA

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ABSTRACT

A herd of 17 southern long-finned pilot whales, *Globicephala melaena edwardii* (Smith, 1834) was found in November 1982 stranded near Punta Tombo, Argentina, at the beach above the high tide line. The herd was composed of nine females, seven males, and an individual of indeterminated sex (5 years, the youngest individual). Using age criteria obtained for the North Atlantic population of the species (Sergeant, 1962) all the females (9–16 years) were estimated as sexually mature, three males (7–11 years) as probably immature, and two males (14 and 16 years) having attained breeding maturity. The reliable estimate of remaining two males, (12 years) was not possible from their ages. Due to the advanced decomposition, no further information on the growth or reproductive status was available.

INTRODUCTION

The mass stranding of Cetaceans attracted the interest of many biologists, and a considerable number of papers dealing with it were published (Geraci, 1978; Sergeant, 1983). The long-finned pilot whale *Globicephala melaena* (Trail, 1809) mass strands like other highly social members of the *Orcininae* (Sergeant, 1983). Sergeant suggested that the frequency of mass stranding in Cetaceans might be a density dependent event of highly social Cetacean species.

Mass stranding of Cetaceans in Argentine coasts has been reported for the sperm whale (Castello and Piñero, 1974) and the southern long-finned pilot whale (Piñero and Castello, 1975). Goodall (1978) has described individual and mass strandings of Cetaceans in Tierra del Fuego.

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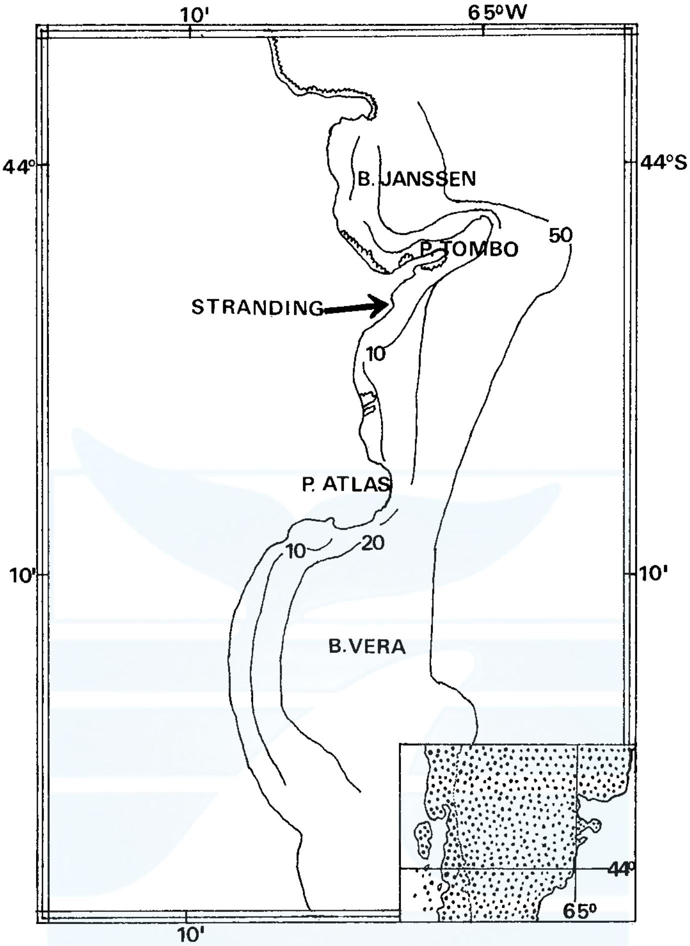

Fig. 1. Location of the stranding. The isobaths are indicated in meter.

The present paper describes the age and body length compositions of a group of southern long-finned pilot whale *Globicephala melaena edwardii* (Smith, 1834), stranded at Punta Tombo, in the Patagonian coast.

MATERIALS AND METHODS

Features of the stranding

The mass stranding took place 2 km south of Punta Tombo (44°02′S, 65°01′W), the Chubut Province Penguin Reserve (Fig. 1). The whales were found stranded on a rocky platform, above sandy and stony beaches, about 3 to 8 m inland side of the normal high tides line.

Nothing is known about the instance of the mass stranding, even if the 17 individuals represent an entire school or part of a lager one. The date of

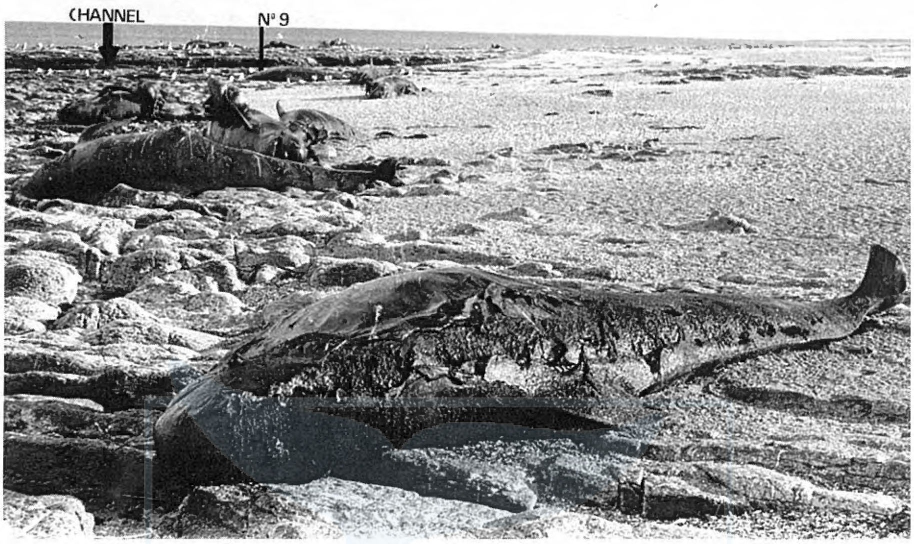

Fig. 2. View of the stranding. Arrows indicate the channel separating the two subgroups, and the largest adult male (Specimen No. 9) found between them.

the stranding was estimated from the degree of decomposition of the whales, and the position of them in the beach, to have occurred around the first days of November, 1982, when the tide was highest. The whales were dispersed along 103 meters of the beach, but as shown in Fig. 2 most of them were in two groups (8 animals each), which were 30 m apart. A large old male (No. 9) was stranded at the middle of the two groups, and opposite to a channel 12 m wide and 3 m deep. Body length and some other external measurements were taken from all individuals by the Gamekeeper of the Penguin Reserve.

Identification of species

The species was identified on the basis of cranial characters and length of the flipper as described by Bree (1971) (Fig. 3 and Table 1), and the presence of whitish eye mark, saddle mark and ventral white patch (Davies, 1960). The mean number of teeth ranged from 9 to 12 in each jaw with a mean of 10.32 (n=56). The mean length of the flippers was 20% of the standard length, again in the range of 18-27% reported for this species (Bree, 1971). Photographs taken by the Gamekeeper of the Reserve one week after the stranding, showed that at least one animal had the eye mark (Fig. 4) and another the ventral patch. They were not confirmed on other animals due to the advanced deterioration or individual variation. It is known that the marks may vary individually even on living or just dead individuals from whitish to dark gray (Davies, 1960).

TABLE 1, NUMBER OF TEETH OF THE PUNTA TOMBO SPECIMEN

Specimen No.	No. of teeth (1)			
	UR	UL	LR	LL
1	10	—	12	—
2	10	10	10	10
3	11	10	10	10
4	9	—	10	9
5	11	11	10	11
6	10	—	10	—
7	9	9	9	9
8	11	10	9	9
9	11	10	10	10
10	10	10	11	11
11	10	10	12	12
12	11	—	10	—
13	11	11	11	10
14	—	11	—	10
15	11	—	10	—
16	—	11	9	10
17	11	12	11	12
mean	10.40	10.40	10.25	10.23

(1) UR: upper right jaw, UL: upper left jaw
LR: lower right jaw, LL: lower left jaw

Skull of Specimen No. 11 was deposited in the mastozoological collection of the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, (Specimen number 3855) (Fig. 3).

Age determination

Two large teeth were taken from a jaw of each individual. The teeth were sectioned longitudinally (sagitally) with a hand saw, and ground with sand paper to a thickness of about 100 μm. Then the teeth were examined for dentinal growth layers under a dissecting microscope (×8 to ×40). Fig. 5 shows the sagital section of Specimen No. 1 and No. 16, and Fig. 6, cementum layers in Specimen No. 2 and No. 8.

The pattern of the dentinal growth layers was the same as described by Sergeant (1962). The outermost dentinal layer was the prenatal dentine, ending in a traslucent neonatal line. The 2nd layer was generally opaque and ended in a clear zone. The opaque layer, sometimes contained a fine clear zone (accesory layer). The 3rd was less than half of the width of the 2nd layer and the thickness of the subsequent layers declined with increasing order. The deposition rate of these layers was assumed as annual without further confirmation (Sergeant, 1962). A double-layer effect was observed in some of

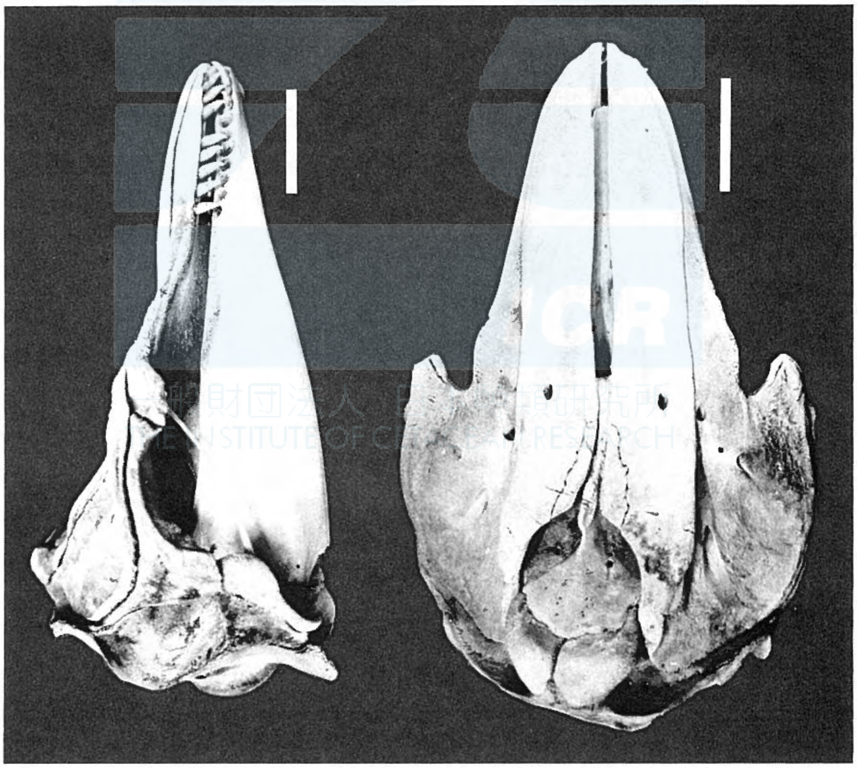

Fig. 3. Lateral and dorsal view of the skull of Specimen No. 11 (F.C.E.N.-U.B.A. Mast. Coll. No. 3855). Scale indicates 10 cm.

Fig. 4. Pigentation of some individuals in the mass stranding. Arrow indicates the whitish mark behind the eye.

Fig. 5. Sagital sections of Specimen Nos 16 (left, 12 years) and 1 (right, 12 years). E: enamel, PC: pulp cavity, PD: prenatal dentine, Circle: neonatal line, Numerals: annual layers in dentine. Scale indicates 0.5 cm.

Fig. 6. Thin ground section of cementum of Specimen Nos 2 (left, 11 years) and 8 (right, 14 years). C: cementum, D: dentine, Numerals: annual layers in cementum. Scale indicates 1 mm.

TABLE 2, LIST OF INDIVIDUALS MASS STRANDED AT PUNTA TOMBO IN NOVEMBER 1982

Specimen No.	Sex	Body length	Age (1)	Estimated sexual maturity (2)
1	male	4.46	12	mature
2	female	4.20	11	mature
3	female	4.68	13	mature
4	female	4.83	12	mature
5	male	3.35	7	immature
6	female	4.00	9	mature
7	male	3.93	8	immature
8	male	5.00	14	mature
9	male	5.38	16	mature
10	female	4.40	13	mature
11	?	3.28	5	immature
12	female	4.10	9	mature
13	male	4.10	11	immature
14	female	4.60	11	mature
15	female	4.28	10	mature
16	male	4.50	12	mature
17	female	4.72	16	mature

(1) Age in number of dentinal growth layers (presumably years).
(2) Sexual maturity is estimated using criteria of Sergeant (1962), i.e. sexually mature at 11 years (male) or 6 years (female).

the teeth, therefore an overestimation of the age of the whale could result.

Nearly same number of layers were observed in dentine and cementum of the same tooth, which suggests a same deposition rate in both tissues.

RESULTS

Sex, standard length and age of the specimens are shown in Table 2. Ages ranged from 9 to 16 years in females and 7 to 16 years in males. The oldest individuals were much younger than what is known for the northern long-finned pilot whale (50 years, Sergeant, 1962) or the short-finned pilot whale (62 years, Kasuya and Matsui, 1984).

The body length ranged from 400 to 472 cm in females and 335 to 538 cm in males. The upper limit of the range was smaller in both sexes than the maximum reported by Sergeant (1962) (females: 536 cm, males: 622 cm).

On the northern long-finned pilot whale, Sergeant (1962) estimated the female age and body length at the attainment of sexual maturity as 4-8 years (mean 6) and 341-386 cm (mean 356), respectively. The ages of males at the attainment of sexual maturity and breeding maturity was 11-16 years (mean 11) and over 12 years, respectively. If these criteria are used tentatively all the nine females (9-16 years and 400-483 cm) are considered as mature, four males (12-16 years and 446-538 cm) as probably have attained sexual matur-

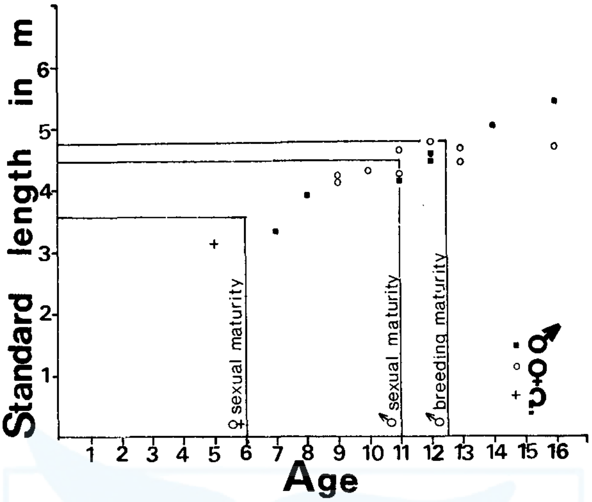

Fig. 7. Scatter plot of body length on age of the mass stranding of *Globicephala melaena edwardii*. Ages and body lengths at sexual maturity are mean values estimated by Sergeant (1962) for the northern long-finned pilot whale.

ity, and three males (7-11 years and 335-410 cm) as immature. An individual of unknown sex (5 years and 328 cm) is estimated as immature (Fig 7 and Table 2). However, this clasification has to be considered as tentative, because there is no base to believe that the growth in the present population is the same as that in the North Atlantic population studied by Sergeant (1962), and because the individual variation of growth is wide in the species. There were no juveniles below 5 years of age.

Of the 16 sexed individuals 9 (56%) were females and 7 (44%) were males. The female/male ratio was 1.28 and the mature female/mature male ratio was probably 2.50 (9/4). This suggests a polygynous school structure as indicated for the North Atlantic long-finned pilot whale (sergeant, 1962) and the short-finned pilot whale in the North Pacific (Kasuya and Marsh, 1984).

DISCUSSION

The southern long-finned pilot whales have been sighted or stranded in the Argentine coast (Piñero and Castello, 1975; Goodall, 1978), although little knowledge is available about the composition of the herds. No explotation of this species exists at least in recent years in the Argentine waters.

According to Sergeant (1962), the sizes of herd of long-finned pilot whale ranged from a few individuals up to 200 or more. The mean herd size of the species driven ashore in Newfoundland and those stranded naturally all over the world was about 85 individuals, with the highest frequency between 21-50 individuals, though the most frequent herd size in sightings in the Labrador Sea made by the U.S. Coast Guard was 11-20 individuals with a mean of 20. This suggest that the pelagic herds tended to be smaller than those stranded or driven ashore (Sergeant, 1962, 1983). He also concludes that the herd size was variable under different circumstances like feeding, stress, migrations, etc, and smaller units may occasionally agregate to form larger ones or viceversa.

The present herd was composed of 17 individuals. Another herd stranded at Punta Norte (Península Valdés - Chubut) on August 30th, 1976, was composed of 25 animals, but except for 2 males and 3 females the remaining 20 individuals were returned to sea (J. C. López, pers. comm.). Castello (1975) reported a stranding of 56 individuals at Isla Trinidad, but there was left no information on the sex ratio. Goodall (1978) recorded a group of 9 animals stranded in Isla de los Estados. These herd sizes are not different from those reported by Sergeant (1962).

Although the pilot whales are known to be sexually dimorphic (Sergeant, 1962; Kasuya and Matsui, 1984), this is not detected in the present materials. This may be related to one or two of these possibilities: (1) small sample size, (2) skewed school composition and (3) that sexual maturity is attained much later in the population (dimorphism appears at later age).

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EFFECT OF EXPLOITATION ON REPRODUCTIVE PARAMETERS OF THE SPOTTED AND STRIPED DOLPHINS OFF THE PACIFIC COAST OF JAPAN*

TOSHIO KASUYA**

ABSTRACT

Age composition and reproductive status of samples from two species of dolphins taken in the Japanese drive fishery are analyzed. A slight decline in the minimum age at attainment of sexual maturity was noted in females of the lightly exploited spotted dolphin. Females of the more intensely exploited striped dolphin underwent a decline in the mean age at sexual maturation from 9.7 years (1956 cohort) to 7.2 years (1970 cohort), accompanied by a decline of the minimum age at maturity. A more tentative finding on the species is the shortening of the mean reproductive cycle from 4.00 years (1955) to 2.76 years (1977). This is a direct result primarily of the probable change in the lactation period but also of the change in the resting period and in the proportion of lactating females simultaneously pregnant. Exploitation and response of the population has probably changed the age composition in the striped dolphin more than that of the spotted dolphin.

INTRODUCTION

The Japanese dolphin fishery was widely distributed along the coast of Japan in the last century but has been limited in recent years to Taiji (driving), Izu coast (driving, Fig. 1), Choshi in Chiba Prefecture (hand harpoon), Okinawa (driving and hand harpoon), Tsushima and Goto Islands off northern Kyushu (driving) and Sanriku coast (hand harpoon) (Bureau of Fisheries, 1911; Wilke, Taniwaki and Kuroda, 1953; Ohsumi, 1972; Miyazaki, Kasuya and Nishiwaki, 1974; Kasuya, 1978; 1982; in press; Miyazaki, 1980; 1983). Although the hand harpoon fisheries can take dolphins of most species, large catches of *Stenella* are limited to the first two locations. Details of the recent geographical distribution of the catch were reviewed by Miyazaki (1983).

Driving or netting of the striped dolphin, *Stenella coeruleoalba* (Meyen,

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1833), has been carried out along the Izu coast since the late 19th century (Fig. 1) and at Taiji (33°36′N, 135°56′E) on the Kii Peninsula only in recent years. The stock of the species has declined since World War II (Kasuya, 1976a; Kasuya and Miyazaki, 1982).

The drive fishery for spotted dolphins, *S. attenuata* (Gray, 1846), was started at Arari on the Izu coast in 1959 (Nishiwaki, Nakajima and Kamiya, 1965). Although small number of this species must have been taken with hand harpoon elsewhere (e.g. Taiji), the catches have been relatively small compared with that of the striped dolphin (Miyazaki *et al.*, 1974; Miyazaki, 1983) (Catch of this species at Arari given by Miyazaki *et al.* (1974) erroneously included "Hasunaga" which is now known to be the bottlenose dolphin, *Tursiops truncatus* (Kasuya, 1976b).)

This study analyzes recent changes in life history parameters of the striped dolphin off the Pacific coast of Japan in comparison with those of the less intensely exploited population of spotted dolphins in the same area.

MATERIALS AND METHODS

Materials

The data are based on schools driven at Kawana and Futo on the Izu coast and Taiji on the Kii Peninsula in the period 1952 to 1980 inclusive. Until recently all the dolphin schools driven by the fishery and examined by any biologist were numbered serially by species. Among these schools only those listed in Table 2 were examined by myself; these constituted the main body of the present material (other schools were not directly accessible to me). These were 13 schools of striped dolphins driven on the Izu coast and 13 schools of

TABLE 1. MATERIALS USED IN THIS STUDY

	Species	Striped dolphin	Spotted dolphin
A.	Main data, school analyses	3,000 individuals in 13 schools caught in 1967-1980	1,319 individuals in 13 schools caught in 1970-1980
B.	Ancillary age data	110 individuals in 6 schools caught in 1960-1967	
C.	Ancillary data on neonatal sex ratio (not included in item A)	287 individuals in 16 schools caught in 1952-1970	22 individuals in a school caught in 1975 (school no. 8)
D.	Published data (Kasuya and Miyazaki, 1982, some included in item A)	Data on pregnancy rates 1952 to 1972	

spotted dolphins driven on the Izu coast or at Taiji (A in Table 1; Table 2). With the exceptions of the schools examined by Dr N. Miyazaki in the 1970 to 1973 seasons (included in D in Table 1, used in analysis of annual change of pregnancy rate), schools examined by biologists tended to be relatively larger schools for which processing started or continued on the day following the drive. The processing and examination of dolphins in these schools were done as follows. In the fishing harbour, a group of fishermen netted a part of the dolphin school and landed them (10 to 30 individuals at one time, alive or

TABLE 2. DETAILS OF SCHOOL CLASSIFIED IN ITEM A IN TABLE 1

School no.	Place of driving	Date of driving	Date of data collection	Number of individuals caught	examined	aged	Remarks
	Striped dolphin						
7	Kawana	26, Nov., '67	28, Nov.	3300	150	0[1]	
8	Futo	15, Nov., '68	17-18, Nov.	1680	372	24[1]	
9	Kawana	16, Nov., '68	16-17, Nov.	322	322	104[1]	
10	Kawana	18, Nov., '68	18, Nov.	600	21	0	Item C in Table 1
12	Futo	12, Oct., '70	14, Oct.	330	84	4[1]	
22	Kawana	14, Dec., '71	15, Dec.	903	306	280[1]	
38	Kawana	17, Nov., '72	20, Nov.	411	201	153	
43	Kawana	15, Nov., '73	19, Nov.	414	249	225	
44	Kawana	20, Nov., '73	22, Nov.	1724	466	222	
45	Kawana	22, Nov., '75	24-25, Nov.	1000	399	362	Two schools mixed after driving
46	Kawana	23, Nov., '75	24-25, Nov.				
47	Futo	3, Nov., '76	4, Nov.	735	161	147	
48	Kawana	24, Nov., '77	25, Nov.	795	250	248	
49	Kawana	27, Nov., '80	28, Nov.	431	140	0[2]	Half of the school was driven.
	Spotted dolphin						
1	Kawana	23, Oct., '70	25, Oct.	264	131	52	
2	Kawana	10, Nov., '70	15, Nov.	1381	272	52	
3	Kawana	4, Nov., '72	4, Nov.	189	46	38	
4	Kawana	13, Nov., '72	13, Nov.	192	117	109	
5	Futo	16, Nov., '72	18, Nov.	67	23	23	
6	Taiji	12, Feb., '73	12, Feb.	146	122	115	
7	Taiji	2, Jul., '73	2, Jul.	60	35	21	
8	Taiji	24, Jan., '75	24-25, Jan.	102	102	0	Item C in Table 1
9	Taiji	16, Jan., '76	17, Jan.	91	43	6	
10	Kawana	19, Oct., '76	19, Oct.	377	45	44	
12	Futo	25, Nov., '77	26-27, Oct.	344	119	118	
13	Futo	13, Dec., '78	14-15, Dec.	756	166	151	
14	Kawana	18, Nov., '80	18, Nov.	308	100	0[2]	
15	Kawana	20, Nov., '80	21, Nov.	750	100	0[2]	

1) Aged using dentine layers: individuals over 11 layers excluded.

2) Age determination not completed.

dead). Another group of fishermen killed the landed animals if necessary and removed the viscera. Biologists (usually a group of three or four persons) working among the latter group of fishermen collected the required data and samples. As soon as that group of dolphins was handled, the next group was landed. From 500 to 1,000 individuals were processed in a day. We tried not to bias our sample by choosing animals of any particular growth or reproductive stages; this was helped by the need to process animals very quickly. The dolphins in the harbour were completely mixed by the repeated operation, and no difference of composition was detected between landings from one school (confirmed in two days of operations on School no. 8). Therefore I believe that the sample was representative of the schools examined.

Another small body of data on the striped dolphin was collected on the Izu coast by other biologists in the period not covered by the above data; these were aged by myself and used in an analysis of recent change in age at attainment of sexual maturity (B in Table 1).

The estimation of neonatal sex ratio is based on 287 striped and 22 spotted dolphins (juveniles) examined on the Izu coast by various biologists in 1952 to 1975 (C in Table 1) in addition to those mentioned above (A in Table 1). Pregnancy rate data on the striped dolphin in Table 3 of Kasuya and Miyazaki (1982) were combined with those collected more recently and used for the analysis of year-to-year change in pregnancy rate.

Methods

Age was determined by myself using growth layers in dentine and/or cementum. Cemental counts were used only for individuals with closed pulp cavities. The method of preparation and reading is described in Kasuya (1976a) and Perrin and Myrick (1980). The deposition rate of these layers was shown to be annual for spotted dolphin and assumed to be annual for the striped dolphin based on the similarity of life history in the two species (Kasuya, 1976a). Ages betwen n and n+1 years are represented by n+0.5 years (n being an integer).

Sexual maturity of females was determined by the presence of a corpus luteum or albicans in the ovaries.

Reproductive status of female dolphins was classified into four stages: resting, pregnant, pregnant and simultaneously lactating, and lactating. The mean length of the reproductive cycle was calculated from the proportion of females at each stage, with necessary corrections for sample bias (see REPRODUCTIVE CYCLE) and assuming a gestation time of 12 months for the striped dolphin (Kasuya, 1972. Although Miyazaki (1984) gave estimation of 13.4 months, the difference is not important because the present study analyzes the trend rather than the absolute values of the reproductive cycle) and 11.24 months for the spotted dolphin (Kasuya, Miyazaki and Dawbin, 1974). The simultaneously pregnant and lactating class was treated as representing an independent phase, and its mean period was estimated as for the other phases.

Pregnancy was determined in 10 schools (nos 7, 8, 9, 43 through 49) by the presence of fetus. However, nonpregnant females of the striped dolphin having a corpus luteum were recorded as pregnant in other schools, for which ovaries were not examined by myself. This overestimates the pregnancy rate. Therefore these data were adjusted, using the proportion of non-pregnant females having a corpus luteum of ovulation in the former schools. Females having more than one corpus luteum of ovulation were rare, and they were dealt as those having one.

Change of fishing operation and scope of samples

Kasuya and Miyazaki (1982) briefly described historical changes in the dolphin fishery along the Izu coast, where most of the present samples were obtained.

Enoshima was once known by the dolphin product (Matsuse, ca 1645, cited by Hawley, 1960, p.181). This is the oldest record of the possible dolphin fishery on the coast of Sagami Bay available to me (Fig. 1).

Kawana village, one of the two places now operating a dolphin fishery on the Izu coast, is known to have established a hunting team in 1888 (recorded on a stone monument at Kawana built in 1922). Another record (Bureau of Fisheries, 1911) shows, however, that the fishery was common in the area in those days and the dolphin species hunted were the Pacific white-sided dolphin, *Lagenorhynchus obliquidens* Gill, 1865, (which is not now hunted because of difficulties in driving it), the short-finned pilot whale, *Globicephala macrorhynchus* Gray, 1846, and the striped dolphin. The main changes in the fisheries have been expansion of the maximum operational distance, through improvement of fishing vessels, from coastal waters (a few nautical miles offshore), to Oshima Island (20 nm), and then to occasional searching up to 50 nm offshore, and a decrease in the number of driving groups (teams of fishermen) on the coast (Table 3). The effect of such changes in the operation on the present study was ignored, because (1) the operation had expanded to the waters adjacent to Oshima Island (20 nm) before the collection of the present materials started in 1952, (2) drives from such a far distance as 50 nm seemed have not been recorded, and (3) all the present samples were obtained from schools taken in Sagami Bay or within a few nautical miles of Oshima Island (25 nm from port, Fig. 1).

At Taiji, the catch of these species was usually below 1,000 individuals per year (Miyazaki *et al.*, 1974). It increased after the establishment of a driveing team in 1973 (Miyazaki, 1980; 1983) and a second team in 1980. Only four schools of spotted dolphins were examined at Taiji for the present study (Table 2). Although there is no direct evidence, the spotted dolphins caught in the two locations are assumed to belong to one population, following the conclusion of Miyazaki *et al.* (1974), deduced from comparison of seasonal changes in oceanographical conditions and the distribution of the dolphins.

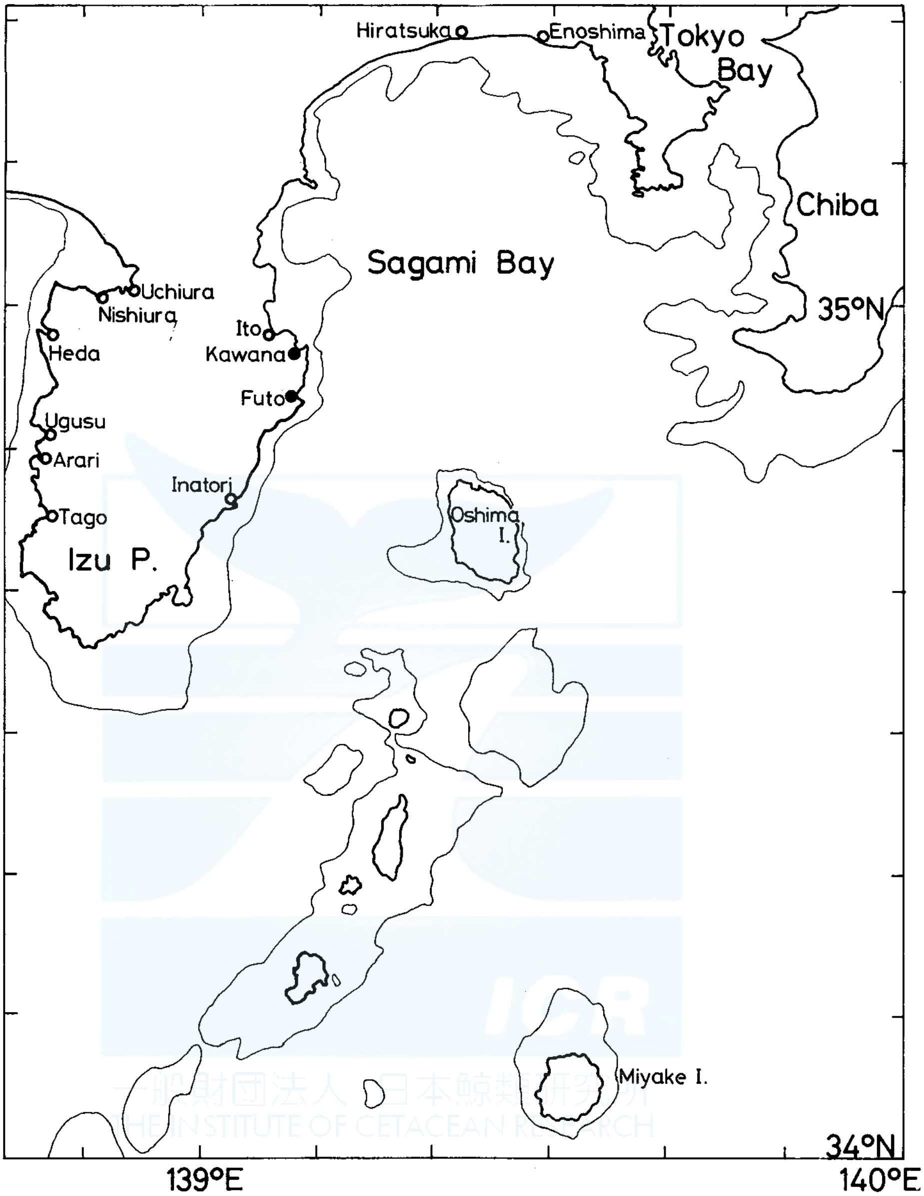

Fig. 1. Map of the area for the dolphin fishery off Izu coast and adjacent area. Thick solid line indicates coastline, and thin solid line the 200 m depth. Ten locations of previous operation (open circle) and two places of present operation (closed circle) are indicated. Types of the fishery were driving (Arari, Futo, Heda, Inatori, Ito, Kawana, Nishiura, Uchiura, Ugusu and Tago), dragnet (Hiratsuka), and unrecorded (Enoshima). (Bureau of Fish., 1911; Hawley, 1960; Kasuya, unpub.)

TABLE 3. CHRONOLOGY OF THE BIOLOGICAL DATA AND DETAILS OF THE FISHERIES FOR STRIPED AND SPOTTED DOLPHINS IN JAPANESE WATERS

year	Dolphin fishery	Biological data
1911	Common on the Izu coast.	
1920's	Expansion of fishing ground to Oshima I. (20 nm) with introduction of motor vessels.	Births of oldest dolphins in the present sample.
1945-'50	Postwar expansion of catch at Arari, Futo, Inatori* and Kawana.	
1952		Start of monitoring of pregnancy rate, striped dolphin.
1956		First cohort examined for annual change of maturation age.
1959	First driving of spotted dolphin.	
1961	Last significant catch (> 100/yr) at Arari on Izu coast. Fishery continues at Kawana and Futo.	
1962	Expansion of searching area close to Miyake I. (50 nm) with the introduction of high-speed boats.	
1968	Last two driving teams on Izu coast joined in operation.	
1970		Last cohort examined for annual change of maturation age.
1973	Start of driving fishery for *Stenella* at Taiji.	Start of monitoring of pregnancy rate, spotted dolphin.
1980	Establish of 2nd driving team at Taiji.	Last data of present study.
1982	Two teams at Taiji joined and set catch limits by species, which were not reached by following operations.	

* Inatori ceased operation between 1945 and 1961.

SCHOOL VARIATION

Fig. 2 shows the age frequency distribution for the eight striped dolphin schools analyzed in this study. Four schools (nos 7, 8, 9 and 12) were excluded from Fig. 2. These were breeding schools containing old individuals, but age for these was determined using only dentinal layers and individual ages over 11 growth layers (presumably years) are often unreliable (Kasuya, 1976a). Data from School no. 22 were for 62 immature females below eight years and 218 males below 13 years (mostly immature); this is considered to be an immature school as described by Miyazaki and Nishiwaki (1978), who listed more examples of this types of school. Six other schools contained immature

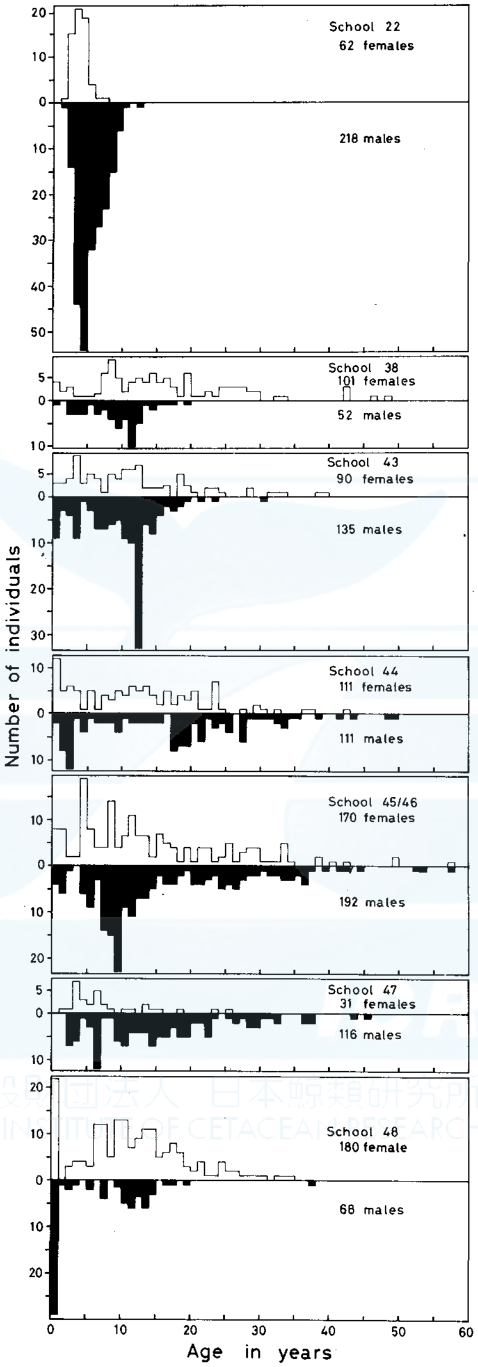

Fig. 2. Age composition of some of the striped dolphin schools used in this study. Only schools with large sample size and listed in item A in Table 1 are indicated.

and mature individuals of both sexes and were considered to be breeding schools. These latter schools show peaks and troughs at various ages below 10 years. This, together with the presence of immature schools, suggests that a group of immature individuals in a breeding school may occasionally segregate to form an immature school (Kasuya, 1972; Miyazaki and Nishiwaki, 1978). This can cause an important bias in the estimates of age frequency and sex ratio of immature individuals.

Fig. 3 shows the age composition of 10 spotted dolphin schools (excluding School 6 that is represented by a small sample). Although they do not include immature schools as observed in the striped dolphin, the presence of troughs at ages below 10 years and the lack of dolphins at around five years of age (ages between weaning and attainment of sexual maturity, see AGE AT SEXUAL MATURITY) in the total age frequency (Fig. 9) suggest the possibility that juveniles of both sexes are segregating from these breeding schools (Kasuya *et al.*, 1974).

Postnatal sex ratios in the schools of striped and spotted dolphins are shown in Table 4. The percentage of females in the sample varies from 22 to 73% (x̄ = 50.5%, SD = 16.4) in the striped dolphin, and from 44 to 66% (x̄ = 57.5%, SD = 6.9) in the spotted dolphin, with smaller between-school variation in the latter species.

Similar analyses were carried out on proportions of sexually mature

TABLE 4. SCHOOL VARIATION IN POSTNATAL SEX RATIO

Striped dolphin (1967-'80)				Spotted dolphin (1970-'80)			
School no.	Males no.	Females		School no.	Males no.	Females	
		no.	%			no.	%
7	51	99	66.0	1	50	81	61.8
8	134	238	63.9	2	108	164	60.2
9	182	140	43.4	3	23	23	50.0
12	35	49	58.3	4	58	59	50.4
22	235	71	23.2	5	8	15	65.2
38	73	128	63.7	6	50	72	59.0
43	146	103	41.3	7	17	18	51.4
44	256	210	45.0	9	15	28	65.1
45/46	206	193	48.3	10	19	26	57.7
47	126	35	21.7	12	40	79	66.3
48	68	182	72.8	13	63	103	62.0
49	57	83	59.2	14	45	55	55.0
				15	56	44	44.0
Total	1,569	1,531	49.4	Total	552	767	58.2
Mean			50.5	Mean			57.5
SD			16.4	SD			6.9
CV			0.3	CV			0.1

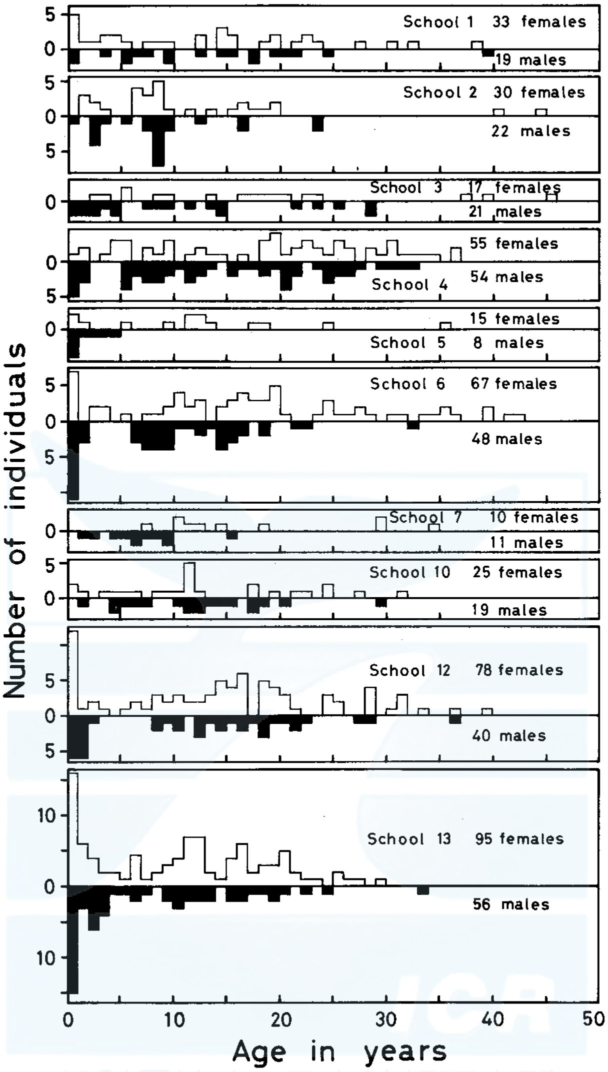

Fig. 3. Age compositions of some of the spotted dolphin schools used in this study. Only schools with large sample size and listed in item A in Table 1 are indicated.

females and reproductive status of adult females (Tables 5 and 6). The between-school variation of these parameters was consistently greater in the striped dolphin, even accounting for differences in school-size frequencies. This means that the between-school variation of these parameters is greater in the striped dolphin schools and suggests that larger sample size may be required for the striped dolphins in order to estimate structure of the population migrating to the fishing ground.

TABLE 5. SCHOOL VARIATION IN FEMALE MATURITY RATE

Striped dolphin (1967-'80)				Spotted dolphin (1970-'80)			
School no.	Immature no.	Mature no.	Mature %	School no.	Immature no.	Mature no.	Mature %
7	46	51	52.5	1	24	48	66.6
8	41	195	82.6	2	67	87	56.4
9	113	20	15.0	3	5	18	78.2
12	15	33	68.7	4	15	42	73.6
22	71	0	0.0	5	5	10	66.6
38	23	103	81.7	6	13	56	81.1
43	38	63	62.3	7	3	15	83.3
44	66	143	68.4	9	10	18	64.2
45/46	69	115	62.5	10	8	18	69.2
47	22	10	31.2	12	22	56	71.7
48	53	129	70.8	13	40	62	60.7
49	31	52	62.6	14	21	31	59.6
				15	13	30	69.7
Total	588	914	60.8	Total	246	491	66.6
Mean			54.8	Mean			69.3
SD			26.0	SD			8.2
CV			0.5	CV			0.1

TABLE 6. SCHOOL VARIATION IN FEMALE REPRODUCTIVE STATUS

Striped dolphin (1967-'80)					Spotted dolphin (1970-'80)				
School no.	Preg	PL	Lact	Rest	School no.	Preg	PL	Lact	Rest
7	2	0	40	9	1	15	3	18	0
8	78	2	86	22	2	17	2	47	17
9	0	0	18	2	3	2	0	15	1
12	7	0	20	4	4	3	1	28	7
22	0	0	0	0	5	4	0	4	0
38	79	1	7	2	6	4	0	21	13
43	20	0	22	5	7	2	0	4	7
44	58	21	47	6	9	1	0	15	1
45/46	34	0	45	19	10	3	1	13	1
47	2	2	1	4	12	11	1	39	5
48	29	9	81	6	13	13	5	36	5
49	19	12	15	5	14	9	2	16	4
					15	1	1	21	6
Total, no.	328	47	382	84	Total, no.	85	16	277	67
Total, %	39.0	5.6	45.4	10.0	Total, %	19.1	3.6	62.2	15.1
Mean, %	32.8	6.5	47.3	13.4	Mean, %	19.5	3.0	62.5	15.0
SD, %	23.8	9.5	25.9	11.5	SD, %	13.7	3.2	15.6	15.1
CV, %	0.7	1.5	0.5	0.9	CV, %	0.7	1.1	0.2	1.0

Preg: pregnant, PL: pregnant and simultaneously lactating, Lact: lactating, Rest: resting

SEX RATIO

Neonatal sex ratio

Neonatal sex ratio was estimated from the sex ratio of fetuses and postnatal individuals below one year of age. Fetuses below 5 cm were excluded, because sex identification is unreliable. All other postnatal individuals below 164 cm (striped dolphin) or below 142 cm (spotted dolphin) were included. These correspond to the age of one year on the respective mean growth curves (Kasuya *et al.*, 1974; Kasuya, 1976a). One of the reasons for the inclusion of calves is to increase the sample size (for further discussions see Kasuya and Marsh, 1984). The results are shown in Table 7.

In the striped dolphin, the sex ratio was not significantly different from 1:1 in all years, in both fetuses and calves (Chi-square test, $p>0.9$). The 841 sexed fetuses and calves yield an estimation of proportion of neonate females of 50.4%.

TABLE 7. NEONATAL SEX RATIO

Species and Season	Fetuses	Calves	Total	
	no.	no.	no.	%
Striped dolphin				
1950-1959 females	5	57	62	51.66
males	6	52	58	
1960-1969 females	55	120	175	49.71
males	53	124	177	
1970-1980 females	103	84	187	50.67
males	93	89	182	
Total females	163	261	424	50.41
males	152	265	417	
Spotted dolphin				
1970-1980 females	48	83	131	44.86
males	62	99	161	

In the sample of spotted dolphins, there were fewer females than males in both fetal and postnatal stages below one year. The neonatal sex ratio estimated from 292 fetuses and calves is 44.9% (females). This is not significantly different from parity ($0.05<p<0.1$).

No change in neonatal sex ratio was detected in either species during the study period.

Postnatal sex ratio

Fig. 4 shows age-related changes in the postnatal sex ratio expressed by the proportion of females. In the striped dolphin, the ratio was low between 2 and 10 years of age. This is an effect of the data from an immature school (no. 22), where males predominated. After this age, change in the sex ratio is slight, the ratio being approximately 1:1.

The spotted dolphin showed different changes. The proportion of females steadily increased till the age of 40 years. This reflects either a higher mortality rate or segregation of adult males (see AGE COMPOSITION AND MORTALITY).

No temporal trend in the postnatal sex ratio was detected in either of the two species.

AGE AT SEXUAL MATURITY

Method

Female age at the attainment of sexual maturity was analyzed for each cohort (defined as the individuals born in the same year, determined from date of death and age at death).

The process is explained below using the following hypothetical age-maturity composition of three years' samples.

Age at death (yr)		0.5	1.5	2.5	3.5	Total
1980 catch,	immature	50	30	10	0	90
	mature	0	10	15	20	45
1981 catch,	immature	100	60	20	0	180
	mature	0	20	30	40	90
1982 catch,	immature	200	120	40	0	360
	mature	0	40	60	80	180

The above data yield the ratios of immature : mature individuals in each cohort at various ages as follows (catch year in parentheses):

Age at death (yr)	0.5	1.5	2.5	3.5
1979 cohort	–	30:10 ('80)	20:30 ('81)	0:80 ('82)
1980 cohort	50:0 ('80)	60:20 ('81)	40:60 ('82)	–

Then the proportion of sexually mature individuals of a cohort at different ages are calculated from these figures. This method assumes that there is no selection in the fishery between mature and immature individuals of the same age caught in a given fishing season. This is certainly not the case for the striped dolphin and possibly also the spotted dolphin (see SCHOOL VARIATION).

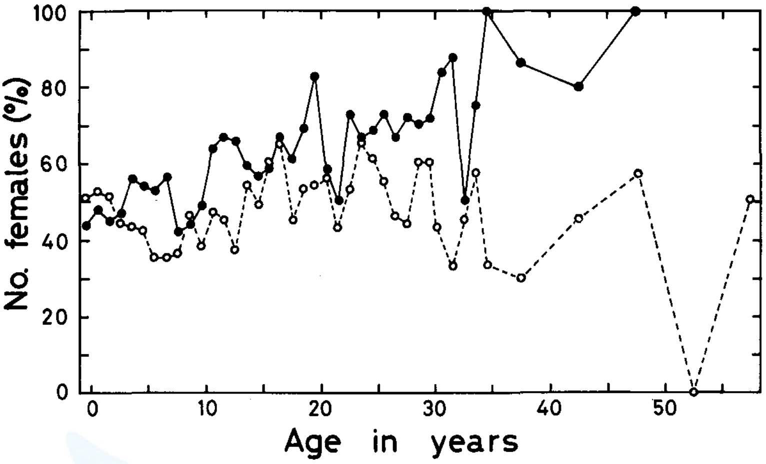

Fig. 4. Age specific sex ratio of striped (open circle and dotted line) and spotted dolphin (closed circle and solid line). Eight striped dolphin schools (nos. 22, 38 and 43 through 48) and 11 spotted dolphin schools (nos. 1 through 13, excluding 8 and 11) are used.

However, the method has the advantage of being free from the sort of bias that occurs, for example, when mean age at sexual maturation is estimated from the transition phase in the earplug of baleen whales (Lockyer, 1972; Cook and de la Mare, 1983; Kato, 1983; Sakuramoto, Kato and Tanaka, 1984).

The age ranges in samples for the earliest cohort and latest cohort were over four years (1950 cohort) and under eight years (1970 cohort), respectively, in the striped dolphin, and over nine years (1961 cohort) and under seven years (1972 cohort) in the spotted dolphin. These earliest and latest cohorts were specified so as to include both mature and immature individuals.

I analyze below the relationships between year of birth and the average age at the attainment of sexual maturity, age of the youngest sexually mature female in the sample, and age of the oldest immature female in the sample. These indices (especially minimum age at the attainment of sexual maturity) seem to be sensitive in some mammals to environmental changes (Laws, Parker and Johnstone, 1975; Ohsumi, in press).

There are several methods for calculating "average" age at attainment of sexual maturity; each can yield different results (DeMaster, 1984). In the present study, it was estimated as the age at 50%-mature on a linear regression weighted by sample size. Even though the proportion of sexually mature individuals may not increase strictly linearly with increasing age, the error can be minimized by using in the regression only the points in the 50%-mature region. Because of the limitation of samples, the analysis was done combining

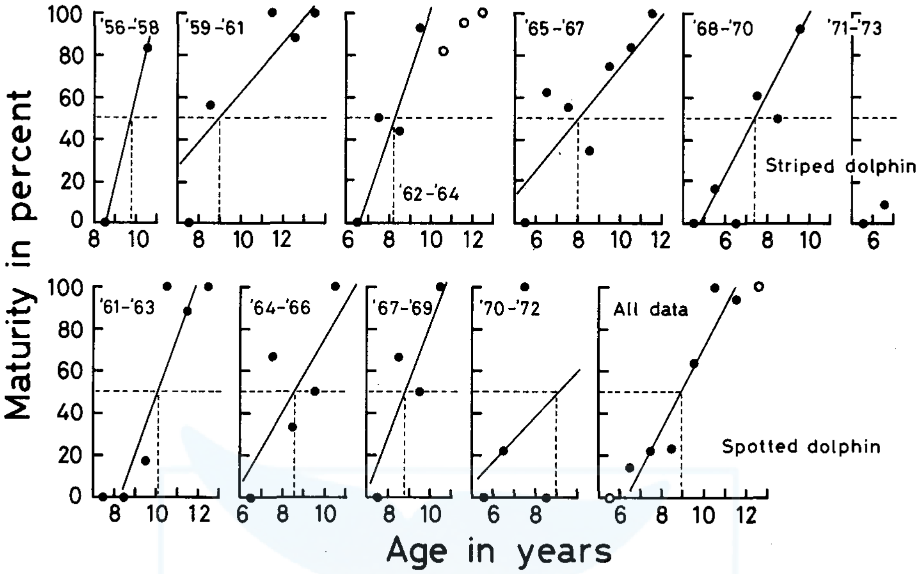

Fig. 5. Estimation of age when half of the females are sexually mature. Cohorts of three successive birth years are grouped. The least-squares regressions are calculated for points indicated by closed circle and weighted by sample size.

data for three contiguous cohorts, yielding five estimates for the striped dolphin and four for the spotted dolphin (Fig. 5).

Striped dolphin, age at sexual maturity

The average age at sexual maturation was estimated at 9.7 years for the 1956-'58 cohorts. It steadily declined to 7.4 years for the 1968-'70 cohorts (Fig. 6). The least-squares regression between the mean age at attainment of sexual maturity (Y, year) and the calendar year of birth (X, using the central year for each cohort group) is expressed by

$$Y = -0.183X + 367.70, \qquad 1957 \leq x \leq 1969, \ r = 0.99$$

Equation 1

The slope is significantly different from zero (t-test, $0.001 < p < 0.01$).

In any of the cohorts before 1962, the observed minimum age of mature females and the maximum age of immature females do not overlap. This is a result of small sample size, as is the apparent increase in maximum age of immature females.

However, in the recent cohorts where sample is large, the age of the youngest mature female seems to be declining (Fig. 6). It was between seven and eight years in the cohorts of 1963 to 1966, but in the more recent cohorts some females matured before six years of age. Also, the age of the oldest im-

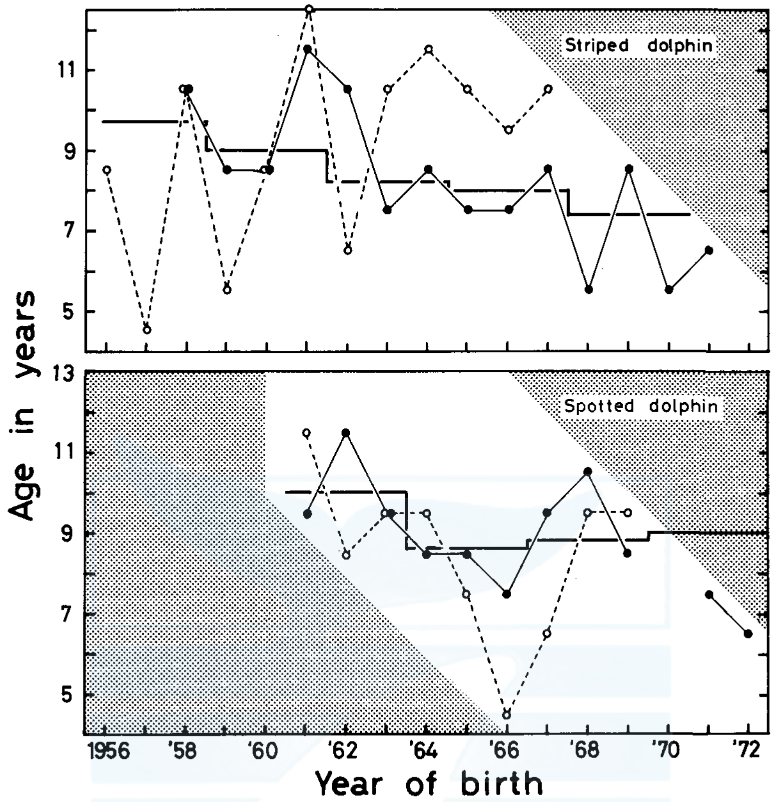

Fig. 6. Annual changes of the age where 50% of females are sexually mature (thick solid line), of the age of the youngest mature female (closed circle and solid line), and of the age of the oldest immature female (open circle and dotted line). Shaded area indicate the ages not included in the analysis.

mature female appears to have declined after the 1963 cohort, but the change is less clear than that of the maturation age.

Spotted dolphin, age at sexual maturity

The average age at sexual maturity for females ranged between 8.6 years (1964-'66 cohorts) and 10.1 years (1961-'63 cohorts) (Fig. 5). The regression coefficient of average age at sexual maturity on year of birth was not significantly different from zero ($p > 0.1$) (Fig. 6.)

A least-squares regression between age of females (X, year) and maturity (Y, %) for all data from 1961 to 1972 yields

$$Y = 27.455X - 194.70, \qquad 6.5 \leq X \leq 11.5, \ r = 0.95$$

Equation 2

Y = 50 when X = 8.9 (Fig. 5). This is not different from the value of 9.0 years obtained in earlier analyses (Kasuya, 1976a).

The age of the youngest mature female was over eight years for the cohorts before 1965, but in more recent cohorts there were some females that matured at an age below seven years

REPRODUCTIVE CYCLE

Mean reproductive cycle

Two kinds of corrections were made before estimating the length of the average reproductive cycle. The first was to separate true pregnant females from nonpregnant females having corpus luteum of ovulation.

For the striped dolphin, only the data for 10 schools (nos 7, 8, 9 and 43 through 49) distinguish between the two cases. The numbers of pregnant, pregnant & lactating, lactating and resting females in these schools were 242, 47, 354 and 78, respectively. Among these, the individuals with corpus luteum of ovulation but no fetus number 15 (14 resting and one lactating). I therefore estimate that (242+47)/(242+47+15) or 0.951 of the "pregnant females" from other schools were probably actually pregnant.

For the spotted dolphin, all the pregnant females were distinguished from nonpregnant females having a corpus luteum of ovulation. The true pregnancies were 0.971 of the number with corpus luteum, close to the result for the striped dolphin.

The second correction is for possible bias in the apparent pregnancy rate. Table 8 shows the number of pregnant females in the sample (corrected as explained above) and the number of calves below a body length corresponding to the age of one year. Since the length of gestation is about one year, the nursing period lasts more than one year, and breeding in these species is seasonally diffuse (Kasuya, 1972; Kasuya *et al.*, 1974; Miyazaki, 1977; 1984), the relative abundances of these two states are expected to be similar (juvenile mortality is ignored). However, they are rather dissimilar, and the differences are opposite in the two species, i.e. pregnant females exceed calves in the striped dolphin sample, but calves exceed pregnant females in the spotted dolphin sample.

I consider the main cause of this discrepancy to be sample bias resulting from the difference in catchability of schools at the two reproductive states (i.e. difference in timing of migration to the fishing ground, geographical segregation, or timing of the breeding peaks). The small number of schools examined could also be a problem. Inaccurate ageing of juvenile is not a likely cause, because the ageing techniques are the same for the two species (for discussion of juvenile growth rates in these species, see Kasuya, 1972; Kasuya *et al.*, 1974; Perrin, Coe and Zweifell, 1976). A similar, but more pronounced, discrepancy was found in a sample of the short-finned pilot whale, *Globicephala macrorhynchus*, caught by the drive fishery (Kasuya and Marsh, 1984).

TABLE 8. COMPARISON OF NUMBER OF PREGNANT FEMALES AND CALVES BELOW AGE OF ONE YEAR, FOR SCHOOLS IN TABLE 2

	Confirmed	Extrapolated*	Total
Striped dolphin (1967-'80)			
Number of pregnant females**	328	34.8	412.6
Females pregnant and lactating**	47	2.8	
Calves at or below 164 cm	262		262.0
Difference			+150.6
Spotted dolphin (1970-'80)			
Number of pregnant females**	85	10.0	112.5
Females pregnant and lactating**	16	1.5	
Calves at or below 142 cm	172		172.0
Difference			−59.5

*: Extrapolated for the mature females examined but without record of reproductive status.
**: Nonpregnant females having corpus luteum of ovulation excluded.

TABLE 9. ESTIMATION OF TRUE REPRODUCTIVE CYCLE, FOR SCHOOLS IN TABLE 2.

	No. individuals		Proportion (%)		Length (year)	
	apparent*	corrected	apparent*	corrected	apparent*	corrected
Striped dolphin (1967-'80)						
Pregnant	362.8	212.2- 362.8	39.0	29.8- 34.1	0.87	0.82-0.88
Preg. and lactating	49.8	49.8- 49.8	5.6	6.5- 4.7	0.13	0.18-0.12
Lactating	409.8	409.8- 560.4	45.6	53.7- 52.6	1.02	1.48-1.36
Resting	91.6	91.6- 91.6	10.0	12.0- 8.6	0.22	0.33-0.22
Total	914.0	763.4-1064.6	100.0	100.0-100.0	2.24	2.81-2.58
Spotted dolphin (1970-'80)						
Pregnant	95.0	95.0- 154.5	19.1	22.0- 28.1	0.79	0.79-0.84
Preg. and lactating	17.5	17.5- 17.5	3.6	4.1- 3.2	0.15	0.15-0.09
Lactating	302.3	242.8- 302.3	62.2	56.3- 54.9	2.57	2.02-1.65
Resting	76.2	76.2- 76.2	15.1	17.6- 13.8	0.62	0.63-0.42
Total	491.0	431.5- 550.5	100.0	100.0-100.0	4.13	3.59-3.00

*Corrected for small number of mature females of unknown reproductive status.

The proportions of the reproductive states were adjusted for the striped dolphin in two alternative ways to yield a range of estimates: by assuming that pregnant females were overrepresented or that calves (i.e. number of lactating females) were underrepresented (Table 9). For example, the corrected number of the pregnant striped dolphins in Table 9 was obtained using figures in Table 8 as 362.8-150.6=212.2 (assuming overrepresentation of pregnant females), and the lactaing females as 49.8+150.6=560.4 (assuming the underrepresentation of lactating females). The latter assumes that females which have been lactating less than one year and those lactating for more than one year are biased in the same way in the present sample. The reverse was assumed for the spotted dolphin. The resting females are thus assumed to be schooling with lactating females or with pregnant females. This may cover the probable range of bias. Table 9 also shows the mean length of each reproductive stage.

With the above correction, the length of lactation (including lactation accompanied by pregnancy) in the striped dolphin increases about 29 to 44% over the uncorrected value, and the resting period is also slightly extended. On the other hand, in the spotted dolphin, the length of lactation is shortened by about 20 to 36% from the uncorrected figure, and the resting period is slightly shortened.

Thus the mean breeding cycle is extended in the striped dolphin from 2.24 years (uncorrected) to 2.58 or 2.81 years. Since there is no reason to prefer one of these two figures, I tentatively consider that the true calving interval will be between the two, or close to their mean (2.70 years). This is 20.3% longer than the uncorrected figure. The corrected calving interval for the spotted dolphin is about 3.30 years, which is about 20.2% less than the uncorrected figure.

This correction for sample bias in apparent pregnancy rate should be considered rather tentative because it does not take into account uncertainties about mortality and growth of juveniles.

Age-specific reproductive cycle

Fig. 7 shows the age specific reproductive cycles for female striped and spotted dolphins. The mean length of each reporoductive stage was claculated using the above described method, but no correction of sample bias in reproductive states rate was done. Five or more year-classes were grouped for each estimate.

Striped dolphin. The oldest female was 57.5 years old and was resting. The two next oldest females were 49.5 years old (one lactating and the other resting), and the oldest (confirmed) pregnant female was 48.5 years old. The oldest simultaneously pregnant and lactating (PL) female was 42.5 years old, but the next oldest female of this status was only 30.5 years old.

The correlation between the length of lactation (Y, year) and age (X, year) is not high, but the data for animals less than 45 years old give the following least-squares regression,

$$Y = 0.0328X + 0.40, \quad X<45, \quad r=0.76, \qquad \text{Equation 3}$$

and the slope is significantly different from zero (t-test, $0.02<p<0.05$).

The resting period (Y, year) is very short in young females being less than 0.2 years, but increases after 30 years of age. The correlation is shown by

$$Y = 0.0293X - 0.49, \quad X>30, \quad r=0.91 \qquad \text{Equation 4}$$

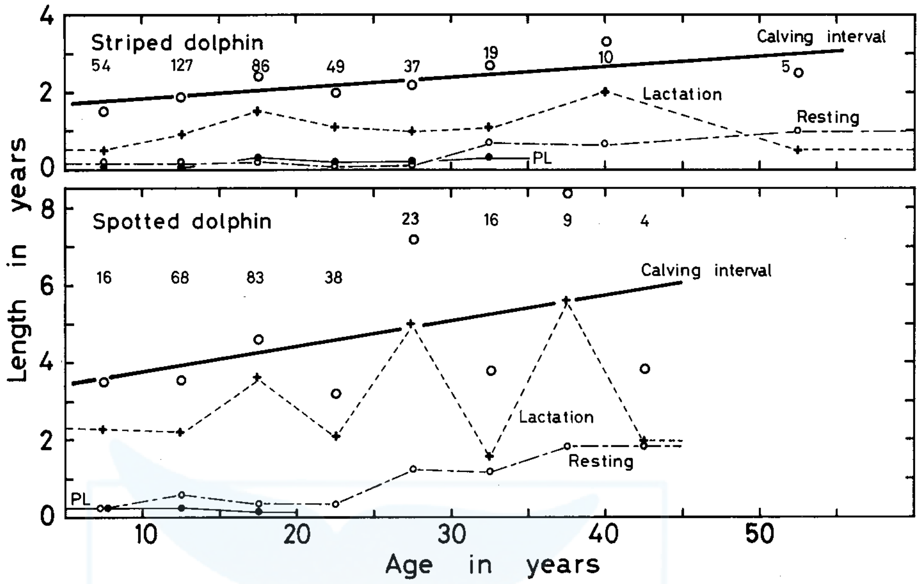

Fig. 7. Age specific reproductive cycle of female striped and spotted dolphins. Contiguous 5, 10 or 15 age classes are grouped for the analysis. Data used are from eight striped dolphin schools (nos 22, 38 and 43 through 48), and 11 spotted dolphin schools (nos 1 to 13, excluding 8 and 11). Figures are calculated from the ratio to pregnant females and are not corrected for sample bias of reproductive stages. Females with corpus luteum of ovulation are not dealt as pregnant. Numerals at the top indicate sample size.

and the regression coefficient is significantly different from zero ($0.02 < p < 0.05$).

The mean length of calving interval (Y, year) shows high correlation for all age range (X, year), giving a least-squares regression,

$$Y = 0.0273X + 1.60, \quad 5 < X < 55, \quad r=0.73, \qquad \text{Equation 5}$$

and the slope is significantly different from zero ($0.02 < p < 0.05$).

The age above which there are no pregnant and simultaneously lactating females coincides with an increase of the resting period from below 0.2 year to about one year. This is an indication that the reproductive potential of female striped dolphins declines after about 30 years.

Spotted dolphin. The oldest female spotted dolphin was 45.5 years old and was lactating. The next oldest female (44.5 years) was resting, and the oldest pregnant female was 40.5 years old. PL females were 20.5 years old or less.

Although the length of lactation seems to be positively correlated with age, the slope of a least-squares regression is not significantly different from zero ($0.8 < p < 0.9$).

The resting stage (Y, year) is short (<0.6 year) below the age (X, year) of 25 years, after which it increases considerably with age. The least-squares regression fitted for points above 20 years is expressed by

$$Y = 0.886X - 13.18, \quad X > 20, \quad r=0.92, \qquad \text{Equation 6}$$

and the slope is significantly different from zero (t-test, $0.02 < p < 0.05$).

The mean calving interval also appears to show positive correlation with age but the linear-regression is insignificant ($0.3 < p < 0.5$).

As described above, the only significant age-related changes in reproductive parameters in female spotted dolphins are in the abundance of PL females and resting females. These two parameters show a negative correlation with each other, as observed in the striped dolphin. Therefore, it is reasonable to conclude that reproductive potential in the species declines with age. The absence of significant correlation between age and calving interval or lactation length may be an artifact of small sample size.

Conclusion. The longevity of the female striped dolphin is probably about 10 years greater than that in the spotted dolphin, and the stage of low reproductive potential (indicated by rapid increase of resting females and disappearance of PL females) starts later in the striped dolphin. The absolute value of reproductive potential of the striped dolphin remain higher even with great age (indicated by the shorter lengths of resting period and calving interval). These differences are at odds with general tendency in mammals for a longer-lived species to have lower annual productivity. Thus I suspect that the difference in the reproductive parameters between the two species may not be entirely due to species-specific differences but relate in some degree to differences in history of exploitation.

Historical change in reproductive cycle

Fig. 8 shows the relationship between mean length of calving cycle (and its components) and the date of capture. Because variation among schools in the proportions for the reproductive stages was large, as mentioned above, years represented by only one school were combined with successive seasons in most cases to reduce year-to-year fluctuation. No correction for sample bias in reproductive states was made.

Striped dolphin. As mentioned above (see MATERIALS AND METHODS), most of the data for the striped dolphin do not distinguish pregnant females from nonpregnant females with corpus luteum of ovulation. Therefore in all the analyses of the striped dolphin in this section all females having corpus luteum are dealt as pregnant. The true number of pregnant females is about 0.951 of the females having a corpus luteum (see Mean reproductive cycle of this section).

Although there is an apparent downward trend for the striped dolphin, only one component of the cycle, proportion of PL females, exhibits a statistically significant increasing trend, and that only in recent years. Correlation of

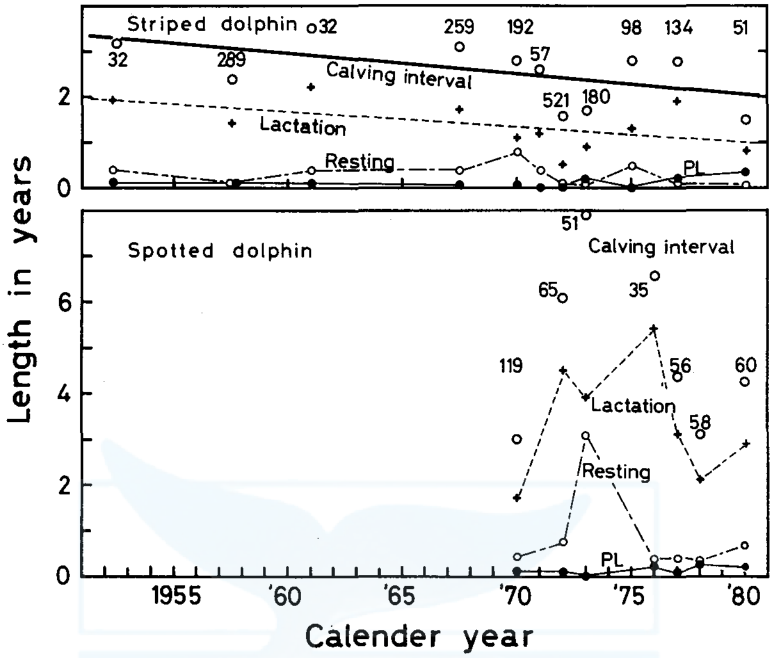

Fig. 8. Annual change in length of reproductive cycle of female striped and spotted dolphins. The data for striped dolphins in the years 1952, '53, '57, '58, '61, '70, '71 and '72 are based on Kasuya and Miyazaki (1982). Figures are calculated from the proportion of pregnant females and are not corrected for sample bias of proportion of reproductive stages. For the striped dolphin, all the females having a corpus luteum of ovulation are dealt as pregnant. Numerals at the top indicate sample size.

the mean length of the PL stage (Y in years, uncorrected for the bias due to segregation) with year (X) for the eight seasons after 1966) is expressed by

$$Y = 2.7590X - 50.25, \quad X \geq 1967, \quad r=0.75, \qquad \text{Equation 7}$$

and the slope is significantly different from zero (t-test, $0.02 < p < 0.05$). This result should be confirmed by collecting more data, because it is not based on a very long period of time.

The mean length of the resting period seems to have a downward trend in recent years, but the regression coefficient is not significantly different from zero ($0.1 < p < 0.2$).

The mean length of lactation also shows an apparent downward trend, but the slope is not significantly different from zero ($0.1 < p < 0.2$).

The mean calving interval (Y in year, uncorrected for bias of corpus luteum of ovulation and segregation) in relation to season (X, after 1952) is shown by the least-squares regression

$$Y = -0.04440X + 89.97, \quad X \geq 1952, \quad r=0.55, \qquad \text{Equation 8}$$

Although the regression coefficient is not significantly different from zero ($0.05 < p < 0.1$), the general downward trend in many of the reproductive parameters mentioned above suggest that more data will prove it significant. This equation and the correction factors for the underrepresentation of lactating female (1.203) and for nonpregnant females having a corpus luteum of ovulation (0.951) give the following estimates of the possible calving interval for the species.

1955 season: 3.160 · 1.203 / 0.951 = 4.00 years
1960 season: 2.938 · 1.203 / 0.951 = 3.72 years
1977 season: 2.183 · 1.203 / 0.951 = 2.76 years

The mean calving interval could have decreased about 1.24 years in the past 22 years between 1955 and 1977.

Spotted dolphin. There are no statistically significant trends over the period sampled.

AGE COMPOSITION AND MORTALITY

Catch data can be used for estimation of mortality rates only when a fishery does not select certain age classes and when the annual recruitment and population size are constant (Caughley, 1966). These conditions are not met for the striped and spotted dolphins. Therefore, the present effort was directed to comparing the age composition of the striped dolphin with that of the less intensively exploited spotted dolphin to attempt to elucidate the possible effect of the longer-term fishery on the age composition of the striped dolphin.

Spotted dolphin

The frequency of juveniles in the present sample is unreasonably low (Fig. 9). This is presumably due to segregation of weaned juveniles from the breeding schools that formed the present sample. Males of adult age classes are consistently fewer than the females of the same age. This could be due to segregation and/or higher mortality rates in males. The two oldest females were aged at 45.5 and 44.5 years, respectively, and the oldest male at 42.5 years. This suggests a slight longer longevity in females.

Caughley (1966; 1977) reviewed the age composition of wild-mammal populations and concluded that mortality rate is dependent on age, i.e., a high juvenile mortality rate that decreases with age, and a lower adult mortality rate followed by a higher rate in older age classes. Males of some polygynous species have a W-shaped mortality curve (Ralls, Brownell and Ballou, 1980).

The age composition of spotted dolphin shows the pattern indicated by Caughly (1966; 1977), except for the juvenile bias, but the data are insufficient to allow detection of details of age-related changes. However the least-

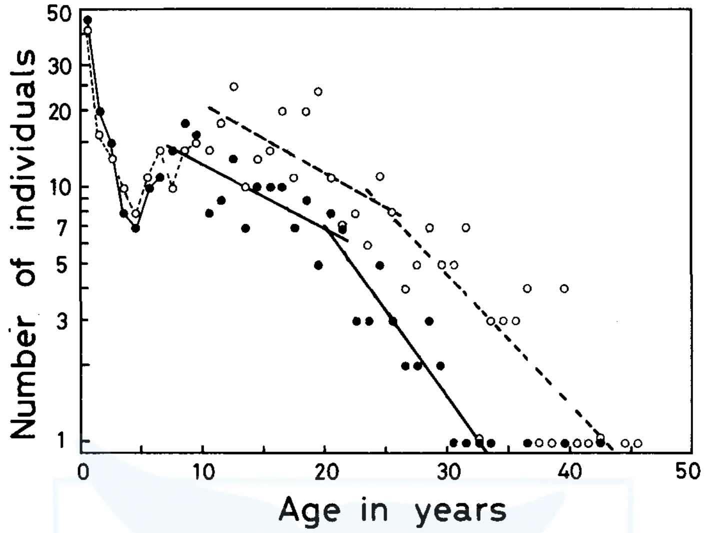

Fig. 9. Age composition of the spotted dolphin. Open circle and dotted line indicate females, and closed circle and solid line males. The thick straight lines (dotted and solid) are least-squares regressions for the indicated age ranges. Eleven schools (nos 1 to 13, except 8 and 11) are included.

squares regressions fitted to the intermediate and older age classes (Fig. 9) suggest higher apparent mortality rate for the older age class (Table 10). The calculations include only data below the age where zero frequency starts to appear in order to avoid bias due to ignoring zero frequency in the calculation. These results are similar to the estimation using the geometric method of Robson and Chapman (1961) (Table 10).

The difference of the apparent mortality rate between medium (approximately from 10 to 22 years of age) and the older age classes is significant (t-test, $p<0.01$). Although the male mortality appeared slightly higher than that of the females of the same age, as suggested by the female sex ratio increasing with age, this difference is not significant in the present small sample.

Assuming a stationary population, a rough estimation of juvenile mortality rate was done as follows. First, the annual production of 43.49 female calves was calculated by (Number of aged females, 431 individuals) × (Proportion of adult females, 0.666) × (Neonatal sex ratio, 0.5) / (Average calving interval, 3.30 years). This annual production is close to the observed frequency of 42 females between 0 and 1 year of age. Then a hypothetical uniform mortality rate was calculated for ages between year 0 (43.49 females) and year 11 (20.01 females calculated from the regression in Fig. 9). This gives 6.9% as the mean annual mortality rate of females between 0 and 11 years of age.

TABLE 10. APPARENT ANNUAL MORTALITY RATE CALCULATED FROM AGE COMPOSITION OF SPOTTED AND STRIPED DOLPHINS

Method	A	B
Spotted dolphin		
Female, 11-26 yr	0.0609	0.0563 ±0.0310
24-43 yr	0.1104	0.1026 ±0.0418
>24 yr	–	0.1348 ±0.0282
Male, 7-22 yr	0.0555	0.0590 ±0.0361
20-34 yr	0.1437	0.1494 ±0.0734
>20 yr	–	0.1618 ±0.0439
Striped dolphin		
Female, 11-22 yr	0.1141	0.1074 ±0.0376
20-34 yr	0.0773	0.0622 ±0.0442
32-41 yr	0.0192	0.2132 ±0.1453
>32 yr	–	0.1408 ±0.0468
Male, 11-22 yr	0.1340	0.1486 ±0.0366
20-34 yr	0.0536	0.0534 ±0.0471
32-46 yr	0.1328	0.1489 ±0.0771
>32 yr	–	0.1419 ±0.0398

A: From least-squares regression in Figs. 9 and 10.
B: After Robson and Chapman (1961), best point estimate with 95% confidence interval.

Striped dolphin

The age frequency below 10 years is largely dependent on the catch of the uncommon immature schools and is not reliable. The oldest individuals were aged at 57.5 years (one male and one female) and the next oldest at 53.5 years. Five males and five females were older than the oldest spotted dolphin (45.5 years old), suggesting a greater longevity in striped dolphins. A sexes difference in longevity is not suggested by the present sample.

The apparent mortality rate was calculated in the same way as for the spotted dolphin (Table 10). Since the population has been exploited probably for more than one century and there are symptoms suggesting decline of the population size (see DISCUSSION), it is not possible to estimate the true mortality rate from these figures. However the general pattern of the steeper slope of the oldest age class (Fig. 10) is similar to that of the spotted dolphin. This will reflect the age specific change of the natural mortality rate.

The slope of the age frequency below 33 years is less steep, but it seems to change at an age of about 21 years (slightly steeper in the younger age). Kasuya and Miyazaki (1982) found a similar change in age frequency data calculated from the ovarian corpora frequency. Although the present sample was insufficient for further analysis, it is probable that it reflects one or both of "the fishing mortality increase" and "increase in the annual recruitment" that might have occurred about 20 years before the commencement of sampl-

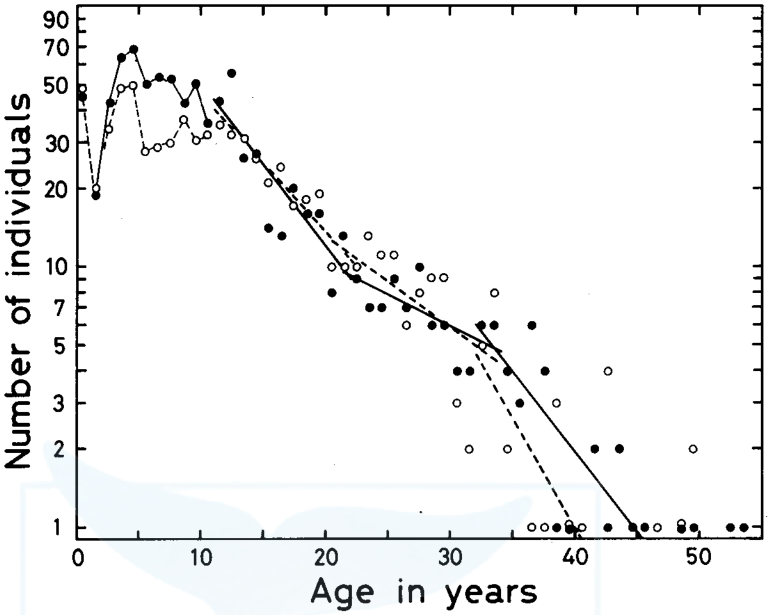

Fig. 10. Age composition of the striped dolphin. Closed circle and solid line indicate males, and open circle and dotted line females. The thick straight lines (dotted and solid) are least-squares regressions for the indicated age ranges. Eight schools (nos 22, 38 and 43 through 48) are included.

ing in 1972 to 1977 as the result of high catches after World War II (Kasuya and Miyazaki, 1982; Miyazaki, 1983).

DISCUSSION

Kasuya and Miyazaki (1982) suggested for the striped dolphin population off the Pacific coast of Japan that the population could not sustain the catch level of the early 1970's, because it exceeded the maximum sustainable yield. Their conclusion was based on the catch curve and changes in the operation pattern such as the number and quality of vessels used, expansion of the fishing ground, and an increased proportion of other delphinids in the catch (their analysis of catch curve was later refined by Kasuya (1976a) using improved age determination, but the conclusion remained unchanged). Although these catch curve analyses may need further examination (Anon., 1981), the changes in the fishing operation will still remain valid as an indication of change of the population level.

Later, Miyazaki (1983) analyzed the catch per unit of effort (CPUE) in the fishery, expressed by the number of captured individuals or the number of schools caught per searching day. Although he was not certain if the

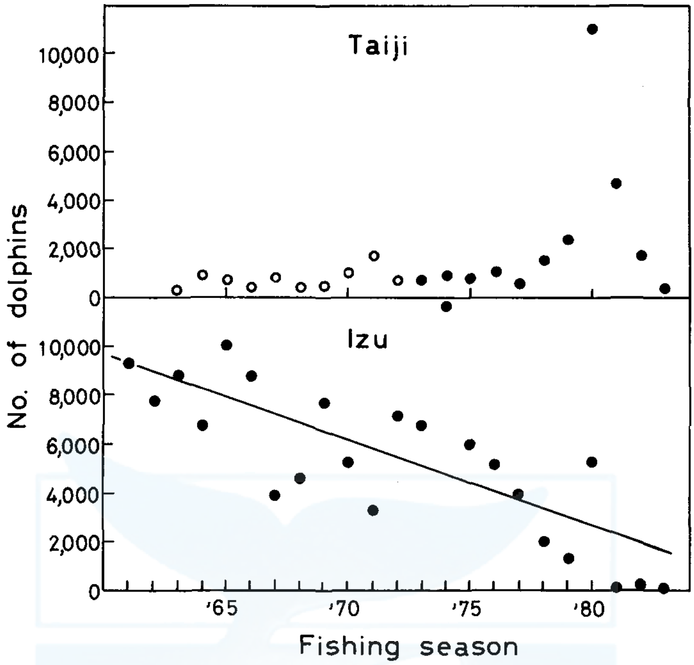

Fig. 11. Landing of the striped dolphin at Taiji and off Izu peninsula (Kawana and Futo) by hand-held harpoon (open circle) and drive fishery (closed circle) for the period where a complete statistics are available. Both equipment and number of hunting teams remained unchanged at Izu coast for the period indicated, but they had changed considerably at Taiji. Straight line represent a linear regression of the annual catch on the fishing season Y = −348.0X + 691,800). The fishing season off Izu coast is indicated by the starting date of the season. The shot-and-lost individuals in the hand-held harpoon fishery at Taiji are not included (see text).

population was stational (Miyazaki, pers. comm.) he could not find a significant decline in the annual catch or in the CPUE serieses.

However, in fisheries such as the drive fishery, where the scouting vessels stop their searching operation for the day and start driving as soon as they find a dolphin school, the change in CPUE underrepresents that of the stock level (Cook, in press). Furthermore, the recent catch of the striped dolphin off the Izu coast has further declined without any change in the equipment used (246 individuals in 1982 and 40 in 1983. Anon., 1984; 1985). The decline of catch after 1961, where complete statistics are available for the two villages (Futo and Kawana) and the equipment remained the same, is significant ($p < 0.001$, t-test of the gradient of the regression coefficient of annual catch on fishing season, see Fig. 11). Using only data from the period of the cooperative operation by the two teams (since 1968) gives the same result

($0.005 < p < 0.01$). The decline of dolphin meat demand was not indicated, because the catch of the Dall's porpoise in the northern Japan increased in recent years (Anon., 1983; 1984).

The fishing season off Izu coast, where they drive southbound schools, has also changed over the period sampled, from October-January (1960's), to October-December (1969 to 1979), to September-December (1980), and finally to September-November since 1981 (most of these data are available in Miyazaki, 1983), although the higher demand for dolphin meat in colder months remained the same.

These changes as well as those pointed out by Kasuya and Miyazaki (1982), suggest the decline of the stock level. However, the catch of the species off Taiji has not shown a significant decline since the start of the drive fishery in 1973. This could be explained if the density change occurred earlier at the periphery of the population's distribution (off the Izu coast) before it happened near the core area (Taiji) (Cook, in press). This could also explain the change in the fishing season off the Izu coast mentioned above.

The possible density dependent changes in the life history parameters of the striped dolphin population may appear too small to account for drastic decline in the catch off the Izu coast. This could be due to either the incomplete mixing of population members or a population decline accompanied by reduction of the range size. The first explanation assumes that the population declined only in the area close to the fishing ground and that the fishery continued to take schools migrating in from the surrounding area that was damaged less by the fishery. The second assumes that, due to the reduction of population range, even with rapid mixing, the density of the remaining stock changed less than would be expected from the apparent decline of the population level in the fishing ground. In both cases, the apparent decline of the population size may result in neither a parallel change of density in the remaining population nor in the expected improvement of its reproductive capacity. It is also true in these cases that the decline of the population level in the periphery of the range may exaggerate the decline of the entire population.

The above discussion, suggesting the decline of the striped dolphin population, is consistent with the density dependent changes of the life history parameters suggested in the present study. Therefore, I consider that the stock of the striped dolphin exploited off the Pacific coast of Japan could not sustain the annual catch of 3,600 to 16,000 individuals ($\bar{x}=7,915$), off Izu and Taiji in 1961 to 1981 (Miyazaki, 1983; Anon., 1984; 1985). This figure does not include the individuals shot and lost by the past harpoon fishery off Taiji, which used hand-held harpoon and shot gun and seemed to have landed only about half of the total kill).

Kasuya and Marsh (1984) suggested for *G. macrorhynchus* that, even when the total catch was the same, the population might respond more effectively to cropping from many schools rather than to the capture of whole schools.

However, because the schools of the striped dolphin seem to be more fluid than those of the pilot whale (Miyazaki and Nishiwaki, 1978) it is questionable if this is strictly applicable to the striped dolphin.

The magnitude of the contribution of the changes in life history parameters to the improvement of population productivity can be roughly estimated as follows.

The average age of female striped dolphins at the attainment of sexual maturity declined from 9.7 years at around 1966 (for the 1957 cohort, using Equation 1) to 7.4 years in 1976 (for the 1969 cohort), i.e. a decline of about 2.3 years during about 10 years. In the 1636 striped dolphins for which ages were estimated (both sexes combined to smooth age frequency), there were 787 individuals over 10 years old and 949 over 8 years old. Thus the observed decline in the age at maturation could have increased population productivity by about 20.6% in this period. However, this figure has to be considered as tentative, because it is affected by the biased juvenile age composition and assumes that the age composition was unchanged for 10 years.

On the other hand, if the calving interval of the striped dolphin really declined in the same period (10 years) to 83.6% of the initial level (Equation 8), it could have contributed to the 19.6% increase in the annual pregnancy rate. If this change was accompanied by the decline in age at maturation mentioned above, the gross reproductive rate could have increased by about 44% ($1.206 \times 1.196 = 1.44$) of the initial level. However, this figure is less certain than that above (20.6% increase), because the change in the pregnancy rate is more uncertain.

The only detectable change in the life history parameters of female spotted dolphins off the Pacific coast of Japan was the possible decline of the minimum age at the attainment of sexual maturity. Ohsumi (in press) analyzed the age of female fin whales at maturation for the exploited population in the North Pacific, using individuals with only one corpus in the ovaries. He found that the density dependent change appeared first as an increase of early-maturing individuals, which had little effect on the age where 50% of the females were sexually mature. This change was followed by a decline in the age of 50% maturation, but some females still attained maturity at a higher age as before. The last phase of the change was the disappearance of these relatively old immature females. Thus females that matured at between 8 and 17 years of age ($\bar{x} = 12.4$) in the 1957–'58 seasons matured in 1974–'75 seasons at about 4 to 11 ($\bar{x} = 7.0$) years of age (Fig. 3 in Ohsumi, in press).

Laws *et al.* (1975) also showed for populations of the African elephant, *Loxodonta africana*, in different habitats, that sexual maturation occurred among females at ages of 10 to 34 years in unfavorable habitat (50% maturation at about 22 years), but at ages of 10 to 22 years in more favorable habitat (50% maturation at about 17 years). Both studies suggest that a change in the age at sexual maturation may not occur equally in all age classes.

I believe that this kind of change could have started recently in the population of spotted dolphins. The drive fishery for the spotted dolphin may have started in 1959 (Table 3), but annual catches were small (less than 1,000) in most of the seasons before 1973 (Miyazaki *et al.*, 1974), and increased only after 1976 to an average of 1,251 (0 to 4,184) concurrent with the decline of the striped dolphin catch (Kasuya and Miyazaki, 1982; Miyazaki, 1983). However, the catch was still low, even in recent seasons (1,441 in 1982 and 629 in 1,983, Anon., 1984; 1985) compared with that of the striped dolphins in the area (Miyazaki, 1983). This suggests that if a change of the minimum age at sexual maturity has really occurred in the spotted dolphin population, it could be the result of not only the decline of the population of spotted dolphins but also that of the striped dolphin population in the same geographical area, due to reduced competition for food.

The limited catches and almost indetectable changes in life history parameters suggest that the apparent mortality rate of the spotted dolphins calculated in this study might be close to the natural mortality rate of the species, even though it may be an overestimate due to the calculation technique (de la Mare, 1984).

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GROWTH OF DALL'S PORPOISE IN THE WESTERN NORTH PACIFIC AND SUGGESTED GEOGRAPHICAL GROWTH DIFFERENTIATION

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AND
SATOSHI SHIRAGA**

ABSTRACT

Some growth parameters of the western North Pacific *dalli*-type Dall's porpoise were estimated from 167 specimens taken with hand-held harpoons on two cruises and compared with data obtained previously from porpoises killed incidentally in the salmon gill net fishery. These parameters were compared with previously published figures for the Japanese coastal population. Individuals from the Pacific coast of Japan (96% were *truei*-type) attained sexual maturity at body lengths 12 to 17cm larger than *dalli*-type individuals in the offshore waters. This is an indication of genetic differentiation between the two populations in addition to the previously reported external pigmentation. The possible usefulness of the growth parameters for the detection of genetic isolation between two major color types off the Pacific coast of Japan is indicated.

INTRODUCTION

Using specimens obtained from a harpoon fishery, Kasuya (1978) analyzed the life history of the Dall's porpoise, *Phocoenoides dalli* (True, 1885), off the Pacific coast of Japan, and suggested that the *dalli*-type individuals which comprised about 4% of the total catch might be migrants from the offshore Pacific or Sea of Japan populations which were mainly composed of *dalli*-type individuals. His conclusion was based on seasonal changes in the frequency of the color types and analysis of mixed schools with both two color types. Miyazaki, Jones and Beach (1984) supported this conclusion by reanalyzing the school structure using additional records of mixed schools. However, there was still uncertainty concerning the genetic isolation of the two color types as suggested by Wilke, Taniwaki and Kuroda (1953) and Houck (1976).

Based on limited number of samples taken in the offshore western North Pacific, Kasuya and Jones (1984) suggested, that both the incidental take by

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the salmon gill net fishery and the intended catch with hand-held harpoons are biased (1) by the tendency of different growth stages to be geographically segregated and (2) bow riding behaviour to be predominant among individuals between weaning and sexual maturity. They also suggested that *dalli*-type individuals in the offshore waters mature at smaller body size than the Japanese coastal population (mostly *truei*-type) studied by Kasuya (1978).

Using additional materials caught by hand-held harpoon, the present study analyzes the effect of different sampling methods on life history parameter analysis, and the growth difference between the Dall's porpoises from the two areas.

MATERIALS AND METHODS

This study is based on *dalli*-type Dall's porpoises taken with hand-held harpoon in the western North Pacific in 1982 (80 individuals) and 1983 (87) during the two cruises of the *Hoyomaru No. 12* chartered by the Fisheries Agency of Japan (Kasuya and Jones, 1984; Ogi and Fujise, 1984). Few *truei*-type individuals taken during the cruises (8 in 1982, and 2 in 1983) were excluded from the analyses, but one black-type taken at 43°27′N, 163°00′E in 1983 cruise was included. Since the black-type, which lacks white area on the flank and is entirely dark, is known in the entire range of the species (Kasuya, 1978; Morejohn, 1979), it is reasonable to assume that it belongs to the same population as that of the major color type of the area.

The periods of sampling were from 21 August to 17 September in 1982 and 16 August to 7 September in 1983. This corresponds to early mating season after the parturition peak in mid June to early August (Newby, 1982). The samples were collected in the area surrounded by the USSR Fishery Control Zone (FCZ), US FCZ, 180° longitude, and 42°N latitude. The majority of animals (82% in 1982 and 92% in 1983) were taken in the Subarctic Convergence Zone and within a radius of 180 nautical miles centered at 45°N and 160°E (Fig. 1). Over 94% of individuals were caught in a region where the surface water temperature was between 11° and 19°C, and where weaned juveniles segregated (Kasuya and Jones, 1984).

In contrast to the present sample, that used by Newby (1982) were collected in early June to late July (during the parturition season), in a northern region (majority of them in an area surrounded by 49°N, 56°N, 170°E, and 175°E), from the incidental take by the salmon gill net fishery, and in the three seasons from 1978 to 1980. Materials used by Kasuya (1978) were taken in winter (January to April), off the Pacific coast of Japan (39° to 40°N), from the harpoon fishery, between 1972 and 1976.

The age determination and classification of female reproductive status were done after Kasuya and Jones (1984). In the case of the 1982 sample male sexual maturity was assessed histologically (Kasuya and Jones, 1984)

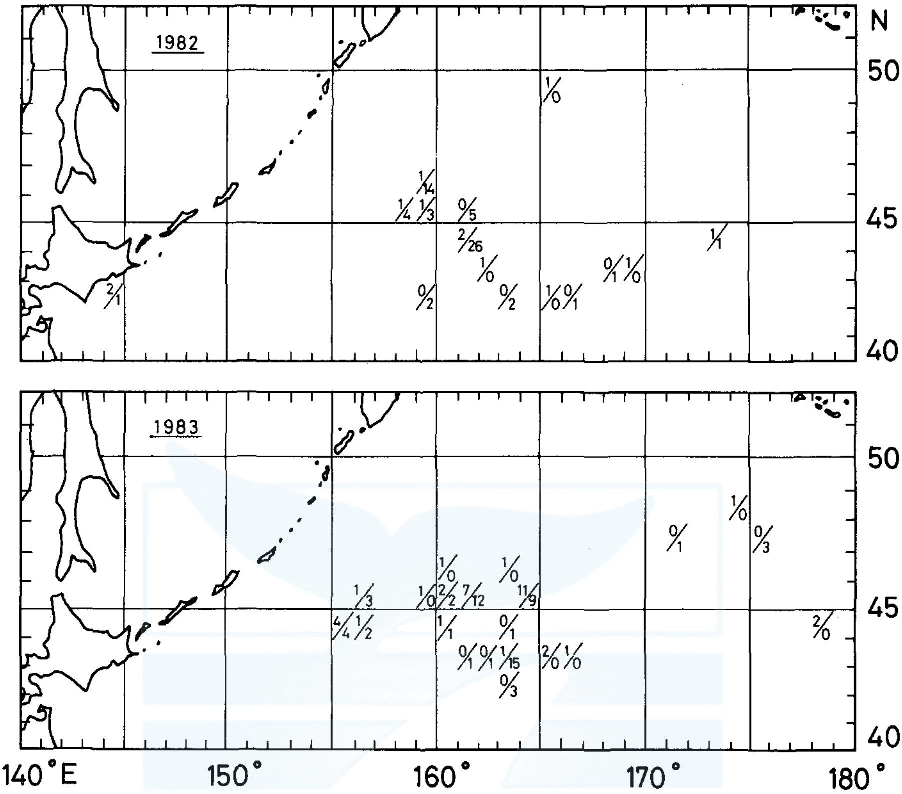

Fig. 1. Position of catch of the present sample. Numbers of females/males are indicated in one degree of longitude and latitude.

However, early (more than 0% and less than 50% of the seminiferous tubules had spermatocyte, spermatid or spermatozoon) and late maturing (50% or more but less than 100% of the tubules had at least one of the cell stages) individuals were included with immature and mature individuals respectively. For the 1983 sample, male maturity was determined using the testis weight criteria of Kasuya and Jones (1984); individuals whose left testis weighed 40g or more in August-September were considered mature and others immature, the inclusion of the late maturing males into mature stage does not cause significant bias in the following analysis, and meets the weight criteria.

RESULTS

Sex ratio, an additional indication of segregation

The number of males in the sample exceeded females for all cruises and maturity groups (Table 1), but the imbalance was statistically significant only for the 1982 sample (Chi-square test, $p < 0.02$). As suggested by Kasuya and

TABLE 1. BODY LENGTH FRENQUENCY OF *DALLI*-TYPES TAKEN BY THE *HOYOMARU NO.12* CRUISES IN 1982 AND 1983

Body length (cm)	Male					Female				
	immature		mature		total	immature		mature		total
	'82	'83	'82	'83		'82	'83	'82	'83	
148-					0		1			1
152-					0					0
156-					0		1			1
160-		4			4		3			3
164-	3	3			6	1	5		5	11
168-	4	6		1	11		2	1	1	4
172-	7	4	2		13	1	2	1	4	8
176-	3	5	3	3	14		1		2	3
180-	10	6	1	4	21		2	2	4	8
184-			8	3*	11*		1	2	3	6
188-	1	5	5	8	19					0
192-		1	4	2	7			1		1
196-	1		4	3	8					0
200-			1		1			1		1
204-			1		1			1		1
208-			1		1					0
212-					0			1		1
216-			1		1					0
Total	29	34	31	24*	118*	2	18	10	19	49

*: Includes one black type.

Jones (1984), there could be more males than females in the Subarctic Convergence. This is supported by the predominance of males in the present sample aged at 2 or 3 years (57:32, see Table 2) and the reverse sex ratio in the gill net sample in the northern area (54:96, see Newby 1982). The sex ratio of immature individuals was significantly different between the 1982 and 1983 samples (Chi-square test, $p < 0.02$). This suggests that there may exist some kind of sexual segregation of immature individuals in the Subarctic Convergence Zone.

Body length frequency

Body length ranged from 148 to 220 cm. However, there were few individuals with body length less than 160 cm or above 188 cm (females) or 196 cm (males) (Table 1), despite the abundance of individuals in these size ranges in the catch of the salmon gill net fishery to the north of our sampling area (Fig. 2).

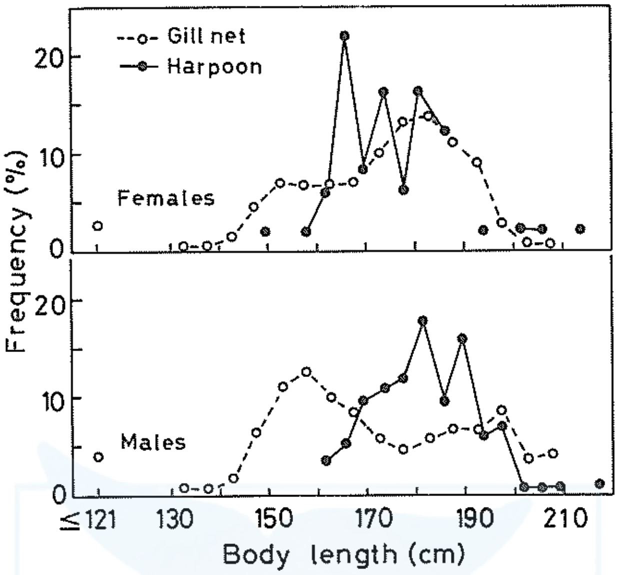

Fig. 2. Body length frequency of *dalli*-type Dall's porpoise taken using hand-held harpoon (present material) or by salmon gill net fishery (Newby, 1982). Sample sizes are 49 females and 118 males (harpoon catch), and 1,140 females and 708 males (gill net catch).

TABLE 2. AGE FREQUENCY OF *DALLI*-TYPES TAKEN BY THE *HOYOMARU NO.12* CRUISES IN 1982 AND 1983

Age (years)	Male					Female				
	immature		mature		total	immature		mature		total
	'82	'83	'82	'83		'82	'83	'82	'83	
0					0					0
1					0		2			2
2	9	11	2	2	24	1	11		4	16
3	6	13	5	9	33		4	2	10	16
4	6	6	6	3	21	1	1	3	1	6
5	4	2	7	5*	18*			1	2	3
6	2	1	3		6				1	1
7	1		1	1	3				1	1
8			1		1					0
9				1	1			1		1
10			1		1			1		1
17			1		1					0
no age	1	1	4	3	9			2		2
Total	29	34	31	24*	118*	2	18	10	19	49

*: Includes one black-type.

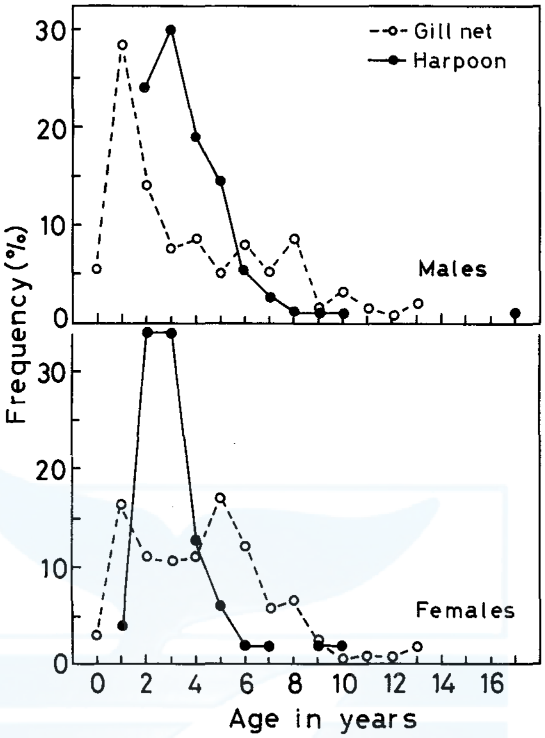

Fig. 3. Age frequency of *dalli*-type Dall's porpoise taken using hand-held harpoon (present material) or by salmon gill net fishery (Newby, 1982). Sample sizes are 47 females and 109 males (harpoon catch), and 427 females and 234 males (gill net catch).

Age frequency

There are some indications that the readability of tooth layers decreases with increasing age (Newby, 1982), but the proportion of individuals which were not aged due to shedding of whole teeth from the jaw or extreme ware of teeth did not differ significantly between mature and immature individuals of the present sample (Chi-square test, $p > 0.2$).

Ages of the present sample ranged from 1 to 17 years, but there were few individuals less than 2 years or older than 6 years (females) or 8 years (males) (Table 2). These results are consistent with the body length frequency data, and quite different from composition of the gill net catch (Newby, 1982; Kasuya, 1978) (Fig. 3). We conclude that the harpoon and gill net samples represent different components of the population because of segregational and behavioral differences related to age and reproductive status (Kasuya and Jones, 1984). Kasuya and Jones (1984) suggested that the waters north of the Subarctic Convergence Zone were inhabited by adult *P. dalli*, weaned calves, and mother-calf pairs all of which were rare in the southern area.

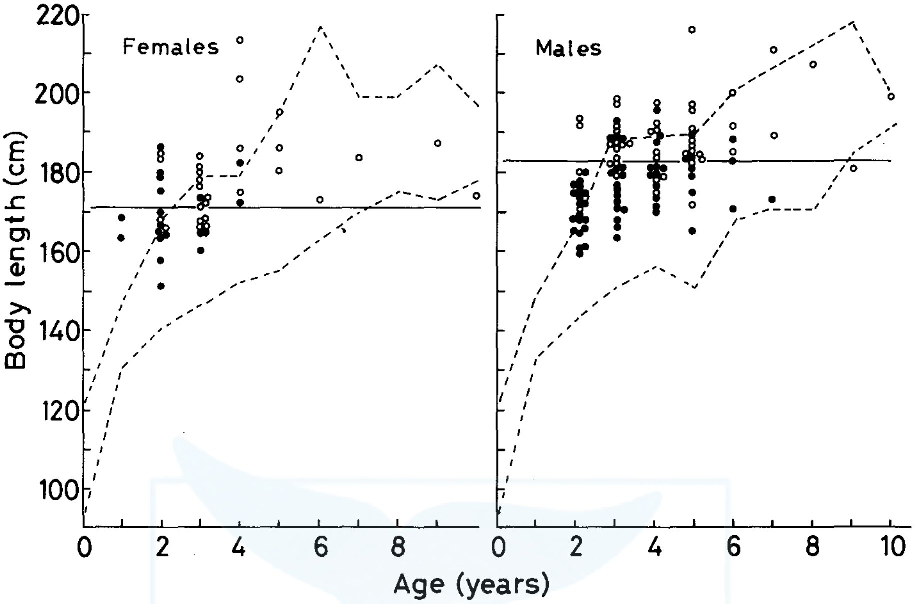

Fig. 4. Age-body length relationship in *dalli*-type Dall's porpoise taken by hand-held harpoon (present material) or salmon gill net fishery (Newby, 1982). Dotted lines indicate range of the gill net sample and circles individuals taken with harpoons (closed circle: immature, open circle: mature). Horizontal line indicates mean body length at the attainment of sexual maturity of the offshore *dalli*-type population.

Growth curve

Newby (1982) estimated the average body length at birth for the offshore population as 94.83 cm. This could be an underestimation because he used all the available fetuses and neonates (363 fetuses and 62 newborns, 61 to 123cm in body length) to correct the unbalanced frequencies of the two categories. It would have been more appropriate to include only length range where both fetuses and calves were present, i.e. 90 to 111 cm. If this procedure is used the average birth length is estimated at about 99 cm. Kasuya (1978) obtained a similar figure (99.7 cm) using a limited number of samples.

Fig. 4 compares the growth curves of the *dalli*-type porpoises suggested by the harpoon and gill net samples. The growth curves generated from the samples from the two harpooning cruises are similar, but different from that suggested by the gill net sample; harpoon samples below 4 (females) or 5 years (males) generally giving larger body size.

A plausible explanation for this is that faster growing individuals migrate to south and start to be attracted to a ship's bow wave at an earlier age than slower growing individuals, and that these individuals mature at younger age and segregate to the mothership gill net fishing ground and become less attracted to vessels at younger age than the slow growing smaller individuals. Thus, neither of the harpoon catch nor the gill net catch alone will correctly indicate the mean growth curve of the population.

Male sexual maturity

Body lengths of the smallest sexually mature male and of the largest immature one were in the body length groups of 168-171 cm and 196-199 cm, respectively (Table 1). The correlation between sexual maturity and body length was high compared with that between age and maturity. The materials from the two different sampling methods indicated an identical pattern (Fig. 5).

The attainment of sexual maturity and accompanying behavioral change in this species apparently depend on body size rather than age. Therefore we consider that the mean body length at the attainment of sexual maturity is correctly estimated by either sampling methods. Newby (1982) gave 182.5 cm, using larger sample, as the body length where 50% of the males were sexually mature. This will be the best available figure for the population.

In the harpoon sample, ages of the youngest mature male and of the oldest immature one were 2 years and 7 years, respectively, and there was observed almost no correlation between the proportion of mature individuals and the age (for ages 3 to 6 years) (Fig. 5). This is different from the result obtained from the gill net sample (Newby, 1982). We interpret this as indicating a balance between males which reach maturity and become takable by harpooning and those which become unavailable for capture by harpooning after a certain stage because of a geographical segregation of reproductive males and/or a change in their response to vessels (Kasuya and Jones, 1984).

Therefore, it is difficult to estimate from the harpoon samples the age where 50% of individuals are sexually mature. A similar phenomenon was reported by Kasuya (1978) for the harpoon sample of the Japanese coastal population of the Dall's porpoise. We do not know how the gill net sample cause bias in estimating the mean age at the attainment of sexual maturity. However, in view of the better correlation between age and maturity and the fact that the mean age estimated from the gill net sample (5.67 years, see Newby, 1982) is within the above range (3 to 7 years), we consider that males of this population will on average be reproductive at about 5 to 6 years of age.

Female sexual maturity

Using the presence of a corpus luteum or albicans as the indicator, the sexual maturity of females was identified more accurately than that of males. The smallest mature female and the largest immature one appeared between body lengths of 164-167 and 184-187 cm, respectively (Table 1). The relationship between the percentage of sexually mature females and body length in the harpooned sample is almost identical with that in the gill net sample (Fig. 5). Newby (1982) estimated the body length at which 50% of individuals were

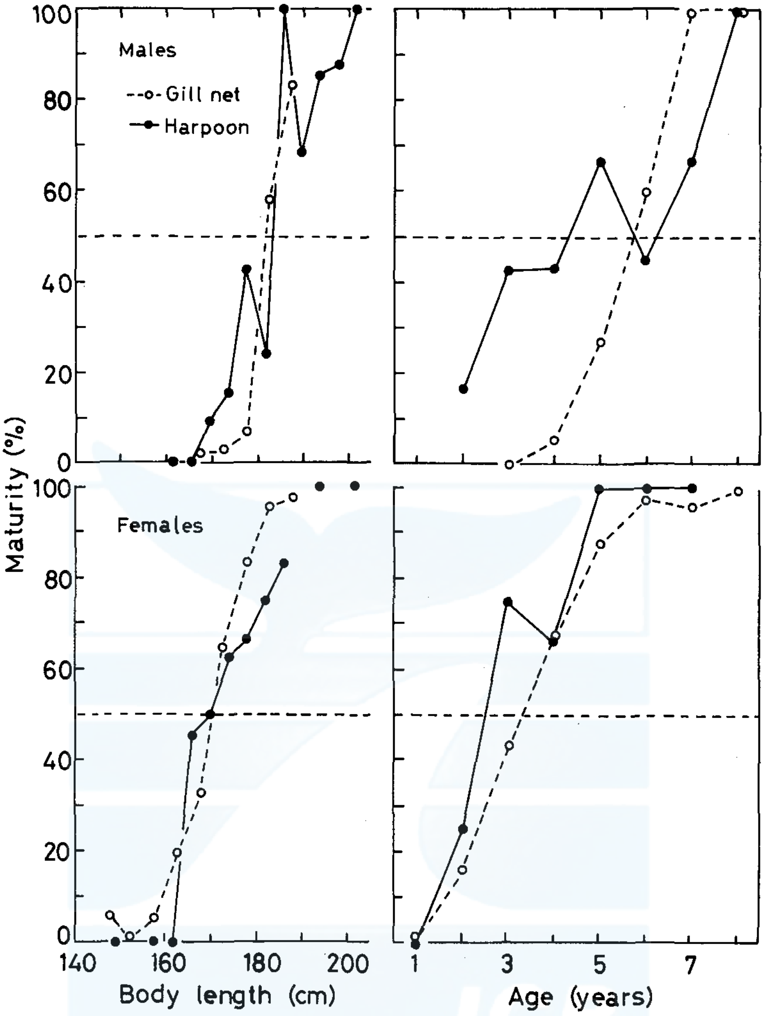

Fig. 5. Body length or age related change of the proportion of sexually mature individuals in *dalli*-type Dall's porpoise taken by harpooning (present material) and gill net fishery (Newby, 1982).

sexually mature as 170.5 cm. This is considered as the present best available figure, because it is based on a large sample.

The mean body length of 21 females in the present material having only one corpus luteum and no corpus albicans ranged from 164 to 186 cm. The mean was 175.0 cm (sd=7.14). The fact that these two figures differ is not necessarily important, because the maturity-body length relationship is not necessarily symmetrical.

The ages of the youngest sexually mature female and the oldest immature one were 2 and 4 years, respectively (Table 2). The disagreement between the maturity-age relationships of the harpooned material and that of the gill net sample is smaller in females than in the males (Fig. 5). The segregation by growth stage may be less intense in females (Kasuya and Jones, 1984). We consider that the age when 50% of the females are sexually mature will be close to 3.3 years as estimated by Newby (1982) using a large number of samples taken in gill nets.

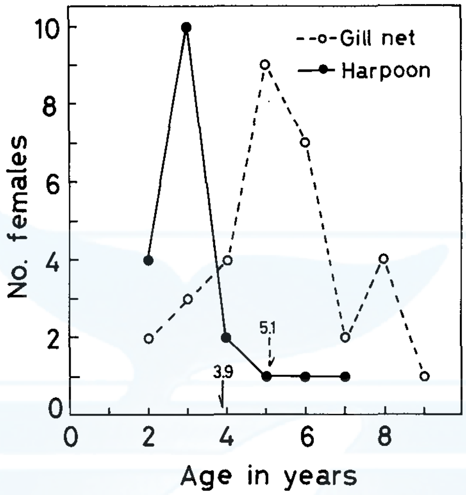

Fig. 6. Age composition of female *dalli*-type Dall's porpoise having corpus luteum of the first ovulation. Arrow indicates mean age.

Another estimate of the age at the attainment of sexual maturity is indicated by the ages of females with only one corpus luteum and no corpus albicans in the ovaries (Newby, 1982). Newby estimated the mean age as 5.1 years (range: 2 to 9 layers (years)). The corresponding figure for the present harpoon sample (19 aged individuals) was 3.9 years (range: 2 to 7 years). There is about one year difference between the two mean values, and two years difference in the peak ages of the two separate samples (Fig. 6). The one year difference of the mean is reasonable because the gill net sample of Newby (1982) was obtained in June and July and was represented by pregnant females with near term fetuses, whereas the present material was taken in August and September, or about 10 months earlier, and was represented by females at the early stage of pregnancy or shortly after ovulation (Table 3).

Even after taking account of the one year difference mentioned above, there still remains another one year discrepancy between the peak ages of the two data sets. The age frequency of females having only one ovarian corpus in the gill net sample was symmetrical (Fig. 6) as expected from the sigmoidal age-maturity relationship (Fig. 5). However that of the harpoon sample is skewed to the left. This suggests that the harpoon sample represents relatively precocious individuals, and will underestimate the age of first ovulation. This also implies that the gill net sample may overestimate the age of first ovulation to some degree. Therefore the mean age of the first ovulation in this population would be between 3 (peak age represented by harpoon sample, Fig. 6) and 4 years (peak represented by gill net sample, with correction for the length of the gestation period). This coincides well with the age of females at which 50% of the individuals are sexually mature estimated above (3.3 years, from Newby, 1982).

TABLE 3. REPRODUCTIVE STATUS OF ADULT *DALLI*-TYPES TAKEN BY THE *HOYOMARU NO.12* CRUISES IN 1982 AND 1983

No. of corpora	Pregnant		Preg. & lact.*		Ovulated**		Total
	'82	'83	'82	'83	'82	'83	
1	1	7			3	11	22
2	1						1
3		1			1		2
4	1						1
5			1				1
6					1		1
12	1						1
Total	4	8	1	0	5	11	29

*: Pregnant and simultaneously lactating.

**: Females having corpus luteum and neither pregnant nor pregnant and lactating. Pregnancy was identified by the presence of embryo recognizable under dissecting microscope or of embryonic membrane (7 embryonic membranes). Among the latter, recognizable embryos (over 4 mm) were found only in those over 10 cm in length (2 individuals), but none in those from 5 to 6 cm (5).

DISCUSSION

The validity of our conclusions relating to segregation and sample bias depend on the correspondence between our age determination technique and those of Newby (1982). We believe that our methods are in good agreement because (1) Kasuya and Newby cross checked each others readings (Newby, 1982), and (2) the age composition of 107 *dalli*-type porpoises that were taken in the gill net fishery and aged by Kasuya (1978) showed features similar to these obtained by Newby (1982), i.e. the highest peak at age one year and subsequent trough (Fig. 3). Similar age related selectivity of hand-held harpoons was reported by Kasuya (1978) on the Dall's porpoise off the Pacific coast of Japan and the striped dolphin, *Stenella coeruleoalba* (Meyen, 1833). Thus, we consider that the conclusions of the present study are not artifacts of age determination error.

Using harpoon sample (96% were *truei*-types), Kasuya (1978) analyzed the life history of Dall's porpoise off the Pacific coast of Japan and concluded that the individuals of the population attained sexual maturity at a mean body length of about 195 cm (male) or 187 cm (female). These figures are larger than the corresponding figures of the offshore western North Pacific population (*dalli*-types) by about 12 cm for males and 17 cm for females.

Age at the attainment of sexual maturity also seems to differ between the two populations. In the harpoon sample from the Japanese coastal population the proportion of the sexually mature individuals in the sample first attains 50% at the age of about 6.5 (male) or between 5.5 and 6.5 years (female). Taking account of the bias of harpoon sample, Kasuya (1978) estimated the mean ages at the attainment of sexual maturity as about 8 years (male) and 6.8 years (female). These are later than the corresponding figures of the offshore population by about 2 or 3 years (0.5 year difference of sampling season adjusted).

Therefore we conclude, as suggested by Kasuya and Jones (1984) based on smaller samples, that individuals in the population off the Pacific coast of Japan mature at a larger body length and possibly later. We believe that the size difference is the more direct information and reliable.

Since maturation is dependent on body size rather than age (see above), if the growth difference between the two populations resulted from a density dependent change in growth rate, we should expect a shortening of the prereproductive period, which may not be accompanied by a change in body length at the attainment of sexual maturity. However, the present study showed the different feature; maturation occurring at a lower age in the population of smaller body size. This suggests that the growth difference between the two populations is not a result of the density dependent change in the growth rate but the result of genetic differentiation.

The differentiation in age and body length at the attainment of sexual maturity indicated above for the two populations of the Dall's porpoise suggests the presence of a parallel difference in the body length at physical maturity. However, the analysis is not possible in the present study because of the sample bias in the catch of the harpoon fishery off the Japanese coast.

Kasuya (1978) suggested that the *dalli*-type individuals off the Pacific coast of Japan might not be inherent to the population but could be migrants from the offshore western North Pacific population or Sea of Japan population. He based his conclusion on the facts that the proportion of *dalli*-type in the catch by the fishery increased during the fishing season, and that the frequency of mixed schools of the two color types was lower than that expected from the assumption of random combination. After this study more data were accumulated to indicate that the geographical segregation of the two color types was rather distinct, and that in the area where both color types were present the occurrence of mixed schools of the two color types was much less than random combination and it was close to frequency of the hetero-specific mixed schools of other dolphin species (Kasuya and Jones, 1984; Miyazaki *et al.*, 1984).

Kasuya and Jones (1984) also showed that the *dalli*-type population in the western North Pacific segregated by growth and reproductive status and that the majority of breeding population was segregated (at least in the mating season) in the northern waters, where the *truei*-type was not recorded. Although it is not known at present how the members of the Japanese coastal population are segregated within its range, this is an additional information suggesting that the interbreeding between the two color types will be less frequent than it might be expected from their geographical coexistence or presence of the mixed schools.

We admit that the results of the present study alone do not provide a firm conclusion on the question of interbreeding between the two color types off the Pacific coast of Japan. However they suggest that the analyses of the growth of the *dalli*-type individuals found among *truei*-types in the Japanese coastal waters will be benefitial. If the growth difference is indicated, it is a strong indication of the genetic isolation between the color types. Then, in view of geographical segregation and minor genetic differenciation other than pigmentation, it will be reasonable to deal them as separate subspecies as proposed by Morejohn (1979). However, if they interbreed, we are unable to individually identify the two populations in the western North Pacific and the idea to deal the two color types as color morphs of one species (Houck, 1976) will be justified.

In view of the recent information on the segregation between the color types, the conclusion of Kuroda (1954; also see Wilke, Taniwaki and Kuroda, 1953) on *truei*-type fetuses found in the *dalli*-type cows should be reexamined based on the knowledge of the ontogenetic development of fetal pigmentation.

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DISTRIBUTION OF COMMERSON'S DOLPHIN, *Cephalorhynchus commersonii*, AND THE REDISCOVERY OF THE TYPE OF *Lagenorhynchus floweri*[*]

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ABSTRACT

Commerson's dolphin, *Cephalorhynchus commersonii*, is well known from the coastal waters of Argentina, from Peninsula Valdes (42°S) southward to the Strait of Magellan, Tierra del Fuego, and around the Falkland (Malvinas) Islands, and Kerguelen Islands. With the possible exception of some Drake's Passage records, there are no confirmed sightings of this species from pelagic areas adjacent to or outside its known range. One of the two type specimens of *Lagenorhynchus floweri*, a synonym of *C. commersonii*, was rediscovered and measurements from it are presented along with those from four other specimens of *C. commersonii*.

INTRODUCTION

Lacépède (1804) described *Cephalorhynchus commersonii (as Delphinus commersonii)* based on observations and a description by Philibert Commerson in a manuscript addressed to Georges Louis Leclerc, Le Comte de Buffon. The type locality was the Strait of Magellan, Tierra del Fuego, Chile. In this paper we review the distribution of *C. commersonii* based on published records, new specimens, and at-sea sightings. We also report on the rediscovery of the type specimen of *Lagenorhynchus floweri* Moreno, 1892.

MATERIALS AND METHODS

At-sea sightings of Commerson's dolphins were made by one of us (RLB)

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[*] *An earlier version of this report was presented to the Subcommittee on Small Cetaceans, Scientific Committee of the International Whaling Commission in 1979 and 1984 as documents SC/30/Doc 16 and SD/36/SM 10 respectively. This report was also presented at the Primera Reunión de Expertos en Mamiferos Acuáticos de América del Sur, Buenos Aires, Argentina, 25-29 June 1984.*

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during the late 1960's and the early 1970's. Both published and some unpublished accounts on this species were reviewed with specific reference to its distribution. Five specimens of *C. commersonii*, including one of the type specimens of *L. floweri*, were examined and measured. Skull measurements were taken as described by Perrin (1975). These specimens are listed below. Full names of institutions are included in the Acknowledgements.

Lagenorhynchus floweri—ARGENTINA: Bahia de Santa Cruz, Provincia Santa Cruz, 1 (MLP 1480: the type).

Cephalorhynchus commersonii—ARGENTINA: Quilmes, Provincia Buenos Aires, 1 (MACNBA 4-421); Tierra del Fuego, 1 (MACNBA unnumbered but 2c marked on cranium). UNKNOWN LOCALITY: 2 (MLP 633; MACNBA, unnumbered).

RESULTS

Specimens and At-sea Sightings of Commerson's Dolphins

During late 1968, Kenneth S. Norris collected two *C. commersonii* specimens in the Strait of Magellan (Norris, 1968; Anonymous, 1969; Aguayo, 1975). These specimens are now in the USNM collection with the numbers 395352 and 395372. There are four other specimens in the USNM collection: (1) USNM 252568, collected by Dr Deane, south of Stanley, East Falkland; (2) USNM 504072; (3) USNM 504073; and (4) the remains of one or more specimens labeled USNM 484889. James G. Mead collected the latter three specimens during February 1973 along the Estancia La Angelina coast approximately 10 km north of Rio Gallegos, Argentina. Mead (personal communication) stated that these specimens were obtained by the local crab fishermen in nets used for *centolla, Lithodes antarcticus*.

On 28 January 1974 M. Canevari obtained a Commerson's dolphin specimen from four km north of Rio Grande on Tierra del Fuego's Atlantic coast. Hugo Castello (personal communication) reported another specimen from Rio Gallegos, Province Santa Cruz, captured in a net used for fishing for *robalo, Eleginops maclovinus,* on 27 or 28 December 1973. Another specimen from Playa La Angelina, Bahia Grande, Province Santa Cruz, was obtained from a *centolla* net on 20 December 1973. Goodall (1978) described 31 specimens (11 fresh and 20 skeletons) netted by fishermen during 1977–78. Three were caught in *centolla* nets and 28 in nets set for *robalo* in the area around Bahia San Sebastian, Tierra del Fuego, Argentina. She also noted an additional 54 skulls collected in distinct parts of the Atlantic coast of Tierra del Fuego, Strait of Magellan, and the Beagle Channel. The localities where these specimens were collected suggest that the species is more common along the northern coast than along the southern coast of Tierra del Fuego.

Sighting and specimen data indicate *C. commersonii* ranges between 42°S and 56°S along South American's Atlantic coast. This distribution is based on the fact that specimens have been collected or described from the following localities: between the Strait of Magellan and Peninsula Valdes (Cummings, Fish and Thompson, 1971); between the Strait of Magellan and Rawson, Comodoro Rivadavia and Puerto Deseado (Mermoz and Goodall, 1980; Gewalt, 1979); Comodoro Rivadavia (Mermoz, 1980); Puerto Deseado (Spotte, Radcliffe and Dunn, 1979); Chubut (Gilmore, 1969); Rio Santa Cruz (Moreno, 1892); Isla de los Estados and Isla Pavon, Santa Cruz (Lahille, 1899); Strait of Magellan (Lacépède, 1804; Harmer, 1922; Norris, 1968; Gilmore, 1971; Goodall, 1977; Goodall, 1978); Isla Desolacion, the westernmost record in the Strait of Magellan (Goodall and Polkington, 1979); Tierra del Fuego (Lacépède, 1804; Dabbene, 1902; Marelli, 1953; Goodall, 1977; Goodall, 1978; Pine, Bridge and Angle, 1978; Lockyer, Smellie, Goodall, and Cameron, 1981); Beagle Channel (Olrog, 1950; Brownell, 1974; Goodall, 1977; Goodall, 1978); and Falkland (Malvinas) Islands (Quoy and Gaimard, 1824; Lesson and Garnot, 1826; Bruce, 1915; Harmer, 1922; Hamilton, 1952; Strange, 1972).

Hart (1935) reported that this species was known to the whalers off South Georgia. This is the only report of this species from the area around South Georgia Island.

We found one specimen (MACNBA 4-421) of this species reported from Quilmes, Provincia Buenos Aires (approximately 34°S). This is about 8 degrees north of the Peninsula Valdez region which we believe is the approximate northern range limit of *C. commersonii*. We and numerous colleagues have worked in the region north of Peninsula Valdez and know of only a few sightings just north (within about one degree) of the Peninsula Valdez area.

Aguayo and Torres (1967) and Aguayo (1975) reported *C. commersonii* from the following geographical positions: 61°59′ S −63°05′ W; 61°50′ S − 63°17′ W; and 58°10′ S −67°58′ W on 27 and 28 February 1966. These localities are in the Drake Passage (Cape Horn is located at approximately 56° S−67°16′ W), and are the only published sightings from that area. We find these three sightings extremely puzzling. Numerous scientific vessels annually traverse Drake Passage in route to the Antarctic Peninsula but we know of no other published or unpublished sightings of *C. commersonii* from this area.

Based on Commerson's dolphins observed along Chile's southern coast between Navarino and Wollaston Islands, Aguayo (1975) amplified the species known geographical distribution by stating that it occurred along the "Atlantic and Pacific coasts of the southern end of South America". In the southermost area of the islands south of Tierra del Fuego, this species is allopatric with *C. eutropia* as shown by observations of Norris (1968) and Aguayo (1975).

At least one sighting of Commerson's dolphin was recorded during a whale-sighting cruise carried out from 1 to 15 February 1982, between 32°S and 38°30′ S and between 75° W and the Chiliean coast (Gallardo, Arcos, Salamanca, and Pastene, 1983). As no specific details are provided on this sighting, we have dismissed it as erroneous. Even if this supposed sighting was made as far south as 38° S, this is still at least fifteen degrees north of the most northern confirmed sighting and well outside the normal range of this species.

Paulian (1953) observed some dolphins similar to Commerson's near the Kerguelen Islands in the southern Indian Ocean. He visited the Kerguelen Islands in 1952 and on his return he took to the British Museum (Natural History) a cranium of a dolphin collected during the voyage. Our inquiries about this specimen have been unfruitful as it cannot be found in the collection of the BM (NH) (F. C. Fraser, personal communication), nor in the Museum National d'Histoire Naturelle de Paris (D. Robineau, personal communication). Angot (1954) captured two male specimens which he determined to be this species in Kerguelen coastal waters. He later wrote to one of us (RLB) on 9 October 1973 that the specimens were harpooned and brought ashore where they were examined but no materials were collected.

Frost and Best (1976) reported this species from the Indian Ocean at 49°44′ S–68°42′ E and 49°44′ S–69°00′ E in the coastal water around Kerguelen. Pascal (1981) reported additional observations on this species in Kerguelen waters.

Gaskin (1972) suggested that a piebald specimen of *C. hectori* recorded by Oliver in the Malborough Sounds, New Zealand, was a Commerson's dolphin. We agree with Morzer Bruyns and Baker (1973) that this proposal has no merit.

Pilleri (1971), in a report on the Franciscana, listed the cetaceans that should be found in Uruguayan waters, including *C. heavisidei* (sic). Marcuzzi and Pilleri (1971) discussed the geographical range of all four *Cephalorhynchus* species (see their Fig. 47), and claimed that *C. heavisidii* was sympatric with *C. commersonii* along a large portion of the Argentine Atlantic coast. These two references are the only ones which expand the distribution of *C. heavisidii* from South Africa, across the whole of the South Atlantic Ocean, to the coast of South America. We know of no specimens, nor any direct observations, published or unpublished, that would support the claim that *C. heavisidii* occurs anywhere in the Atlantic Ocean other than along the western coast of southern Africa.

We give a series of new sightings where *C. commersonii* has been observed, mostly by RLB during several voyages in the waters of the western South Atlantic Ocean, in Table 1. Most of these records were plotted on plate 8 in Brownell (1974). No pelagic sightings of this species were ever made during these voyages.

In summary, *C. commersonii* is well known in the western South Atlantic Ocean along the coast of Argentina from Peninsula Valdes (approximately 42°S) southward to the Strait of Magellan, around most of Tierra del Fuego and around the Falkland (Malvinas) and Kerguelen Islands. Its occurrence around South Georgia Island and in the Drake Passage needs to be reconfirmed. With the possible exception of the Drake's Passage reports, there are no confirmed sightings of this species from pelagic areas adjacent to or outside of its known range.

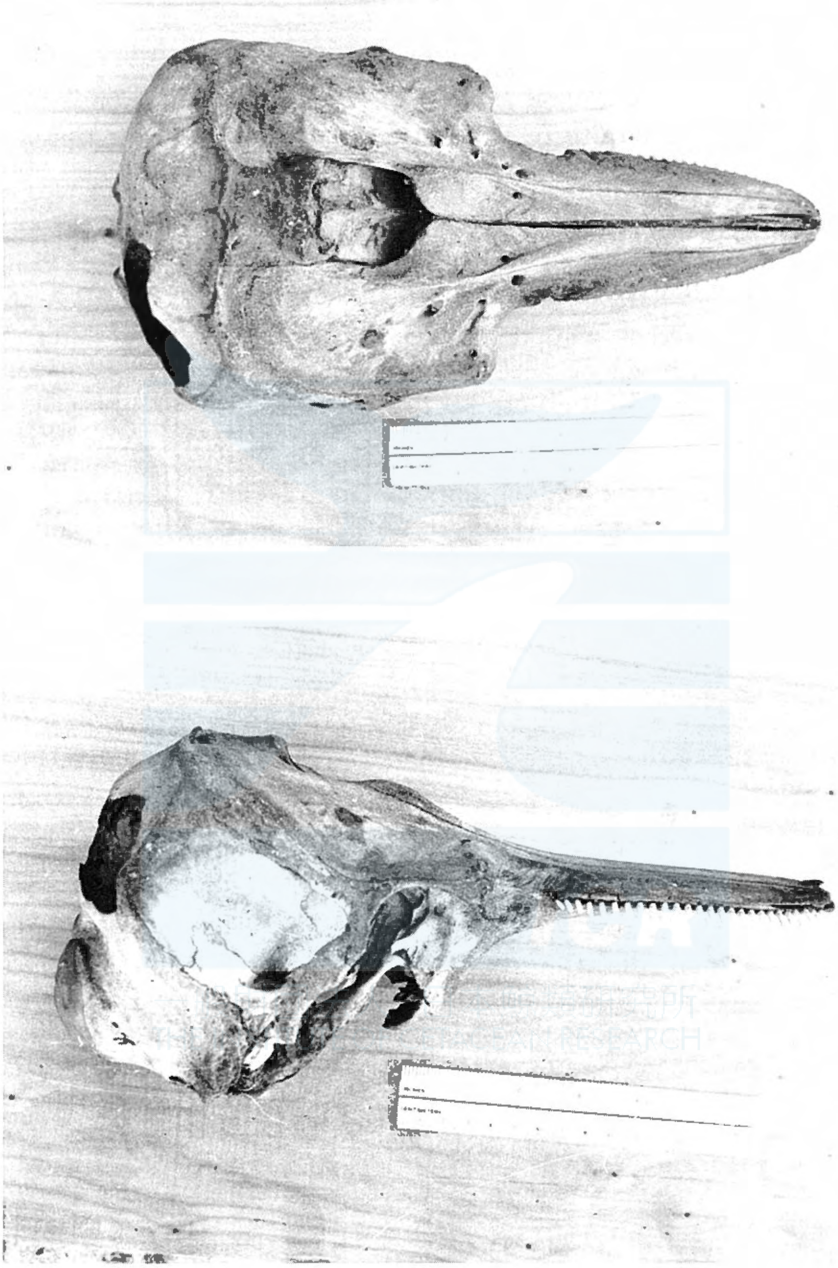
Rediscovery of the type of Lagenorhynchus floweri

In 1892, Moreno described *Lagenorhynchus floweri* on the basis of specimens observed in the mouth of the Rio Santa Cruz and along the coast of Chubut Province, Argentina, and two specimens (male and female) obtained by Sr. Tonini del Furia from Bahia de Santa Cruz and Tierra del Fuego.

Lagenorhynchus floweri was considered a separate species until Harmer (1922) made it a synonym of *C. commersonii* in his revision of the genus *Cephalorhynchus*, although he noted, "It is unfortunate that Moreno's specific name, which was based on a good and well-illustrated account of external and cranial characters, cannot be accepted." We accept Harmer's conclusion as have others before us. Moreno (1892) thus provided the first description of the cranial characters for *C. commersonii*.

TABLE 1. AT-SEA SIGHTINGS OF COMMERSON'S DOLPHINS, *CEPHALORHYNCHUS COMMERSONII*

Date		Hour	Locality	Number of dolphins	Observer
21. VI	1971	10:30	20 miles E. of Punta Norte de Peninsula Valdes 42°00′ S. – 63°30′ W.	3	Cummings (Pers. Com.)
29. VI	1971	15:20	41°26′ S. – 63°00′ W.	2	Cummings (Pers. Com.)
16. VII	1969	10:10	43°18′ S. – 64°53′ W.	2	Brownell & Gilmore, 1973
16. VII	1969	10:35	43°20′ S. – 64°55′ W.	2	Brownell & Gilmore, 1973
16. VII	1969	10:40	43°21′ S. – 64°56′ W.	1	Brownell & Gilmore, 1973
19. VII	1969	12:54	47°25′ S. – 65°39′ W.	1	Brownell & Gilmore, 1973
19. VII	1969	14:10	47°35′ S. – 65°45′ W.	1	Brownell & Gilmore, 1973
21. VII	1969	08:39	47°55′ S. – 65°40′ W.	2	Brownell & Gilmore, 1973
21. VII	1969	16:15	48°35′ S. – 66°46′ W.	1	Brownell & Gilmore, 1973
15. VI	1971	15:43	48°53′ S. – 68°15′ W.	3	Cummings (Pers. Com.)
13. VI	1971	12:00	Bahia San Julian 49°20′ S. – 67°40′ W.	2	Cummings (Pers. Com.)
22. VII	1969	16:25	49°35′ S. – 67°39′ W.		Brownell & Gilmore, 1973
23. VII	1969	10:05	50°04′ S. – 67°54′ W.	1	Brownell & Gilmore, 1973
24. VII	1969	15:00	51°35′ S. – 68°58′ W.	1	Brownell & Gilmore, 1973
26. VII	1969	12:41	51°39′ S. – 68°25′ W.	2	Brownell & Gilmore, 1973
26. VII	1969	12:45	51°39′ S. – 68°25′ W.	1	Brownell & Gilmore, 1973
12. VIII	1969		53°07′ S. – 70°50′ W.		Brownell & Gilmore, 1973
			Punta Arenas, Chile	2	Brownell & Gilmore, 1973



Figs. 1 and 2. Dorsal and lateral (from top to bottom) view of the cranium (No. 1) of the type of *Lagenorhynchus floweri* Moreno, 1892.

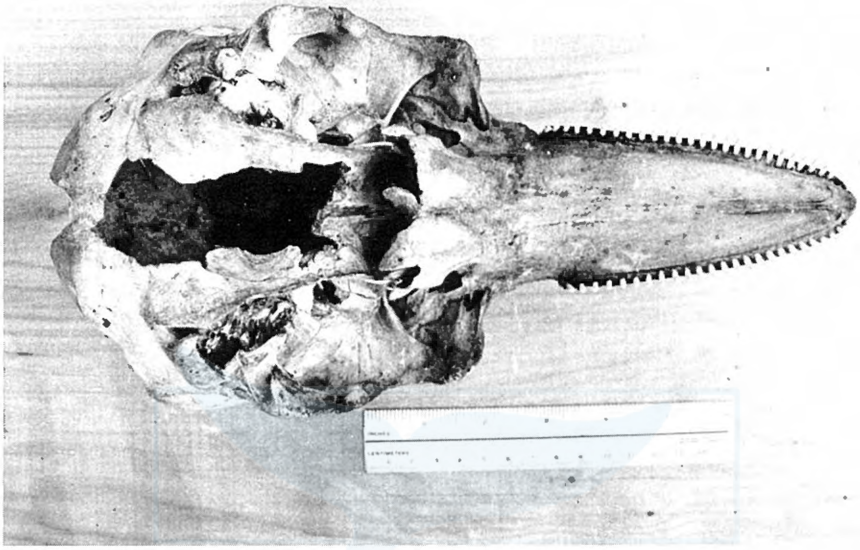


Fig. 3. Ventral view of the cranium (No.1) of the type of *Lagenorhynchus floweri* Moreno, 1892.

The two specimens described by Moreno were considered by Harmer and others to be unavailable, and no further mention of them has been made. Recently, however, while studying the cetacean collection in the MLP, we found a cranium (MLP 1480) without date or locality, recorded in the MLP catalogue as *Phocaena*. After examining this specimen in detail, we concluded that it was cranium No. 1 figured by Moreno (1892); therefore it is one of the two types of *L. floweri*.

The cranium is of a male. The right lateral side of the supraoccipital is broken; a large fracture occurs in the occipital-sphenoid region; the left tympanic bulla is missing; and there is a break in the external border of the left superior maxillary between the end of the tooth row and the antorbital notch (Figs 1 to 3). These characteristics and the dimensions of the partial cranium coincide exactly with those given by Moreno (1982) for his male specimen number one.

Moreno (1982) pointed out that the associated mandible does not belong to the cranium, but that it "procede del mismo punto donde fue recogido. He notado esto, despues de terminar el dibujo que conservo porque creo que esta mandibula pertenece a un *L. Burmeisteri* (*nomen lapsus* for *L. floweri* used in osteological description), pues en la Bahia de Santa Cruz no he observado otros delfines de este tamaño ni tengo noticia de que hayan sido vistos por otras personas". He added that "ha pertenecido a un individuo mas adulto, de

TABLE 2. SKULL MEASUREMENTS OF *CEPHALORHYNCHUS COMMERSONII* (IN MM.)

Measurements	1	2	3	4	5*)
1. Condylo-basal length	287	302	303	295	298
2. Rostrum length	135	146	143	142	139
3. Rostrum basal width	66	67	73	68	69
4. Rostrum width 60 mm. anterior to ant. ob. notches	52	51	52	49	53
5. Rostrum width at middle	50	53	51	47	50
6. Premaxillae width at same point.	23	23	27	22	24
7. Tip of snout to blowhole	173	180	172	177	177
8. Tip of snout to pterygoid	174	192	–	189	–
9. Preorbital width	125	128	121	118	129
10. Post-orbital width	140	143	135	136	146
11. Orbital width	125	127	124	120	130
12. Blowhole, width at	140	146	140	141	149
13. Zygomatic breadth	36	37	38	39	39
14. Greatest width pmx.	44	44	47	49	48
15. Width of braincase across parietals	139	138	134	134	139
16. Number of teeth upper R.	29	30	30	30	31
17. Number of teeth upper L.	26+	30	30	30	30
18. Length of tooth row upper R.	113	123	123	123	119
19. Length of tooth row upper L.	108+	122	123	123	121
20. Hinder end of upper tooth row R.	118	128	130	129	128
21. to tip of pmx. L.	110+	124	–	129	126
22. Number of teeth lower R.	28	33	30	30	29
23. Number of teeth lower L.	28	31	30	32	29
24. Length of lower tooth row R.	112	125	115	116	115
25. Length of lower tooth row L.	113	124	120	117	116
26. Hinder end of lower tooth row R.	118	125	125	125	121
27. to tip of mandible L.	118	125	125	124	121
28. Mandible length	223	234	233	229	226
29. Coronoid height	53	58	54	53	49
30. Length of symphysis	17	13	18	20	18
31. Post-temporal length	65	67	69	65	68
32. Post-temporal height	47	47	50	49	46
33. ¾ rostrum length-width at	38	37	35	35	39
34. Cranial height	128	132	128	126	134

*)

1 – M.L.P. 1480, Bahia de Santa Cruz, Provincia Santa Cruz, Rep. Argentina. Type of *Lagenorhynchus floweri* Moreno, 1892.

2 – M.L.P. 633, No data.

3 – M.A.C.N.B.A. 4-421, Quilmes, Provincia Buenos Aires, Rep. Argentina.

4 – M.A.C.N.B.A. 2c, Tierra del Fuego, Rep. Argentina.

5 – M.A.C.N.B.A., No data.

TABLE 3. SKULL MEASUREMENTS OF *CEPHALORHYNCHUS COMMERSONII* EXPRESSED AS A PERCENT OF THE CONDYLO-BASAL LENGTH

Measurements	1	2	3	4	5*)
1. Condylo-basal length	100.0	100.0	100.0	100.0	100.0
2. Rostrum length	48.4	48.3	47.1	48.1	46.6
3. Rostrum basal width	22.9	22.1	24.0	23.0	23.1
4. Rostrum width 60 mm. anterior to ant. ob. notches	18.1	16.8	17.1	16.6	17.7
5. Rostrum width at middle	17.4	17.5	16.8	15.9	16.7
6. Premaxillae width at same point	8.0	7.6	8.9	7.4	8.0
7. Tip of snout to blowhole	60.2	59.6	56.7	60.0	59.5
8. Tip of snout to pterygoid	60.6	63.5	–	64.0	–
9. Preorbital width	43.2	42.3	39.9	40.0	43.2
10. Post-orbital width	48.7	47.3	44.5	46.1	43.9
11. Orbital width	43.2	42.0	40.9	40.6	43.6
12. Blowhole, width at	48.7	48.3	46.2	47.7	50.0
13. Zygomatic breadth	12.5	12.2	12.5	13.2	13.5
14. Greatest width pmx.	15.3	14.5	15.5	16.6	16.1
15. Width of braincase across parietals	48.4	45.6	44.2	45.4	46.6
18. Length of tooth row upper R.	39.3	40.7	40.5	41.6	39.9
19. Length of tooth row upper L.	–	40.3	40.5	41.6	40.6
20. Hinder end of upper tooth row R.	41.1	42.3	42.9	43.7	42.9
21. to tip of pmx. L.	–	41.0	–	43.7	42.2
24. Length of lower tooth row R.	39.0	41.3	37.9	39.3	38.5
25. Length of lower tooth row L.	39.3	41.0	39.6	39.6	38.8
26. Hinder end of lower tooth row R.	41.1	41.3	41.2	42.3	40.6
27. to tip of mandible L.	41.1	41.3	41.2	42.0	40.6
28. Mandible length	77.7	77.8	76.8	77.6	75.8
29. Coronoid height	18.4	19.2	17.8	17.9	16.4
30. Length of symphysis	5.9	4.3	5.9	6.7	6.0
31. Post-temporal length	22.6	22.1	22.7	22.0	22.8
32. Post-temporal height	16.3	15.5	16.5	16.5	15.4
33. 3/4 rostrum length-width at	13.2	12.2	11.5	11.8	13.0
34. Cranial height	44.5	43.9	42.2	42.7	44.9

*) Same abbreviations in Table 2

craneo algo mas estrecho." Nevertheless, we conclude that this mandible has all the characteristics typical of *C. commersonii*.

The MLP and MACNBA collections contained four crania of *C. commersonii* (1 MLP and 3 MACNBA). We have included the measurements from these specimens and their relative percentages here for comparison with those from the type of *L. floweri* (Tables 2 and 3). The small variation among these specimens and those reported by Harmer (1922) falls within the intraspecific variation of *C. commersonii* .

SUMARIO

Se analizan las citas bibliograficas para tonina overa, *Cephalorhynchus commersonii*, en lo relativo a su distribution geográfica, y se proporcionan nuevas localidades basadas en observaciones directas. Medidas craneométricas y fórmulas dentarias son presentadas de cinco especimenes en museos Argenti nos, incluido el tipo de *Lagenorhynchus floweri* Moreno, 1892.

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A NOTE ON A STRANDING OF THE HUMPBACK WHALE ON THE SOUTHERN COAST OF BRAZIL

MARIA CRISTINA PINEDO*

A humpback whale (*Megaptera novaengliae*) stranded alive on a beach 89 km north of the mouth of Patos Lagoon (31°38′S, 51°21′W), Rio Grande do Sul, in southern Brazil, on August 26, 1980. Fig. 1 shows a map of the position. According to fishermen, a school of approximately ten humpback whales was sighted swimming parallel to the beach on the previous day, and one of them stranded on a sand bank near the beach suddenly. Then, a strong southern wind pushed the whale to the beach. When I arrived there on August 28, the animal was still alive burying its belly into the sand. Although we intented to rescue the animal, it was too large in size to return it to the water.

The animal was male and 11.15 m long. I took some photographs (one of them is shown in Fig. 2), and measured its body proportions based on Leatherwood, Caldwell and Winn (1976), as shown in Table 1. It was estimated from the body length to sexually mature bassed on Chittleborough (1965). Cirripeds (*Coronula diadema*) infested the animal heavily on tubercles of both jaws and knobs of anterior margins of flippers. Cyamid amphipods which were identified as *Cyamus catodontis* (Arvy, 1977) were also found on the surface of its both jaws.

Fishermen obtained permission from the local fisheries fiscalization agency to kill the animal, and it was slaughtered by about ten fishermen on the beach. The whale oil was sold for leather tanning, and the whale meat was consumed locally. After flensing of the carcass, number of baleen plates of left side were counted by touching the base of each plate, and the length of the longest baleen plate was measured as shown in Table 1. Cervical and caudal vertebrae, some right ribs and right scapula were collected by a team of the Rio Grande Oceanographic Museum, and they were deposited in the museum as the Specimen No. 104.

Fig. 1 summarizes previous records of positions of humpback whales caught or sighted in the waters near Brazil, Uruguay and Argentina in past and suggest that they visited the brazilian coast more frequently in winter. Catch history of humpback whales in the northeastern Brazil indicates that brazilian humpback stock had decreased largely. According to Williamson (1975), the average an annual catch of humpback whales in the whaling

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ground changes from 222.6 whales in the 1910-1914 period to 9.8 in 1960-1963 period, and the last record of catch of humpback whales in brazilian waters was 1963.

Furthermore, in seven years of monthly observations over 120 km along the coast and three years of on board observations on the R/V "Atlântico Sul" (FURG), this is the first record of a humpback whale in Rio Grande do Sul. This record suggest that the brazilian stock could be returning to the places they frequented at the begining of this century, in a similar way as the right whale is doing (Pinedo, 1984).

Fig. 1. Distribution of catch areas and records of *M. novaeangliae* accordaing Lahille (1903) (⊙), Townsend (1935) (▲), Hinds (1965) and Paiva & Grangeiro (1965) (▨), Hinds (1965) (□), Vaz-Ferreira (1970) (●), Cummings et al. (1974) (○) and present record (✳).

TABLE 1. MEASUREMENTS OF THE STRANDED *M. NOVAEANGLIAE* ON AUGUST 26, 1980 AT RIO GRANDE DO SUL COAST, BRAZIL (AND % OF TOTAL LENGTH)

		cm	n°	%
1.	Tip of upper jaw to deepest part of fluke notch	1,115.0		100
2.	Tip of upper jaw to blowholes	222.0		19.9
3.	Tip of upper jaw to angle of gape	320.0		28.7
4.	Length of eye (left)	24.0		2.2
5.	Rostrum maximum width	91.0		8.2
6.	Flipper length-tip to anterior insertion (right)	420.0		37.7
7.	Flipper width (right)	110.0		9.9
8.	Dorsal fin base	128.0		11.5
9.	Dorsal fin height	37.0		3.3
10.	Fluke span	432.0		38.7
11.	Fluke width	130.0		11.7
12.	Blubber thickness (lateral)	19.0		1.7
13.	Baleen plates, length longest	45.0		4.0
14.	Baleen counts (left upper)		256	
15.	Number of maxillar notches (right)		15	
	(left)		14	
	(middle)		7	
16.	Number of vibrissae present in the notches		9	
17.	Vibrissae length range	2.3-4.5		

Fig. 2. Male *Megaptera novaeangliae* stranded at Rio Grande do Sul coast (31°38'S, 51°21'W) on August, 1980.

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