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FOODS AND FEEDING OF BOWHEAD WHALES
IN WESTERN AND NORTHERN ALASKA

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ABSTRACT

Samples were collected from the gastrointestinal tracts of 20 bowhead whales taken by Eskimo whalers at several locations on the western and northern coast of Alaska. A probable total of 56 species of prey was found, including 50 species of crustaceans, 3 molluscs, and 3 fishes. Most of the prey species (23) were gammarid amphipods, which occurred in 13 of the samples examined. Of the individual prey species, the most frequently encountered were a euphausiid, *Thysanoessa raschii* (11 occurrences); a copepod, *Calanus hyperboreus* (10 occurrences); and a hyperiid amphipod, *Parathemisto libellula* (8 occurrences).

In samples from stomachs containing appreciable amounts of recognizable food, copepods were the dominant prey in nine, euphausiids in six, and gammarid amphipods in one. The latter was a whale taken at Gambell in May; the others were all taken at Barrow in May, or at Barrow or Kaktovik in September-October. Based on volumetric composition of the samples, euphausiids were the dominant (90.3% total contents) prey at Barrow in autumn (n=2). Whales taken there in May (n=4) had eaten substantial amounts of copepods (30.7%), as well as euphausiids (59.1%). Copepods (66.1%) and euphausiids (31.2%) were the dominant prey of whales taken at Kaktovik in autumn (n=8). The organisms most commonly eaten ranged from about 3 to 30 mm in length.

Based on stomach contents and other information, two important feeding areas in Alaska can at present be identified: the area between Barter Island and the U.S.-Canada demarcation line, and the region from Point Barrow to approximately Pitt Point. The organisms eaten in the Beaufort Sea in autumn are extremely high in fat and caloric content when compared to other species and more southern areas. Calculations indicate that prey densities are adequate for whales to obtain their annual energy needs during a 130-day feeding season, and that annual production in most years is probably adequate to support populations of bowheads and other consumers of zooplankton. Arctic cod are the major consumers of copepods and euphausiids in the area. Aspects of feeding ecology are obviously of great importance to the recovery of the presently reduced bowhead whale population. A major question is whether bowheads can reoccupy portions of the Bering and Chukchi seas that were once used as summer feeding areas.

INTRODUCTION

Bowhead whales, *Balaena mysticetus*, make extensive annual migrations from wintering areas in the Bering Sea to summering grounds in Amundsen Gulf and the Beaufort and Chukchi seas (Braham *et al.* 1982). It has generally been assumed that bowheads, like other mysticete cetaceans, feed principally during the summer, and that their migration therefore is undertaken in order to reach preferred feeding areas. However, aspects of the feeding biology of bowheads are very poorly known.

The foods of most species of baleen whales are well documented since they have been the objects of commercial harvests in the 19th and 20th centuries and the contents of stomachs of harvested whales have been carefully examined (e.g., Nemoto 1957, Tomilin 1957). Bowheads were also extensively harvested by commercial whalers in the late 1800's and early 1900's. However, since they usually were processed only for baleen and sometimes for oil, the contents of stomachs were rarely, if ever, examined. Tomilin (1957) concluded based on indirect evidence that copepods (*Calanus finmarchicus*) and pteropods (*Limacina helicina*) were major food items. MacGinitie (1955) in a report based on work done at Point Barrow indicated that bowheads ate euphausiids, mysids, pteropods, and copepods. Johnson *et al.* (1966) examined the stomachs of two bowheads taken at Point Hope in April 1960 and May 1961. One stomach was empty; in the other, they found fragments of polychaetes, crabs, snails, crustaceans, and echinoderms. Mitchell (1975) stated that bowheads eat principally small and medium-sized zooplankton but sometimes also eat benthic organisms such as amphipods and mysids.

Since 1976 we have obtained and examined samples of the stomach contents of bowhead whales taken by Eskimo whalers at several locations on the western and northern coasts of Alaska. Those samples were collected for us through the cooperation of the Alaska Eskimo Whaling Commission and the National Marine Fisheries Service. Results of our analyses of the samples have been in part reported (Lowry *et al.* 1978, Lowry and Burns 1980). In this paper we will report and summarize all our observations on stomach contents of bowheads, examine the importance of various prey species in their diet, identify major feeding areas in Alaskan waters, and discuss the overall feeding strategy of bowheads in the western Arctic.

METHODS

Samples of bowhead whale foods were collected for us by a number of different persons. All samples were from the gastrointestinal tracts, usually the forestomachs, of whales taken by Eskimo subsistence hunters and were generally obtained within a few hours of the time the whales were killed and landed. The samples which we obtained were usually preserved in buffered 10% formalin and ranged in volume from a few mL to over 2L. The total volume of food present in the

stomach of each whale was usually estimated and recorded in the field.

In the laboratory, samples were drained and gently washed on a 1.00-mm mesh sieve. Food material was then sorted macroscopically into major taxonomic groups, and the water displacement volume of each group was determined. The organisms in each group were examined microscopically when necessary and identified to species if possible. Identifications were made using appropriate keys and reference specimens in collections at the Alaska Department of Fish and Game and the University of Alaska. The number of individuals and total volume of each prey species were determined, and lengths of representative specimens were measured. In the case of abundant, small organisms such as copepods, the volume and number of the various species were estimated from subsamples.

RESULTS

We examined samples of prey items from the gastrointestinal tracts of 20 bowhead whales. With three probable exceptions, all were collected from stomach contents. Seven of the samples were from whales taken near Point Barrow, nine from whales taken near Kaktovik, two from Point Hope, and one each from Shaktoolik and Gambell (Table 1). All of the samples from Kaktovik and two of those from Barrow were from whales taken in the autumn (September or October); all of the others were from whales taken in the spring (May).

TABLE 1. BOWHEAD WHALE SPECIMENS FROM WHICH SAMPLES
OF PREY ITEMS WERE OBTAINED

Specimen number	Location	Date of kill	Sex	Total length (m)	Comments
76-B-6F	Barrow	10 Sep 76	female	16.0	reported to be an ingutuk
76-B-7F	Barrow	20 Sep 76	female	14.3	
77-B-5	Barrow	5 May 77	male	10.6	killed at 1600 hrs local time
79-B-3	Barrow	27 May 79	male	8.3	sample from colon
80-B-3	Barrow	25 May 80	male	8.5	killed at 0630 hrs local time
80-B-5	Barrow	25 May 80	male	10.4	killed at 0616 hrs local time
80-B-9	Barrow	27 May 80	female	13.7	killed at 1800 hrs local time
79-KK-1	Kaktovik	20 Sep 79	male	12.7	recovered on 22 September
79-KK-2	Kaktovik	6 Oct 79	female	10.5	
79-KK-3	Kaktovik	8 Oct 79	male	10.3	
79-KK-4	Kaktovik	10 Oct 79	male	10.6	
79-KK-5	Kaktovik	11 Oct 79	male	10.6	killed at 1740 hrs local time
80-KK-1	Kaktovik	14 Sep 80	male	9.1–10.7	sample probably from small intestine
81-KK-1	Kaktovik	8 Sep 81	female	17.4	killed at 1430 hrs local time
81-KK-2	Kaktovik	11 Sep 81	male	14.0	killed at 1700 hrs local time
82-KK-1	Kaktovik	23 Sep 82	male	16.0	killed at 2100 hrs local time
78-H-2	Point Hope	4 May 78	male	9.7	
79-H-3	Point Hope	6 May 79	male	9.1	
80-SH-1	Shaktoolik	9 May 80	male	10.1	sample from colon
82-G-2	Gambell	1 May 82	female	8.8	killed at 1533 hrs local time

Depending on the state of digestion of the samples, it was more or less difficult to determine the specific identity of the prey. Some prey could be identified only to phylum, family, or genus when only fragments occurred in the samples. Small, fragile organisms such as copepods were difficult to identify to species except in comparatively fresh stomach contents. Larger, more durable organisms such as amphipods and molluscs could generally be identified in mostly digested stomach or intestinal samples. The presence of euphausiids was easy to detect due to the persistent and characteristic nature of the eyes which detach from the body during digestion. Entirely soft-bodied animals such as coelenterates, salps, chaetognaths, and pteropods may not have been detected in some samples examined, although they would have been readily observed in those which were in fresh condition.

Eliminating those organisms which could not be identified to species but which probably represented species found in other samples (e.g., *Calanus* sp., *Gammarus* sp., Family Lysianassidae, and Family Crangonidae), a probable total of 56 prey species was found in the 20 whales containing identifiable food remains (Table 2). With the exception of three species each of molluscs and fishes, all identified prey were crustaceans. The distribution of prey species among the major groups of crustaceans was: gammarid amphipods—23; copepods—10; hyperiid amphipods—5; shrimps—3; euphausiids, mysids, and crabs—2 each; and isopods, cumaceans, and ostracods—1 each. The number of times each of the major prey groups occurred in the samples was: gammarid amphipods—13; copepods—12; euphausiids and hyperiid amphipods—11 each; mysids and shrimps—6 each; fishes—5; molluscs—4; crabs and cumaceans—2 each; and isopods and ostracods—1 each. Of the individual prey species, the most frequently encountered were *Thysanoessa raschii* (11 occurrences), *Calanus hyperboreus* (10 occurrences), and *Parathemisto libellula* (8 occurrences). All the remaining prey species occurred in fewer than five stomachs, while 41 species occurred in only one or two samples. Pebbles, generally less than 1 cm in size, occurred in six samples.

Copepods or euphausiids were the dominant component of all except five of the samples we examined (Table 2). Two of those were from colons and contained shrimp fragments and small clams. Two others contained a single amphipod and a single snail. The fifth contained gammarid amphipods, cumaceans, and other benthic organisms. In the other 15 samples, euphausiids were the major food in six, and copepods were dominant in nine. In most of the samples, either *Thysanoessa raschii* or *Calanus hyperboreus* was the dominant prey species. At Barrow, *T. raschii* was the dominant prey in both whales taken in September, while in samples from spring *T. raschii* and copepods (*Calanus hyperboreus*, *Euchaeta glacialis*, and *Metridea longa*) each predominated in two. In samples from whales at Kaktovik, all of which were taken in late September and early October, copepods (principally *C. hyperboreus*) were dominant in seven and *T. raschii* in two.

Eliminating the samples obtained from small intestines or colons and those from stomachs which contained only a single food item, food remains were found in the stomachs of 15 whales. One of those (82-G-2) was a whale taken in the Bering Sea near Gambell on 1 May 1982. The stomach of that whale was recorded

TABLE 2. PREY IDENTIFIED FROM GASTROINTESTINAL TRACTS OF BOWHEAD WHALES. DOMINANT PREY SPECIES ARE INDICATED BY ××

	BARROW							KAKTOVIK									OTHER AREAS			
	76-B-6F	76-B-7F	77-B-5	79-B-3¹	80-B-3	80-B-5	80-B-9	79-KK-1	79-KK-2	79-KK-3	79-KK-4	79-KK-5	80-KK-1²	81-KK-1	81-KK-2	82-KK-1	78-H-2	79-H-3	80-SH-1¹	82-G-2
COPEPODS																				
Calanus cristatus					×								××			×				
C. finmarchicus											×									
C. glacialis			×																	
C. hyperboreus					××	×××	××	××	××	×	××	×		××	××	××				
Calanus sp.					×	×	×		×	×		×								
Chiridius obtusifrons			×		×		×			×	×									
Euchaeta glacialis			××		××		×		×	×	×					×				
Heterorhabdus sp.									×		×					×				
Metridea longa			××																	
M. lucens								×	×	×	×			×		×				
Pseudocalanus sp.			×											×						
EUPHAUSIIDS																				
Thysanoessa inermis	××	×	×		×		×					×		×						
T. raschii		××			××	×××	××		×	×××	×	××		×						
MYSIDS																				
Mysis litoralis					×		×	×	×	×	×	×								
Neomysis rayi					×	×	×				×									
HYPERIID AMPHIPODS																				
Hyperia galba					×		×		×											
H. medusarum							×				×									
Hyperia sp.									×											
Hyperoche medusarum			×				×													
Parathemisto abyssorum										×				×		×				
P. libellula	×	×						×	×	×	×	×		×	×	×				

Continued...

TABLE 2. Continued.

GAMMARID AMPHIPODS	BARROW 76-B-6F	76-B-7F	77-B-5	79-B-3[1]	80-B-3	80-B-5	80-B-9	KAKTOVIK 79-KK-1	79-KK-2	79-KK-3	79-KK-4	79-KK-5	80-KK-1[2]	81-KK-1	81-KK-2	82-KK-1	OTHER AREAS 78-H-2	79-H-3	80-SH-1[1]	82-G-2
Acanthostepheia behringiensis		×																		×
A. incarnata																				
Ampelisca macrocephala																	×			
Anonyx compactus																				×
A. nugax							×													
Apherusa glacialis											×			×						
Atylus atlassovi																				×
A. carinatus										×		×								×
Bathymedon sp.																				
Gammaracanthus loricatus		×								×		×								
Gammarus zaddachi																				
Gammarus sp.									×											×
Hippomedon denticulatus										×	×									×
Monoculodes zernovi		×								×										
Monoculodes sp.													×							
Munnopsis c.f. *M. typica*																				
Onisimus glacialis									×	×				×		×				
O. litoralis								×							×					
O. nanseni																				
Orchonome sp.																				
Pontoporeia femorata	×																			×
Rozinante fragilis		×									×	×								×
Weyprechtia heuligini																				
W. pinguis											×		×							
Family Lysianassidae																				
Family Synopiidae																				×

ISOPODS
  Saduria entomon
SHRIMP
  Eualus fabricii
  E. gaimardii
  Sabinea septemcarinata
  Family Crangonidae
CRABS
  Chionoecetes opilio
  Family Paguridae (zoea)
CUMACEANS
  Diastylis bidentata
  Diastylis sp.
OSTRACODS
MOLLUSCS
  Limacina helicina
  Natica clausa
  Nuculana sp.
  Order Pelecypoda
FISHES
  Boreogadus saida
  Myoxocephalus quadricornis
  Pungitius pungitius
  Family Cottidae
PEBBLES

[1] Sample from colon.
[2] Sample probably from small intestine.

as full and contained an estimated 30L of food.   Based on the sample we examined, the prey was composed of 92% gammarid amphipods, 7% cumaceans, and 1% other benthic organisms.   Four small pebbles also occurred in the sample.

The quantitative composition of stomach contents samples from the remaining 14 whales is shown in Tables 3 and 4.   Euphausiids dominated in the stomach contents of whales taken at Barrow in the autumn.   Whales taken at Barrow in the spring contained principally euphausiids and copepods in variable proportions, with substantial amounts of mysids in three.   Total quantities of food in whales taken during spring were very small.   In whales taken in the autumn at Kaktovik,

TABLE 3. QUANTITATIVE DATA (% OF TOTAL SAMPLE VOLUME) ON STOMACH CONTENTS OF BOWHEAD WHALES TAKEN AT BARROW

Prey type	AUTUMN 1976			SPRING 1977 AND 1980				
	Whale specimen number		Overall mean % of contents[1]	Whale specimen number				Overall mean % of contents[2]
	76-B-6F	76-B-7F		77-B-5	80-B-3	80-B-5	80-B-9	
Copepod	—	—	—	97.0	24.2	—	1.4	30.7
Euphausiid	97.1	86.7	90.3	1.0	48.5	95.4	91.6	59.1
Mysid	—	—	—	—	15.2	3.8	5.4	6.1
Hyperiid amphipod	2.3	3.0	2.7	<0.1	3.0	—	1.0	1.0
Gammarid amphipod	0.6	10.3	6.9	—	—	—	0.6	0.2
Other invertebrate	—	<0.1	<0.1	2.0	—	—	—	0.5
Sample volume (ml)	17.5	33.0		20.0	3.3	73.4	139.7	
Estimated total volume of contents (liters)	unknown	109		unknown	"a few invertebrates"	1	2	

[1] Calculated as the percent of combined total volume in the two samples.
[2] Calculated as the average of the percent of total volume in each of the samples.

TABLE 4. QUANTITATIVE DATA (% OF TOTAL SAMPLE VOLUME) ON STOMACH CONTENTS OF BOWHEAD WHALES TAKEN AT KAKTOVIK, AUTUMN 1979-1982

Prey type	Whale specimen number								Overall mean % of contents[1]
	79-KK-1	79-KK-2	79-KK-3	79-KK-4	79-KK-5	81-KK-1	81-KK-2	82-KK-1	
Copepod	99.7	99.0	23.4	88.3	<0.1	99.0	99.0	98.7	66.1
Euphausiid	—	0.3	67.8	4.9	97.9	0.7	—	—	31.2
Mysid	—	0.3	7.0	—	0.8	—	—	—	1.2
Hyperiid amphipod	<0.1	0.1	0.5	0.4	—	<0.1	—	<0.1	0.1
Gammarid amphipod	0.1	0.1	0.3	2.4	0.1	0.3	1.0	1.3	0.4
Other invertebrate	<0.1	<0.1	—	2.3	1.1	<0.1	—	—	0.5
Fish	<0.1	0.1	1.0	1.7	—	—	—	—	0.3
Sample volume (ml)	2406.2	545.2	399.7	131.3	357.9	145.5	19.2	95.2	
Estimated total volume of contents (liters)	44	18	22	18	36	18	3	"a few"	

[1] Calculated based on the volume and percent composition of each sample and the estimated total contents volume of stomachs from which samples were taken.

TABLE 5. SIZES OF PREY ORGANISMS IN STOMACHS OF BOWHEAD WHALES

	Length (mm)[1]	Volume (mL)
Copepods	3.5-7.0	0.002-0.02
Euphausiids	18-30	0.1-0.15
Mysids	23-33	0.1-0.2
Hyperiid amphipods	8-21	0.05-0.1
Gammarid amphipods	7-55	0.02-4.0
Isopods	52-86	3.4-5.7
Fishes	31-83	0.1-2.9

[1] Measurements are total length for all groups except copepods, which are cephalothorax length.

copepods and euphausiids in aggregate comprised 91.2–99.7% of the contents of individual samples and 97.3% of the overall prey in all samples combined. The stomach contents in individual whales varied from 99.7% copepods to 97.9% euphausiids; overall, copepods comprised about twice as much of the stomach contents as did euphausiids. The total volume of stomach contents in the whales varied from 3 to 44L, with an average of 23L.

Sizes of representative species of the major prey groups eaten by bowheads are shown in Table 5. The organisms most commonly eaten (copepods, euphausiids, mysids, and amphipods) range from about 3 to 30 mm in length and have a volume of 0.002 to 0.2 mL. Organisms such as isopods and fishes are considerably larger but were rarely found in stomach contents samples. The largest item we found in bowhead stomach contents was the shell of a snail (*Natica clausa*), 3.4 cm high and 2.6 cm in basal diameter, weighing 8.0 g. The smallest items were *Pseudocalanus* copepods, which are approximately 1.3 mm in cephalothorax length and weigh about 0.1 mg.

In addition to the whales from which samples were collected, some additional animals were examined in the field and the presence or absence of food in their stomachs recorded. Of whales taken in the Bering Sea in spring, two had prey in the stomach: one taken at Gambell (82-G-2) contained gammarid amphipods, cumaceans, and other benthic organisms; the other (78-S-1) taken at Savoonga was reported to contain " a few euphausiid-like creatures." Three had empty stomachs: two of those reportedly had material in the intestines, and the third had crustaceans in the baleen. Of four whales taken in the Chukchi Sea in spring, two had empty stomachs, one contained a snail, the other a single gammarid amphipod. Four whales taken at Barrow in spring have contained food remains, and seven have been recorded as having empty stomachs. Three of the latter had some food residues in the intestines. All whales that have been taken and examined in the autumn (2 at Barrow and 10 at Kaktovik) have contained substantial quantities of food.

We examined the relationship between whale size and the principal type of prey found in samples based on 18 animals of known length which contained recognizable prey. Whales that had eaten principally copepods ranged from 10.5 to 17.4 m, with a mean length of 13.1 m (n=7). Those that contained mostly eu-

phausiids ranged from 8.5 to 16.0 m, with a mean of 12.0 (n=7). Five whales
in which we found only benthic organisms were 8.3—10.1 m, with a mean length
of 9.2 m. Only one of the whales that had eaten copepods or euphausiids was less
than 10.3 m in length.

DISCUSSION

We identified a wide array of organisms from samples taken from the gastrointes-
tinal tracts of bowhead whales. Most of the prey species (53/56) were inverte-
brates, and most of those (35/53) were primarily benthic organisms. However,
with few exceptions, benthic species composed a very small proportion of the overall
stomach contents. Four of the five exceptions were whales taken in spring in the
Bering and Chukchi seas; the fifth was a whale taken at Barrow in spring whose
colon contained three small clams. The two taken in the Chukchi Sea each con-
tained single items. One of those taken in the Bering Sea had an empty stomach
but shrimp fragments in the colon; the other had a stomach filled with benthic
invertebrates. The five whales were all small, the largest being 10.1 m long, and
were undoubtedly subadult animals (Marquette 1978). We conclude, based on
the samples we examined and field records, that some bowheads feed while passing
through the northern Bering Sea in May. The incidence of feeding during the
northward migration appears to be less in the Chukchi Sea than in the Bering.
Feeding whales may be predominantly juveniles, and their prey are mostly benthic
invertebrates.

Four of 11 whales taken and examined at Barrow in the spring have contained
food in their stomachs, generally a few liters or less of copepods and euphausiids.
We conclude that some feeding occurs near Barrow during the spring migration
and that planktonic organisms are the main prey. However, based on the high
proportion of empty stomachs and the small volumes of contents in those contain-
ing food, it appears that the main feeding season has not yet commenced.

Many bowhead whales summer in the eastern Beaufort Sea (Fraker and
Bockstoce 1980), where they are presumed to feed extensively (Griffiths and Buch-
anan 1982). Whales that have been taken and examined while moving westward
through the Alaskan Beaufort Sea in autumn have all contained food. Whales
taken at Barrow have contained mostly euphausiids, while in those taken near
Kaktovik both copepods and euphausiids occur, with copepods overall predominat-
ing in the samples. Benthic organisms are quantitatively unimportant near Kak-
tovik but comprised a small and perhaps significant proportion of the samples ex-
amined from Barrow. Feeding of whales in autumn is obviously directed primarily
at organisms in the water column, with benthic organisms being taken incidentally
during near-bottom feeding.

Several lines of evidence point to the existence of at least two areas of the
Alaskan Beaufort Sea where bowheads regularly feed during September-October.
First, of course, is the occurrence of substantial quantities of food in the stomachs
of all the whales taken and examined at Kaktovik and Barrow during autumn

hunts. Whalers from Kaktovik have indicated that they regularly find bowheads feeding in the area to the east of Barter Island (D. Ljungblad, pers. commun.; G. Jarrell, pers. commun.). In discussing bowheads in the area to the east of Point Barrow, Durham (1979) stated that " the hunters sometimes encounter herds of 50 to 60 whales along the Plover Islands (Thomas Brower, pers. commun.). This area may be a rest stop for the whales and provide an opportunity for them to feed, judging from stomach contents."

The feeding area east of Barrow appears to extend to approximately Pitt Point. On 18 September 1974, 57 whales were counted in this area (Braham *et al.* 1982), while on 20 September counts ranged from 81 to 136 (Ray and Wartzok 1980). On 8 August 1976, a single whale was seen just offshore from the Plover Islands (Lowry, unpublished). Two ringed seals (*Phoca hispida*) collected in the immediate area within minutes of sighting the bowhead had been actively feeding on euphausiids (Lowry *et al.* 1980). On 19 August 1976, four bowheads were seen northeast of Point Barrow, and on 21 September 47 whales were counted in the area (Braham *et al.* 1982). As indicated in this report, whales taken at Barrow on 10 and 20 September 1976 had both been feeding on euphausiids. A group of 20 whales which appeared to be feeding was seen north of Point Barrow on 22 October 1978 (Braham *et al.* 1982).

The feeding area in the eastern Beaufort Sea extends from Barter Island east to at least the U.S.-Canada demarcation line (141°W longitude). In 1979, 35 whales were seen milling east of Beaufort Lagoon on 24 September, and 37 were observed north of Demarcation Bay on 26 September (Ljungblad *et al.* 1980). In 1980, single whales that appeared to be feeding were sighted north of Beaufort Lagoon on several occasions from 9 to 21 September, and a group of nine was seen east of Barter Island on 14 September (Frost and Lowry 1981, Ljungblad 1981). On 22 September 1982, 128 bowheads were counted in the area north of Demarcation Bay. Most of the animals were milling around near the surface (S. Johnson, pers. commun.).

Although bowheads may feed regularly or occasionally in other parts of the Alaskan Beaufort Sea, such occurrences cannot be verified by observations of stomach contents since very few whales are taken elsewhere than the areas discussed above. Ljungblad (pers. commun.) has seen bowheads engaged in behavior that might indicate feeding in the areas north of Flaxman Island and northeast of Pingok Island.

The smallest organisms which are regular foods of bowheads are the copepods *Metridea* spp. (cephalothorax length 2.7–3.1 mm) and *Calanus glacialis* (2.4–3.3 mm). The most commonly eaten species of copepod, *Calanus hyperboreus*, is much larger, ranging in length from 3.6 mm (copepodite stage IV) to 6.4 mm (adult). The smaller copepods, *Pseudocalanus* sp. (1.1–1.6 mm long) and *Derjuginia tolli* (1.4–1.8 mm long), although very abundant in the Beaufort Sea (Frost and Lowry 1981), virtually never occur in bowhead stomach contents. It appears, therefore, that organisms smaller than about 2.5 mm are not effectively retained by bowhead baleen. The largest prey regularly consumed appear to be about 30 mm long and

TABLE 6. CALORIC VALUES OF REPRESENTATIVE SPECIES OF ARCTIC
ZOOPLANKTON AND BENTHOS, ARRANGED IN ORDER OF DECREAS-
ING CALORIC VALUE. ALL VALUES ARE FROM SAMPLES TAKEN
IN SEPTEMBER UNLESS OTHERWISE INDICATED.
(ADAPTED FROM PERCY AND FIFE 1980.)

Taxon	Cal/g wet weight	% of maximum
Copepod (*Calanus* sp.)		
September	2,983	100
mid-late August	2,660	90
late July-early August	2,018	69
Euphausiid (*Thysanoessa inermis*)	1,974	67
Hyperiid amphipod (*Parathemisto libellula*)	1,364	46
Gammarid amphipod (*Anonyx nugax*)	1,299	44
Chaetognath (*Sagitta elegans*)	517	18
Isopod (*Saduria* (=*Mesidotea*) *sabini*)	367	12
Pteropod (*Clione limacina*)	296	10
Ctenophora (*Mertensia ovum*)	98	3
Cnidaria (*Aglantha digitale*)	89	3

include euphausiids, mysids, and amphipods.

The fact that bowheads migrate several thousands of kilometers annually to summer and feed in the Beaufort Sea implies that the quantities and kinds of food available to them there are adequate, and also perhaps that feeding conditions are superior to those found in other areas. The abundance of copepods in the Beaufort Sea is not remarkably high (Griffiths and Buchanan 1982). The abundance of euphausiids is extremely difficult to quantify (Brodie *et al.* 1978), but observations of predator stomach contents indicate that they may be locally abundant (Frost and Lowry 1981). One way in which arctic marine zooplankton are remarkable is their tendency to accumulate storage lipids during the summer which are used for maintenance and reproduction during winter months (Lee 1975). In samples of *Calanus hyperboreus* collected from Fletcher's Ice Island in October, lipids comprised 64% of the dry weight (Lee 1975). In samples collected in September at Frobisher Bay, lipids comprised 52.4% of the dry weight of *Thysanoessa inermis* and 57.4% of *Calanus* spp. (Percy and Fife 1980). Caloric values of representative species of arctic marine zooplankton and benthos are shown in Table 6. Values are expressed in terms of calories per gram wet weight, which is the most appropriate consideration from the perspective of a consumer. Organisms which are the primary foods of bowheads (copepods and euphausiids) have very high caloric values. Those eaten with some frequency (hyperiid and gammarid amphipods) have intermediate values. Those organisms which are rarely or never consumed have very low caloric values. Of interest also is the fact that copepods in September contain almost 50% more calories than those sampled in late July and early August. Therefore, given equivalent prey densities, late summer feeding may be of greater value to the whales than that which occurs earlier in the year.

Although it is probably true in general that arctic zooplankton are richer in calories than those in more southern latitudes (Percy and Fife 1981), there are few

data available with which to verify this hypothesis. Nishiyama (1977) sampled zooplankton in Bristol Bay, Alaska and determined the caloric value of *Calanus* and *Thysanoessa* to be 5,512 and 5,554 cal/g ash-free dry weight. Those values are 44% and 19% lower than comparable measurements for the same species collected at Frobisher Bay (Percy and Fife 1980). The values for caloric content of Frobisher Bay copepods are the highest published values for any marine organism (e.g., see Braun *et al.* 1968, Tyler 1973, Laurence 1976).

Several authors have attempted to assess the relationship between availability of food in the marine environment and the food requirements of whales. Studies dealing with fin whales (*Balaenoptera physalus*) have concluded that either whales swim exceedingly fast, or densities of prey are much greater than those found using standard sampling techniques (Klumov 1961, Brodie *et al.* 1978). Similar results were derived by Brodie (1980) and Griffiths and Buchanan (1982), dealing with bowheads. However, those studies did not take into account the energetic richness of prey available in the Arctic.

We have made similar calculations, starting with the energetic assumptions used by Brodie (1980), who concluded that a bowhead 13.72 m long would need to ingest approximately 4,000 kg of lipids during the feeding season in order to maintain itself throughout the year. Based on data in Percy and Fife (1980), 16.8% of the wet weight of *Calanus* copepods collected in late July and August is lipid; therefore, a whale would need to consume 23,810 kg of copepods during the feeding season. A bowhead 13.72 m long would have baleen approximately 2.4 m long (Alaska Eskimo Whaling Commission, unpubl. data). We assume that while feeding the mouth opening is 2.4 m high and tapers from 2.0 m wide at the bottom to 1.0 m at the top and a whale swims at about 4.2 km/hour (2.8–5.6 km/hr in Ljungblad *et al.* 1981). Using those assumptions, 15,120 m³ of water would be filtered each hour. Griffiths and Buchanan (1982) observed biomasses of *Calanus* ranging from 0.623–0.903 g/m³ at certain depths in areas of the Canadian Beaufort Sea where bowheads appeared to be feeding on organisms in the water column. To acquire 23,810 kg of copepods would require filtering 26,367,000–38,218,000 m³ of water (assuming the above prey densities and 100% filtering efficiency), which would involve 1,744–2,528 hours of feeding. Frost and Lowry (1981) estimated a feeding season of 105 days in the Canadian Beaufort and 25 days in the Alaskan Beaufort Sea, which suggests 3,120 hours available for feeding. Therefore, it appears that bowheads can obtain their annual food requirements with a 130-day feeding season in the Beaufort Sea, if they feed for somewhat over half the time they are on the feeding grounds and concentrate their efforts in areas where prey are relatively abundant. Based on the above assumptions and an average weight for copepods of 0.004 g (Bain *et al.* 1977), the ingestion rate of copepods would be approximately 50,000 individuals per minute.

A further consideration with respect to the bowhead whale stock in the western Arctic is whether the total annual production of prey in the feeding areas is sufficient to supply the energetic requirements of all the whales summering in the area. Although the summer feeding range of the bowhead once included much

of the Bering and Chukchi seas as well as the Beaufort Sea (Bockstoce and Botkin 1980), at present the Beaufort Sea is the primary feeding area, although some late season feeding may occur in the Chukchi Sea (Frost and Lowry 1981). Calculations such as those done for an individual whale feeding on copepods cannot be expanded to the entire population because euphausiids, a major prey species, have not been quantitatively sampled properly in the Beaufort Sea (see Frost and Lowry 1981 and Griffiths and Buchanan 1982) and bowhead prey are also eaten by other consumers in the Beaufort Sea. Frost and Lowry (1983) estimated the quantities of prey eaten on an annual basis by populations of major vertebrate consumers in the Alaskan Beaufort Sea. They considered only species which feed primarily on organisms connected to the pelagic/planktonic food web—bowhead whales, white whales (*Delphinapterus leucas*), ringed seals, seabirds, and arctic cod (*Boreogadus saida*). Results indicated that arctic cod are by far the major consumer of zooplankton. They were estimated to eat 97.8% of the total copepod and 65.8% of the total euphausiid biomass consumed annually by all species of predators combined. Estimates for bowhead consumption were 2.2% of the total copepod biomass and 31.5% of the total euphausiid biomass consumed. Although these results suggest the possibility of considerable competition for food, some resource partitioning occurs since many of the copepods eaten by arctic cod are small forms (*Derjuginia* and *Pseudocalanus*), which are not major foods of bowheads (Frost and Lowry in press). Based on extrapolations from measurements of primary production, Frost and Lowry (1981) estimated that 0.3–4.4 million t of zooplankton are produced annually in the Alaskan Beaufort Sea. When compared to the estimated total amount of zooplankton consumed annually (approximately 1.1 million t (Frost and Lowry in press)), this suggests that food availability may be limiting in years of low production, while in other years a surplus of food may be available. Causes of annual variations in productivity and their effects on consumer populations are largely unknown.

What then is the feeding strategy of western arctic bowhead whales? Bowhead whales are robust-bodied animals, possessing long baleen with fine fringes capable of efficiently retaining very small prey. Although our study has shown that some feeding occurs in the northern Bering and Chukchi seas during the spring northward migration, the major known summer feeding grounds are in the Beaufort Sea. The quantities and kinds of organisms there are adequate, and the extraordinarily high fat content (and caloric value) of prey facilitates accumulation of blubber reserves necessary to maintain the animals during periods of fasting. Extensive blubber reserves may help sustain animals through years of low summer productivity which may occasionally occur.

Some late summer and early autumn feeding may occur in the Chukchi Sea. There is no direct information to indicate whether bowheads feed on their wintering grounds in the Bering Sea. However, based on considerations such as the seasonal distribution and abundance of prey, and their probable caloric content, we speculate that winter feeding in the Bering Sea, if it occurs, is of little significance in the annual nutrition of bowheads. Bowhead whales swim from the Ber-

ing Sea to the Beaufort Sea to feed because of the high-energy foods available there, and perhaps also because competition for food from other organisms occurs at tolerable levels. No other baleen whale penetrates northward into what is presently the principal feeding grounds for bowheads. In years past, bowheads mingled with other species in the Bering Sea in summer until they were eliminated by predation from commercial whalers. Whether the portions of their feeding range that were lost decades ago will ever be regained is a most interesting question, and one of great significance when contemplating the ability of the western arctic bowhead population to regain its former abundance.

ACKNOWLEDGMENTS

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OBSERVATIONS ON THE OCCURRENCE AND BEHAVIOUR OF MINKE WHALES OFF THE COAST OF BRAZIL

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ABSTRACT

Field observations on minke whale morphology and physiology, the hydrography and topography of the Brazilian whaling ground and catch statistics from 1963 to 1982 are presented.

In the past 20 years, 12,494 minke whales have been taken off Brazil; only 3 were taken prior to 1963. Of those animals thought to be mature, females predominate in the catch (sex ratio, 2 females: 1 male). The population appears to remain at an exploitable level, although other species in the area have been considerably reduced.

The most important environmental conditions associated with the arrival of the minke whale in these tropical breeding grounds appear to be an optimum temperature of 26–27°C, day-length, reduced turbulence and an amiable surface current.

The behaviour of minke whales in response to various stimuli is described, and in particular their escape reactions, normal swimming speeds, co-ordinated swimming, affinity for mates and response to electric shocks.

INTRODUCTION

The minke whale, *Balaenoptera acutorostrata* (Plate I), is one of the most valuable marine mammals and is now the most common species of baleen whales in the Antarctic. Perhaps, due to its high yield of meat, relative to the rest of the components (Table 1), this species has become an important natural food resource and thus making the commercial whaling economically viable. Despite the claims that the minke whales are increasing in the Antarctic and now considerably more abundant as they were in 1910 (FAO, 1982), the exploitation of this species is regulated by IWC.

The minke whales taken off Brazil are considered as a part of the Area II management stock as defined by the IWC (0°–60°W) although there is some controversy over the applicability of these Areas (originally developed for blue and fin whales) to minke whales (IWC, 1981; 1982). However, much of the whaling would depend on natural population which varies both geographically and seasonally due to fluctuations in the rate of recruitment, mortality, including level of exploitation, growth rate, supply of planktonic krill as food (Ohsumi, Masaki and Kawamura, 1970; Ohsumi, 1979) and other causes of environmental factors. The catch statistics and catch per unit effort (CPUE) values over the past 20 years have

TABLE 1. PRIMARY MATERIALS DERIVED FROM MINKE WHALES BASED ON
ACCUMULATED FACTORY DATA

Primary Products		Mean Weight (Kg/Whale)	%
1.	Meat	3,500	50.00
2.	Bone	1,260	18.00
3.	Cartilage	7	0.10
4.	Baleen plates	35	0.50
5.	Viscera: Tongue	70	1.00
	Lungs	56	0.80
	Heart	21	0.30
	Kidneys	14	0.20
	Liver	63	0.90
	Stomach	14	0.20
	Intestine	63	0.90
6.	Blubber: Dorsal	980	14.00
	Ventral	280	4.00
7.	Fins	42	0.60
8.	Lost Materials: Blood etc at sea & factory	595	8.50
	Total	7,000	100.00

shown that the recruitment of this species in this area has remained very constant
(Singarajah, 1983). With the advent of their breeding seasons, the minke whales
arriving off Brazil are characteristically migratory, but the reasons to select this
area as their breeding ground with such regularity are little understood.

Previous work on Brazilian minke whales is scanty (Williamson, 1975) and in
this paper some aspects of minke whale biology are examined and the feasibility of
continuing to exploit this species, together with some of the factors which may
influence their migratory behaviour to the breeding ground off Brazil, are dis-
cussed.

MATERIALS AND METHODS

Field observations were made on board the catcher boat *Cabo Branco*. The normal
operation pattern is that the boat leaves port at about 0330–0400 hours and re-
turns to the factory with its catch at about 2230–2300 hours. Samples were taken
both on board the catcher and at the factory though most measurements were made
at the latter.

Past data on catches, lengths, reproductive state of the whales and informa-
tion on stomach contents were kindly provided by SUDEPE (Superintendência Do
Desenvolvimento Da Pesca) but some of the early data were missing or considered
unreliable. The selected data, covering the whole period of minke whaling, were
then transferred to an IBM computer for processing. Blood counts were made on
board the catcher; most observations on behaviour patterns were confirmed by
photographs, 35 mm colour slides and " Super 8 " cine films. Where necessary,
appropriate parts of the whale, including entire baleen series, were transported to
the laboratory for confirmation.

RESULTS

MORPHOLOGY

General appearance :   The minke whales are the smallest of the rorqual whales which are well adapted for exclusively marine life.   The body is somewhat less streamlined with triangular and dorsoventrally compressed head with a strong central ridge (see Plate I).   The paired nostrils or " blow holes " are situated at the summit of the head about a metre from behind the tip of the snout which is about 8 cm shorter than the lower jaw.   The blow holes are highly dilatable, especially when the animal gasps for breath, which otherwise remain closed by valve-like muscular folds of skin.   The blow holes lead to a common median tubular canal about 50 cm long and 8 cm in diameter before leading to the tracheae.

The eyes are small, when compared to the huge body, and dorsolaterally placed.   The eye-ball, on dissecting out, measures about 10 cm in diameter and well controlled by the powerful eye muscles and the optic nerve.

No external ear is visible, but the external ear aperture is a horizontal slit of extremely small size, about 5 mm long; normally remains closed by valvular folds within a narrow groove about 9 mm wide and 9 cm long.   The centre of the aperture lies about 44 cm behind and on the same level as the eye.   The external aperture leads into a complicated tubular canal which is about 6 mm in diameter and its inner surface is lined by fine longitudinal grooves and ridges and having the same colour as the skin, perhaps due to invagination of the skin.   The canal, after running about 8 cm towards the tympanic bulla, leads into a " gizzard-like " structure which is often filled with bone marrow-like substance.   The canal is now continued from the centre of one side of the muscular gizzard structure and extends until it establishes contact with the ear plug.   The conical ear plug (Plate II) fits closely over a membranous, but strong, teat-like structure or " glove finger " (Plate III) and similarity in ear aperture was noticed in fin whales (Laws & Purves, 1956). The broad margin of the glove finger is attached to the hollow part and surrounded by the bony elements in the posterior-ventral region of the tympanic bulla.   The canal, connecting the gizzard-like structure and the ear plug, is smooth and devoid of any ridge or groove and the grey colour is generally lacking.   The ear bones or tympanic bullae are kidney-shaped, each about 9 cm long and 6 cm broad and weighing 450 g wet and 250 g dry weight.   It is perhaps the hardest part of the whole body and is located just anteriodorsal to the foramen magnum and is separated from the external aperture by about 50 cm, on each side.

Ventral grooves :   The ventral grooves run lengthwise and parallel to one another reaching anteriorly the chin and posteriorly close to the umbilicus, and extend laterally to a line between the eye and the flipper insertion.   The median groove extends from the posterior end of the mandibular symphysis to just short of the umbilicus.   This distance between the end of the median groove and the umbilicus has a mean of 84.9 cm, though it varies in the different sexes.   However, the minimum distance between the umbilicus and the nearest 6th groove, on either

side of the median groove, remains constant in both sexes at 40.7 cm.   This ob-
servation is in close agreement with measurement given by Ohsumi *et al.* (1970) to
the Antarctic minke whales.

The number of ventral grooves of 660 animals (223 males and 437 females)
were counted in 1979 and the mean number in both males and females was 47 (8).
Da Rocha (1980) examined 220 males and 452 females and her values (for half the
total number) were 21 for males (range 16–35) and 22 for females (range 15–31).
The difference in the values may be due to differences in the method of count-
ing; in da Rocha's study, the grooves were counted while the whales were lying
in their sides on the flensing platform; while in the present study the grooves were
counted while the whale was tied by its tail alongside the vessel, which facilitated
the counting.

Skin and colour pattern: The skin is about 3 mm thick, smooth and slippery, sup-
ported by a thick layer of panniculus adiposus or the " blubber " from below
(Fig. 1).   The colour of the skin changes from dark grey on the dorsal aspect of
the body to creamy white ventrally.   The dark grey colour continues from tip of
the snout to the dorsal surface of the caudal fluke, but dips down just below the
eye and the dorsal end of the flipper insertion to form a small arch and again mid-
way between the flipper and the caudal fluke thus forming a wider arch; the end
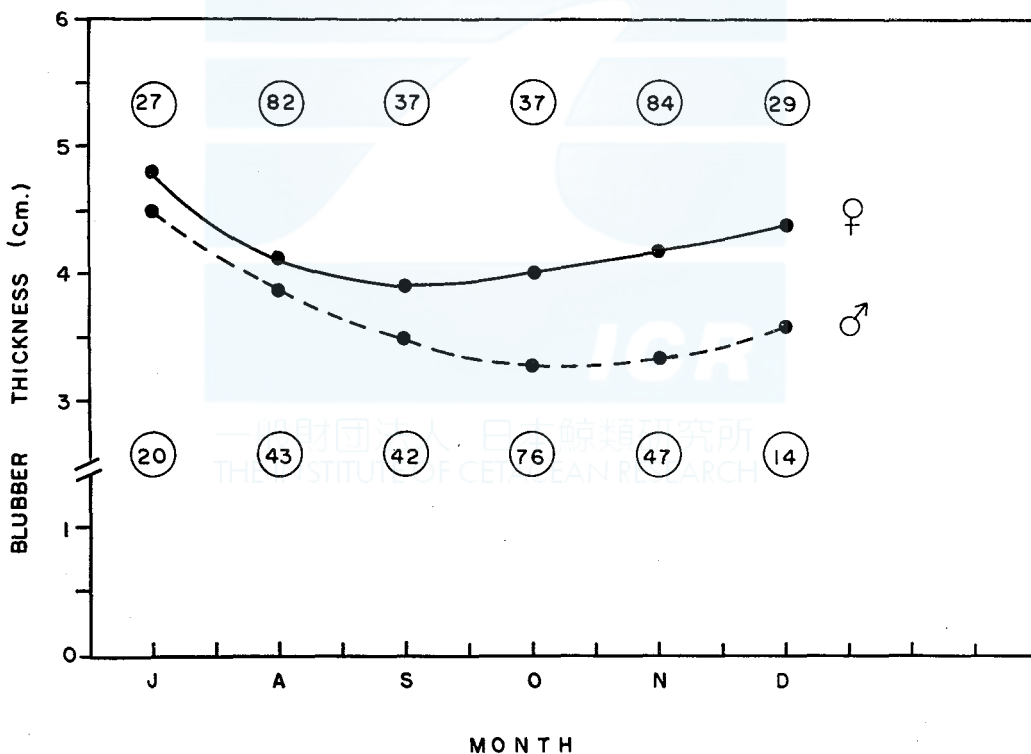
Fig. 1.   Blubber thickness of males and females of the same whaling season.   Num-
bers shown within circles represent mean sample.

of this second arch then curves up, like a broad inverted dorsal fin, to a median lateral line to merge with the dorsal surface of the fluke, on each side. The cream colour extends from chin to the caudal end, including the ventral surface of the fluke though the margins of the latter are usually edged with dark grey. The creamy bracket marks above the flipper are usually inconspicuous.

These colour patterns are essential in identifying the Antarctic stocks of minke whales, and seem to be of adaptive value. Usually with the slightest tilt of the body in the water, these peculiar colour patterns cause to reflect a bright bluish-green light, particularly when the whales swim up side down, which enables them to be easily recognized from a distance of about 800 meters.

Jaws: The two jaws are symmetrical, but the lower jaw is about 8 cm longer than, and protrudes beyond, the upper jaw (see Plate I). The upper jaw on each side measures, on an average, 186 cm between the tip of the snout and the gape of the mouth. But, beyond this point, the baleen laminae are carried in by a short segment, about 28 cm long, which curves inward and terminates bluntly as a triangular end. It is along this rear end that the greatest number of smaller baleen laminae are arranged in multiple rows.

Baleen plates: The strongly keratinized horny structures though called baleen plates, all are not truly plates. These horny structures are fused together at their top ends by interlaminar cement-like substance to form the " baleen series " (Plate IV) and suspended from each side of the upper jaw. The cemented part, which apparently represents the " gum ", varies in height and width according to the size of the plates inserted.

On the basic characteristics of size, shape and position, the plates could be grouped into mainly four categories:

1. The smallest rod-like structures in the anterior segment of the jaw, usually 8 in number, are arranged in double rows fairly close to each other. Each of these rod-like structures measures about one cm from below the line of fusion and provided with usually 4 very stiff filaments (Plate V A).

2. These are followed by the transitional plates which are small rectangular laminae and variable in number (Plate V B).

3. Next in series, occupying the major part of the jaw, are the larger plates, on an average 237 of them, arranged transversely at intervals of 0.4–1 cm between laminae. They are inserted by the smallest side and run undivided between lingual and labial margins in a single row (see Plate IV). However, the size of the individual plates varies and the largest plates are always confined to the mid-region while others, in gradually diminishing order of size, run towards both extremities of the jaw until they merge with the transitional laminae. These laminae are not typically triangular as commonly described, but rather combinations of inverted triangles and rectangles; the triangular part increases in size at the expense of rectangular part as the plates reach the mid-region of the jaw. The labial side of the largest plates measures about 40 cm and is smooth and devoid of any filaments, but on the lingual side only the hypotenuse, just below the rectangulr part, is frayed out into fine flexible

filaments (see Plate IV). The filaments also vary in number and length; the largest plate on the average consists of 380 filaments and the longest of these being 10 cm.

4. By contrast, the " plates " on the rear end of the baleen series are very much reduced in size, about 2 cm tall and rectangular type of laminae which are disproportionally numerous and grossly overlap and relatively difficult to count, unless the series is cut into segments. The bristles are less stiff and vary between 4 and 12 per plate (Plate V C).

Perhaps for this reason, Williamson (1973) concluded that for rorquals, it was too difficult to accurately count the rear plates and he called them, including the anterior rod-like plates, as " hairs ". Previous studies (van Utrech *et al.* 1978; Ohsumi *et al.* 1970; da Rocha, 1980) have clearly not included all the " hairs " in their counts. Best (1978) followed the procedure followed by Williamson (1983).

During the 1981 season, the baleen plates from 26 whales, 13 males and 13 females, were examined. Except for the colour pattern, no asymmetry was observed between the right and the left hand side of the blaeen series. The baleen laminae can be further divided into 3 on the basis of colour: (i) creamy white; (ii) creamy white with black edge and (iii) black (see Plates IV & V). The results are given in Table 2. The baleen series on the right side comprised an average of 111 all white plates, including the rod-like " plates " or " hairs ", at the anterior end, covering about 50 cm of the jaw. The plates in the mid-region comprised an average of 127 white/black plates. The posterior all black laminae include about 87 plates and about 2,050 smaller laminae. The pattern on the left hand side is the same but the proportion of all white plates is lower; on average there are only 63 all white plates covering 20 cm.

While the function of the colour difference on the two sides remains curious, but the enormous number of the smaller laminae, though look vestigeal in form, are adaptations that are functionally more evolved to increase the efficiency and rapidity perhaps during filter-feeding.

Flippers: Between 1979 and 1981, 1,745 animals, 619 males and 1126 females, were examined for flipper colouration. The flippers are elongated and more wing-like. There appeared to be no difference between the sexes; the flippers are about 1 m in length (Plate VI) and 30 cm wide, being light grey apart from a dark grey calyx shaped on the dorsal surface next to the body. No white stripes were observed in Brazilian minke stock, but the under margins turn out to be slightly

TABLE 2. MEAN NUMBER OF BALEEN LAMINAE FOR MINKE WHALES FROM BRAZIL

		Colour pattern		
		(i)	(ii)	(iii)*
Males	right	106.6	128.3	2131.5
	left	73.7	156.7	1913.0
Females	right	116.0	126.3	2051.0
	left	51.8	187.5	2112.0

* posterior black laminae are from approximate estimates.

whitish.

Flukes: In 1980, the flukes from 49 animals, 20 males and 29 females, were examined. The flukes were on average about 118 cm in length, and narrower in males than in females. The notch was about 7 cm deep and 4 cm at its widest part. A considerable strength is centered just anterior to the fluke, the tail-stock (Pl. VII).

Dorsal fin: A fleshy dorsal fin about 38 cm in height is situated about two thirds of the length of the body, more proximal to the flukes, and neatly curved (Pl. VIII) pointing caudally. Both dorsal fins and caudal flukes are devoid of any bony elements.
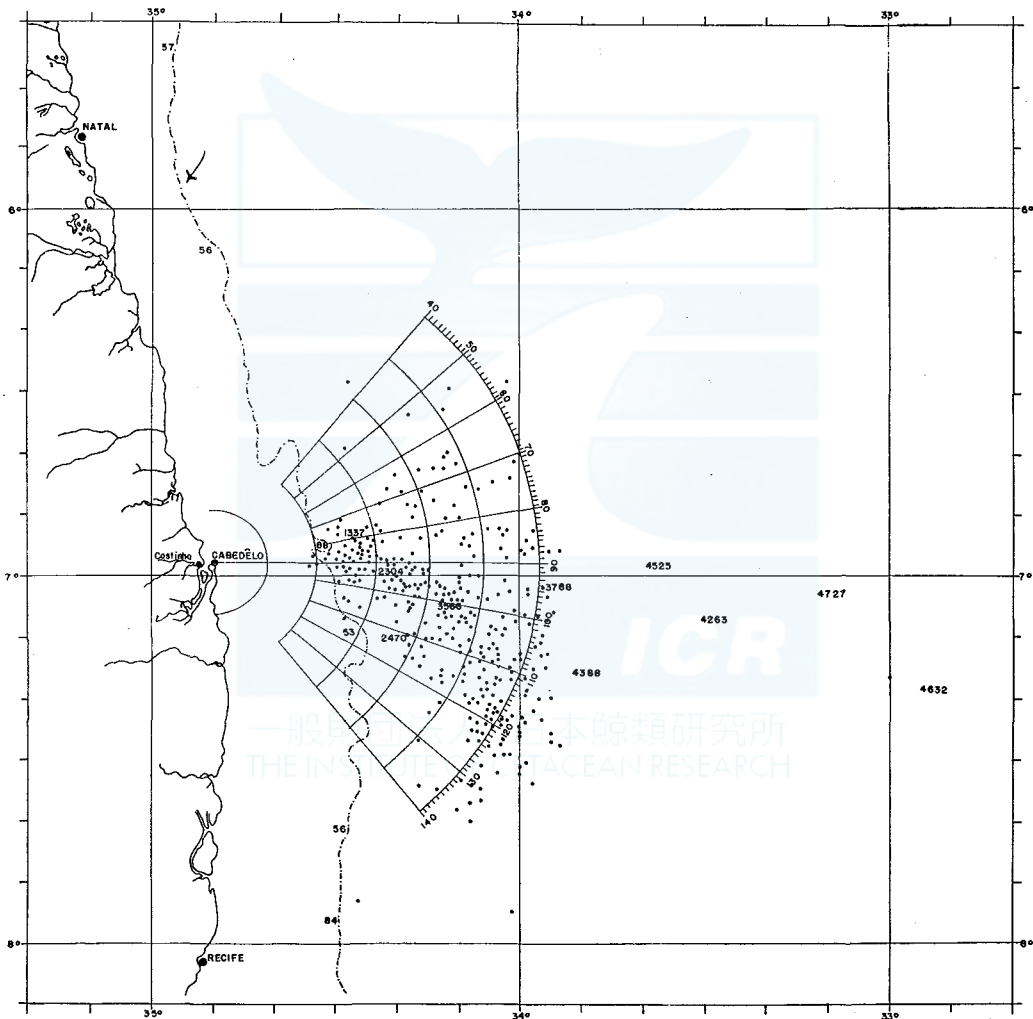
Fig. 2. Positions of minke whales caught during 1980 season, superimposed on tract chart. The broken line represents the continental edge of Brazil and the discrete numbers indicate depths in meters.

Hairs: Very few hairs were seen; usually on the rostrum and on the sides of the mandible. The hairs, particularly from the latter, arise from 7 small pits (each*
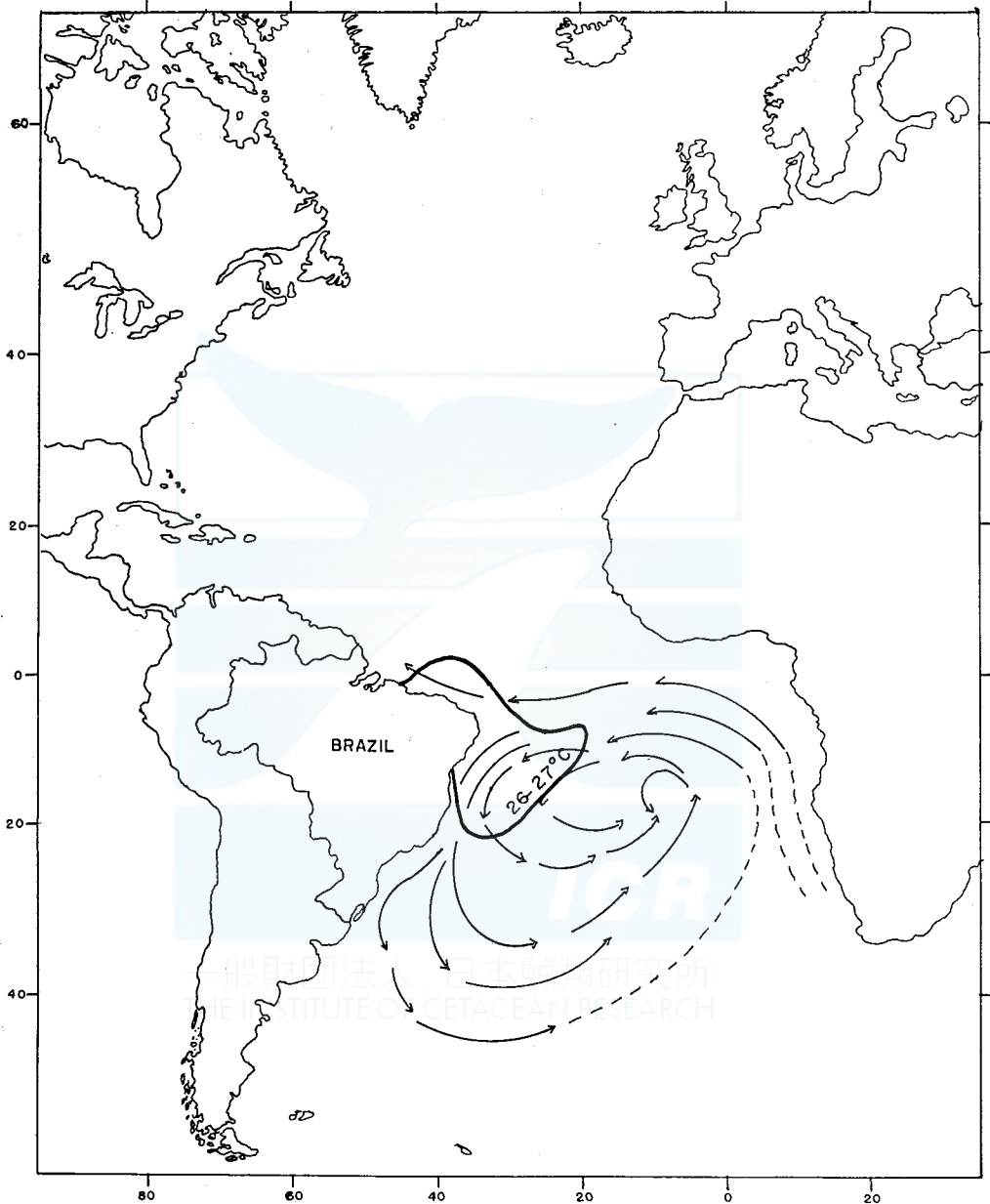
BRAZIL

Fig. 3. Surface currents and an isothermic stretch of the whaling area off Brazil, in the Southwest Atlantic. Surface temperature distributions are based on 20 years daily recordings during each whaling season.

* Since this paper going to the press, asymmetrical disposition and variation of number of pits, particularly in a few females had been observed.

side).   The hairs are creamy colour and about 4 cm tall and can be easily pulled out.
External sexual characteristics: As in the other whale species, the vaginal orifice lies
immediately anterior to the anus whereas the penal slit is clearly separated from
the anus.   In many females a creamy yellow substance was found in the vagina;
which may have meant that they had recently copulated.   Histological analysis
is required to confirm this.

WHALING AREA

Topography and hydrography: The tract records of the whaling boats over several
years reveal the whaling grounds off Brazil, which extend from 6°–8°10′S and
32°20′–35°00′W, to have remained very constant.   The continental shelf ex-
tends to about 20 miles from the coast where it drops abruptly from 60 m to
3–4,000 m (Fig. 2).   The sea floor in the shelf area is irregular and rocky.   The
most important hydrographic feature of the area is its proximity to the equatorial
current systems.   The south equatorial current flows westwards near the equator
towards South America.   On reaching the Brazilian coast it divides into two:
most of the warm water moves northwards towards the Caribbean while the
remainder turns south forming the weak Brazil current.   This meets the cold
Falkland current (Fig. 3).   The whaling area is largely under the influence of the
south equatorial current.   From June, when it is particularly strong, to September,

TABLE 3.   MONTHLY MEAN TMPERATURES (°C) BASED ON DAILY RECORDINGS
FROM JUNE TO DECEMBER EACH YEAR OF THE WHALING AREA, LAT.
6°S–8°10′S AND LONG. 32°20′W–35°00′W.

Year	June	July	August	September	October	November	December
1963	*25.00	26.10	26.05	27.74	26.35	—	—
1964	27.23	27.12	27.74	27.00	26.35	—	—
1965	27.35	26.98	26.26	26.97	26.71	—	—
1966	27.70	27.14	26.64	26.15	27.01	26.71	—
1967	27.45	26.70	26.16	26.13	26.95	26.42	—
1968	26.10	26.41	26.01	26.01	26.80	27.02	—
1969	27.73	26.42	26.77	26.80	26.74	27.03	27.56
1970	27.20	26.80	26.40	26.40	26.90	27.90	27.00
1971	27.80	27.10	26.50	26.40	26.50	26.90	—
1972	28.00	27.60	27.10	26.90	27.00	27.30	27.80
1973	28.10	27.60	26.40	26.80	27.00	27.90	27.80
1974	27.80	27.60	26.40	26.80	27.00	27.90	27.80
1975	27.90	27.50	26.70	26.60	27.10	27.60	27.80
1976	27.30	26.90	26.60	26.60	27.00	27.40	—
1977	28.30	28.30	28.00	26.60	26.90	27.70	27.80
1978	—	—	26.90	27.00	27.40	27.70	27.80
1979	—	27.40	27.50	27.70	27.80	28.00	28.40
1980	28.50	27.80	27.70	27.40	27.60	27.90	28.10
1981	—	27.62	26.86	26.91	27.77	27.84	—
1982	—	27.89	27.38	27.25	27.53	27.70	27.83

* Based on only 4 days recordings.

TABLE 4. SOME ENVIRONMENTAL PARAMETERS OF THE WHALING AREA OFF THE COAST OF BRAZIL (LAT. 6°S-8°10'S AND LONG. 32°20'W-35°00'W), AVERAGE BASED ON *DAILY AND **MONTHLY RECORDINGS DURING 4 YEARS 1979-1982.

Month	Current velocity* Knot/Hr	Salinity** ‰	Oxygen** ml/l	Extinction** Coefficient
June	1.04	34.60	7.80	0.15
July	0.97	34.82	8.04	0.90
August	0.83	35.00	7.60	0.11
September	0.98	35.00	8.20	0.09
October	0.74	35.40	7.90	0.10
November	0.60	35.50	8.00	0.14
December	0.60	35.50	8.20	0.17

there is a strong southerly wind, which from mid-September until December becomes easterly.

Measurements of temperature, current velocity and salinity (Tables 3 and 4) reveal that the temperature and salinity remain fairly constant throughout the year. The velocity of the current decreases from 1.04 knots in June to 0.60 in December. Visibility under water improves considerably after July partly due to decrease in precipitation.

Biotic factors: Flying fish, *Exocoetus sp.*, are very common in the whaling grounds and schools of dolphins (12–20 animals) are also often seen. The whale louse, *Cyamus balaenopterae*, is found on minke whales (Ohsumi *et al.*, 1970). As the whales move into warmer waters, these ectoparasites fall off, probably in response to the warmer water, leaving small oval shaped scars which are about 5 cm×4 cm×4 cm. The large white shark, *Carchardon carcharias* and the hammerhead shark, *Sphyrna zygaena* are quite common in the whaling area, and often tear chunks of meat from the ventral side of dead, buoyed whales. Occasionally, Remoras or suckerfish and lampreys were seen to be attached towards the ventral side of the buoyed whales.

BEHAVIOUR

Behaviour during the hunt: Off Brazil, minke whales are commonly seen in small groups, 2–6 animals, and only rarely as singles or in larger groups, about 10–14 animals. The animals in pairs swim fairly close to one another (10–12 m) and sometimes very close. Undisturbed minke whales swam at about 8–10 knots; estimated by comparison with the velocity of the boat. Some authors (Kasuya *et al*, 1965; Mitchell, 1978) have reported " ship seeking " behaviour for minke whales although no such evidence was found in tropical waters and the minke whales off Brazil appeared to be indifferent to the presence of the vessels. Absence of " ship seeking " behaviour in the Antarctic minke whales also has been reported particularly during the last IWC/IDCR cruise (IWC, 1982).

During chasing, the whales can swim faster than the boat (17 knots) for short periods. However, after about 10–12 n miles they surface regularly and more

frequently, often cutting right across the bow of the ship, when, of course, they are easy to harpoon. When hit with the harpoon some animals attempt to escape with such force that they break the loop end of the whale line and swim rapidly (estimated at about 24 knots) away, usually following a fairly straight course and profusely bleeding which was traceable for more than a killometer. In all harpooned whales, it was noticed that the spray of water during blowing was mixed with blood. Direct evidence indicated that this was due largely to rupture of blood vessesls, even though an explosive charge in the lungs could not be ruled out.

Epimeletic behaviour: On one occasion, a pod of three whales, later found to be two females and one male, were pursued at full speed. A female was harpooned and was eventually brought to the ship, during which time the other two whales remained with the female, swimming in large circles around her. Within an hour the second female was harpooned and took out the full 700 m whale line, diving and circling in an attempt to escape. During this time the male swam close to the female, diving and blowing in synchrony. This continued for some 13 minutes before the female was brought to the side of the boat and killed by electricution. Even then the male made no attempt to escape and fell easy prey to the gunner.

Electric shocks: Most of the harpooned whales do not die instantly and are frequently winched back and shot a second or even a third time after which an

TABLE 5. COMPARISON OF CATCHES, SEX RATIOS AND PERCENTAGES OF MINKE WHALES FOR THE PERIOD FROM 1963 TO 1982.

Year	Male /	Female /	Indeterminate*	Total	Sex Ratio Male : Female	CHI Square/P Values
1963	—	2	—	2	— —	— —
1964	16	28	—	44	1 : 1.75	0.06<0.8
1965	26	42	—	68	1 : 1.62	0.73>0.5
1966	119	233	—	352	1 : 1.96	0.04<0.9
1967	154	334	—	488	1 : 2.17	0.69<0.5
1968	151	305	—	456	1 : 2.02	0.01>0.9
1969	204	413	—	617	1 : 2.02	0.02<0.9
1970	227	474	—	701	1 : 2.09	0.28<0.7
1971	330	570	—	900	1 : 1.70	4.01<0.5
1972	231	470	1	702	1 : 2.03	0.33>0.5
1973	210	440	—	650	1 : 2.10	0.15<0.7
1974	246	515	4	765	1 : 2.09	0.87>0.5
1975	380	658	1	1,309	1 : 1.73	5.21<0.1
1976	279	497	—	776	1 : 1.78	2.04>0.2
1977	330	664	6	1,000	1 : 2.01	0.01>0.9
1978	225	463	2	690	1 : 2.05	0.92<0.8
1979	242	496	1	739	1 : 2.05	0.09<0.8
1980	315	587	—	902	1 : 1.86	1.03<0.3
1981	244	504	1	749	1 : 2.25	0.17<0.7
1982	288	566	—	854	1 : 1.96	0.06<0.9
Total	4,217	8,261	16	12,494	1 : 1.95	

* Due to loss

electric shock is applied.   Initially intermittent shocks are applied to which the
whales respond violently.   After these, a continuous current is applied for three
minutes during which even the strongest whale becomes restrained, apart from
some lashing of the flukes.   This is soon followed by the drooping of the lower jaw.
Perhaps, it might be safest for the crew to wait until the lower jaw droops before
tying the whale to the ship.

CATCH STATISTICS FOR BRAZIL

Paiva (1961) and Williamson (1975) gave some details of catches from Brazil for
the period of 1910, when whaling began, to 1974, but these include mostly the
larger species.   Prior to 1966, larger whales (humpbacks up to 1928 and then sei
and Bryde's whales and occasional blue, fin and sperm whales) dominated the
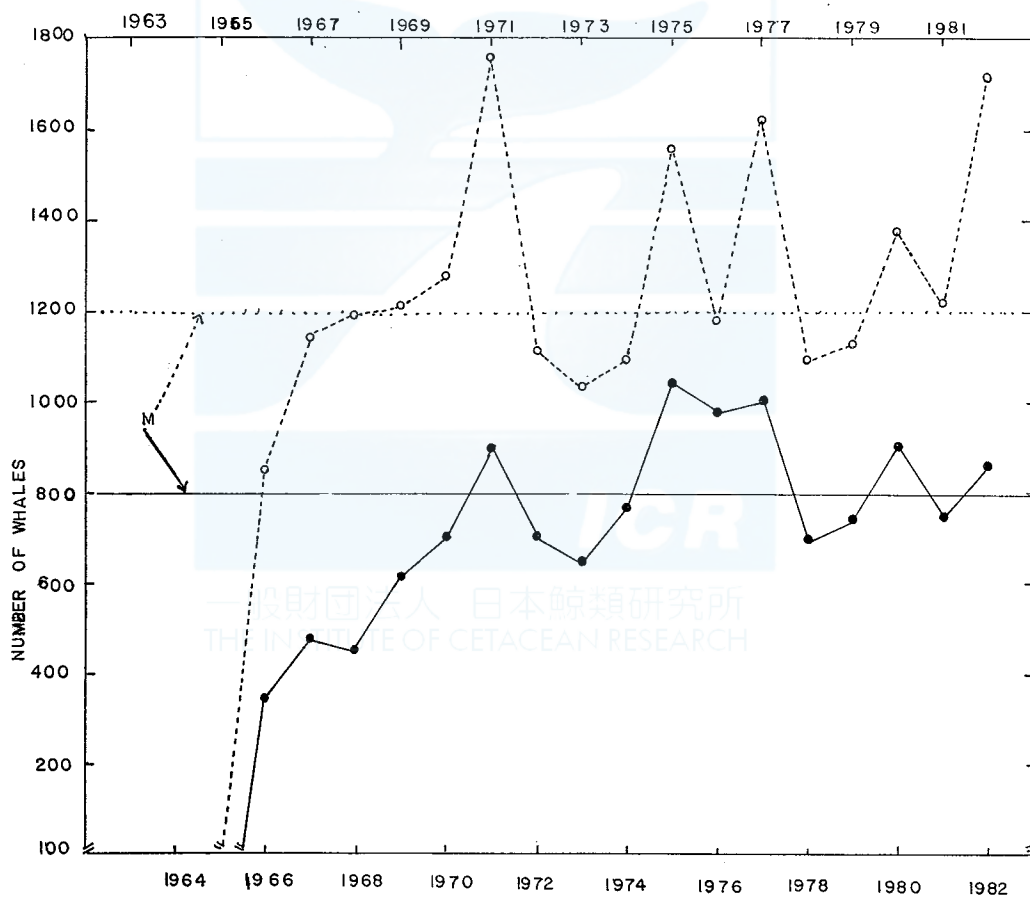
Fig. 4.   The relationship between catch (●) and sighting (○); the pattern of minke
whales caught fluctuates almost correspondingly with changes in population sighted.
M indicates means.

catch. Only 3 minke whales were taken prior to 1963. However, catches of minke whales increased only during the last 20 years (Singarajah, 1983) while most of the others are now protected.

Table 5 gives details of Brazilian catches between 1963 and 1982. The season generally lasts from June to December but for a variety of reasons no whaling occurred in either of those months in 1967, 1968, 1971, 1976, 1978, 1979 or 1981. During the period 1963–1982, 12,494 minke whales have been caught: prior to 1963 3 were caught making a total for the area of 12,497.

Fig. 4 shows the number of minke whales sighted and the number of minke whales caught between 1963–1982.

SEX RATIO

Fig. 5 shows the catch composition by year and month for the greater period of minke whaling and the average lengths of males and females. There is a significant difference between the number of males and females in the catches and the overall ratio is 1 male: 1.95 females; not significantly different from 1: 2. This remains fairly constant by month although the percentage of females is lowest at the beginning of the season (Fig. 5). This factor, along with the sex ratio in captured schools, often 1 male: 2 females or 2 males: 3+females, may suggest that minke whale are not monogamous.

DISCUSSION

Although a comprehensive anatomical description of southern minke whales has been given by Ohsumi et al., (1970), the present study has provided additional information with respect to the whales off Brazil. Despite somewhat vestigeal in form and character, the omission by previous workers (Williamson, 1961; van Utrecht et al, 1962; Ohsumi et al, 1970; da Rocha, 1980) to include in the count of the very large number of the baleen plates of the posterior segment was perhaps solely due to their size. Nevertheless, these are true baleen plates and they could not be justifiable excluded.

Variation in flipper colour patterns have been described by several authors (Taylor, 1957; Williamson, 1959; Ohsumi et al, 1970; Doroshenkho, 1975; Best, 1978). Data from Brazilian operations show that a single flipper type, devoid of a white stripe, predominates. However, on rare occasions (e.g. in 1980 and 1981, about 0.2% of the annual catch) a second type, with a white stripe, was recorded. The animals were small, about 7 m, and Best (pers. commun.) informed me that " they might be a diminutive form of the species ".

The morphology of minke whales off Brazil and in the Antarctic and the temporal distribution of the whales strongly suggest that the whales migrate between these two areas. Data collected over several years on the distribution of minke whales off Brazil clearly show that they generally occur in a relatively small area (<15,000 n. miles²). Their high density in this tropical habitat is further confirmed by the CPUE estimates.
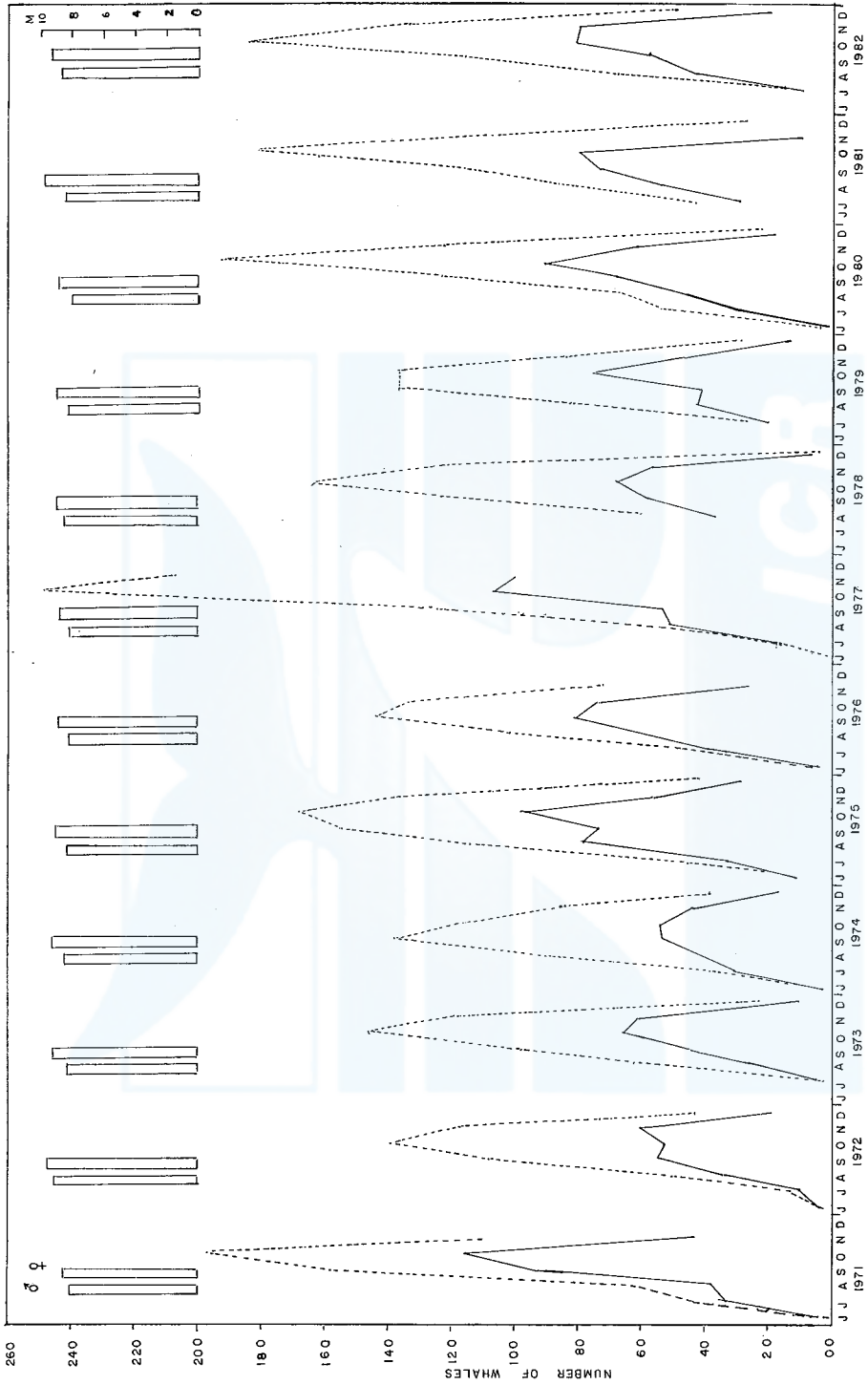
Fig. 5. Relationship between numbers of males (solid line) and females (broken line) minke whales taken monthly. Open histograms compare the mean lengths of males and females on yearly basis.

The concentration of the minke whales into this area for breeding is presumably a result of the physical and biotic characteristics of the environment. Temperature and perhaps day length seem likely to be important factors influencing the migrations of whales. Minke whales begin to arrive in the region in the latter part of June, although the peak months are September, October and November by which time:

1) precipitation has considerably diminished;
2) the strong SE wind has changed to a moderate E wind concomitant with reduced turbulence;
3) the water is more transparent;
4) the temperature has dropped very slightly (perhaps to an optimal level);
5) the surface current is less strong;

and these factors may influence the minke whales. However, it must be remembered that the first three points also have the practical effect on making the whales easier to see and so the increase in sightings may to some extent be due to this. In addition, the increasing numbers of whales from June to September may in fact have more to do with the conditions in the Antarctic which affect the rate of leaving there rather than the prevalent conditions on arrival off Brazil.

It is interesting to note that the testes from males which were caught in the peak period are generally larger than those taken earlier (Table 6 and Fig. 6). A similar trend is seen in ovary weights although the range is greater.

As yet, we have not found a satisfactory technique for estimating the age of the minke whales taken off Brazil: Christensen's (1980) method using the tympanic bullae was tried but found to be too tedious for routine samples; problems were also found with the reading of ear plugs, particularly of younger animals, and often the counts of the left and the right plugs were different. As a result of this we have no estimate of age at sexual maturity for the animals off Brazil.

Masaki (1979) examined age at sexual maturity in minke whales taken by Japanese expeditions in the Antarctic using four techniques: (i) the age (from ear plugs) at which 50% of the animals are sexually mature, i.e. have either at least one corpus luteum or albicans, or have one testis of at least 0.4 kg; (ii) the relationship between age (from ear plugs) and the number of ovulations; (iii) using length at sexual maturity and the growth curve (age from ear plug); (iv) from the transition phase of the ear plug. The results from all four methods suggested a female age at sexual maturity of about 6–7 years. Direct evidence for males was more limited due to the scarcity of immature animals in the catches and the need for further histological analyses to confirm to 0.04 kg criterion of Ohsumi et al. (1970). However, assuming that the transition phase in the ear plug was formed at sexual maturity then the age at sexual maturity for males was about 6 years. If the 0.4 kg criterion is true then almost all the males caught in Brazilian waters are mature (Table 6). Using the maturity criterion of technique 1, da Rocha (1980) estimated the lengths at maturity of males and females off Brazil to be about 25 ft and 26.5 ft respectively. This is slightly higher than Masaki's Area II values of 23.3 ft and 26.1 ft.

TABLE 6. FREQUENCY DISTRIBUTIONS OF WEIGHTS OF TESTES

Weight (g)	July Left	July Right	August Left	August Right	September Left	September Right
50					1	1
100	1	1	1	1		
150	2	1			1	
200	1	2			1	2
250			1	1	1	1
300			1	3	1	1
350	1	1	3	1		
400			1	2		
450			1			
500	1	1	4	4		
550			3	2		
600	1	2			2	1
650	1		1	1	1	
700	1		1	3	4	4
750					1	2
800		1	1	1	2	3
850				1		
900			2		1	1
950						
1,000	2	1	3	2	1	
1,100	1	2		2	4	8
1,200	2	1	2	2	2	1
1,300		1	2	1	3	1
1,400					2	3
1,500				1	1	1
1,600			2	1	2	1
1,700	1		1	2	1	1
1,800		2	3	2	2	1
1,900	2	1	1	1	1	1
2,000			1			3
2,100	1	1	1	4	1	1
2,200					1	2
2,300			3	1	1	
2,400	1	1	1			
2,500						
2,600	1					
2,700						
2,800		1	1	2		2
2,900			1		1	
3,000					2	1
3,200						
3,400						
3,600						
3,800						
4,000						
4,200						
4,400			1			
4,600				1		
Σ	20	20	43	42*	41*	42
Mean	1,052.5	1,100.0	1,296.5	1,207.5	1,237.8	1,242.9
Combined Mean	1,076.3		1,252.4		1,240.4	
Overall Mean=	1,428.53					

* 1 lost during flensing.

OF BRAZILIAN MINKE WHALES BASED ON 1979 SEASON

October		November		December	
Left	Right	Left	Right	Left	Right
2	2				
1	1				
2	1	1	1		
	1				
1					
		1	1		
2	3	1			
	1				
4	4		1		
2	1				
1	1	1	1		
3	1			1	
1					
4	6				
11	12	2	2	1	2
3	3	2	2		
2	2	1	1		
6	8	2	2	2	2
2	1	1	2	1	2
2	2	2	3	1	1
	2	4			
6	2	4	8	1	1
1	6	3	3	1	1
3	2	6	4	1	
	4	3	1	1	1
2	1	3	5		
1	2	2		1	
1		2	2		1
			1		
	1	1	1	2	1
1	1			1	2
1	2	2	2		
3	1	3	3		
1	1	2			
1					
1	1				
		1			
75	75	47	47	14	14
1,386.7	1,429.3	1,839.4	1,833.3	1,877.4	1,864.3
1,408.0		1,836.1		1,867.9	
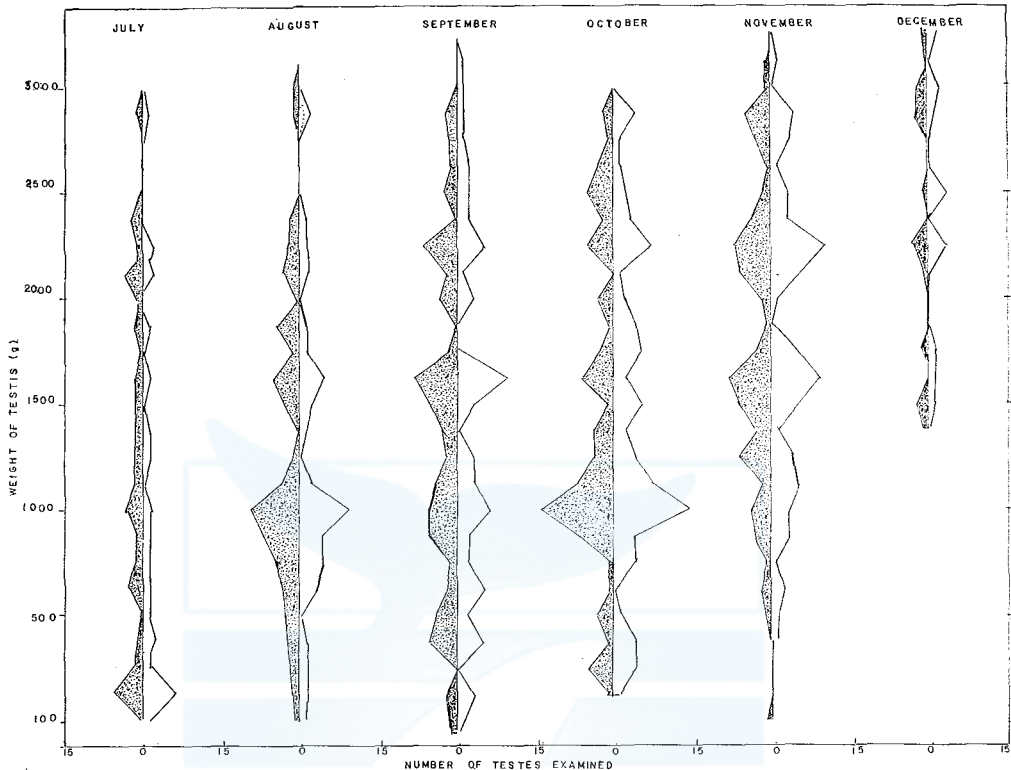
Fig. 6.   Weight frequency histogram for the testes of minke whales caught off the
coast of Brazil during the 1980 season.

Masaki (1979) estimated the gestation period for minke whales to be about 9 1/2 months, with the peak mating period in early to mid-October and the peak calving period in late July using the method of Laws (1959), and data from the whole Antarctic.   If this is true, then if the waters off Brazil were calving grounds, one might expect to see large numbers of calves in the area.   However this is not the case.   This may be because the females calve elsewhere or because calving occurs much later in the season.   If the latter is true then one might expect to find a high proportion of pregnant (near term) females in the catch in the early part of the season, decreasing as the season progresses.   Unfortunately, there are few reliable records on pregnancy off Brazil to date.

Population estimates of minke whales in southern hemisphere is far from complete at the present; and there is no close agreement among previous estimates (Ohsumi *et al*, 1970; Williamson, 1975; Best, 1979; Chapman, 1979; Holt, 1980). Although minke whales in the Antarctic are claimed to be increasing (FAO, 1982), Watson & Riche (1981) place the population of southern minke whales at 150,000–300,000.   However, the minke whales arriving off the coast of Brazil to breed are variations of the southern stock (Williamson, 1975), but no estimates on absolute population for the Southwest Atlantic has been worked out.   Recent
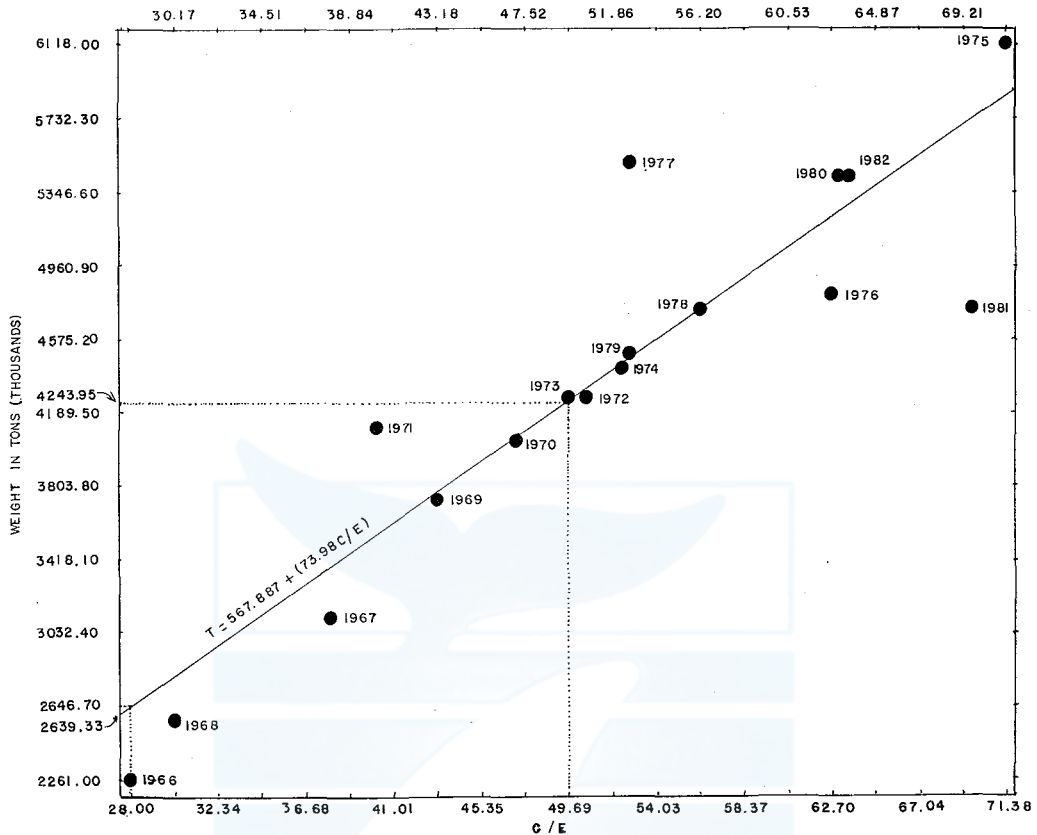
Fig. 7. Correlation between the catch per unit effort (C/E) and the abundance of minke whales. Regression line calculated from 17 years consistent data.

marking experiments to relate stock identity and estimates of its population have met with only limited success; of the 29 minke whales marked off the coast of Brazil (Butterworth & Best, 1982) none so far has been recaptured.

The regression line (Fig. 7) for the more consistent peak seasons, covering almost the entire minke whaling period from the Brazilian whaling ground, shows that the relationship between catch per unit effort and abundance is fairly constant with a few exceptions. The significant variablity in abundance particularly during 1966, 1971, 1977 and 1981 might be due to a variety of causes, the chief being operational and other factors peculiar to Brazil, including the quota system imposed by IWC.

Sex data, throughout the whaling period, both monthly and annual catch, show characteristically that the females far out number the males, and these observations are quite contrary to those reported in the Antarctic (Kasuya & Ichihara, 1965; Ohsumi et al, 1970). The reversal of the sex ratio of the same species in varying geographical conditions perhaps suggests the segregation of the sexually mature whales which may be associated with hormonal state of the individuals.

In respect of the sex ratio, the Brazilian minke whales resemble the population of
the Arctic pattern where Jonsgard (1951) noted that the females numerically dom-
inated the males.

Several lines of evidence indicate that the Brazilian minke whales could be
regarded as spatial and temporal stock in a transient habitat, but their biotic po-
tential or capacity to increase in population will very much depend on the limiting
factors which prevail in their native relatively stable Antarctic habitat.

ACKNOWLEDGEMENTS

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EXPLANATION OF PLATES

PLATE I

Breathing and escape reaction of a female minke whale for harpoon shot. Also, note
the difference of length between the lower and upper jaw and the triangular rostrum
with the strong central ridge.

PLATE II

The ear-plugs which fit snugly upon the conical end of the " glove-finger " ; the right
and the left side plugs often vary considerably in size.

PLATF III—A & B

The pair of ear bones or tympanic bullae of the same female whale measuring 9.20 m
body length. Macrophotography ; the marker represents 1 cm. The surface view
of the photograph is actually the vertical plane of the tympanic bullae, facing each
other in the natural position, with their membranous " glove finger " pointing pos-
terior and ventrally. A : inner aspect. B : outer aspect.

PLATE IV

A small segment of the baleen series just anterior to mid-region of the jaw. Note the
colour pattern (black/white) ; the lingual margin of the hypotenuse of the triangular
part of the plate is frayed out into fine flexible filaments. Note also the height of
the cementation.

PLATE V

The different types of reduced baleen plates. A ; anterior rod-like plates ("hairs"),
B ; the transitional rectangular laminae, C ; the posterior reduced rectangular
laminae (see text).

PLATE VI

The flipper, more like a wing and a calyx shaped mark on the dorsal surface next
to the body. Note the distinct absence of stripes or patches on the flipper of the
Brazilian minke whales.

PLATE VII

The fluke of a male which is usually narrower than that of the female. The whale
strikes the tailstock in response to harpoon shot and in an atttempt to escape.

PLATE VIII

The dorsal fin ; situated more toward the caudal end of the body.

(PL. I)

(PL. II)

PLATE III-A & B   SINGARAJAH

(PL. IV)

(PL. V)

(PL. VI)

(PL. VII)

PLATE VIII
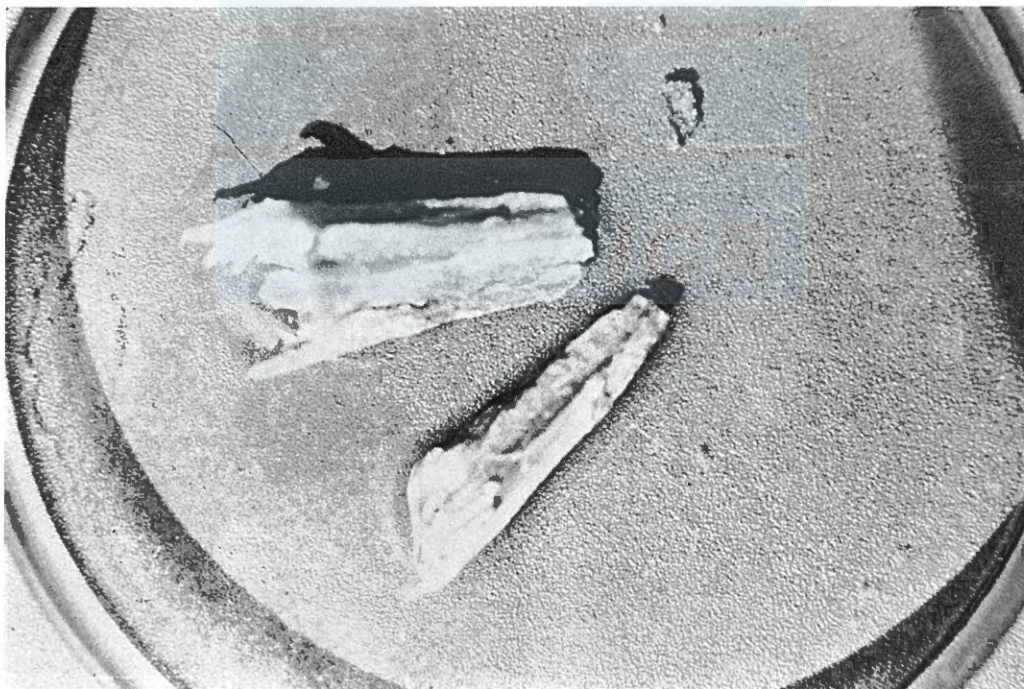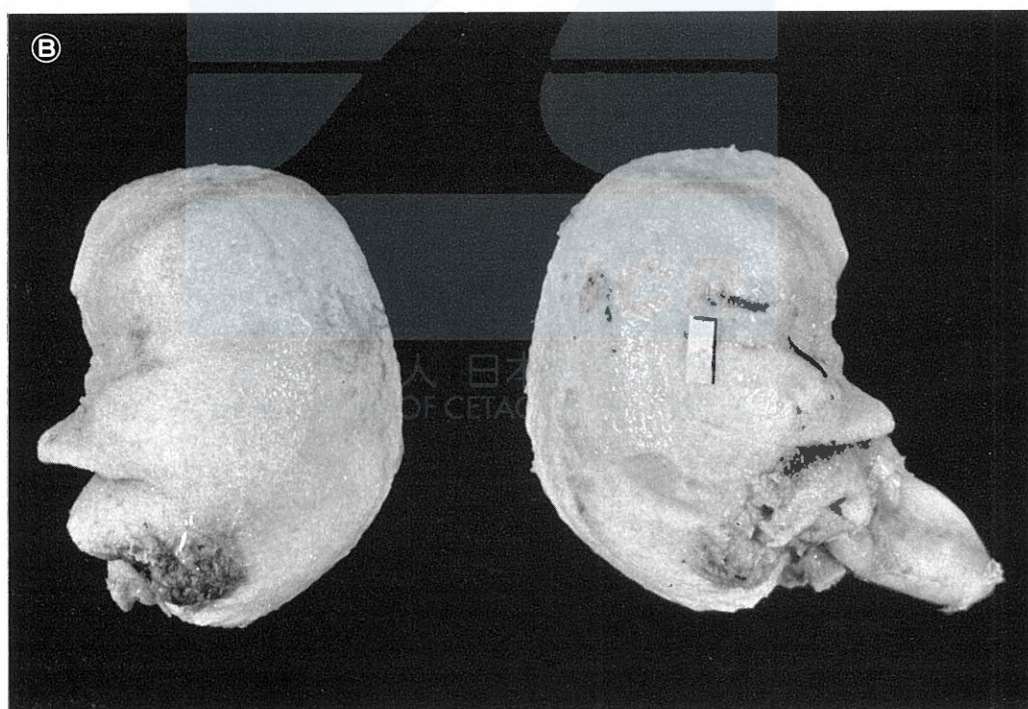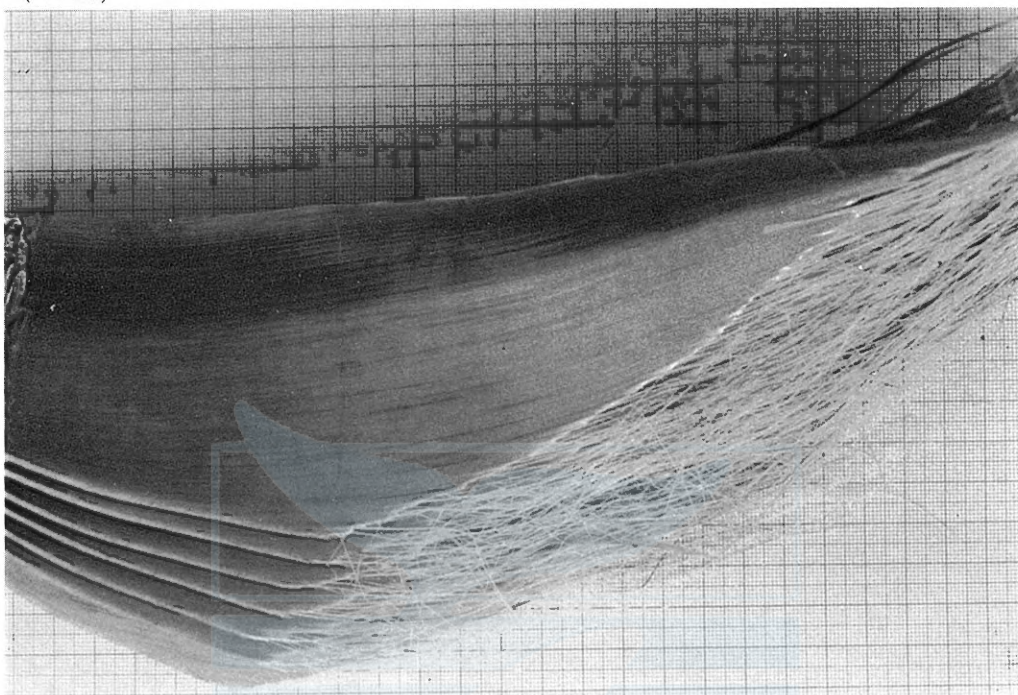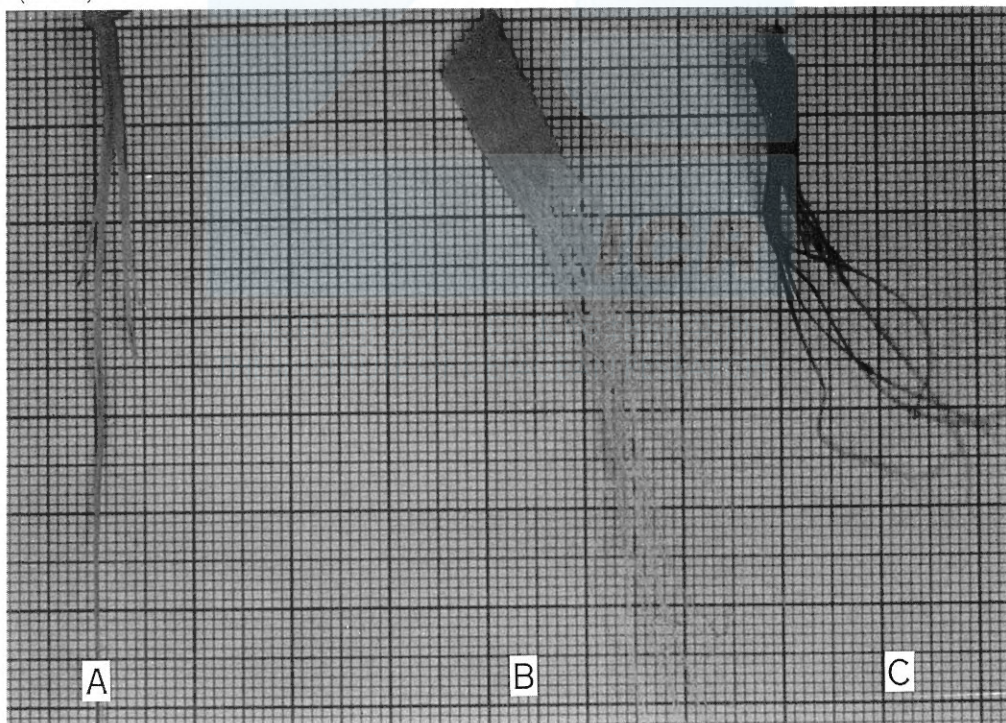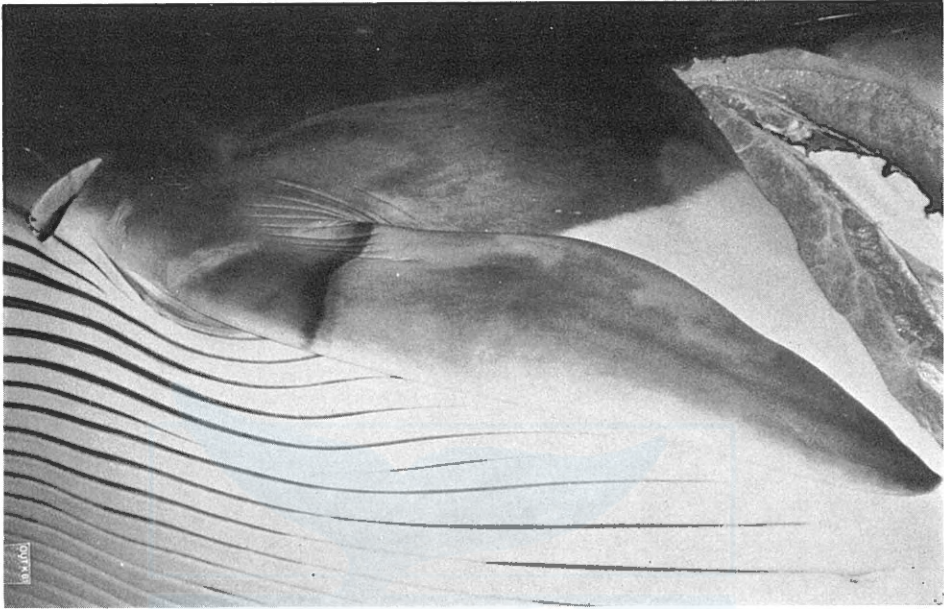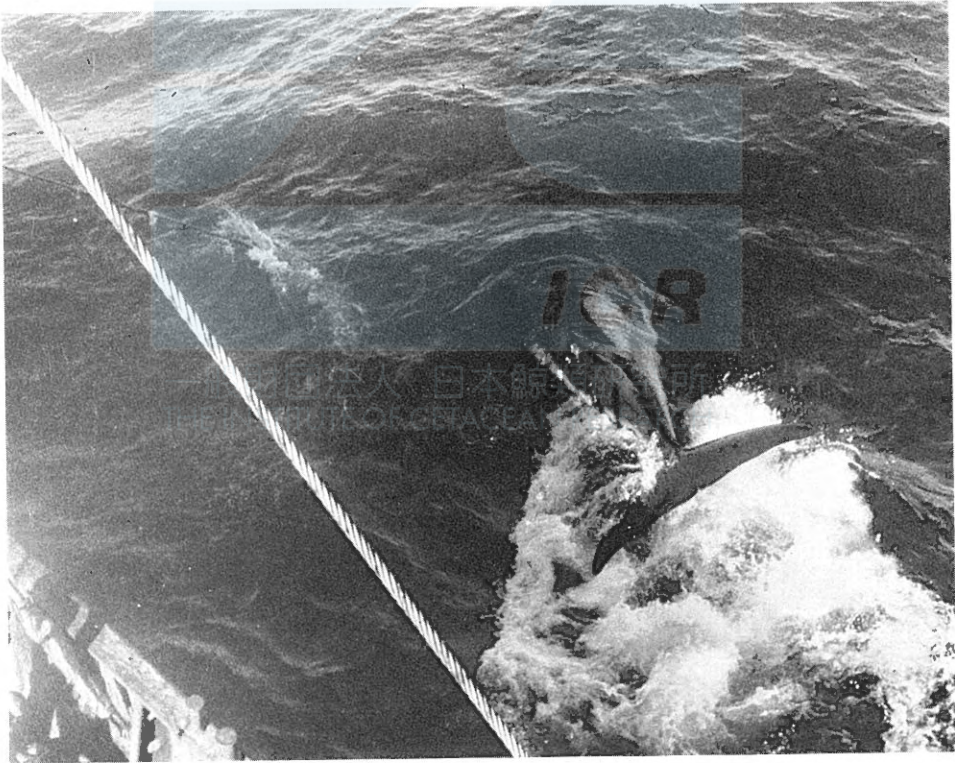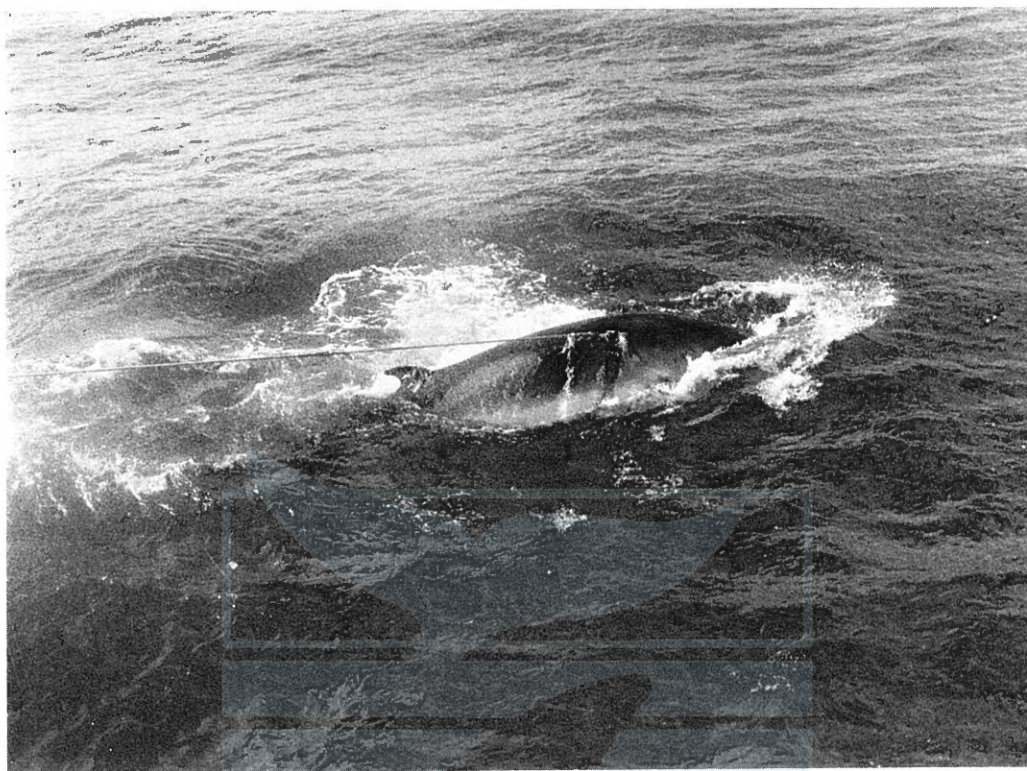
OBSERVATION OF TOOTH SCARS ON THE HEAD OF MALE SPERM WHALE, AS AN INDICATION OF INTRA-SEXUAL FIGHTINGS

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ABSTRACT

In order to examine the relation between intra-sexual fightings and sexual maturity, observations of tooth scars on the head of sperm whales (*Physeter catodon*) were made collected in South Pacific Oceans during 10 to 18 March 1979 on the *Nisshin maru No. 3*. Tooth scars on the head were observed on 48 males based on the following four relative stages; none, indistinct, distinct and heavy. Distinct tooth scars including " pallarel scar " which suggest intra-sexual fightings occurred among whales over 43 ft, and scars of most heavey stage were observed among whales over 46 ft in body length. Whales having relatively heavier scars were taken in solitary or a pair in either high latitudes (>40°S) or northern parts of females's range. Although no whales was directly taken from *mixed school*, three solitary large males taken around the *mixed school* had scars of most heavy stage. From the informations of body length, school size and catch position, most of these whales having relatively heavy scars were classified to *large bachelor*, these suggest intra-sexual fightings took place among *large bachelors*.

The relation between tooth scar stage and testes weight were also examined. Mean weights of single testis (heavier) for males were 4.88 kg (combined both sides, 9.26 kg) and 2.68 kg (4.70 kg) at scar stages of heavy and distinct, respectively. Comparing testis weights among the whales of same body length, whales with heavier scar tend to have heavier testis.

In conclusion, it can be said that sexual maturity rate tend to increase with increasing of body length and with development of scar stages. This suggests that tooth scars indicate one of the evidences of sexual maturity.

INTRODUCTION

Polygyny is the most characteristic behaviour among the social structure of sperm whale, *Physeter catodon*. Ohsumi (1971) estimated that a school master may serve up to 14 mature females in a breeding season, and Best (1970) gave an estimation of 10–20 females.

Although there is sexual unbalance in the adult population of the sperm whale due to the male's slower attainment of sexual maturity, it is only such a low magnitude as 2.6: 1 (Best, 1979). However, as suggested by Ohsumi (1966) and Best (1979) only 10–25% of mature males can become school master and join breeding school in a year. There has to be expected large surplus males and serious intra-

sexual competition in the male population.

Although no direct observation on the intra-sexual competition was made, Ohsumi (1971), Best (1979) and Gaskin (1982) suggested the presence of tooth scars on the head and/or the body might be one of the evidences of the fighting among mature males. No analysis on the tooth scars have not been done previously.

I had an opportunity to observe tooth scars on carcases of sperm whale on board of a whaling factory ship in the 1978/79 Antarctic whaling season, and to analyze in relation to the growth stage.

MATERIALS AND METHOD

In the 1978/79 Antarctic whaling season, *Nisshin maru No. 3* fleet, on which I was on board, mainly caught sperm whales in pre (25 Nov.–3 Dec. 1978, southern areas of Indian Ocean) and post minke whaling season (10–18 March 1979, South Pacific
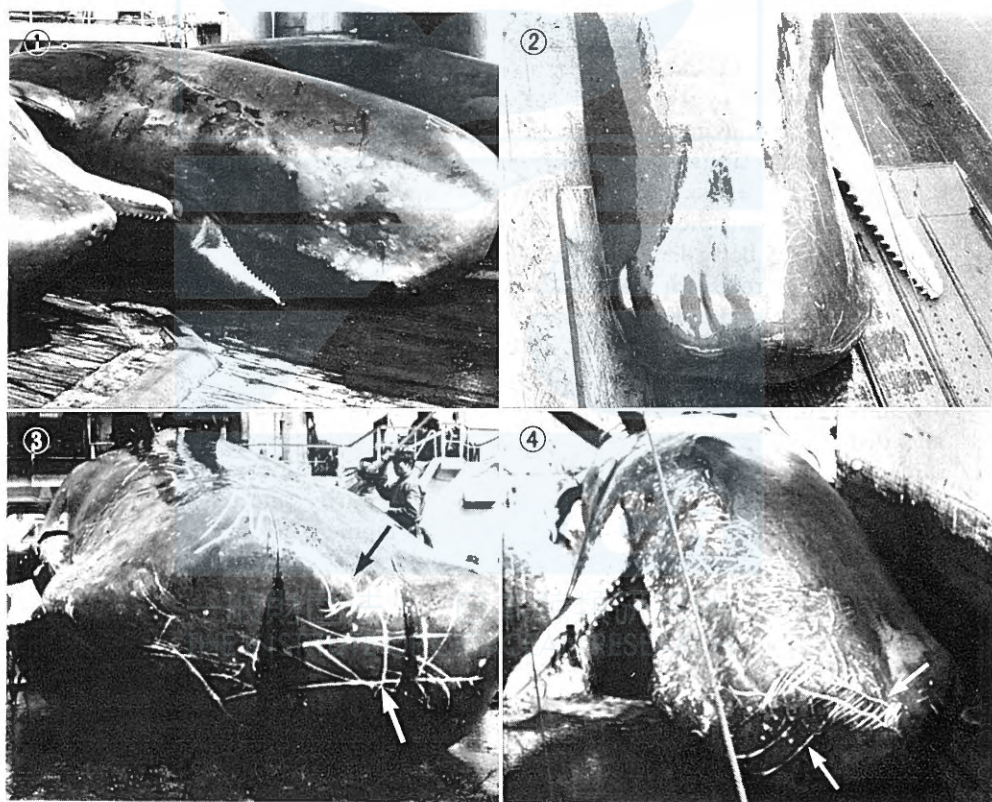
Fig. 1.   Typical appearances of tooth scars on the head of sperm whale in each scars stage, arrows show examples of " parallel scar ".
1:   Stage 0, photograph from North Pacific. (in the possession of WRI)
2:   Stage I, from Antarctic. (WRI)
3:   Stage II, from North Pacific. (WRI)
4:   Stage III, from the Antarctic. (WRI)

TABLE 1. CRITERIA OF TOOTH SCAR STAGES ON THE HEAD OF SPERM WHALES

Tooth scar stage		Criterion
0	None	No tooth scar present on the head.
I	Indistinct	Small number of indistinct and sparse scars present.
II	Distinct	Scars distinct, at least a pair of "parallel scars" present.
III	Heavy	Tooth scars including "parallel scar" are more frequent than previous stages.

Ocean). The catches were 43 (all males) and 157 whales (70 males and 89 females), respectively.

I observed tooth scars on 48 males out of 70 males caught in the latter periods, the approximate position of catch of those samples were on a line connecting two points; 41°S, 154°E and 26°S, 173°E. Tooth scars on the head region were observed on the flensing deck. Scars presumably caused by sucker and hooks on cephalopod tentacles or by some other accidental scratchers were excluded. The density of tooth scars was classified into following four relative categories; none " 0 ", indistinct " I ", distinct " II " and heavy " III " (Fig. 1 and Table 1).

Both testes were weighed to nearest 50 g on the deck, school size and position caught for each whale were taken from the operation report of respective catcher boats.

RESULTS AND DISCUSSION

Gaskin (1970) and Ohsumi (1971) recognized six types of school as the principally social units of sperm whale school; nursely school, harem school, juvenile school, bachelor school, bulls school and lone bull. While Best (1979) proposed somewhat different interpretation of the social structure. He considered the *mixed school*, which was composed of adult females, their calves and juveniles of both sex as a basic social unit. This school changes into breeding school in breeding season. Furthermore, he classified mature males into three developmental stages; *small bachelor* (31–39 ft in body length), *medium-sized bachelor* (40–45 ft) and *large bachelor* (over 46 ft). Best (1979) considered that, in a breeding season *large bachelors* will join *mixed school* to serve as a school master only for short periods. For the convenience of the analyses, above three male body length criteria were adopted below without further consideration. Furthermore, although the term of " social maturity " has recently been used for male's sexual maturity mainly by International Whaling Commission (1979) due to unique social breeding behaviour of this species, the term of " sexual maturity " was adopted in the present study.

Tooth scars were abundant on the side and front portions of the head, but sometimes few were seen even on the back of body. None of them were new. This suggests that the intra-sexual fighting did not take place considerably before the season of the present observation (March).

Body length
Table 2 shows relationship between body length and tooth scar stage in 48 male

TABLE 2. LENGTH DISTRIBUTIONS OF OBSERVED WHALES
BY EACH STAGE OF TOOTH SCAR

Length (ft)	Stage of tooth scar				Total
	0	I	II	III	
31	2	—	—	—	2
32	—	—	—	—	—
33	2	—	—	—	2
34	2	2	—	—	4
35	1	3	—	—	4
36	1	8	—	—	9
37	—	6	—	—	6
38	—	3	—	—	3
39	—	3	—	—	—
40	—	2	—	—	2
41	—	—	—	—	—
42	—	—	—	—	—
43	—	1	1	—	2
44	—	—	1	—	1
45	—	—	—	—	—
46	—	—	2	1	3
47	—	—	1	2	3
48	—	—	1	1	2
49	—	—	—	1	1
50	—	—	—	1	1
Total	8	28	6	6	48
Mean length (ft)	33.71	36.72	45.67	47.83	

sperm whales.   Mean body lengths for scar stages " 0 ", " I ", " II " and " III " were 33.71, 36.72, 45.67 and 47.83 ft, respectively.   The difference between stages of " I " and " II " was significant (t-test, $0.005 < P < 0.01$).   It is clear that magnitude of scars on the head increase with increasing body length.

Best (1979) reported that the presence of " parallel scar " (Fig. 1), which he considered as attributable to attack of another sperm whale, is one of the evidence of intra-sexual fightings.   This type of scars were peculiar to whales classified to the scar density stages of " II " and " III " (Fig. 1), and observed among whales at 43 ft in body length or more (Table 2).   This result coincides with the result obtained off the west coast of South Africa (Best, 1979).   The heaviest scars (" III ") were observed only whales over 46 ft in body length.

School size and position of catch
Best (1979) and Gaskin (1982) showed that males segregate latitudinally by growth stages (or by groups mentioned above) in Southern Hemisphere, the southern limits of migration for *small* and *medium-sized bachelors* are about 35°S and 45°S, respectively, and *large bachelors* migrate to the Antarctic region.

The mean size of bachelor schools relates to the above mentioned growth stage, *i.e.* 15 whales, 4–6 whales and solitary (or sometimes a pair) for *small, medium-sized* and *large bachelor*, respectively (Best, 1979).   Table 3 shows the relationship

TABLE 3. SCHOOL SIZES OF OBSERVED WHALES RECORED BY RESPECTIVE
CATCHER BOATS IN EACH TOOTH SCARS STAGES

School size	Tooth scars stage			
	0	I	II	III
1.0	—	7	1	4
1.1–1.5	1	6	4	2
1.6–2.0	1	5	—	—
2.1–2.5	—	—	—	—
2.6–3.0	3	3	—	—
3.1–3.5	—	—	—	—
3.6–4.0	2	1	—	—
≥4.1	1	6	—	—
Unknown	—	—	1	—
Total	8	28	6	6

between tooth scar stage of whales and school size of those whales. Mean school
sizes decreased with increasing scar stage, 3.27 (stage " 0 "), 2.58 (" I "), 1.30
(" II ") and 1.13 (" III "). However, since the school size tended to be recorded
after disruption of the original school by chasing, these school sizes might be under-
estimated, and the actual value of group size would be less important rather than
the trend. It is notable that whales having the relatively heavier scars (" II " and
" III ") were mainly taken from solitary whales or those in a pair.

Fig. 2 shows the latitude of catch positions of present materials (males) to-
gether those of females which were not analysed in the present study. Whales
having relatively heavier scars (" II " and " III ") were mainly caught either in
higher latitudes (>40°S) outside of females range or in northern parts of the range
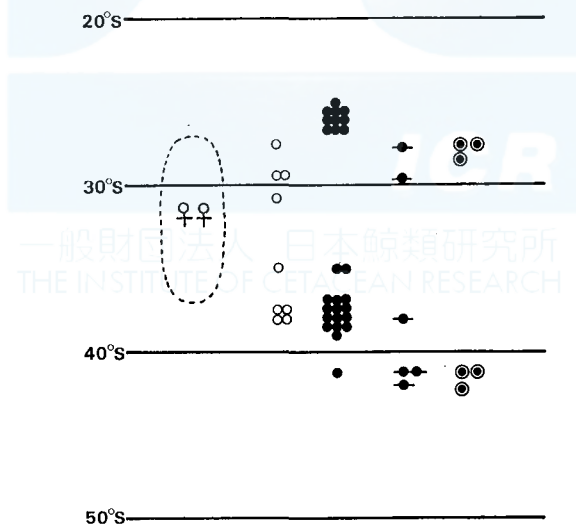
Fig. 2. Latitudinal catch positions of male sperm whales in each tooth scar stage
and females (unobserved).
○: Stage 0   ●: Stage I   ●: Stage II   ◉: Stage III

TABLE 4. NUMBER OF MALES IN THE PRESENT MATERIALS CLASSIFIED BY TYPE
OF GROUP, SCARS STAGE AND KINDS OF SCHOOLS TAKEN FROM

Scars stage	Type of group	From bachelor school n (%)	From mixed school n (%)
0	Small bachelor	5 (62.5)	3 (37.5)
I	Small bachelor	23 (78.5)	1 (7.2)
	Medium-size bachelor	3 (10.7)	1 (3.6)
II	Medium-size bachelor	1 (16.7)	—
	Large bachelor	5 (83.3)	—
III	Large bachelor	6 (100.0)	—

(Fig. 3). Although three solitary males having scars of stage " III " were not
caught from the *mixed school*, they were found relatively near a mixed school
(26°44′S, 165°04′E) from which five resting females and one pregnant female
were taken. Their positions were 27°21′S, 163°57′E; 27°14′S, 164°27′E; 27°13′S,
164°24′E. Distances from the mixed schools ranged from 44.7 to 70.5 nautical
miles. There is no observation on the social relationship between these males and
the *mixed school* above.

Male group type
Table 4 was constructed using male growth stage criteria mentioned above (Best,
1979) and information of schools recorded by the catcher boats. All the six whales
at scar stage " III " and five of six whales at scar stage " II " belonged to body
length stage of *large bachelor*. Although the presence of " parallel scars " are not
recorded for all individuals, as mentioned previously, only stages of " II " and
" III " had " parallel scars " which indicate possible intrasexual fighting (Best,
1979), therefore, it can be said that most of intrasexual fightings take place be-
tween large bachelor whales.

Testes weight
Best (1969) reported that rapid increase of testes weight relative to body length
start at around 43–46 ft, which almost coincides with the length where 50% of in-
dividuals are sexual mature by his histological criteria. Furthermore, Gambell
(1972) found on sperm whales off Durban that the increase in growth rate of testes
weight start at a body length of 45.4 ft or at a combined weight of both testes of
4.85 kg. They concluded that mean body length at sexual maturity is about 45–
45 ft, and Gambell (1972) suggested whales having combined weight of testes of
4.85 kg are sexual mature.

Fig. 3 shows the relation between weight of testis, body length and tooth scar
stages. It is apparent that testis weight increases with increasing body length. And
if compared among the whales of same body length, the whales having heavier
testes tend to have heavier scars on the head. This trend is more evident among
the whales over 43 ft in body length. Mean weight of single testis (heavier in both
side) for males at scar stage " III " were 4.88 kg (range, 2.75–7.50 kg), which was
much larger than 2.68 kg (range, 1.45–3.80 kg) for males at the stage " II ". The
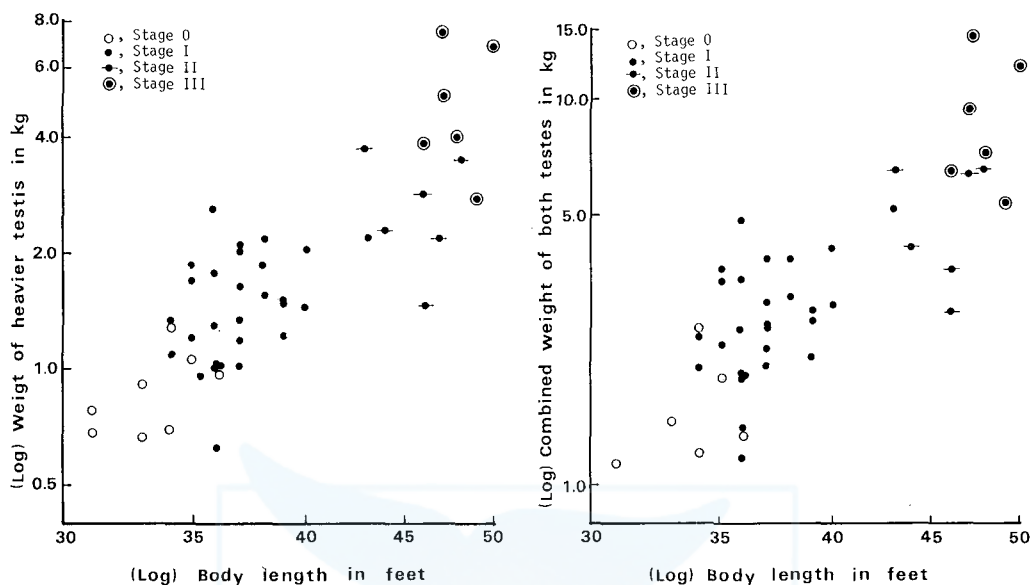
Fig. 3. Relationship between body length (in logalithmic scale), tooth scar stage and weight (in logalithmic scale) of heavier testis (left) or combined weight of both testes (right).

difference of above two weights was statistically significant (t-test, $0.01 < P < 0.05$). The combined weights of testes for whales ranged 5.30–14.80 kg ($\bar{x}=9.26$ kg) for scar stage " III " and 2.85–6.60 kg ($\bar{x}=4.70$ kg) for stage " II ". The difference of two mean values was also statistically significant (t-test, $0.01 < P < 0.05$).

Adopting the criterion of sexual maturity of the combined testes weight of 4.85 kg (Gambell, 1972), all males at stage " III ", three of six males at stage " II " and one of 27 males at stage " I " can be sexually mature (Table 5).   On the other hand, comparing with body length criteria of male's group type and adopting the above mentioned criterion of testes weight as sexual maturity, eight of 12 males in *large bachelor*, two of four males in *medium size bachelor* can be sexually mature (Table 5).

TABLE 5.   RELATIONSHIP BETWEEN BODY LENGTH (FT), TOOTH SCAR STAGES
AND SEXUAL STATUS OF SPERM WHALES

Type of group (length)	Sexual status	Tooth scar stage				Total
		0	I	II	III	
Small bachelor	Immature	8	25	—	—	33
(31–39 ft)	Mature	—	—	—	—	0
Medium-size bachelor	Immature	—	2	—	—	2
(40–45 ft)	Mature	—	1	1	—	2
Large bachelor	Immature	—	—	3	—	3
(46 ft)	Mature	—	—	2	6	8
Total	Immature	8	27	3	0	38
	Mature	0	1	3	6	10

Judging from testes weight, among the *large bachelors* all males having scars of stage III are sexually mature, while three of five males of stage " II " are sexually immature (Table 5). Among four *medium-size bachelors* two sexually matured males also exist; one from tooth scar stage " I " and the other from stage " II " (Table 5). But it's doubtful whether males having scar of stage " I " actually contribute to reproduction of this species or not.

Summarizing the above, judging from testes weight of the present materials, it can be said that sexual maturity rate tends to increase with increasing of body length and with development of scar stages. Moreover, even in males of the *large bachelors*, although all males attained sexual maturity in the tooth scar stage " III ", both of sexually matured and immature males coexist in stage " II ". These suggest that magnitude of tooth scar closely relate to sexual maturity.

In conclusion, tooth scars on the head of sperm whales seem to increase with growth and presumably indicate the experience of intra-sexual fighting. For the further examination of this point, individual age information should be taken in account. It will be examined in future study.

ACKNOWLEDGMENT

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ANATOMICAL STUDIES ON THE CELL COLUMN LOCATED CLOSELY MEDIAL TO THE NUCLEUS OF THE SPINAL ROOT OF THE TRIGEMINAL NERVE IN THE SPERM AND THE PYGMY SPERM WHALES

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ABSTRACT

A specific cell column was examined anatomically, which was located closely medial to the nucleus of the spinal root of the trigeminal nerve of the medulla oblongata in two sperm whales and a pygmy sperm whale.

This cell column was observed extending at the level from the obex to the uppermost medulla in the sperm whale and at the level of the middle one third of the medulla oblongata in the pygmy sperm whale.

After the precise comparative anatomical and histological investigations, the author has come to the conclusion that the cell column is thought to be the structure corresponding to the lateral cervical nucleus which has highly developed in the level of the medulla oblongata.

INTRODUCTION

In the previous report (1977) of a noteworthy cell group located closely medial to the nucleus of the spinal root of the trigeminal nerve in the sperm whale, the author pointed out the high possibility that the cell group might belong to the spino-bulbo-thalamic relay system because of the striking similarity between the characteristics of the cell group and those of the lateral cervical nucleus.

While Matsumoto (1953) described a specific cell group situated closely medial to the nucleus of the spinal root of the trigeminal nerve in the pygmy sperm whale. He thought the cell group might belong to the sensory trigeminal nucleus because of the partial continuance of the gray substance at the oral level of the cell group to that of the spinal trigeminal nucleus.

In this research, the author investigated comparative anatomically and histologically the specimens of two sperm whales and a pygmy sperm whale, and found out that the cell group Matsumoto described in the pygmy sperm whale showed just the same characteristics as those of the cell group reported by the author in the sperm whales.

MATERIALS AND METHODS

Two adult sperm whales (*Physeter catodon* Linnaeus) were parts of those which had been collected by Dr T. Kojima when he was on a whaling expedition in the

Antarctic Ocean in 1949–50.   The first sperm specimen was the portion covering
almost full length of the medulla oblongata and the first cervical cord, and the
second sperm was the part, extending from the level 10 mm above the obex to that
part which included the first cervical cord.   Both materials, after having been pre-
served in formalin, cut off to meet the purpose, and refixed in Müller's solution in
37°C for 2 to 3 weeks and mounted in celloidin through the usual manner.   Serial
sections of 30 to 45 μm in thickness, along the transverse plane for the first sperm,
and the horizontal plane for the second sperm, were made.   Each 5th sections
(the first and sixth and so forth with the last order of each figure being 1 and 6)
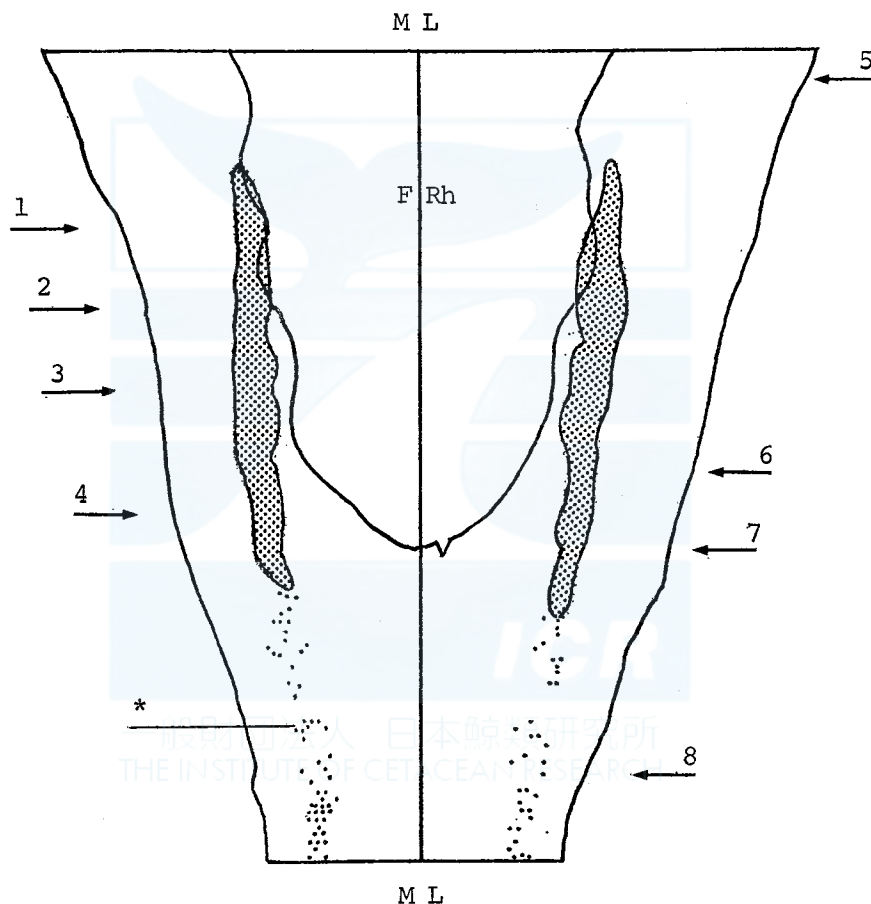
Fig. 1.   Approximate location and size of the cell column in question projected
   from transverse sections on the horizontal plane (dorsal view) in the 1st sperm
   whale, Klüver-Barrera, ×3, Arrows show levels: 1=Plate 1, Fig. 1, 2=Plate 1,
   Fig. 2, 3=Plate 2, Fig. 3, 4=Plate 2, Fig. 4, 5=cranial end of the nucleus of the
   posterior funiculi, 6=caudal end of the inferior olive, 7=level of the obex, 8=
   cranial limit of the dorsal roots.   *: Cranial extension of the lateral cervical
   nucleus.   ML: Midline, FRh: Fossa rhomboidea.

were stained by the Klüver-Barrera's method and each 10 sections (10th, 20th, 30th—etc.) were treated by the Weigert-Pal's or Kultschitzky's method for myelin staining. Silver impregnation method was also applied sporadically on some sections according to needs.

The pygmy sperm (*Kogia breviceps* Blainville) whale specimen was a case which had been collected by Dr T. Ogawa in 1937 at Shiogama, and the whole brain stem was treated into the serial section preparates stained by the Pal carmin method at the Brain Research Institute of the University of Tokyo.
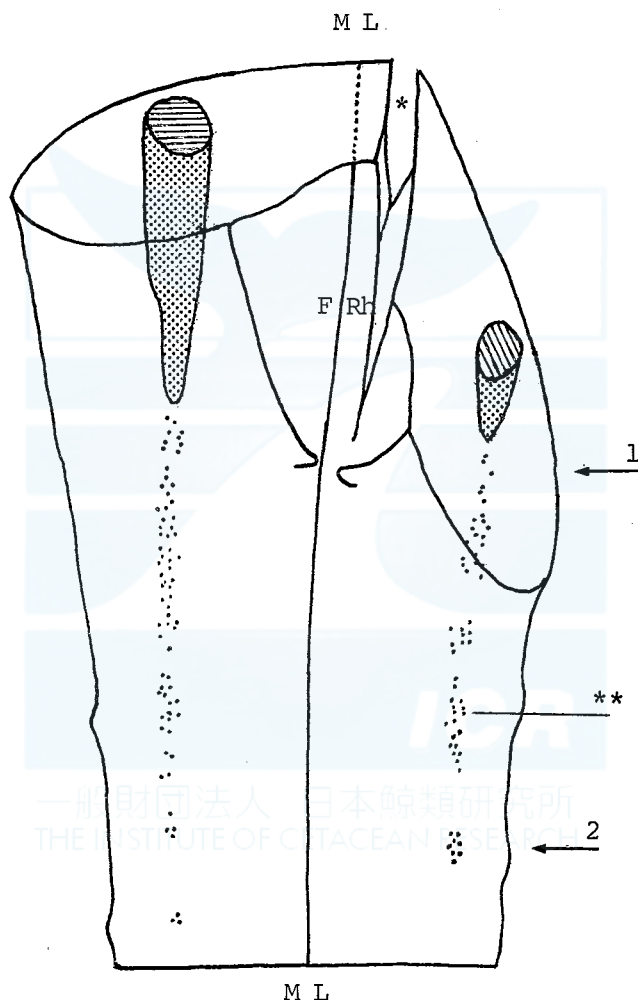
Fig. 2. Approximate location and size of the cell column in question superimposed from horizontal sections on the horizontal plane (dorsal view) in the 2nd sperm whale, Klüver-Barrera, ×4, Arrows show levels: 1=level of the obex, 2=cranial limit of the dorsal roots. *: Artificial cleft, **: Cranial extension of the lateral cervical nucleus, ML: Midline, FRh: Fossa rhomboidea.

RESULTS

In the sperm whales, the cell group in question was found as an evident cell column extending longitudinally from the level of the obex to the uppermost medulla and located closely medial to the nucleus of the spinal root of the trigeminal nerve (Plate 1 and 2).

This cell column was surrounded by the coarse myelinated fibers of the lateral funiculus and seemed oval, fusiform or club shape in appearance at the transverse sections, and measured 4.0–3.2 mm in dorso-ventral direction, 1.5–1.2 mm in width at the midmost level of the column, and extended 21 mm on the left side and 23 mm on the right side in rostrocaudal direction (Figs 1 and 2).

Inside the cell column, it was filled by rather dense net of fine myelinated fibers, and some of small bundles of coarse fibers were seen penetrating longitudinally through the gray substance of the column. Such penetrating fiber bundles were observed numerous in the caudal levels and decreased in number gradually in the higher levels of the column (Plates 1, 2 and 5, Fig. 9).

Nerve cells contained in the column were thought to be classified in two types; one was quite numerous and middle sized, somewhat rounded polygonal or sometimes spindle shaped, measured 60–40 μm in long diameter and 40–20 μm in short one, enclosed fine Nissl granules and stained in light colour, the other one was less in number and a little smaller in size, measured 50–30 μm in long diameter and 25–18 μm in short one, triangle or multipolar in shape, usually stained darkly. These cells were disseminated almost evenly in the cell column and they scarcely made crusters or groups of cells inside the gray substance of the column (Plate 6, Fig. 11).

These structures noted above were quite characteristic to the cell column in question, and made it easy to discriminate from certain other structures in the neighbourhood, *i.e.* nucleus of the spinal root of the trigeminal nerve, nucleus ambiguus, nucleus reticularis lateralis etc. (Plates 1, 2, 5 and 6, Figs 11–14).

At the level near the rostral end of the column, although the gray substance of the column was observed contacting partly with that of the nucleus of the spinal root of the trigeminal nerve (Plate 1, Fig. 1), identification of both structures was easily recognized as the characteristics of the nerve cells were different from each other (Plate 6, Figs 11 and 12).

In the sperm whales, a small lateral cervical nucleus was able to recognize at the uppermost cervical segment, though less distinct. This nucleus, slender and reticular in appearance, was observed continuous farther cranialwards to the medulla oblongata and finally reaching and fused with the cell column in question at the level of the obex (Figs 1 and 2).

In the pygmy sperm whale, the cell group Matsumoto described was observed as a conspicuous cell column extending longitudinally at the level of the middle one third of the medulla oblongata and located closely medial to the nucleus of the spinal root of the trigeminal nerve (Plates 3 and 4).

M L

F|Rh

1
2
3
4

5

6

7

8

M L
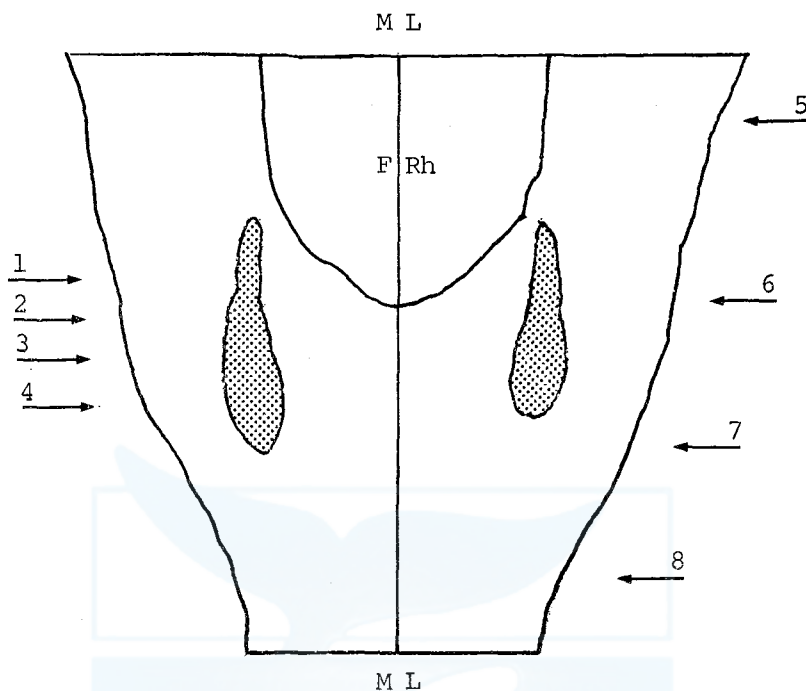
Fig. 3. Approximate location and size of the cell column in question projected from tranverse sections on the horizontal plane (dorsal view) in the pygmy sperm whale, Pal carmin, ×4, Arrows show levels: 1=Plate 3, Fig. 5, 2=Plate 3, Fig. 6, 3=Plate 4, Fig. 7, 4=Plate 4, Fig. 8, 5=caudal end of the lateral recessus, 6= level of the obex, 7=caudal end of the inferior olive 8=rostral limit of the dorsal roots. ML: Midline, FRh: Fossa rhomboidea.

This cell column was surrounded by the coarse myelinated fibers of the lateral funiculus and seemed oval, fusiform or club shape in appearance at the transverse sections, and measured 4.2–3.8 mm in dorso-ventral direction, 1.3–1.0 mm in width at the level of the obex, and extended 8.8 mm on the left side and 7.3 mm on the right side in rostro-caudal direction (Fig. 3).

Inside the cell column, it was filled by rather dense net of fine myelinated fibers, and some of small bundles of coarse fibers were seen penetrating longitudinally through the gray substance of the column. Such penetrating fiber bundles were observed numerous in the caudal levels and decreased in number gradually in the higher levels of the column (Plates 3 and 4).

Two types of nerve cells were investigated in the column; one was numerous and middle sized, somewhat rounded polygonal or sometimes spindle shaped, measured 40–30 μm in long diameter and 30–20 μm in short one, stained in light colour, the other one was less in number and a little smaller in size, measured 30–20 μm in long diameter and 25–15 μm in short one, triangle or multipolar in shape, usually stained darkly by the carmin. These cells were disseminated almost evenly in the cell column and they scarcely made crusters or groups of cells inside the

gray substance of the column.

These structures noted above were quite characteristic to the cell column in question in the pygmy sperm whale, and made it easy to discriminate from certain other structures in the neighbourhood, *i.e.* nucleus of the spinal root of the trigeminal nerve, nucleus ambiguus, nucleus reticularis lateralis etc. (Plates 3 and 4).

At the level near the rostral end of the column, although the gray substance of the column was observed contacting partly with that of the nucleus of the spinal root of the trigeminal nerve, identification of both structures was easily recognized as the characteristics of the nerve cells were different from each other.

In the pygmy sperm whale, the lateral cervical nucleus was hardly recognized at the uppermost cervical segment or the lower medulla in the Pal carmin stained sections.

DISCUSSION

Dr Matsumoto was the earliest researcher who described the cell column in question. In his anatomical studies on the brain stem of the pygmy sperm whale (1953), he made precise and accurate descriptions on the cell column. Although he paid attention to the fact that the cells were observed disseminating in the cell column, he thought this column might belong to the sensory trigeminal nucleus because of the partial continuance of the gray substance at the oral level of the cell column to that of the nucleus of the spinal root of the trigeminal nerve. He also emphasized that the cell column is a quite exceptional structure to the pygmy sperm whale, and denied such a structure in the dolphin, Sei and Beaked whales.

In the previous report (1977), present author described a noteworthy cell group observed at the level from the obex to the uppermost medulla and located closely medial to the nucleus of the spinal root of the trigeminal nerve, and pointed out the high possibility that the cell group might belong to the spino-bulbo-thalamic relay system because of the striking similarity between the characteristics of the cell group and those of the lateral cervical nucleus.

In this research, specimens of the sperm whales were examined carefully, and further, with the permission of the Institute of the Brain Research, University of Tokyo, the serial section preparate of the specimen of the pygmy sperm whale was investigated, which was the case Dr Matsumoto examined before. After the precise comparative anatomical and histological investigations, the author found out that the noteworthy cell group in question in the sperm whales showed quite the same characteristics as those of the specific cell group in the pygmy sperm whale described by Dr Matsumoto, with the exception of the levels of location of these cell groups; the former was higher in the medulla and the latter was lower and at the level almost middle one third of the medulla oblongata.

In the previous study on the comparative anatomy of the lateral cervical nucleus (1965), present author reported that the nucleus was observed at the uppermost cervical segment in the common dolphin (*Delphinus delphis* Linnaeus), and

pointed out an interesting fact that the nucleus was extended farther cranialwards to the lower medulla up to the level of the obex as the gray substances arranged longitudinally in stepping stone pattern. From the findings of the present investigation, the cell column in question was thought to be locating on the upwards elongated line of the lateral cervical nucleus, and moreover, in the sperm whales, the lateral cervical nucleus was found also in the uppermost cervical segment, though less distinct, and the nucleus was observed continuous farther cranialwards to the medulla oblongata, as islands-like cell collections in appearance, and finally reaching and fused with the cell column in question at the level of the obex.

According to these findings noted above, the cell column in question, found in the sperm whales and a pygmy sperm whale, was considered to be the structure corresponding to the cell group highly developed in the level of the medulla oblongata showing just the same characteristics as those of the lateral cervical nucleus.

Matsumoto (1953) noted certain degree of asymmetrical development of the cell column in question; the left side column being larger than the right side one, and he thought it might be some relation with the asymmetrical structure of the nasal meatus in the pygmy sperm whale, without an explanation of the reason on this fact. From the present examination, Matsumoto's finding about the asymmetrical development of the column was reconfirmed distinctly. Ogawa (1949, a and b), in the pygmy sperm whale, described the striking development of the facial nucleus of the right side than that of the left side, and suggested that there should be certain relation with the asymmetrical structure of the nasal meatus in this whale. Hosokawa (1950) reported some asymmetrical structure of the larynx in the sperm whale. In spite of the extraordinarily asymmetrical nasal passage, after the present examination, as far as the extent of the gray substance is concerned, the cell column in question in the sperm whale was hardly recognized the significant asymmetry. At the present stage of the research, it is thought to be difficult to say something on the relation between the difference of the largeness of the cell column in each side and the asymmetrical structures of the nasal meatus or the larynx in these whales.

Matsumoto (1953) stated that the partial continuance of the gray substance at the oral level of the cell column in question with that of the nucleus of the spinal root of the trigeminal nerve, and accordingly he thought that the cell column might belong to the sensory trigeminal nucleus. In the present examination of the specimen of the pygmy sperm whale, the characteristics of the cell column in question was observed different from those of the nucleus of the spinal root of the trigeminal nerve, and the situation was interpreted as the gray substance of the cell column being in contact with that of the trigeminal nucleus. Concerning this matter, in this research, the structural difference of both gray substances was reconfirmed clearly in the first specimen of the sperm whale, after the examination of the additional sections treated by the Klüver-Barrera's and silver impregnation methods.

In the cat or in certain other mammals, it is well known that the lateral cervical nucleus receives afferent fibers originating from the lower levels (Brodal and

Rexed 1953, Morin 1955, Ha and Liu 1966, Craig 1978, etc.). Craig (1978) reported medullary input of the lateral cervical nucleus originating from the nucleus of the posterior funiculi and the nucleus of the spinal root of the trigeminal nerve. Similar relationships, referring the findings of the present examination, could be suggested also in the whales, such as the possibility that a certain amount of fibers of the lateral funiculus might terminate in the cell column.

Although holding a different opinion from that of Dr Matsumoto as to the meaning of the cell column in question, the present author should like to make a proposal, in memory of his first description, to name the cell column as " the nucleus of Matsumoto ", at least for some time until it receives an adequate nomenclature in the future.

SUMMARY

A specific cell column was examined anatomically, which was located closely medial to the nucleus of the spinal root of the trigeminal nerve of the medulla oblongata in two adult sperm whales and an adult pygmy sperm whale.

This cell column was observed extending at the level from the obex to the uppermost medulla in the sperm whales and at the level of the middle one third of the medulla oblongata in the pygmy sperm whale.

The cell column was surrounded by the coarse myelinated fibers of the lateral funiculus and bordered in an oval, fusiform or club shape in appearance at the transverse sections and seemed considerably outstanding from the neighbouring structures.

Inside the cell column, two types of nerve cells were contained; one was middle sized and polygonal, somewhat rounded or spindle shaped, palely stained, and the other one was a little smaller in size, triangle or multipolar, stained darkly. The characteristics of these cells contained seemed very similar to those of the lateral cervical nucleus.

This cell column was thought to be located on the upwards elongated line of the lateral cervical nucleus and moreover, in the sperm whales, the direct continuance was recognized between the lateral cervical nucleus and the cell column at the level of the obex.

According to these findings noted above, the cell column in question was considered to be the structure corresponding to cell group highly developed in the level of the medulla oblongata showing just the same characteristics as those of the lateral cervical nucleus.

Although none of the definite finding about the fiber connection of the cell column was obtained, at the present stage of research, it seems there is a high possibility that the cell column belongs to the spino-bulbo-thalamic relay system.

precious materials (Sperm 1 and 2) for this study.   Many thanks are due to Dr
T. Ogawa and Dr T. Kusama, formerly directors of the Brain Research Institute,
University of Tokyo, for their kind permission to my investigation of the research
material (*Kogia*).   Throughout my study on the *Kogia*, good assistance of Dr T.
Kamiya, formerly a staff of the Department of Anatomy, School of Medicine,
University of Tokyo, is also acknowledged.

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EXPLANATION OF PLATES I—VI

PLATES I AND II

Figs 1 and 2 and Figs 3 and 4:   Transverse sections of the medulla oblongata in the 1st Sperm, arranged from cranial to caudal, Kultschitzky, ×6.

PLATES III AND IV

Figs 5 and 6 and Figs 7 and 8:   Transverse sections of the medulla oblongata in the Pygmy sperm, arranged from cranial to caudal, Pal carmin, ×8.

PLATE V

Fig. 9:   The same section as Plate I, Fig. 2, a little enlarged (×10), left side; note the location and shape of the cell column in question and neighbouring structures.

Fig. 10:   The section very near to that of Fig. 9, ×20, silver impregnation; note the structural difference of the cell column and the neighbouring nuclei.

PLATE VI

Nerve cells in high magnification (×100), Klüver-Barrera.

Fig. 11:   The cell column in question.

Fig. 12:   Nucleus of the spinal root of the trigeminal nerve.

Fig. 13:   Nucleus reticularis lateralis.

Fig. 14:   Nucleus ambiguus.

ABBREVIATIONS IN PLATES

FL	Funiculus lateralis
FLM	Fasciculus longitudinalis medialis
FP	Funiculus posterior
NA	Nucleus ambiguus
NFP	Nucleus funiculi posterioris
NQ	The cell column in question
NRL	Nucleus reticularis lateralis
NSV	Nucleus tractus spinalis nervi trigemini
NXII	Nucleus nervi hypoglossi
OL	Nucleus olivaris inferior
RX	Radix nervi vagi
RXII	Radix nervi hypoglossi
S	Fasciculus solitarius
TSV	Tractus spinalis nervi trigemini

Fig. 1.

Fig. 2.

PLATE II   SEKI

Fig. 3.

Fig. 4.

PLATE III

Fig. 5.

Fig. 6.

PLATE IV   SEKI
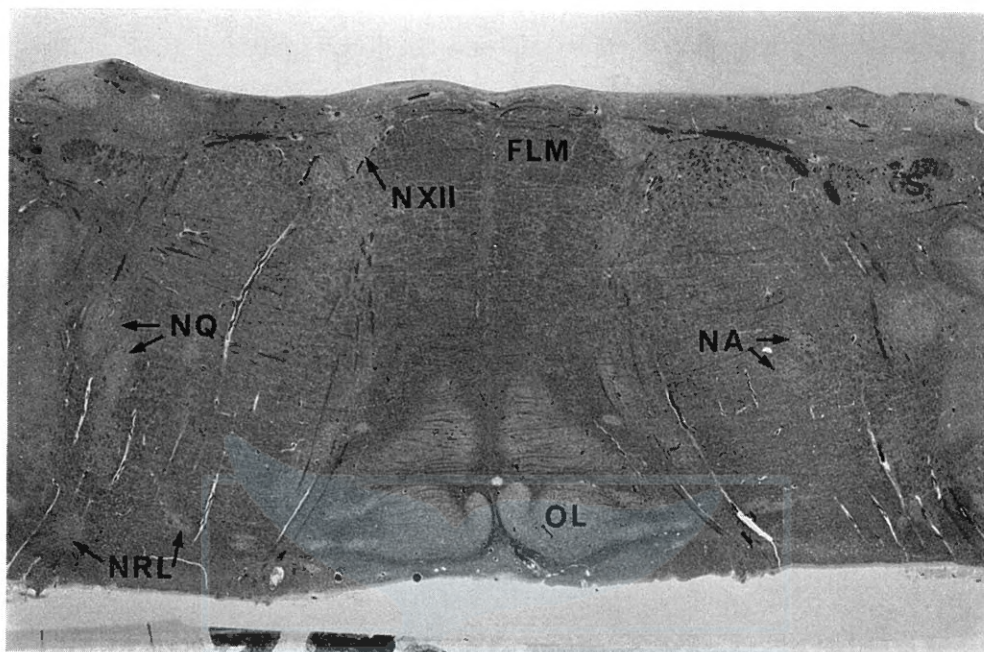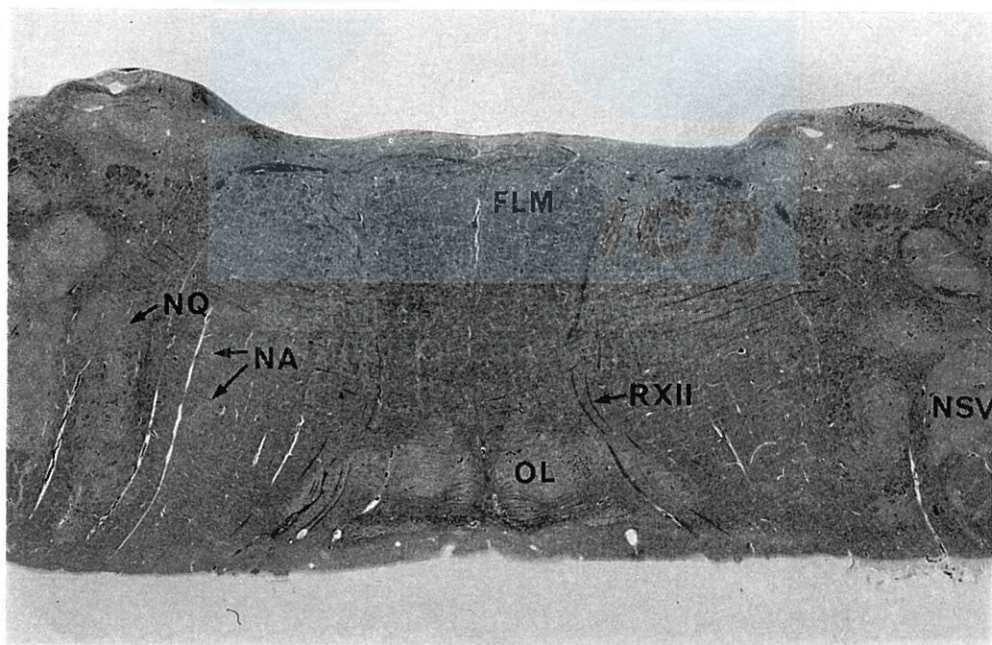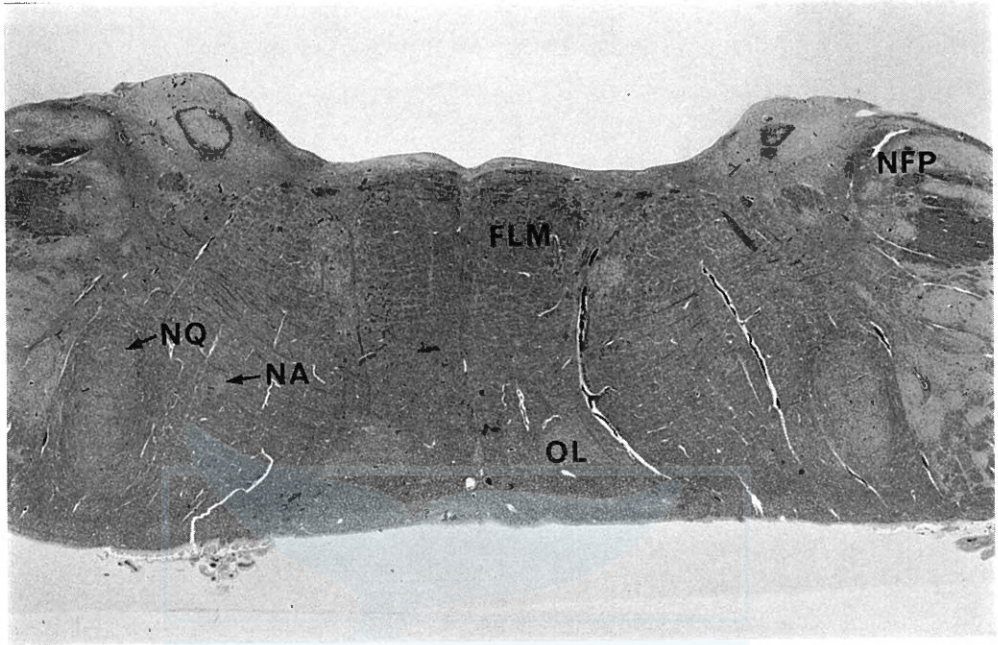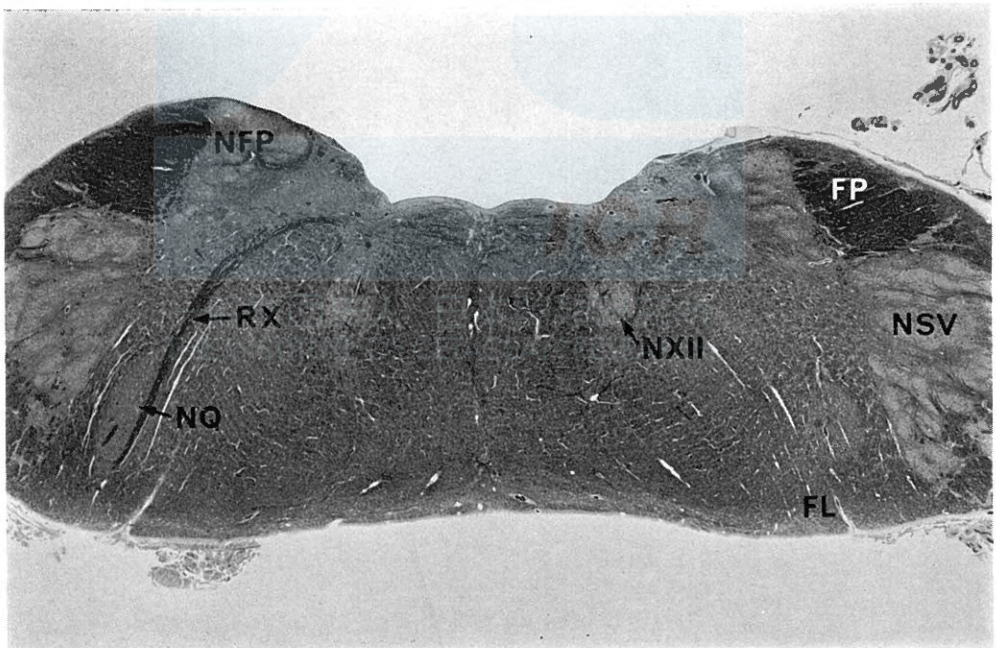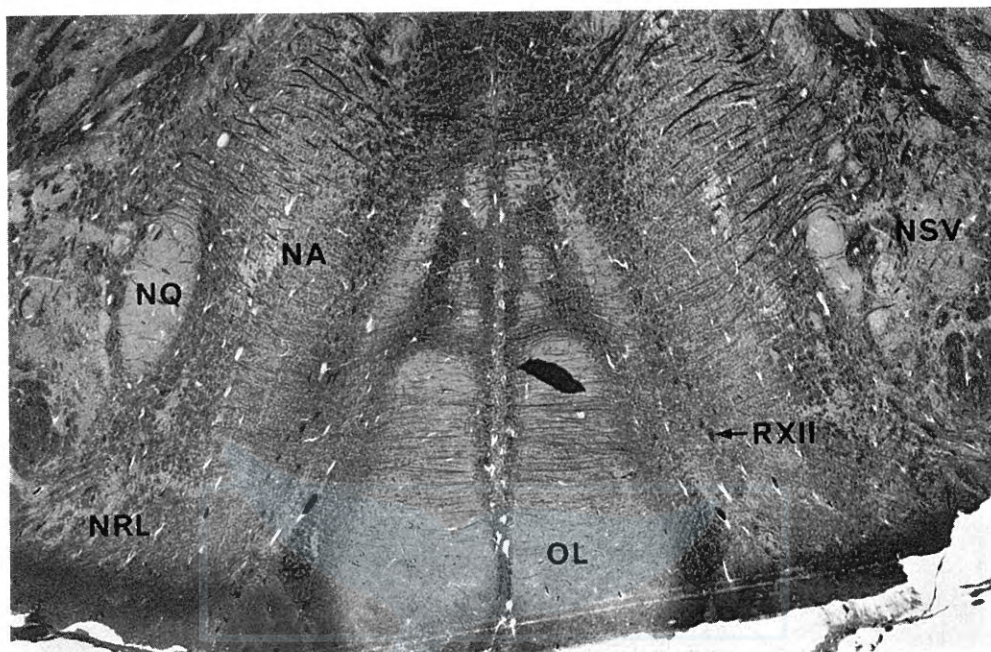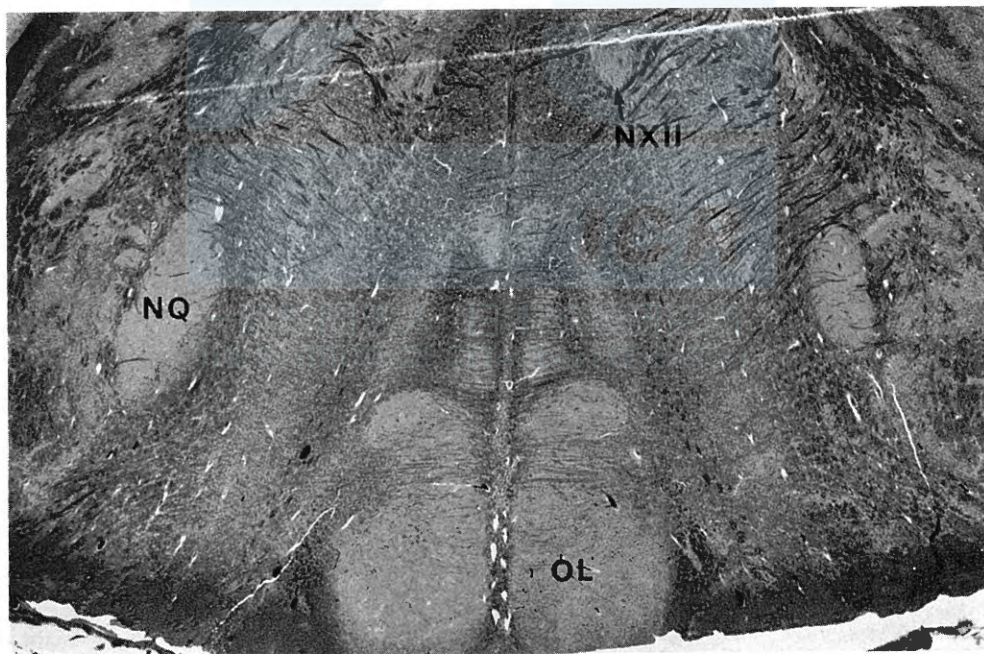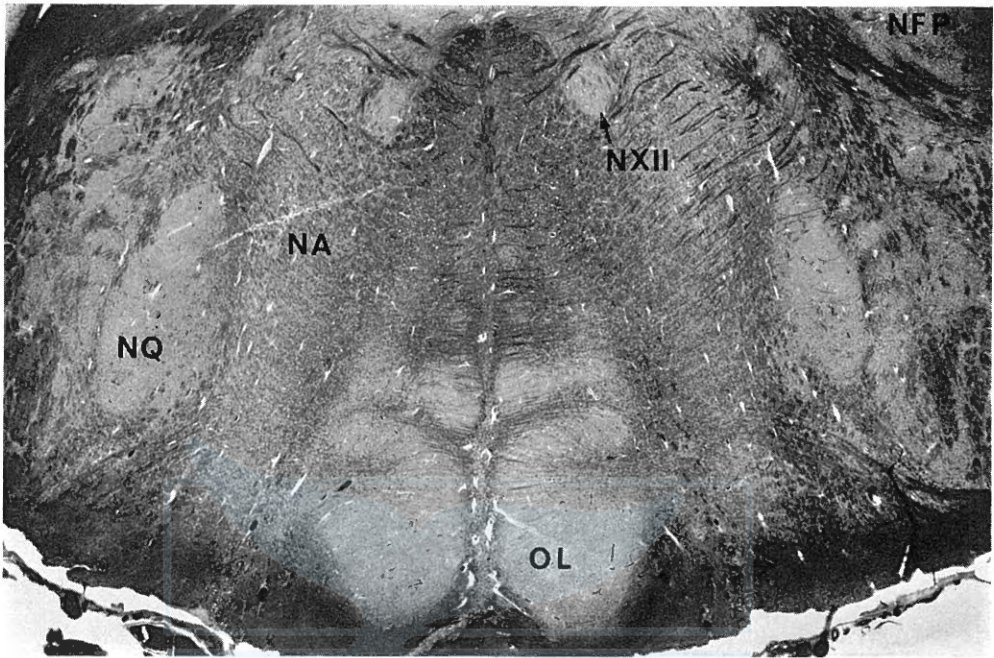
Fig. 7.

Fig. 8.

Fig. 9.

Fig. 10.

PLATE VI   SEKI
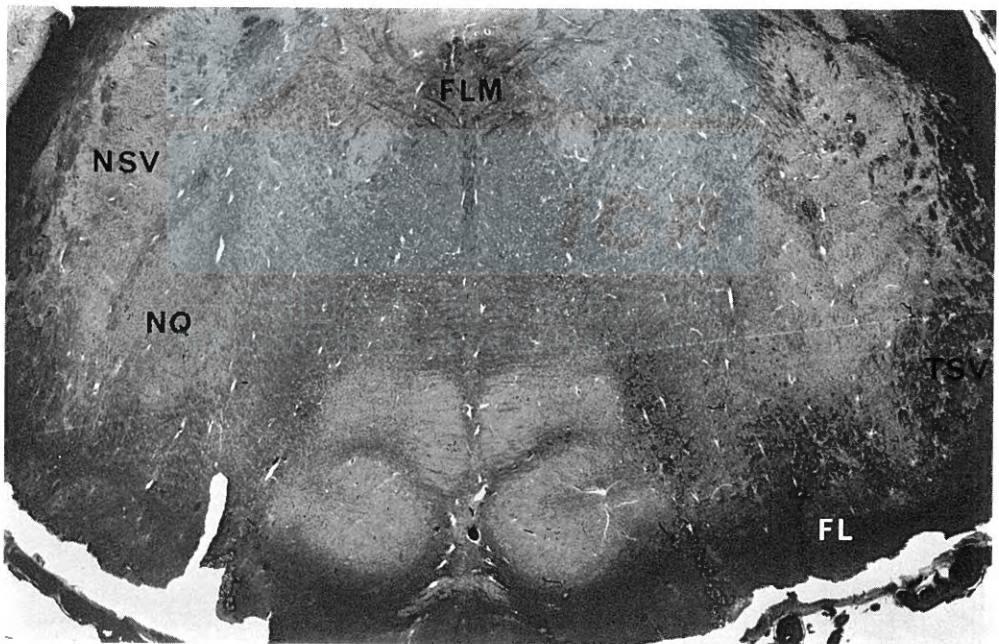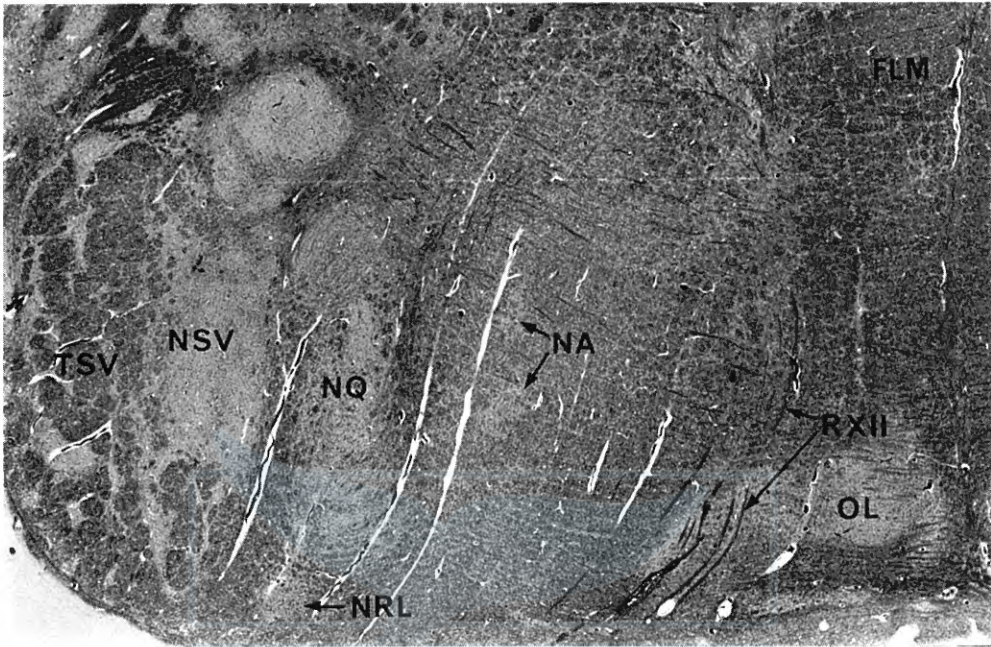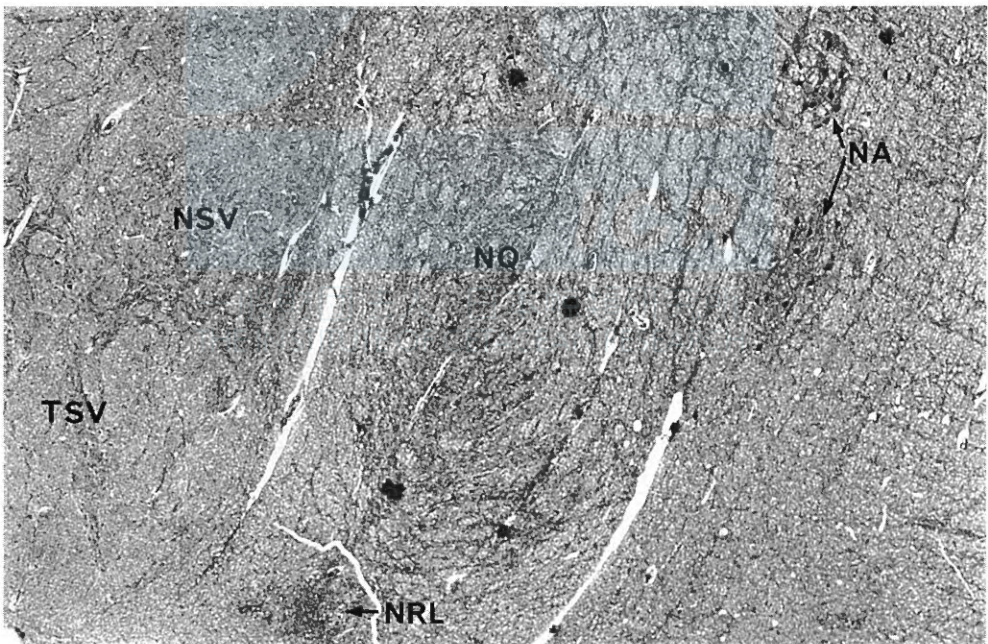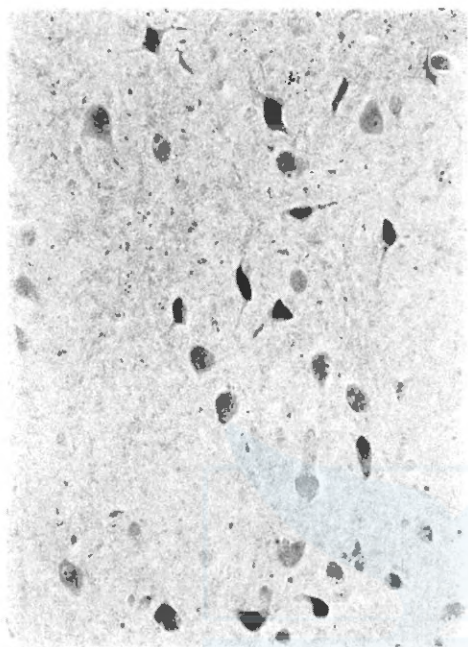
Fig. 11.
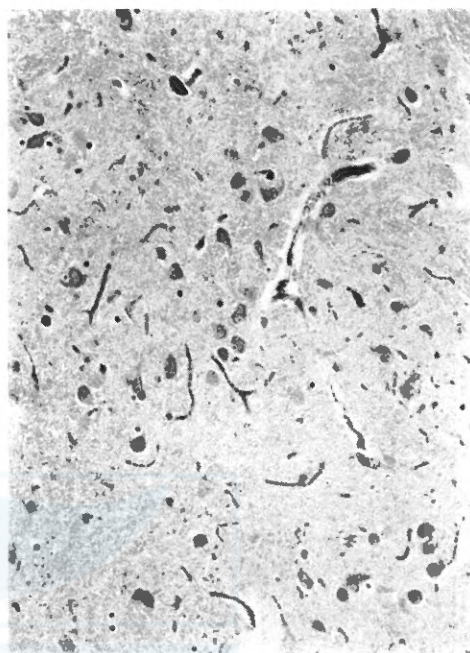
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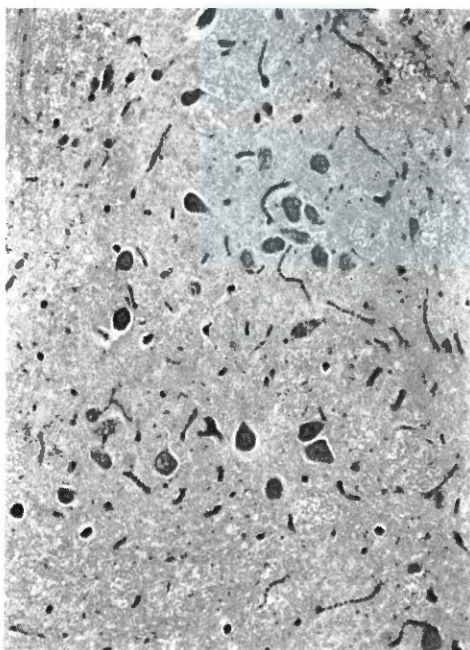
Fig. 13.
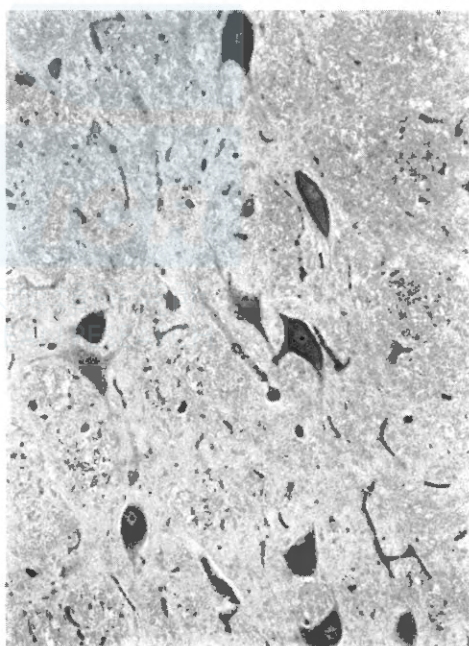
Fig. 14.

AGE DETERMINATION AND GROWTH OF THE SHORT-FINNED PILOT WHALE OFF THE PACIFIC COAST OF JAPAN

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ABSTRACT

This study is based on data and specimens from 373 female and 170 male *Globicephala macrorhynchus* collected off the Pacific coast of central Japan and covering eight months of the year. The deposition rate of dentinal growth layers was annual, the haematoxylin-stainable layer being formed from May to October and the unstainable from December to February. The annual deposition of cemental layers continued after dentine deposition ceased, thus enabling the age of old individuals to be determined. The maximum age attained by females was 62 years, that of males 45 years. Females almost ceased growth at sexual maturity (nine years) and reached the asymptotic length of 364.0 cm at age 22 years. Male growth was similar to that of females until age nine years, when the secondary male growth spurt started. Males attained an asymptotic length of 473.5 cm at 27 years. Body length could be converted into age with an accuracy of ± 2 years, up to a body length of 280 cm (females; equivalent to age 5 years) or 320 cm (males; age 8 years). The relationship between body weight (W, kg) and body length (L, cm) of fetal and postnatal individuals of both sexes was described by $\log W = 2.8873 \log L + \log (2.377 \times 10^{-5})$.

INTRODUCTION

Sergeant (1959) examined the dentinal growth layers in the tooth of long-finned pilot whale, *Globicephala melaena* (Traill, 1809), and suggested that these layers might be used to estimate absolute age. He used this technique in his analysis of the life history of *G. melaena* in Newfoundland waters (Sergeant, 1962). Sergeant also observed cemental growth layers in this species and suggested that they might be used to age animals in which dentine deposition had ceased. However, he did not use the technique, presumably because of technical difficulties.

Dentinal layer counts have subsequently been used in the study of the life

history of several odontocetes as reviewed by Scheffer and Myrick (1980), despite the limitations of the technique for determining the age of old individuals. In recent years, however, the methods of preparing teeth for cemental and dentinal layer counts have been greatly improved (Perrin and Myrick, 1980).

The improved age determination techniques have been used to study the life history of the short-finned pilot whale *Globicephala macrorhynchus* Gray, 1846. We report on age determination and growth in *G. macrorhynchus* in this paper.   Related studies on the life history and reproduction of this species (Kasuya and Marsh, in press) and on fundamental anatomy of the ovaries (Marsh and Kasuya, in press) will be published elsewhere.

MATERIALS AND METHOD

Data source

Most of the data and specimen materials were collected between 1965 and 1980 inclusive from 24 schools of *G. macrorhynchus* (Schools 1 through 24 in Table 1) caught on the Pacific coast of Japan by the driving fishery at Taiji (33°34′N, 135°54′E), Futo (34°54′N, 139°09′E), or Arari (34°49′N, 138°46′E), and from one school stranded at Choshi (35°43′N, 140°52′E) in the Chiba prefecture. The

TABLE 1.   MATERIALS USED IN THIS STUDY

School no.	Locality	Date of		No. of individuals			
		catch	data collection	driven	examined	aged	lost
1	Arari	20 Oct. '65	21 Oct. '65	33	18	8	15
2	Choshi	13 Dec. '66	15 Dec. '66	ca. 90	9	3	80
3	Arari	— June '67	27, 28 June '67	>30	14	4	16
4	Taiji	22 July '69	July–Aug. '69	31	9	2	22
5	Taiji	27 July '69	July–Aug. '69	46	23	10	23
6	Taiji	24 Feb. '71	24 Feb. '71	24	12	0	12
7	Taiji	17 Jan. '75	18, 19 Jan. '75	28	28	26	0
8	Taiji	21 Jan. '75	21, 22 Jan. '75	52	47	0	5
9	Taiji	24 June '75	25 June–4 Jul.	ca. 230	173	125	57
10	Taiji	22 July '75	22–24 July '75	33	32	18	1
11	Taiji	13 Jan. '76	13–17 Jan. '76	28	26	21	2
12	Taiji	4 Feb. '76	5, 6 Feb. '76	20	20	18	0
13	Taiji	7 Oct. '76	8, 9 Oct. '76	38	38	38	0
14	Futo	20 Dec. '77	21 Dec. '77	25	25	22	0
15	Futo	24 Dec. '77	25 Dec. '77	48	48	45	0
16	Taiji	20 Feb. '78	20, 21 Feb. '78	27	27	27	0
17	Futo	4 Dec. '78	5 Dec. '78	52	52	49	0
18	Futo	13 Dec. '78	13, 14 Dec. '78	28	28	28	0
19	Taiji	6 Jan. '80	6 Jan. '80	26	23	0	3
20	Taiji	17 Jan. '80	17, 18 Jan. '80	14	14	7	0
21	Taiji	2 Feb. '80	2 Feb. '80	19	17	0	2
22	Taiji	20 Feb. '80	23 Feb. '80	15	15	15	0
23	Taiji	21 Feb. '80	24 Feb. '80	23	23	23	0
24	Taiji	30 May '80	31 May–3 June	38	38	38	0

linear distance between the southernmost location, Taiji, and the northernmost, Choshi is about 500 km.

The quality and quantity of data and samples varied between the schools. In the early period of the study (Schools 1 to 6), effort was directed to the collection of materials for taxonomy, and the data obtained for the present analyses were limited and biased to adult individuals. Information from four schools (schools 8, 19, 20 and 21) examined by volunteers was usually limited to sex and body length. The 14 schools (Schools 7, 9 through 18, 22, 23 and 24) caught in the seven years from 1975 to 1980 and examined by Kasuya constituted the major source of data used for the study.

Field procedures

The information and samples listed below were collected by Kasuya, volunteers or both, when the fishermen were flensing. At this stage each pilot whales was assigned a sample number which is a hyphonated combination of the school number followed by the number of the animal within the school.

1. *Sex*

2. *Body length* Measured to the nearest 1 cm on a straight line parallel to the long axis of the body from the anteriormost point to the bottom of the tail fluke notch. Although the tip of the upper jaw is the anteriormost point of the body of juveniles, it lies posterior to the front end of the melon after the whale is about 240 cm long and becomes difficult to distinguish (Yonekura, Matsui, and Kasuya, 1980). Thus the measurement of body length is not exactly comparable for adults and calves less than one year old.

3. *Teeth* One to three contiguous teeth were collected from the center of the lower tooth row with a hammer and chisel and preserved in 10% buffered formalin. The largest available teeth were selected.

4. *Other specimens* Mammary gland, testis, epididymises, ovaries, uteri and stomach contents were collected as detailed in Kasuya and Marsh (in press).

Laboratory procedures

1. *Tooth preparation* The age determination was done by Kasuya who counted the annual growth layers in dentine or cementum. (One growth layer is equivalent to an *annual* Growth Layer Group of Perrin and Myrick (1980)). The bone and connective tissue surrounding tooth selected were removed with a knife. The tooth was then cut longitudinally with a low speed diamond saw. The cut surface was then polished with coarse (about 1,200 mesh) and fine (about 3,000 mesh) whetstones to expose the center of the tooth. The polished surface was dried and glued on a clear perspex plate (1 mm thick) with cyanoacrilate monomer. After the glue had hardened, the other side of the tooth was similarly sawed off leaving a 0.3 to 0.5 mm thick section on the perspex slide. This section was polished with the whetstones to a thickness of 30 to 40 μm. The polished section was then decalcified in 5% formic acid for about 24 hours at room temperature, rinsed in running water for 5 to 12 hours, stained with Mayer's haematoxylin for 30 minutes,

rinsed in running water for several hours and mounted in Canadian balsam. (A complete removal of acid by long rinse or ammonia after staining prevent fading.)

2. *Reading growth layers* The counting of annual growth layers was done under transmitted light with a compound microscope (20 to 100x) using the following procedure. An ontogenetic series of 20 slides was initially prepared for each sex. Factors taken into account in the selection of these slides included the quality of preparation and the relative age suggested by the thickness of dentine and by the size of the pulp cavity. The dentinal and cemental growth layers in the slide of these 40 teeth were counted. In most cases, there was reasonable coincidence between the number of growth layers in both tissues.

However, there were a few cases where the reading did not correspond. These slides were re-examined for indication that dentine deposition had ceased. All counts were then plotted against body length and sexual maturity for males and females separately. The pattern of increase suggested that the growth layer counts were a reliable index of absolute age.

The age of the other whales were then determined based on the standard established above but without reference to biological data. First the cementum was read three or more times. The medium count was then taken as the true value. Then the dentinal layers were counted three times without referring to the cemental counts. The medium value was again used. If the deposition of dentine was considered to have been continuing on at least part of the wall of the pulp cavity, the dentinal count was used. In a few cases the range of dentinal and cemental counts differed on a tooth with open pulp cavity. In these cases the growth layers in both tissues were repeatedly checked until a good agreement was reached between the counts for both tissues. Kasuya used this method to train himself to be able to make accurate cemental layer counts, enabling him to age whales with closed pulp cavities, the age of these animals being determined from cemental layer count only.

The age of each individual was principally expressed as the number of growth layer cycles, which was equivalent to years (see below). The age of individuals below 10 years was roughly estimated to the nearest 1/4 year by considering the thickness and nature of the first and last postnatal dentinal layers of incomplete thickness. For whales over 10 years, the age was grouped into the nearest n+0.5 years (n=integer).

3. *Other procedures* The method used to determine the reproductive status of each whale are detailed in Kasuya and Marsh (in press) and Marsh and Kasuya (in press).

AGE DETERMINATION

Description of dentinal growth layers (Plates I to III)
The prenatal dentine is capped by an enamel layer, which dissolves in the decalcification reagent. In decalcified and haematoxylin stained sections, the prenatal dentine appears as either a moderately or strongly-stained layer in which

10 to 20 indistinct short cycle layers can be detected with careful study. The proximal border of the prenatal dentine is lined with a thin unstainable layer in most postnatal animals. This is the neonatal line (Fig. 2 in Plate I). The thickness of the neonatal line ranges from 16 to 64 μm ($\bar{x}=38$ μm; n=25). The neonatal line could not be distinguished in four newborn individuals ranging from 136 to 142 cm in body length. Two of these whales (males 136 cm and 142 cm long), had an erect dorsal fin, an indication that birth had occurred not less than several hours before (Kasuya, Miyazaki and Dawbin, 1974). In contrast, the neonatal line was clearly seen in the teeth of five individuals from 154 to 190 cm in body length and aged between 0.1 to 0.5 year (estimated from body length). This indicates that the neonatal line in *G. macrorhynchus* is identifiable only after the deposition of ordinary more stainable postnatal dentine.
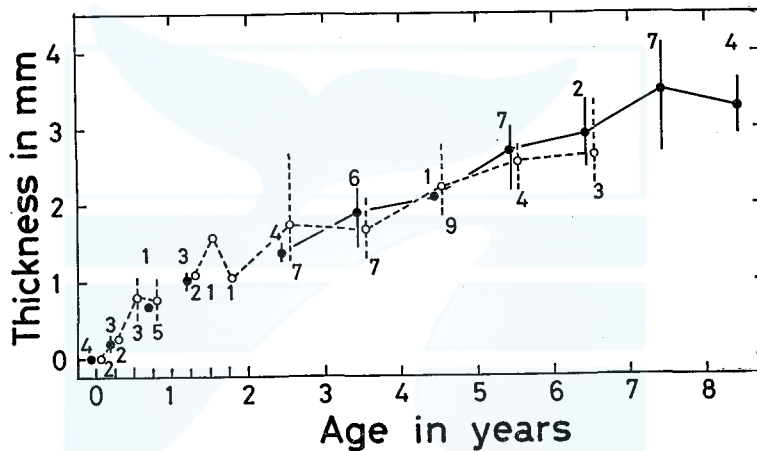
Fig. 1. Thickness of postnatal dentine of *G. macrorhynchus*. The ranges, means and sample sizes are indicated. Open circles and dotted line represent females, closed circles and solid line males.

In decalcified and stained sections, the growth layers in postnatal dentine are seen as layers of alternating stainability. The thickness of the annual growth layers is about 0.5 to 0.6 mm in both the first and second complete layers (measured at the level of the base of the prenatal dentine). This thickness decreases to about 0.1 mm at the 30th and subsequent layers (measured at the midlength of the pulp cavity). No sexual dimorphism was observed in dentine thickness of young whales (Fig. 1). Within one annual growth layer, short cycle layers are usually detectable. These tend to be conspicuous where the growth layers are wide, *i.e.* in the dentine laid down near the tooth apex while the whale is young. Occasionally some of these short cycle layers are as prominent as ordinary annual growth layers.

The appearance of dentinal growth layers is variable within a tooth. The layers deposited in the juvenile stage in the root of the tooth are composed of wide stainable and narrow unstainable layers (Fig. 4 in Plate I). However if a stainable layer is traced to the tip of the tooth its outer border gradually looses stainability,

while the stainability of its inner border increases.   Furthermore, an accessory layer (Hohn, 1980) of strong stainability may appear in the unstainable layer near the tip. Thus the pattern of stainability of these layers often appears to be reversed with a resultant apparent lag of about half a growth layer cycle between the cusp and the root portions of the tooth.   This feature is usually absent or negligible in sub-sequent layers.   The annual growth layer deposited in the root of the tooth in adult whales is usually composed of a narrow stainable layer and a wide unstainable layer (Figs 2 and 3 in Plate II).   Although accessory layers are still common in these layers, they are less conspicuous than in the apex.
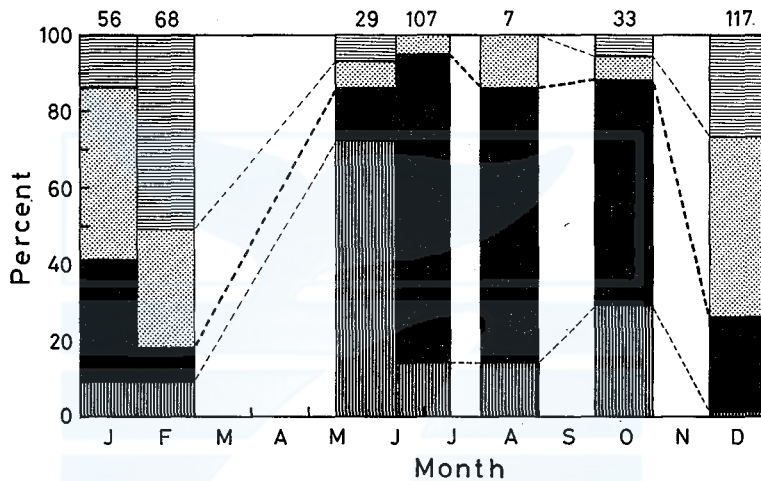
Fig. 2.   Seasonal change in the nature of the last incomplete dentinal layer of *G. macrorhynchus*.   Numerals at the top indicate sample size.   Thin horizontal lines: wide unstainable layer.   Stippling: thin unstainable layer.   Black: wide stainable layer.   Thick vertical lines: thin stainable layer.

Deposition rate of dentinal growth layers

Seasonality of stainability: Data were obtained from 270 females and 147 males in which the deposition of dentine was certainly continuing.   The nature of the last incomplete dentinal layer in the root of the tooth was classified as either a thin or a thick, stainable or unstainable layer.   The thickness was judged by eye in com-parison with the corresponding tissue in the previous cycle.   Fig. 2 shows the sea-sonality of stainability of the last deposited dentine.   In May/June most of the 29 individuals (86.2%) have started depositing stainable dentine.   This continues in most individuals until October.   The number of individuals depositing an unstain-able layer increases from 12.2% in December to 82.4% in February.   Although data are lacking from March to early May, we suspect that deposition of the un-stainable layer peaks in February and March, and suggest that the alternations of dentinal layers from unstainable to stainable and from stainable to unstainable may occur in April to early May and in November, respectively.   Thus each of the two major components of a dentinal layer seems to represent approximately six months.
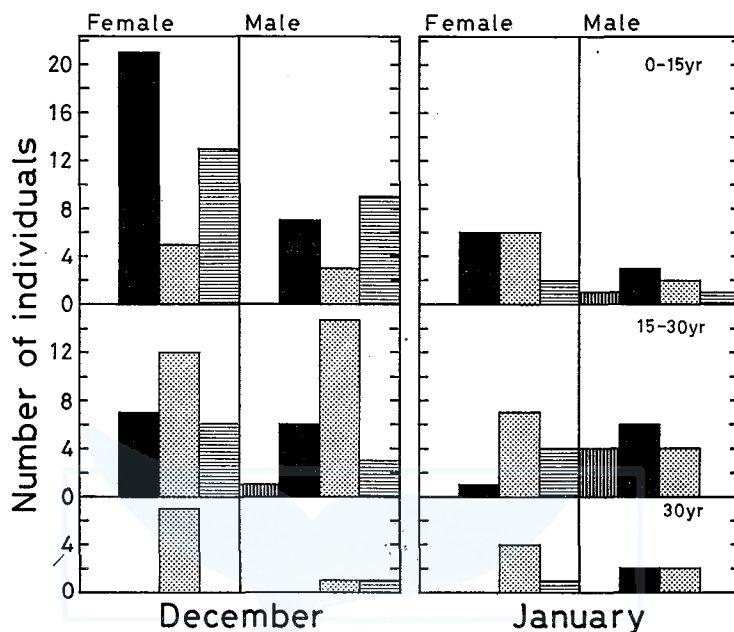
Fig. 3. Age and sex differences in the season when the stainable and unstainable layers within a dentinal growth layer alternate in *G. macrorhynchus*. Thin horizontal lines: wide unstainable layer. Stippling: thin unstainable layer. Black: wide stainable layer. Thick vertical lines: thin stainable layer.

Approximately 10 to 20% of our sample was not depositing dentine in accordance with this pattern. This may have been due to (1) exceptional individuals (2) errors in layer-identification due to the short cycle layers or (3) sex or age differences in dentine deposition. To test the last possibility the data for each month were subdivided according to sex and then into three age groups (1) below 15 years, (2) from 15 to 30 years and (3) over 30 years (Fig. 3). Age/sex differences in the relative frequency of the four deposition stages was then statistically tested for each month (Chi-square test). A statistically-significant difference ($P<0.05$) was found only for samples obtained in December and January. The only combination where a significant difference was obtained between sexes was in intermediate age class (15–30 years) in January ($P<0.01$). Although this result indicates that males of intermediate age were more likely to deposit a stainable layer than females, we consider this is probably an error caused by small sample size because a similar trend was not observed in December (Fig. 3). A significant difference in the proportion of animals of the same sex laying down a stainble layer was also found for the following age combinations in December:

    Females   young: intermediate, $P<0.01$
                intermediate: old, $0.02<P<0.05$
                old: young, $P<0.001$
      Males   young: intermediate, $P<0.01$

Thus as the whales get older, proportionately fewer females tend to be accumulating a stainable layer in December. Although not always statistically-significant, the same trend is also observed in the male. The change in the deposition pattern from stainable to unstainable dentine seems to occur slightly later in younger individuals possibly due to the larger relative width of the stainable dentine in young animals (see " Description of dentinal growth layers ").
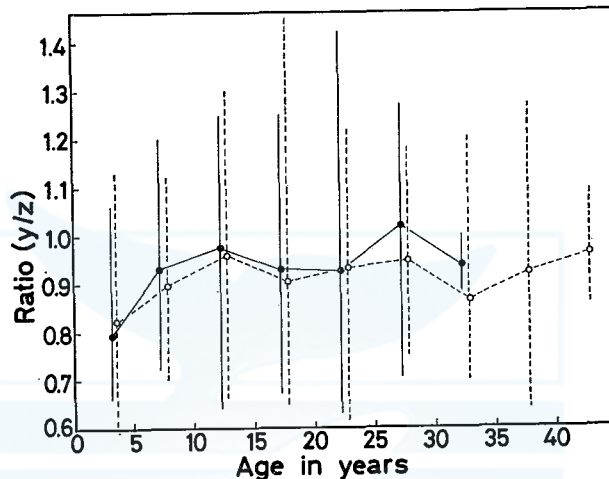
Fig. 4. Rate of decrease in the width of dentinal growth layers indicated by the thickness of the last complete layer (Y) and penultimate layer (Z) in *G. macrorhynchus*. The ranges and means for males (closed circles and solid line) and females (open circles and dotted line) are indicated.

Seasonal changes in dentine thickness: The thickness of dentinal growth layers was measured with an ocular micrometer. The measurement was taken from the center of one stainable layer to the center of the next, except in the case of the last incomplete set, the width of which was measured from the center of the last complete stainable layer to the predentine-dentine boundary near the edge of the pulp cavity (irrespective of nature of dentine being laid down). This latter measurement was often thicker than that of the penultimate measurement because each stainable layer was defined only after the next unstainable layer had been deposited. The uncorrected degree of deposition of the last growth layer (R_n) can be defined as;

$$R_n = \frac{X_n}{Y_n}$$

where X_n is the thickness of the last (incomplete) growth layer of an n-year old whale and Y_n is the thickness of the (complete) penultimate growth layer of the same individual. As the thickness of a dentinal growth layer varies with the whales's age, R_n has to be corrected for this variation. The correction factor C_n for an n-year old whale can be defined as;

$$C_n = \left(\sum_{j=1}^{m} \frac{Y_{n+1,j}}{Z_{n+1,j}} \right) \cdot \frac{1}{m}$$

where m is the number of whales aged $(n+1)$-years and Z is the thickness of the layer one cycle prior to Y. Then the corrected deposition rate for the last incomplete layer of an n-years old individual can be defined as R_n/C_n. This method is only applicable for whales older than two years.
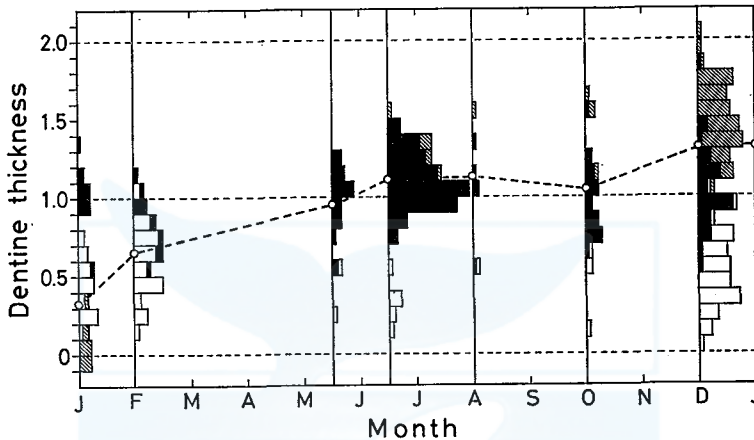
Fig. 5. Seasonal change in the relative thickness of the last incomplete dentinal layer in *G. macrorhynchus*. The dotted line joins the monthly means (open circles). Black squares represent individuals depositing a stainable layer; white squares those depositing an unstainable layer. The shaded areas indicate indiviuals that are moved back (January) or forward (June/July—December) for one cycle in order to correct for the individual variation in the seasonality of dentine deposition.

The relationship between age (n) and Y_n/Z_n is shown in Fig. 4. The means of the five-year age classes increase until the whales are about 15-years old, and stays almost constant thereafter. The values for males are slightly higher than the corresponding values for females indicating that the decline of growth layer thickness with age is slower in males. This may relate to the earlier cease of dentine deposition in males mentioned below (see " Pulp cavity "). Because Y_n/Z_n shows such large individual variation, it is not practical to calculate C_n for each age class and sex. Therefore, we have calculated C_n for both sexes and for four age classes as follows;

2–5 yrs	$C_n = 0.804$
5–10 yrs	$C_n = 0.902$
10–15 yrs	$C_n = 0.963$
≥15 yrs	$C_n = 0.922$

The resultant corrected values of the relative thickness of the dentinal layer being deposited at the time of death in various months are shown in Fig. 5. In January, about 40% of the individuals are still depositing stainable dentine while
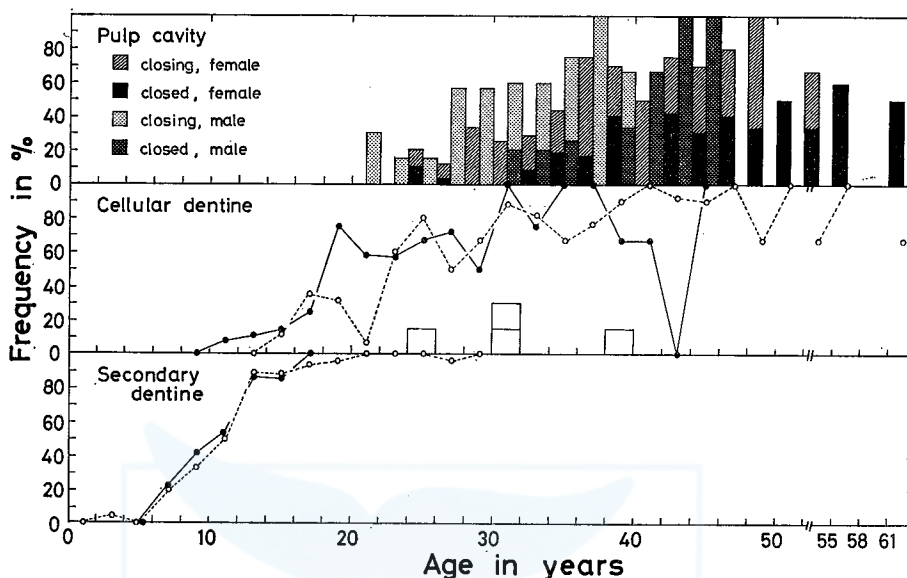
Fig. 6. Growth of *G. macrorhynchus* teeth. Top: condition of pulp cavity. Middle: deposition of cellular dentine. The boxes represent four males whose pulp wall was completely covered by cellular dentine. Bottom: deposition of secondary dentine. The open circles and dotted line represent females, and closed circles and solid line males.

the remainder have already started to deposit unstainable dentine. Therefore the values of the former individuals need to be moved backward for one cycle. In the same way, the values for individuals depositing an unstainable layer after July need to be moved forward one cycle. The mean monthly values of the corrected thickness of the last dentinal layer thus calculated are shown by the open circles in Fig. 5. The values increase from 0.3 in January to 1.3 in December. The increase is 1.0/year, and indicates that the deposition of the dentinal growth layers is annual.

Growth of dentine

The postnatal growth of dentine is shown in Fig. 1. The thickness is measured on the convex ramus of the tooth section from the proximal end of the prenatal dentine to the pulp wall. Because the apex of the pulp cavity reaches the level of the base of the fetal dentine, this measurement is not possible on some males after 8.5 years of age or on some females after 6.5 years. The deposition of dentine is rapid between 0.25 and 0.5 year of age. This period may correspond with the time of tooth eruption and more indirectly with the start of taking solid food (see Kasuya and Marsh, in press). After 0.5 year of age the thickness increases at a slightly decreasing rate. The mean annual increment of the dentine in the juvenile stage is calculated from Fig. 1 as about 0.95 mm in the first year, 0.40 mm in the second year, 0.33 mm in the 3rd year, and 0.30 mm in the 4th year.

The deposition of secondary dentine starts in some pilot whales of both sexes at the age of seven years, and in most individuals by 16 years of age (Fig. 6). Although secondary dentine starts to form during the years when pilot whales mature sexually, there is no correlation between the two phenomena in individual whales and the age at which secondary dentine first forms varies between different teeth in the same jaw (Table 3). Secondary dentine deposition starts at several points on the pulp cavity wall as discussed by Sergeant (1962), and comprises increasingly more of the tooth tissues as the whale ages. It appears translucent on thin undecalcified sections and is less stainable in the decalcified and stained sections (Plate II, Figs 1, 2, 3, and 6). The annual growth layers in secondary dentine are less regular than in ordinary dentine and the contrast between stainable and unstainable layers is usually less pronounced (Plate II, Fig. 2). However, we consider that secondary dentine is not a real obstacle to age determination in *G. macrorhynchus*, because (1) even in old individuals some small areas of ordinary dentine are usually evident along the wall of the pulp cavity and (2) reading the layers in secondary dentine is not very difficult in the decalcified and stained sections (Plate II, Figs 2 and 3).

Another characteristic of the short-finned pilot whale tooth is the deposition of a tissue on the wall of the pulp cavity that we have tentatively called " cellular dentine " (Plate III, Figs 3 to 7). In decalcified and stained sections, this tissue looks rather like cementum. Although the " cellular dentine " contains minute growth layers, the spacings are irregular making counting almost impossible. The deposition of " cellular dentine " starts at the base of the pulp cavity, but progresses further along the cavity in some individuals 10 years or more in age. The boundary between the " cellular dentine " and cementum is less obvious than between this tissue and both other types of dentine.

While preparing teeth for age determination, it was noted that " cellular dentine " tended to be laid down by unusually fibrous pulp which adhered closely to the wall of the pulp cavity. In few exceptional males, the entire wall of the (still open) pulp cavity was lined with " cellular dentine " making it impossible to count the dentinal growth layers (Fig. 6).

Pulp cavity

We classified the condition of the pulp cavity as follows:

1. *Open pulp cavity* All dentinal growth layers continuous in a longitudinal tooth section, dentine being deposited along the entire pulp cavity wall. Similar numbers of dentinal and cemental growth layers.

2. *Closing pulp cavity* Some of the dentinal growth layers (at least the latest one) discontinuous in a longitudinally sectioned tooth. Growth layers deposited along a limited portion of the pulp cavity wall only, the remainder being lined with a strongly-stainable thin layer of uniform structure, which does not contain cells in it. The number of dentinal growth layers may coincide with the number of cemental layers within the range of reasonable error if the best portion of the pulp wall is used for counting.

TABLE 2. LIST OF WHALES WITH CLOSED PULP CAVITV

Sample no.	Age (yrs) dentine	cement	Gonad*	Reproductive status	B.L. (cm)	Sample no.	Age (yrs) dentine	cement	Gonad*	Reproductive status	B.L. (cm)
Male						**Male**					
9- 1	26.5+	30.5	2235	—	510	16- 5	30.5+	33.5	1850	Mat.	473
9-23	30.5+	42.5	1475	Mat.	478	18- 1	31.5+	45.5	1360	Mat.	431
9-75	34.5+	41.5	2150	Mat.	491	18- 3	40.5+	45.5	1750	Mat.	463
13-16	28.5+	34.5	2010	Mat.	479	18-49	40.5+	41.5	880	Mat.	444
15- 8	35.5+	39.5	1570	Mat.	438						
Female						**Female**					
1-16	33.5+	52.5	—	Mat.	378	15-33	46.5+	57.5	12	Rest.	358
5-N3	22.5+	38.5	1+	Preg.	340	15-37	29.5+	35.5	8	Lact.	339
7- 2	22.5+	26.5	13	Preg.	335	16- 8	47.5+	62.5	—	Rest.	363
7- 4	22.5+	32.5	9	Preg.	354	16-19	38.5+	43.5	16	Lact.	353
9- 3	34.5+	38.5	—	Rest.	360	17-20	33.5+	38.5	5	Rest.	368
9-38	35.5+	38.5	—	Rest.	364	17-41	35.5+	47.5	7	Lact.	353
9-47	29.5+	45.5	—	Lact.	381	20- 7	25.5+	36.5	—	—	375
9-55	29.5+	34.5	—	Rest.	368	22- 2	30.5+	55.5	13	Rest.	381
12- 4	33.5+	48.5	7	Mat.	354	22- 7	34.5+	43.5	14	Rest.	382
12-11	32.5+	43.5	10	Lact.	376	22- 9	40.5+	44.5	9	Rest.	380
12-18	22.5+	37.5	12	Rest.	368	23- 8	32.5+	47.5	14	Rest.	363
13-10	42.5+	42.5	13	Lact.	381	24-12	37.5+	45.5	8	Rest.	365
15- 2	38.5+	42.5	6	Rest.	350	24-14	38.5+	50.5	13	Lact.	382
15- 4	35.5+	55.5	4+	Rest.	382	24-19	41.5+	46.5	6	Rest.	377
15- 5	40.5+	47.5	10	Rest.	352	24-24	24.5+	35.5	15	Lact.	372
15-13	42.5+	51.5	8	Rest.	355	25- 3	37.5+	39.5	17	Rest.	—
15-18	22.5+	25.5	10	Rest.	371	25-30	38.5+	45.5	12	Rest.	352
						26-12	34.5+	48.5	12	Lact.	348

* Weight of one testis in gram or number of corpora in ovaries (Data from Kasuya and Marsh (in press) and Marsh and Kasuya (in press)).

Abbreviations: B.L.: body length; Mat.: mature; Preg: pregnant; Rest.: resting; Lact.: lactating.

3. *Closed pulp cavity* Dentinal growth layers discontinuous in a longitudinally-sectioned tooth. The wall of the pulp cavity entirely covered by a thin uniform layer of stainable dentine. The number of cemental layers equal to or greater than the number of dentinal layers irrespective of where the dentinal layers counted.

A closing pulp cavity may occur in males over 21.5-years old and in females over 24.5-years old, and the closed pulp cavity in males over 31.5-years old and in females over 24.5-years old (Table 2). At ages between 20 and 45 years, the proportion of closing or closed pulp cavities is higher in males than in females suggesting that dentine deposition tends to cease earlier in males. About 25 to 50% of females over the age of 40 years still have an open pulp cavity (Fig. 6).

Figure 7 documents the changes in the (maximum) diameter of the pulp cavity that occur with increasing age. The diameter of the pulp cavity tends to be greatest at the proximal end in animals less than a year old and in the middle region in older whales. There is no sexual dimorphism in this character. The diameter of the pulp cavity decreases from about 10 mm for whales less than two-
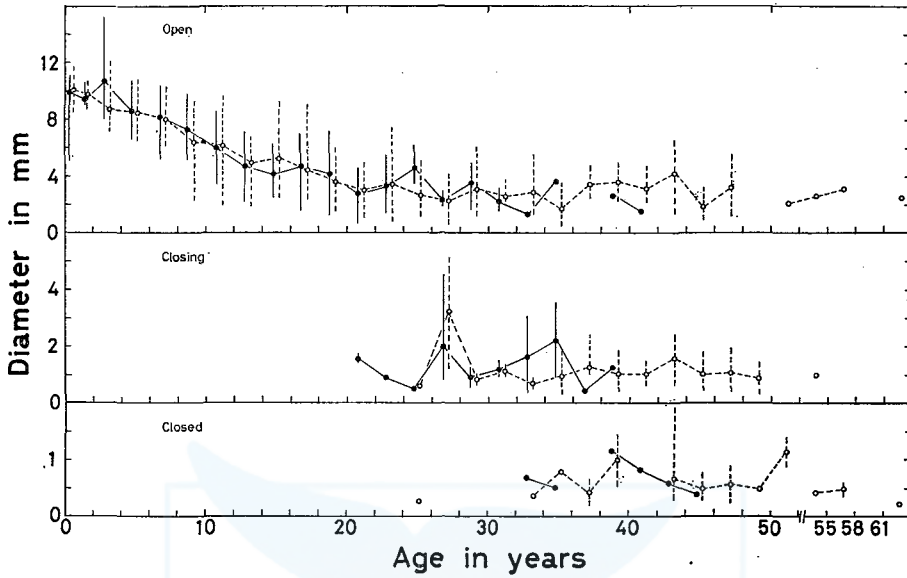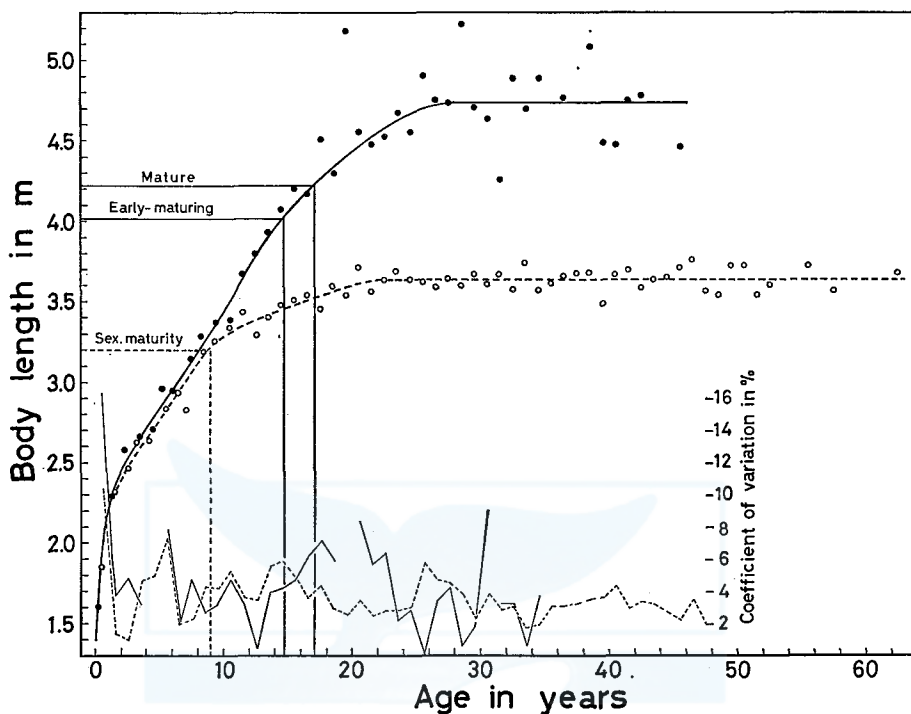
Fig. 7. The mean and range of the diameter of the pulp cavity in *G. macrorhynchus*. Open circles and dotted line represent females, and closed circles and solid line males.
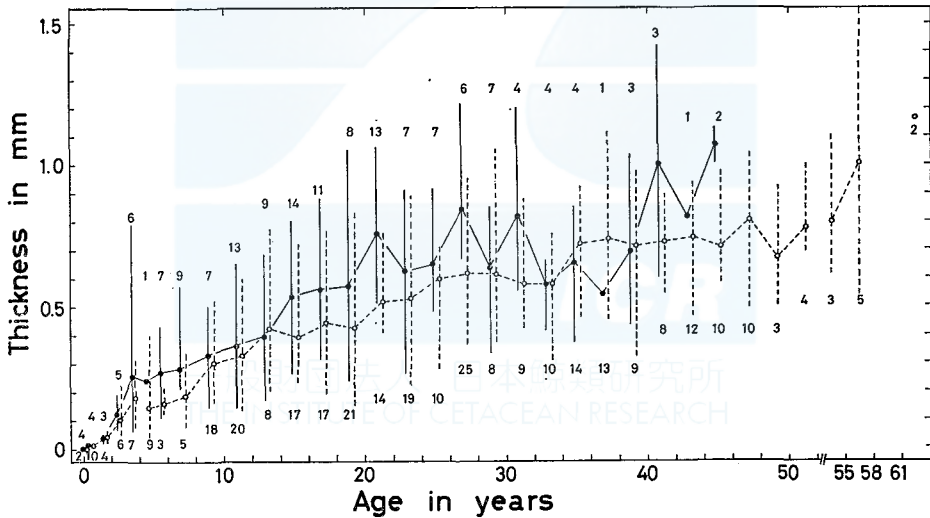
Fig. 8. Thickness of cementum in *G. macrorhynchus* showing means, ranges, and sample sizes. Open circles and dotted line represent females and closed circles and solid line males.

years old to about 3 mm in whales over 20-years old when the cavity starts to close. " Closing " pulp cavities tend to have a relatively constant mean diameter of about 1 mm while the mean diameter of a " closed " pulp cavity ranges from 0.5 to
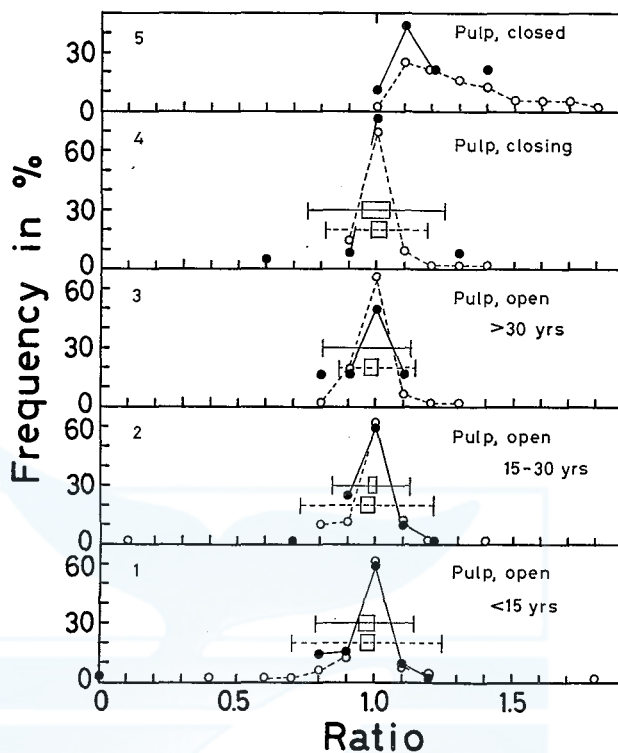
Fig. 9. Ratio of the number of cemental growth layers to the number of dentinal growth layers in *G. macrorhynchus*. 95% confidence interval for the mean (box) and 2×SD range (bar) are indicated on each side of the mean. Open circles and dotted line indicate females, and closed circles and solid line males. 1: 68 males and 61 females below 15 years of age. 2: 53 males and 121 females between 15 and 30 years of age. 3: six males and 45 females over 30 years of age. 4: 22 males (20–40 years) and 46 females (25–52 years). 5: nine males (30–45 years) and 32 females (25–63 years).

1.0 mm and shows no decline with age. These observations are consistent with dentine being deposited only along limited parts of the pulp cavity wall in the " closing " stage and deposition ceasing in the " closed " stage.

Cemental growth layers
Figure 8 shows the maximum cementum thickness plotted against age. Cementum is absent from the teeth of very young postnatal whales. The largest individual without cementum was a male 154 cm long and aged about 1.5 months (age estimated from body length). The smallest individual with a cemental layer was a 163 cm long female (estimated from its length to be two or three-months old). Seven whales less than 200 cm long had tooth cementum. Therefore, we conclude that the deposition of cemental layers starts in *G. macrorhynchus* at a few months of age. Cemental growth is rapid between two and four years of age (Fig.

8). After that the thickness increases at a lower rate, but continues throughout life. After two years of age, males tend to have thicker cementum than females (Fig. 8).

Although the cemental growth layers are much narrower than the dentinal growth layers, the accessory layers are less conspicuous and we consider that the readability of both tissues is about the same (compare figures in Plates I, II, and III). When reading the cemental growth layers it is important to remember that (1) the first or second layer is usually limited to the distal portion of a tooth and (2) in older whales the later layers are usually very thin or absent in the distal part of the tooth. Therefore a whole set of cemental growth layers of an old individual cannot be seen in one cross section of the tooth. It is necessary to read the layers from the inner distal layers to the outer proximal layers as in *Berardius bairdii* (Kasuya, 1977).

Figure 9 shows the number of cemental growth layers expressed as a proportion of the number of dentinal layers. In young whales there is a tendency to underestimate the number of cemental growth layers compared with the number of dentinal growth layers.

For most whales with an open or closing pulp cavity, the counts of dentinal and cemental growth layers were very close. The mean difference from parity of the ratio of cemental layer count: dentinal layer count was only 3.4%, even though there were some exceptional individuals in which the ratio was as high as 1.8 (Fig. 9). We therefore conclude that the deposition of cemental layers is also annual.

Even though we have not otherwise calibrated the cemental layer deposition rate, we consider that cemental layers continue to be deposited after dentine deposition has ceased, for the following reasons. (1) The age at which dentine deposition ceases is very variable and the cessation occurs concomitant with redution of pulp cavity after the transitional " closing " stage. Thus there is no evidence to suspect that cessation is caused by a physiological change which would also affect cementum deposition. (2) The thickness of cemental growth layers decreases constantly throughout life with no indications of an abrupt decline. (3) The technique of reading cemental growth layers was repeatedly standardized by checking young teeth.

Errors in age determination

Errors due to the position of the teeth used for age determination: Hui (1980) reported that in *Tursiops truncatus* the deposition of dentinal growth layers ceases earlier in teeth near the anterior and posterior ends of the row than in the other teeth. In order to test whether this was also true in *G. macrorhynchus*, we counted the growth layers in a series of teeth from five jaws from three whales. Each of the growth layer counts shown in Table 3 is the middle value of three repeat counts. Even though the pulp cavities of all the teeth of the youngest whale (No. 17–7, estimated age 19.5 years) were open, the dentinal growth layer counts of the teeth at the ends of the row were significantly less than those of the other teeth probably because the posterior teeth were smaller and tended to have irregular growth layers. In con-

TABLE 3. COMPARISON OF GROWTH LAYER COUNTS OF SEVERAL
TEETH FROM THE SAME WHALE

| Sample no. | 17-7 | | | 23-5 | | | 18-3 | | |
| BL, Sex | 437 cm, male | | | 366 cm, female | | | 463 cm, male | | |
	C	D	S	C	D	S	C	D	S
Upper teeth (numbered from anterior to posterior)									
1	20	13	11				44	20	11
2	20	20	11				47	32+	11
3	18	20	13				44	31	17
4	17	19	13				44+	27+	7+
5	17	17	9				45+	28+	12+
6	19	19	11				45+	22+	13+
7	19	16	11				45+	19+	—
Lower teeth (numbered from anterior to posterior)									
1	21	17	11	29	30	12	46	32+	12+
2	20	20	9	30	29	13	46	34+	15+
3	19	20	14	29	30	9	46	41	13
4	20	20	13	29	30	7	47	41	15
5	21	20	13	28	31	8	46	35	14
6	20	20	11	30	30	9	48	46	13
7	20	19	12	30	31	9	46	40+	13+
8	19	17	12	25	28+	10+	42	22+	9+
9	19	17	14	—	—	—	—	—	—
10	20	15+	—	—	—	—	—	—	—

Code: C: No. of cemental layers; D: No. of dentinal layers; S: Age (no. of layers) when secondary
dentine first deposited; +: Neonatal line or first cemental layer lost by abrasion; BL: Body
length.

trast, similar differences were not observed in the 29.5-year old female (No. 23–5).
All the teeth of the oldest animal (No. 18–3, 45.5 years) had closed pulp cavities
with the exception of the 6th tooth of the lower jaw which had a " closing " pulp
cavity.   Dentine probably ceased to be deposited in this animal when it had laid
down between 36 and 46 dentinal layers.   However, only 20 dentinal layers were
counted in the anterior teeth.

In contrast, no significant differences were observed between the cemental
growth layer counts of different teeth from the same whale except for the two
smallest teeth of No. 18–3 (Table 3).

These results suggest that errors in age determination due to tooth position
will not occur if the largest tooth near the center of the row is used.

Calibration errors: Errors can occur when the growth layer count is converted into
absolute age.   The age of *G. macrorhynchus* older than 10 years was expressed as
the nearest n minus 0.5 years where n was the number of stainable layers counted
(Any incomplete stainable layers in the first or last cycle were regarded as complete
and unstainable layers were ignored).   As each complete stainable or unstainable
layer represents about six months, the true age of an individual with n stainable
layers is between $n-1.5$ and $n+0.5$ years *i.e.* a mximum error of ±1.0 year.   For

TABLE 4. INDEX OF ERROR IN AGE ESTIMATION (I, %): DIFFERENCE BETWEEN
THE MIDDLE COUNT AND ITS CLOSEST COUNT IN THREE READINGS OF
THE SAME TOOTH EXPRESSED AS PERCENTAGE
OF THE MIDDLE COUNT

Error (I)	Age (yr) and Tissue used[1]			
	0–15 (D)	15–30 (D)	>30 (D)	>30 (C)
Males				
<−5.0	1.2	4.5	0.0	0.0
−5.0~−2.5	0.0	7.6	7.1	0.0
−2.5~+2.5	95.1	87.9	85.8	55.6
+2.5~+5.0	2.5	0.0	0.0	44.4
≥+5.0	1.2	0.0	7.1	0
Total, %	100.0	100.0	100.0	100.0
No. of whales	81	66	14	9
Mean	+0.07	−0.52	+0.27	−1.97
SD	1.22	1.57	1.93	2.04
Females				
<−5.0	1.9	3.1[2]	3.4	0.0
−5.0~−2.5	0.0	6.2	5.7	6.5
−2.5~+2.5	97.2	80.6	78.3	80.6
+2.5~+5.0	0.0	7.0	11.5	9.7
≥+5.0	0.9	3.1	1.1	3.2
Total, %	100.0	100.0	100.0	100.0
No. of whales	107	129	87	31
Mean	−0.10	+0.10	+0.02	+0.60
SD	1.38	2.18	2.24	1.88

[1] Age based on counts of growth layers in dentine (D) (teeth with open or closing pulp cavities) or cementum (C) (teeth with closed pulp cavities).

[2] One reading of cemental layer included.

G. macrorhynchus less than 10 years of age, the number of growth layers was counted to the nearest 0.25 deposition cycle by estimating the thickness of the first and last incomplete layers. The maximum error of this is 0.5 cycle (=year).

Counting errors: Since three repeat counts were done by the same reader for both cementum and dentine with the middle value considered the best, the index of error (I, %) is calculated by the following formula:

$$I = \frac{C-M}{M} \cdot 100$$

where M indicates the middle reading and C the reading closest to the middle reading. The result is shown in Table 4 arranged by sex, age, and tissue type. The standard deviation of the index or error increases with the age of animals from less than 1.4% to over 2.2%. The error expected for repeat counts done by the same person has a standard deviation of about 2%, giving a 95% confidence range of about 2%×2=4% of the middle reading.

If the errors due to calibration and counting are added together, the 95%
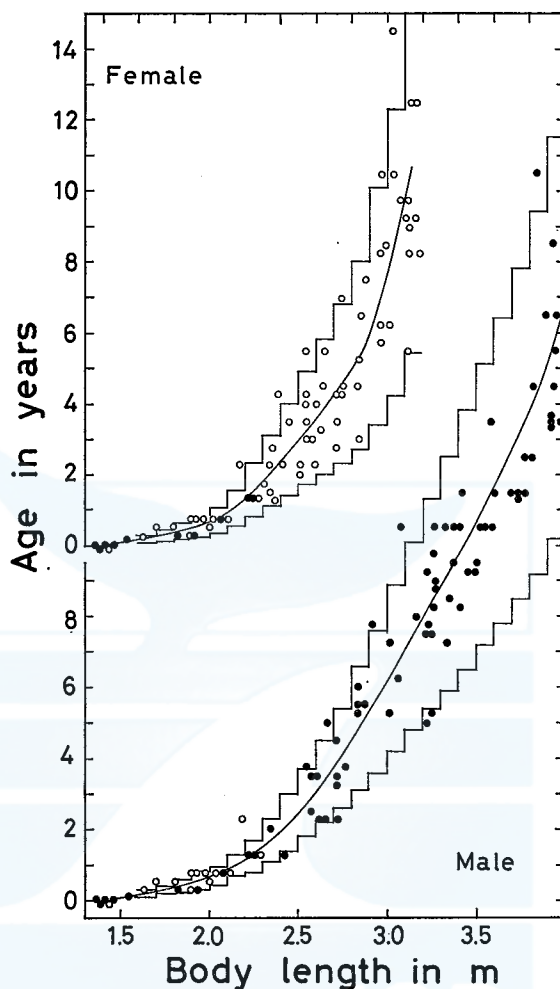
Fig. 10. Conversion of body length into age in *G. macrorhynchus*. Means and 95% confidence intervals are indicated. Open circles represent females and closed circles males.

confidence range for the age estimates at ages 10, 20, 40 and 60 years are estimated to be ±0.9, ±1.8, ±2.6, ±3.4 years respectively. The confidence range for the youngest ages may be slightly narrower than indicated, because the value of *I* tends to be overestimated in this instance.

Conversion of body length into age
The ages of juveniles from which teeth for age determination were not available were estimated from their body lengths as follows. For whales in each 10 cm size-class below 400 cm (males) and 320 cm (females), the mean and coefficient of variation of the ages were calculated. (For whales less than 230 cm long, data for

both sexes were combined). As these mean ages fluctuated due to sampling error they were smoothed by eye as in Fig. 10. For females, the coefficients of variation were nearly constant and had a mean of 0.234. In the male, the coefficients of variation tended to decrease with increasing age (because males tend to be larger) and had a mean of 0.182. The 95% confidence interval of the age corresponding to each size class was calculated (assuming that age was normally distributed for each size class and that the coefficient of variation was constant) as:

(smoothed age)±(smoothed age)×(coefficient of variation)×2

The results are shown as squares in Fig. 10. In females and males less than 330 cm long, the confidence interval approximately coincides with the range of observed values. In larger males the observed range tends to be smaller than the confidence interval, probably because the coefficient of variation was actually decreasing not constant as assumed.

Using this technique it is possible to estimate age within two years for females below 280 cm (mean converted age about 5 years) or for males below 320 cm (mean age about 8 years).

GROWTH CURVE AND BODY WEIGHT

Body length frequencies

The body length frequencies in Fig. 11 are based on the data from 18 schools (Schools 7 through 24). The frequencies are biased, because the catch of a driving fishery may under-represent the juveniles in the population (see Kasuya and Marsh, in press) and because the whales below length 320 cm are missing from one large school (School 9) (see Kasuya and Marsh, loc. cit.).

The largest of the 449 females was 405 cm long. The next longest females were two animals of 400 cm. The adult female length frequency has a single mode at about 360 cm (Fig. 11).

The maximum male body length measured in the present study was 580 cm (No. 9–171), which was followed by much smaller males of 525 and 520 cm. The largest individual, which was measured by Ms C. Goebel, had testes weighing 1.7 and 1.8 kg but no other biological data were collected. We consider that this individual was exceptional among the 201 males examined and may have belonged to the larger of the two types of pilot whale recently recorded from Ayukawa*, and that the maximum body size expected for males of the form usually taken off central Japan will be 525 cm. The male length frequency is more diffuse than

* Since completing this study, Miyazaki and Kasuya (unpublished) have observed two types of pilot whales off Ayukawa (38°20′N) on the Pacific coast of northern Japan in November. This is near the northern boundary of the range of *G. macrorhynchus* at this time of year. Both types have skull feature characteristic of *G. macrorhynchus* as described by Bree (1971). The smaller type is identical to those taken off central Japan and studied in this paper. The other type is possibly a boreal form. It is from one to two meters larger, and has more pronounced saddle mark. The forehead of the adult male is roundish rather than square as in the smaller type. The two forms are presumably geographical races corresponding to those reported by Polisini (1980) from the eastern North Pacific.
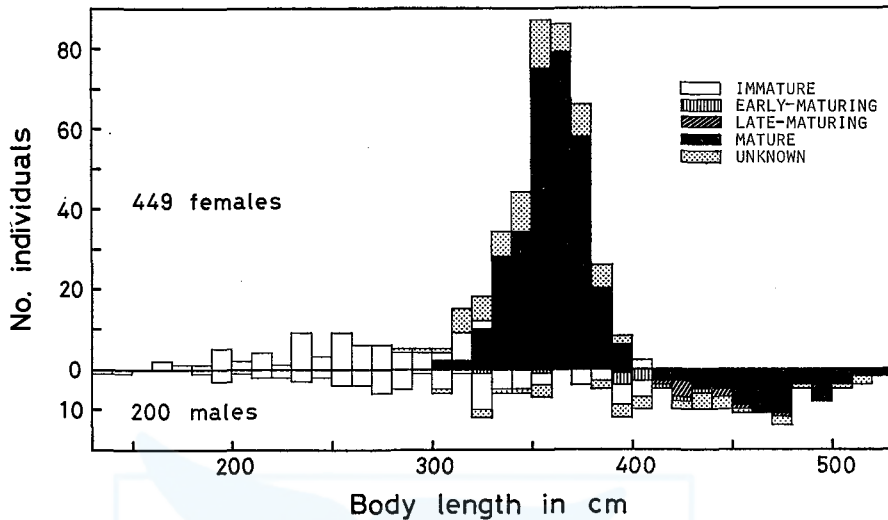
Fig. 11. Frequency histogram of body lengths and growth stages in *G. macror-hynchus*. All data from schools 7 to 24 are included. In school 9, individuals below 320 cm are underrepresented. " Early-maturing " stage represent males with testes where more than 0 but less than 50% of tubules are mature, " late-maturing " those males with testes where from 50% to 100% (exclusive) of tubules are mature, and " mature " those males whose seminiferous tubules are all mature (equivalent to social maturity) (Kasuya and Marsh, in press). For further description of the stages of sexual maturity see Kasuya and Marsh (in press).

that of the female with a possible adult mode at about 470 cm body length. Both the maximum and modal lengths of males are about 110 to 120 cm larger than the corresponding figures for females.

Growth curve

In Fig. 12, the mean body length of each age group is plotted against the corresponding age for each sex. The mean growth curve between the mean birth length of 139.5 cm (Kasuya and Marsh, in press) and asymptotic length has been drawn by eye for each sex as an indication of the general growth trend. The coefficients of variation of body length for each age group for each sex are shown at the bottom. Age-length keys for the samples have been included as Appendices 1 and 2.

The mean growth curves are divided into the four phases; (1) a phase of rapid neonatal growth, (2) a juvenile phase of less rapid but almost linear growth, (3) growth between puberty and mean asymptotic length, and (4) a phase of no increase in body length.

The first phase, in both sexes, is similar and seems to end at about 1.25 years of age. The mean growth in this period (mean length at 1.25 years (230 cm)—mean length at birth (139.5 cm)=90.5 cm) represents a mean annual growth rate of 72.4 cm, slightly smaller than that in the first year after birth (225 cm—

Fig. 12. Mean growth curve of *G. macrorhynchus*. Open circles and dotted line represent females, and closed circles and solid line males. The mean ages and body lengths at the onset of sexual maturity (females), of the " early-maturing " stage (male), and of the ' mature " stage (male) are indicated. Curves between birth and asymptotic length are fitted by eye. For description of the stages of sexual maturity see Fig. 11.

139.5 cm=85.5 cm or 62.1% of the neonatal length). This phase may last slightly longer in males because by the age of 2.5 years, males average 254 cm long, 6 cm longer than females.

The second growth phase lasts, in females, until about the mean age of first ovulation (9.0 years, see Kasuya and Marsh, in press). During this phase the body lengths of females tend to be several centimeters smaller than those of males of similar age. The mean growth rate for females between 2.5 and 9 years is 11.4 cm per year ((322−248) cm/6.5 years). In males, this second growth phase lasts slightly longer until about 10 years of age but the mean growth rate is fairly similar, about 12 cm per year ((344−254) cm/7.5 years).

The third growth phase ends, in females, at about 22 years when the growth curve reaches the mean asymptotic length. The mean growth rate for females during this phase is (364−322) cm/(22−9) years=3.2 cm per year. In males, the corresponding growth phase begins at about 10 years of age with slightly accelerated prepubertal growth followed by a gradual decrease in the growth rate until the growth curve reaches the asymptote at about 27 years. Under these circum-
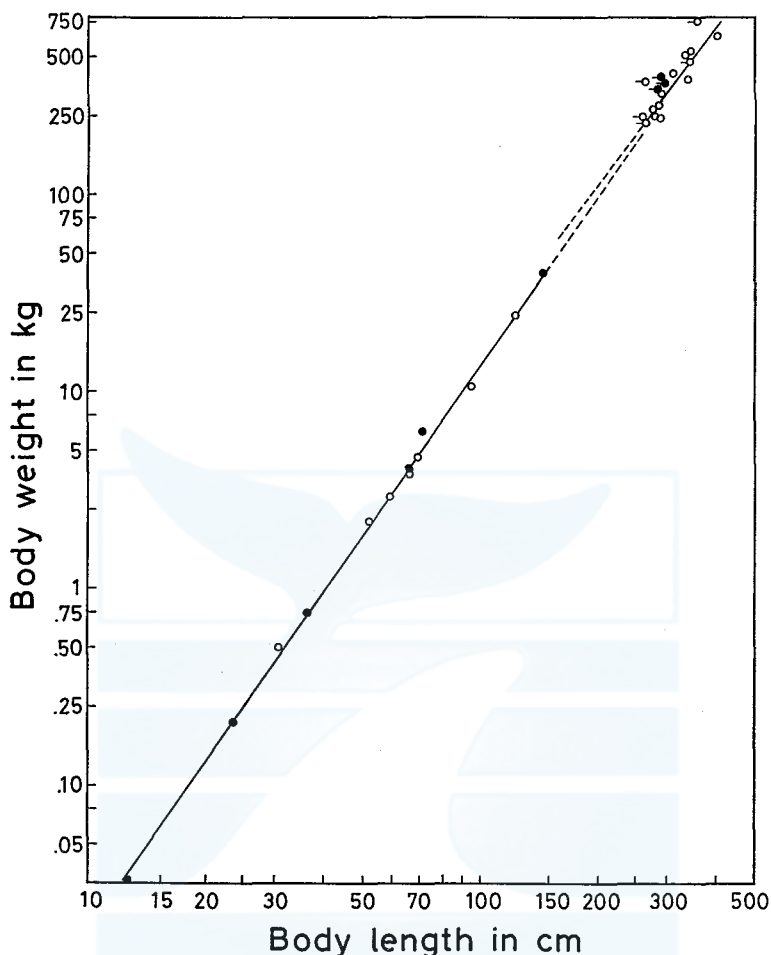
Fig. 13. Relationship between body length and body weight in *G. macrorhynchus* plotted on a double logarithmic scale. Open circles indicate females, closed circles males, and circle with bar individuals which died in an aquarium.

stances, calculation of a mean growth rate over this entire period is not meaningful. The mean growth rate for males between ten years and fourteen years of age is (397−344) cm/4 years=13.3 cm per year while that of males between 23 years and 27 years of age is (473.5−461) cm/4 years=3.1 cm/year.

The last phase starts at 22 years in females and at 27 years in males, when all individuals stop growing. Presumably some individuals will cease growing at a younger age and the proportion of individuals ceasing growth will increase with age until the ages mentioned above. The " mean asymptotic lengths " (in the sense usually accepted for cetaceans) for *G. macrorhynchus* are as follows:

Sex	Number of samples	Mean asymptotic length	95% confidence interval of mean
Female	181	364.0 cm	±1.9 cm
Male	35	473.5 cm	±9.1 cm

These figures are close to the modal lengths in the body length frequencies.

TABLE 5. BODY WEIGHT OF *G. MACRORHYNCHUS*

No.	Body length (cm)	Body weight (kg)	Sex	Remarks		
1	12.5	0.0328	♂	Fetus		
2	23.3	0.2112	♂	,,		
3	30.6	0.500	♀	,,		
4	36.5	0.750	♂	,,		
5	52.0	2.20	♀	,,		
6	59.5	2.94	♀	,,		
7	65.5	3.97	♀	,,		
8	66.5	4.15	♂	,,		
9	69.5	4.75	♀	,,		
10	72.0	6.40	♂	,,		
11	95.0	10.70	♀	,,		
12	123	24.50	♀	,,		
13	144	40.20	♂	,,		
14	275	275	♀	At capture		
15	275	250	♀	,,		
16	285	285	♀	,,		
17	286	245	♀	,,		
18	290	325	♀	,,		
19	310	410	♀	,,		
20	330	520	♀	,,		
21	335	380	♀	,,		
22	340	530	♀	,,		
23	400	650	♀	,,		
24	260	255	♀	At death after 547 days in captivity		
25	263	237.19	♀	,,	270	,,
26	265	377.90	♀	,,	225	,,
27	281	348	♂	,,	311	,,
28	290	406	♂	,,	362	,,
29	291	379.22	♂	,,	192	,,
30	335	484.60	♀	,,	11	,,
31	355	751.90	♀	,,	228	,,

Body weight

Table 5 shows the intact body weights of 13 fetuses and 18 postnatal individuals. As shown in Fig. 13, whales weighed at death after being kept in the museum tend to be heavier than those measured at capture. We considered this to be the result of over-feeding and/or lack of exercise, and excluded those data from the following analyses.

Figure 13 shows the relationship between body length (L, cm) and body

TABLE 6. BODY WEIGHT OF *G. MACRORHYNCHUS* AT SEVERAL GROWTH STAGES
CALCULATED FROM BODY LENGTH-BODY WEIGHT RELATIONSHIP

Growth stage and sex		Mean body length (cm)	Body weight (kg)
Birth	(♀♂)	139.5	37.0
Sexual maturity	(♀)	315.6	391
Asymptotic length	(♀)	364.7	593
Early-maturing stage*	(♂)	401.1	781
Mature stage*	(♂)	422.1	904
Asymptotic length	(♂)	473.5	1260

* For definitions see Fig. 11, and for detailed descriptions of these stages see Kasuya and Marsh (in press).

weight (W, kg) of specimens of *G. macrorhynchus* plotted on logarithmic scales. The least squares regression of 10 postnatal females is,

$$\log W = 2.6642 \times \log L + \log (8.403 \times 10^{-5})$$
$$275 \leq L \leq 400 \qquad r = 0.93$$

The similar relationship of 13 fetuses of both sexes is,

$$\log W = 2.8772 \times \log L + \log (2.432 \times 10^{-5})$$
$$12.5 \leq L \leq 144 \qquad r = 0.99$$

The gradients of these equations are not significantly different (T-test, $P > 0.3$). Although a larger sample may provide evidence of significantly different gradients for the fetal and postnatal stages, we consider that a single equation fitted to fetal and postnatal individuals is more appropriate with the present sample size. This equation is,

$$\log W = 2.8873 \times \log L + \log (2.377 \times 10^{-5})$$
$$12.5 \leq L \leq 400 \qquad r = 0.85$$

This equation does not include postnatal males, which as adults develop a bulbous melon larger than that of females (Yonekura, Matsui, and Kasuya, 1980). Yonekura *et al* (1980) described the changes in shape which occur in *G. macrorhynchus* from a slender head with a pointed rostrum during early postnatal life to the moderately bulbous head of adult females or subadult males. This change does not significantly affect the body length-body weight relationship mentioned above. Therefore, we suspect that the above equation will approximately describe the body length-body weight relationship throughout life for both sexes and have accordingly used it in calculating the body weights shown in Table 6.

DISCUSSION

Our technique of determining the age of *G. macrohynchus* by counting dentinal and/or cemental growth layers in haematoxylin-stained *longitudinal* tooth sections proved very satisfactory. We were able to age all 543 animals in our sample using this

technique.

In contrast Perrin and Myrick (1980, p. 19) recommended that cemental layers in *G. macrorhynchus* should be counted in transverse tooth sections. Even though they appreciated that it was possible to lose the first cemental layer using this technique, Perrin and Myrick (1980) considered that transverse sections were superior to longitudinal sections because they were both easier to prepare and to read.

However, our study indicates that, even when the position of the section was carefully selected, more than one cemental layer (either the earliest or latest layers) could be missed from the transverse section of a relatively old tooth (Plates I to III). We consider that the cemental layers are easier to read in longitudinal sections. A wider range of tissue can be scanned in longitudinal sections thus enabling us to eliminate the accessory layers from the count. The variability of repeated cemental layer counts was similar to that of dentinal layers. The difficulty of preparation was minimal by using the method we have developed. In addition, if transverse sections are used for counting dentinal layers, the count is often difficult in older teeth in which secondary dentine is being deposited (Perrin and Myrick, 1980). However, using longitudinal sections enabled us to observe whole pulp cavity and to choose the most readable portion of the tooth (Plates II and III).

Our result indicated that the stainable growth layers in dentine was formed in spring to fall and unstainable dentine in winter to spring, although the time of alternation of dentinal layers was not precisely defined. This seasonality of dentine deposition in *G. macrorhynchus* coincides with that of *Tursiops truncatus* studied by Sergeant (1959) and *Pontopori blainvillei* studied by Kasuya and Brownell (1979), but differs from that of *Stenella attenuata* in the western North Pacific reported by Kasuya (1976). The seasonality of deposition of haematoxylin stainable dentine and/or correspondence of the stainability with optical density can be different between species.

Ogden, Lee and Conlogue (Ms.) listed body lengths of 46 male and 108 female *G. macrorhynchus* stranded on the east coast of the North America. In males, the highest body length frequencies were in the ranges 470 to 480 cm (three individuals) and 480 to 489 cm (three individuals). The largest male had a body length of 535 cm, while the next largest was 525 cm long. In females, the highest body length frequency was in the 360 to 369 cm range (18 individuals). The largest female was 397 cm long and the next largest 392 cm long. These figures are identical to our results from central Japanese coastal waters. Alagarswami, Bensam, Rajapandian and Fernando (1973) reported the body length frequency of 77 whales in a mass stranding of 147 *G. macrorhynchus* in the Gulf of Manar on the southeast coast of India. The identification of the species was based on the skull, teeth and flipper length. The body lengths ranged from 220 to 575 cm (sex was not given). There were two modes in the length frequency, one at 375 to 425 cm, the other at 525 to 550 cm. We suspect that the smaller and larger modes may correspond to the asymptotic lengths of females and males respectively. Be-

cause these body lengths are larger than those of known *G. macrorhynchus* but almost identical with those of *G. melaena* as reported by Sergeant (1962), we initially suspected that the method of measuring body length (not detailed in the report) differed from ours.   However Alagarswami (pers. comm.) has since confirmed that the body lengths were measured on a straight line from the tip of upper jaw to the notch of flukes.   Thus there exists a possibility that the body length of *G. macrorhynchus* in the Indian Ocean may be intermediate between the two geographical forms in the western North Pacific (see footnote on page 75).

Kasuya (1972, 1976) showed that the increase in body length in the first year after birth is between 55 and 65% of neonatal length in several odontoceti *i.e.*, *Stenella coeruleoalba*, 64%; *S. attenuata*, 60%; *Tursiops truncatus*, 55%.   Collet (1981) obtained a corresponding value of 61.3% for *Delphinus delphis*.   Thus the value we estimated for *G. macrorhynchus*, 61.2%, is in good agreement with the results for other species.

Perrin, Coe, and Zweifel (1976) found for several odontocetes the following relationship between body length at birth (X, cm) and the difference between the fetal growth rate during the linear phase and the average growth rate during an initial postnatal period equal to the gestation period (Y, cm/month),

$$\log Y = -1.33 + 0.997 \, (\log X)$$

Substituting the appropriate values for *G. macrorhynchus* (*i.e.*, gestation time 452 days, neonatal length 139.5, and fetal growth rate in the linear phase 10.3 cm/month (for values see Kasuya and Marsh, in press), the above equation predicts a body length of 197.4 cm, 452 days after birth.   The corresponding figure, roughly estimated from the growth curve (Fig. 12), is 228 cm.

Ralls, Brownell and Ballou (1980) concluded that males of polygynous cetacean species will have larger body size and higher natural mortality rate compared with the females of the same species.   The result of present study (males growing 1.30 times larger than females and living 17 years shorter) and the polygynous social structure of the the species reported by Kasuya and Marsh (in press) agree with their conclusion.

Sergeant (1962) obtained for *G. melaena* the following body length (L, cm)-body weight (W, kg) relationship,

$$W = 0.000025 \, L^{2.895}$$

using fetuses and juveniles below 235 cm in body length.   This relationship is almost identical with the corresponding equation that we have obtained for *G. macrorhynchus*.

ACKNOWLEDGEMENTS

collect the necessary samples. The hunters also provided information on the schools which they had driven.

The Taiji Whale Museum provided laboratory facilities. Dr N. Miyazaki collected the body-length frequency data for one school. The field study was done with the help of many biologists including Dr R. L. Brownell Jr., Dr S. Ohsumi, Mr K. Kureha, Dr N. Miyazaki, Dr T. Otake, Ms E. Miyahara, Mr S. Shiraga, Dr T. Kajihara, Dr K. Hirose and Dr S. Tanaka. Dr D. E. Sergeant kindly cooperated in the cross-reading of several tooth slides of *G. macrorhynchus*. We thank Ms C. Goebel for her collaboration. This study was initially prepared for the Report of the International Whaling Commission (special issue on cetacean reproduction) as a part of a paper on the life history and reproduction of the species, but it had to be split by the financial difficulties. We wish to express our thanks to the two anonymous referees and editor of the IWC volume for their suggestions and criticism. Dr H. Marsh critically read the manuscript and corrected the English. Their cooperation largely improved this paper.

The histology slides were prepared by Ms M. Oya. Ms T. Shirai, Ms M. Nakagiri, Ms Y. Oka and Ms S. Wada assisted in data analyses, typing and drawing.

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APPENDIX TABLES

APPENDIX TABLE 1. AGE-LENGTH KEY OF *G. MACRORHYNCHUS*, FEMALE

Age		Body length																												No.	Mean	S.D.
n	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40			
0	1	1		1	1	1	4	2																					11	185.45	19.26
1									1	1	3																		3	231.00	3.26
2									1		2	1	2	1	1														8	245.50	15.61
3												1	3	1	1	1													7	262.00	12.07
4												1	2	2	3	1													9	264.00	12.85
5													1	1			1	1	1										5	282.60	20.71
6																	1	1				1							3	294.33	6.01
7															1	1													2	281.50	6.50
8																	1	1	2	3		1							8	317.50	13.81
9																	1	1	4	1	3	2							11	325.27	13.18
10														1			1	1	1	1	3	4	1						11	332.81	17.33
11																				1	3	1	3	1					9	343.33	12.25
12														1					1	2	3	1							4	328.75	11.29
13																			1			1	1	2					5	340.22	18.90
14																		1		1	2	4	1	2	2				12	346.58	20.27
15																				1	1		1	1	1				5	350.00	16.67
16																				1	2	2	3	1	2				9	352.66	12.78
17																				1	3	1	1	1	3				8	345.00	14.73
18																					1	1	4	4	3				13	359.30	10.36
19																					1	2	3	4					10	354.10	8.87
20																							1	2	1	1	1		6	370.66	12.53
21																					1		7	2	2				10	355.60	8.74
22																							5	4	3	1			9	363.55	10.32
23																							2	4	4	1	1		11	369.00	10.15
24																							3	1	1	1			6	364.33	10.97
25																							1		1	1	1		4	363.00	20.59
26														1				1		1		3	3	4	4	2	1		15	359.46	16.74
27																						3	2	1	4				11	363.81	16.23
28																						1	1		2				4	360.25	13.53
29																						2	1	3	1	1			5	367.20	8.42
30																						2		1	2	1			5	360.80	13.80
31																							2		2		1		4	366.50	10.57

Age	n	Mean body length	SD
32	8	358.12	10.79
33	3	373.66	6.34
34	8	357.12	6.75
35	8	360.75	10.75
36	7	365.00	10.92
37	6	367.33	11.79
38	8	367.37	13.04
39	2	348.50	12.50
40	4	367.25	15.78
41	4	369.75	10.70
42	5	359.40	11.72
43	7	363.85	11.30
44	5	365.40	9.62
45	5	371.40	8.21
46	4	375.75	13.32
47	6	356.83	6.84
48	2	354.50	0.50
49	1	373.00	
50	3	373.33	6.94
51	1	355.00	
52	3	361.33	12.39
53	0		
54	0		
55	4	373.25	9.62
56	0		
57	1	358.00	
58	0		
59	0		
60	0		
61	0		
62	2	369.00	6.00

Age: $n \leq$ Age in years $< n+1$. Body length: $10 n \leq$ Body length in cm $\leq 10 n+9$.

SD of this table $= [\sum (x-\bar{x})^2/n]^{0.5}$

APPENDIX TABLE 2.   AGE-LENGTH

Age																						Body
n	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
0	2	2	1			1	1	1														
1										2		1										
2											1		1	2	1							
3													2	1	3							
4															1							
5														1		3		1		2		
6																1		1				
7																	1	2		3	1	
8																			1	2	1	1
9																				3	1	2
10																		1		1	2	1
11																						1
12																						
13																						
14																						
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45																						

Age : n≤Age in years<n+1.   Body length : 10 n≤Body length in cm≤10 n+9.   SD of this table=[∑(x−

KEY OF *G. MACRORHYNCHUS*, MALE

length

35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	No.	Mean	S.D.
																		8	161.62	26.31
																		3	229.00	8.52
																		5	258.00	12.29
																		6	265.50	8.51
																		1	271.00	
																		7	296.00	20.06
																		2	294.00	13.00
																		7	314.28	14.52
																		5	328.00	8.85
1																		7	337.42	10.67
3																		8	339.37	15.91
		1	4															6	366.50	11.91
		1	1															2	379.50	1.50
1				4	1	1												7	393.14	15.18
			1	1	2		1	1										6	406.50	16.89
				1	2			1	2									6	420.00	19.85
				2	1		1	1			1							6	417.16	25.85
					1	2					1	1			1			6	451.33	31.95
				1		1	3			1		1						7	430.00	25.16
																1		1	519.00	
			1							1	1	1		1				5	455.80	37.64
					2		2		2				2					8	447.75	25.66
						1		1	1					1				4	452.75	28.64
									1			2						3	468.33	10.20
							2	1	1	1								5	456.20	12.79
														2				2	490.50	0.50
									1					1				2	474.50	15.50
								1		2	1			1				5	473.60	19.94
																	2	2	522.50	2.50
										2	1	2						5	470.80	8.54
					1				1					1		1		4	463.50	41.65
						1												1	427.00	
												1						2	488.50	15.50
											1	1						2	470.00	3.00
												1						4	489.00	18.31
																		0		
												1						1	477.00	
																		0		
															1			1	509.00	
										1		1						2	448.50	10.50
											1							1	448.00	
										1				1				2	474.50	16.50
												1						1	478.00	
																		0		
																		0		
										1		1						2	447.00	16.00

$\bar{x})^2]^{0.5}$.

EXPLANATION OF PLATES

PLATE I

All scale bars represent 0.1 mm.

FIG. 1. Decalcified and haematoxylin-stained section from a newborn female *G. macrorhynchus* (No. 17–46, 163 cm, 0.25-year old, tooth length 22 mm). N indicates the neonatal line in the dentine, and 2 and 3 the positions enlarged in Figs 2 and 3 (this plate) respectively.

Fig. 2. Higher magnification of position 2 in Fig. 1 (this plate). Arrow indicates neonatal line in dentine, and E, cast of dissolved enamel.

Fig. 3. Higher magnification of the position 3 in Fig. 1 (this plate). Arrow and circle indicate a stainable cemental layer (annual layer).

Fig. 4. Decalcified and stained tooth section of an immature male *G. macrorhynchus* (No. 9–73, 326 cm, 5.25 years old with five annual stainable layers of full thickness and 6th (last) stainable layer of incomplete thickness (circles), tooth length 38.4 mm). N indicates the neonatal line, and 5 through 7 the positions enlarged in Figs 5 through 7 of this plate.

Fig. 5. Higher magnification of position 5 in Fig. 4 (this plate), showing cemental growth layers near the neck of the tooth. Circles and arrow indicate 1st to 4th annual stainable layers.

Fig. 6. Cemental layers at position 6 in Fig. 4 (this plate). The 2nd to 5th annual stainable layers are indicated by circles.

Fig. 7. Cemental layer at position 7 in Fig. 4 (this plate). Circles indicate the 3rd to 6th annual stainable layers.

PLATE II

All scale bars represent 0.1 mm.

Fig. 1. Decalcified and haematoxylin-stained tooth section from a lactating female *G. macrorhynchus* (No. 24–22, 366 cm, 27.5–years old, tooth length 42.8 mm). Dentine is still being deposited along the entire pulp cavity wall. C indicates cementum, E cast of dissolved enamel, N neonatal line in dentine, and the numerals the positions enlarged in Figs 2 through 4 of this plate. The dots indicate the annual stainable layers in dentine.

Fig. 2. Higher magnification of position 2 in Fig. 1 (this plate). Annual growth layers are clearer in ordinary dentine (circles) than in secondary dentine. P indicates predentine.

Fig. 3. Higher magnification of position 3 in Fig. 1 of this plate. Annual growth layers are clear in secondary dentine (circles). P indicates predentine.

Fig. 4. Cemental layers at position 4 in Fig. 1 (this plate). Dots indicate 1st to 28th annual cemental layers.

Fig. 5. Cemental layers at position 5 in Fig. 6. (this plate). Dots indicate 2nd to 36th annual cemental layers.

Fig. 6. Decalcified and stained section of a tooth from a resting female *G. macrorhynchus* (No. 17–36, 35.5–years old, tooth length 39.5 mm). Deposition of dentine is about to cease. C indicates cementum, E cast of decalcified enamel, N neonatal line, 5 the position shown in Fig. 5 of this plate.

PLATE III

All scale bars represent 0.1 mm.

Fig. 1. Higher magnification of pulp of the tooth in PLATE II Fig. 6. P indicates predentine. Deposition of dentine is limited to this portion of the pulp wall.

Fig. 2. Cemental layers at position 2 in Fig. 7 (this plate). Dots indicate 1st to 51th annual growth layers.

Fig. 3. Top of the pulp cavity of tooth in Fig. 7 (this plate). A strongly-stainable uniform thin layer of dentine (S) indicates the cessation of dentine deposition along most of the wall of the pulp cavity, but thin predentine (P) is still visible at the top and an irregular thin unreadable layer of " cellular dentine " (C) is being deposited. Formation of the cellular dentine has started secondarily on the pulp wall.

Fig. 4. Middle portion of the pulp of tooth in Fig. 7 (this plate). The last two dentinal layers merge in the pulp wall cavity which is covered by thin strongly-stainable uniform dentine (S). Secondary deposition of " cellular dentine " (C) is also visible.

Fig. 5. Base of the pulp cavity of tooth in Fig. 7 (this plate). The last readable dentinal growth layer was deposited as indicated by the arrow. " Cellular dentine " (C) is still being deposited.

Fig. 6. Higher magnification of position 6 in Fig. 7 (this plate). Thick " cellular dentine " is being deposited.

Fig. 7. Decalcified and stained section of a tooth of a lactating female *G. macrorhynchus* (No. 24–14, 382 cm, 50.5–years old, tooth length 38.3 mm). There are 39 annual stainable layers in the dentine and 51 in the cementum. C indicates cementum, E cast of dissolved enamel, N neonatal line in dentine, and 2 and 6 the positions shown in Figs 2 and 6 of this plate respectively.

PLATE II   KASUYA AND MATSUI
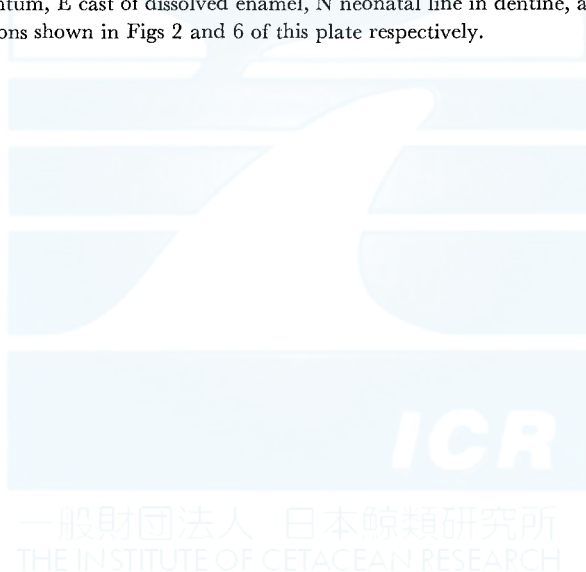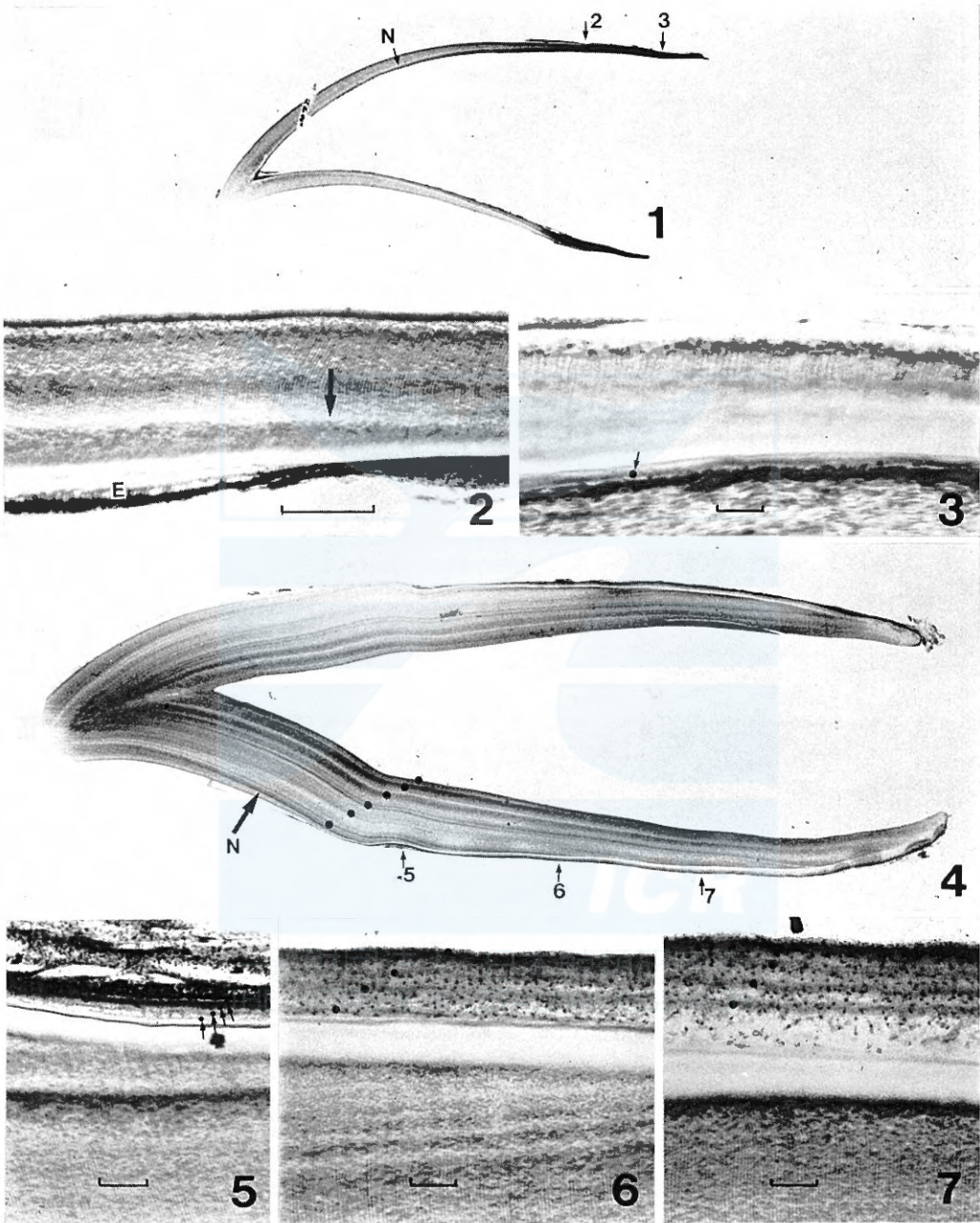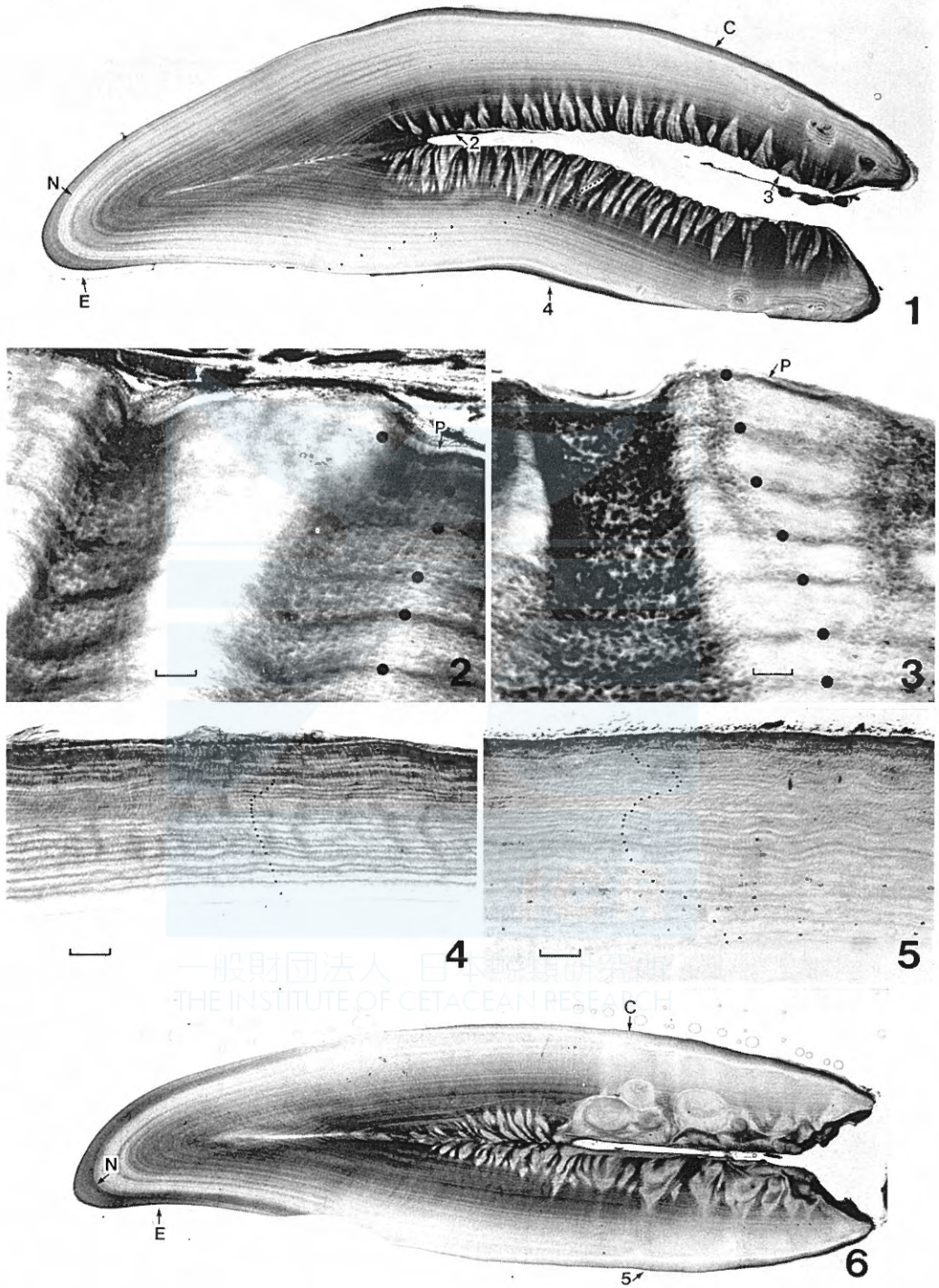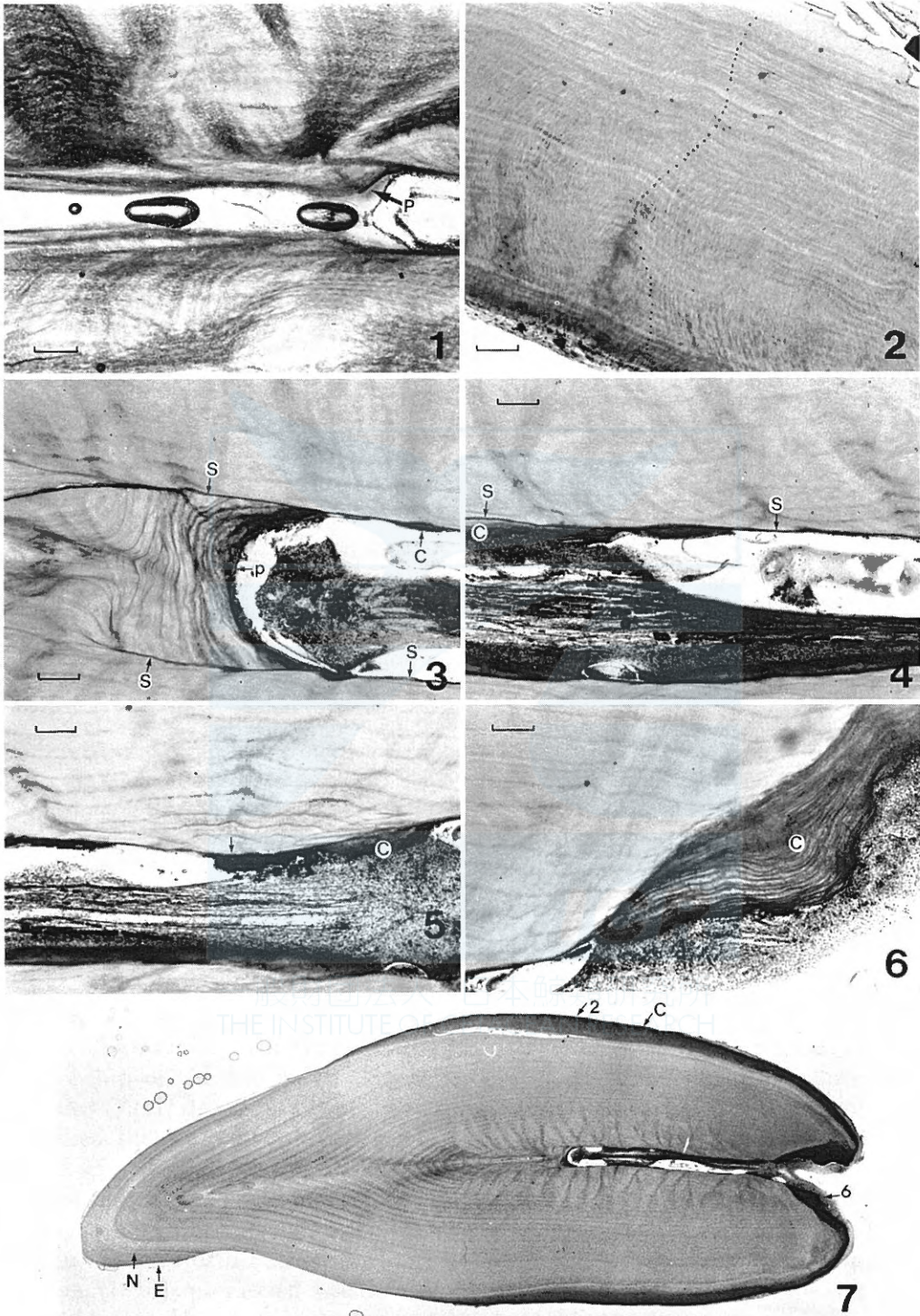
SOME OBSERVATIONS ON THE SCHOOLS OF *DALLI-* AND *TRUEI*-TYPE DALL'S PORPOISES IN THE NORTHWESTERN PACIFIC

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ABSTRACT

During 349 hours of sighting surveys conducted from late June to early August 1979 in the northwestern North Pacific Ocean and the southern Bering Sea, 167 schools of *Phocoenoides dalli* were sighted. Three kinds of schools (*dalli*-type, *truei*-type and mixed schools composed of both types) were observed in the southern areas surveyed while only *dalli*-type schools were seen in the northern areas. School size of *dalli*-type schools was smaller than that of the *truei*-type or mixed schools. *Truei*-type as well as mixed schools tended to occur in warmer waters (above 13°C) than *dalli*-type schools during the second part of the survey. Behavior of animals in mixed schools was not apparently different than in the segregated schools. Mixed schools were composed of all sizes of animals including an adult-calf pair. The relationship between the two color types is discussed.

INTRODUCTION

Phocoenoides dalli (True, 1885) is widely distributed in the cold waters of the northwestern North Pacific (Nishiwaki, 1972; Ohsumi, 1975; Kasuya, 1976; Kasuya, 1978). Two major color types exist but little is known concerning the systematic relationship of the two types. Based on five external morphological differences Andrews (1911) described them as two species: *P. truei* and *P. dalli*. Kuroda (1954) described them as two subspecies. He concluded based upon sighting records of mixed schools of the *truei*-type and the *dalli*-type, and the presence of a *truei*-type fetus in a *dalli*-type pregnant female, that the *truei*-type is a small population (race) evolved in the Japanese waters by a dominant mutation from the *dalli*-type distributed in the North Pacific Ocean, the Okhotsk Sea and Sea of Japan. However Kasuya (1978) questioned whether the fetus in the *dalli*-type female was a *truei*- or *dalli*-type. Houck (1976) observed a mixed school of the two color forms off

northern Honshu, Japan.   Based on the ecological and morphological considerations of the genus, he concluded that *P. dalli* is polymorphic in color pattern with two major color morphs, the *dalli*- and the *truei*-types, and that there are not separate geographical races or subspecies.

From sighting records of *P. dalli* and an analysis of the school structure, Kasuya (1978) concluded that the school formation is to some degree dependent on color pattern and that all the *dalli*-type individuals found off the Pacific coast of Japan may not be from the Japanese coastal population, but that at least some of them, especially those in the schools not containing the *truei*-type, migrate from the offshore population in the northwestern North Pacific and the western Bering Sea or from the Sea of Japan-Okhotsk Sea population.   He considered that interbreeding between the populations would be less frequent than expected on the basis of the apparent coexistence of the two color types.

The discussion above makes it clear that the taxonomic problem of the two color forms of *P. dalli* has not been completely resolved.   This report provides additional information on school composition and distribution for two color types of Dall's porpoises and a discussion on their relationship, including the possibility of interbreeding between the two color types.

METHODS

A Japanese salmon research vessel, the R/V *Hoyomaru No. 67* (size: 299 gross tons; cruising speed: 10 knots), was chartered by the Japan Fisheries Agency for a US-Japan cooperative Dall's porpoise research project.   A marine mammal sighting survey was conducted on board this vessel in the northwestern North Pacific Ocean and the Bering Sea from 29 June to 9 August, 1979.   The cruise track is shown in Fig. 1.   Total observation time was 349 hours.   Observations were made by Miyazaki and Beach from the upper bridge except during night time, heavy rain and heavy fog.   Since the main objectives of this cruise were experimental salmon gillnetting and study of the incidental catch of Dall's porpoises, most of the survey effort was spent during the transits between the coast of Japan and the western Bering Sea.

For each sighting, data were recorded on estimated body size, color type and number of porpoise and surface water temperature.   Estimates of body size were made for Dall's porpoises coming close to the bow of the vessel, within about 20 m. Animals were classified as small (less than 150 cm in body length), medium (150–180 cm) or large (more than 180 cm).   Calves were distinguished by their small size and continued association with a larger animal.

RESULTS

Distribution

During this survey, 655 Dall's porpoises were sighted in 167 schools.   There were 68 schools of the *dalli*-type, 24 schools of the *truei*-type and 7 mixed schools
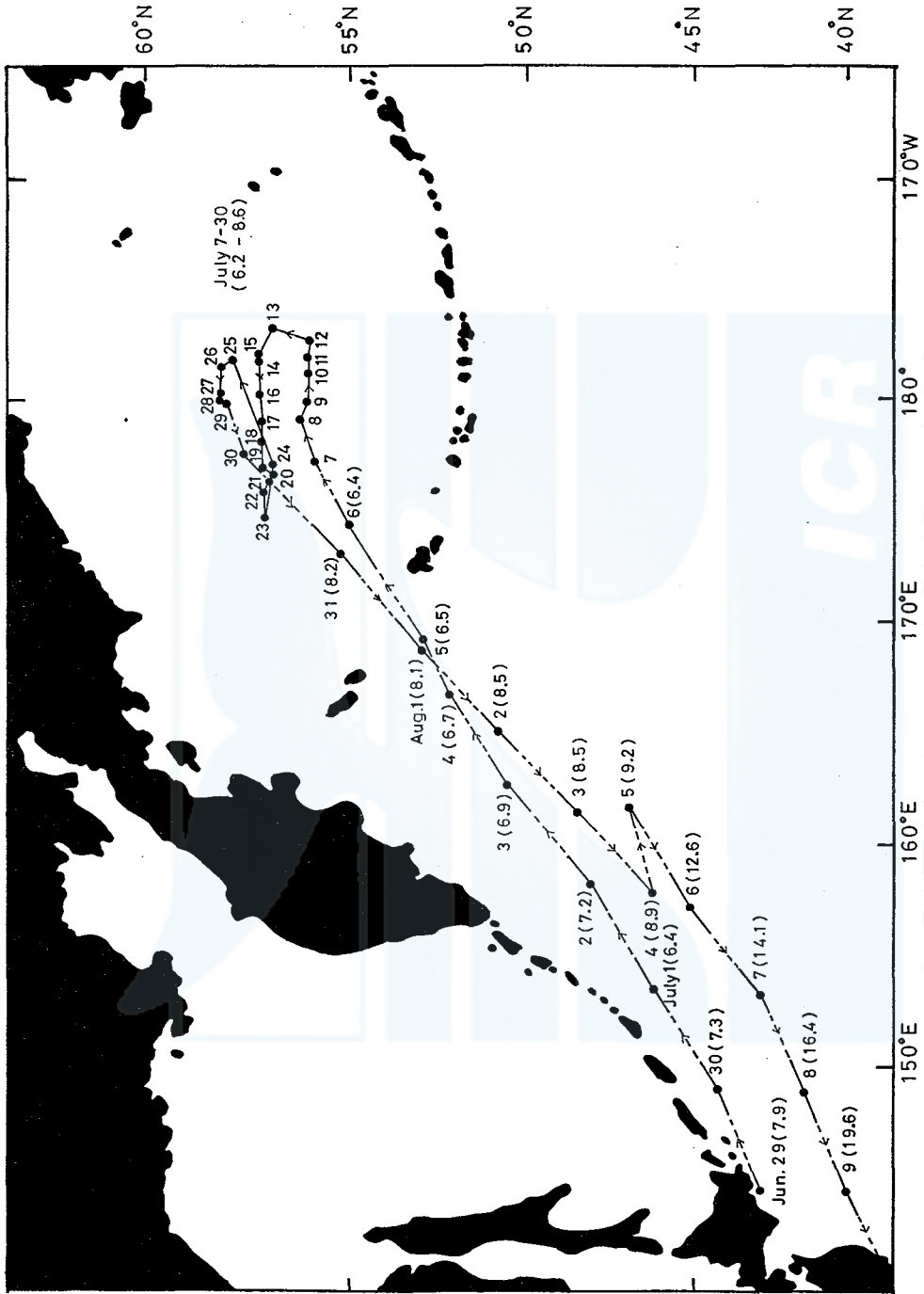
Fig. 1. The cruising course of the R/V *67th-Hoyomaru* during 29 June and 9 August, 1979. Numbers indicate dates, closed circles, noon position; solid lines, sighting course; and broken lines, course passed in darkness. Figures in parentheses indicate the surface water temperatures (°C) at noon. The temperatures of noon positions during 7 July and 30 July range from 6.2° to 8.6°C.

TABLE 1. SIGHTING RECORDS OF THE SCHOOLS OF DALL'S PORPOISES IN THE
NORTHWESTERN NORTH PACIFIC AND THE BERING SEA IN 5° BY 10° AREAS

Areas		dalli-type		truei-type		mixed		unknown	Total No.
		No.	%	No.	%	No.	%	No.	
I	40°–45°N 140°–150°E	4	25.0	10	62.5	2	12.5	8	24
II	40°–45°N 150°–160°E	4	21.1	13	68.4	2	10.5	11	30
III	45°–50°N 150°–160°E	7	77.8	1	11.1	1	11.1	9	18
IV	45°–50°N 160°–170°E	4	100	0	0	0	0	0	4
V	50°–55°N 160°–170°E	11	84.6	0	0	2	15.4	3	16
VI	50°–55°N 170°E–180°	5	100	0	0	0	0	5	10
VII	55°–60°N 170°E–180°	13	100	0	0	0	0	8	21
VIII	55°–60°N 180°–170°W	20	100	0	0	0	0	24	44
Total		68	68.7	24	24.2	7	7.1	68	167

of the two types.   The remaining 68 schools could not be identified as to color type.

The sighting records were grouped into eight areas of 5° latitude by 10° longitude (Table 1).   All three kinds of schools, dalli-type, truei-type and mixed, were sighted in areas I, II and III, while only schools of the dalli-type were observed in areas IV, VI, VII and VIII.   The ratio of the dalli-type schools to total identified schools was about 21–25% in the southern areas (I and II), increased to 78% in area III, and to 84% or more in the remaining northeast areas.   The ratio of mixed schools to total identified schools was 10–12% in the areas where both the dalli-type and the truei-type schools were sighted.

As shown in Fig. 2, the truei-type schools were sighted more frequently in the southern part of the northwestern North Pacific than in the northern region. The area where the truei-type schools were sighted was south of 45°46′N and west of 153°39′E, while dalli-type schools were observed north of 42°52′N and east of 144°32′E.   All mixed schools of the two color types were observed in the area between 41°09′N to 50°56′N and 147°55′E to 163°58′E.   Three of them were sightd in the area where the dalli-type schools were predominant (Fig. 2, Areas III and V), and four in the area where the truei-type schools were predominant (Fig. 2, Areas I and II).

Table 2 shows a comparison of the density and school structure of P. dalli in the North Pacific and the Bering Sea areas.   Although the total number of Dall's porpoises per observation hour is the same in the two areas, the number of schools per observation hour is somewhat larger in the Bering Sea.   Especially, the number of dalli-type schools per observation hour in the Bering Sea is about twice as large
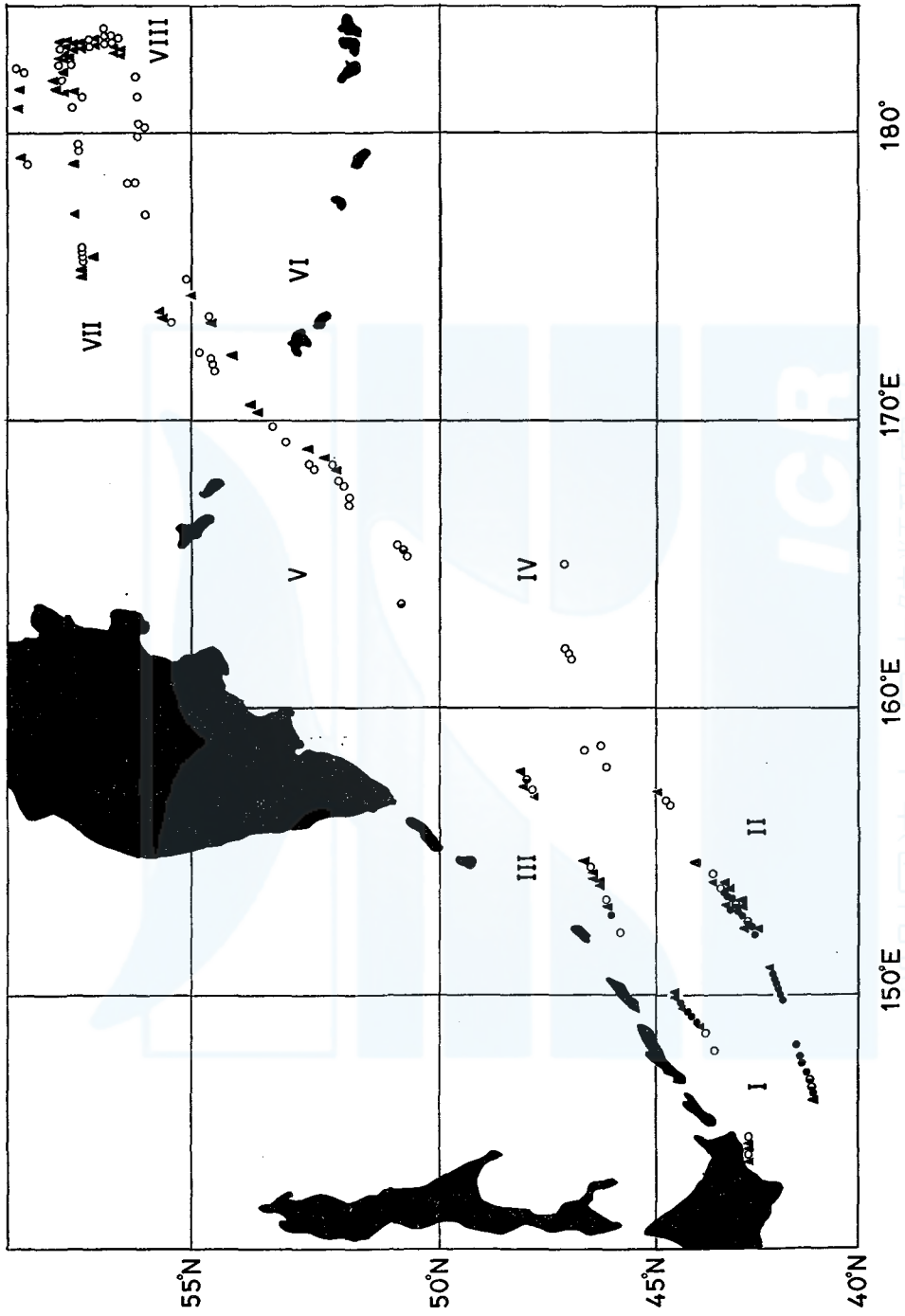
Fig. 2. Sighting records of the school of *Phocoenoides* in the northwestern North Pacific. Open circles indicate the schools of the *dalli*-type; closed circles, the schools of the *truei*-type; half closed circles, the mixed schools of the *dalli*-type and the *truei*-type; and closed triangles, the schools of unknown color type of *Phocoenoides*. For I, II, III, IV, V, VI, VII and VIII see text and Table 2.

TABLE 2.   COMPARISON OF RELATIVE DENSITY OF DALL'S PORPOISES

Areas and color types	Pacific area				
	T	D	M	U	Total
No. of schools	24	30	7	33	94
No. of porpoises	133	114	38	128	413
Mean school size	5.5	3.8	5.4	3.9	4.4
Observation hours	—	—	—	—	220
No. of school/hour	0.11	0.14	0.03	0.15	0.43
No. of porpoises/hour	0.61	0.52	0.17	0.58	1.88

T indicates a school of *truei*-type; D, a school of *dalli*-type; M, mixed school of two color types; and

as that in the North Pacific.

School size

Table 3 shows the school size of the various types of *P. dalli*.   School size ranged from 1 to 16 individuals.   Schools of 10 or less individuals were 91.7% (22 out of 24 schools) of the *truei*-type schools and 98.5% (67 out of 68) of the *dalli*-type.   About 60% of all the schools were composed of two to four individuals. The range in school size was similar in the three types of schools (*truei*, *dalli*, and mixed schools).   The mean school size of the *dalli*-type was about 3.8 individuals in both the Bering Sea and the Pacific (Table 2).   The mean school size of the *truei*-type was 5.5 individuals and was significantly larger than that of the *dalli*-type in both areas (t-test, $p<0.01$).   The mean school size of the mixed schools was 5.4 individuals, and was not significantly different from either the *truei*-type or the *dalli*-type (t-test, $p>0.8$), however, the sample size is small (n=7).

TABLE 3.   SCHOOL SIZE OF DALL'S PORPOISES IN THE NORTHWESTERN
NORTH PACIFIC AND THE BERING SEA

School size	School type				Total
	truei-type	*dalli*-type	mixed	unknown type	
1	0	11	0	7	18
2	3	8	3	22	36
3	5	19	1	17	42
4	3	9	0	8	20
5	4	6	0	7	17
6	2	9	0	1	12
7	3	2	1	2	8
8	0	3	1	1	5
9	1	0	0	0	1
10	1	0	0	2	3
11	0	1	0	0	1
12	1	0	0	0	1
13	0	0	0	0	0
14	0	0	1	1	2
15	0	0	0	0	0
16	1	0	0	0	1
Total	24	68	7	68	167

BETWEEN THE NORTHWESTERN NORTH PACIFIC AND THE BERING SEA

	Bering Sea					Total			
T	D	M	U	Total	T	D	M	U	Total
0	38	0	35	73	24	68	7	68	167
0	139	0	103	242	133	253	38	231	655
0	3.7	0	2.9	3.3	5.5	3.7	5.4	3.4	3.9
—	—	—	—	129	—	—	—	—	349
0	0.29	0	0.27	0.57	0.07	0.19	0.02	0.19	0.48
0	1.08	0	0.80	1.88	0.38	0.72	0.11	0.66	1.88

U, a school of unknown color type.

Table 4 shows the observed percentages of each school type for each school size in the area between 41°N and 51°N, and between 144°E and 166°E, where the three school types were observed in the present survey. Of the 247 Dall's porpoises in 52 schools sighted in this area, 157 individuals (63.6%) were the *truei*-type and 90 (36.4%) were the *dalli*-type. The probability of these two color types for each school size was calculated using this proportion, assuming random combination of two color types. The calculated percentages for the mixed schools were higher than those actually observed. These data suggest that the schools of *P. dalli* are not formed by the random combination of the two color types, but that school formation of the species is related to color type. This is the same conclusion reached by Kasuya (1978) based on observations off Sanriku coast of Japan during January, February, May and June.

TABLE 4. THE OBSERVED AND CALCULATED PERCENTAGES OF EACH COLOR TYPE FOR EACH SCHOOL SIZE OF DALL'S PORPOISES IN THE SOUTH OF 51°N, WHERE THREE COLOR TYPES ARE DISTRIBUTED

School size	No.	Observed			Calculated		
		truei	mixed	*dalli*	*truei*	mixed	*dalli*
1	3	0	0	100	63.6	—	36.4
2	10	30.0	30.0	40.0	40.4	46.3	13.3
3	11	45.5	9.0	45.5	25.7	69.3	4.8
4	6	50.0	0	50.0	16.3	81.9	1.8
5	6	66.7	0	33.3	10.4	89.0	0.6
6	3	66.7	0	33.3	6.6	93.2	0.2
7	4	75.0	25.0	0	4.2	95.7	0.1
8	4	0	25.0	75.0	2.7	97.3	0
9	1	100	0	0	1.7	98.3	0
10	1	100	0	0	1.1	98.9	0
11	0	—	—	—	0.7	99.3	0
12	1	100	0	0	0.4	99.6	0
13	0	—	—	—	0.3	99.7	0
14	1	100	0	0	0.2	99.8	0
15	0	—	—	—	0.1	99.9	0
16	1	100	0	0	0.1	99.9	0
Total	52	46.2	13.5	40.4	20.9	73.0	6.0

TABLE 5. SURFACE WATER TEMPERATURE OF THE SIGHTING POSITIONS OF

								School
Surface water temperature (°C)	truei-type				dalli-type			
	J to B	B to J	Be	T	J to B	B to J	Be	T
5	0	0	0	0	1	0	0	1
6	1	0	0	1	6	0	7	13
7	4	0	0	4	2	0	16	18
8	0	0	0	0	1	7	6	14
9	0	0	0	0	0	6	0	6
10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0
12	0	0	0	·0	0	2	0	2
13	0	3	0	3	0	0	0	0
14	0	7	0	7	0	0	0	0
15	0	0	0	0	0	1	0	1
16	0	6	0	6	0	0	0	0
17	0	2	0	2	0	0	0	0
Total	5	18	0	23	10	16	29	55

J to B indicates transit from Japan to the Bering Sea; B to J transit from the Bering Sea to Japan;

Surface water temperature

The frequency of sightings of each school type and surface water temperatures is shown in Table 5. The temperature for the *dalli*-type ranged from 5.9° to 15.8°C, similar to that for the *truei*-type (6.5° to 17.1°C). On the way from Japan to the Bering Sea (late June to early July), the number of sightings is low and the temperature ranges of the two types overlap, however the mean surface water temperature of the 5 *truei*-type schools was 7.4°C (range: 6.0°–7.9°C) while the mean for the 10 *dalli*-type schools was slightly lower, 6.8°C (range: 5.0°–8.9°C). On the return from the Bering Sea (early August), the mean temperature of the sightings of the 18 *truei*-type schools was 15.3°C (range: 13.6°–17.7°C) and was higher than the mean temperature of 9.8°C for the 16 *dalli*-type schools (range: 8.0°–15.8°C) which were predominantly in waters below 10°C (13 out of 16 schools). These results indicate that the *truei*-type school tends to be distributed in relatively warmer waters than the *dalli*-type school. The water temperatures during sightings of the mixed schools were from 5.9° to 16.4°C (mean: 11.7°C) and therefore were within the range of both the *truei*-type and *dalli*-type. During the return to Japan from the Bering Sea, the mixed schools tended to be in the warmer waters (4 out of 5 schools).

Observations of the mixed schools

Seven mixed schools (two in July and five in August) were observed in this survey (Table 6).

At 1215 hour (Japanese standard time) of 7 August, a mixed school of 14 porpoises were sighted. A mixed group of 12 porpoises among them firstly approached the vessel and rode the bow wave. Several minutes later, a mixed pair

DALL'S PORPOISES IN THE NORTHWESTERN NORTH PACIFIC AND THE BERING SEA

type

mixed				unknown				Total			
J to B	B to J	Be	T	J to B	B to J	Be	T	J to B	B to J	Be	T
1	0	0	1	0	0	0	0	2	0	0	2
1	0	0	1	4	0	3	7	12	0	10	22
0	0	0	0	1	0	14	15	7	0	30	37
0	1	0	1	3	2	3	8	4	10	9	23
0	0	0	0	0	0	0	0	0	6	0	6
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	1	0	3	0	3
0	0	0	0	0	4	0	4	0	7	0	7
0	2	0	2	0	5	0	5	0	14	0	14
0	0	0	0	0	1	0	1	0	2	0	2
0	2	0	2	0	1	0	1	0	9	0	9
0	0	0	0	0	0	0	0	0	2	0	2
2	5	0	7	8	14	20	42	25	53	49	127

Be, the Bering Sea; and T, Total.

of large *truei*- and *dalli*-type porpoises joined the first group. In this mixed pair, one swam slightly ahead of the other (Plate 1, Figs 1 and 2), alternating the lead and these two porpoises behaved similarly swimming side by side, keeping a direction and surfacing simultaneously to breathe (Plate 1, Figs 3 and 4). This may indicate that there is no dominant-recessive relationship in social status between them. The mixed pair left the bow after several minutes but the other 12 porpoises remained without apparent change in their behavior. In the other 12 porpoises, one *dalli*-type and two *truei*-type small porpoises (about 1.5 m in body

TABLE 6. COMPOSITION OF MIXED SCHOOLS OF DALL'S PORPOISE SIGHTED IN 1979 IN THE WESTERN NORTH PACIFIC OCEAN

School no.	Date	Time	Total group size	*Truei*-type		*Dalli*-type		Un-known type	Comments
				No.	Size	No.	Size		
1	2 July	0805	7	1	large	1	large	5	mixed pair moved some distance from other porpoises
2	3 July	1540	3	1	medium	2	medium	0	
3	2 August	1045	2	1	medium	1	large	0	
4	7 August	1215	14	11	2 small; 9 medium and/or large	3	1 small; 2 medium and/or large	0	
5	7 August	1700	8	5	2 large; 1 large with a calf; 1 medium	1	large	2	
6	8 August	1545	2	1	large	1	large	0	
7	8 August	1700	2	1	large	1	large	0	

length) were found.   As these three young porpoises were not accompanied by large porpoises, they seem to be at the stage after the weaning.

Later in the day (1700 hour) a mixed school of 8 porpoises was observed in an apparent feeding behavior, swimming in a circle, making frequent dives.   Five of them came to the bow in three groups (a pair of *truei*-type of adult size; an adult *truei*-type with a calf of *truei*-type and an adult *dalli*-type; and a medium *truei*-type). These two adult porpoises with the calf swam together throughout the 30-minute observation period.

From these observations, we conclude that the two color types of different growth stages, including adults with a calf, can form a single group and there were no apparent differences in the behavior of the mixed school compared to schools of uniform color type.

Formation of mixed schools

Only three mixed schools of the *truei*-type and the *dalli*-type have been studied off Hokkaido on 13 July 1954 (Kuroda, 1954), off northern Honshu in February (Houck, 1976) and off Sanriku in winter (Kasuya, 1978).   However, present sightings of seven mixed schools and Miyazaki's observations of other two mixed schools off the Sanriku coast of Japan on 27 March 1972 and on 8 March 1979 (unpublished data) suggest that the mixed school is not necessarily rare in the overlapped area of two color types.   There is no trend in the sighting time of the mixed school during the observation time (0500–0900 hour) (Table 6).   The mixed school was sighted not only in the coastal waters (Kasuya, 1978; Miyazaki, unpublished data) but also during the present cruise in the waters up to approximately 180 nautical miles offshore.   From these informations it can be safely said that in the overlapped area of two color types the mixed school seems to be formed in any time in the day, throughout most of the year and in both coastal and offshore waters.

Composition of seven mixed schools sighted in the present cruise (Table 6) suggests that there are three types of mixed schools, Type I: Combination of single *truei*-type porpoise with single *dalli*-type porpoise; Type II: Combination of single porpoise of one color type with two or more porpoises of other color type; Type III: School containing two or more porpoises of *truei*-type and two or more porpoises of *dalli*-type.   Three mixed schools (school nos 3, 6 and 7 in Table 6) and one mixed school (school no. 2) belonged to Type I and II, respectively.   The mixed school no. 4 (11 *truei*-type and 3 *dalli*-type porpoises) belonged to Type III. This was sighted in the higher density area, where 52 porpoises in 6 schools were sighted in the 51 minute-observation (1215 to 1306 hour on 7 August) corresponding to approximately 3×10^5 m² research areas.   Two mixed schools (school nos 1 and 5) should be classified into Type II or III when several individuals of unknown color type are considered.

DISCUSSION

Based on information on *P. dalli* in the northwestern North Pacific Ocean off the Kuril Islands, Ohsumi (1975) indicated that the northern limit of the *truei*-type was 48°N and the eastern limit was 167°E. Kasuya (1978) reported that the *truei*-type seemed to be distributed in the summer season from 42° to 54°N and from the east coast of the Kuril Islands to 168°E. Sightings of the *truei*-type have been made subsequently to 180° (NMML, unpublished data). The sighting positions of the *truei*-type obtained in the present study are distributed within the limits of these studies. Most of the *truei*-type were distributed in the southern areas off the Pacific coast of Japan whereas the *dalli*-type were less in number in this area.

During the present survey, *P. dalli* were sighted in surface water temperatures from 5.8° to 17.1°C. Within this range, there is no significant difference in the temperature preference between the two color forms. However, in August during the transit from the Bering Sea to Japan, the *truei*-type schools were usually sighted in warmer waters than the *dalli*-type. Mixed schools also tended to be in warmer waters at this time (4 out of 5 schools).

In the winter season, *P. dalli* (mostly *truei*-type) migrates into the waters off the Sanriku region (Pacific coast of Japan) where the surface water temperature is 5° to 8°C (Miyazaki, unpublished data). Few *dalli*-type schools are reported there at this season (Kasuya, 1978). Small numbers of mixed schools are seen during the same season (Kasuya, 1978; Miyazaki, unpublished data). From February to March, the southern range of the *truei*-type schools reaches off Choshi (34°44'N, 140°50'E) where the surface water temperature is about 14°–17°C (Kasuya, 1978; Miyazaki, unpublished data). Thus, most of the *truei*-type schools appear not to migrate into areas warmer than 18°C. On the contrary, the water temperature of the *truei*-type in the northern range certainly overlaps that of the *dalli*-type. From these informations it can be said that the northern range of the *truei*-type schools may not be limited by the surface water temperature only but also by other factors such as competition with the *dalli* type.

Sightings of the mixed school of the large *dalli*- and *truei*-types porpoises (body length $\geq$ 180 cm) in the present cruise during 29 June to 9 August suggest that the two color types may interbreed because of the beginning of the breeding season for *P. dalli* in early to mid-August (Mizue *et al.*, 1966; Kasuya, 1978). Kuroda (1954) reported a *dalli*-type female having a *truei*-type fetus, although Kasuya (1978) questioned whether the fetus was a *truei*-type because of his belief on the difficulty of separating two color types in the fetal stage. Newby (1982) also reported that a *dalli*-type fetus was found in a *truei*-type female and the reverse case, and a *dalli*-type fetus was found in a black variant female. These evidences support the hypothesis that the two color types may interbreed.

ACKNOWLEDGEMENTS

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EXPLANATION OF PLATE

PLATE I

A portion of a mixed school (no. 4 in Table 6) composed of 11 *truei*-type and 3 *dalli*-type porpoises sighted at 42°48′N, 153°05′E, 1215 hour, 7 August 1979.

Fig. 1. A pair of adult *truei*-type and adult *dalli*-type (the left two porpoises) were coming close to the bow of the research vessel.

Fig. 2. The *dalli*-type was swimming behind the *truei*-type in a line with a characteristic splash of water.

Fig. 3. A pair of the *truei*-type and the *dalli*-type were surfacing simultaneously to breathe with turning their heads to a direction.

Fig. 4. A pair of the *truei*-type and the *dalli*-type were just diving into water after breathing.

BEHAVIOR AND SEGREGATION OF THE DALL'S PORPOISE IN THE NORTHWESTERN NORTH PACIFIC OCEAN

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ABSTRACT

To improve knowledge of the life history of Dall's porpoise, *Phocoenoides dalli* (True, 1885) that are incidentally caught by the Japanese salmon mother-ship fishery in the northwestern North Pacific, a 34-day cruise was conducted during August-September, 1982, after the fishing season. A total of 710 Dall's porpoise were sighted and 80 were caught using hand-held harpoons. The species' southern limit was at 41°N latitude, at a surface water temperature of 18°–19°C, and overlapped the range of *Lissodelphis* and *Lagenorhynchus*. Distribution of the *truei*-type was limited to the Japanese coastal waters and the number sighted was negligible east of 155°E. Density of Dall's porpoise was higher in the western and northern parts of the research area, and somewhat lower in the southeast. More Dall's porpoise rode the ship's bow wave during mid-day than in the morning or evening, and in areas where the surface water temperature was 11°C or above. In areas with a surface water temperature of 11°C or below, most of the Dall's porpoise avoided the ship. The latter areas had a high number of mother-calf pairs and calves possibly weaned, none of which rode the bow wave. Adults not accompanying calves were sighted in both areas. School size was not different between the two areas. Most of the specimens were taken in the southern part of the study area. Males predominated and most were 2 to 6 years old, around the age of attainment of sexual maturity. Lactating individuals were significantly scarce in the sample. The *dalli*-type reached sexual maturity at a smaller body length than the *truei*-type.

Based upon comparisons of results from this cruise with those obtained from the salmon mothership fishery since 1978, we conclude that, during the season from June through September, (1) females in the state of late pregnancy, lactation, or pregnancy and simultaneous lactation are mainly distributed in the northern area, and (2) the southern area is mainly occupied by males and some females not accompanied by calves.

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INTRODUCTION

Dall's porpoise, *Phocoenoides dalli* (True, 1885), was first reported by Mizue and Yoshida (1965) to be taken incidentally in the northwestern North Pacific Ocean by the Japanese salmon drift net fisheries that started offshore operation in 1952. Little information was available on the magnitude of the incidental take or on the biology of Dall's porpoise prior to the implementation in 1978 of the U.S.-Japan cooperative research program under the auspices of the International Convention for the High Seas Fisheries of the North Pacific Ocean. Beginning in 1978, biological samples were collected from Dall's porpoise captured in gillnets and returned to the salmon motherships for examination and dissection by U.S. biologists onboard. The specimens were analyzed to obtain information on the life history parameters. However, since the biological data were collected in the salmon mothership gillnets during the limited annual fishing season (June-July) and in a limited portion of the porpoise geographic range (Nishiwaki, 1967), there was concern about the representativeness of the sample and whether there was any bias in the data. To address these questions the Japanese Government, in 1982, conducted a cruise to observe and catch porpoise outside the fishing area and season. This paper reports information obtained through this cruise on the life history of the Dall's porpoise.

MATERIALS AND METHOD

1. *Outline of Cruise*

The vessel was the *Hoyomaru No. 12* (overall length: 42 m, gross tonnage: 299), chartered by the Fisheries Agency of Japan. The research period was 34 days, sailing from the port of Kesennuma on 17 August 1982, and returning on 17 September 1982. The research was conducted in the northwestern North Pacific between 140°E and 174°E, and between 40°N and 50°N outside the US and USSR Fishery Conservation Zones (FCZ) (Fig. 1).

During the study period, there were two days (8 and 11 September) when research was not conducted due to rough seas (Beaufort wind scale 6 or higher). On September 16, the ship was in the USSR FCZ, and no Dall's porpoise were chased or captured although there were sightings.

2. *Method of Sighting*

Sighting surveys were conducted from the upper wheel deck, from which the observers' eye height was 8.5 to 9 m above the sea level. A small cabin on the port side limited observations somewhat in the area from 45° to 90°. Sighting surveys were conducted continuously from sunrise to sunset when visibility was greater than 50 m and Beaufort wind scale was less than 5 or 6.

The observation range was 180° in the direction of travel (90° port and starboard). Any changes of weather, visibility and wind force were recorded, regardless of sighting of marine mammals. The surface water temperature was recorded
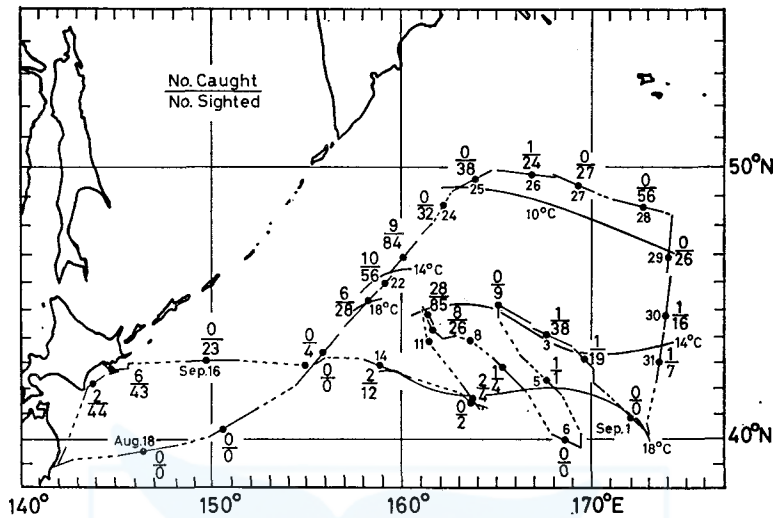
Fig. 1. Cruise track of the *Hoyomaru No. 12* (solid lines), noon position (closed circle, JST), surface water temperature, and number of Dall's porpoises sighted and caught during the cruise. The dotted lines indicate area where the sighting survey was not conducted. There was no chase or catch of porpoise on 16 September.

every hour from the auto-thermorecorder placed on the ship's hull. A difference of about 0.5°C was observed between the temperature of the thermorecorder and sampled surface water. Ship's position calculated by the navigation system was imprecise during the interval between satellite overflights (about 1 to 4 hours) if ship's speed was frequently changed for chase, catch and retrieval of Dall's porpoise. Hand held binoculars (7× or 10×) were used.

Two to eight observers conducted surveys, including ship's crew, up to three marine mammal biologists (T. Kasuya, Y. Fujise and C. Thomson), and one or two harpooners (T. Fukushi, experienced in Dall's porpoise hunting and Mr Y. Ishida experienced in sightings on a whale catcher boat). The senior author observed all cetacean schools.

Each time marine mammals were sighted, time (Japan Standard Time), direction, radial distance, sighting cue, species, number, and estimates of growth stages were recorded. Ship's position was calculated later. The radial distance to the animals was estimated visually when the school was close, or if the distance was large, was calculated based on the ship's speed (10 knots, or 300 m per min.) and the time interval between sighting and approach to the school.

3. *Capture and Shipboard Processing of Porpoise*

With rare exceptions, whenever Dall's porpoise was sighted, the ship was directed towards the school. When the porpoises rode the bow wave, the ship's speed was decreased to 5 knots or less and the harpooners used hand-held harpoons to catch them. Some porpoises were caught while they rode the ship's side wave.

In most cases, harpoons equipped with an electric shocker (50 volt, 60 Hz) were used and death occurred within 2 to 3 minutes. When Dall's porpoise did not ride the ship's wave, they were followed as long as possible to record behavioral observations and to approach closely enough for harpooning. The catch consisted of 80 Dall's porpoises (*dalli*-type 72; *truei*-type 8), 3 *Lagenorhynchus obliquidens*, 3 *Lissodelphis borealis*, 2 *Delphinus delphis* and 2 *Stenella coeruleoalba*.

Body weight (to nearest 1 kg), body length (to nearest 1 cm) and external measurements of most porpoises were obtained on ship. However the body length of 6 Dall's porpoises were calculated from the body weight. Reproductive status of females was determined and teeth and gonads were collected from all individuals. The teeth were taken from the lower jaw or from both upper and lower jaws and fixed with 10% formalin or 70% ethanol solution. The left testis with the epididymis was collected, cut transversely at the midlength for better fixation, and fixed in 10% formalin solution. For the mammary glands, color was recorded, thickness was measured at the center, and a sample for histological examination was collected and fixed in formalin. The width of the left and right uterine horns was measured, and a small piece of endometrium was fixed in formalin with the ovaries. If an ovary had a corpus luteum and the uterus was small, 10% formalin solution was injected into both uterine horns after measurement, and the whole uteri and ovaries were placed in formalin. Some skeletons, stomachs, and various tissue samples were also collected for other researchers.

4.   *Laboratory Procedures*

After weighing the testis, smears were taken from all testis and epididymis samples and stained in toluidine blue. Presence and relative quantity of spermatozoa were recorded. The sperm density in the smear was recorded in 5 categories (from none to abundant). Histological sections were made from testis tissue at the center of aforementioned cut surface and epididymis in the same area and stained with haematoxylin and eosin for permanent preparations. Sexual maturity for each male was determined from these preparations, mainly based upon the testis tissue.

The weight of the left and right ovary was measured separately, and the number of corpora albicantia (CA) and corpora lutea (CL) were counted. In two females, a fetus (4.4 cm and 13.1 cm) was observed on board the ship. For the other seven females, although a CL was present in the ovary, pregnancy was not apparent. These uteri were opened in the laboratory, washed in water, and both the wash and uteri were examined for small embryos.

Tooth preparations for age determination were made using two methods. The method used by Kasuya (1978), was used for all females, and males of a body length up to 180 cm (aged by TK and LJ). In the remaining samples, the whole tooth was decalcified in 5% formic acid for two to three days, embedded in paraffin and sectioned in the usual method (15 μm), and stained in haematoxylin (aged by TK only). For age determination, the number of haematoxylin stainable layers in the cementum was counted. Conversion of these values into ages was done ac-

cording to Kasuya (1978), assuming deposition of haematoxylin stainable layers occurs from fall to winter. Therefore, for the samples collected in the present cruise, the number of stainable layers coincides with the approximate age of the porpoise.

RESULTS

1. *Segregation between Dall's Porpoise and Other Delphinids*
       During the cruise, Dall's porpoises were sighted during the period from 20 August to 18 September, with the exception of 6 days (17–19 August, 1, 6 and 19 September) when the ship cruised south of 41°N (Table 1 and Fig. 1). Therefore it is concluded that the southern limit of this species in the northwestern North Pacific Ocean during this season is about 41°N.
       To determine the distribution of the species, it is desirable to analyse the segregation between Dall's porpoise and other delphinids. As shown in Tables 1, 2 and 3, nine delphinid species were observed during the cruise. There was a correlation between surface water temperature and the occurrence of certain species. Sightings of Dall's porpoise were limited to surface water temperatures below 20°C.
       Warm water delphinids, such as *Delphinus*, *Tursiops*, *Globicephala*, and *Stenella*, were sighted in waters above 17°C. Dall's porpoise accounted for about half of all the schools sighted in surface water temperatures of 18°C to 19°C, and since the size of Dall's porpoise schools was small, we conclude this species will be dominant in August-September in the waters below 18°C. This temperature is slightly higher than the figure obtained by Kasuya (1982) but agrees with data obtained by Ohsumi and Takaki (unpublished manuscript) for this season. The lower limit of the water temperature for Dall's porpoise was not determined in the present study. They have been sighted in this area in temperatures to 2°C (NMML unpublished data).
       Two boreal species, *Lissodelphis* and *Lagenorhynchus*, were sighted at surface water temperatures between 12°C and 19°C. Near the southern limit of the range of the Dall's porpoise, the distribution of these three species overlaps. Although *Phocoena phocoena* also occur in this temperature range, they inhabit coastal waters, and were only sighted on the continental shelf off the east coast of Hokkaido.

2. *Segregation between the Two Colour Types*
       The two major colour types, *dalli*-type and *truei*-type, are not currently distinguishable by characteristics other than pigmentation. Geographically *dalli*-type lives in the northern North Pacific and waters adjacent to it, and the *truei*-type lives off the Pacific coast of the southern Kuril Islands and northern Japan. Although it is clear that there are at least two stocks of Dall's porpoise in the northwestern North Pacific (Kasuya, 1978), little is known about the taxonomic relationship of the two color types or about the variation in color pattern in these stocks.
       On the northbound offshore route, Dall's porpoise first appeared at 43°20′N and 155°54′E, and were the *truei*-type. On the return, the *truei*-type appeared at

TABLE 1. SIGHTINGS OF DALL'S PORPOISE DURING THE CRUISE ABOARD *HOYOMARU NO. 12*

Date	Noon position	*Truei-*type	*Dalli-*type	Type uni-dentified	Mother-calf pairs	Rode ship's[1] wave,. %	Surface temperature (°C)[4]
Aug. 17	Lv. Kesennuma	0	0	0	0	—	20.8–23.4
18	39°27'N, 146°30'E	0	0	0	0	—	20.9–22.6
19	40°36'N, 151°31'E	0	0	0	0	—	20.2–23.7
20	43°32'N, 155°54'E	4	0	0	0	50	18.5–19.6
21	45°17'N, 158°21'E	1	27	0	0	82	17.5–18.7
22	45°59'N, 159°15'E	0	23	33	0	32	16.6–17.8
23	46°49'N, 160°00'E	0	43	41	1	87	12.5–16.6
24	48°37'N, 162°22'E	0	24	8	0	63	11.8–12.5
25	49°41'N, 163°58'E	0	10	28	0	5	9.8–10.2
26	49°46'N, 166°55'E	0	12	12	3	4	9.1– 9.5
27	49°13'N, 169°22'E	0	15	12	4	7	9.2– 9.9
28	48°38'N, 172°41'E	0	22	34	20	0	9.5–10.0
29	46°58'N, 174°02'E	0	15	11	8	0	9.7–11.1
30	44°55'N, 173°47'E	0	13	3	1	6	11.6–12.8
31	43°08'N, 173°31'E	0	7	0	0	71	12.1–16.7
Sept. 01	40°59'N, 172°01'E	0	0	0	0	—	16.0–18.0
02	43°09'N, 169°37'E	0	17	2	0	100	13.7–17.6
03	44°05'N, 167°44'E	0	31	7	1	45	13.1–14.0
04	45°10'N, 165°13'E	0	7	2	0	22	13.7–14.1
05	42°20'N, 167°48'E	0	1	0	0	100	15.0–18.9
06	40°00'N, 168°49'E	0	0	0	0	—	19.4–19.8
07	42°48'N, 165°23'E	0	4	0	0	100	15.8–18.4
08	43°58'N, 163°37'E	0	2[3]	0	0	100	14.4–15.4
09	44°14'N, 161°41'E	1	23	2	0	85	14.6–17.1
10	44°50'N, 161°27'E	1	59	25	0	76	14.8–16.8
11	43°52'N, 161°30'E	No sighting surveys conducted					14.1–16.8
12	41°29'N, 163°54'E	0	2	2	0	50	16.7–18.2
13	41°31'N, 163°50'E	0	0	2	0	0	18.0–20.6
14	42°50'N, 158°52'E	0	7	5	1	58	14.4–18.3
15	42°56'N, 155°03'E	0	0	0	0	—	16.0–17.6
16[2]	43°02'N, 149°51'E	5	1	17	1	22	13.8–17.6
17	42°46'N, 144°52'E	12	15	16	2	63	14.1–18.0
18	42°14'N, 143°53'E	31	0	13	0	30	15.0–18.5
19	Ar. Kesennuma	0	0	0	0	—	19.1–20.1
Total		55	380	275	42	46	

[1] Porpoise came to the ship's wave, either at bow or side.
[2] No porpoises were chased or caught by the vessel.
[3] Porpoise were sighted on bow, but sighting survey was not conducted due to rough weather.
[4] Temperature ranges during sighting surveys, or during the day if surveys were not conducted.

around 43°N and 151°E, and the proportion increased as the ship moved toward the southwest, reaching about 50% on the edge of the continental shelf off Ochi-ishizaki to Daikokujima, Hokkaido (42°46'N and 144°52'E). Slightly south of this area, all the Dall's porpoises sighted were of the *truei*-type (18 September).

Surface water temperature at the boundary of the two types was about 18°C

TABLE 2. OTHER DELPHINOID SPECIES SIGHTED DURING THE
HOYOMARU NO. 12 CRUISE, 1982

Date	Position	No. schools	No. indi- viduals	Surface water temperature (°C)	Remarks
Delphinus delphis					
8.18	39°–40°N, 146°–148°E	2	143	22.2–22.4	
8.19	40°–41°N, 150°–152°E	4	245	20.7–23.4	Two schools with *Stenella*
9.01	40°18′N, 172°50′E	1	25	17.5	
Stenella coeruleoalba					
8.19	39°–41°N, 150°151°E	4	160	23.0–23.7	Two schools with *Delphinus*
Orcinus orca					
8.20	43°45′N, 156°10′E	1	35	18.5	
8.21	44°58′N, 157°53′E	1	35	18.7	
8.25	49°50′N, 164°35′E	1	4	9.8	
9.10	44°58′N, 161°18′E	1	1	15.1	
9.18	42°42′N, 145°07′E	1	15	18.2	
Lagenorhynchus obliquidens					
8.21	45°27′N, 158°43′E	1	1	17.5	With *P. dalli*
8.30	44°43′N, 173°43′E	1	500	12.3	With *Lissodelphis*
9.03	43°–45°N, 167°–168°E	4	1565	13.5–13.9	Three schools with *Lissodelphis*
9.04	44°–45°N, 166°–167°E	4	39	13.7	
9.08	43°44′N, 163°–164°E	2	450	14.6–15.4	With *Lissodelphis*
9.14	42°43′N, 159°–160°E	2	8	16.5	
9.15	43°08′N, 155°58′E	1	30	16.0	
9.18	42°02′N, 143°22′E	1	50	18.3	
Lissodelphis borealis					
8.30	44°43′N, 173°47′E	1	150	12.3	Found with *Lagenorhynchus*
9.03	43°45′N, 167°–168°E	3	1210	13.5–13.9	,,
9.08	43°–44°N, 163°–164°E	2	450	14.6–15.4	,,
Phocoena phocoena					
9.17	42°–43°N, 144°–145°E	6	12	16.5	
9.18	41°–42°N, 143°–144°E	3	13	18.5	
Tursiops truncatus					
9.18	41°36′N, 143°16′E	1	40	18.3	Found with *Globicephala*
9.19	39°17′N, 142°08′E	1	15	19.6	,,
Globicephala macrorhynchus					
9.18	41°36′N, 143°16′E	1	50	18.3	Found with *Tursiops*
9.19	39°17′N, 142°08′E	1	25	19.6	,,
Unidentified		4	6+		

in the offshore waters and 14°C–15°C off Hokkaido. In the area east of 160°E, however, only the *dalli*-type was observed even in waters of 14°C–18°C. The proportion of the *truei*-type sighted became lower in the eastern area, regardless of water temperature. This indicates that surface water temperature was not the determining factor for habitat selection of the two color types.

Mixed schools in which both the *dalli*-type and *truei*-type were present were sighted on five occasions (one school each on 21 August, and 9, 10, 16 and 17 September). Mixed schools were sighted each day when both color types appeared. During these five days 38 schools were sighted in which all identified individuals were *dalli*-

TABLE 3. NUMBER OF SCHOOLS OF DELPHINOID SPECIES OBSERVED
AT SURFACE WATER TEMPERATURES FROM 9°-24°C DURING
THE *HOYOMARU NO. 12* CRUISE, 17 AUG. TO 19 SEPT. 1982

Species		9–9.9	10–10.9	11–11.9	12–12.9	13–13.9	14–14.9	15–15.9	16–16.9	17–17.9	18–18.9	19–19.9	20–20.9	21–21.9	22–22.9	23–23.9
Phocoenoides:	dalli-type	19	6	3	8	27	10	7	16	12	8					
	truei-type						3		9	2	2	1				
	unidentified	26	8	2	3	10	10	8	16	6						
Lissodelphis borealis					1	3	1	1								
Lagenorhynchus obliquidens					1	8	1	1	3	1	1					
Orcinus orca								1			3					
Phocoena phocoena									6		3					
Delphinus delphis										1			1	1	2	2
Tursiops truncatus											1	1				
Globicephala macrorhynchus											2	1				
Stenella coeruleoalba																4
Total		45	14	5	13	48	25	18	50	22	20	3	1	1	2	6

TABLE 4. EFFECT OF WEATHER CONDITIONS ON SIGHTING
OF DALL'S PORPOISE 20 AUG. TO 18 SEPT., 1982 AND
CORRECTION FACTOR FOR WEATHER

Beaufort scale	Sighting Effort (hours)	No. porpoise sighted	No./sighting hour	Effort correction factor
1	16.25	88	5.41	1.252
2	112.90	279	2.47	1.000
3	87.94	155	1.76	0.798
4	50.64	152	3.00	0.637
5	15.57	20	1.28	0.508
6	2.68	4	1.49	0.406
Total	285.98	705	2.46	—

type, and four schools were all *truei*-type. The number of schools in which both types were present accounted for about 11% of the total number of identified schools. On 16 and 17 September, when the numbers of individuals of the two types were about equal (16: 17), the number of mixed schools was two out of nine schools. This is not higher than the frequency of mixed schools of other dolphin species observed in the cruise. In other words, we sighted a total of 27 schools of *Lagenorhynchus*, *Lissodelphis*, *Delphinus*, *Stenella*, *Tursiops*, and *Globicephala*, out of which mixed schools were sighted on 10 occasions (37%). Of the five mixed schools of Dall's porpoise we encountered, composition was recorded for four. The proportions of *dalli*-type to *truei*-type to unidentified type for each school were 1: 1: 0, 3: 1: 0, 1: 1: 0, and 3: 1: 0.

As shown in Table 1, the number of *truei*-type porpoises was only seven individuals out of a total of 371 Dall's porpoises (2%) sighted and identified during the 27 days from 20 August to 15 September. In the following analyses, we re-

garded all the unidentified Dall's porpoises sighted in the period as the *dalli*-type.

3. *Geographical Difference in Dall's Porpoise Density*

As described earlier, Dall's porpoises were sighted mostly in surface water temperatures of 18°C or below, with only a few sightings between 18°C and 19°C. Within the temperature range, the number of individuals sighted daily varied from 5 to 85. There was a tendency that more were sighted in the western and northern parts of the research area and fewer in the southwestern part (Fig. 1). Such an apparent geographical difference in sightings may occur if there is (1) a geographical difference in porpoise density, (2) a difference in sightability due to geographical differences in porpoise behavior, or (3) a geographical difference in sighting rate due to differences in weather conditions such as wind force, wind direction and visibility. The second factor is analyzed below. We attempted to correct for weather conditions. We consider that difference in visibility was not a key factor since it changed often during daily sighting hours. Wind direction affected sightings in that, even with the same wind force, sighting was easier in a tail wind than in a head wind. However, this factor was also ignored since there were no wind direction data adequate for use in the analysis.
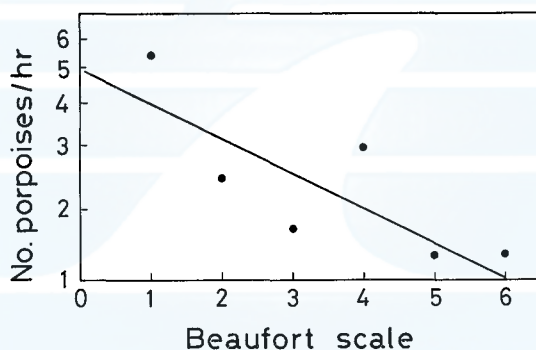
Fig. 2. The relationship between the number of Dall's porpoise sighted per sighting hour (y) and Beaufort wind force (x) during cruise of *Hoyomaru No. 12*. The y-axis is in a logarithmic scale. The solid line is the least squares regression, ln y = ln 4.98−2.253x, r=0.8.

Table 4 shows the time of initial sighting and number of sighted Dall's porpoises for each Beaufort wind scale. The numbers in this table are limited to those observed during sighting surveys, and, therefore, do not correspond to values in Table 1. Beaufort wind scale 2 was the most frequent, accounting for 39% of the total sighting hours, and 40% of Dall's porpoise sightings. The number of sighted individuals per survey hour decreased exponentially as the wind force increased (Fig. 2). The least squares regression between the number of sightd Dall's porpoises per hour (y) and the Beaufort wind scale (x) is:

$$\ln y = -2.253x + \ln 4.98, \quad r = 0.8$$
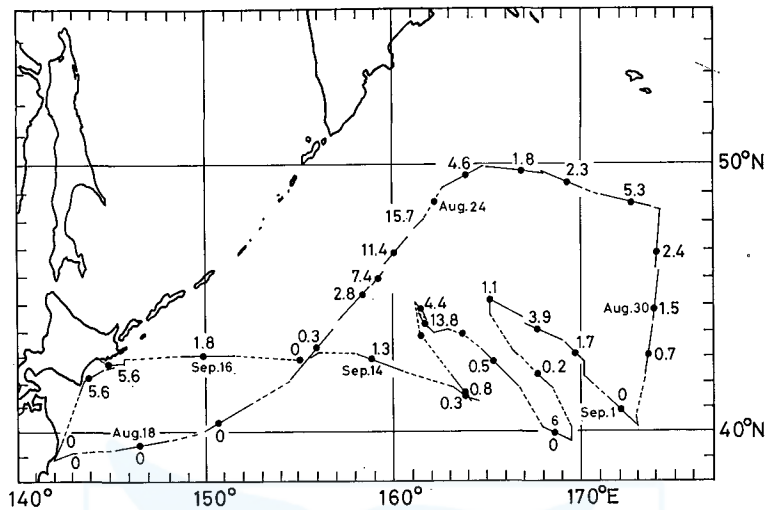
Fig. 3. Number of Dall's porpoise sighted per sighting hour with the correction for
wind force, during cruise of *Hoyomaru No. 12* (17 August-19 September, 1982).
The closed circles are noon positions (JST). The solid lines are the ship's track
and dotted lines are tracks on which there was no sighting effort.

In this equation the number of sighted individuals does not become zero even if
the wind force increases. This agrees with our observations of porpoise approach-
ing the vessel even in rough weather. The value of $y_{x=n}/y_{x=2}$ was calculated
using the above equation, and used as the effort correction factor for wind scale n
(Table 4). In other words, sighting effort is standardized to that in the state of
Beaufort wind scale 2, which was the most frequent during the cruise.

Fig. 3 shows the density of Dall's porpoise per hour of sighting, after correc-
tion for the wind force. The trend in the density distribution discussed above re-
mains unchanged after this wind force correction. The density is highest in a
comparatively narrow area centering at 45°N and 160°E. During the cruise there
was an intrusion of a warm water mass with surface temperatures of 14°C to 16°C
in this area (Japan Meteorological Agency, 1982) and this may be related to the
concentration of Dall's porpoise in the area. Presumably there was a shift of
the high density area of 22–23 August to the area of high sightings on 9 September
(Fig. 3). This is supported by the meteorological data. The concentration of
delphinids in areas of particular oceanographic conditions is also documented for
Stenella coeruleoalba (Miyazaki, Kasuya and Nishiwaki, 1974) and baleen whales
(Gaskin, 1982).

The next highest density of Dall's porpoise was found between 48°N and 50°N
(Fig. 3). The surface water temperature was about 10°C, and the same oceano-
graphic conditions extended over a wide area, including further north. Therefore,
this density may continue further north. Also, as discussed in the next section,
sightability of Dall's porpoise in this area may have been less than in the south,
and therefore density in the north may have been higher than observed. Dall's

TABLE 5. DIURNAL CHANGE OF SHIP'S WAVE RIDING BEHAVIOR
OF DALL'S PORPOISE OBSERVED DURING THE *HOYO-*
MARU NO. 12 CRUISE 1982

Time Period	*Dalli*-type (20 Aug.–15 Sept.)		*Truei*-type (16–18 Sept)	
	Number sighted	Number that rode wave (%)	Number sighted	Number that rode wave (%)
Morning[1]	207	69 (33.3)	55	18 (32.7)
Day time[2]	221	125 (56.5)	53	20 (37.7)
Evening[3]	166	55 (33.1)	2	2 (100.0)

[1] Before 1000 hr (local time);   [2] From 1000 hr to 1400 hr;   [3] After 1400 hr.

porpoise density off the east coast of Hokkaido was also high (Fig. 3). To sum-
marize, Dall's porpoise density was high in the western and northern parts of the
study area.

4. *Geographical Difference in the Wave Riding Behavior*

Dall's porpoises ride waves created by vessels. They usually ride the bow
wave, but will also ride side or stern waves. In most cases they alternately ride
these various waves once they have approached a ship. During the cruise, when
they did not approach the ship, they were chased to attempt to get them to ride
the ship's waves in order to harpoon them, and whether they rode the ship's waves
was recorded.

Table 5 shows the relationship between time of day and number of Dall's
porpoises that rode the ship's wave. In the offshore waters (20 August to 15 Sep-
tember) where the *dalli*-type was predominant, wave riding was about twice as
frequent during mid day as in the morning and late afternoon (Chi-square test, $p <$
0.001). This may be related to their habit of feeding during the night time (More-
john, 1979).

Among 202 Dall's porpoises sighted from 20 to 24 August off the eastern
boundary of USSR FCZ, 136 (67%) porpoises rode the ship's wave. On 24
August, 63% of the sighted individuals rode the wave, but the catch was low. This
is probably attributable to the unfavorable weather conditions.

From 25 to 29 August, in the area off the southern boundary of US FCZ,
where the surface water temperature was around 11°C, only six individuals (3%) of
187 Dall's porpoises sighted rode the ship's wave. In addition, 25 out of 56 schools
sighted in this area were not resighted, even though we attempted to approach
them after sighting the schools. The remaining 31 schools were chased for various
lengths of time, from two to 48 minutes (average 12 minutes). When chased in
this area, Dall's porpoise escaped by swimming faster than the ship's speed and
then rolled slowly after gaining a distance of 300 to 500 m. When the ship ap-
proached again, they resumed running, and repeated the behavior sequence. The
ship could not approach within 50 m to 100 m. Except for three schools, the Dall's
porpoise in this area eventually escaped by swimming at high speed.

The period from 31 August to 15 September was spent mainly south of the

TABLE 6. RELATIONSHIP BETWEEN SURFACE WATER TEMPERATURE
AND PROPORTION OF DALL'S PORPOISE THAT RODE
SHIP'S WAVE, 20 AUG.–18 SEPT., 1982

Water temperature (°C)	Dalli-type (20 Aug.–15 Sept.)		Truei-type (16–18) Sept.	
	Number sighted	Number that rode wave (%)	Number sighted	Number that rode wave (%)
9– 9.9	132	3 (2.3)	—	—
10–10.9	39	1 (2.6)	—	—
11–11.9	12	5 (41.6)	—	—
12–12.9	36	16 (44.4)	—	—
13–13.9	119	73 (61.3)	0	0
14–14.9	51	46 (90.2)	22	4 (18.2)
15–15.9	55	18 (32.7)	0	0
16–16.9	76	42 (55.3)	71	24 (33.8)
17–17.9	45	25 (55.6)	10	6 (60.0)
18–18.9	25	18 (72.0)	7	6 (85.7)
19–19.9	4	2 (50.0)	—	—
Total	594	249 (41.9)	110	40 (36.4)

14°C surface isotherm.   In this area, the number of Dall's porpoises that rode the ship's wave increased and 146 out of 209 Dall's porpoises (70%) rode the bow wave. This proportion was about the same as that in the period of 21 to 24 August.

Table 6 shows the relationship between the proportion of the Dall's porpoise that rode the ships wave and surface water temperature.   In the offshore area where the *dalli*-type was predominant (20 August to 15 September), less than 3% of the Dall's porpoises sighted north of the 11°C isotherm rode the wave.   As the temperature increased above 13°C, the percentage increased to exceed 60%.   The difference in behaviour in the two temperature ranges was conspicuous.   Off the east coast of Hokkaido (16–17 September), where the *truei*-type was abundant, the data are limited and the situation is not completely clear.   However, in general, the number of individuals that rode the bow or side wave increased as the surface water temperature rose.   In this coastal area, the number of Dall's porpoises that rode the wave exceeded 60%, in surface water temperatures greater than 17°C. The difference in temperatures between two areas reflects the distribution pattern of the *truei*-type.

We conclude there is a marked difference in the behavioral response to ships between *dalli*-type porpoise that live north of 11°C surface isotherm and those that live south in the Subarctic Convergence at temperatures of 11°C to 19°C.

5.   *Segregation of Mother-Calf Pairs*
Although it is difficult to estimate body lengths of Dall's porpoise in the water, it is not difficult to identify mother-calf pairs if observed at a close distance (less than 100 m).   In the present study we identified mother-calf pairs using the difference in body length or splash size of two individuals swimming together at close distance (Table 1 and Fig. 4).

Out of 41 mother-calf pairs sighted in the offshore area where *dalli*-type
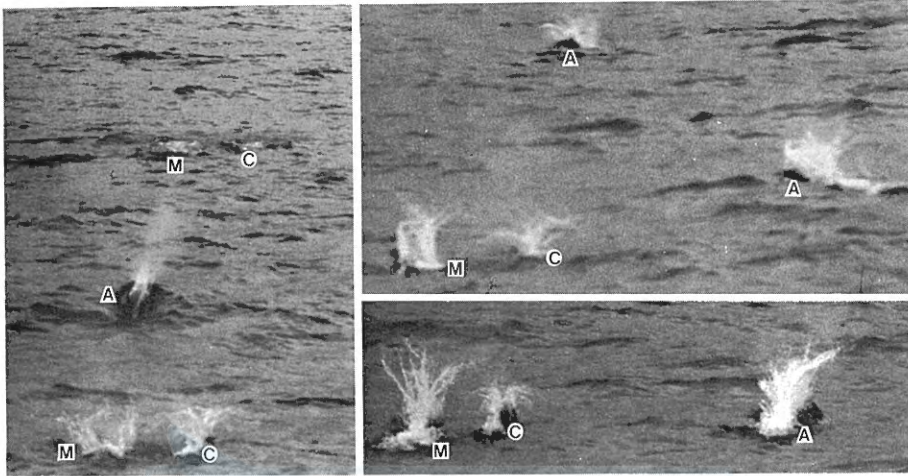
Fig. 4. Dall's porpoise school (School No. 118, 28 August 1982, 48°53′N, 171°10′E). When sighted initially at 0352 (JST), this group consisted of 2 mother-calf pairs and 2 adults, but during the chase (at 0403), another mother-calf pair joined the group. At 0405, they escaped from the vessel. All 8 were of the *dalli*-type. A: Adult, M: probable Mother, C: Calf

was predominant, 36 pairs (86%) were sighted in the period from 26 to 30 August. A particularly notable day was 28 August. Forty individuals (20 pairs) out of the 56 individuals encountered were identified as mother-calf pairs. Throughout the entire cruise period, no mother-calf pair rode the ship's wave. This is one reason for the infrequent wave riding behavior of porpoise in the northern area (25 to 30 August). However, this is not the complete explanation, since mother and calf pairs accounted for only 72 individuals (36 pairs) out of 187 individuals that were sighted in the cruise period. Even if there were additional mother-calf pairs that were not recorded, there were obviously many individuals other than mothers-calves.

Among the Dall's porpoise schools sighted in the northern area from 25 to 30 August, 29 schools were closely observed during the chase. Among these 29 schools, 13 schools had at least one mother-calf pair, and seven of these consisted of only mother and calf pair(s) as follows:

1 mother-calf pair : 2 schools
3 mother-calf pairs: 2 schools
4 mother-calf pairs: 2 schools
7 mother-calf pairs: 1 school

When first sighted, the last school was composed of two separate groups of three mother-calf pairs and four mother-calf pairs. These joined when the vessel approached.

The remaining six schools with mother-calf pair(s) consisted of:

1 mother-calf pair and 1 adult: 3 schools
2 mother-calf pairs and 1 adult: 1 school
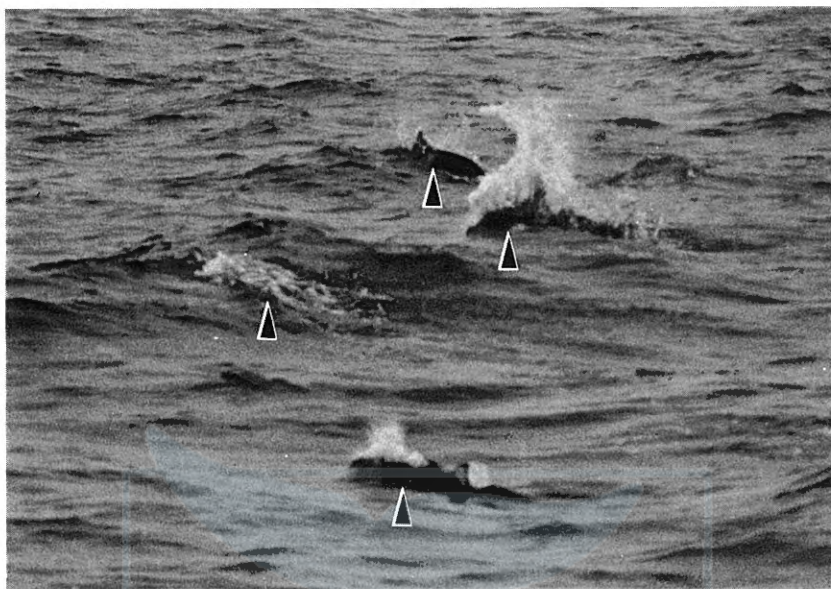
Fig. 5. A school consisting of 4 *dalli*-type porpoises of about the same size (School No. 143, 30 August 1982, 45°55′N, 173°56′E). This school joined School No. 142 (3 *dalli*-type porpoises: Large+Medium+Small) after 46 minutes (from 0730 to 0818) of following School 142. Of the four, 1 rode the bow wave and was caught (No. 31). It was a 174 cm long female, 10 years old, and was not pregnant or lactating but had 1 corpus luteum and 2 corpora albicantia in the ovaries.

2 mother-calf pairs, 1 adult and Unknown: 1 school
3 mother-calf pairs with 2 adults: 1 school

In one of the groups of three individuals, there was one adult and one medium sized individual followed by a smaller calf (School No. 142). This could have been a mother-calf pair accompanied by a calf of the preceding year.

In the remaining 16 schools, there were no mother-calf pairs. In four of these schools, the growth stage of the individuals was estimated as:

3 small individuals: 2 schools
5 small individuals: 1 school
4 large individuals: 1 school (Fig. 5)

The following inferences can be drawn from the above data:

(1) Several mother-calf pairs may aggregate to form a school.
(2) Mother-calf pair(s) may form a school with one or more other adults.
(3) Weaned calves or immatures may form schools.
(4) In the northern area where mother-calf pairs appear frequently, other schools are also present.

In the 29 schools, 45 individuals (41%) were not associated with mother-calf pairs. These 45 individuals rarely rode the ship's wave. Since only two of them were caught (2 resting females with CA and CL in the ovaries, age 3 and 10 years respectively), there is not enough direct information on their sex, age and reproduc-

tive status.   However, it is likely that adult males were also with these oestrus females (see *School structure*).   In this northern area, the proportion of mother-calf pairs out of the total number of individuals sighted per day fluctuated as follows during the interval from 25 to 30 August: 0%, 25%, 30%, 71%, 72% and 13% (Table 1).   Therefore, among the areas studied in this cruise, mother-calf pairs were highest north of 46°N and east of 165°E (Table 1).

6.   *School Structure*

In the offshore area where the *dalli*-type was predominant, schools were composed of one to 14 individuals (Table 7).   The mode was two individuals, and the average was about 3.5 to 3.8 individuals.   This is similar to values for *dalli*-type reported by Kasuya (1978) and Bouchet, Braham and Tsunoda (1983 ms).   No significant difference was detected between the school sizes in the northern and southern parts of the offshore area.   Kasuya (1978) reported that the *truei*-type formed larger schools than the *dalli*-type.   The reason for the apparent larger school size off Hokkaido (16 to 18 September) may be attributable to the presence of *truei*-type.   The sizes of 13 schools in which only *truei*-type were identified are as follows: 20 August: 4; 16 September: 1 and 3; 17 September: 1, 6, and 7; 18 September: 2, 3, 4, 5, 6, 6 and 10.

Sighting information on school structure of Dall's porpoise distributed south of the 11°C isotherm indicates that there were very small numbers of mother-calf pairs and small individuals that could be considered as weaned.

Information on the composition of Dall's porpoise schools was obtained from multiple collections of animals from schools that came to the bow of the vessel.

TABLE 7.   SCHOOL SIZE FREQUENCY OF DALL'S PORPOISE FOR SURFACE
WATER TEMPERATURES ABOVE AND BELOW 11°C.   DATA FOR BOTH
COLOUR TYPES ARE POOLED.   DATA FOR 16–18 SEPTEMBER
ARE PREDOMINANTLY TRUEI-TYPE

School size	Below 11°C	Above 11°C	
	25–29 Aug.	20–24 Aug. 30 Aug.–15 Sept.	16–18 Sept.
1	8	4	2
2	14	29	4
3	5	25	6
4	9	21	6
5	2	8	3
6	5	10	3
7		4	1
8	3	1	1
9		1	1
10		1	1
12		2	
14	1		
Total	47	106	27
Mean	3.51	3.77	4.07

Of the 70 *dalli*-type porpoise collected during this cruise, 54 (77%) were collected with one or more additional porpoise from the school. These animals were taken from at least 19 different schools. Interpretation of the results is complicated because more than one school was probably present during some collections.

Trends with respect to age, sex and reproductive status in the school composition were not clear. The composition of the samples from individual schools was:

Composition	No. of schools	School numbers
All immature males	4	35, 48, 50, 218
Mature males	2	219, 226
Mature and immature males	7	43, 49, 197, 206, 208, 209, 215
Males and a female	6	24, 39, 202, 204+205, 243

A mature female was present in four of the five schools containing both males and females. In two of these (school 24 and 243) there was a mature male, and in one case the female was pregnant and lactating (fetal length 4.4 cm), and in the other the female had a corpus luteus and possible fetal membrane in the uterus. In school 204+205 a resting female and a mature male were collected from a group of six individuals. In school 39, four out of six individuals came to the bow, and an immature female, immature male and a mature male were collected. The final mixed sex sample (school 202) was collected from a large group of animals that probably comprised several schools. Eleven individuals were taken, including a resting female with a corpus luteum, immature and mature *dalli*-type males and an immature *truei*-type male. These data indicate that schools with mature females without calves often contain mature males. Schools comprised of immature animals also exist.

7. *Analyses of the Catch*

Eight *truei*-type Dall's porpoises were caught during the cruise, seven of which were males, and one, an immature female (Table 9).

Of the *dalli*-type, 72 individuals, including 12 females, were caught. Of the females, 2 mature females were caught in the northern area where the surface water temperature was 11°C or less (see *School structure* and Fig. 5). The body lengths of the 12 females were 164 cm to 215 cm, and the ages from 2 to 10 years. Two were sexually immature and 10 were mature. Of the 10 mature females, two were pregnant (fetus lengths of 1.4 cm and 13.1 cm) and one was pregnant and simultaneously lactating (fetus length: 4.4 cm). These three had total corpora counts of 2, 12 and 5 respectively. Two females had a CL (and no CA) and a tissue (about 3 cm and 4 cm in the length) in the uterus that appeared to be embryonic membrane. The remaining five females had CL in various developmental stages in the ovary, but no embryonic tissue was observed in the uterus. Their corpora numbers were 1, 1, 3, 4 and 6 respectively. The seven mature females in which pregnancy was not confirmed were not lactating. These findings add three interesting points

TABLE 8. BODY LENGTH FREQUENCIES AND SEXUAL MATURITY OF DALL'S PORPOISE CAUGHT IN THE *HOYOMARU NO. 12* CRUISE, 1982

Colour type	*Dalli*-type								*Truei*-type		
Sex	Male					Female			Male		Female
Body length (cm)	I	E	L	M	Total	I	M	Total	I	M	I
164–167	3				3	1		1	1		
168–171	4				4		1	1	1		
172–175	7		1	1	9	1	1	2	1		
176–179	3			3	6				1		
180–183	7	3		1	11		2	2			1
184–187				8	8		2	2	2		
188–191	1		1	4	6						
192–195				4	4		1	1		1	
196–199	1			4	5						
200–203				1	1		1	1			
204–207				1	1		1	1			
208–211				1	1						
212–215							1	1			
216–219				1	1						
Total	26	3	2	29	60	2	10	12	6	1	1

I: Sexually immature, E: Early maturing, L: Late maturing, M: Sexually mature

TABLE 9. AGE FREQUENCIES OF DALL'S PORPOISE CAUGHT IN THE *HOYOMARU NO. 12* CRUISE, AUGUST TO SEPTEMBER 1982

Colour type	*Dalli*-type								*Truei*-type	
Sex	Male					Female			Male	Female
Age (yr)	I	E	L	M	Total	I	M	Total	I	I
2	9			2	11	1		1		
3	6			5	11		2	2	1	
4	6		1	5	12	1	3	4		1
5	3	1	1	6	11		1	1		
6	1	1		3	5					
7	1			1	2					
8				1	1					
9							1	1		
10				1	1		1	1		
17				1	1					
Total	26	2	2	25	55	2	8	10	1	1

I: Sexually immature, E: Early maturing, L: Late maturing, M: Sexually mature

to our knowledge of adult female behavior.   The first point is that while mothers accompanied by calves do not ride the ship's wave (described previously), female individuals that are not lactating (that is, they are probably not accompanied by a calf) do so.   This is what Kasuya (1978) assumed with the *truei*-type.   The second point is that most of these non-lactating mature females seem to be segregated in the southern area where the water temperature is comparatively high.   The

third point is that the ovulation rate of non-lactating mature females is very high. It is probable since the research was conducted in the mating season that most of the females with CL in the ovaries were in a very early stage of pregnancy that could not be confirmed visually. Therefore, the pregnancy rate of these non-lactating adult females in the sample may have been underestimated.

The body lengths of the 60 *dalli*-type males ranged from 164 cm to 219 cm, and the ages from 2 to 17 years. As in the case of females, no male shorter than 164 cm or younger than 2 years was caught. This indicates that the young individuals are either (1) segregated in the northern area, or (2) are in the southern area with surface water temperatures above 11°C, but do not approach ships. In either case, since individuals below 2 years of age did not ride the ship's wave, they could not be sampled. The same is true for the *truei*-type in the Japanese coastal waters (Kasuya, 1978).

Male sexual maturity was determined from histological examination of the testis. If no spermatozoa, spermatid or spermatocyte was observed in the testis tissue (usually 0.5×0.5 cm taken from the center), the indidividual was determined to be " immature ". " Early maturing " stage indicates males in which the proportion of seminiferous tubules containing any one of these stages was between 0 and 50%; " late maturing " are those with these stages present in 50% to less 100% of the tubules. Individuals in which all tubules had any of these stages present were determined to be " mature ". Even in the individuals which were determined to be " mature " using this classification, some showed active spertogenesis and some did not. Also, some individuals did not have one or two of these spermatogenetic stages. This may indicate that the male mating peak is not totally synchronized. This will be studied separately.

These maturity criteria were compared with the sperm density in the epididymal smears. The results indicate that two out of the 31 males that were determined to be " mature " did not have sperm in the epididymis, and in another 3 males the sperm density was " scanty " (1 sperm in several fields). The sperm density of the other " mature " males was " common " (one to three sperm in one field) or higher. Only three males of the 34 which were classified " immature " had " scanty " sperm present and no sperm was observed in the epididymis of the others. As shown in Fig. 6, the correlations between maturity and testis weight and between maturity and body length are reasonable. Therefore, we conclude that these classifications of male sexual maturity are appropriate. Generally, the testis weight of 40 gm could be used as the threshold between " immature " and " mature ".

As shown in Table 8, male *dalli*-type attain sexual maturity at body length between 172 cm and 199 cm. The body length where half of the males are mature is assumed to be somewhere in the range of 176 cm to 187 cm. The corresponding body length of mature females is between 172 cm and 183 cm. These body lengths are 10 to 15 cm smaller than the values for *truei*-type in the Japanese waters obtained from the samples caught by the same method (Kasuya, 1978).

For male *dalli*-type, the ages of the youngest mature individual and oldest
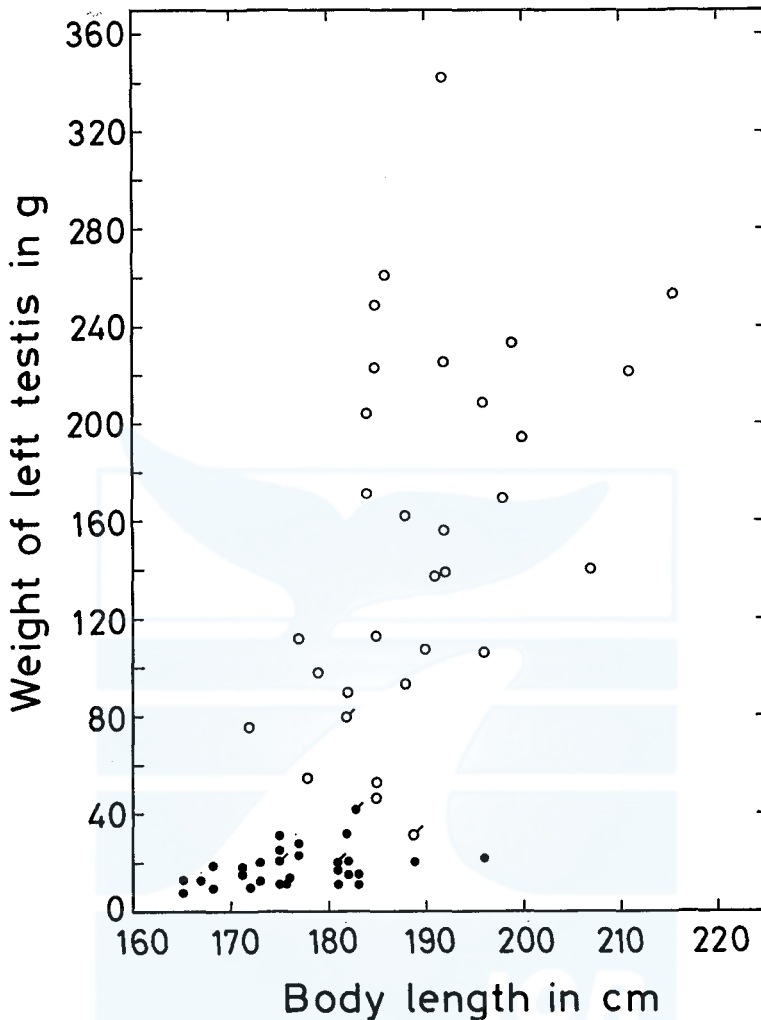
Fig. 6. Relationship between body lengths and left testis weights of Dall's porpoise caught with hand harpoons during the cruise of *Hoyomaru No. 12* (17 August— 19 September, 1982). Open circle without bar: Mature. Open circle with bar: Late maturing. Closed circle with bar: Early maturing. Closed circle without bar: Immature.

immature individual are 2 years and 7 respectively. For females, although the sample is small, it is 3 years and 4 years respectively (Table 9). These values agree with the corresponding figures obtained from the salmon gillnet fishery in 1967 (Kasuya, 1978) and in 1978 to 1980 (Newby, 1982).

The proportion of mature males does not significantly change from 4 to 7 years of age. If the sample is not biased, one expects the proportion of mature individuals to increase with age. Another interesting point is that the age fre-

quency does not change between 2 and 5 years, but abruptly drops at ages over 6 years. We interpret this to mean, as is the case for *truei*-type off the Japanese coast (Kasuya, 1978), that the proportion of individuals available for sampling by hand harpoon increases as maturity approaches and decreases after individuals have reached maturity. Since the majority of the mother and calf pairs were distributed in the northern area, almost none of Dall's porpoises in that area rode the ship's wave, and about 70% of the individuals in the southern area rode the ship's wave, we conclude that wave riding behavior of Dall's porpoise is common in only certain growth or reproductive stages (especially in females).

The data on the *dalli*-type obtained in the present study was biased towards males (male 60: female 12). In the southern area, the proportion of individuals that did not ride the ship's wave was 30% of the total number of Dall's porpoises sighted. If all of them are assumed to be females, the sex ratio of Dall's porpoise in the area would be $(12+72 \times 0.3 \div 0.7)/(12+72 \times 0.3 \div 0.7+60)=0.42$. Even with such an extreme assumption, it is difficult to explain the unbalanced sex ratio of the catch. One interpretation is that more males live in the southern area. The fact that there are fewer females than males in all age groups (Table 9) may indicate that sexual segregation is present in all age groups over 2 years.

DISCUSSION

Since 1978, a large number of samples and data have been collected from Dall's porpoise killed incidentally by the Japanese salmon mothership gillnet fishery (Anon. 1981). The majority of these samples were collected annually in June and July, in the area between 46°N–58°N latitude and 168°–175°E longitude. There are three major differences in the sampling between the present study and the previous. In the present study, although there was some areal overlap (27–29 August), emphasis was placed on collections south of the mothership fishing area, in the Subarctic Convergence. In this study, samples were collected during the mating season (August-October) rather than the parturition season (June-July). The third difference is that samples were obtained using a hand-held harpoon as animals rode the ship's wave rather than from gillnets as in the previous collections.

In the sample collected from the mothership fishery, body length frequency is characterized by the presence of some newbornes (about 100 cm) and juveniles (130–160 cm) which correspond to an age of about 1 gear are abundant (Kasuya, 1978; Newby, 1982). This corresponds to the presence of mother and calf pairs and presumably weaned juveniles sighted in this study in August-September north of the Subarctic Convergence.

The age of individuals obtained in the Subarctic Convergence was 2 years or older. This indicates that the bow wave riding behavior does not necessarily start at the time of weaning. Therefore, Kasuya's estimate (1978) of the suckling period of the *truei*-type off the Japanese coast might have been an overestimation. In the present study no estimation of the weaning period has been obtained.

The female ratio in all the Dall's porpoise caught by the salmon gillnet fishery

was about 63%, and that in the adult individuals 76% (Anon., 1981). In this sample, twelve out of 72 Dall's porpoise (17%) were female and 23% of the mature animals were female. This supports our conclusion that more males are distributed in the Subarctic Convergence and more females are distributed north of the Convergence. Dall's porpoise have also been collected in the western North Pacific near Monterey Bay, California (36°48′N and 121°47′W) in the southern portion of the species range from strandings and by hand-held harpoons (Loeb, 1972; Morejohn, 1979). Although the sample sizes are small, the proportion of females taken by harpoon was 19% (4 out of 21 animals), similar to the percentage in the present study. However, in stranded animals from the Montery Bay area, the sex ratio was about 1:1 (n=9) (Loeb, 1972). Data on maturity or age were not presented. In the finless porpoise, possibly reflecting the age specific mortality rate, most of the strandings were juveniles below 2 growth layers and adults over 8 layers (Kasuya and Kureha, 1979). If this is true for Dall's porpoise, additional biological data will be required for further analysis of the stranded individuals.

In the samples collected in the gillnets, 690 out of 752 mature females (92%) were pregnant. This corresponds to the observation of large numbers of mother-calf pairs north of the Subarctic Convergence in August-September, after the peak of the parturition season. The high pregnancy rate in the sample collected during the parturition season (June-July) indicates an annual pregnancy for this species. For this to be true, almost all of the adult females of this species would have to ovulate within a month or so after parturition and enter the next gestation. Therefore, the majority of adult females must be lactating and simultaneously in the early stage of pregnancy in August-September. To clarify this point, we expected to obtain mother-calf pairs in this cruise, but it was not possible because of their behavior of avoiding the vessel. However, in this study, we are able to clarify these points: (1) some of the mature females are distributed in the Subarctic Convergence, and all of these have recently ovulated since all had a CL present, and only one was lactating; and (2) a few nonlactating mature females may occur north of the Subarctic Convergence during this time of year. This indicates that many of them may become pregnant every year but some individuals do not, and most of these are segregated in the Subarctic Convergence.

The present study clarified that the Dall's porpoise is geographically segregated by growth stage, sex and reproductive status and that their reaction to vessels is not uniform. This suggests that the sighting rate of Dall's porpoise from ships may vary by the areas and seasons. Care must be paid to this point when estimating the Dall's porpoise population by sighting.

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DISTRIBUTION, SEASONAL MOVEMENTS, AND ABUNDANCE OF PACIFIC WHITE-SIDED DOLPHINS IN THE EASTERN NORTH PACIFIC*

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ABSTRACT

All relevant data available through 1979 on Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, in the eastern North Pacific were examined for patterns of distribution, movements, and abundance. In waters east of longitude 180° white-sided dolphins occur from about latitude 20°N to latitude 61°N, on the continental shelf and offshore. They are present in the mouth of the Gulf of California and in inland marine waters of Washington, British Columbia, and Southeast Alaska, but apparently they do not usually enter the Bering Sea or regularly penetrate Prince William Sound. They appear to be continuously distributed across the temperate North Pacific. Seasonal movements cannot be unequivocally demonstrated in any area, although observed peaks in numbers suggest regular seasonal influxes into waters north of latitude 40°N in spring and summer and between latitudes 25°N and 30°N in fall. Evidence for seasonal presence is most convincing off Southern California, between latitudes 30°N and 35°N, where peak numbers occur inshore in November through April. No population estimate is possible with currently available data. On aerial surveys in the well-studied Southern California Bight, Pacific white-sided dolphins were observed to occur at a peak frequency of 1.42 individuals per nm flown; because perpendicular sighting distances were not recorded consistently for these sightings, we are unable to estimate survey strip-width or translate the frequency of individuals sighted into an estimate of density. In a region off Baja California, Pacific white-sided dolphins have been estimated to occur in densities up to 0.06 individuals per nm². They appear to be the second or third most abundant delphinid in Southern California waters in winter, after common dolphins and northern right whale dolphins. The Pacific white-sided dolphin may be the most abundant delphinid in the temperate eastern Pacific. The 1300 herds sighted averaged 88 individuals (s=366). Herds were significantly larger in southern

($<$30°N) and northern ($>$55°N) than in central (30°–55°N) portions of the range (one-way Anova, n=1268, F=3.69, P$<$0.01).

INTRODUCTION

The Pacific white-sided dolphin, *Lagenorhynchus obliquidens* (Fig. 1), is one of the most widely distributed delphinids in the eastern North Pacific.   It has been reported from temperate waters between about latitude 23°N (Leatherwood and Reeves, 1978; Leatherwood, Reeves, Perrin, and Evans, 1982) and latitude 61°N (Scheffer, 1950), from the North American coast to at least the edge of the continental shelf.

Within their eastern North Pacific range, Pacific white-sided dolphins are a highly visible resource, interacting with human activities in various ways.   An estimated 80 to 115 individuals have been live-captured for public display or research
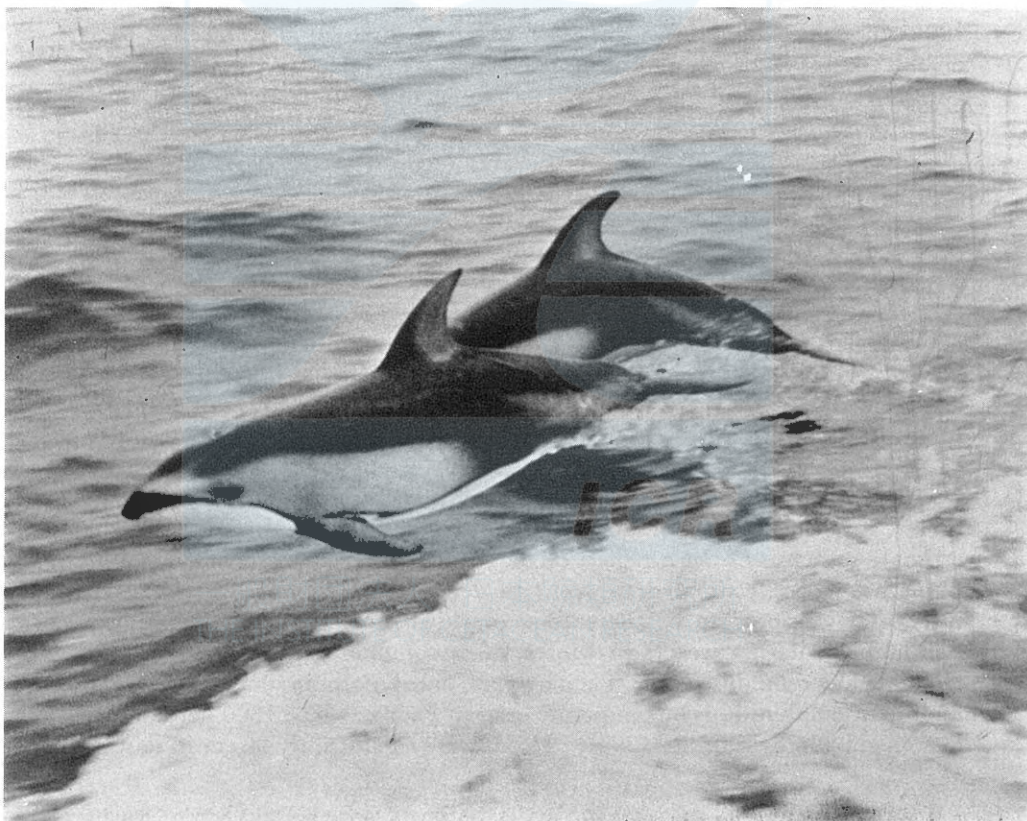
Fig. 1.   Pacific white-sided dolphins " porpoising " beside a fishing vessel south of Adak, Alaska.   The prominent bicolored dorsal fin, absence of a well demarcated beak, and striking pattern of black, gray, and white markings make these dolphins easy to recognize at sea [Photo courtesy of NMFS, National Marine Mammal Laboratory (NMML)].

since 1966 (Walker, 1975; National Marine Fisheries Service (NMFS), Washington, D. C., 1982, unpublished records; Reeves and Leatherwood, 1984). Small numbers have been taken incidentally in fishing operations for tuna, anchovy, and salmon in subtropical, midtemperate and northern temperate waters, respectively (U.S. Dept. of Commerce, 1981). These dolphins prey on commercially valuable fish and squid (Jones, 1981; Stroud, Fiscus, and Kajimura, 1981).

In 1979, under contract from the Southwest Fisheries Center, NMFS, a study was begun on the population biology and ecology of Pacific white-sided dolphins in the eastern North Pacific. This paper reports on distribution, seasonal movements, and abundance of the species in North Pacific waters east of longitude 180°, as surmised from all data available through 1979. Results of the remainder of the NMFS-sponsored study, addressing morphology, geographic variation, and general biology, will be published elsewhere by Leatherwood, William A. Walker and William F. Perrin.

BACKGROUND AND PREVIOUS LITERATURE

Gill (1865) initially described *L. obliquidens* from two specimens (U.S. National Museum Numbers 1963 and 3886) taken off the California coast. Scammon (1874), referring to those dolphins with which he had become acquainted while whaling in the eastern North Pacific, reported that " this species has a wider range and congregates in larger numbers than any other of the dolphin family." True (1889) gave the Pacific white-sided dolphin's distribution as the North Pacific Ocean, Puget Sound, and the coast of California. Subsequent accounts have added limited regional and seasonal information while restating the more generalized descriptions of range made by these early authors.

In the eastern North Pacific, individuals of *L. obliquidens* have been reported from the southern tip of Baja California (about latitude 23°N) northward along the coasts of California, Oregon, Washington, British Columbia, and Alaska to 61°N (Scheffer, 1950) and westward through the Gulf of Alaska and North Pacific to Amchitka Island (Scheffer and Slipp, 1948; Cowan and Guiguet, 1956; Brown and Norris, 1956; Pike, 1956, 1960; Norris and Prescott, 1961; Brownell, 1964; Fiscus and Niggol, 1965; Walker, 1975; Wahl, 1977; Barham, 1978; Leatherwood and Reeves, 1978; Everitt, Fiscus, and DeLong, 1979; Dohl, Norris, Guess, Bryant, and Honig, 1980; Consiglieri and Braham, 1982).

In the western North Pacific these dolphins have been reported to occur from Taiwan northward along the coasts of Japan and Asia to the Kurile and Commander Islands (Okada and Hanaoka, 1939; Tomilin, 1957; Sleptsov, 1961; Nishiwaki, 1967; Mitchell, 1975). They have not been reported reliably from the Bering Sea (Nishiwaki, 1967; Consiglieri and Braham, 1982).

The statement that *L. obliquidens* " can be seen in the center of the North Pacific including the Hawaiian Islands " (Nishiwaki, 1967) has not been substantiated, although recent sightings at about latitude 40°N, longitude 180° (G. Naftel, Honolulu, Hawaii, personal communication) indicate that they do occur in the

pelagic mid-Pacific at temperate latitudes. Nishiwaki (1967) also claimed that Pacific white-sided dolphins are known from as far south as Panama in the eastern Pacific, but we are not aware of any confirmed records from south of 20°N. Their occurrence in partially enclosed areas, such as Osaka Bay (Kuroda, 1953), Puget Sound (Scheffer and Slipp, 1948), and the Inside Passage along the coast of British Columbia (Pike and MacAskie, 1969) is well documented. They have been reported to penetrate the Gulf of California to as far north as Gorda Bank (23°00'N, 109°30'W) (Leatherwood and Reeves, 1978; Leatherwood et al., 1982). Although a skeleton was collected from Valdez, Alaska, in Prince William Sound (latitude 61°N) in 1901 (Scheffer, 1950), no Pacific white-sided dolphins were seen inside the Sound during recent extensive aerial and ship surveys (Hall, 1979).

Seasonal shifts in distribution have been reported. Pacific white-sided dolphins are said to be more common in coastal waters during fall and winter, moving offshore during spring and summer (Brown and Norris, 1956; Cowan and Guiguet, 1956; Norris and Prescott, 1961; Brownell, 1964; Pike and MacAskie, 1969; Barham, 1978; Leatherwood and Reeves, 1978; Everitt et al., 1979; Dohl et al., 1980). They are thought to occur only in warmer seasons in the northeastern Gulf of Alaska (Consiglieri and Braham, 1982) and to be more numerous in cooler seasons south of Point Conception, California (Leatherwood and Reeves, 1978). It has been suggested that such movements are related to changes in prey distribution (Norris and Prescott, 1961; Brownell, 1964; Barham, 1978) and water temperature (Leatherwood and Reeves, 1978; Dohl et al., 1980).

Since Scheffer's (1950) summary of records along the North American coast, no comprehensive review of the Pacific white-sided dolphin's distribution and movements in the northeastern Pacific has appeared in the literature. The only published estimates of popluation size are Nishiwaki's (1972) statement that there are 30,000 to 50,000 in Japanese waters and Fox's (1977) estimate that about 24,000 inhabit an approximately 1.5 million km² area off California and Baja California. Leatherwood and Walker (1979) considered L. obliquidens one of the three most abundant delphinids, along with Delphinus delphis and Lissodelphis borealis, in Southern California waters during midwinter.

In this report we examine information available through 1979, from sightings and collections made north of latitude 15°S and east of longitude 180°, for patterns of distribution, movements, and abundance of the species in the eastern North Pacific.

MATERIALS AND METHODS

Records of sightings of Pacific white-sided dolphins in the eastern North Pacific for the years 1949 through 1979 were available from the literature and various unpublished sources. A complete file containing all the distribution data obtained for this report has been deposited with the Southwest Fisheries Center. Principal contributors are listed in Table 1, and their approximate areas of coverage are shown in Fig. 2. As in three previous efforts of this kind to investigate other

TABLE 1. PRINCIPAL SOURCES OF UNPUBLISHED RECORDS OF SIGHTINGS OF PACIFIC WHITE-SIDED DOLPHINS IN THE EASTERN NORTH PACIFIC (MODIFIED FROM DAHLHEIM, LEATHERWOOD AND PERRIN, 1982). THE NOTATIONS IN THE MIDDLE COLUMN INDICATE WHETHER, FOR PURPOSES OF THIS REPORT, THE LISTED PROGRAM'S SURVEY EFFORT HAS BEEN CHARACTERIZED SUBJECTIVELY (★), QUANTITATIVELY (+) OR NOT AT ALL (O).

Institution/Activity	Principal Area(s) Covered	Effort	Period(s) and Effort	Total No. Used
I. U.S. National Marine Fisheries Service				421
A. Southwest Fisheries Center				
1. Dolphin-tuna observer program and associated research cruises, 1968 through 1973.	Latitudes 35°N to 15°S, coast to approximately longitude 160°W.	★	Heavy effort nearshore Jan— Feb declining and moving seaward March through remainder of year. Some coastward research Qtr. 4.	
2. Dolphin-tuna observer program and associated research cruises, 1974 through 1979.	Latitudes 35°N to 15°S, coast to approximately longitude 160°W.	+	Same as above, but effort data available as number of ship survey hours per 5° square (see Fig. 3).	
3. Albacore observer program and associated research cruises, 1971 through 1979.	Latitudes 25°N to 46°N, within 250 nm of coast.	★	33 vessels, May through September, generally moving south to north through season.	
B. National Marine Mammal Laboratory				410
1. Pelagic fur seal program				
a. 1958 through 1979	Latitudes 32°N to 62°N, east of USA/USSR Convention line in Bering Sea, east of longitude 180° in remainder of Gulf of Alaska and N. Pacific.	O	Sporadic coverage, largely in summer, principally searching for and collecting fur seals. (See various reports of North Pacific Fur Seal Commission; Kajimura et al., 1980; Stroud et al., 1981). Effort characterized but summary unavailable in useable format.	
b. 1960's	Latitudes 21°N to 35°N, within 150 nm offshore and offshore Baja California as far as Islas Revillagigedos.	O	Cruises working north to south in winter and spring, January through April (Fiscus and Niggol, 1965; Rice 1963a, b; 1974). Effort characterized subjectively but summary unavailable in useable format for this report.	
2. Dall porpoise program 1978 and 1979	Southern Bering Sea and northern Pacific Ocean, near Aleutian Islands. Some cruises in Gulf of Alaska.	O	Observers aboard mother ships and research vessels much of summer. Sighting conditions often poor. Effort summaries described by Bouchet (1981) but unavailable in useable format for present report.	
3. Platforms of opportunity	All areas.	O	Coverage opportunistic, no effort data available.	

TABLE 1.   Continued.

Institution/Activity	Principal Area(s) Covered	Effort	Period(s) and Effort	Total No. Used
II. Naval Ocean Systems Center				140
A. Ship surveys 1965 through 1975	Within 150 nm of coast from latitudes 22°N to 35°N including Gulf of California. Some cruises north to Kodiak, Alaska in spring.	O	Effort data not consistently recorded. Cruises conducted all seasons, but principal effort winter and spring.	
B. Aerial surveys 1968 through 1975	Continental Shelf waters (Shore to longitude 121°W) between latitudes 31°30′N and 34°N (Southern California Bight).	+	Total 29,000 nm surveyed, all months. Effort data retained as transect lines by month (see Fig. 4).	
III. University of California				54
A. Scripps Institution of Oceanography—La Jolla	Principally within 100 nm of coast of California and Baja Calif. and in Gulf of California.	O	1950–1979—miscellaneous cruises with no indication of survey effort by area or season.	
B. Coastal Marine Laboratory Santa Cruz				
1. Ship surveys	Continental Shelf waters between latitudes 31°N and 34°N (Southern California Bight).	+	Effort available as total nm surveyed by month.	
2. Aerial surveys	Continental Shelf waters between latitudes 31°N and 34°N (Southern California Bight).	+	Effort available as total nm surveyed by month.	
IV. Smithsonian Institution Pacific Ocean Biological Survey	Latitudes 27°N to 35°N, coast to longitude 120°W.	O	1967–1968—unable to quantify effort by area or season.	47
Additional sources include: The University of Southern California, the Natural History Museum of Los Angeles County, San Diego Museum of Natural History, Marineland of the Pacific, Sea World, and numerous colleagues.				33* 196**

* unpublished. ** published.

small cetaceans of the eastern North Pacific (Leatherwood and Walker, 1979; Leatherwood, Perrin, Kirby, Hubbs, and Dahlheim, 1980; Dahlheim *et al.*, 1982), we pooled all acceptable data to describe overall distribution and to search for trends in distribution and abundance by season and latitude.   Many of the sightings represented incidental observations from programs for which no measure of survey effort was available; such records were of limited value.   Other incidental records came from programs for which survey effort could be subjectively described, e.g., in terms of general periods and areas of coverage.   These records were somewhat more useful.   The most important records, however, were those obtained from the following three programs which provided quantitative data on survey effort.

Southwest Fisheries Center (SWFC), NMFS
   Scientific observers aboard American tuna vessels and U.S. government re-
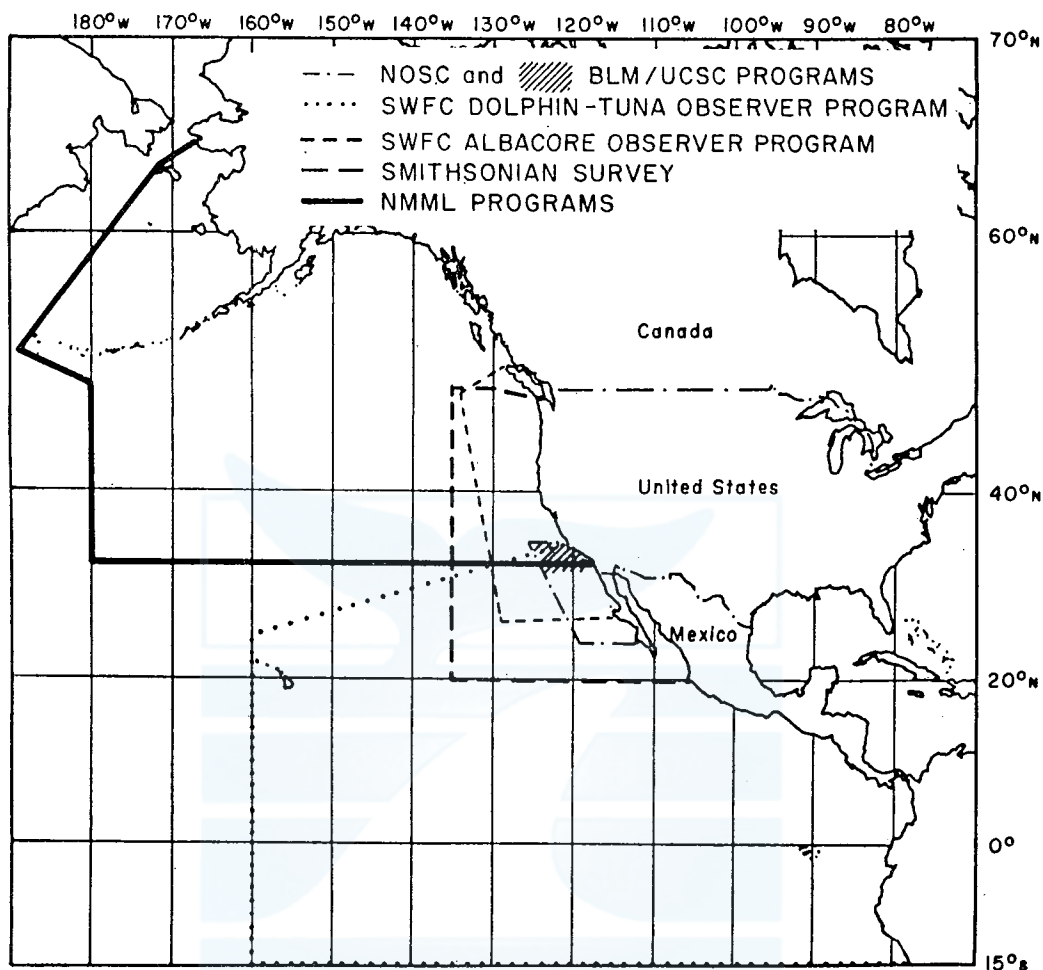
Fig. 2. Approximate areas covered by the principal programs providing sightings of Pacific white-sided dolphins (modified from Leatherwood *et al.*, 1980).

search vessels operating in the eastern tropical Pacific have supplied sightings made in the area from about latitudes 15°S to 35°N, between the shore and about longitude 160°W (Table 1). Sightings from this program were subjected to critical scrutiny using methods explained in detail by Leatherwood (1978). Unverifiable sightings were discarded. Effort (time during which a NMFS marine mammal observer was on watch) was calculated as number of hours of watch within each 5-degree block (Fig. 3). All minutes in a watch series were assigned to the 5-degree block in which the watch series began. Additional information concerning the protocol for data collection in this program is available in the NMFS Observer's Handbook (unpubl. manuscr., SWFC, La Jolla).
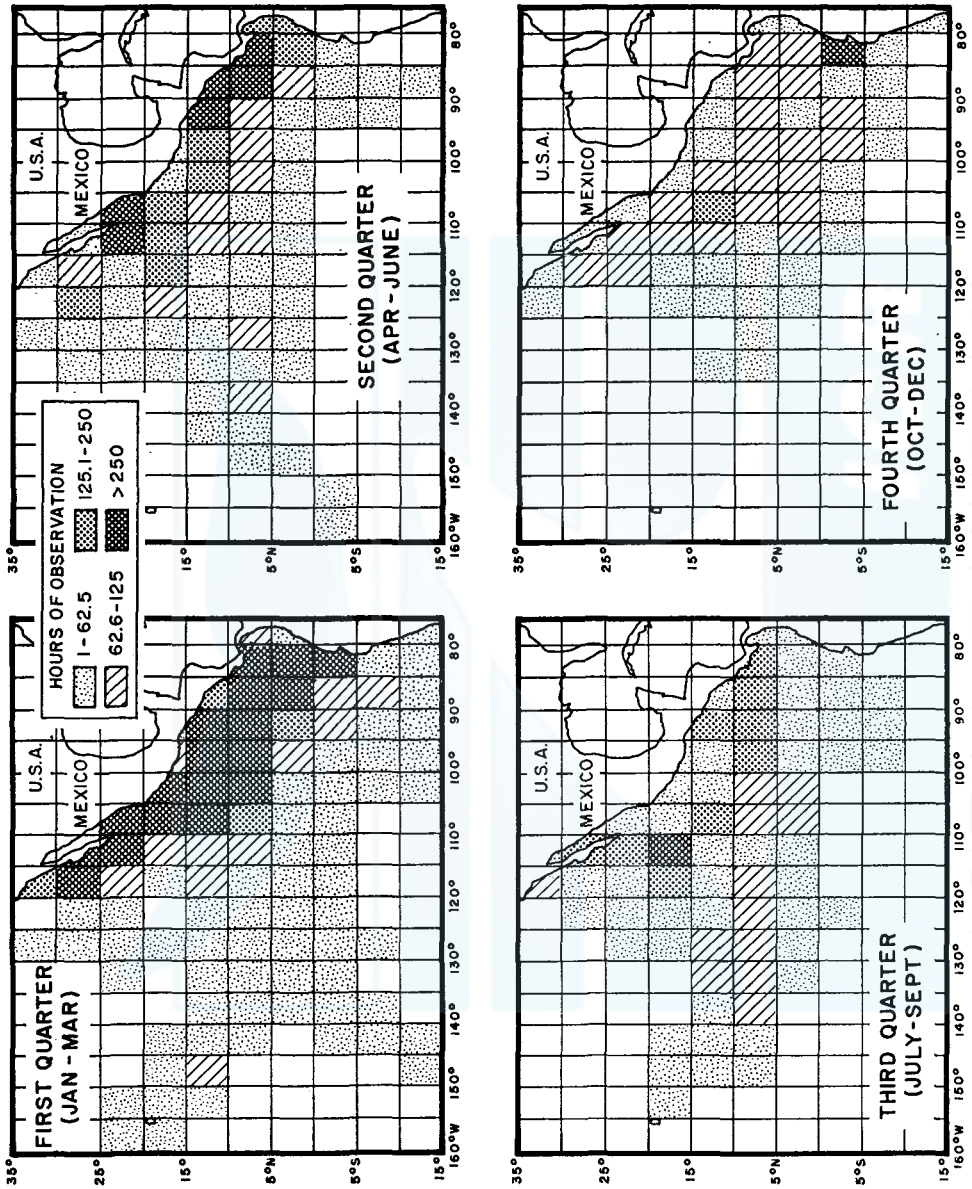
Fig. 3. Ship survey effort by NMFS dolphin-tuna observer program, 1974 to 1979, by quarter.
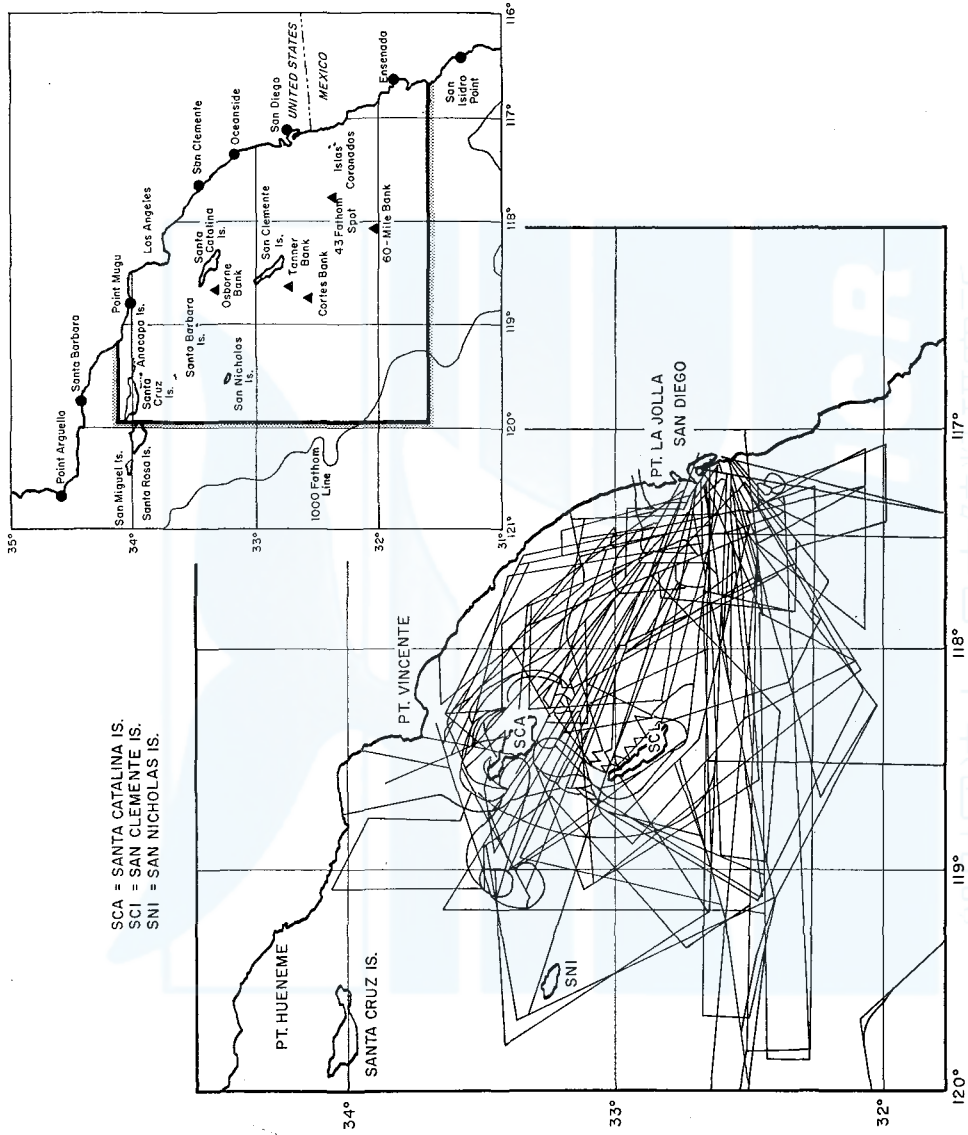
Fig. 4. Area covered by Naval Ocean Systems Center (NOSC) aerial surveys, 1968 through 1976. The lower left figure shows principal transects flown.

Fig. 5. Aerial survey effort by UCSC, May 1975 through March 1976. Numbers in 5-degree blocks denote number of times that area was surveyed by air during the study period. The blocked area corresponds to the area covered by NOSC aerial surveys, 1968 to 1976 (see Fig. 3). The diagonal lines are the UCSC transects (from Dohl *et al.*, 1980).
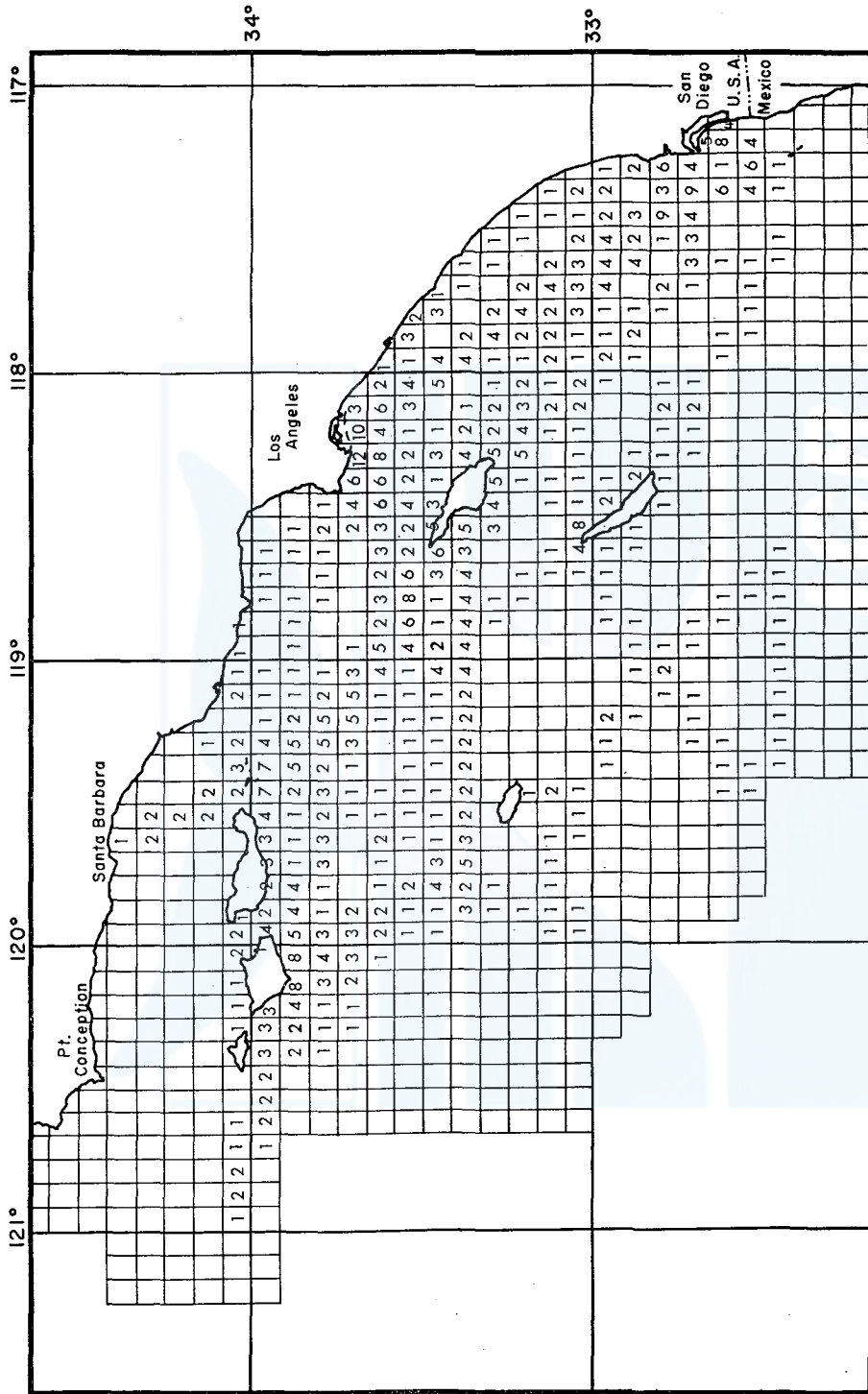
Fig. 6. Ship survey effort by University of California, Santa Cruz (UCSC), April 1975 to March 1976. Numbers in 5-degree blocks denote number of times that area was surveyed by ship during the study period (Dohl *et al.*, 1980).

Naval Ocean Systems Center (NOSC)

Aerial surveys were conducted regularly by the Naval Undersea Center (now NOSC) from January 1968 through April 1976 over the California continental shelf, principally between latitudes 32°N and 34°N (Table 1; Fig. 4). The methods employed in these surveys were described in detail by Leatherwood (1974), Evans (1975), Leatherwood and Walker (1979), and Leatherwood *et al.* (1980). Sightings were critically evaluated using the review procedures of the SWFC system referred to above, and unverifiable sightings were discarded. Effort was given as plots of transect lines (Fig. 4) and estimates of nautical miles (nm) flown.

University of California, Santa Cruz (UCSC)

Shipboard and aerial surveys sponsored by the U.S. Department of the Interior, Bureau of Land Management (BLM), were conducted in the Southern California Bight during 1975 and 1976 by the Coastal Marine Laboratory, University of California, Santa Cruz (Dohl *et al.*, 1980) (Table 1). Transects were designed to provide uniform coverage of the entire study area throughout the year. Methods of quality control on sightings data were not reported. Therefore, because original data entries were unavailable to us for review, we have simply accepted sightings on the assumption that they were subjected to adequate quality control by the program's internal review process. Effort was characterized as the number of times each 5-minute block was surveyed (Figs 5 and 6) and as the number of nautical miles covered (Table 4). Note the substantial overlap in aerial coverage between NOSC and UCSC surveys (Figs 4, 5, 6).

Other Sources

In addition to the unpublished sources of data, we examined scientific publications and extracted sighting records from them. For all these records, we collected, as available, date, location, number of animals, and information source. We assembled a total of 1300 reliable records, 1104 unpublished accounts from various programs and 196 previously published. Except for obvious misidentifications or obscure references with irreconcilable disparities, we assumed published records reflected correct identification. Sightings published twice or more were only entered in the data base once. Each known at-sea collection for which date, location, and number of animals was available was also considered to represent a sighting of a herd. For each map and analysis we used all appropriate sightings. For those sightings in which herd size was recorded as a range (e.g., 45–50 animals), we used the midpoint rounded to the lowest integer (e.g., 47).

Data were grouped by various combinations of quarter, 1- and 5-degree latitude belts, and depth zones (inside or outside the approximately 1,000 fm isobath). Maps, histograms, descriptive statistics, and frequency distributions were prepared, and grouped or paired samples were compared to detect patterns of occurrence (Table 2). For numbers of herds and numbers of animals, we determined sample sizes (N), sum, mean (x), standard deviation (s), standard error (s_x) and range (Table 3).

TABLE 2. THE VARIOUS COMBINATIONS IN WHICH AVAILABLE SIGHTINGS
DATA WERE EXAMINED

	Overall			Quarterly					Depth zone by 5° belt and quarter	
				1° belt			5° belt			
No. Herds	M	D	H	M	D	H	D	H	D	H
No. Individuals	M	D	H	M	D	H	D	H	D	H
Herd size		F	D		—			—		—	

M=maps
H=histograms
D=descriptive statistics
F=frequency distribution

TABLE 3. NUMBER OF HERDS, TOTAL NUMBER OF ANIMALS, AND HERD
SIZES FOR PACIFIC WHITE-SIDED DOLPHINS, BY QUARTER AND
5° LATITUDE BELT, FROM LATITUDE 20°N TO 60°N

Latitude belt	Quarter	No. Herds	Total no. animals	Mean herd size	St. dev.	St. error	Min. herd size	Max. herd size
20–25	I	23	6,196	269.39	682.28	142.27	1	3,000
20–25	II	7	210	30	44.99	17.00	1	125
20–25	III	3	105	35	35	—	10	75
20–25	IV	4	46	11.50	9.95	4.98	1	20
25–30	I	99	9,096	91.88	466.24	46.86	1	3,500
25–30	II	85	5,544	65.22	250.72	27.19	1	2,000
25–30	III	105	30,665	292.05	936.48	91.39	1	6,000
25–30	IV	55	6,570	119.45	321.03	43.29	1	1,750
30–35	I	87	8,722	100.25	217.41	13.31	1	1,000
30–35	II	49	4,324	88.24	209.02	29.86	1	1,000
30–35	III	38	5,425	142.76	417.03	67.65	1	2,500
30–35	IV	66	3,217	48.67	115.84	14.26	1	750
35–40	I	154	3,565	23.15	59.57	4.80	1	500
35–40	II	119	2,444	20.54	64.20	5.89	1	500
35–40	III	38	851	22.39	49.31	8.00	1	300
35–40	IV	16	996	62.25	125.10	31.28	1	450
40–45	I	8	522	65.25	112.68	39.84	2	300
40–45	II	28	1,731	61.82	160.69	30.37	1	725
40–45	III	56	2,220	39.64	61.58	8.23	1	275
40–45	IV	8	71	8.88	14.67	5.19	2	45
45–50	I	17	184	10.82	10.31	2.50	1	30
45–50	II	47	3,914	83.28	210.74	30.74	1	1,000
45–50	III	39	2,658	68.15	163.68	26.21	1	900
45–50	IV	6	484	80.67	94.09	38.41	2	250
50–55	I	9	535	59.44	43.41	14.47	5	250
50–55	II	8	1,399	174.88	337.83	119.44	3	100
50–55	III	15	204	13.60	15.32	3.96	1	1,000
50–55	IV	11	748	68	107	32.26	1	50
55–60	I	—	—	—	—	—	—	—
55–60	II	12	2,215	184.58	572.17	165.17	2	2,000
55–60	III	15	2,057	137.13	258.15	66.65	1	1,000
55–60	IV	3	529	176.33	280.31	161.84	12	500

For analysis of latitudinal effects, only groupings by 5-degree latitude belt resulted in adequate sample sizes. One-degree belts were retained for mapping. Maps were produced showing number of herds (Figs 7 and 8) and number of animals (Figs 9 and 10), by one-degree blocks for all samples combined. Charts were made on a DEC-PDP 11/34 using the AMPS Mapping Package (Analytical Software, Inc.). Densities for each block on the sighting charts were calculated by summing the number of herds and number of animals sighted in each block each quarter. For example, all the animals sighted from longitudes 117°00′W to 117°59′W and from latitudes 32°00′N to 32°59′N were counted as being in the block 32°N by 117°W.

The following problems with data ruled out the use of significance tests on any of the data sets: (a) sightings were not collected at random; (b) sightings could not be assumed to be independent of one another, because of the animals' tendency to aggregate and variability among observers in defining and scoring groups as
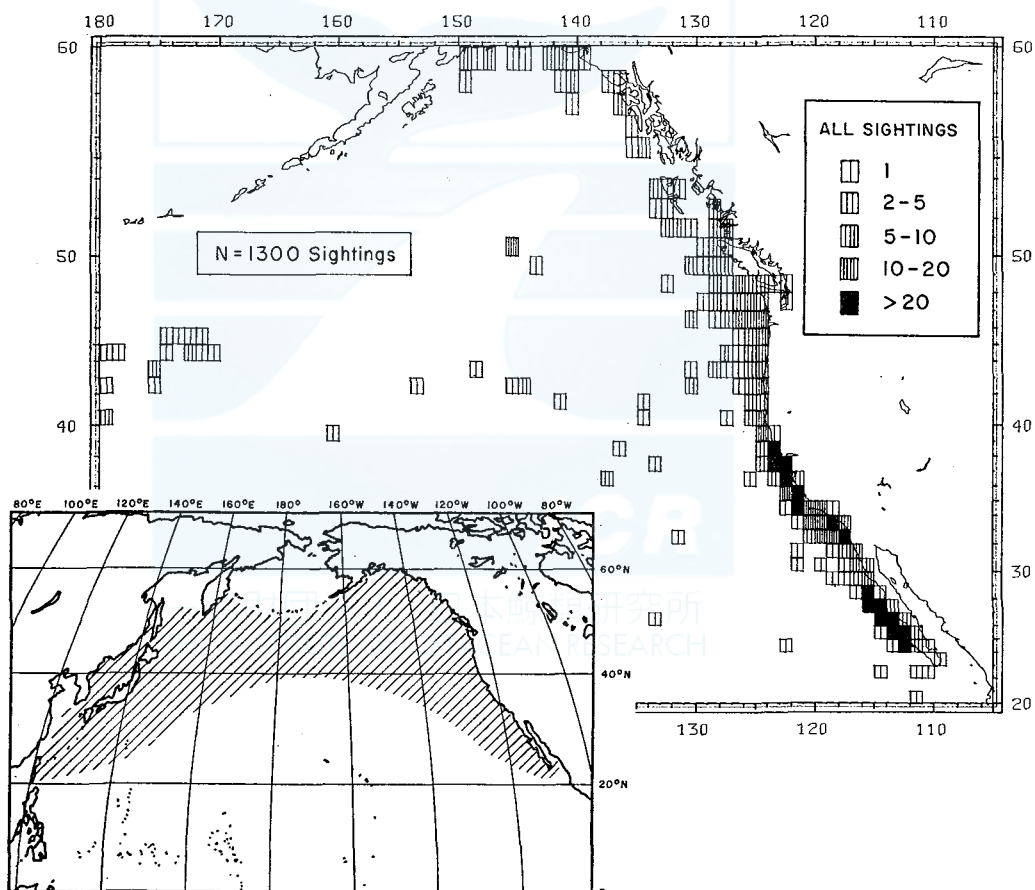
Fig. 7. Number of sightings (herds) of Pacific white-sided dolphins by 1-degree block from all seasons and all sources, 1949 to 1979. The inset illustrates the species' probable range.

Fig. 8. Number of sightings (herds) of Pacific white-sided dolphins by 1-degree block, by quarter, from all sources, 1949 to 1979.
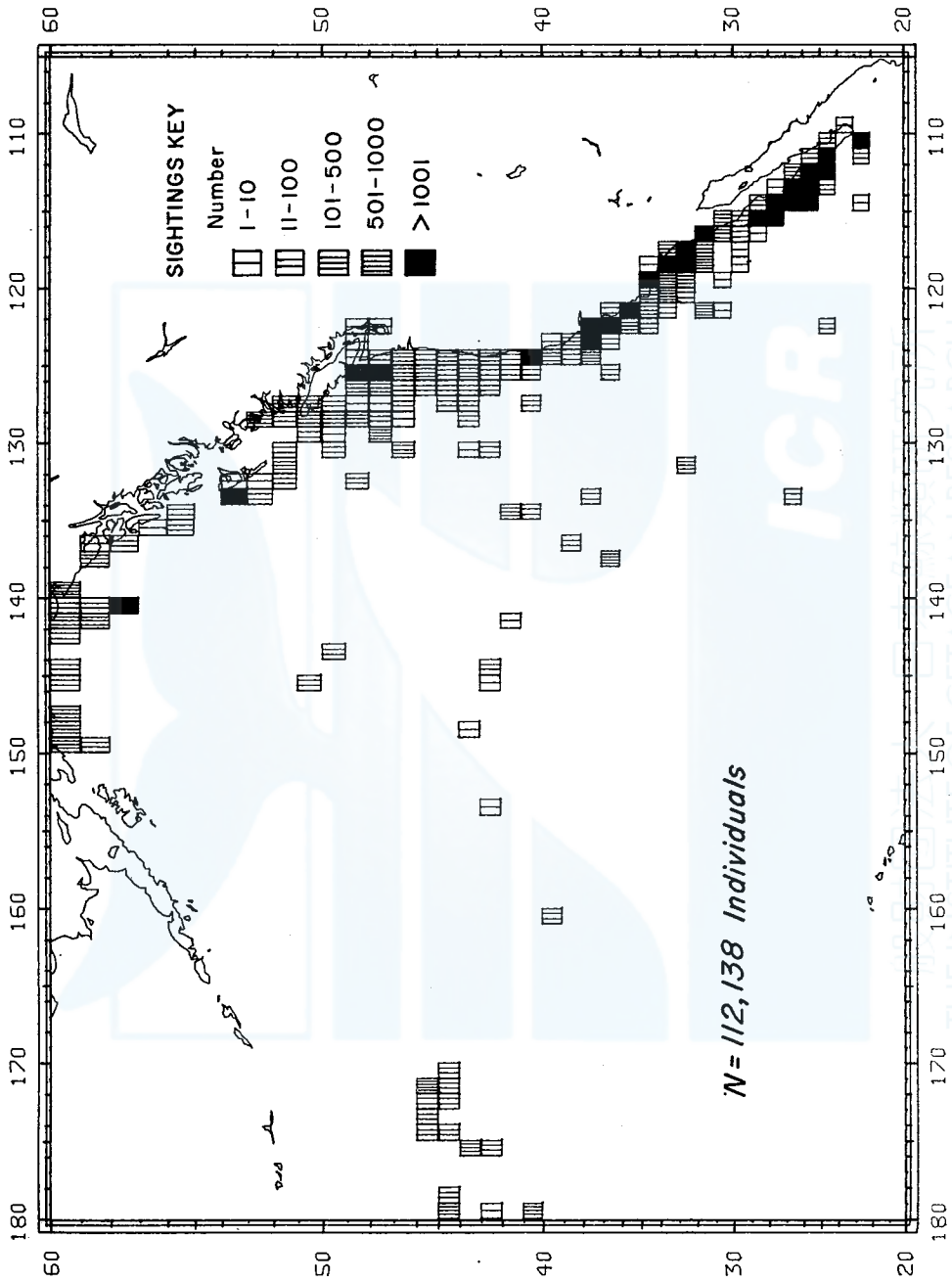
Fig. 9.   Total number of Pacific white-sided dolphins observed by 1-degree block, from all sources, 1949 to 1979.
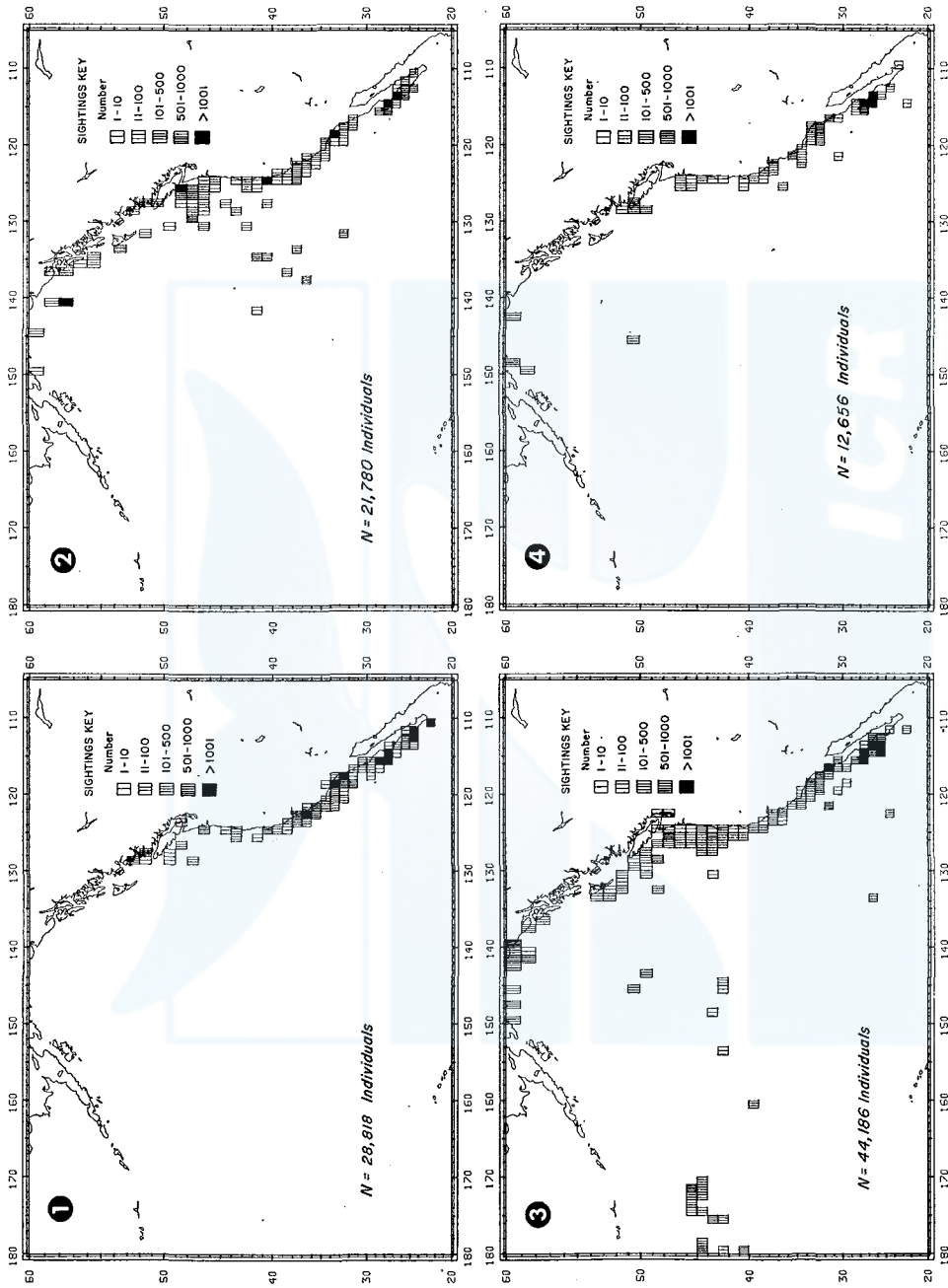
Fig. 10. Total number of Pacific white-sided dolphins observed by 1-degree block, by quarter, from all sources, 1949 to 1979.

separate small herds or "superherds"; and (c) pooled effort was impossible to quantify. We feel that even if statistical significance were demonstrated, it would not be possible to ascribe any biological significance to the results. Therefore, to define patterns for the area overall, we depended solely on direct examination of graphic presentations of the data.

Data from the Southern California Bight were examined in somewhat greater detail. For the NOSC aerial surveys, we calculated number of herds per hundred nautical miles and number of dolphins per nautical mile flown (Table 5, I_1 and I_2,

TABLE 4. SUMMARY OF EFFORT AND SIGHTINGS OF PACIFIC WHITE-SIDED DOLPHINS BETWEEN LATITUDES 32°N AND 35°N AND A CALCULATED INDEX OF DENSITY FROM UCSC AERIAL SURVEYS, MAY 1975–MARCH 1976

Period	Nautical miles flown	Number of animals seen	I_2 Number of dolphins per n.m.
May	954	2,024	2.120
July	2,080	2,540	1.220
August	1,383	70	0.050
September	765	100	0.140
October	1,935	292	0.150
November	2,034	1,892	0.930
December	934	0	0.000
January	3,255	12	0.003
February	2,520	7	0.003
March	1,800	768	0.043

TABLE 5. INDICES OF DENSITY OF PACIFIC WHITE-SIDED DOLPHINS (*L.o.*) IN THE SOUTHERN CALIFORNIA BIGHT (32°N TO 34°N), 1968–1976, FROM NOSC AERIAL SURVEYS. THE TOTAL NUMBER OF HERDS SEEN IS FOLLOWED IN PARENTHESES BY THE NUMBER OF HERDS FOR WHICH ESTIMATES OF NUMBERS WERE AVAILABLE. ALSO SHOWN ARE INDICES OF DENSITY FOR NORTHERN RIGHT WHALE DOLPHINS (*L.b.*) FOR THE SAME AREA (FROM LEATHERWOOD AND WALKER, 1979)

Month	Effort flown in n.m.	Total no. of herds *L.o.*	I_1-Herds per 100 n.m. *L.o.*	I_1-Herds per 100 n.m. *L.b.*	Total no. of indiv. *L.o.*	I_2-Dolphins per n.m. *L.o.*
January	1,890	16 (15)	0.85	3.30	2,687	1.42
February	2,005	12 (18)	0.60	11.48	1,626	0.81
March	2,645	7	0.26	1.38	766	0.29
April	4,475	23 (15)	0.51	2.04	3,626	0.81
May	2,150	3	0.14	0.39	90	0.04
June	1,390	1	0.07	0	50	0.04
July	2,120	4	0.19	0	268	0.13
August	2,267	1	0.04	0	6	<0.01
September	1,470	3	0.20	0	68	0.05
October	1,795	3 (2)	0.17	0.36	296	0.16
November	550	3 (2)	0.55	0.54	159	0.29
December	2,025	19 (13)	0.94	1.77	2,123	1.05
Totals	24,762	95 (72)	0.384	—	11,766	0.48

respectively). Because herd size was not estimated for each sighting, in calculating the I_2 values we: (a) found that no significant variability in herd sizes among months could be demonstrated and (b) assumed that those for which herd size estimates were available (72) were representative of all 95 herds. Therefore, in estimating number of animals seen per month, each empty cell was filled with the overall
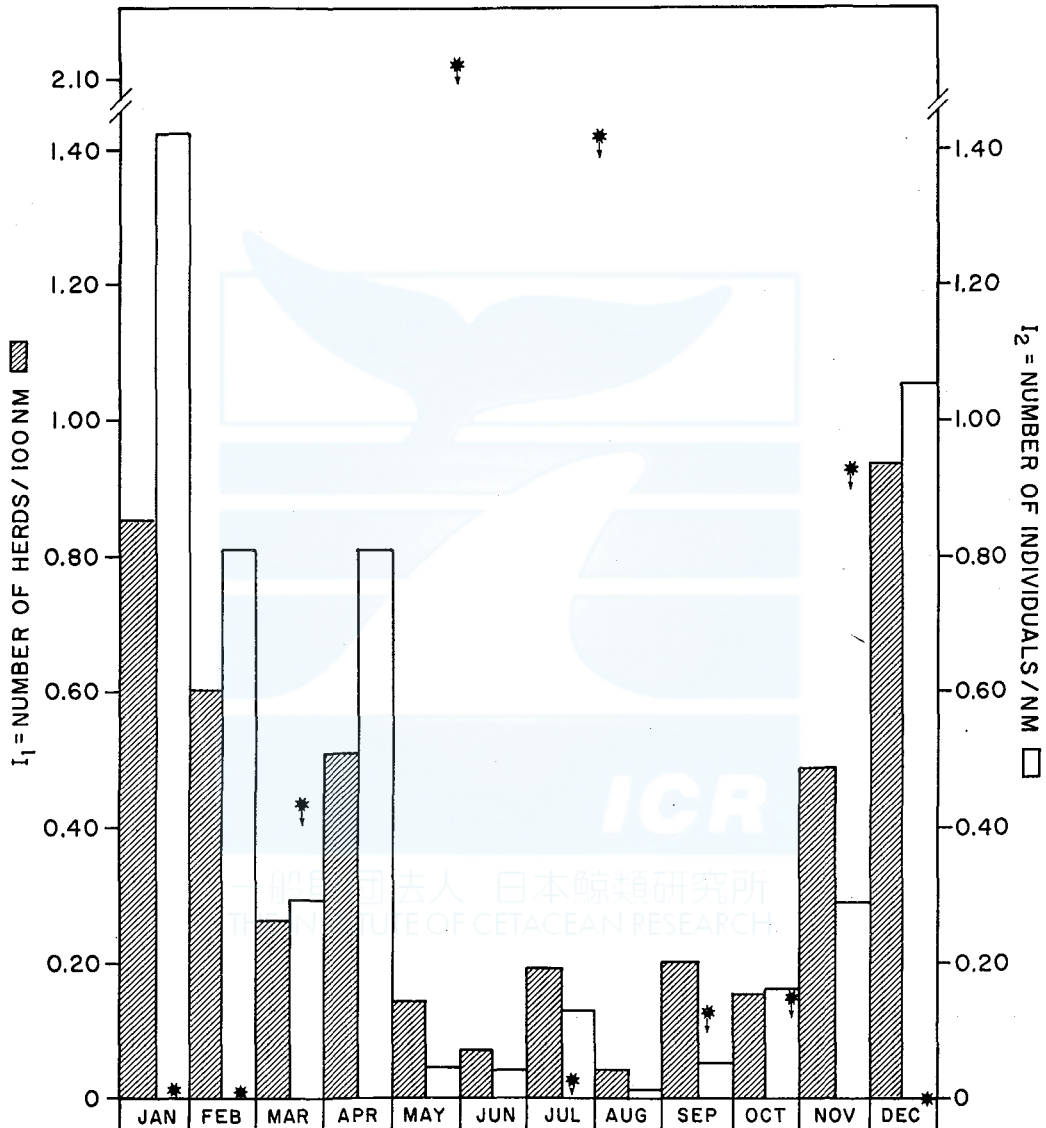
Fig. 11. Indices of abundance of Pacific white-sided dolphins off Southern California 1968 through 1976, based on NOSC aerial surveys. The * indicates I_2 values calculated from Dohl et al., 1980, Table III-93, for aerial surveys of the same area, May 1975 to March 1976.

mean (x=145.7, s=271.2).

For comparison, we converted indices of density for northern right whale dolphins in the same area, reported by Leatherwood and Walker (1979) as the number of herds or animals per square nautical mile, to I_1 and I_2 values and presented those in Table 5. For the UCSC aerial survey data (Dohl *et al.*, 1980), we also calculated monthly I_2 values (Table 4).* Trends indicated by the two programs (NOSC and UCSC) were compared graphically (Fig. 11), but no attempt was made at a rigorous analysis of observed patterns.

RESULTS AND DISCUSSION

Overall Pattern of Distribution

Herds of Pacific white-sided dolphins were seen in all 5-degree latitude belts between latitudes 20°N and 60°N in all quarters of the year, except for latitudes 55°–60°N in quarter I, January–March. The 1,300 herds (112,138 individuals) included in the analysis were widely distributed from the continental shelf throughout the pelagic temperate eastern North Pacific, although records were more abundant within the few coastal 1-degree blocks in each latitude belt (Figs 7 through 10). The apparent coastward concentration as well as the areas of higher density observed north to south along the coast probably reflect levels and centers of observational effort (Fig. 12), with sightings clustered near Seattle, near the Monterey / Santa Cruz area, and within the 35° to 30°N and 30°N to 25°N latitude belts.

The steady decreases in number of sighting records throughout the year, from 407 herds in the first quarter to 177 herds in the fourth quarter, also probably reflect effort. In fact, for all the data combined, there were no detected trends in distribution of herds which could not be explained readily on the basis of the survey effort alone. It is only when records are examined regionally, with emphasis on the three programs permitting quantitative analysis, that any patterns can be discerned which might be considered biologically meaningful.

The probable North Pacific range of white-sided dolphins, inferred from records presented herein and published records from the western North Pacific, is shown in the inset to Fig. 7. Available data suggest a continuous range across the North Pacific. In the area covered by this paper, sightings decrease in the area west of longitude 135°W and south of latitude 45°N, but there has been insufficient observational effort in pelagic areas to confirm the existence of a hiatus between eastern and western North Pacific " populations ".

Distribution North of Latitude 40°N

Sample sizes are small and effort unquantifiable north of latitude 40°N. Sightings do occur there throughout the year, although almost all the more north-

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* Estimates of density and indices of density from previous programs are presented in the units reported. Original data were unavailable to us; so, we were unable to translate to common units.
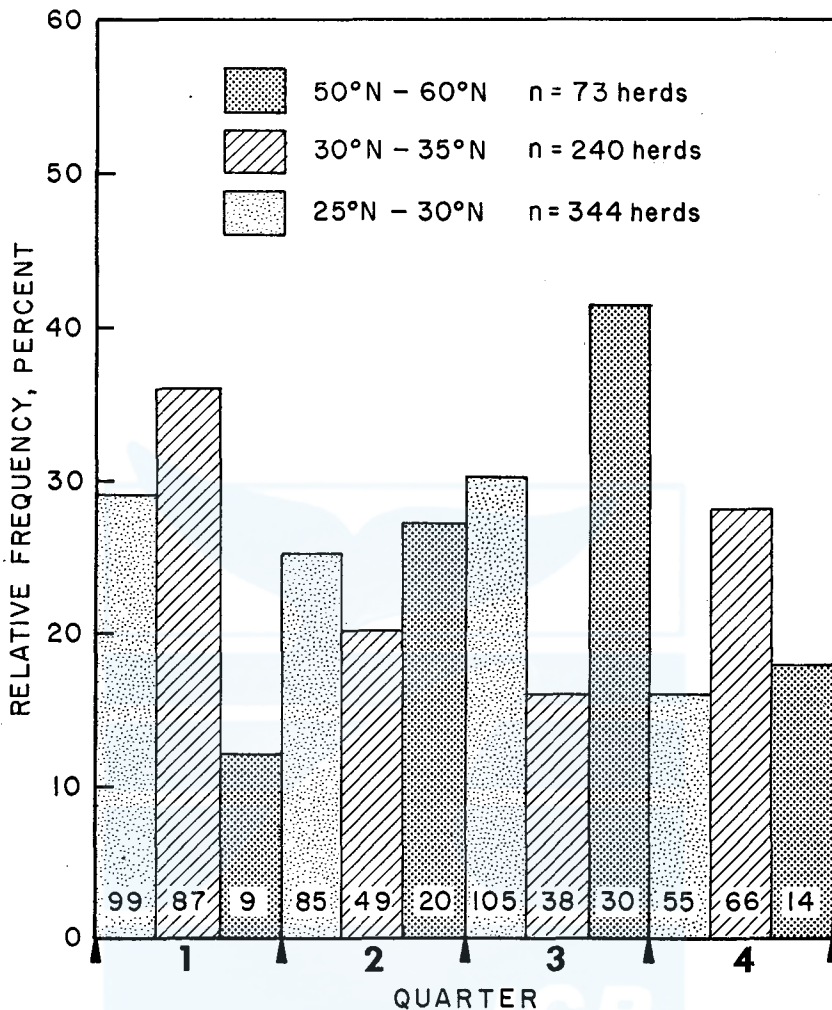
Fig. 12.   Relative distribution of sightings by quarter within the three areas of greatest interest.   The number of herds comprising each class interval is shown.

ern records refer to quarters II and III (spring through fall), and almost all the sightings for quarters IV and I are in coastal regions.   In the Gulf of Alaska, the seasons when Pacific white-sided dolphins are reported most frequently and widely are also the periods of most intensive fishing and research activity.   We have no way of determining whether this apparent seasonal pattern in dolphin distribution is real or an artifact of observational effort.   Based on opportunistic sightings of 3, 8, 50, and 15 herds in quarters I through IV, respectively, Consiglieri and Braham (1982) concluded that this species, indeed, occurs seasonally in the Gulf of Alaska. They further concluded, based on the same set of sightings, that in southeastern and southern Alaskan waters Pacific white-sided dolphins occur principally on the continental shelf.   Further evidence that Pacific white-sided dolphins are present

seasonally off southern Alaska is provided by Hall and Tillman (1977) and Hall (1979), who reported that despite extensive year-round aerial and ship surveys in Prince William Sound and immediately adjacent to its entrances, Pacific white-sided dolphins were observed only once—in October just outside Montague Strait. Currently available data are opportunistic in nature or limited in region, and therefore inconclusive. The question of seasonality of occurrence of Pacific white-sided dolphins in the Gulf of Alaska and North Pacific north of latitude 40°N, particularly in pelagic regions, cannot be resolved without systematic seasonal sampling over a broader area than has been surveyed to date (1982).

From available data, we are unable to verify the reported occurrence of Pacific white-sided dolphins in the Bering Sea (Clark, 1945). The various programs of NMML (see Table 1), the sources of incidental sightings used by Consiglieri and Braham (1982), and 8 one-hundred hour aerial surveys of the eastern Bering Sea conducted between March 1982 and April 1983 (Leatherwood, 1983) likely provided adequate coverage of the waters north of the Aleutians to judge whether these dolphins occur regularly in the Bering Sea. The absence of records is taken to mean that they do not.

Distribution South of Latitude 23°N

Similarly, we regard the evidence that Pacific white-sided dolphins do not occur regularly south of about latitude 23°N to be convincing (see Figs 7 and 9). Coverage of the waters south of Baja California has been extensive in both area and season.

Although observational effort in the NMFS dolphin-tuna program generally decreased from quarter I to quarter IV according to the fishing schedule of the tuna fleet, there was some effort in a broad area south of latitude 30°N year-round (Figs 2 and 3). In addition to the shipboard observations, three extensive aerial surveys of the eastern tropical Pacific tuna grounds have been conducted by NMFS (Smith, 1975; Barham, Evans and Coe, 1975; Barham and Powers, 1977; Powers and Barham, 1977; Holt and Powers, 1982). Therefore, we consider the low number of sightings there—five confirmed south of latitude 23°N, the southernmost at 20°N—to be biologically meaningful. If appreciable numbers of Pacific white-sided dolphins had been present, there undoubtedly would be more records.

Depth Preferences

Northern and southern limits of the species' range are more readily defined than are its inshore-offshore limits. There have been a few sightings in water as shallow as 20 fathoms (Consiglieri and Braham, 1982; NOSC unpublished records; Leatherwood, personal observations) though these appear exceptional excursions into shallow water. Otherwise, these dolphins are encountered widely in continental shelf, continental slope, and offshore zones. Because of uncertainty in position records, we cannot report the maximum depth of water where Pacific white-sided dolphins have been seen. However, the westernmost records in the study area were plotted at locations in which surrounding water for a radius of at

least 100 nm was more than 3000 fms deep.

Little can be said about the relative frequency of occurrence of Pacific white-sided dolphins in waters of different depth. The fact that, overall, most sightings were made inshore of the approximately 1000 fm isobath probably reflects effort patterns rather than an aspect of dolphin distribution.

There does appear, however, to be a tendency for Pacific white-sided dolphins to occur nearer to the coast south of about latitude 30°N. The effort in pelagic waters between latitudes 20°N and 30°N was appreciable and the encounters with Pacific white-sided dolphins few.

Seasonal Trends in Distribution

The only two portions of the study area in which observed distribution patterns are not likely an artifact of sampling effort are the waters off Baja California and in the Southern California Bight. Off Baja California, the effort is tied to fishing and research activities of the tuna fishery, essentially declining steadily throughout the calendar year with a slight increase in the fourth quarter associated with research cruises and early departures from San Diego by fishing vessels bound for the eastern tropical Pacific (Fig. 3). Despite this declining trend in effort, the number of sightings and number of animals per quarter off Baja California did not decline consistently through the calendar year (Figs 8 and 10, Table 6). In fact, for the area between latitudes 25°N and 30°N, the number of sightings and total number of animals observed in the third quarter were substantially greater than the number observed during the previous two quarters (Table 3). This sharp increase in numbers during a period of relatively low sampling effort is of interest. It suggests an influx of animals to this area during late summer and early fall. There is no reason to believe such an influx would consist of animals moving inshore from the west. Rather, judging by published accounts about the seasonal movements of Pacific white-sided dolphins south of Point Conception (e.g. Brown and Norris, 1956; Leatherwood and Reeves, 1978; Leatherwood *et al.*, 1982), it seems most reasonable to us that these are dolphins moving southward from the area off Southern California between latitudes 30°N and 35°N.

The monthly indices of density from the NOSC aerial surveys indicate that Pacific white-sided dolphins are at their peak density and peak number off Southern California from November through April, and are less common from late spring

TABLE 6. DETAILS OF EFFORT AND SIGHTINGS OF PACIFIC WHITE-SIDED DOLPHINS, 25°N AND 30°N, FROM NMFS DOLPHIN-TUNA PROGRAM, 1974 THROUGH 1979. I_1 AND I_2 VALUES ARE NUMBER OF HERDS AND NUMBER OF INDIVIDUALS PER SURVEY HOUR, RESPECTIVELY.

Quarter	Approximate number of survey hours	Number of sightings	I_1	Number of animals	I_2	Mean herd size $\bar{H}$
I	>375	99	<0.27	9,096	<24.26	92
II	565	85	0.15	5,544	9.83	65
III	250	105	0.44	30,665	3,738.66	292
IV	190	55	0.29	6,570	34.58	119

through late fall (Fig. 11, Table 5).　This seasonal pattern is consistent with that reported for the area by previous investigators, based on subjective impressions (e.g., Norris and Prescott, 1961; Leatherwood *et al.*, 1972) or on preliminary analysis of the NOSC data (Leatherwood and Reeves, 1978; Leatherwood *et al.*, 1982).　It is also very similar to the seasonal pattern reported by Leatherwood and Walker (1979) for the northern right whale dolphin, a sympatric species with which Pacific white-sided dolphins have a strong affinity in coastal waters (Table 5). From these data, Pacific white-sided dolphins appear to reach their lowest densities off Southern California during the periods discussed above, when they are apparently at their highest densities off Baja California.　We emphasize that the argument for a relationship between these two phenomena is only circumstantial; there is no direct evidence of a coast-wise migration.　The origin of the apparent " immigrants " to Baja California waters in quarter III and the destination of the " emigrants " from Southern California in quarters II and III remain unknown. The peak density off Southern California is 1.42 individuals per nm (Fig. 11); off Baja California it is reported to be 0.06 individuals per nm^2 (Fox, 1977).

The trends indicated by the UCSC aerial surveys are slightly inconsistent with those indicated by the NOSC program; the latter covered a slightly more coastal area.　Densities derived from data collected in the 10-month UCSC program fluctuate considerably, with about 1–2 individuals per nm^2 in May, July, and
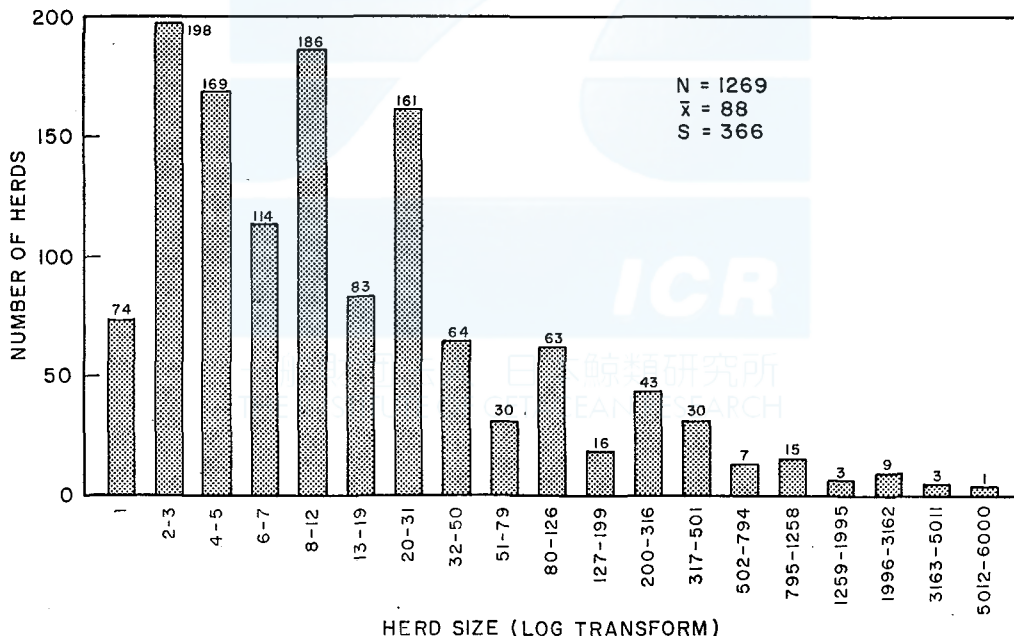
Fig. 13.　Log transform of sizes of herds of Pacific white-sided dolphins observed in the eastern North Pacific, 1949 to 1979.　Number of herds comprising each class interval is shown.　The log transform was performed strictly for presentation.　No analysis was conducted on logs of data.

November, and much lower densities in all other months (Table 4). The differences may be due to small sample sizes and the short period of coverage in the UCSC program. However, if they are not, then the results may indicate a shift of the Southern California portion of the population offshore and northwestward in quarters II and III.

Hubbs (1961) described a major transition zone for marine fauna along the outer coast of Baja California at about 24°N latitude, in the vicinity of Magdalena Bay. Au, Perryman and Perrin (1979) noted another water-mass change at the mouth of the Gulf of California, where the fauna tends to change from temperate to tropical. As a temperate-zone species, the Pacific white-sided dolphin probably is influenced by these oceanographic changes. In the areas of most intensive observational effort, between latitudes 20°N and 30°N, it was observed mainly shoreward of the outer margin of the California current (Owen, 1974), suggesting that it is principally an inhabitant of rich upwelling waters.

Trends in Herd Size

The overall distribution of herd sizes is shown in log-transform as Fig. 13.
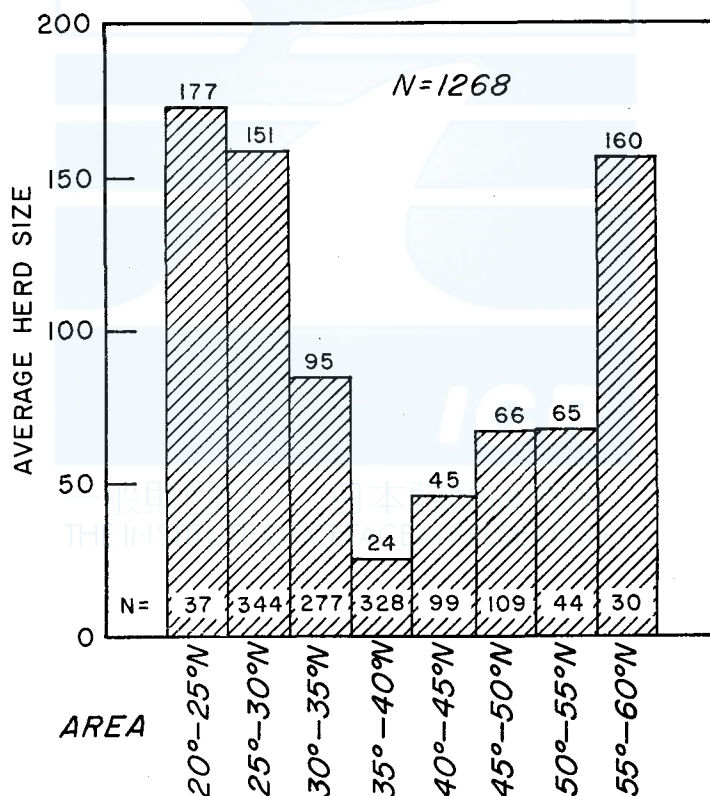
Fig. 14. Mean herd sizes by 5-degree latitude belts, from all sources, 1949 to 1979. Mean values are shown above each class interval. Number of herds comprising each class interval is shown.

The number of animals in the 1,269 sightings for which "group" size estimates were available ranged from 1 to 6,000, about a mean of 88. Above about 20 individuals, the apparent "pulses" in group size are probably spurious, being caused by the tendency of observers to classify estimates into rounded units. Herd sizes varied over the entire geographic range of the sightings (Fig. 14). Those north of latitude 55°N and south of latitude 30°N were significantly larger than those between 30°N and 55°N (n=1,268, F=3.69, p<0.01). In the northernmost area (north of 55°N), where sea-surface conditions are consistently inhospitable to cetacean surveys, it is possible that bad weather and observer bias resulted in a tendency to see and record only large herds. In the other two areas (south of 30°N and between 30°N and 55°N), we assume that observers could detect herds of various sizes and that most participants were able to estimate herd size in a relatively accurate and consistent manner. Therefore, we do not believe the observed differences are artifactual. It is unclear why herds would be larger off Baja California than elsewhere. Perhaps there are inherent differences in herd-size estimation from aircraft (the principal platform used for observations between latitudes 30°N and 35°N) and ships (the platform used almost exclusively south of 30°N).

ACKNOWLEDGEMENTS

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SECOND RECORD OF SPECTACLED PORPOISE
FROM SUBANTARCTIC SOUTHWEST PACIFIC

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ABSTRACT

An incomplete skull of unknown sex of a sub-adult spectacled porpoise
(*Phocoena dioptrica* Lahille, 1912) was collected at Macquarie Island (54°30′S,
159°00′E) in July 1957. Cranial measurements are given, and the specimen
is compared with other phocoenids. This is the second specimen of *P. dioptrica*
reported from the subantarctic southwest Pacific, and this record adds sup-
port to the suggestion that the species may have a circumpolar distribution in
subantarctic latitudes.

INTRODUCTION

The spectacled porpoise (*Phocoena dioptrica* Lahille, 1912) is a little-studied austral
species of the Family Phocoenidae. It is known primarily on the basis of speci-
mens from the southwest Atlantic Ocean (Brownell, 1975), particularly Tierra del
Fuego (Goodall, 1978; Goodall and Cameron, 1979). Hitherto, the only speci-
men collected outside South American waters was National Museum of New
Zealand (NMNZ) Ma1670, from Auckland Islands, southwest Pacific (Baker,
1977). The species apparently has been sighted alive near New Zealand (Caw-
thorn, 1977), and possibly Kerguelen (Frost and Best, 1976). Here we report de-
tails of a second specimen of *P. dioptrica* from the subantarctic southwest Pacific.

DESCRIPTION OF SPECIMEN

The specimen is an incomplete skull (Plates I and II, Figs 1–4) of unknown sex,
collection number C10323, in the National Museum of Victoria (NMV), Melbourne,
Victoria, Australia. It was collected at Aerial Cove, Cataline Point, Macquarie
Island (latitude 54°30′S, longitude 159°00′E) by S. Csordas (Australian National
Antarctic Research Expedition) on 24 July 1957. The skull is damaged, and lacks

TABLE 1. CRANIAL MEASUREMENTS OF *PHOCOENA DIOPTRICA*,
NMV C10323, TO NEAREST MILLIMETRE

Measurement	Millimetres
Condylobasal length	283
Length of rostrum	111
Width of rostrum at base	81
Width of rostrum at mid-length	54
Width of premaxillae at mid-length	28
Width of rostrum at 60 mm anterior to rostrum base	52
Width of rostrum at three-quarters length, measured from posterior end	43
Distance from tip of rostrum to external nares	153
Distance from tip of rostrum to broken anterior border of right internal naris	154
Preorbital width at level of most ventrally-produced portion of frontal	127
Supraorbital width, level with anterior border of right external naris	136
Greatest postorbital width	159
Greatest width of external nares (immediately posterior to broken tips of premaxillae)	34
Greatest width of premaxillae (level with anterior edge of right external naris)	46
Greatest parietal width (at parietal-squamosal-exoccipital suture)	138
Vertical external height of braincase from mid-line of basisphenoid to summit of supraoccipital	107
Internal length of braincase from hindmost limit of condyles to foremost limit of cranial cavity along mid-line	107
Greatest length of left temporal fossa	>59
Minor diameter of left temporal fossa	30
Projection of premaxillae beyond maxillae at tip of rostrum	3
Distance from foremost end of junction between nasals to estimated hindmost point of margin of supraoccipital crest	41
Length of right orbit, from most ventrally produced preorbital portion of frontal to broken anterior edge of postorbital process	45
Length of antorbital process of right lacrimal	32
Greatest width of internal nares estimated (width of right internal naris, 28)	56
Length of upper right alveolar groove	89
Deviation of skull from symmetry in dorsal view	ca. 4 degrees

teeth, posterior ends of the premaxillae, part of the left supraorbital process of the frontal, the apices of both postorbital processes, lateral portions of the supraoccipital, both squamosals, all but a fragment of left pterygoid, the hamulus and outer lamina of right pterygoid, and the left and partial right paroccipital processes. The vertex and the apices of the rostrum and right supraorbital process are abraded. The specimen exhibits no noteworthy differences from previously described individuals of *P. dioptrica*.

The absolute age of the specimen cannot be determined, as teeth, which might exhibit incremental growth lines, are absent. Other cranial features suggest that the animal is sub-adult. Traces of the frontoparietal suture remain, and the basisphenoid-presphenoid suture was not fused, which suggest immaturity, but the fusion of interparietal and parietal indicates that the specimen is at least older than the equivalent of age-class III of *Stenella attenuata* as defined by Perrin (1975).

Measurements of NMV C10323 (after Perrin, 1975: Table 2) to the nearest 1 mm are given in Table 1.

DISCUSSION

Extant species of phocoenid are generally differentiated on the basis of external morphology, and the only comparative description of the skulls of species of *Phocoena* that we are aware of is that of Norris and McFarland (1958).   Only two phocoenid skulls (*P. phocoena*, NMV C24749; *P. dioptrica*, NMNZ Ma1670) were available to us for comparison with the Macquarie Island specimen.   Thus, we base our identification of NMV C10323 primarily on descriptions and/or illustrations of phocoenid skulls given by Norris and McFarland (1958), and other authors, as follows: *Phocoena phocoena*, Hamilton (1941), Norris and McFarland (1958), Van Bree *et al.* (1977); *P. dioptrica*, Marelli (1922), Hamilton (1941), Praderi (1971), Brownell (1975), Baker (1977), Goodall (1978), Goodall and Cameron (1979); *P. sinus*, Norris and McFarland (1958); *P. spinipinnis*, Allen (1925), Praderi (1971), Goodall (1978); *Phocoenoides dalli*, True (1885), Andrews (1911), Miller (1930); and *Neophocaena phocaenoides*, Allen (1923), Shaw (1938), Pilleri and Gihr (1975).

On the basis of information provided in the above literature, it appears that adult specimens of *P. dioptrica* differ from those of *P. phocoena*, *P. sinus*, and *P. spinipinnis* in that the dorsal surfaces of the rostrum and supraoccipital are in the same plane, the dorsal surface of the rostrum is more flattened, the premaxillae are elevated less above the maxillae, the dorsal and ventral surfaces of the rostrum are more nearly parallel, the apex of the rostrum is attenuated more abruptly (dorsal and lateral views), the face slopes more steeply from the vertex to the external nares (note vertex wear in C10323), and particularly from the vertex to the nasal tubercules, the nasals are placed more ventrally, the vertex is longer, the postorbital portion of the cranium and temporal fossa are shorter and deeper, the postorbital process of the frontal is more robust and has an elongate base, the zygomatic processes are exposed less in dorsal view, and the teeth are smaller, and more loosely inserted in less prominent alveolar grooves.   *P. dioptrica* differs also from *P. phocoena* in its longer, broader skull, and convex maxillary portion of the palate, and from *P. sinus* in the larger skull, posterior margin of palate with broad W shape indentation, convex maxillary portion of the palate, and relatively less exposure of frontal on the dorsolateral portion of braincase.

Phocoena dioptrica appears to differ from *Neophocaena phocaenoides* in all cranial features listed above except possibly the structure of the postorbital and zygomatic process.   Also, the skull of *P. dioptrica* is relatively larger, the rostrum is relatively longer, and the rostrum is bent less relative to the basicranial axis.   Cranial differences between *Phocoena dioptrica* and *Phocoenoides dalli* are not clear from a perusal of literature, and these species appear to be similar in that, for example, the dorsal surfaces of the rostrum and flat-topped supraoccipital are in the same plane, the dorsal surface of the rostrum is relatively flat, the face slopes steeply from the vertex to the external nares (noted by Brownell, 1975; although in the specimen of *Phocoenoides dalli* figured by Miller 1930, this appears more shallow), the nasals are placed relatively ventrally, the postorbital process is robust with a relatively long base, the zygomatic process is poorly exposed to dorsal view, and the teeth are

relatively small, and inserted in a poorly developed alveolar groove. The main cranial differences between these species (discerned from published figures) appear to be that the postorbital part of the cranium and the temporal fossae are relatively shorter and deeper in *P. dioptrica*. The postcranial skeletons of *Phocoena dioptrica* and *Phocoenoides dalli* are, however, very different (compare Brownell, 1975: fig. 1 and Goodall and Cameron, 1979: fig. 5, with Miller, 1930: plate 1). *Phocoena dioptrica* is similar to other species of *Phocoena* while *Phocoenoides dalli* possesses very tall, anteroposteriorly narrow neural spines with reduced zygapophyses and anteroposteriorly narrow centra.

We identify NMV C10323 as *Phocoena dioptrica* because it exhibits features which can be used to separate positively-identified specimens of *P. dioptrica* from other species of phocoenid. However, limited information on the comparative cranial osteology of phocoenids, as well as our limited access to specimens, makes the above comparisons provisional and the former indicates the need for a general review of phocoenid osteology.

The Macquarie Island record, which is only the second positive occurrence outside southern South American waters, certainly indicates that *P. dioptrica* has a wider distribution than was known only a few years ago (e.g. Brownell, 1975). This record, and sightings apparently of *P. dioptrica* near New Zealand (Cawthorn, 1977) and Kerguelen (Frost and Best, 1976), support Barker's (1977) suggestion that the species may have a circumpolar distribution in subantarctic latitudes. Undoubtedly, much new information on the species will result from the recent work of Goodall (1978; Goodall and Cameron, 1979) in Tierra del Fuego. Whereas Brownell (1975) observed that only ten occurrences then were known of *P. dioptrica*, Goodall (1978) listed 112 specimens, and mentioned another 29, from Tierra del Fuego alone. These beach collections suggest that the spectacled porpoise is the most common small cetacean in inshore waters around Tierra del Fuego, but the absence of sightings of live animals even in areas of high stranding densities attests to the cryptic behaviour of the species. It is likely that strandings, rather than sightings of live animals, will constitute further records of the species from the subantarctic southwest Pacific and, in view of the northward distribution of the porpoise into temperate South American waters (Brownell, 1975), strandings might be expected in New Zealand.

ACKNOWLEDGEMENTS

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EXPLANATION OF PLATES

PLATES I AND II

Skull of *Phocoena dioptrica*, NMV C10323.   Skull length 283 mm.

Fig. 1.   Dorsal view.
Fig. 2.   Left lateral view.
Fig. 3.   Anterior view.
Fig. 4.   Ventral view.

Fig. 1.

Fig. 2.

PLATE II　　　　　　　　　　　　　　　　　FORDYCE, MATTLIN AND DIXON
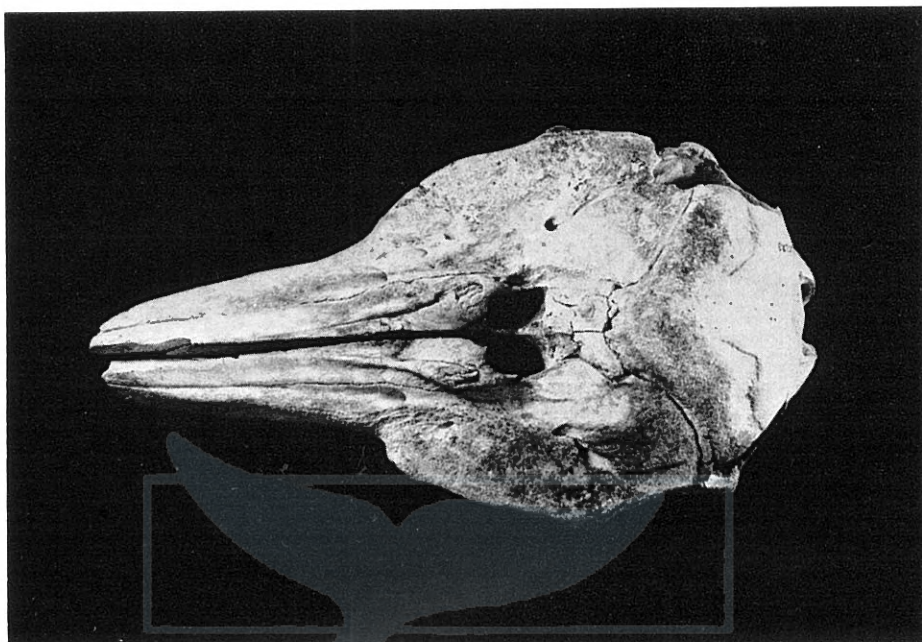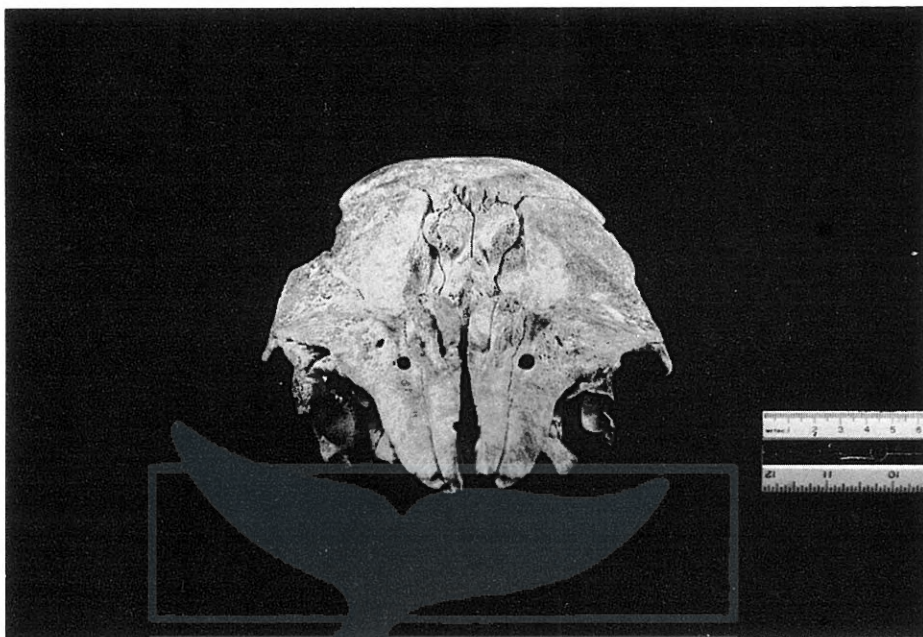
Fig. 3.

Fig. 4.

A MORPHOLOGICAL NOTE ON THE INTESTINE OF THE BOUTU WITH EMPHASIS ON ITS LENGTH AND ILEO-COLIC TRANSITION COMPARED WITH OTHER PLATANISTIDS

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ABSTRACT

The intestine of the Boutu, *Inia geoffrensis* (body length 204 cm, female), was examined macroscopically and light microscopically. The intestine of the *Inia* examined was grossly divided into three portions: the small intestine, the smooth-walled portion, and the colon. The lengths of these parts were approximately 4150 cm, 80 cm, and 40 cm, respectively. The total intestinal length of the *Inia*, including the 5 cm long rectum and 3 cm long anal canal, was 4278 cm. Therefore, the intestine was nearly 21 times as long as the body length. In the interior of the small intestine, except for the proximal half of the duodenum, a single distinct longitudinal fold involving both the mucosa and submucosa could be seen. The smooth-walled portion was thicker than the small intestine, and had no fold, but its inner surface became flat and smooth. The colon, which had several longitudinal folds in its interior, was thinner than the smooth-walled portion in the initial one-third and thicker in the remaining portion. Histological differences between the small intestine and the smooth-walled portion and the colon could not be clearly distinguished in our specimen, except for the abundance of goblet cells in the latter two portions. The ileo-colic transition of the *Inia* observed was unclear and this region was compared with other kinds of platanistids.

INTRODUCTION

Morphological investigation of the internal organs, as well as of other body features, is very important in order to clarify the phylogenetic relationship among the fresh water dolphins of the family Platanistidae, *Platanista*, *Pontoporia*, *Lipotes*, and *Inia*. Concerning the morphology of the intestine, there are some observations previously reported on *Platanista* (Anderson, 1879; Slijper, 1962/1979; Takahashi and Yamasaki, 1972), *Pontoporia* (Burmeister, 1869; Yamasaki, Takahashi and Kamiya, 1975), *Lipotes* (Chen and Chen, 1975; Zhou and Li, 1981), and *Inia* (Zhou, Li and Pilleri, 1982). However, our morphological knowledge of the *Inia*'s intestine is still insufficient because the investigation by Zhou *et al.* (1982) treated only *Inia boliviensis*, and no detailed description on the intestine of *Inia geoffrensis* has so far been reported except for a partial reference to the morphology of the intestine (Yamasaki *et al.*, 1975). The present paper, as the second report on the morphological study

of the digestive tract of *I. geoffrensis* (cf. Yamasaki and Kamiya, 1981, on the stomach), deals with the macroscopical characteristics of the intestine, some of which were not observed by Zhou *et al.* (1982) in *I. boliviensis*, and discusses the intestinal length and the ileo-colic transition as compared with other platanistids.

MATERIAL AND METHODS

The intestine of the Boutu (Amazonian dolphin), *Inia geoffrensis* (body length 204 cm, female) used for this study was provided by the Kamogawa Sea World, Chiba, Japan, after death from unidentified disease. The intestine taken from the abdominal cavity was preserved in 10% formalin solution and transported to our laboratory. After macroscopical observations, small pieces for the light microscopy were taken from several parts of the intestine, and were embedded in paraffin. Sections were stained with hematoxylin and eosin.

OBSERVATIONS (PLATE I AND II)

The intestine of *I. geoffrensis* was observed to be grossly divided into three portions: the small intestine, the colon, and the portion which was located between these two. The intermediate portion was thicker than the small intestine and was also characterized by its smooth interior. It was difficult to determine whether this portion belonged to the last part of the small intestine or the initial part of the large intestine; therefore, for convenience, we called it a " smooth-walled portion " of the intestine in this study.

The initial part of the small intestine, the duodenum, consisted of the duodenal ampulla and the duodenum proper. The former was continuous with the pyloric stomach with a small opening 2 mm in diameter. It was funnel-shaped, approximately 2.5 cm in diameter at the widest proximal part, about 3 cm in length, and continued to the duodenum proper. The hepato-pancreatic duct opened in the duodenal lumen about 9 cm away from the commencement of the duodenum proper and formed a distinct plica longitudinalis duodeni about 1.5 cm long and 0.6 cm wide. Although the border between the duodenum and the jejunum was unclear, and fairly difficult to determine, the length of the duodenum proper appeared to be roughly 20 cm. The small intestine, except for the proximal half of the duodenum, formed a number of coiled loops suspended by a broad mesentery, which was 7–12 cm in width. The small intestine was approximately 0.7–0.8 cm in diameter but in several parts there was a slight dilation, about 1 cm in diameter, extending over a length of about 5–10 cm. The length of the small intestine, from the initial part of the duodenum to the beginning of the smooth-walled portion, measured nearly 4,150 cm. No circular folds could be seen in the interior of any parts of the small intestine. The inner surface of the duodenal ampulla exhibited several folds, which might be not present in the living state, being slightly irregular; and at about 5 cm from the opening of the hepato-pancreatic duct one single distinct longitudinal fold began and continued throughout almost the whole interior of the

small intestine (Fig. 1). This single fold projected into the intestinal lumen beyond a half diameter of the lumen and was generally found on the antimesenteric border (Fig. 6). The fold became slightly smaller and irregular in the several dilated parts of the small intestine mentioned above, and also near the smooth-walled portion (Fig. 2). The smooth-walled portion of the intestine measured about 80 cm long. This portion, about 1 cm or more in diameter, was clearly thicker than the small intestine. The longitudinal folds could not be seen in this portion and the inner surface became flat and smooth (Fig. 3). However, from one to three short longitudinal folds, 2–5 cm long, were seen in some places of this portion. The smooth-walled portion formed an intestinal loop but its mesentery was shorter than in the small intestine. The vessels in the mesentery made an acade and many vasa recta reached the smooth-walled portion as seen in the small intestine, though this pattern tended to become irregular in the distal part. The last part of this portion ran upwards and flexed dorsal, and continued to the next colon.

The colon descended straightly and continued to the rectum. The mesentery of the colon was short, about 5–6 cm wide, and gradually reduced in width analwards, disappearing in the anal part. The initial one-third of the colon was somewhat thinner than the smooth-walled portion, with a width of approximately 1 cm or less, and the last two-thirds became thicker, being about 1.5 cm in diameter. In the interior of the colon there could be seen from two to five distinct folds running longitudinally (Fig. 4), which became more marked in the last two-thirds (Fig. 5). These folds were broader than those in the small intestine. Most folds continued throughout the entire length of the colon, but short ones, 2–3 cm long, were present in some places. The colon was approximately 40 cm long, and the rectum and the anal canal were 5 cm and 3 cm long, respectively.

The thickness of the mucosa of the duodenal ampulla was 0.6–0.7 mm, and that of the rest was slightly thinner, being 0.4–0.5 mm in thickness. Since the specimen observed was in poor condition for histological examinations, typical villi could not be clearly observed in the small intestine (Fig. 7) and it could not be determined whether villi were present or not in the smooth-walled portion (Fig. 8). Intestinal glands were mucous in the duodenal ampulla. Those of the rest of the intestine morphologically resembled each other. But the glands of the smooth-walled portion and colon showed some tertuous courses and goblet cells became abundant, especially in the bottom of the glands (Figs 8–10). Musclaris of the whole intestine, consisting of thick inner circular and thin outer longitudinal layers, was 0.3–0.5 mm thick in the small intestine (Fig. 6) and smooth-walled portion, and 0.5–0.8 mm thick in the colon. The inner muscular layer was 4–5 times as thick as the outer one. The sphincteric structure could not be seen at either the border between the small intestine and the smooth-walled portion or between this portion and the colon. The folds observed in the whole intestinal tract involved both the mucosa and the submucosa (Fig. 6). Some accumulations of lymphoid tissue were found in the lamina propria of the colon but well-developed lymphatic nodules could not be seen in any portion of the intestinal tract of the observed

specimen.

DISCUSSION

The total length of the whole intestine of the *I. geoffrensis* (body length 204 cm) was 4,278 cm; thus the ratio of the intestinal length to the body length is nearly 21 to 1. This agrees well with the ratios, 19 and 20 to 1, obtained in *I. boliviensis* (body lengths 145 cm and 174 cm, respectively, Zhou *et al.*, 1982). The ratios in other fresh water dolphins reported by previous investigators are shown in Table 1*. *Platanista*'s ratio is notably low and *Pontoporia*'s is higher by far than that of other dolphins. Since there appears to be a tendency for the intestinal length to increase with age in our collected specimens of *Platanista* and *Pontoporia* (cf. Takahashi and Yamasaki, 1972; Yamasaki *et al.*, 1975), the ratio becomes slightly higher when specimens are limited to adults.

TABLE 1.   THE RATIO OF THE INTESTINAL LENGTH TO THE
BODY LENGTH IN PLATANISTIDS

Species	Ratio	Authors and Remarks
Inia		
boliviensis	19.0–20.0	Zhou *et al.* (1982)
geoffrensis	21.0	Yamasaki *et al.* (1975) and present study (1983)
Platanista		
gangetica	4.1–4.4	Anderson (1879)
	7.3	Slijper (1962/1979), no descriptions on the length of body and intestine
	3.6–4.9	Takahashi & Yamasaki (1972)
Pontoporia		
blainvillei	32.0	Burmeister (1869)
	24.0–37.0	Yamasaki *et al.* (1975), examined in unfixed state in most cases
Lipotes		
vexillifer	15.0	Chen & Chen (1975), ratio of whole length of the digestive tract, from mouth to anus, to the body length
	12.5–14.9	Zhou & Li (1981)

In the small intestine of the *Inia* observed there are no circular folds, but a single distinct longitudinal fold projecting into its lumen can be seen as in *Pontoporia* (Yamasaki *et al.*, 1975). Although Zhou *et al.* (1982) did not mention this fold in *I. boliviensis*, the fold in *I. geoffrensis* is plainly visible as a permanent structure and can also be easily felt through the wall of the intestine when the intestine is grasped between the fingers. In *Platanista*, well-developed circular folds are present on the inner surface of the small intestine but the surface of about the last 50 cm of the ileum becomes flat and smooth, and a distinct longitudinal fold, about 30 cm long, is present at this portion (Takahashi and Yamasaki, 1972). The presence of the circular or longitudinal folds in the small intestine is due to the struc-

* The ratios of *Platanista*, *Pontoporia*, and *Inia* misquoted in our previous paper (1981) are corrected as shown in Table 1.

tural specializations that serve to increase the area of the surface exposed to the lumen. It is assumed that numerous well-developed circular folds are a much more effective means of augmenting the surface area of the mucosa than a single longitudinal fold. This fact may have some relation to the short intestine of *Platanista* and to the long intestine of *Inia* and *Pontoporia*. In the reports of the intestine of *Lipotes* (Chen and Chen, 1975; Zhou and Li, 1981) there are no macroscopical descriptions of its internal structure, and therefore it is unclear whether *Lipotes'* intestine has such longitudinal folds or not.

In cetaceans it is generally known that there is no clear external transition between the small and the large intestines; except for *Platanista* and mysticetes which have a short caecum. In *Pontoporia* the external appearance of the transition between the small and the large intestines was not so difficult to determine because of the differences in thickness, the supply of the mesenteric vessels, and the interior equipped with a single longitudinal fold in the small intestine while there were two folds in the large intestine (Yamasaki *et al.*, 1975). However, in the case of our *Inia*, it was very difficult to determine the transition between the small and the large intestines. In the smooth-walled portion the single longitudinal fold disappears and the inner surface becomes flat and smooth. Nevertheless, the pattern of the blood supply, the vasa recta, seen in the small intestine was observed until the distal part of the smooth-walled portion. Since our specimen was, unfortunately, in poor condition for histological examination, neither the presence of typical villi, which is one of the most important characteristic features of the small intestine, nor the disappearance of the villi in the large intestine could be observed. In addition, other histological findings generally found in each small and large intestine in mammals in general could not be observed, so that we did not confirm the transition region from the small to the large intestine. However, goblet cells of the intestinal glands of our *Inia* were abundantly observed in the smooth-walled portion and the colon, unlike in the small intestine. This distribution of the goblet cells in the smooth-walled portion and colon in *Inia* appears to correspond well to that in the ascending and descending colons in *Pontoporia*.

Zhou *et al.* (1982) did not mention this smooth-walled portion, and they considered the colon to be only the portion, about 35 cm long, which ran caudally connecting with the rectum, and they described the presence of villi in the small intestine. The length of the large intestine of *Pontoporia* was 80 cm or more (Yamasaki *et al.*, 1975) and in *Lipotes* it is about 100 cm (Zhou and Li, 1981). As the structure of the intestine of our *Inia* resembles that of *Pontoporia*, and probably *Lipotes*, rather than that of *Platanista*, the 35 cm long colon of *I. boliviensis* seems to be proportionally too short. Although in our previous paper (Yamasaki *et al.*, 1975) the smooth-walled portion was considered as ascending colon, there are no conclusive characteristics to determine whether the smooth-walled portion belongs to the small or the large intestines, as is discussed in this study. In order to clarify the subject of the ileo-colic transition, it is necessary to investigate cetacean species having no caecum from comparative morphological viewpoints.

Zhou *et al.* (1982) observed no goblet cells in the intestinal glands in *I. bolivi-*

ensis and also stated that this is one of the characters common to *Inia* and *Platanista*. We found abundant goblet cells in *I. geoffrensis*, as in *Pontoporia* and *Lipotes* (cf. Yamasaki *et al.*, 1975; Zhou and Li, 1981). Though present, the cells were much less abundant in *Platanista* (Takahashi and Yamasaki, 1972). Therefore, the absence of the goblet cells may be peculiar to *I. boliviensis* among the fresh water dolphins previously reported.

Although well-developed lymphatic nodules in the lamina propria were present from the last part of the ileum to the initial part of the colon in *Platanista* (Takahashi and Yamasaki, 1972) and in *Pontoporia* (Yamasaki *et al.*, 1975), development of lymphatic tissues of the intestinal tract was very poor in our *Inia*. Zhou *et al.* (1982) described numerous lymphatic nodules aggregating from the last part of the ileum (probably corresponding to the last part of the smooth-walled portion in our case) to the anal part, and well-developed anal tonsils. Since the anal tonsils in our *Inia* were poorly developed (Yamasaki, Komatsu and Kamiya, 1977), poorly developed lymphatic tissue in the intestinal tract seems due to individual characteristics; well-developed lymphatic nodules could not be seen anywhere in the intestinal tract.

Pilleri and Gihr (1977, 1980) and Pilleri, Marcussi and Pilleri (1982) stated that there were clear morphological and morphometric differences between the Bolivian and Amazonian *Inia*, based on the observations of their brains and teeth. The stomachs of both *I. geoffrensis* and *I. boliviensis* quite resemble each other in structure (cf. Yamasaki and Kamiya, 1981; Zhou *et al.*, 1982). However, as mentioned above, there are some remarkable macroscopical differences in their intestines. It remains a problem whether such differences in the intestine were interspecific or not, because the present observations on *Inia* were based on one case. Therefore, further observations of this subject, based on the sufficient materials, should be done in order to compare with each other.

ACKNOWLEDGEMENTS

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EXPLANATION OF PLATES

PLATES I AND II

Inner views of several parts of the intestine of *Inia geoffrensis* (1–5).   The intestine is opened wide to show its interior at the mesenteric border.   Figs 1–5, actual size.

Fig. 1.   Inner surface of the ileum at about 5 m proximal to the smooth-walled portion.   Note that a single distinct longitudinal fold can be seen and no circular folds are present in the small intestine.

Fig. 2.   The transitional part between the small intestine (left) and the smooth-walled portion (right).   The longitudinal fold becomes slightly irregular in the last part of the small intestine and the inner surface becomes smooth in the smooth-walled portion.

Fig. 3.   Mid-part of the smooth-walled portion, which is thicker than the small intestine.   Short longitudinal folds are seen in some places in this portion.

Fig. 4.   The last part of the smooth-walled portion (left) and the initial part of the colon (right).   Two or three longitudinal folds are present in the initial part of the colon.

Fig. 5.   Mid-part of the colon.   Marked longitudinal folds can be seen in the surface.

Fig. 6.   Cross section of the mid-part of the small intestine.   A prominent longitudinal fold, involving both the mucosa and the submucosa, projects into the lumen from near the antimesenteric borders.   ×11.

Fig. 7–10.   Same magnification photomicrographs of the mucosa of the several parts of the intestinal tract.   ×10.   Mid-part of the small intestine (Fig. 7), mid-part of the smooth-walled portion (Fig. 8), initial part of the colon (Fig. 9), and mid-part of the colon (Fig. 10).   Typical villi could not be seen in the small intestine in our specimen.   The intestinal glands of the small and the large intestines are rather straight.   Goblet cells become abundant in the smooth-walled portion and the colon.

PLATE II   YAMASAKI AND KITO
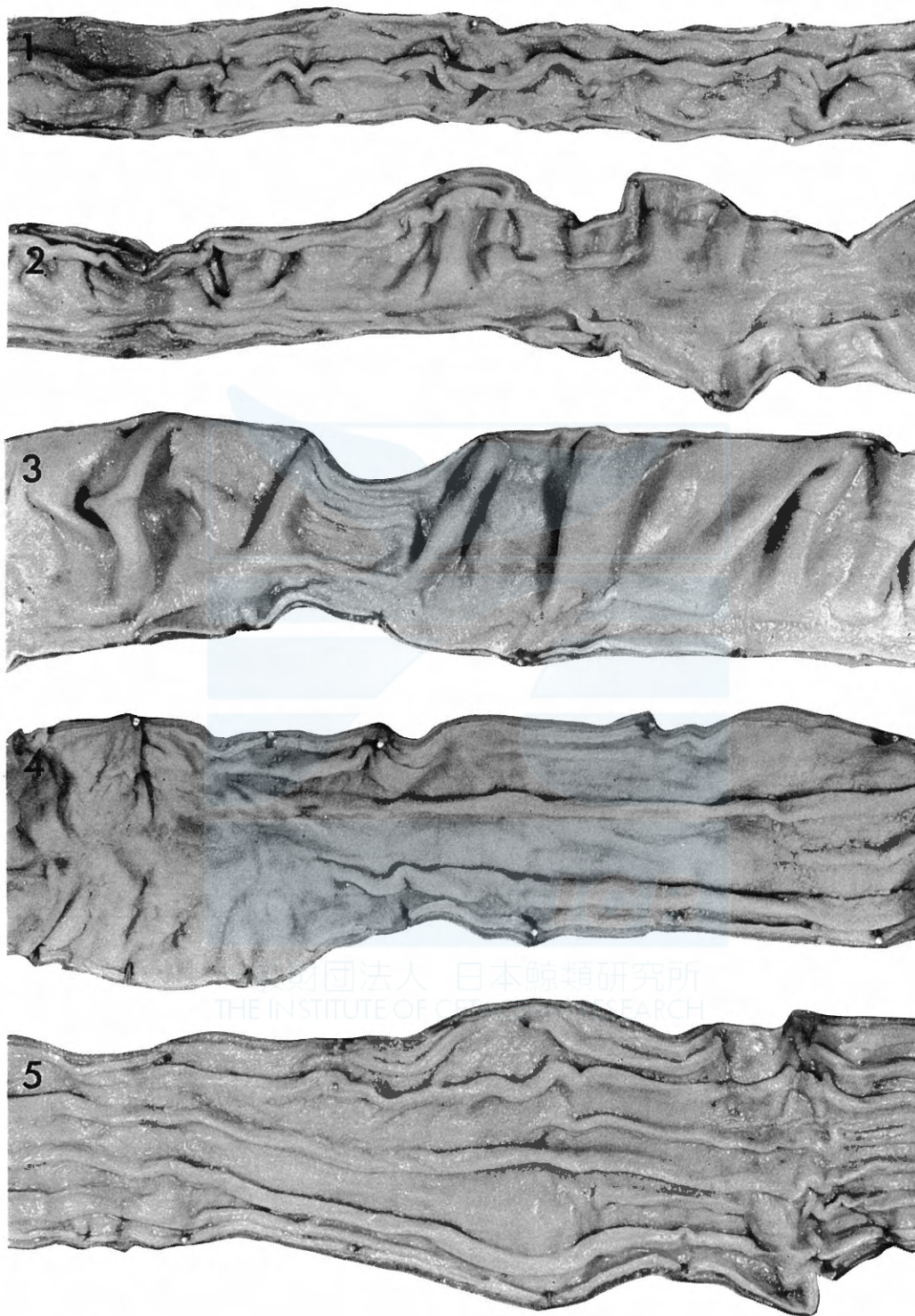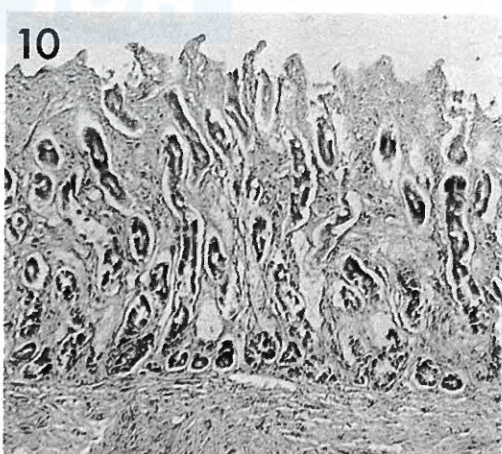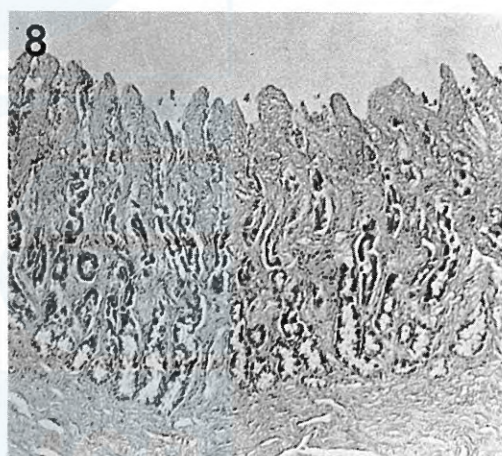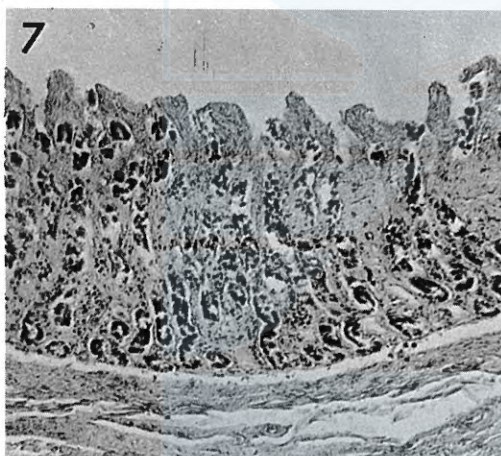
FIRST DISCOVERY OF A TERTIARY PLATANISTOID FOSSIL FROM ASIA

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ABSTRACT

A new genus and species of Lipotidae, *Prolipotes yujiangensis* collected from the bank of Yujiang River and considered roughly as Miocene in age, is the first discovery of Platanistoid fossil from Asia. The holotype is a fragment of mandible with teeth, including posterior part of symphysial portion and initial part of free portion of mandibular rami. Comparison of the new specimen with the mandible of *Lipotes* and *Kampholophos* indicates that *Prolipotes yujiangensis* is the fossil odontocetes species most closely related to *Lipotes* known thus far.

The superfamily Platanistoidea is a declining group consisting four modern families which are found in areas far away from each other. Lipotidae occurs in China. Platanistidae is found in the Indian subcontinent. Another two live in South America: Iniidae lives in Amazon and Orinoco river basins and Pontoporiidae occurs in coastal central Atlantic waters of South America. In each family only one or two species restricted to very narrow areas are living. Our knowledge concerning the history of the Platanistoids is still scanty. Fossil studies indicate that they were widely distributed in America, Europe and Africa during Miocene and Pliocene. No Platanistoid fossil from Asia, however, has been reported so far. A fragment of mandible belonging to Lipotidae collected from the bank of Yujiang River in Guiping County, Guangxi in 1981 and considered roughly as Miocene in age is the first discovery of Platanistoid fossil from Asia.

SYSTEMATICS

Order CETACEA Brisson, 1762
Superfamily PLATANISTOIDEA Simpson, 1945
Family LIPOTIDAE Zhou, Qian et Li, 1978
Prolipotes, new genus

Type species: *Prolipotes yujiangensis*
Diagnosis: See diagnosis of *Prolipotes yujiangensis* (generic type).

Prolipotes yujiangensis, new species
(Figs 1–3, Plates I–II)

Holotype: A fragment of mandible with teeth, including posterior part of symphysial portion and initial part of free portion of mandibular rami.

Type locality: Bank of Yujiang River 500 m SE of Oucun village in Mengwei Commune, Guiping County, Guangxi Zhuang Autonomous Region, People's Republic of China.   Coordinates of the type locality are 23°17′20″N latitude, 110°3′30″E longitude.

Age: The specimen was collected from " Yongning Group " (upper part?) of Tertiary age.   At first the " Yongning Group " was considered to be as new Tertiary (Pliocene?) in age according to the molluscs discovered.   Later the geological age of this Group was revised on the basis of a large number of fossils of reptiles (crocodiles) and mammals found successively from Yongning Group beds or corresponding beds in Baise and Yangle Basins (Tiandong and Tianyang County), assigned Early Tertiary and further determined Late Eocene to Early Oligocene in age (Tang *et al.*, 1974).   Our Platanistoid fossil was found from the upper part of this Group and is of later age.   Its differences from the extant species are not very big.   The phylogenetic history of the superfamily indicates that they probably arose at the end of Early Tertiary.   At present, in the light of the general stratigraphic condition of the type locality and data for the geohistorical distribution of Platanistoidea, we suggest that the new specimen is of Miocene age.

Diagnosis: Mandibular symphysis long, its posterior end very thick; deep longitudinal furrow between two tooth rows; anterior part of two rami in shape of a curve where they join symphysial portion; teeth closely spaced; crowns of teeth slightly compressed antero-posteriorly, their upper half recurved interiorly, cingulum rounded and broad; enamel of crowns ornamented with irregular vertical striae and ridges; tip of roots not widen to form an anterior and posterior projection.

Description: The mandibular symphysis is very long, its preserved posterior part measures 80 mm in length.   A deep broad longitudinal furrow extending gently to the posterior end is found between the two tooth rows of the symphysial portion of the mandible.   The posterior end of mandibular symphysis is slightly thinner than the anterior break (seven teeth from the posterior end of mandibular symphysis), about half of the height of the lingual side of the anterior end of the free portion of the ramus.   The preserved free portion of the two rami is very short.   The anterior part of the two rami is in the shape of a curve where they join the symphysial portion.   The angle between the two lines extending from the anterior end of the two rami is about 37.5°.   Several mental foramens located below the 1st, 3rd and 6th-7th teeth respectively before the hind extremity of the mandibular symphysis, are found at the labial side of the lower jaw.

Additional one is found on the left mandible below the 5th tooth situated before the posterior end of the symphysis.   A faint groove runs longitudinally below the mental foramens near the lower rim of the mandible.

Eight teeth (two broken) and two alveolus are found on the preserved right
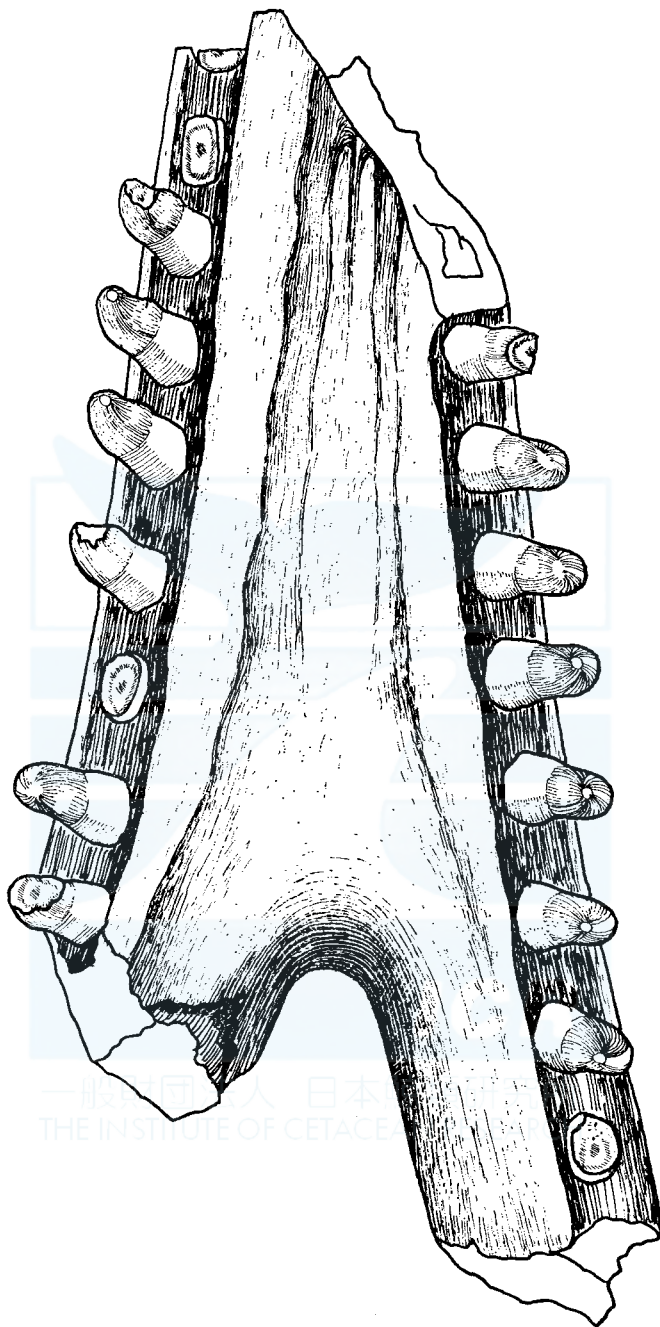
Fig. 1. *Prolipotes yujiangensis*, holotype, occlusal view of mandible, ×1.5.

TABLE 1. MEASUREMENTS (MM) OF MANDIBLE, HOLOTYPE

	Left	Right	Symphysial portion
Length of mandible as preserved	100.0	111.6	
Length of free portion of ramus as preserved	13.7	27.7	
Height of labial side of anterior end of ramus	27.0	27.0	
Height of labial side of anterior break of mandible	21.5[1]	23.8[2]	
Thickness of mandibular symphysis at posterior end			15.0
Thickness of mandibular symphysis at anterior break			18.3
Transverse diameter of mandible at posterior end of symphysial portion			51.0
Transverse diameter of mandible at front edge of the 3rd tooth before posterior end of symphysis			40.0
Transverse diameter of mandible at front edge of the 6th tooth before posterior end of symphysis			32.0
Length of tooth row of last six teeth of symphysial portion	57.5	55.6	

[1]   Eight teeth from posterior end of symphysial portion.
[2]   Six teeth from posterior end of symphysial portion.

mandible, of which three are located on the free portion of the ramus.   Only the lower half of the anteriormost part of the free portion of the left ramus has been preserved and all of the preserved nine teeth (four broken) of the left mandible are situated on the symphysial portion.   The alveoli are transversely elliptical in outline, about 7 mm in antero-posterior and 6 mm in labio-lingual diameter.   They are located on the mid-line of the mandible of the symphysial portion.   The position of the three teeth on the anterior part of the free portion of the right ramus is slightly lateral to the lingual side.

The teeth are closely spaced.   The intervals are about 3 mm between the anterior teeth and 4 mm between the hinder ones.   In the posterior part of the symphysial portion, there are as an average one tooth per 9.2 mm on the right mandible and one per 9.6 mm on the left.   The crown of the teeth is inclined labially conspicuously and slightly compressed anterior-posteriorly.   Its upper half is recurved interiorly and places the apices of the mandibular teeth which are slightly worn in an upward direction.   The lower half of the lingual side of the crowns is a broad, rounded cingulum where the largest diameter of the crown cross. The enamel of the whole crown is ornamented with irregular vertical striae and ridges.   The bases of the crowns constrict to join the roots.   The exposed portion

TABLE 2. MEASUREMENTS (MM) OF RIGHT MANDIBULAR TEETH, HOLOTYPE

	0[1]	1	2	3	4	5
Length of labial side of root above alveolus	3.5	3.5		3.7	4.2	3.9
Length of lingual side of root above alveolus	3.1	3.2	3.3	3.6	3.6	3.5
Greatest anteroposterior diameter of exposed portion of root	6.2	6.2	6.0	6.2	6.4	6.5
Greatest labio-lingual diameter of exposed portion of root	5.8	5.9		6.1	6.0	5.9
Greatest anteroposterior diameter of crown	4.6	4.5	4.5	4.4	4.3	4.3
Greatest labio-lingual diameter of crown	6.3	6.3	6.4	6.3	6.2	6.0
Length of crown	7.8	7.8	7.7	7.5	7.4	7.2

[1]   Counting ahead from the 1st tooth behind the symphysis, the Nos. are 0, 1, 2, 3, 4, 5 in proper order.
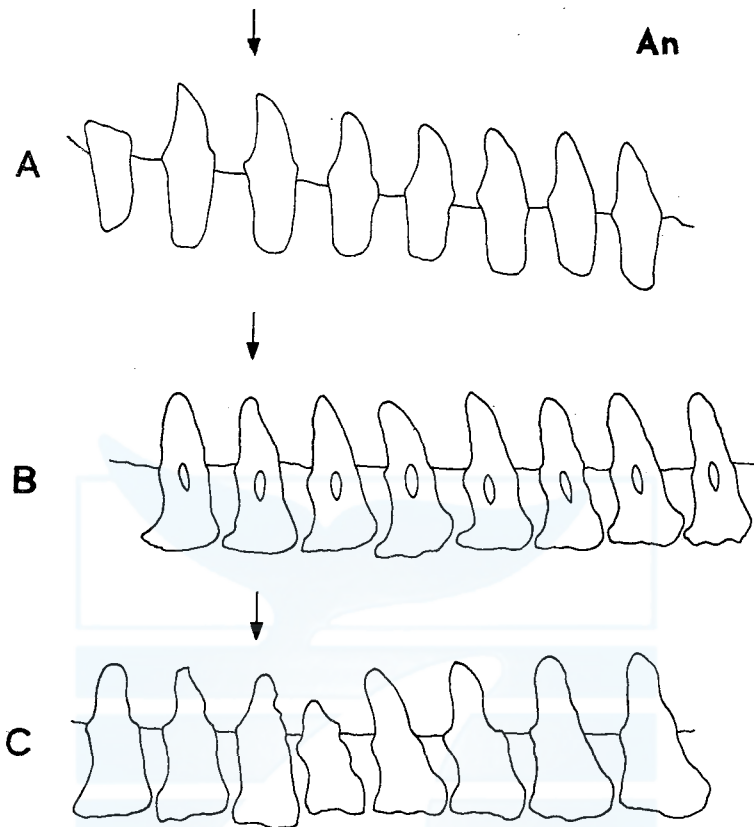
Fig. 2. Lateral view of part of teeth of right mandible, trace over radiographs, ×1.
Arrow indicating posterior end of mandibular symphysis. An: anterior.
A. *Prolipotes yujiangensis*, holotype
B. *Lipotes vexillifer*, NNC (Nanjing Normal College) 7909
C. *Lipotes vexillifer*, NNC 7405

of the roots is larger in diameter than the crowns and the anterior-posterior diameter of the former is larger than its labiolingual diameter. The radiograph of the mandibular teeth shows that the base of the roots is not widen to form an anterior and posterior projection.

Comparison: In the Yujiang specimen, the hind part of the mandibular symphysis as preserved is rather long. The intervals between the teeth are relatively short, as an average there is one per 9.3 mm (right) or 9.6 mm (left) on the hind part of the mandibular symphysis. The crowns are ornamented with vertical irregular striae and ridges, recurved interiorly and with a well developed cingulum on the lower half. The above mentioned characters resemble those of the *Lipotes vexillifer*. Rensberger (1969) has concluded that among the described fossil odontocetes only the Miocene *Kampholophos serrulus* is related to *Lipotes vexillifer*. But the teeth of the former are widely spaced, only one per 21.3 mm on the posterior
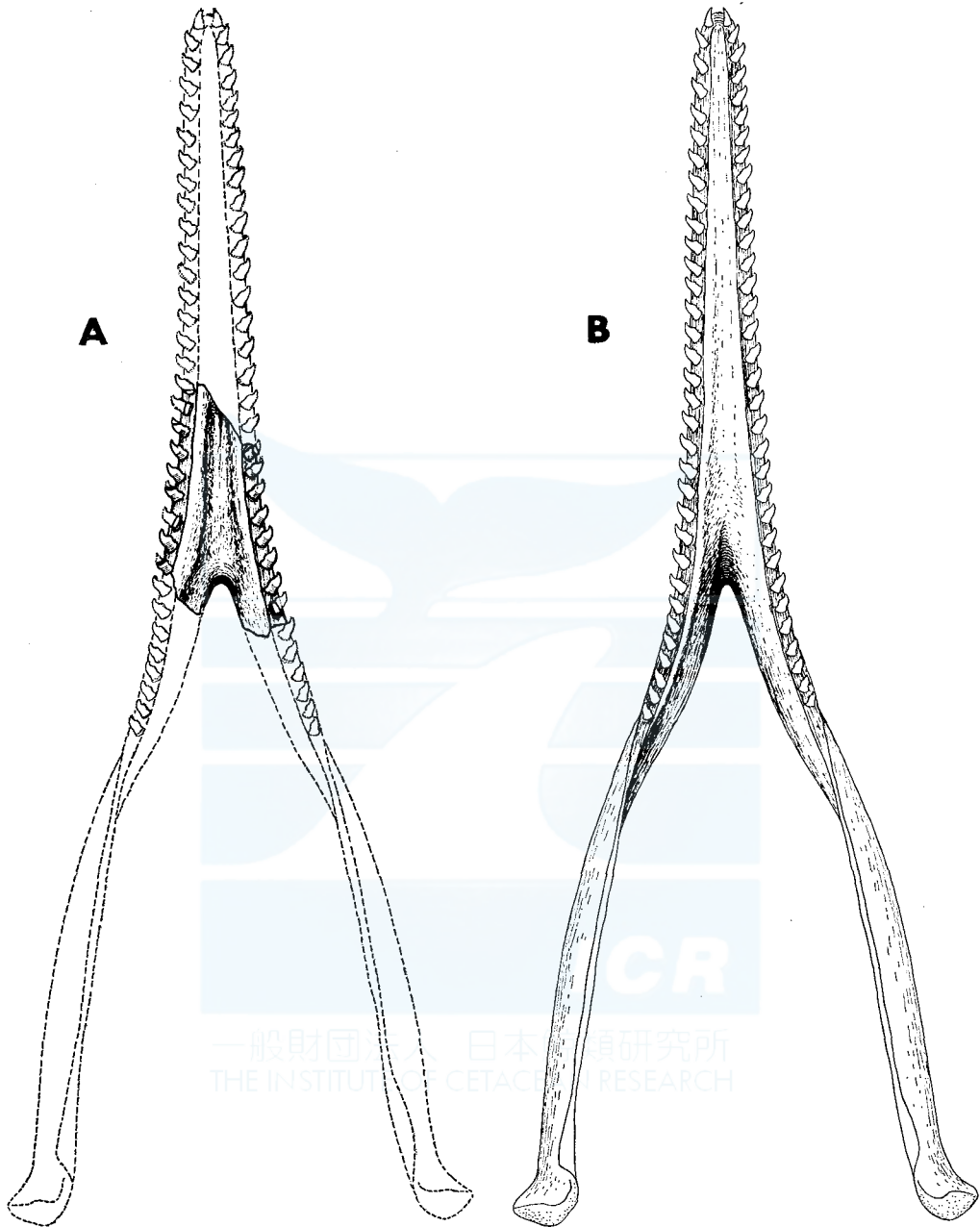
Fig. 3. Comparison of (A) restored mandible of *Prolipotes yujiangensis* with (B) mandible of *Lipotes vexillifer*, about ×1/3.

part of the right mandible. In an old adult of *Lipotes vexillifer* (NNC 7405), the teeth along the posterior part of symphysial portion are closely spaced, or one per 9.3 mm (right) or 9.8 mm (left). The posteriormost teeth of *Kampholophos serrulus* bear a prominent-based accessory cusp which is absent on the anterior teeth. Their crowns are laterally compressed with vertical striae and ridges which are most prominent on the lower two-thirds of each crown. They are coarsest on the labial and anterior sides (Rensberger, 1969). The structure of all the teeth of *Lipotes vexillifer* is alike. The crowns are slight antero-posteriorly compressed with vertical striae and ridges which are most prominent on the upper two-thirds of each crown. They are coarsest on the lingual side. Since the differences of the teeth between *Kampholophos* and *Lipotes* are more than those between the Yujiang specimen and *Lipotes*, it is beyond all doubt that the new specimen is the fossil odontocetes species which is most closely related to *Lipotes* known thus far and should be placed in the family Lipotidae.

Five mandibles of different ages of young and adult of *Lipotes* (NNC 5601, 7808, 7909, 7907, 7405) were examined for comparison. The longitudinal furrow between the tooth rows of the symphysial portion is shallow and narrow in the anterior part and descends abruptly to form a valley-like steep depression at about last 3–4 mm of the posterior end of the mandibular symphysis. The posterior end of the mandibular symphysis is very thin, inferior to half of the thickness of the symphysis at the 7th tooth before its posterior end (corresponds to the anterior break of the Yujiang specimen), or less than one-third of the lingual height of the front end of the free portion of the rami. The anterior part of the two rami is in the shape of an acute angle where they join the symphysial portion. The vertical striae and ridges of the crowns are relatively shallow and are fewer at anterior and posterior side. The base of the labial side of the crowns is comparatively smooth. The tip of the roots widens to form an anterior and posterior projection. On the basis of the above mentioned differences between the Yujiang specimen and *Lipotes*, we therefore proposed to name the former as a new genus and new species.

Because of the paucity of the available material, which is confined to a fragment of lower jaw with corresponding teeth, the finding of the skulls and postcranial skeletons of this new species for the further studies of the characters of the genus and species is expected.

We thank Wang Zhefu of the Institute of Vertebrate Paleontology and Paleoanthropology for took the photographs and Xu Xinrong of the Nanjing Normal college for drawings.

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EXPLANATION OF PLATES

PLATE I

Prolipotes yujiangensis, holotype, ×1.
A, occlusal view; B, ventral view; C. lateral view.

PLATE II

Prolipotes yujiangensis, holotype, ×3.
1st tooth on the right mandible behind the posterior end of the mandibular sym-
    physis, left,
labial view; middle, lingual view; right, posterior view.

PLATE II
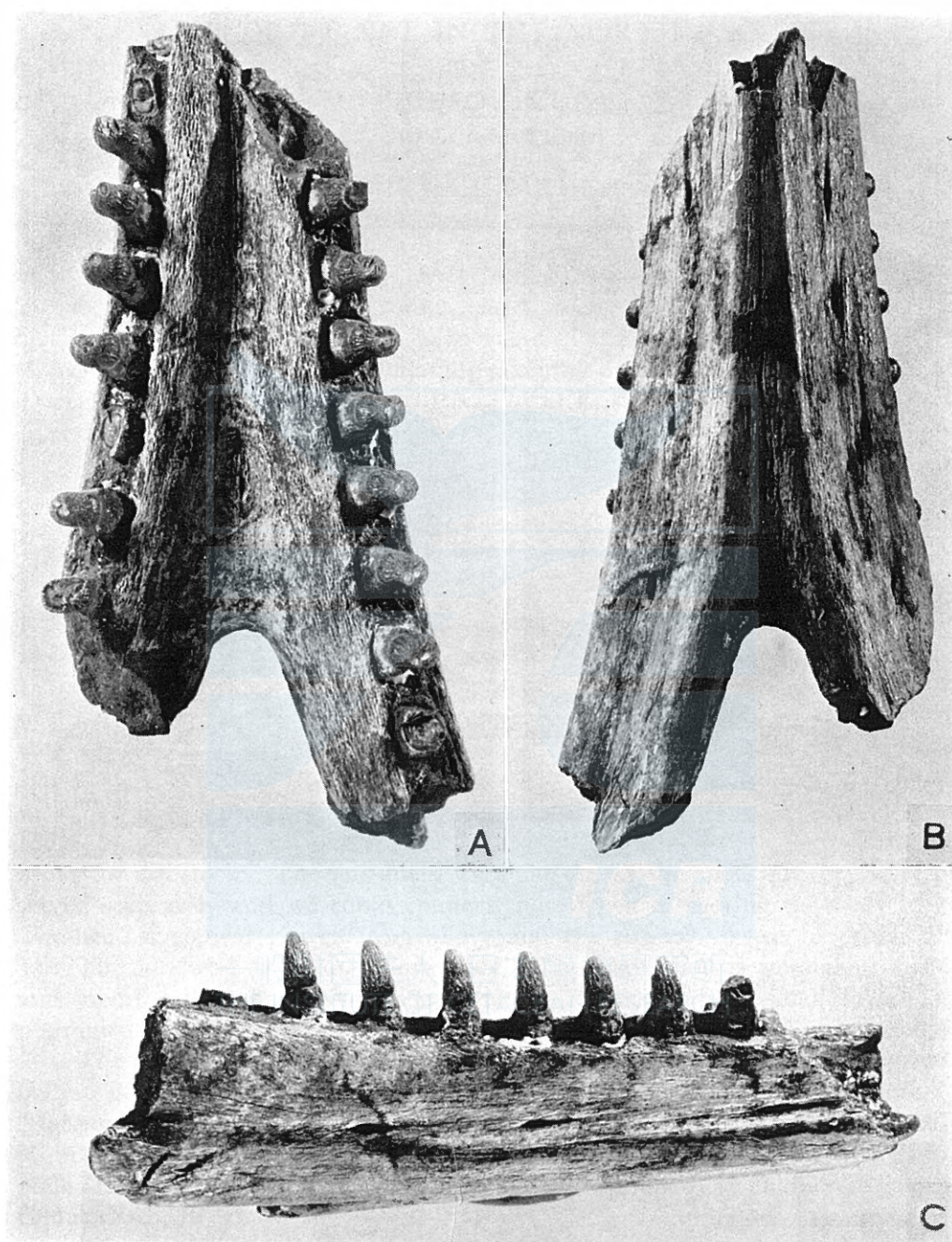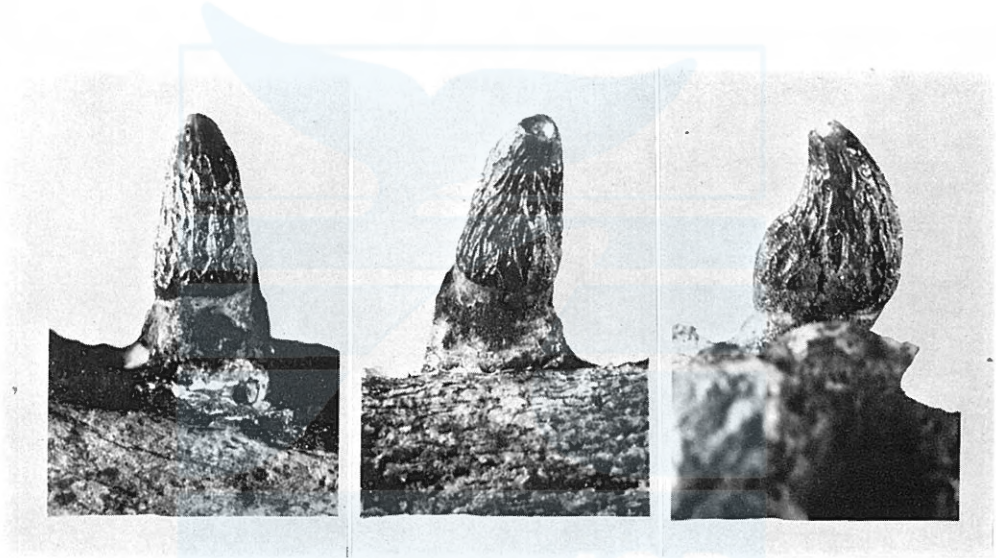
A PYGMY SPERM WHALE ACCIDENTALLY TAKEN
BY DRIFT NET IN THE NORTH PACIFIC

HIDEO OMURA

Whales Research Institute

MIKI SHIRAKIHARA

Shimonoseki-shi, Yamaguchi-ken

HARUKA ITO

National Science Museum

A pygmy sperm whale was accidentally taken by drift net called Omenagashi on 1 December 1981 at a position 34°01′N, 176°17′E, during an experimental fishing operation for tunas.

This whale was frozen on the spot and kept in an ice-chamber of about −20°C until towards the end of March of the following year. Then it was transported to Whales Research Institute for identification of the species. On 6 April 1982 we made observation and dissection of the carcass after melting the body. Dr Toshio Kasuya of the Ocean Research Institute, Dr Nobuyuki Miyazaki of the National Science Museum and Mr Hidehiro Kato of the WRI have cooperated in the works. We are very grateful for all of them.

This whale was a femele calf of 1,731 mm in length. It was said that several other whales of the same species were concurrently taken. They were larger than this specimen, but the smallest was selected for the sake of convenience. There remains no record of the number, size and sex of these animals, but presumably included among them the female which was accompanied by the calf.

This whale has a robust body with a small but distinctively shaped head and a narrow tail stock. The tail flukes were cut off on the spot, but they were preserved separately and we could connect them when measuring the body length. The head is conical viewed from above and also conical viewed in profile (Fig. 1). The forehead overhangs noticeably. The lower jaw is small and narrow, and superficially resembles to a shark's jaw. The dorsal fin is small, falcate, and positioned behind midback. The flippers are located well forward on the body.

The color of the body is dark gray on the back, shading to lighter gray on the belly. Between eye and flipper there was present a so-called " bracket mark " or " false gill " on each side of the body (Fig. 2). This mark was first described by Hubbs (1951) and followed several subsequent authors, *e.g.* Caldwell *et al.* (1960), Hale (1963), Roest (1970) and Ross (1979). It appears to be characteristic of the Genus (Ross, 1979).

Yamada (1954) also noted similar mark was present in two *Kogia* taken at Taiji, Japan, and in one specimen obtained from Tamashima, Okayama-ken. This pattern of his specimens, however, different in shape from the " bracket-like "
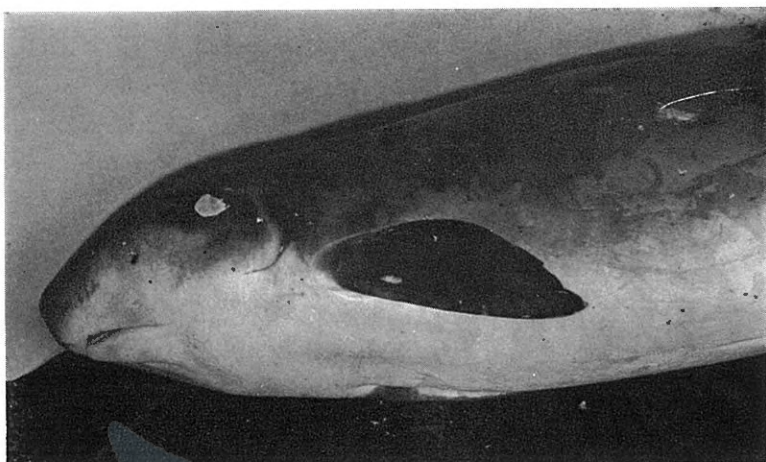
Fig. 1.   Obliquely lateral view of head and trunk of the present specimen of the pygmy sperm whale.

Fig. 2.   Head of the present specimen, showing the typical " bracket mark " after eye.

mark.   The position of this mark is quite similar to those of other specimens, *i.e.* it is located behind the eye and in front of the flipper.   This pattern was consisted of two processes of the ventral white color upwards into the dorsal black region and both pointing to ear hole, thus forming black island between them.

Since then no paper deals with this marking of the Japanese specimen. Omura and Takahashi (1981) reported a pygmy sperm whale stranded at Tokai-mura, Japan.   In this case, however, the carcass was already half-decomposed and no marking was observed.   In the present specimen the marking is clearly typical

TABLE 1. BODY PROPORTION OF THE PRSENT SPECIMEN

	Measurements	in mm	% of Total length
1.	Tip of snout to notch of flukes (Total length)	1,731	100.0
2.	Tip of snout to center of eye	215	12.4
3.	Tip of snout to ear	283	16.3
4.	Center of eye to ear	54	3.1
5.	Tip of snout to blowhole	185	10.7
6.	Tip of snout to ant. insertion of flipper	360	20.8
7.	Tip of snout to ant. insertion of dorsal fin	902	52.1
8.	Tip of snout to tip of dorsal fin	1,050	60.7
9.	Length of gape	109	6.3
10.	Length of blowhole	15	1.0
11.	Width of blowhole	42	2.4
12.	Length of eye	26	1.5
13.	Tip of snout to umbilicus	859	49.6
14.	Tip of snout to midpoint of genital slit	1,151	66.5
15.	Tip of snout to anus	1,168	67.5
16.	Projection of snout beyond lower jaw	69	4.0
17.	Half girth on transverse plane at eye	402	23.2
18.	Half girth on transverse plane at axilla	505	29.2
19.	Half girth on transverse plane at ant. insertion of dorsal fin	556	32.1
20.	Half girth on transverse plane at umbilicus	570	32.9
21.	Half girth on transverse plane at anus	350	20.2
22.	Length of flipper, ant. insertion to tip	275	15.9
23.	Length of flipper, axilla to tip	203	11.7
24.	Maximum width of flipper	105	6.1
25.	Width, base of flipper	123	7.1
26.	Height of dorsal fin	67	3.9
27.	Length of dorsal fiin	166	9.6
28.	Width of flukes, tip to tip	444	25.6
29.	Noteh of flukes to tip, right	228	13.2
30.	„ , left	220	12.7
31.	Anterior insertion of flukes to notch	183	10.6
32.	Anterior insertion of flukes to tip(r)	349	20.2

" bracket mark " or " false gill " (Fig. 2), but this specimen was obtained from the high seas of the North Pacific and not from the coast of Japan. Yamada's opinion (1954) was that " kogiids from the Japanese waters differ to a certain extent from those from the American coasts both Pacific and Atlantic." To our regret since then this has not been proved or disproved yet.

In Table 1 the body proportions of this specimen and in Table 2 the weights of various parts of the body are shown. The dorsal fin starts from about midpoint of the body and its height is 3.9% of the body length, which is in the ranges of the value for *K. breviceps* given by Ross (1979).

This whale was identified as *Kogia breviceps* because there was present no creases on throat, and a falcated dorsal fin was small and situated behind midback as stated above. Further it had 25 small teeth in all on lower jaw and none on upper jaw. Later this was confirmed by examination of the skull.

TABLE 2. BODY AND ORGAN WEIGHTS OF THE PRESENT SPECIMEN

Item	Weight in gr.		% of the total
Muscle		32,795	39.8
Blubber		31,580	38.3
Bones		7,050	8.5
Skull	1,410		
Ribs	1,350		
Vertebrae	3,970		
Others	320		
Internal organs		8,191	9.9
Brain	685		
Heart	840		
Spleen	22		
Lung	1,135		
Stomach	755		
Intestine	1,660		
Liver	2,330		
Kidney	450		
Uterus and ovary	64		
Others	250		
Others		3,845	3.5
Total		82.461	100

Skull and postcranial bones were obtained by boiling the carcass about one month later from the dissection, during which period they were soaked in water. Skull of this specimen is shown in Fig. 3 and mandibles in Fig. 4. The bones which consisted of the skull are very loosely fused each other and very easily be separated. Handley (1966) listed up distinguishing characteristics of *Kogia breviceps* and *K. simus* in his Table 1. The majority of these differences refer to features of the cranium and mandible. The most distinctive cranial characters are the shape of the dorsal sagittal septum and the dorsal cranial fossae. These were confirmed by Ross (1979) who studied a considerable number of specimens. In *K. breviceps* the dorsal sagittal septum near vertex is broad, whereas in *K. simus* it is narrow.

This breadth of the present specimen of a calf is 22 mm, as seen in Table 3. Accroding to Handley (1966) this breadth is 20–38 mm in *K. breviceps*, whereas in *K. simus* it is only 6–14 mm (both in adult specimens). In *K. simus* the dorsal cranial fossa is cupped posteriorly and sub-symetrical, but in the present specimen each fossa slopes gradually from the dorsal rim of the skull and giving no cupped appearance. These two are the most conspicuous character which separates the two species. We concluded, therefore, that the present specimen is *K. breviceps*.

The measurements of the skull of this specimen are shown in Table 3. In this table the measurement numbers are the same to those used by Ross (1979). From these measurements, excepting above stated, no definite conclusion will be drawn at present and further collection of material is needed. There are rather wide range of variation in measurements presented by Ross (1979).

The seven cervical vertebrae are ankylosed into a single unit (Fig. 5), but the
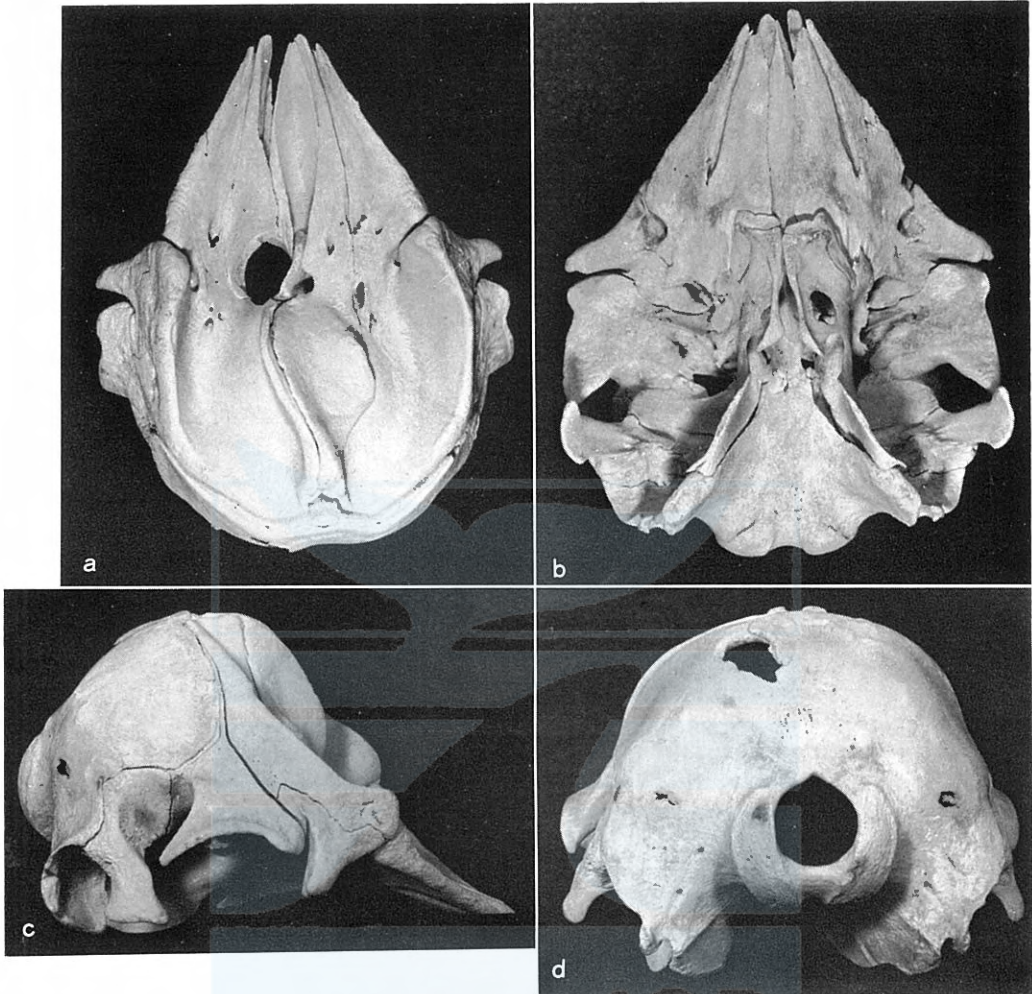
Fig. 3.   Skull of the present specimen.
a.   Dorsal view.   b.   Ventral view.
c.   Lateral view.   d.   Posterior view.

posterior epiphysis of the seventh vertebra is not fused to its centrum.   In other vertebrae all of the epiphyses were not fused to their centra.   In all there are 52 vertebrae and the formula is C7, D12, L9, Ca24, Total 52 (Fig. 6).   The dorsal or thoracic vertebrae are the vertebrae which are accompanied rib.   The lumbar vertebrae have no relationship with a rib and the last lumbar is separated from the first caudal by absence of chevron bone at its ventro-posterior end.   In all 14 chevron bones were present, and in each of them the right and left laminae were fused into a mass.   Measurements of vertebrae are shown in Table 4 and their photograph in Fig. 6.

It seems that the problem of the number of vertebrae has not been cleared
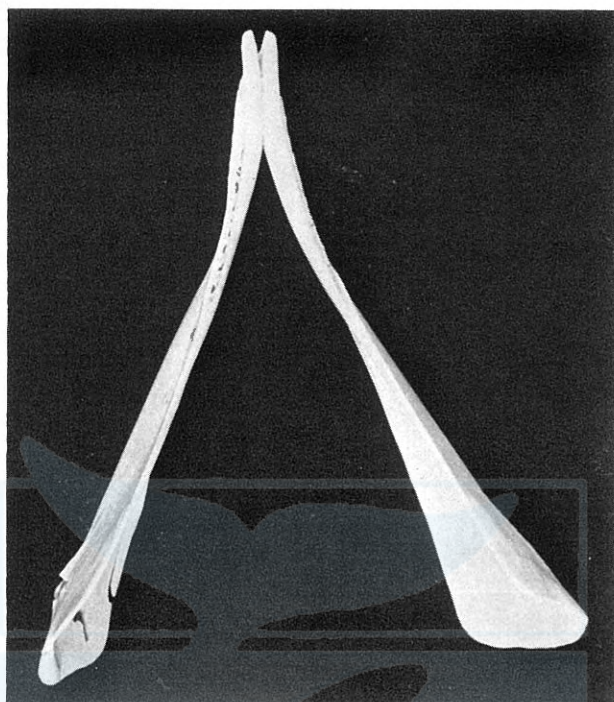
Fig. 4.   Mandibles of the present specimen.

TABLE 3.   SKULL MEASUREMENTS OF THE PRESENT SPECIMEN

	Measurements	in mm	% of Total length
1.	Total (condylobasal) length	247	100
2.	Rostrum length*	96	38.8
3.	Rostrum, basal width*	102	41.3
4.	Rostrum, width at its middle*	84	34.0
5.	Breadth across pre-orbital angles of supra-orbital processes	190	76.9
6.	Breadth across post-orbital processes	196	79.3
7.	Zygomatic width	197	79.8
8.	Height to vertex	151	61.1
9.	Width of vertex	22	9.0
10.	Width of supra-occipital at narrowest part between posterior margins of temporal fossae	153	62.3
11.	Tip rostrum - left naris	106	42.9
12.	Height of ventral border of foramen magnum	46	18.6
15.	Width outer margins oceipital condyles	64	25.5
16.	Tip rostrum - hind margin pterygoids	142	57.5
17.	Length of mandible	201	81.4
20.	Height mandible at coronoid	51	20.6
21.	Length mandibular synphysis	31	12.6
24.	Height dorsal border of foramen magnum to vertex	67	27.1

* Measured ventrally.
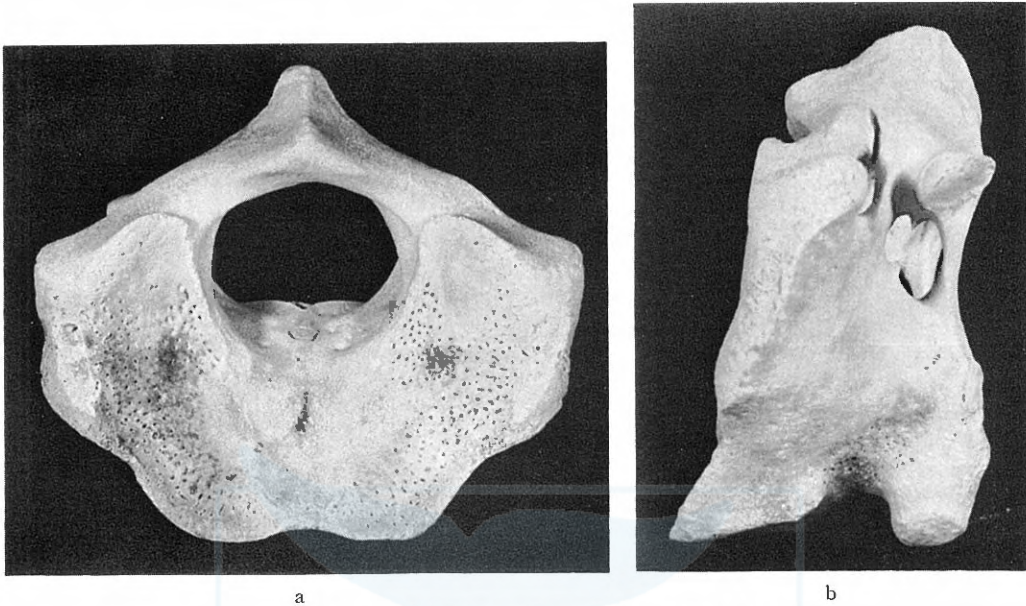
Fig. 5. Cervical vertebrae of the present specimen.
a. Anterior view. b. Lateral view.

yet for *K. breviceps* and *K. simus*. Both Handley (1966) and Ross (1979) discussed nothing on this matter, though this might be an essential character to separate the two species. Ogawa (1936–37, 1939), Hale (1947, 1959) and Yamada (1954) counted the number of vertebrae of genus *Kogia*. These are compared with the culculation of the present specimen in Table 5.

As seen in Table 5 the smallest number of vertebrae is 52 and the largest 57. In Ogawa's specimen (1939) and present specimen the total number of vertebrae is 52. Ogawa identified this specimen as *Kogia breviceps*. This is supported by photograph of the skull (Fig. 2 of his thesis). The dorsal sagittal septum near vertex is broad and the dorsal cranial fossa is not cupped posteriorly. The present specimen is without doubt *K. breviceps*, as stated already. Yamada (1954) made no distinction of the species of his specimens. Omura and Takahashi (1981), however, conjectured his specimen Nos. 1, 3, and 4 to be *K. simus* and Nos. 2, 5, and 6 to be *K. breviceps*. Hale's specimen (1959) (young male) was possibly *K. simus*, because he described that the falcate dorsal fin is much larger and commences slightly anterior to the middle of the total length of the animal.

As to the Ogawa's specimen (1936–37) (his No. 2 specimen) he identified this specimen to be *K. breviceps*, but he described that according to Mr Arai who collected the specimen there were present longitudinal wrinkles near the lower lip. This explanation in Japanese is not clear, but if this means the creases on throat it is possible that this specimen was in fact a *K. simus* (Leatherwood *et al.*, 1982). Yamada's No. 5 specimen was judged from his photograph in which the dorsal sagittal septum near vertex seems broad, but dorsal cranial fossa seems to have
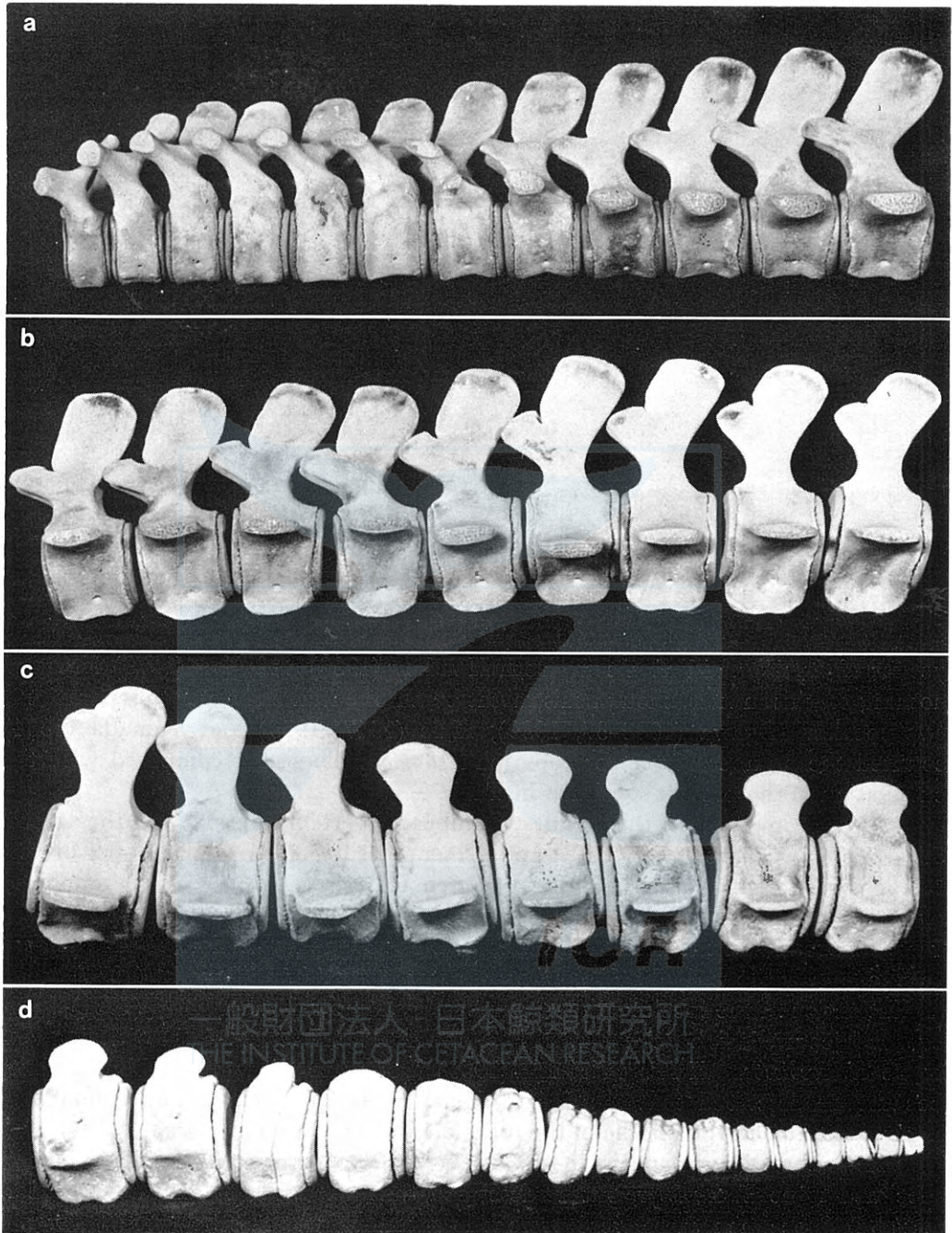
Fig. 6. Vertebrae of the present specimen.
a. 1–12 dorsal vertebrae. b. 1–9 lumbar vertebrae.
c. 1–8 caudal vertebrae. d. 9–24 caudal vertebrae.

TABLE 4. MEASUREMENTS OF VERTEBRAE OF THE PRESENT SPECIMEN (IN MM)

Serial No.	Vertebral No.	Greatest breadth	Greatest height	Centrum Breadth	Centrum Height	Centrum Length	Note
1	C 1						
2	2						all fused into a
3	3						mass, but pos-
4	4	82	74	44	29	35	terior epiphysis
5	5			(posterior)		(inferior)	of No. 7 is not
6	6						fused to centra.
7	7						
8	D 1	73	60	35 (anterior)	27	18	
9	2	70	69	38	27	20	
10	3	66	73	29	28	23	
11	4	61	76	29	28	25	
12	5	58	78	29	27	26	
13	6	56	79	29	27	27	
14	7	54	81	30	27	28	
15	8	67	81	34	28	29	
16	9	73	83	37	28	29	
17	10	77	85	38	29	30	
18	11	78	87	38	31	31	
19	12	80	87	38	31	31	
20	L 1	81	90	41	34	32	
21	2	81	91	41	39	33	
22	3	81	93	43	42	34	
23	4	82	93	43	39	34	
24	5	83	94	43	42	35	
25	6	85	95	42	43	35	
26	7	86	95	42	45	36	
27	8	89	93	42	45	36	
28	9	86	92	43	46	35	
29	Ca 1	84	80	43	43	35	
30	2	82	74	43	39	35	
31	3	78	71	43	40	34	
32	4	74	64	41	39	33	
33	5	66	61	40	37	33	
34	6	60	59	39	37	31	
35	7	55	55	39	37	31	
36	8	49	52	38	36	29	
37	9	43	49	36	36	28	
38	10	38	45	36	35	28	
39	11	—	40	35	33	25	
40	12	—	38	33	33	25	
41	13	—	30	31	30	23	
42	14	—	28	30	27	19	
43	15	—	—	27	22	16	
44	16	—	—	26	20	12	anterior epiphysis
45	17	—	—	24	16	12	missing
46	18	—	—	22	15	12	
47	19	—	—	19	14	12	
48	20	—	—	18	12	11	
49	21	—	—	16	10	10	
50	22	—	—	14	9	9	
51	23	—	—	12	7	8	
52	24	—	—	11	6	6	both epiphyses missing

TABLE 5. NUMBER OF VERTEBRAE IN GENUS KOGIA COUNTED
BY VARIOUS AUTHORS

Author	C	D	L	Ca	Total	Remarks
Ogawa (1936–37)	7	13	9	27	56*	*simus?*
Ogawa (1939)	7	12	10	23	52	*breviceps*
Hale (1947)	7	13	9	26	55	?
Yamada (1954)						
No. 3	7	13	12	25	57	*simus*
No. 4	7	13	11	26	57	*simus*
No. 5	7	13	10	27	57*	*simus?*
No. 6	7	13	11	24	54	*breviceps*
Hale (1959)	7	14	10	26	57	*simus*
Present	7	12	9	24	52	*breviceps*

* See text.
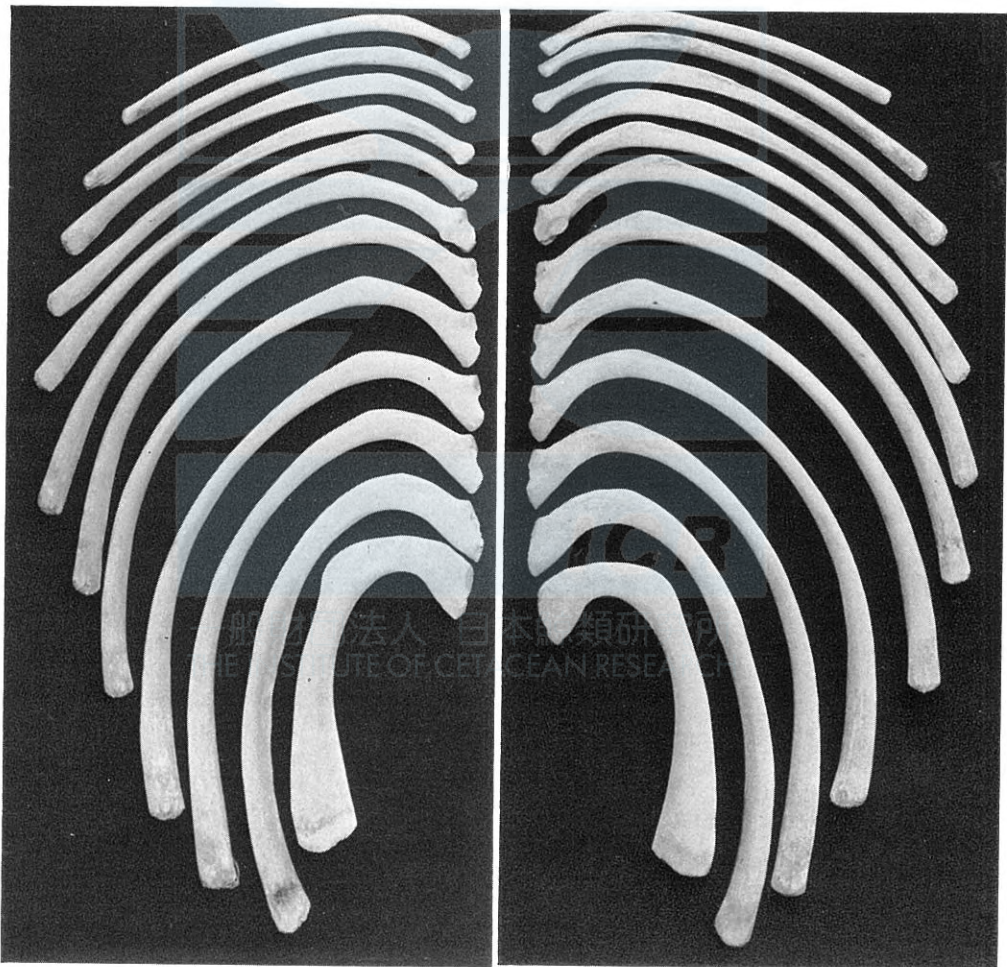
Fig. 7. Ribs of the present specimen.

TABLE 6. LENGTH OF THE RIBS OF THE PRESENT SPECIMEN (IN MM)

No.	Right*	Left*
1	131	137
2	194	197
3	215	217
4	222	235
5	230	224
6	234	223
7	224	226
8	217	212
9	201	202
10	192	192
11	178	179
12	157	159

Measured in straight line.
* In which 7 ribs are double headed.

cupped appearance.

From the above it will be concluded that the total number of vertebrae would be 52–54 in *K. breviceps* and 55–57 in *K. simus*, pending further studies in future with more samples.

In the present specimen 12 pairs of ribs are present (Fig. 7). Their straight lengths are shown in Table 6.

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NOTE ON A GRAY WHALE FOUND IN THE ISE BAY ON THE PACIFIC COAST OF JAPAN

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A gray whale, *Eschrichtius robustus* (Lilljeborg, 1861), was sighted at 1245 hour of 27 March 1982 within a few hundreds meters from the shore of the Mikimoto Pearl Island at Toba (34°28′N, 136°53′E; water depth 8 to 15 m), which locates in the Shima Archipelago near the entrance of the Ise Bay on the Pacific coast of central Japan (Fig. 1).   The species was identified by the shape of rostrum (Fig. 2) and about 10 dorsal humps (Fig. 3).   The body lengh was estimated at about 12 m.   Most of its body surface was covered by barnacles and white/yellow falling skin presumably covering healing scars (Figs 2 and 3).   Remaining portion of the body was dark gray.   Several parallel scars present on the right side of head (Fig. 2) were presumably caused by screw propeller of a small boat.   This whale was swimming toward the Ise Bay, and disappeared at 1700 hour (27 March).

On 12 April, 16 days after the first sighting, the same whale (identified by the scars) was sighted in a shallow water in the Ise Bay off Tsu City.   After this date, the whale was sighted frequently by the flights of the press and television companies, and some shipboard observation was done.   All the confirmed records being in the same area, it was suspected that the whale had settled down the place. The last sighting was recorded by the Chunichi Press on 31 May at the same location, and the whale was considered to have left the Ise Bay thereafter.   The minimum duration of the stay in the coast was 64 days since 27 March.

Since the sea was shallow (7 to 15 m), the whale's movement off the coast of Tsu city was traced easily by the cloud of mud along its passage.   The interval of dives was 5 to 6 seconds (short dives) or 3 to 4 minutes (long dives).   The blow was heart shaped.   The spyhopping posture was once observed.

Omura (1974) indicated in his review that there was a low level of constant catch of the gray whale by the Japanese net-whaling along the Pacific coast till the end of the last century.   However, the gray whale records have been extremely limited in the Pacific coast in recent years (Nishiwaki and Kasuya, 1970).   The present record is the third one known to science off the Pacific coast after the start of complete protection in 1937.

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Inst.*, 26: 1–14.
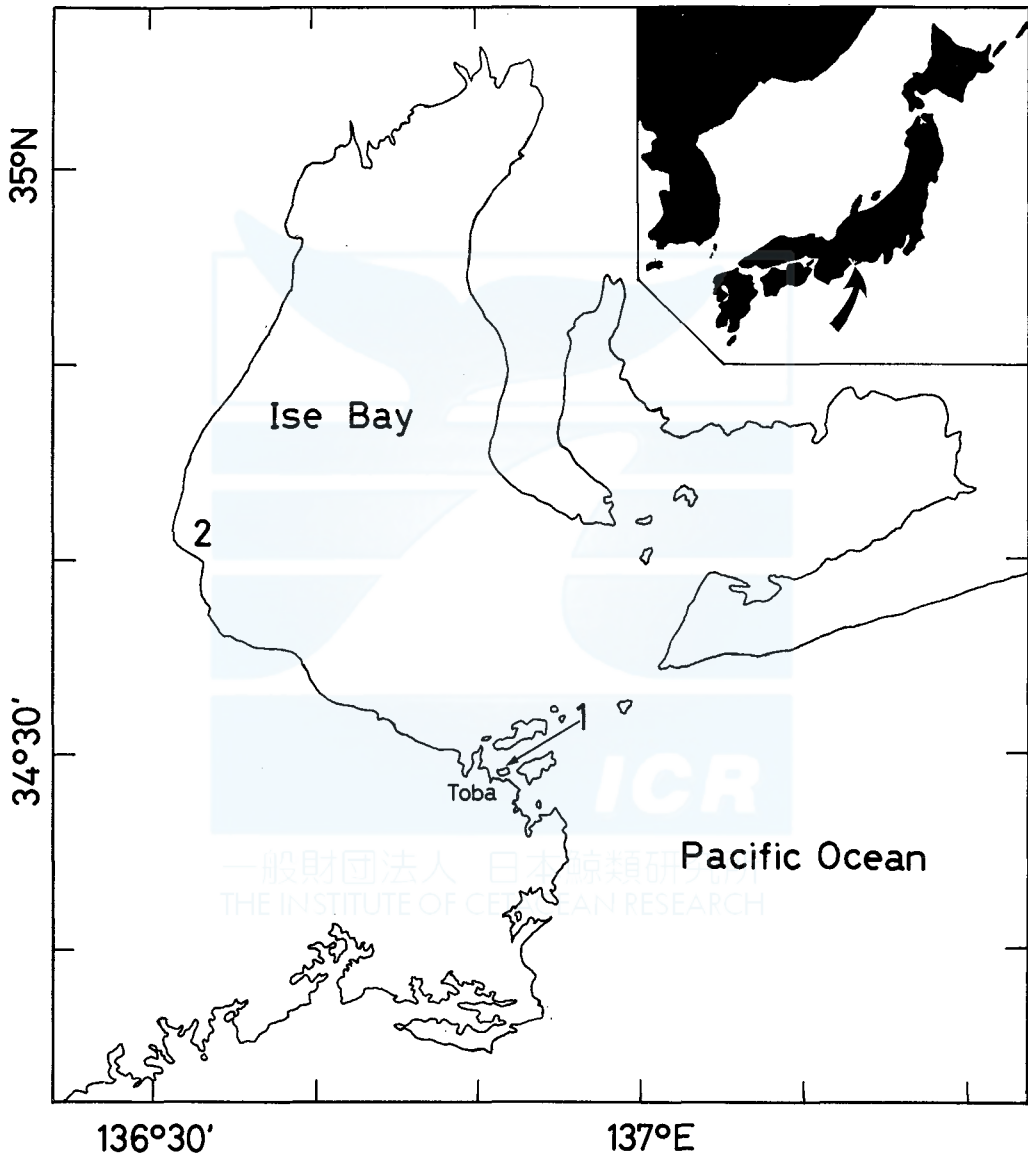
Fig. 1.   Map of Toba and the Ise Bay region.   1: Mikimoto Pearl Island where the
whale was first sighted; 2: off Tsu city where the whale stayed for minimum of
45 days.

Fig. 2.   Right side of head region of the whale, off Tsu City.
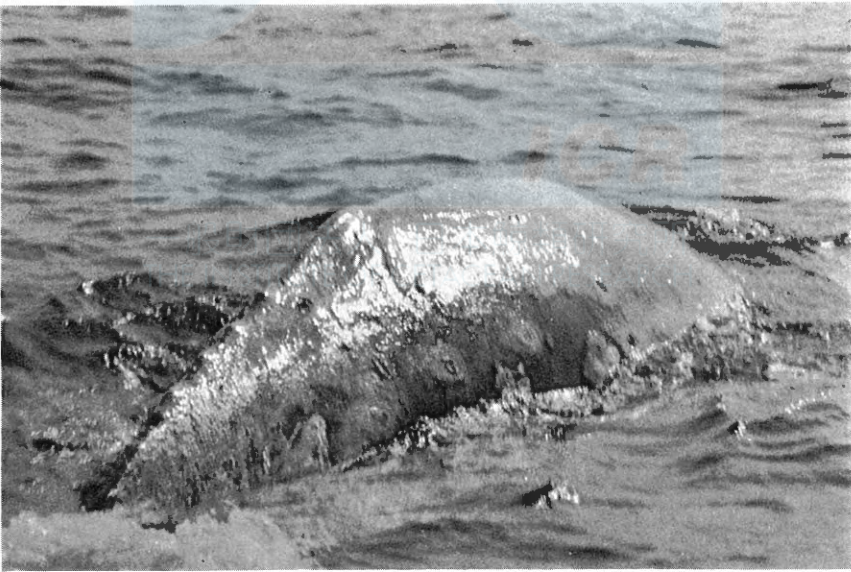
Fig. 3.   Dorsal humps of the whale, off Tsu City.

Appendix

MEASUREMENTS OF BODY PROPORTIONS OF THE PYGMY BLUE WHALE, LEFT BY THE LATE DR TADAYOSHI ICHIHARA

INTRODUCTION BY EDITOR

One of the most prominent works of The Late Dr T. Ichihara is the discovery of the " Pygmy Blue Whale ". The name pygmy blue whale was first given by Ichihara (1961) on blue whales inhabiting the waters around Kerguelen Island, recognizing differences in the external characteristics from the blue whales elsewhere in the Antarctic. Since then researches on this population have been carried out by various authors *i.e.* Ichihara, 1963 and 1966; Gambell, 1964; Ichihara and Doi, 1964; Zemsky and Boronin, 1964; Omura, Ichihara and Kasuya, 1970.

The subspecies *Balaenoptera musculus brevicauda* was proposed by Ichihara in a paper read in 1963 at the First Symposium on Cetacean Research held in Washington, D. C. His paper was not published until 1966, due to delay in printing. Meanwhile the name *brebicauda* was published by Zemsky and Boronin (1964). This is a nomen nudum according to van Bree, pers. comun.; and the first valid publication of the name was by Ichihara 1966 (Rice, 1977).

His conclusion is mainly based on the differences in the external morphology between the ordinary and pygmy blue whales. To our regret the basic data of the measurements of body proportions of each whale he measured (Table 1) were not appended to this important thesis. Accordingly these valuable data could not be used by researchers who desire to use them. This is the reason why we publish them here at this moment. (H.O.)

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TABLE 1.   MEASUREMENTS OF BODY PROPORTIONS OF THE PYGMY
(Measurement of 1 are in metres and other

1.   Total length, tip of snout to notch of flukes   3.   Tip of suout to blow-hole
of snout to anterior end of flipper   7.   Eye to ear, centres   8.   Notch of
11.   Notch of flukes to umbilicus   12.   Notch of flukes to end of system of
vertical height   15.   Dorsal fin, length of base   16.   Flipper, tip to axilla
21.   Skull, greatest width   22.   Skull length, condyle to tip of premaxilla

Serial no.	1	3	5	6	6′	7	8	10
	[MALE]							
602 N 0000	18.00	17.67	19.39	44.88	33.67	5.50	21.56	27.50
612 K 0974	18.05	19.67	20.78	47.09	35.46	5.26	24.10	28.25
60 K J 1025	19.30	—	21.24	43.52	—	3.63	19.17	27.98
612 K 0987	19.30	16.58	19.27	—	29.53	5.38	22.79	27.05
612 K 0960	19.90	18.59	19.10	—	34.17	6.53	22.61	25.63
60 K J 0876	20.00	—	19.75	42.00	—	5.25	22.00	26.00
60 K J 0795	20.50	—	20.49	45.37	—	4.39	20.49	25.37
612 K 0938	20.00	19.50	21.25	46.50	35.75	5.25	21.00	26.00
613 N 1334	20.40	18.48	20.74	44.80	—	5.44	23.04	26.86
60 K J 0878	21.00	—	21.90	42.86	—	4.77	20.95	27.62
60 K J 1149	21.50	19.53	20.00	42.33	32.56	5.58	21.40	25.12
602 T 1216	21.60	15.28	—	44.44	—	—	23.15	25.00
612 K 0954	21.30	16.67	18.07	—	28.64	6.81	28.09	27.46
613 K 1876	21.30	—	20.66	42.72	31.46	4.69	19.72	25.35
613 K 1875	21.30	—	20.19	39.44	29.58	4.69	21.60	24.41
60 K J 1116	22.00	18.18	—	43.18	35.45	—	20.45	23.64
602 T 1578	22.10	18.55	21.27	—	31.22	—	23.98	—
60 K J 0619	22.20	—	20.27	43.69	34.68	4.96	20.36	24.77
613 K 1863	22.10	18.55	23.98	38.91	29.86	—	23.53	26.70
60 K J 0640	23.10	—	18.61	—	—	—	—	24.67
60 K J 1261	23.10	—	19.91	—	—	—	—	27.27
	[FEMALE]							
60 K J 1015	18.60	—	18.28	40.32	—	4.03	24.73	26.88
612 T 0845	19.10	19.90	22.25	46.07	35.60	4.87	21.62	27.23
60 K J 1022	20.30	—	21.92	43.34	—	3.20	21.67	27.09
60 K J 0941	20.50	—	20.00	43.41	—	4.39	22.44	26.83
60 K J 0875	20.80	—	20.43	42.31	—	5.29	22.60	27.88
60 K J 0796	21.00	—	20.95	42.86	—	6.19	22.86	27.62
60 K J 0912	21.10	—	22.27	42.18	—	2.85	22.27	27.01
60 K J 1117	21.30	18.31	19.72	40.85	33.33	6.10	22.54	25.82
602 N 0924	21.30	17.37	19.01	—	31.46	5.07	24.55	25.96
60 K J 0770	21.30	16.43	20.19	42.25	32.39	4.69	23.47	24.88
602 T 1231	21.30	17.84	19.72	—	32.39	5.16	23.00	25.35
60 K J 0944	21.40	19.16	20.56	44.39	34.11	6.54	20.09	26.17
602 T 1656	21.40	19.63	22.36	—	36.45	5.14	22.43	27.10
602 T 1212	21.50	16.28	—	42.79	—	—	23.26	30.23
60 K J 0914	21.60	—	20.14	43.52	—	3.70	—	28.70
602 N 0848	21.70	18.89	21.01	—	33.18	2.95	25.35	27.88
602 N 0804	21.70	18.66	20.05	—	31.34	4.83	21.01	25.99
60 K J 0858	21.80	20.18	21.10	44.04	33.49	5.51	21.56	26.15
613 N 1326	21.25	17.88	20.14	41.88	—	5.13	20.71	25.65
613 N 1845	21.30	20.33	21.64	43.66	—	5.26	—	24.13

BLUE WHALE, LEFT BY THE LATE DR TADAYOSHI ICHIHARA.
are percentages against the total length)

5.   Tip of snout to centre of eye   6.   Tip of snout to tip of flipper   6'.   Tip
flukes to posterior emargination of dorsal fin   10.   Notch of flukes to anus
ventral grooves   13.   Anus to reproductive aperture, centres   14.   Dorsal fin,
17.   Flipper, tip to anterior end of lower border   19.   Flipper, greatest width
(23).   Flukes, greatest width

11	12	13	14	15	16	17	19	21	22	(23)
42.89	41.00	7.22	0.89	3.28	—	—	—	12.44	26.00	—
44.88	43.21	6.65	0.66	2.49	—	—	—	—	—	—
44.04	—	8.29	—	—	12.18	15.13	3.74	—	—	—
45.08	40.41	7.89	1.24	2.85	—	—	—	—	—	—
42.21	37.19	—	—	—	—	—	—	—	—	—
44.00	—	8.50	—	—	9.50	12.25	3.40	—	—	—
43.90	—	6.83	—	—	11.22	13.66	3.66	—	—	—
40.00	39.00	6.30	1.15	3.00	—	—	—	—	—	—
42.65	36.76	6.96	0.98	3.77	—	—	—	—	—	—
44.76	—	6.19	—	—	10.48	13.10	3.90	—	—	—
40.93	—	6.97	—	—	—	—	—	—	—	—
41.67	31.48	7.87	1.06	—	—	—	—	—	—	—
42.96	38.97	5.87	1.13	2.58	—	—	—	—	—	—
40.85	37.09	7.04	0.99	3.05	—	—	—	—	—	—
39.91	38.03	7.51	0.85	2.82	—	—	—	—	—	—
40.91	39.09	8.18	0.77	3.18	—	—	—	—	—	—
—	—	—	0.90	3.17	—	—	—	—	—	—
40.54	37.39	6.76	0.81	2.25	—	—	—	—	—	—
43.89	42.08	8.60	1.09	2.49	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
41.93	—	2.68	—	—	9.68	12.90	3.12	—	—	—
42.15	43.36	3.14	1.10	5.08	—	—	—	12.04	25.92	—
43.84	—	2.96	—	—	10.04	12.81	3.89	—	—	—
44.39	—	3.41	—	—	10.54	13.71	3.95	—	—	—
44.71	—	2.89	—	—	9.62	12.74	3.65	—	—	—
42.86	—	2.86	—	—	10.00	12.86	3.57	—	—	—
43.13	—	2.85	—	—	9.48	11.80	3.51	—	—	—
41.78	36.62	2.35	0.89	2.35	—	—	—	—	25.35	—
41.60	38.31	3.48	0.66	3.66	—	—	—	—	—	—
45.07	42.72	2.35	0.99	2.82	—	—	—	—	24.88	—
42.25	37.56	2.82	0.70	2.11	—	—	—	—	—	—
40.65	38.32	2.33	0.98	3.27	—	—	—	—	26.17	—
42.99	40.65	1.87	1.12	2.10	—	—	—	—	—	—
45.12	42.79	2.79	1.26	2.05	—	—	—	—	—	—
42.13	—	3.24	—	—	10.19	12.96	3.61	—	—	—
44.47	43.09	3.46	1.38	4.06	—	—	—	—	—	—
43.09	38.57	3.04	0.92	4.10	—	—	—	—	—	—
42.66	38.07	2.29	0.87	2.75	—	—	—	—	26.15	—
42.82	38.21	2.59	0.75	3.67	—	—	—	—	—	—
41.55	37.55	5.07	—	—	—	—	—	—	—	—

TABLE 1. Continued

Serial no.	1	3	5	6	6′	7	8	10
613 K 1884	21.40	17.29	21.03	—	—	—	20.09	24.77
613 K 1859	21.50	19.53	—	42.33	—	—	23.26	27.91
613 N 1324	21.82	15.99	19.25	42.67	—	5.04	22.91	27.27
613 N 1328	21.90	17.58	19.95	43.38	—	4.79	21.37	27.58
613 K 1858	21.90	19.18	23.74	42.46	—	—	21.92	27.40
60 K J 0581	22.00	15.91	19.09	—	32.27	5.00	20.00	24.09
602 N 0897	22.10	17.65	18.78	—	32.13	4.84	22.35	24.38
60 K J 0808	22.10	—	20.81	42.53	—	4.98	21.72	27.60
602 T 1723	22.10	19.00	20.81	—	32.13	—	22.62	26.70
602 T 1767	22.10	19.00	21.27	—	34.39	4.97	21.72	25.79
602 T 1275	22.30	18.83	19.73	—	32.29	4.49	22.42	29.15
602 T 1591	22.30	16.59	20.18	—	32.74	6.73	23.32	25.11
60 K J 0801	22.30	18.83	20.18	43.05	32.74	5.38	21.97	26.91
60 K J 0798	22.50	—	20.44	42.22	—	5.78	22.67	28.44
602 T 1693	22.60	17.26	20.35	—	34.51	5.31	23.45	27.43
602 T 1612	22.60	16.81	22.57	—	37.17	—	20.80	22.57
602 N 0896	22.70	19.82	21.32	—	34.10	5.20	22.91	27.31
602 N 0907	22.80	17.06	18.95	—	31.45	4.38	23.90	22.63
602 N 0805	22.80	17.98	20.04	—	30.26	5.18	20.18	23.90
60 K J 0897	23.00	—	21.20	44.57	—	3.90	21.20	28.13
60 K J 0624	24.20	—	19.42	—	—	—	—	26.86
[FOETUS, MALE]								
60 K J 0912	2.52	—	15.82	40.79	—	7.99	23.81	30.16
60 K J 0946	2.70	—	17.15	44.44	—	6.92	24.81	29.63
602 N 0924	3.25	14.15	16.31	—	32.62	6.46	22.46	28.92
602 T 0805	3.57	14.00	17.09	—	33.89	—	22.97	29.41
60 K J 0945	3.65	—	16.44	43.84	—	8.77	27.40	31.51
602 T 0772	4.15	14.46	18.32	—	35.42	—	24.10	30.12
60 K J 0941	4.52	—	17.26	45.13	—	8.18	23.67	27.88
60 K J 0889	4.70	—	15.77	42.13	—	7.21	25.53	31.06
60 K J 0858	6.30	13.81	18.10	44.44	32.22	5.56	25.08	30.63
[FOETUS, FEMALE]								
602 T 0736	2.30	15.22	—	—	35.65	—	23.91	29.57
602 T 0771	2.30	13.48	16.09	—	—	—	23.04	29.13
60 K J 0875	2.70	—	17.04	45.56	—	9.63	24.44	30.37
602 T 0769	3.15	14.92	17.14	—	33.65	—	25.08	29.21
60 K J 1040	4.35	—	15.86	44.14	—	8.97	26.67	29.66
602 N 0896	4.73	15.22	17.97	—	33.62	5.29	25.37	29.61
60 K J 0872	4.81	—	17.05	44.91	—	8.11	25.57	27.03
60 K J 0801	5.20	14.42	16.35	45.58	33.08	—	24.04	—
602 T 0816	5.36	14.93	17.16	—	32.46	6.16	24.25	29.85

11	12	13	14	15	16	17	19	21	22	(23)
—	39.25	2.80	0.70	1.87	—	—	—	—	—	—
46.51	44.19	2.79	0.51	2.28	—	—	—	—	—	—
44.63	39.92	2.43	0.78	4.22	—	—	—	—	—	—
45.16	38.36	2.51	0.87	3.70	—	—	—	—	—	—
42.01	40.64	2.28	0.82	2.97	—	—	—	—	—	—
40.91	39.09	2.27	0.82	5.91	—	—	—	—	—	—
41.18	36.92	2 54	0.77	3.35	—	—	—	—	—	—
42.99	—	3.17	—	—	9.28	12.22	3.39	—	—	—
42.53	40.72	1.81	1.00	2.94	—	—	—	—	—	—
42.08	40.27	3.17	1.18	2.26	—	—	—	—	—	—
45.29	40.36	2.69	1.12	2.02	—	—	—	—	—	—
41.70	38.16	0.91	0.99	2.24	—	—	—	—	—	—
42.15	39.46	2.24	0.94	2.02	—	—	—	—	25.56	—
41.78	—	2.64	—	—	9.33	11.78	3.56	—	—	—
42.48	39.82	2.22	0.88	1.99	—	—	—	—	—	—
44.69	42.48	4.86	—	—	—	—	—	—	—	—
43.52	39.47	2.65	1.37	3.52	—	—	—	—	—	—
44.12	34.21	4.12	1.05	3.46	—	—	—	—	—	—
40.39	36.75	4.17	0.70	3.73	—	—	—	—	—	—
42.84	—	3.03	—	—	10.39	12.77	3.50	—	—	—
—	—	—	—	—	—	—	—	—	—	—
46.03	—	7.94	—	—	11.11	15.48	4.37	—	—	—
44.44	—	7.41	—	—	11.52	15.56	4.44	—	—	—
42.46	46.46	7.70	1.54	5.54	—	—	—	—	—	—
45.94	43.98	—	1.68	4.34	—	—	—	—	—	—
47.67	—	6.85	—	—	13.15	17.81	4.38	—	—	—
45.30	42.65	6.27	1.69	4.82	—	—	—	—	—	—
45.80	—	8.40	—	—	12.83	17.26	5.09	—	—	—
47.23	—	6.39	—	—	13.19	16.38	4.38	—	—	—
46.98	43.17	7.47	1.59	4.13	—	—	—	—	—	—
45.22	—	2.17	1.74	3.48	—	—	—	—	—	—
46.09	43.48	2.61	1.30	4.35	—	—	—	—	—	27.39
47.41	—	2.59	—	—	12.22	16.67	4.81	—	—	—
43.81	41.27	2.22	1.59	3.44	—	—	—	—	—	22.22
44.60	—	1.83	—	—	12.64	16.32	4.37	—	—	14.25
47.36	44.40	2.74	1.90	5.07	—	—	—	—	—	—
40.96	—	1.66	—	—	12.46	16.22	4.57	—	—	—
—	—	—	2.31	4.81	—	—	—	—	—	—
46.27	45.90	2.24	1.31	3.17	—	—	—	—	—	—

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