ISSN 0083-9086

THE
SCIENTIFIC REPORTS
OF
THE WHALES RESEARCH INSTITUTE

No. 34

THE WHALES RESEARCH INSTITUTE
TOKYO · JAPAN

DECEMBER 1982

Sci. Rep. Whales
Res. Inst., No. 34

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THE WHALES RESEARCH INSTITUTE
3-32-11 OHJIMA, KOTO-KU, TOKYO

THE SCIENTIFIC REPORTS OF THE WHALES RESEARCH INSTITUTE

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MASS STRANDINGS OF TOOTHED WHALES (ODONTOCETI) AS A POPULATION PHENOMENON

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Sci. Rep. Whales Res. Inst.,
No. 34, 1982, 1–47

ABSTRACT

From a study of *Globicephala melaena* and *Lagenorhynchus acutus* in the northwest Atlantic, and *Physeter catodon* at North Island, New Zealand, it is shown that mass strandings of Odontoceti occur at high population densities. Moreover, within the range of a single species, mass strandings occur within the " core " of the range but not at its periphery. They occur at high frequency among species of the subfamily Orcininae. In *Globicephala* spp. and *Pseudorca crassidens* the stranded herds include all sizes of animals of both sexes, and these species are therefore highly social. Amongst most Delphininae, mass strandings occur at lower frequency. Herds consist of reproductively mature animals and calves, or of immatures, or solitary immatures may strand. These species are therefore less social and, in captivity, an adult male *Tursiops truncatus* is aggressive towards immature animals. The social Orcininae nevertheless show greater sexual dimorphism than the Delphininae, a more delayed sexual maturity and a lower frequency of males, features usually associated with polygyny. The sperm whale *Physeter catodon* shows frequent mass strandings of harem herds and occasional mass strandings of adolescent males in warm seas, singleton strandings of solitary males in cool seas.

Age-specific mortality rates of Odontoceti and Mysticeti were studied from length-frequencies of stranded as compared with randomly-captured animals. Two Mysticetes (minke, humpback) showed a high mortality of newly-weaned animals, and minke—a high mortality at greatest lengths, among strandings. A weakly social Odontocete (*Phocoena phocoena*) showed the first feature. Three Delphinid species showed evidence of more even mortality through all ages. This feature is related to their sociality, including long parental care. Nevertheless there is evidence for enhanced mortality of immatures of both sexes in species showing aggression by adults. There is also evidence for density-dependent reproduction in several species of Odontoceti, though not so far in the most highly social Orcininae. Since most mortality in these latter species is mass mortality, mass mortality must regulate their populations. Psychological mechanisms leading to mass strandings remain to be investigated, but could include stress. The animals about to strand are regarded as being in a passive, moribund state, drifted to the coastline by currents.

INTRODUCTION

The Cetacea are divided into two suborders which differ in many ways, not least in size. The baleen whales or Mysticeti are all large (6 to 30 m adult body length) and feed by engulfing organisms much smaller than themselves which they trap and strain with their baleen plates. The toothed whales or Odontoceti are smaller (2 to 15 m) and feed on fish or squids not so much smaller than themselves. Very often, active cooperation aids capture of their prey, a habit which may have resulted in their commonly found and highly-developed social behaviour. Only among the Odontocetes, especially in the most highly social families, do we find the very curious tendency to come ashore and die in groups; the phenomenon of mass strandings. Mysticetes are found stranded en masse in only one circumstance, when pressed by pack ice on to the shore, a phenomenon found also in Odontocetes that live in cold seas (Taylor 1957; Sergeant, Mansfield and Beck 1970). This seems to be an accidental phenomenon, which does not necessarily imply social behaviour, other than that individual whales may be feeding or travelling together.

Mass-stranded animals are not obviously diseased or in an abnormal body state, and the phenomenon has so far defied explanation (Geraci 1978). Observers who have sought the cause at the level of the specific site and set of circumstances have so far produced no convincing explanations. While the stranding animals must be exhibiting abnormal behaviour, since it is almost always lethal, I have found it useful to look first at the phenomenon at the level of the population. Opportunity to do this came from the lucky chance that 30 years' data existed, from 1950 to date of writing (1981), on the abundant north Atlantic pilot whale *Globicephala melaena* at Newfoundland. I also found some less complete data on another delphinid, the white-sided dolphin *Lagenorhynchus acutus* in the northwest Atlantic, and on the sperm whale *Physeter catodon* at New Zealand. I have also been fortunate in that networks of published strandings have increasingly developed in recent years, notably in France and the United States.

THREE CASE HISTORIES

a. *North Atlantic pilot whale Globicephala melaena in the northwest Atlantic.*

Northern pilot whales have long been known to mass-strand in cool waters of the North Atlantic, from Cape Cod to Newfoundland, in Greenland, and from France to Iceland (Figure 1). In several regions of their abundance, especially at the Faeroes and at Newfoundland, inshore fishermen have taken advantage of this tendency to drive the animals ashore (Mitchell 1975a).

Catching in Newfoundland was intensive, with an organised industry, from 1947 to 1971 (Fig. 2). In the later years of this drive-fishery, annual catches became very low. It appeared that a population, of ill-defined extent, but probably inhabiting the area east of Newfoundland, had been decimated; the total catch had been approximately 54,000 animals (Mercer 1975). Figure 2 shows that high catches at the outset, peaking in 1956, were steadily reduced, lesser fluctuations being associated with variable abundance of the main food, the squid *Illex illecebrosus*, from year to year. There was, however, no overall decline of squid over the period of decline of pilot whales.

Fig. 1. Part of a herd of 58 pilot whales *Globicephala melaena* stranded at Port Maitland, Nova Scotia (44°01′N, 66°10′W) August 1–2, 1960. Photo by Ken Oxner, Yarmouth, N.S.

The area inhabited by *G. melaena* throughout the year is over deep water, extending in to the Continental Slope, where the species is generally abundant (Fig. 3). In late summer water temperatures become warm enough to allow the squid and pursuing pilot whales to concentrate over the continental shelf and inshore.

During the period of the drive fishery, there were no natural strandings in eastern Newfoundland. This is scarcely surprising since fishermen actively drove pilot whales ashore in much of the area (Conception, Trinity, Bonavista and Notre Dame bays). However, there was one stranding in 1957 in western Newfoundland (Sergeant, Mansfield and Beck 1970) where no driving took place (Table 1).

While pilot whales appeared to be scarce east of Newfoundland in the late

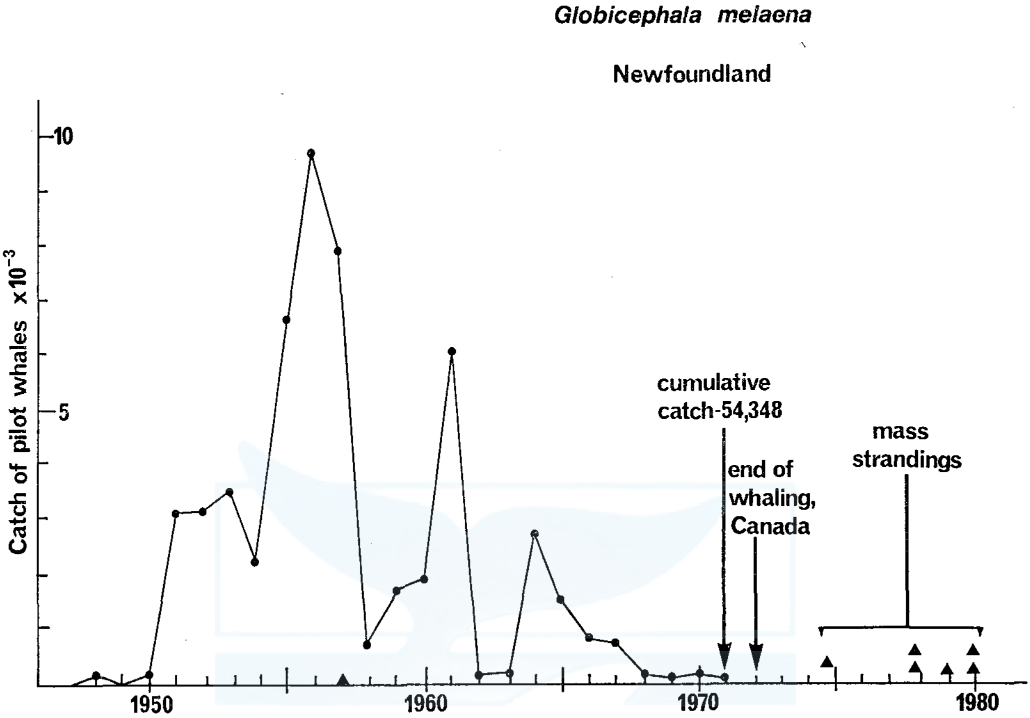

Fig. 2. *Globicephala melaena.* Catches and strandings at Newfoundland, 1948 to 1980.

1950's to early 1970's, they were still common off Nova Scotia (Fig. 3), and natural mass strandings took place both on the mainland and at offshore Sable Island (Table 1). This adjacent population must have contributed to the rather rapid recovery that took place when hunting stopped at Newfoundland, where by 1980 pilot whales were again abundant off the eastern coast (K. Hay, unpublished MS 1981).

In 1972 all whale hunting in Canada, with the exception of aboriginal hunting in the arctic, was prohibited. In 1975, natural strandings of pilot whales began to occur at Newfoundland (Mitchell 1977, Geraci and St. Aubin MS 1975; Table 1). Such had been the change in the world climate of opinion about Cetacea that fishermen were employed to save the animals by towing them to sea. In 1978 two mass strandings occurred at Miquelon Island off Newfoundland's south coast, and one in Notre Dame Bay on the east coast. In 1979 one large stranding occurred on the Burin Peninsula on the south coast. In 1980 strandings occurred on the south and northeast coasts of Newfoundland, and one at Prince Edward Island (Table 1). In 1981 there were two mass strandings in Newfoundland, one at the Magdalen Islands, Quebec, four in Nova Scotia and Cape Breton Island, and one at Cape Cod, Massachusetts. In 1980 K. Hay (unpublished MS 1981) estimated from aerial survey at least 14,000 pilot whales in Newfoundland's eastern waters up to 150 km offshore, and animals were seen to enter inshore waters in large numbers

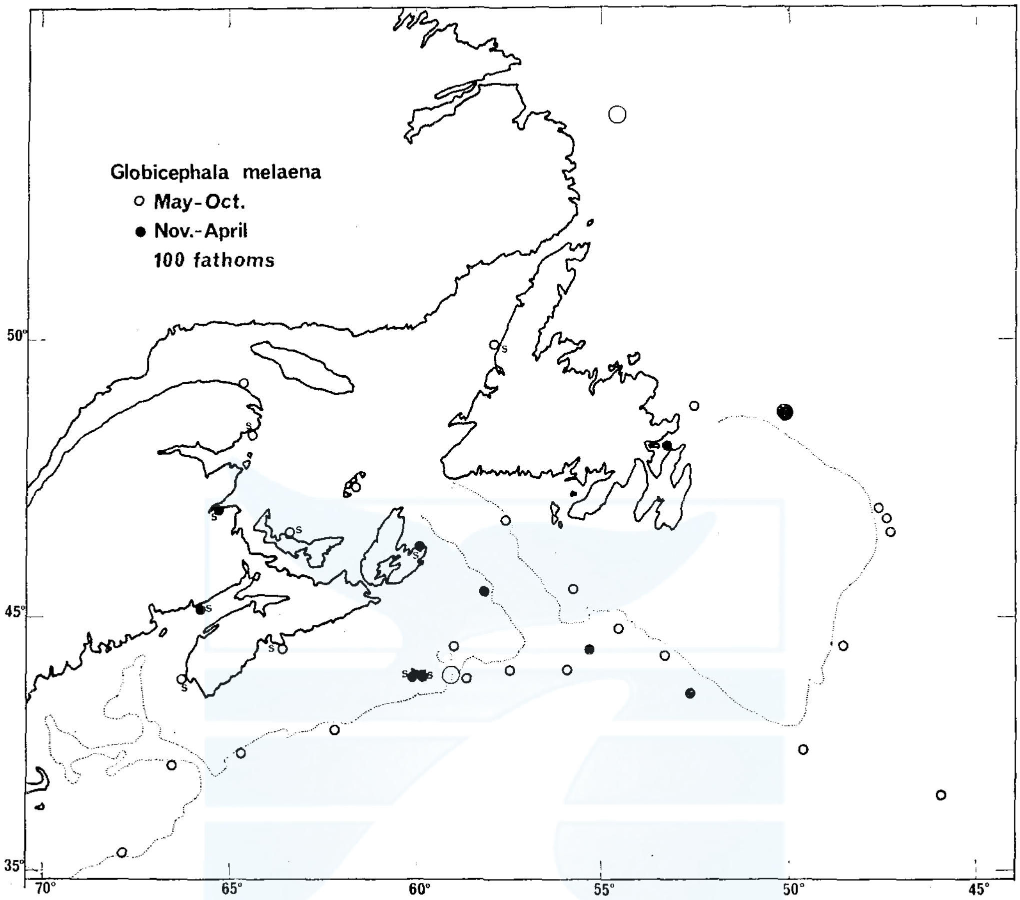

Fig. 3. Sightings and strandings (s) of *G. melaena* in the northwest Atlantic, 1957 to 1972 (from Sergeant 1979).

in early September (M. Moore, pers. comm.). In 1981 large numbers again entered inshore waters in late summer.

Mass strandings had therefore begun, coming from a population which had increased again and resumed its habit of moving inshore in late summer. A rough assessment of mortality due to mass strandings of *G. melaena* at Newfoundland in 1975 to 1980 can be made from the mean number stranded (Table 1), which is not less than 150 out of the population estimate of at least 14,000, or about 1%; this assumes that all animals were vulnerable to this kind of death, and excludes animals further than 150 km offshore. This is not a large proportion, but from the 1980 and 1981 data, mass strandings seem to be increasing in frequency and in area affected, if not in total number of animals dying.

b. White sided dolphin Lagenorhynchus acutus in the northwest Atlantic.

Lagenorhynchus acutus was observed at Newfoundland (Sergeant and Fisher

TABLE 1. MASS STRANDINGS OF PILOT WHALES IN EASTERN CANADA, 1957–1980
Sources: Sergeant, Mansfield and Beck (1970); Geraci and St. Aubin (1975, 1977), Mitchell (1977, 1980, 1981, MS 1981).

Date	Lat.	Long.	Locality	Province/State	Number
4 VIII 1957	49°51′	57°48′	Cow Head	Newfoundland	12 or more
2 X 1959	43°58′	59°48′	Sable I.	Nova Scotia	18
1 VIII 1960	44°	66°10′	Yarmouth	Nova Scotia	58
24 XII 1967	46°13′	59°57′	Glace Bay, Cape Breton I.	Nova Scotia	15
28 IX 1975	48°35′	53°30′	Charleston, Bonavista Bay	Newfoundland	300
26 XII 1976	43°58′	59°48′	Sable I.	Nova Scotia	130 or more
19 IX 1978	47°	56°15′	Miquelon-Langlande	(France; S. of Nfld.)	93+63
3 X 1978	49°28′	53°56′	Musgrave Hbr., Notre Dame Bay	Newfoundland	70
16 VII 1979	46°54′	55°33′	Pt. au Gaul, Burin Peninsula	Newfoundland	135
18 X 1980	49°09′	55°20′	Pt. Leamington, Notre Dame Bay	Newfoundland	75
25 X 1980	47°15′	55°30′	Grand Beach, Burin Peninsula	Newfoundland	18
9–18 XI 1980	46°23′	63°48′	Bedeque Bay	Prince Edward Island	52

1957) and at New England (Schevill 1956) in the early 1950's and its noteworthiness, as well as the infrequency of previous reports, suggests that it was not a particularly abundant species in the northwest Atlantic at this time. The same was true in the 1960's when Mercer (1973) recorded it in southern Newfoundland and far to the east of the island over deep water, and Sergeant, Mansfield and Beck (1970) recorded it stranded on Sable Island. During the 1970's, however, it has very often been reported in the waters off New England and Nova Scotia, and in summer in the Gulf of St. Lawrence (Katona, Testaverde and Barr 1978; Sergeant, St. Aubin and Geraci 1980; Testaverde and Mead 1980). While some of this increase must be due to an increase in observers, it seems certain that a real increase of population has occurred. The aerial surveys carried out by the University of Rhode Island's Cetacean and Turtle Assessment Program (CETAP; see Hain, Edel, Hays, Katona and Roanowicz 1981) found *Lagenorhynchus acutus in* 1979 to be the most numerous cetacean along the northeastern seaboard of the U.S.A., exceeding 10,000 individuals observed. The species occurred throughout the Gulf of Maine, especially in the vicinity of Cape Cod and over Georges Bank, and south to waters off Chesapeake Bay.

During the 1970's there were two mass strandings of *L. acutus*: at Cape Cod in May 1973 and in the northern Gulf of Maine in September 1974. There was a third multiple stranding at almost the same site in the Gulf of Maine in September 1981 and also a small multiple stranding at Prince Edward Island in the Gulf of St. Lawrence in November 1979 (Mitchell 1981). There have been numerous single strandings in New England, Nova Scotia and the Gulf of St. Lawrence throughout the 1970's. In September and October 1981, the species several times entered the waters of Bedford Basin, Halifax Harbour, Nova Scotia. Thus irregular mass strandings, and frequent single strandings, have been a feature of the biology of *L. acutus* during the period of its population abundance in the northwest Atlantic.

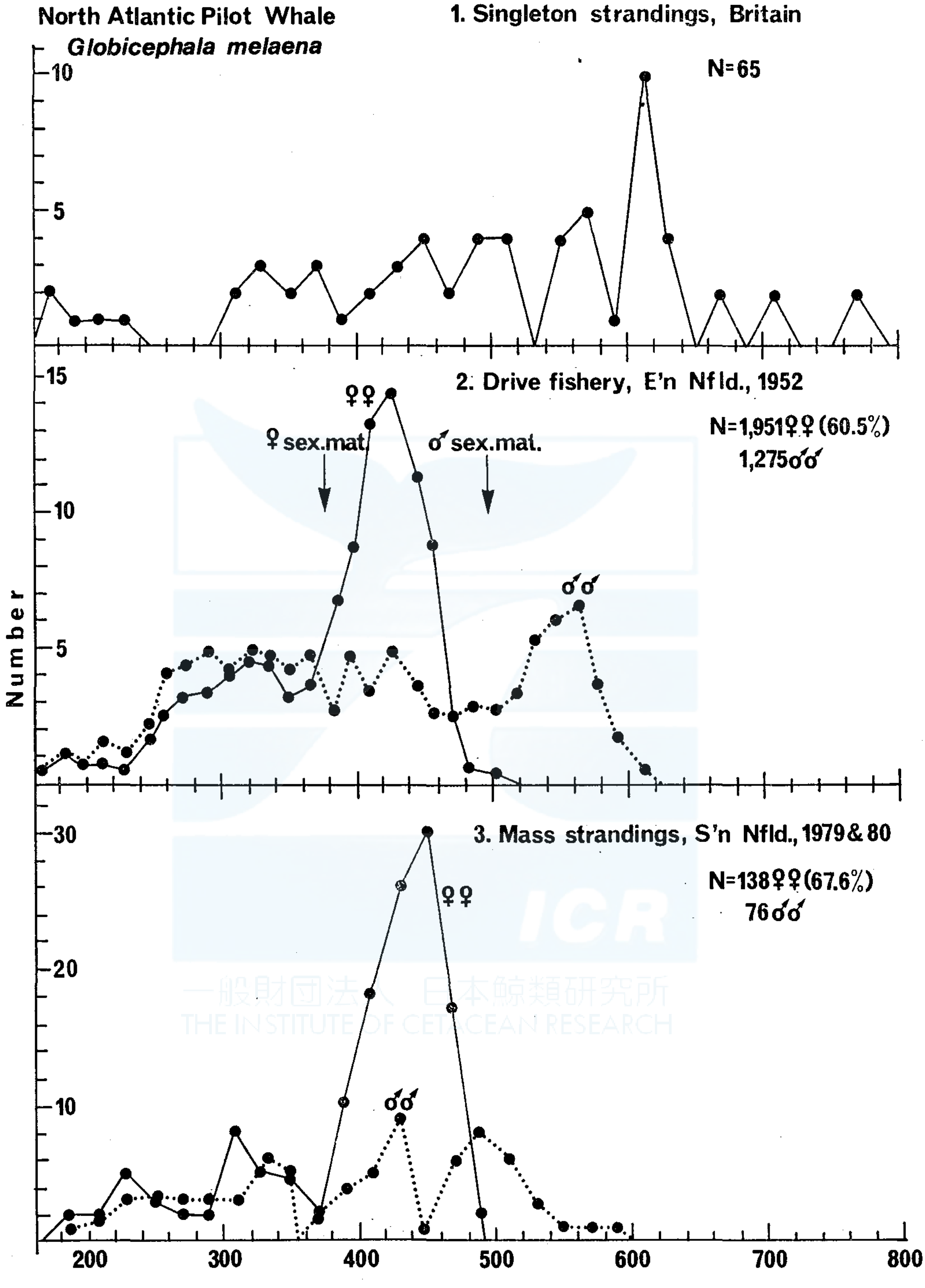

Fig. 4. Length frequencies of *G. melaena*, stranded naturally and driven shore.

c. *Sperm whale Physeter catodon at New Zealand*

At North Island, New Zealand, multiple strandings of harem herds of sperm whales have repeatedly occurred up to at least 1972 (Gaskin 1968; Robson and Van Bree 1971; Stephenson 1975). Best (1974, Figs.–1 and 11–2) shows that the surrounding area of sea has one of the highest known densities of sperm whales, and the highest known density of female sperm whales, in the southern hemisphere.

d. *Conclusions*

From the preceding review of three commonly-stranding species one may conclude that mass strandings come from a dense population and not from a reduced one. In ecological parlance, they are either density- or resource-dependent (DeMaster 1981). As to the condition of naturally-stranded *G. melaena*, I am indebted to K. A. Hay (*in litt.* 1979) and J. Lien and staff (*in litt.* 1981) for measurements and sexings of animals in three herds stranded at Newfoundland in 1979 and 1980. The distribution of lengths (Fig. 4) differs little from length frequencies which were obtained from large samples of driven animals in the 1950's (Sergeant 1962). The sex ratio is more variable, being low for males in the two 1980 samples, and high for a stranding at Sable Island in 1976 described by Geraci and St. Aubin (1977), but with little difference if the samples are summed (Table 2). The length-specific blubber thickness is comparable (Table 3). There is therefore no obvious difference between the state of animals driven ashore by man and those naturally stranded. Both sets of beachings result from the dense herds which form up in the coastal waters when the population is abundant.

TABLE 2. SEX RATIOS OF NORTHWEST ATLANTIC PILOT WHALES, DRIVEN AND STRANDED. Date from Sergeant (1962) Geraci and St. Aubin (1977), Hay (pers. comm.), and Lien (pers. comm.).

Sample	Date	Males	Females	Male ratio
Driven	1952—1957	1,825	2,778	.395
Stranded	1977—1980	141	173	.450

TABLE 3. MID-LATERAL BLUBBER THICKNESS OF FEMALE PILOT WHALES AT NEWFOUNDLAND, DRIVEN AND STRANDED Data from Sergeant (1962, Table IV) and Hay (pers. comm.).

Sample	Date	N	Range of body lengths (cm)	Blubber thickness (cm)	
				Range	Mean
Driven	August 1952	40	185—470	2.1—3.2	2.7
Stranded	July 1979	74	206—470	2.3—4.0	3.3

DISTRIBUTION OF MASS STRANDINGS AMONG THE ODONTOCETI

a. *Definition*

I define a mass- or multiple-stranding as one consisting of two or more animals, other than the simultaneous stranding of a female and her calf.

b. *Offshore and onshore mortality*

Although I have assumed up to now that all dead cetaceans arrive on the coastline, this cannot be true. Skulls of pilot whales *G. melaena* are dredged by trawlers from Georges Bank off New England (Lord and Chandler 1969). This bank is separated by channels from the land, showing that animals which die at sea may sink there. Mass strandings, by definition, occur on the coast and it is difficult to imagine mass, almost simultaneous deaths occurring at sea among a herd of Cetacea. If they do occur, no concentrations of carcasses have been reported at sea, to my knowledge, nor of a sequence of carcasses drifting ashore. Mass strandings are of live animals, though singleton animals can arrive on the beach dead or alive. That some dead singletons do not reach the shore could bias upward the percent of animals recorded dead en masse. Other sources of bias work in the same direction.

c. *Reporting bias*

For most past reporting, it is likely that multiple strandings are over-reported as compared with single animals because they are the more conspicuous phenomenon.

It is extremely hard to quantify this statement, but it seems likely that the more intensive the stranding network, the more this bias is removed. I have identified three relatively intensive stranding networks: that of Great Britain from 1913 to 1966, of France from 1971 to the present, and of the United States from 1976 to the present. Since none of these is complete or perfect, not all bias has been removed. For France I compared reports of strandings of pilot whales in the period 1961–1960 (Duguy and Baudouin-Bodin 1965, Budker 1968 and Le Tallec 1968) to those in 1971–1980 (Duguy and Budker 1972, Duguy 1973, 1974, 1975, 1976, 1977, 1978, 1979, 1980, 1981). In the earlier decade, there were reports of 310 individual *G. melaena* of which 303 (97.7%) were mass-stranded. In the later decade there were only 5 out 80 (6.25%) *G. melaena* mass-stranded. Clearly the change cannot be due solely to a change in sighting intensity since the absolute frequency of mass strandings of pilot whales decreased. This could be due, in part, to chance: mass-strandings are rare events and more than a decade may be necessary to obtain an index of their frequency. Unfortunately, the density of the population involved may change during a decade (see section 4 d (ii), so that solution of the problem seems impossible There seems little left to do except to use the most complete data available, and to use the much more evenly distributed singleton strandings, together with the mass strandings, as an index of natural mortality rate, and therefore of abundance.

The classification of the Odontoceti as usually divided (Rice 1977, Fraser and Purves 1960) is shown in Table 4.

d. *British strandings*

Systematic observations of stranded Cetacea around the British coasts were begun in 1913 and I have drawn freely on this long-continued record (Harmer

TABLE 4. SYSTEMATIC ORDER OF ODONTOCETI ACCORDING TO RICE (1977)
Genera including species known to mass-strand shown with an asterisk.

Ziphiidae	*Tasmacetus*
	* *Mesoplodon*
	* *Ziphius*
	* *Hyperoodon*
	Berardius
Physeteridae	* *Physeter*
	Kogia
Platanistidae	
Stenidae	*Sotalia*
	Sousa
	* *Steno*
Phocaenidae	* *Phocoena*
	Phocaenoides
Delphinidae	
Delphininae	* *Delphinus*
	* *Grampus*
	* *Lagenorhynchus*
	Lagenodelphis
	* *Stenella*
	* *Tursiops*
Cephalorhynchinae	*Cephalorhynchus*
Lissodelphinae	* *Lissodelphis*
Orcininae	? *Feresa*
	* *Globicephala*
	Orcaella
	* *Orcinus*
	* *Peponocephala*
	* *Pseudorca*

1929; Fraser 1934, 1946, 1953, 1974.) While it is impossible to define its completeness, the existence of a reporting network, together with a responsible central museum over a long period of time, makes it a good starting point.

(i) Frequency of mass strandings:

As stated at the outset, there are no mass strandings of Mysticeti. The British records give the number of individual Odontoceti in each mass stranding and also the number of singleton strandings of each species. Table 5 summarises these data. There are rare species, such as the arctic white whale *Delphinapterus leucas* and narwhal *Monodon monoceros*, and the more southerly blue-white or euphrosyne dolphin *Stenella coeruleoalba*, that give few records. The others can be divided into a group of mainly mass-stranders, comprising pilot whale *G. melaena*, false killer whale *Pseudorca crassidens* and white-sided dolphin *Lagenorhynchus acutus* and a group of species stranding mainly as individuals, comprising killer whale *Orcinus orca*, several other dolphin species (*Lagenorhynchus albirostris*, *Grampus griseus*, *Delphinus delphis*, *Tursiops truncatus*), bottlenose whale *Hyperoodon ampullatus* and common porpoise *Phocoena phocoena*. All sperm whales *Physeter catodon* stranded singly, although

TABLE 5. FREQUENCY OF MASS-STRANDED TO TOTAL STRANDED INDIVIDUAL ODONTOCETI BY SPECIES IN BRITAIN, 1913 TO 1966
Data from Harmer (1927) and Fraser (1934 to 1974).

Species	Number of animals			Percent multiple
	single	multiple	total	
Delphinapterus leucas	1	—	1	(—)
Delphinus delphis	121	14	135	10.4
Globicephala melaena	66	429	495	86.7
Grampus griseus	63	4	67	5.9
Hyperoodon ampullatus	61	11	72	15.3
Lagenorhynchus acutus	24	67	91	78.2
Lagenorhynchus albirostris	78	9	87	10.3
Monodon monoceros	2	—	2	(—)
Orcinus orca	36	6	42	14.2
Phocoena phocoena	596	35	631	5.5
Physeter catodon	13	—	13	0.0
Pseudorca crassidens	5	227	232	97.8
Stenella caeruleoalba	3	—	3	(—)
Tursiops truncatus	175	14	189	7.4

the species is known to mass-strand elsewhere and has done so in western Europe (Boschma 1938). However, mainly solitary males reach northern seas, and singleton strandings are the rule also in Norway (Haug and Gulliksen 1981) and in Newfoundland (J. Lien MSS 1980, 1981).

(ii) Consistency of mass strandings through time:

Because of the uniquely long (53 year) period of the British strandings, it is instructive to examine the consistency through time of mass-strandings of a species. In Table 6 I have done this for 6 species, retaining the unequal time periods into which Harmer and Fraser divided their reports. [To use decades, as S. G. Brown (1975) did, would not materially alter results.] The analysis shows that one species, *Pseudorca crassidens*, stranded at high frequency during its short occurrence in seas around Britain. Three species, *Grampus griseus*, *Lagenorhynchus albirostris*, and *Tursiops truncatus*, mass-stranded at low frequency throughout the 5 episodes of time. Two species remain. *Lagenorhynchus acutus* decreased markedly after 1932, whereas *Globicephala melaena* increased markedly after 1937. Not unexpectedly, both species

TABLE 6. MULTIPLE STRANDINGS PER TIME PERIOD IN BRITAIN
Number of individuals stranded in multiple strandings and in total.

Years Species	1913–1926 (14)	1927–1932 (6)	1933–1937 (5)	1938–1947 (10)	1948–1966 (19)
G. melaena	2/10	0/6	2/6	20/26	405/447
G. griseus	2/10	0/9	0/10	2/19	0/19
L. acutus	32/40	35/39	0/3	0/3	0/6
L. albirostris	2/30	0/8	2/14	0/7	5/28
P. crassidens	—	150/150	77/82	—	—
T. truncatus	4/27	2/27	4/23	2/35	2/77

TABLE 7. FREQUENCY OF SINGLE (S), MULTIPLE (M) AND TOTAL (T) STRANDED INDIVIDUAL ODONTOCETI IN NEW ZEALAND (Gaskin 1968, Fraser 1955), Tasmania (Guiler 1978) and South Australia (Aitken 1971)

Species	New Zealand				Tasmania				S. Australia				Overall			
	S	M	T	%M	S	M	T	%M	S	M	T	%M	S	M	T	%M
Berardius arnouxi	17	0	17	0.0	1	—	—	0	1	—	—	0	19	0	19	0.0
Cephalorhynchus commersoni	16	0	16	0									16	0	16	0
Delphinus delphis	15	0	15	0	6	114	120	95.0	7	—	7	0	28	114	142	80.2
Globicephala melaena	3	856	859	99.7	9	908	917	99.0	—	5	5	(high)	12	1,769	1,781	99.3
Grampus griseus	1	0	1	—									1	—	1	(0)
Hyperoodon planifrons	2	0	2	(0)					1	—	1	0	3	—	3	(0)
Kogia breviceps	21	1	22	4.5	1	—	1	0	10	—	10	0.0	32	1	33	3.0
Lagenorhynchus obscurus	17	3	20	15.0									17	3	20	15.0
Lissodelphis peroni	—	3	3	(100)									—	3	3	(100)
Mesoplodon bowdoini	6	—	6	0	1	—	1	0					7	—	7	0.0
M. densirostris	—	—	—	—	1	—	1	0					1	—	1	(0)
M. grayi	24	25	49	51.0	3	—	3	0	0	—	3	0	30	25	55	45.5
M. hectori	—		—	—	1	—	1	0					1	—	1	(0)
M. layardi	19	0	19	0	3	—	3	0					22	—	22	0.0
Orcinus orca	4	20	24	83.3	1	—	1	0	1	—	1	0	6	20	27	76.9
Physeter catodon	16	65	81	80.2	13	129	142	90.8	3	—	3	32	32	194	226	85.8
Pseudorca crassidens	4	148	152	97.4	6	243	249	97.5	(a few)	250	( )	(high)	10	391	401	97.5
Tasmacetus	6	0	6	0									6	—	6	(0)
Tursiops truncatus	8	2	10	(20.0)	6	15	21	71.4	12	—	12	0.0	26	17	43	39.5
Ziphius cavirostris	19	0	19	0.0	8	—	8	0.0	1	—	1	—	28	—	28	0.0

show high mass stranding rates with high overall stranding rates. None of these data support the idea that mass-stranding rates vary with time, in contrast to the French data discussed earlier (section 4-c). The data do, however, support the concept that populations of Odontocetes may change in abundance with time.

e. *Strandings in the southern hemisphere*

In amplification of the British stranding records, there is an excellent set of tabulated data on strandings on New Zealand coasts, chiefly due to Gaskin (1968). To these I have appended details given for Tasmania by Guiler (1978) and for south Australia by Aitken (1971), since all are cool-water coasts with much the same fauna (Table 7).

In these seas *Globicephala melaena* and *Pseudorca crassidens* retain a very high percentage of individuals mass-stranded (97.5–99.3%). Nearly as high are *Physeter catodon* with 85.8% of individuals mass-stranded, *Delphinus delphis* with 80.2% and *Orcinus orca* with 76.9%. High values are also found for *Mesoplodon grayi* (45.5%), *Tursiops truncatus* (39.5%) and *Lagenorhynchus obscurus* (15.0%). Other Ziphiidae (*Berardius arnouxi*, *Ziphius cavirostris* and other *Mesoplodon* spp.) had no multiple strandings, nor did the pigmy sperm whale *Kogia breviceps*.

f. *Strandings in Florida*

Table 8 shows strandings from a well-documented sub-tropical region, that of Florida with its extensive sandy coasts.

High multiple stranding frequencies are again shown by pilot whales, this time the tropical short-finned species *Globicephala macrorhyncha*, and by false killer whales *Pseudorca crassidens*, which are here within their normal range of distribution at sea in the sub-tropical North Atlantic (Morzer-Bruyns 1969), Gulf of Mexico (Bullis and Moore 1956; Brown, Caldwell and Caldwell 1966) and Caribbean Sea (Caldwell, Caldwell, Rathjen and Sullivan 1971). *Stenella longirostris* shows a high mass-stranding rate (92.7%) with two mass strandings, and *Steno bredanesis* with but a single one. Both *Tursiops truncatus* and *Kogia breviceps* show singleton strand-

TABLE 8. STRANDINGS IN FLORIDA

Sources: [1]Moore, 1953; [2]Layne, 1965; [3]Caldwell, Caldwell and Walker, 1970; [4]Mead, Odell, Wells and Scott, 1980; [1]Odell, Asper, Baucom and Cornell, 1980.

	Single	Multiple	Total	%M
Globicephala macrorhyncha[1]	1	323	324	99.7
Globicephala macrorhyncha[2]	6	212	218	97.2
Kogia breviceps[1,2]	12	—	12	0.0
Mesoplodon europaeus[1]	1	—	1	—
Physeter catodon[1,2]	5	—	5	0.0
Pseudorca crassidens[1,3,5]	3	241	242	99.6
Stenella longirostris[4]	5	64	69	92.7
Steno bredanensis[2]	—	16	16	(100.0)
Tursiops truncatus[1,2]	13	—	13	0.0
Ziphius cavirostris[1]	3	—	—	(0)

ings only; for other species data are scarce.

g. *United States Eastern Seaboard*

Six years' intensive observations, from 1976 to 1981, were available to me for this region from the monthly reports of strandings given in SEAN (Smithsonian Scientific Event Network).

The resulting summary of data (Table 9) refers to 32 species, such a large fauna being the result of the wide geographical extent of the coast from a cold to a warm sea. Some cold-water species, e.g. *Hyperoodon ampullatus*, were absent, others, e.g. *Orcinus orca*, were rare.

TABLE 9. UNITED STATES EASTERN SEABOARD. STRANDINGS, 1976–1981 (Source—SEAN monthly reports).

Species	1977–1981		Multiple Frequency
	Total	Multiple	
Balaenoptera acutorostrata	27	—	—
B. borealis	—	—	—
B. edeni	3	—	—
B. musculus	—	—	—
B. physalus	22	—	—
Delphinapterus leucas	1	—	—
Delphinus delphis	29	4	.138
Eubalaena glacialis	3	—	—
Feresa intermedia	4	—	—
Globicephala macrorhyncha	43	28	.651
G. melaena	42	18	.429
Grampus griseus	21	5	.238
Hyperoodon ampullatus	—	—	—
Kogia breviceps	105	—	—
K. simus	30	2	.066
Lagenorhynchus acutus	78	19	.245
L. albirostris	1	—	—
Megaptera novaeangliae	10	—	—
Mesoplodon bidens	—	—	—
M. densirostris	3	—	—
M. europaeus	14	—	—
M. mirus	3	—	—
Orcinus orca	3	—	—
Phocoena phocoena	177	(12)	(.062)
Physeter catodon	30	11	.366
Pseudorca crassidens	30	30	1.000
Stenella caeruleoalba	45	6	.133
S. longirostris	32	29	.906
S. plagiodon/attenuata	32	—	—
Steno rostratus	23	21	(.913)
Tursiops truncatus	543	(7)*	(.013)
Ziphius cavirostris	6	—	—

* Strandings of several animals close in space and time were reported but it could not be determined if these were in fact multiple strandings.

The data allowed comparison with older data (Table 8) from parts of the same seaboard. Thus, multiple strandings of *Globicephala macrorhyncha* fell from 99.7–97.2% for earlier data from Florida to 65.1% for the whole coast. At first, I thought this was the result of more thorough examination of beaches for singletons. However, examination of SEAN records by state showed a geographical trend. A high multiple stranding rate was still recorded for Florida but northward this decreased to zero. I therefore analysed data for *G. macrorhyncha* and *G. melaena* by latitude in order to quantify such geographical changes (section h).

The strandings from the east coast of the United States show a similar sequence of frequency of mass-strandings to that found in other regions. Ten species show multiple stranding frequencies exceeding 10%, in order of descending rank:

Species	Frequency	Number of	
		animals	mass events
Pseudorca crassidens	1.000	30	1
Steno rostratus	.913	23	2
Stenella longirostris	.906	32	1
Globicephala macrorhyncha	.651	43	4
G. melaena	.429	42	1
Physeter catodon	.366	30	1
Lagenorhynchus acutus	.245	78	4
Grampus griseus	.236	21	2
Delphinus delphis	.138	29	1
Stenella caeruleoalba	.133	45	2

The three commonest species to strand: *Tursiops truncatus*, *Phocoena phocoena* and *Kogia breviceps*, all showed extremely low rates of multiple strandings, as noted earlier by Mead (1979). Indeed, for *P. phocoena* and *T. truncatus*, there was doubt whether animals that stranded at the same time and place were, in fact, from the same group. These data agree with those from Britain (Table 5), although mass strandings of *Tursiops truncatus* were noted from the southern hemisphere (Table 7), where perhaps a different species or stock with different social behavior is involved.

h. *Geographical variation in mass stranding rate within a species.*

This problem is sufficiently common to require resolution. In order to study it I selected the east coast of North America where the excellent data from the U.S.A. (from SEAN and from earlier faunal studies) could be supplemented by less complete data from Canada. I selected the two pilot whale species *G. melaena* and *G. macrorhyncha* because of their high mass stranding frequency, and listed all strandings known to me by geographical position, and whether single or multiple, then analysed these by half-degrees of latitude (Table 10).

The table shows that the cold-water species *G. melaena* mass-strands mainly in the northern part of its range north of 46°N. Sable Island, located at 44°N, accounts for most mass strandings south of this latitude. There are in modern times few mass strandings at Cape Cod, at ca 41°30′N Lat., although the species was

TABLE 10. STRANDINGS OF THE PILOT WHALES *GLOBICEPHALA MELAENA* AND *G. MACRORHYNCHA* ALONG THE EASTERN SEABOARD OF CANADA AND THE UNITED STATES

The records are summed by half degrees of latitude, and separated into single and multiple strandings. Sources: Various, from varied starting dates up to end 1981 in SEAN.

G. melaena			*G. macrorhyncha*		
Latitude Zone	(1)	(2)	Latitude Zone	(1)	(2)
51°31′—52°	1		39°00′—39½°	3	
—51½°					
—51°			35°31′—36°	4	
—50½°			—35½°	3	
—50°		12	—35°	1	
—49½°	1	129	—34½°	1	5
—49°		125	—34°	1	19
—48½°			—33½°		
—48°	3		—33°		13+
—47½°	4	18	—32½°		26
—47°	3	291	—32°		3
—46½°		15	—31½°	1	30
—46°			—31°		
—45½°	1		—30½°		150
—45°	1		—30°		72
—44½°	3		—29½°	2	57+
—44°	2	203	—29°		63
—43½	1		—28½°		
—43°	1		—28°	1	64
—42½°			—27½°	1	
—42°	5		—27°	2	51
—41½°	4	18	—26½°		
—41°	3		—26°		
—40½°	1		—25½°		70+
—40°	1		—25°	2	12
—39½°	3		24°00′—24½°	1	50
—39°	(1)*				
—38½°	1				
—38°					
—37½°					
—37°					
—36½°					
35°31′—36°	1				

(1) Number of animals stranded singly.
(2) Number of animals in multiple strandings.
* Species uncertain.

driven here in the past and herds are sometimes seen (*e.g.* by Starrett and Starrett 1955). Singleton strandings occur further south as far as about 36°N.

The warm-water *G. macrorhyncha* has its highest frequency of mass-strandings in the southern part of its range. Mass strandings occur along the U.S. east coast from the Florida Keys at 24°30′N to about 34°30′N. Northward only singleton strandings occur, as far as 39°N. Thus, both species show a " core " area where mass-strandings occur, and a peripheral area where they do not. I would deduce from this that mass-strandings occur where the population of the species is high. Mass strandings of *G. macrorhyncha* continue through the West Indies southward to at least Isla Margarita, Venezuela, at 12°N Lat. (Casinos and Bou, 1980). Thus in *G. melaena* there seems to be no northern limit to the mass strandings (in relation to the population as a whole), in *G. macrorhyncha* no southern limit, suggesting that it is inter-specific competition between the species that determines density of both.

I know no other pair of contiguous species where such an analysis is possible, but note other cold-water species that show mass strandings towards the north of their range, *e.g. Orcinus orca* in Norway but not in Britain, see footnote this p.; other warm-water species that show mass strandings mainly in the south of their range, *e.g. Delphinus delphis* in west Africa but not in Europe, see pp. 37 and 11 respectively.

i. *Individual species considered.*

The false killer whale *Pseudorca crassidens* is unusual in that virtually all of its mortality on the coasts of Britain, New Zealand, Tasmania, South Australia, South Africa (Smithers 1938) and Florida, occurs as mass strandings. It is a warm-water species (Bullis and Moore 1956, Morzer-Bruyns 1969), that does not normally occur round the British coasts; thus the mass strandings that occurred there in 1927, 1935 and 1936 were in the nature of immigrations followed by mass mortality. However, its mass strandings in Florida occur within the species' normal range. As its diet consists of large fish and squids, including tuna which it frequently takes off long-line hooks (Moore 1953, Brown, Caldwell and Caldwell 1966, Mitchell 1975), we have the impression of a top carnivore exerting pressure on its food supply.

In tropical seas, the short-headed electra dolphin *Peponocephala electra* has mass-stranded in eastern Australia (Dawbin, Noble and Fraser 1970), the New Hebrides (Rancurel 1974) and Japan (T. Kasuya, pers. comm.). Analysis of some of these records by Perrin (1975) gives a very high frequency (about 95%) of individuals mass-stranded. The genus is placed within the Orcininae as is another tropical genus *Feresa*, of which we know little. We now have three genera from among this subfamily: *Globicephala*, *Pseudorca* and *Peponocephala*, which show high frequencies of multiple strandings. The killer whale *Orcinus orca* has shown a low incidence of mass strandings in Britain[1], but a high incidence in New Zealand. Killer whales mass-stranded in British Columbia before live captures for aquaria started in 1964 (Ford and Ford 1981). Carl (1946) and Pike and MacAskie (1969) together record 39 animals stranded in the period 1941–1967, of which 36 or 92.3% represented multiple strandings.

Among the typical dolphins (Delphininae) many species have been recorded

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[1] None were recorded by Harmer or by Fraser from 1913 to 1966, but Turner (1871) described a drive-hunt of 18 *Orcinus orca* at Bressay Sound, Shetland in February 1871, which makes it seem likely that mass strandings might occur to the north of Britain. A pod of 14 animals indeed stranded at Lofoten, Norway in June 1981 (Haug and Sandnes, 1982).

with a high frequency of strandings, yet there is considerable variability in this feature; *e.g. Delphinus delphis* and *Tursiops truncatus* may show a low incidence in one region and a high incidence in another. There is also a high incidence of strandings in the pelagic long-snouted dolphin *Stenella longirostris* in Florida. The species *Stenella coeruleoalba* and *S. attenuata* are driven ashore in large groups by fishermen in Japan, which makes one believe that they would mass-strand there naturally, if not being hunted.

Among the porpoises Phocoenidae, the harbour porpoise *Phocoena phocoena* normally strands singly or in groups of 2–4 animals. It is known to be weakly gregarious, with schools of 9 animals or less observed by Gaskin, Arnold and Blair (1974).

There are about 20 known mass strandings of *Physeter catodon* in the world in the last 300 years and more than half of these have come from New Zealand (Anon 1979). I have also heard of two unpublished mass strandings (in the Seychelles and Falkland Is.) since beginning this study. Most mass strandings are of harem herds (Robson and van Bree 1971, Stephenson 1975). Considering that the main mass of harem herds of sperm whales live in the tropical oceans, which are grossly under-reported for Cetacea (consider the late discovery of tropical genera such as *Feresa*, *Peponocephala* and *Lagenodelphis*), the scarcity of reported mass strandings of *Physeter* is not surprising. At high latitudes most strandings of sperm whales are of single adult or subadult males. The pigmy sperm whale *Kogia breviceps* seems always to strand singly or in numbers not exceeding three, suggesting a group size no larger than a family.

Mass strandings are also known among several genera of the Ziphiidae: *e.g.* a herd of 25 *Mesoplodon grayi* at the Chatham Is., New Zealand (Gaskin 1968); a herd of 4 *Ziphius cavirostris* at the Netherlands Antilles; and records of *Hyperoodon ampullatus* in Britain (van Bree and Kristensen, 1974). There are no known mass strandings from among the freshwater Platanistidae, nor from among the small group Cephalorhynchinae, but we have noted one of three animals from among the Lissodelphinae (*Lissodelphis peroni* at New Zealand, Fraser 1955).

Considering the high incidence of mass strandings among members of the Orcininae it is worth looking at the biological characteristics of the subfamily, as compared with those of members of the typical dolphin subfamily Delphininae. There are now sufficient studies of life histories of a number of genera to make such a comparison possible. The social structure of the sperm whale *Physeter* is also well known.

SOCIAL STRUCTURES COMPARED

a. *Orcininae*

As Norris and Dohl (1980) have previously observed, mass strandings occur especially in the group Orcininae of the Delphinidae, which contains the genera *Pseudorca*, *Orcinus*, *Orcaella*, *Globicephala*, *Feresa*, and *Peponocephala*. Of these only *Globicephala* is well known bionomically, *Orcinus* is beginning to be so (Bigg 1981), and knowledge on *Pseudorca* must be assembled from the few data of various authors.

I studied the social structure of *G. melaena* from a drive fishery in Newfoundland in the 1950's (Sergeant 1962), having a large number of animals available to examine. Main features relevant were: (1) a marked sexual dimorphism, males reaching 20 ft (6 m) in length compared with 16 ft (5 m) for females; (2) an extremely delayed sexual maturity for males—16 ft (5 m) length and 12 years of age compared with 12 ft (4 m) and 6 years of age for females; (3) a higher male mortality rate throughout life. The last two features resulted in a low ratio of adult males to adult females. Most importantly (4), the composition of 91/92 schools was homogeneous, consisting of all sizes of both sexes of animals. The only atypical herd was a group of adult males with a few very large females. I deduced that the species was exceptionally social, with no signs of aggressiveness, there being no segregation of size groups associated with aggression.

McCann (1974) found tooth scars or scratches on the body of almost all Odontocete genera studied which he attributed to various behaviour patterns, including play between younger animals and aggression by adult males. In driven *G. melaena* I found fresh scratches on all animals, which I attributed to the panic of the drive, since I could find no old scars. Norris and Prescott (1961) found tooth scratches on young male *G. scammoni* and not on adult males, leading Norris

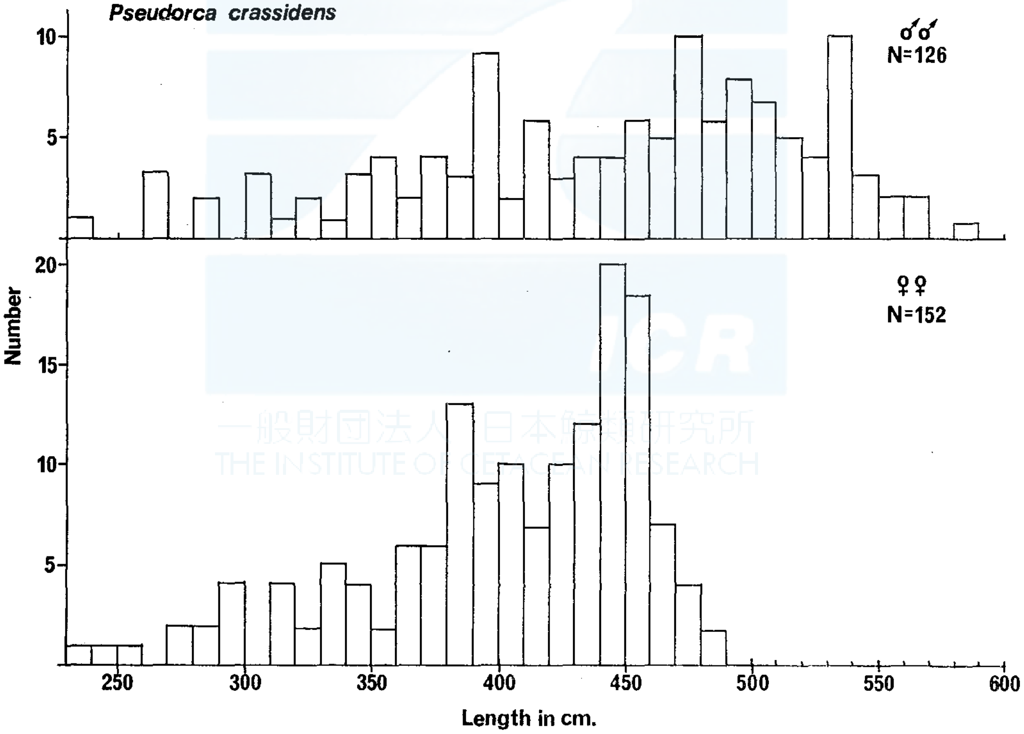


Fig. 5. Length frequencies of naturally stranded male and female *Pseudorca crassidens*.

(1967) to deduce that these were produced by schoolmates in play. Thus I suppose that tooth scratches are not necessarily an index of aggression. McCann noted that Ziphiids have deeper scars than most Delphinidae and he believed that such less social species show more aggression.

Information on *Pseudorca crassidens* comes from samples examined by Hinton (1928), Fraser (1936), Peacock, Comrie and Greenshields (1936), and Yamada (1956) from animals stranded in Britain; by Smithers (1938) from strandings in South Africa; by Scott and Green (1975) from strandings in Tasmania; and by Odell, Asper, Baucom and Cornell (1980) from strandings in Florida. Comrie and Adam (1938) examined reproductive tracts collected by Peacock *et al.* (1936). Figure 5 shows length frequencies which indicate clearly that the species is sexually dimorphic. Extreme recorded lengths in all these strandings are males 589 cm and females 489 cm, or a ratio of about 1.2: 1, which compares with 1.3: 1 in extreme and peak lengths for large samples of *G. melaena* (Sergeant 1962). If one omits the length frequencies of Scott and Green (1975), who examined part of the same set of females twice, the sex ratio is about 53.5% females for a sample size of 198. Lengths at first maturity of female *Pseudorca* were well-studied by several authors, as follows:

	Body length (cm)	
	largest immature	smallest mature
Hinton 1928	—	427 (pregnant)
Fraser 1936	418	429 (several corpora albicantia)
Comrie and Adam 1938	284	425 (9 corpora albicantia)
Harrison, Brownell and Boice 1972	293	414 (large corpus luteum plus corpora albicantia)
Scott and Green 1975	337	360 (pregnant)
Odell *et al.* 1980	358	440 (8 corpora albicantia)
Highest/lowest	418	360

This analysis gives a range of 360 to 420 cm for length at first pregnancy, a wide spread. One wonders if all workers measured length in the same way, or whether the populations differed in size. For males, we know only that a large male 520 cm in length was mature, with testis in active spermatogenesis weighing 8.2 kg (Odell et al. 1980), and that a male 366 cm was immature, while males 511, 530 and 534 cm in length were mature with testis volumes 50×16×8 cm or larger (Fraser 1936). Thus, we can only say that male *Pseudorca crassidens* mature at body lengths of 511 cm or less. Since the animal measured by Fraser as 511 cm in length had a testis significantly smaller in volume (50×16×8 cm) than those of 530 and 544 cm in length (60×20×16 cm and 62×22×11 cm) it is possible that it was just mature; this compares with a 520 cm male *P. crassidens* measured by Odell *et al.* (1980), the testis of which weighed 8.2 kg (see also Sergeant 1962, Fig. 19 for a curve relating testis length to body weight in *G. melaena*). If *P. crassidens* males mature at about 500 cm body length, as compared with about 400 cm for females, then the ratio of numbers of mature females to mature males from the data of Fig. 5 is about 90/34 or 2.65: 1, a ratio comparable with that

TABLE 11. RATIO OF ADULT LENGTHS OF ODONTOCETES (cm)

Species	Region of Study	Sample size	Peak		Extreme		Ratio M/F	Authors
			M	F	M	F		
Delphininae								
Delphinus delphis	Black Sea	4,217	170	170	205	200	1.02	Sleptsov 1941
Stenella attenuata	E. Tropical Pacific	3,504	—	—	200	190	1.05	Perrin, Coe & Zweifel 1976
Tursiops truncatus	Florida	46			270	250	1.08	Sergeant, Caldwell & Caldwell 1973
Tursiops truncatus	N. W. Atlantic	120			250	250	1.00	Hohn 1980
Tursiops aduncus	S. Africa	16			254	252	1.01	Ross 1977
Lagenorhynchus acutus	N. W. Atlantic				260	245	1.06	Sergeant, St. Aubin & Geraci 1920
Orcininae								
Orcinus orca		567	655	609	944	822	1.15	Nishiwaki & Handa 1950
			890	780	—	—	1.15	Bigg 1981
Globicephala melaena					610	503	1.21	Sergeant 1962
Pseudorca crassidens					590	490	1.20	(see p. 21)
Physeter catodon			15.8				1.44	Lockyer 1976

TABLE 12. ATTAINMENT OF SEXUAL MATURITY OF ODONTOCETES

Species	Length (cm)		Age (yr)		Ratio lengths	Authors
	M	F	M	F		
Delphininae						
Delphinus delphis	170	158			1.08	Sleptsov 1941
Stenella attenuata	195	181	12	9	1.08	Perrin, Coe & Zweifel 1976
Tursiops truncatus	245	235	13	12	1.05	Sergeant, Caldwell & Caldwell 1973
Lagenorhynchus acutus	230	210	(10)	(9)	(1.11)	Sergeant, St. Aubin & Geraci 1980
Orcininae						
Orcinus orca	579	488	12	8	1.18	Bigg 1981 and in litt.
Globicephala melaena	487	366	12	6–8	1.33	Sergeant 1962
Physeter catodon	12 m	8.5 m	19	9	2.1	Best 1974

TABLE 13. SEX RATIO OF ODONTOCETES

Species	Overall			Mature			Authors
	No. of males	No. of females	Male ratio	No. of males	No. of females	Male ratio	
Delphininae							
Delphinus delphis	2,079	2,138	0.493	890	1,179	0.435	Sleptsov 1941
Stenella attenuata			0.449			0.43	Perrin, Coe & Zweifel 1976
Orcininae							
Orcinus orca	247	320	0.436	60*	72*	0.455	Nishiwaki & Handa 1958; Bigg 1981
Globicephala melaena			0.396	418	1,364	0.234	Sergeant 1962
Pseudorca crassidens	92	106	0.465	90	34	0.265	(See discussion)

* excluding juveniles and calves.

found in *G. melaena*. Unfortunately the variance of estimate of this ratio is high as between samples: using Scott and Green's (1965) mean female maturity length of 348 cm it would be 128/34 or 3.8: 1, using Fraser's (1936) value of 423 cm it would be 68/34 or 2: 1 (Fig. 5).

For *Orcinus orca*, Nishiwaki and Handa (1958) and Bigg (1981 and *in litt.*) provide good data on body lengths of adult males and females, allowing calculation

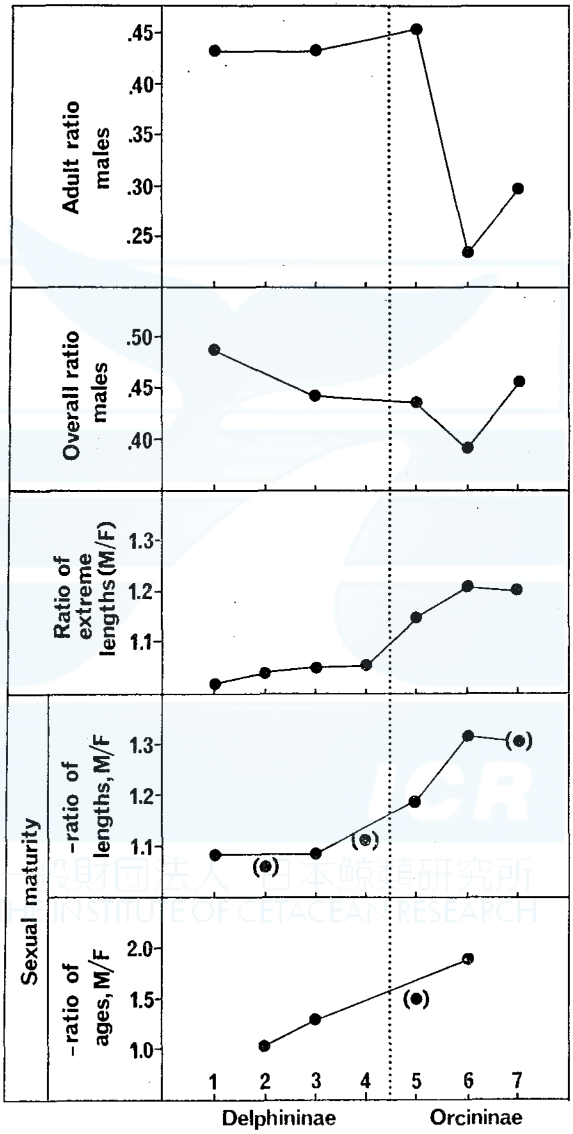


Fig. 6. Summary of information on sexual dimorphism within the Delphinidae. 1. *Delphinus delphis*, 2. *Tursiops truncatus*, 3. *Stenella attenuata*, 4. *Lagenorhynchus acutus*, 5. *Orcinus orca*, 6. *Globicephala melaena*, 7. *Pseudorca crassidens*. (The ordering of species within each subfamily was random.)

of the degree of sexual dimorphism, which seems to be somewhat less than in *Globicephala* and *Pseudorca*. There is less good information on lengths and ages at sexual maturity. Data are summarised in Tables 11 to 13 and Figure 6. One gains the impression that *Orcinus* in some ways is an intermediate between the strongly sexually dimorphic Orcininae and the weakly dimorphic Delphininae (see below).

For *Peponocephala electra*, data are as yet too few to assess the degree of sexual dimorphism in length and at sexual maturity with any accuracy (see Bryden, Harrison and Lear 1977).

b. *Delphininae*

Good information on the bionomics exists for several genera. Sleptsov (1941) studied large numbers of *Delphinus delphis* in the Black Sea, this species proving to show very little sexual dimorphism in either body size or length at sexual maturity. Perrin, Coe and Zweifel (1976) studied equally large numbers of *Stenella attenuata* in the eastern tropical Pacific with rather similar results. There is some information for the species *Tursiops truncatus* (Sergeant, Caldwell and Caldwell 1973, Hohn (1980); and *T. aduncus* (Ross, 1977), summarised in Tables 11 and 12.

In *Lagenorhynchus acutus* (Sergeant, St. Aubin and Geraci, 1980) mass stranded herds were found to be composed of adults, mostly females, together with young calves. Singly-stranded animals by contrast were found to be made up chiefly of adolescents. This kind of heterogeneity could account for much of the variability which we have found in the frequency of mass strandings in various members of the Delphininae, as discussed in section 4 above.

In both *Stenella attenuata* and *S. coeruleoalba* driven ashore in Japan, abundant data show the existence of juvenile schools and adult schools, with the juveniles rejoining the adult, mating schools at puberty (Kasuya, Miyazaki and Dawbin 1974; Miyazaki and Nishiwaki 1978).

A valuable study on living animals, which indicates the behaviour that may be involved in such segregation, comes from the work of Tavolga and Essapian (1957) and Tavolga (1966) on the former captive colony of *Tursiops truncatus* at Marineland, St. Augustine, Florida. This colony in the 1950's was not subjected to heavy pressure to perform in public; it was large (13 animals) and composed of variably sized animals. Its behaviour was thus probably close to that of a wild herd. In this colony a dominant male drove off three immature males and maintained a harem structure of females and calves. There was also a dominance hierarchy of adult females, although other pubertal and older females took much care of the calves. Another study, from the USSR, gave similar findings. Shurepova (1973) states that a large male in a group of 11 captive animals " had the dominating position in the school: it grabbed fish from the others during feeding, chased young females which shied away from its mating advances, chased young males, bit them, beat them vigorously with its tail and snout and so on."

Aggressiveness and dominance hierarchies could give rise to the segregation of immature animals seen among the Delphininae, and we have seen, at least in

Lagenorhynchus acutus, that it is often these immature animals which strand singly. Indeed such animals may attach themselves to a group of one of the social species, such as *Globicephala melaena* (Sergeant and Fisher 1957) or *Orcinus orca* (Sergeant, St. Aubin and Geraci 1980 *fide* R. D. Elliot). Hence, probably, arises the lower frequency of mass strandings among the Delphininae. But of course in all species sick and injured animals can strand singly.

In summary the Orcininae are more sexually dimorphic than the Delphininae, males having a greater excess of asymptotic body length over females. There is also a greater delay in attainment of male sexual maturity, and with this delay comes a greater male mortality, resulting in a lower overall male sex ratio than in the Delphininae.

All these features are usually associated with polygyny and male aggression in sea mammals (*e.g.* in elephant seals, fur seals and the sperm whale). Yet, paradoxically, the polygynous Orcininae are the more highly social of the Delphinidae, with a more homogeneous herd composition and with a higher mass stranding rate. Thus polygyny is not necessarily associated with male aggression.

c. *Phocaenidae*:

Phocoena phocoena shows a larger size of females than males (Mohl-Hansen 1954). It seems likely that this is due to the need to produce a neonate which is large enough to be viable in cold water (Kanwisher and Sundnes 1965). In support of this, a larger member of the family Phocoenidae, *Phocoenoides dalli*, has a male asymptotic length about 1.05 times that of the female (207 and 198 cm, Kasuya 1978), as typical for Delphininae. I have noted previously (Sergeant 1969) that *Phocoena phocoena* has a high metabolic rate throughout life, as determined from its food consumption and heart weight/body weight ratio, and that the same is true for *Phocoenoides dalli*. The high activity appears to be an adaptation to life in cold water with a thin blubber layer.

d. *Sperm whale*

The sperm whale *Physeter catodon* is a well-researched species because of its commercial importance. Because of the migrations of males to high latitudes we already know that its sociality is not total. A number of mass-strandings have been well-documented (*e.g.* by Robson and van Bree (1971) and by Stephenson (1975) in New Zealand), and these are usually harem herds. It seems likely from the records of Gilmore (1957, 1959) and Bryant (1979) in the Gulf of California that herds of adolescent males may also strand. This distribution of strandings would accord with the types of sperm whale schools classified by Gaskin (1970) and Best (1979), which include bachelor schools of young males. As the males mature, they become less and less social and some become the harem bulls, loosely attached to the schools of females and calves, others the northern wanderers. Sexual maturity in male *Physeter* is much delayed as compared with the female (Best 1969, 1974), sexual dimorphism is marked and harem-masters are intolerant of other adult males. The social structure of the sperm whale therefore comes closer to that of the Delphininae than of the highly social Orcininae, which fits the sperm whale's lower frequency of mass-strandings to total strandings.

HERD SIZE

Herd size is extremely difficult to define. As Norris and Dohl (1979) and others have shown, there is a whole range of groupings within a species (pod, herd, school) from the family up to large schools with varying cohesion and varying stability. The basic subgroup does not vary very much and is thus not a useful measure of sociality. Thus for *Pseudorca crassidens*, which we would judge from its stranding behaviour to be a species travelling in large aggregations, Morzer-Bruyns (1969) has this to say from observations of animals feeding at sea:

" The normal school of *Pseudorca crassidens* contains 20 to 30 animals divided into " family " groups of four to six animals, covering an area of about 0.5 mile in diameter."

About the only generalisation possible is that inshore species *e.g. Sousa plumbea* have only small school sizes, while in offshore species, *e.g. Delphinus delphis*, *Stenella coeruleoalba*, large aggregations can occur (Saayman, Bower and Tayler 1972, Saayman and Tayler, 1979); but the basic unit remains small, a family of females and calves with loosely attached males of all ages older than calves in *Stenella longirostris* (Pryor and Kang 1980), much as in *Tursiops truncatus* (Tavolga 1966). In both these species in the wild groupings may have a very temporary, changing existence (Norris and Dohl 1979, Wursig and Wursig 1979).

There seem to be two features which must be separated in considering the relation of mass strandings to school size: 1. Species such as *Phocoena phocoena*, *Kogia breviceps* and perhaps also some of the Ziphiidae (Morzer-Bruyns 1968) have small herd size; that is, one scarcely or never finds large aggregations. These show mass strandings rarely because they are rarely in groups; 2. Social species may have aggressive adult males, which split the herd into harem (or reproducing) herds and the rest, chiefly immature (occasionally adult) males, and immature females. Harem herds tend to mass-strand, presumably because females and calves are closely associated and females are rarely aggressive (Tavolga 1966 for *Tursipos truncatus*). The rest tend to strand singly because they are weakly associated, so mass stranding frequency is reduced.

For *Globicephala melaena* I noted (Sergeant 1962) that the mean number of animals in groups driven ashore was about 85, the same as in natural mass-strandings reported around the world; however the mean number for animals observed far to sea was about 20. This could be due to aggregation of herds as they increase in density in inshore waters. For *Orcinus orca* stranded herd sizes recorded are: in British Columbia 20, 11 and 5 (Carl 1946); 10 for an ice-stranded herd in Newfoundland (Dearden 1958); 19 for a herd stranded in Norway (Haug and Sandnes 1982), for an overall mean of 14. This compares with means of 10.5 and 11.4 for observed pod sizes in the southern and northern components of the killer whale population observed in the sounds of British Columbia and

Washington by Bigg, MacAskie and Ellis (MS, 1976).

AGE-SPECIFIC MORTALITY IN CETACEA

a. *General*

It is rather generally assumed that age-specific patterns of mortality in Cetacea are similar; that Odontocetes can be lumped together with Mysticetes, in spite of their very different social structure. I shall here show that this is not the case, and the evidence I shall use is again from strandings.

b. *Mysticetes*

British strandings again prove useful and the source is a compilation by Fraser (1953) of strandings of the minke whale *Balaenoptera acutorostrata* on British coasts, reproduced here as Figure 7. Fraser showed a peak stranding length of 16 ft (5 m) and one again at the greatest lengths attained. The latter peak, one must assume, contains a good many estimated lengths. However the peak at 16 ft must be measured or estimated accurately and I believe it is significant that this is the length at which weaning occurs (Jonsgaard 1951). In other words, minke whales strand (die) especially at the length of first independence, and again in old age.

These peaks do not represent the normal occurrence of these length-classes in the North Sea, as can be seen from data (1951) on length-frequencies of catches from different areas around Norway given by Jonsgaard (1951). For areas such as Lofoten, immature whales were commonly hunted, but in Jonsgaard's area 1 (Skagerrak and the eastern North Sea), catches consisted mainly of adults (Fig. 7). Thus the evidence suggests that newly weaned animals strand selectively.

For a long time I was unable to obtain information on mortality patterns of other Mysticetes owing to the paucity of stranding information. However, recently there became available information on the length frequency of humpback whales *Megaptera novaeangliae* caught in nets at Newfoundland (Perkins and Beamish 1979, Lien MS 1981), and further information on some natural deaths and several accidental deaths from gill-netting and a ship collision on the U.S. east coast (Mead

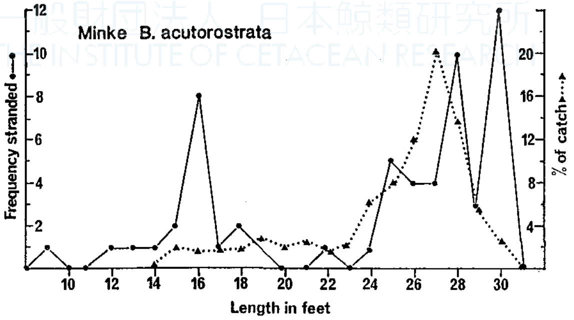
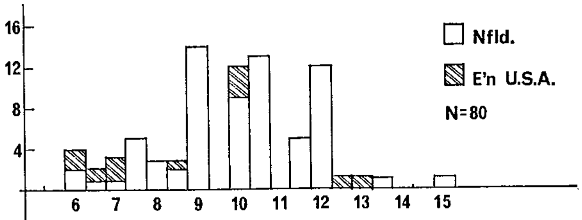
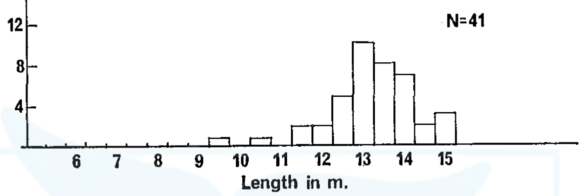


Fig. 7. Solid line: mortality by length for minke whales *B. acutorostrata* stranded on British coasts. Dotted line: catches by length in the North Sea.



(a) Netted and stranded, 1978-1980



(b) Caught with minimum length limit, Nfld., 1969-1971

Fig. 8. Lengths of humpback whales *M. novaeangliae* caught in nets (a) and harpooned at sea with a lower length limit (b).

1980). Both sets of data come from the same population, which migrates between the Caribbean in winter and the Gulf of Maine and eastern Newfoundland in summer (Kellogg 1929).

Analysis of these data (Fig. 8) shows that the dead humpbacks, many of which were imperfectly measured because of their entrapment in floating nets, were largely immature animals, 6 to 12 m in length. Weaned immatures, about 9–10 m in length, greatly exceeded younger calves and older animals, though sometimes an adult female entrapped itself with its calf. The lower frequency distribution in the Figure essentially shows the length of adults, upwards of 12 m, from this population; it is derived from a selective and specially licensed catch taken in 1969–1971 off eastern Newfoundland (Mitchell 1973). Thus, mainly immature humpbacks die in nets, owing to their inexperience. I infer that immature humpbacks probably have a higher death rate than adults to other forms of hazard which might be considered more " natural " than nets. Putting minke whales and humpbacks together, I would expect that Mysticetes as a whole show similar patterns of mortality. Allen (1980) can throw little light on the subject, doubtless because of the imposition of a lower size limit on whaling for all species except the minke whale.

c. *Odontocetes*

Natural mortality rates of Odontocetes are profitably examined from strandings, owing to the large numbers of animals involved and to some precision of size estimation. For several genera (*Phcooena*, *Delphinus*, *Tursiops*, *Globicephala*) some comparison is possible between length frequencies of stranded animals and non-selective length-frequencies coming from fisheries made by mass-netting or driving.

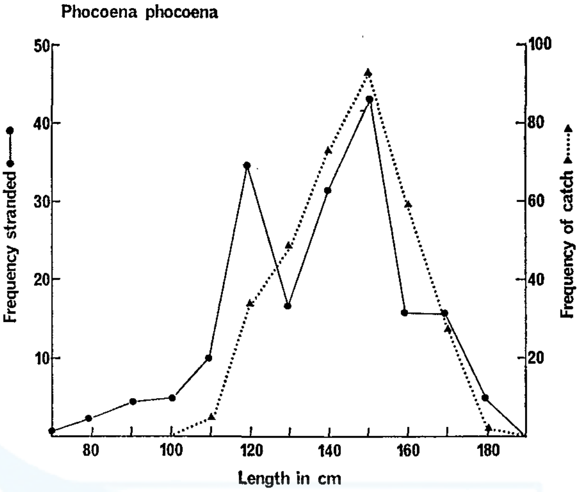


Fig. 9. Common porpoise *P. phocoena*. Length frequencies of animals stranded in Britain (solid line) and taken by driving in Denmark (dotted line).

Phocoena phocoena (Fig. 9). Size frequency of strandings in the U.K. (from Fraser 1934 to 1974) is compared with a revived drive-fishery in Denmark during the second world war (from Mohl-Hansen 1954). The size range of the animals is the same, as might be expected from the nearness of the two samples. The main difference is a peak of stranded animals at 4 ft (120 cm) which seems to be real, in spite of rounding of estimates of size in strandings. This size corresponds to animals aged about 1 year, which is also the age at weaning (Fisher and Harrison 1970). Thus it is possible that *Phocoena phocoena* endures a somewhat higher mortality rate at weaning than at younger or older ages, just as do minke whales. The distribution of older deaths seems to be proportional to the abundance of animals.

Delphinus delphis (Fig. 10). The distribution of stranded animals comes from British strandings (Fraser, *op. cit.*); that of unselected hunted animals from Soviet fihseries in the Black Sea (Sleptsov 1941). Black Sea *D. delphis* constitute a dwarf race (Kleinenberg 1956), although exceedingly abundant. Thus, the peak of adult lengths is very different. However there is no sign of a peak of juvenile deaths in either graph.

Tursiops truncatus (Fig. 11). The sample of stranded animals again comes from Britain. The very small sample of driven animals comes from Cape Hatteras, North Carolina, as described by True (1890). From what is known about relative sizes of *T. truncatus* from Europe and North America (Hohn 1980), adults from the second area should be considerably smaller. There seems to be no difference in the distribution of deaths.

Globicephala melaena. If one compares driven and naturally-stranded animals from Newfoundland, there are no differences in the size frequencies (Fig. 4). Owing to the high percentage of multiple strandings there are only small numbers

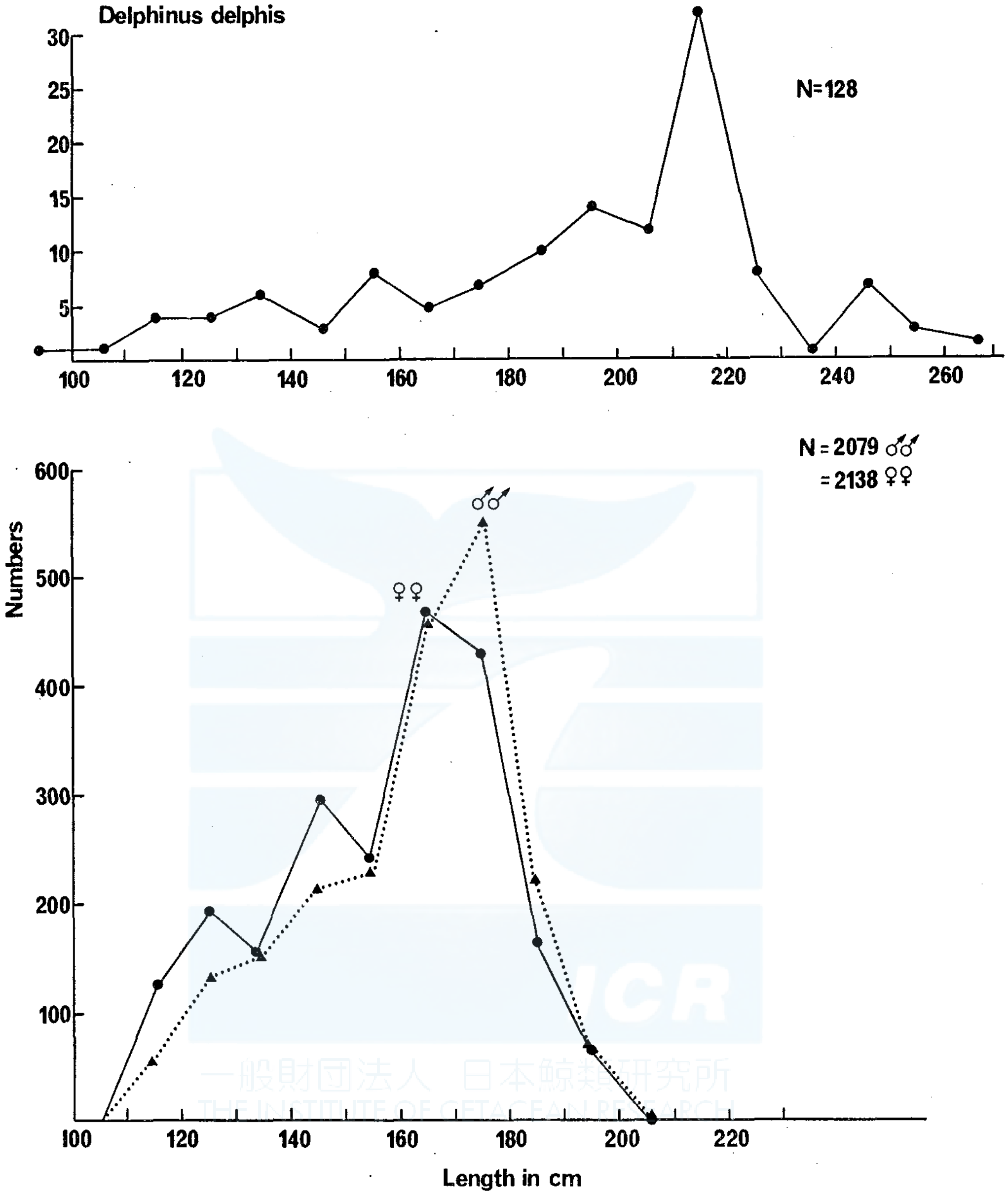


Fig. 10. Length frequencies of saddleback dolphin *D. delphis* stranded in Britain (above) and taken in net fisheries in the Black Sea (below).

of measured, singly-stranded animals from Britain. Thus, although there may be a tendency for neonates and old animals to die selectively in these strandings, the number of animals involved must be small.

In summary, the porpoise *Phocoena phocoena* may show raised juvenile mortality,

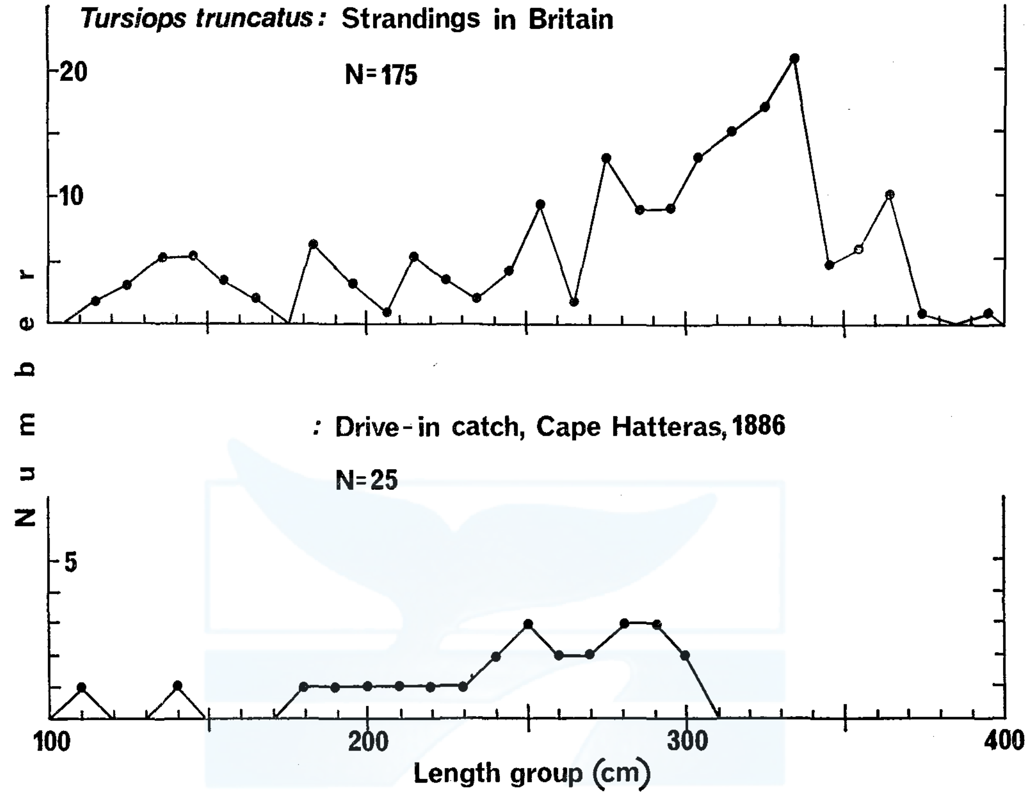


Fig. 11. Length frequencies of bottlenosed dolphin *T. truncatus* stranded in Britain (above) and taken in a drive fishery at Cape Hatteras (below).

but the three Delphinid genera examined show no sign of this phenomenon. Their natural mortality, as measured by their strandings, appears to occur in proportion to the abundance of animals of different sizes in the population. If this is so, then the Delphinidae (at least) must have evolved adaptations to reduce juvenile mortality. What these adaptations might be involve a comparison of Mysticete and Odontocete reproductive cycles (see next section).

However, many weaned, immature dolphins remain independent of the reproductive herds: in *Lagenorhynchus acutus* they may travel as singletons or in loose immature herds (Sergeant, St. Aubin and Geraci 1980); in *S. coeruleoalba* they may keep together in semi-permanent herds (Miyazaki and Nishiwaki 1978), and perhaps in *Stenella attenuata* also when not aggregated by purse-seining (Pryor and Kang 1980). Perrin and Powers (1980) found a higher incidence of skull lesions caused by the nematode *Crassicauda* sp. in juvenile than in older *Stenella attenuata*; highest rates were at 2–8 years, which are just those animals expected to be in separate schools. A higher mortality is implied because of the permanent scars left by the parasite on the skulls. Therefore in this species, there is evidence from a unique source for higher immature than adult mortality; there are not sufficient strandings of the same species to make a comparison by the method we have used for the more inshore species.

REPRODUCTIVE CYCLES IN MYSTICETES AND ODONTOCETES

As Laws (1959) made clear, the length of gestation in most Balaenopterid whales is one year. This feature involves an accelerated foetal growth rate in late pregnancy. Coupled with it is a short lactation period of 6–11 months (Gambell 1973). Since pairing occurs in winter, and a migration to high latitudes in summer, the two features appear to ensure that birth will occur in the winter, and independence in the following summer, so that the lactating female and young animal are loosed upon a rich food supply. The whole process of gestation and lactation is extremely rapid for such large animals.

The Odontocetes by contrast have gestation lengths which increase with the size of the animals, from 10–11 months in *Phocoena phocoena* (Fisher and Harrison 1970), 11–12 months in genera such as *Stenella* (Perrin, Coe and Zweifel 1976; Kasuya 1976) and *Delphinus* (Sleptsov 1941), to 16 months in large Delphinidae such as *Globicephala* (Sergeant 1962) and 14–15 months in the Monodontid genus *Delphinapterus* (Sergeant 1973). The sperm whale *Physeter catodon* also has a gestation of 16 months (Best 1968).

The lactation period also increases with body size, being 8 months (as short as in a Mysticete) in *Phocoena phocoena* (Fisher and Harrison 1970), ranging up to two years in *Tursiops*, *Globicephala*, *etc.* From *Tursiops truncatus* in captivity it is known that, though solid food may be taken at 6 months, lactation may continue intermittently to 2 years (Tavolga and Essapian 1957).

Care of juveniles continues during this period or beyond (Tavolga 1966), and adult females (" aunties ") other than the mother may share this task. Care-giving or succorant behaviour is well-known in many Delphinids, in sperm whales and in Ziphiids (Caldwell and Caldwell 1966; Best 1979; Benjaminsen and Christensen 1979). It is little wonder, then, that juvenile mortality is reduced among Odontocetes.

We may suppose, therefore, that one major direction of evolution in Odontocetes has been towards increasing the length of the reproductive cycle coupled with an increase in size. The resulting lowered reproductive rate is offset by a decrease in juvenile mortality. One may ask, therefore, if density-dependent control of reproductive rate still occurs in the Odontoceti.

Mysticeti (*Balaenoptera* sp.) exhibit a shorter period between pregnancies, and age at sexual maturity falls, when populations are reduced (Gambell 1973). Attempts to find the same phenomenon in Odontoceti have been more recent and have shown less clear-cut results. Let us start with the examination of a time series within one population which has been reduced by hunting—or the reverse, a population which has been allowed to increase by relaxation of hunting—and pass to comparisons of adjacent populations of the same species believed to exist at higher and lower population densities.

Density-dependence:

a. Time series within one population

In 1952 to 1954 and again in 1957 I measured the reproductive rate in unselected samples of *Globicephala melaena* in search of a change of reproductive rate (Sergeant 1962, Table XIX). I failed to find such a change (Table 14), there being a decrease rather than an increase of pregnancy rate and no change in lactation length. Yet we now know (Fig. 2) that 15% of the population had been removed at the mid-point of the first sample, 50% at the beginning of the second. At the time, I put the failure to find a change in reproductive rate to the short time period between samples and to a possible lag in the system, since female pilot whales take 6 years to reach sexual maturity. This still seems a reasonable explanation. However, had I returned to resample, it might not have been possible to obtain adequate further data owing to depletion of the population (Fig. 2).

Perrin, Coe and Zweifel (1976) studied the reproductive rate of a population of the spotted dolphin *Stenella attenuata* in the eastern tropical Pacific from 1968 to 1973. Perrin, Miller and Sloan (1977) continued these studies up to 1975. Reproductive rate was best calculated as the proportion of females in the population, times the proportion of females reproducing, times the annual pregnancy rate; this was 0.146 in 1968–73, 0.14∓0.008 in 1973, 0.135∓0.008 in 1974, 0.140∓0.007 in 1975 and 0.140∓0.004 in 1973–75, thus showing no significant change in 7 years. In 1974 this population was at or near its maximum productivity, with a kill of about 80,000 to 100,000 occurring annually in a purse-seine fishery for tuna (Perrin, Smith and Sakagawa 1975). Kills had been higher in 1971 to 1973 and the population was believed to have declined, though the amount was unknown.

Length of lactation period was 11.2 months in 1968–1973.

Henderson, Perrin and Miller (1980) calculated a reproductive rate of about 0.12 for northern *S. attenuata* from the eastern Pacific in 1974–1978. Length of lactation increased steadily from 8 to 36 months between 1973 and 1978. They noted a "dramatically decreased (porpoise) kill over the same period" in tuna purse-seines. These data would tend to suggest that length of lactation can be very sensitive to exploitation rate in *Stenella* spp., given a long enough time for study. Here it increased, making the reproductive rate fall, as the rate of exploitation slackened.

TABLE 14. REPRODUCTIVE RATES OF PILOT WHALES THROUGH TIME
Data from Sergeant (1962, Table XIX).

Females	1952–1954		1957	
	No.	%	No.	%
Mature	415	100	114	100
in active reproduction in oestrus	395	95.2	105	92.1
or ovulated	35	8.4	16	14.0
pregnant	140	33.7	29	25.4
lactating	220	53.0	60	52.6
Percent animals removed from population	15		50	

TABLE 15. INCIDENCE OF FEMALE SPERM WHALES IN EARLY AND LATE PREGNANCY FOR TWO TIME PERIODS
from Best (1980).

	1962–1967	1973–1975
No females examined	1,029	1,127
Percent in early pregnancy	17.1	20.7
Percent in late pregnancy	4.5	3.1
Percent with large corpus luteum but no foetus	2.2	6.2
Total	23.8	30.0

Kasuya (1976) studied *Stenella coeruleoalba* off eastern Japan. The population was depleted to about half its initial size between about 1945 and 1972–73. The mean calving interval became shorter, changing from 3.2 years in 1952 to 2.4 years in 1972–73, with a decrease in lactation period of from two years to less than one year. This is the same process in reverse as seen by Henderson et al. (1980) in *S. attenuata*.

Best (1980) studied female sperm whales off Natal, South Africa (Table 15). Sampling was done twice with an interval of 10 years, during which period the female population was believed to have been halved. The results are a little hard to interpret, because a category " females with large corpus luteum but no foetus " might have been either females with large foetuses lost in towing, or recently calved females. The total number of pregnant females, if this category is included, increased from 23.8% to 30.0%, if excluded, from 21.6% to 23.5%. Even though each sample exceeded 1000 animals, Best regarded them as barely adequate. It cannot be said that this example is clear-cut, but the conditions of sampling were not ideal.

Judging from the studies reported above, about a decade of studies is needed on a population subject to a changing exploitation pattern, probably because of the long time required to attain sexual maturity in the genera studied.

b. Comparisons of two populations of the same species

(1) by the same author

Perrin and Henderson (1979) compared reproductive rates in two populations of spinner dolphins *Stenella longirostris* which had been exploited at markedly different rates. There was no difference in gross reproductive rates (proportion of females times proportion mature times pregnancy rate) although there were differences in these individual components of reproduction.

(2) by different authors

These comparisons are listed separately since methodology cannot always be closely compared.

Perrin, Coe and Zweifel (1976) and Perrin, Miller and Sloan (1977) examined the reproductive rate of *Stenella attenuata* in the eastern tropical Pacific Ocean, a population which had sustained a heavy fishery. Kasuya, Miyazaki and Dawbin (1974) examined the reproductive rate of the same species off Japan, from a popu-

TABLE 16. WHITE WHALES: A COMPARISON OF LIFE HISTORY PARAMETERS IN TWO POPULATIONS
from Brodie 1971, Sergeant 1973.

Character	Western Hudson Bay	Cumberland Sound
Sample size:		
Hunted	257	17
Netted	293	107
Total	550	124
Maximum no. tooth layers	50	40
Maximum no. corpora albicantia	15	9
Mean age at sexual maturity (tooth layers):		
male	16–18	16
female	8–13 (10)	9–11 (10)
Gestation	14 months	14.5 months
Lactation	20 months	2 years
Frequency of calving	1 in 3 years	1 in 3 years

lation which had only been exploited for about 10 years at a low rate (6000 caught in 1963–1973), both fisheries exploiting populations of unknown size. Reproductive rate was calculated in a different way from Perrin *et al.*, but the data allow recalculation by Perrin *et al.*'s (1976) method: thus percent females (193/323)=0.60; percent reproductive females (124/193)=0.64; and annual pregnancy rate=0.256, including simultaneously pregnant and lactating females assigned half to each category. This gives a reproductive rate close to 0.100 as compared with Perrin *et al.*'s rate of 0.140 to 0.145. The difference appears to be due to a lower rate of ovulation prolonging lactation in the population from the Japanese seas.

Brodie (1971) examined the reproductive rate of a population of white whales *Delphinapterus leucas* as Cumberland Sound, Baffin I. This population has undoubtedly been under heavy exploitation for a long time (Brodie, Parsons and Sergeant 1981) and should show the maximum reproductive rate of which the species is capable. Sergeant (1973) examined a population of white whales in western Hudson Bay which he later believed (Sergeant 1981) to be in a balanced though not low state of exploitation. No differences are apparent (Table 16) in mean age at female sexual maturity, nor in frequency of calving. It is unfortunate that the western Hudson Bay population was not sampled for these features around 1950 at the outset of the industrial fishery at Churchill, Manitoba.

Thus the majority of the comparative population studies show a difference in reproductive rates between lightly and intensively exploited populations. Sergeant and Brodie's populations of white whales may have been exploited at similar rates, or the parameters may not have been measured sufficiently accurately. No change in mean age at first reproduction has yet been demonstrated in any of the within-population or between-population studies; the changes are all changes in length of lactation. Probably the mechanism is between a lactation anoestrus in females within a denser population, and ovulation during lactation in better-fed females within a heavily exploited population. There is therefore a density-dependent reproductive rate within an Odontocete population. It remains to be shown whether or not a calf suckled for only 8 months by its mother has a higher mortality rate than a calf suckled for 24 months. Probably, the length of lactation has little significance, since later lactation is intermittent (Tavolga and Essapian 1957; Tavolga 1966) in *Tursiops truncatus*; and the existence of " aunties " from among younger or anoestrous females safeguards an older calf when the mother has a new one. Therefore, a higher reproductive rate is probably not necessarily associated in Odontoceti with a higher calf mortality rate. It is only when the adolescents form herds on their own account that their mortality rate may rise, as demonstrated by the high singleton death rate of adolescent *Lagenorhynchus acutus*, and by Perrin and Powers (1980) in *Stenella attenuata* from infections with *Crassicauda* (p. 31). These mortalities might be density-dependent. However the existence of social mechanisms maintaining calves within the herds will continue to keep calf mortality low.

Thus in Odontocetes survival of juveniles is maximixed by a high degree of parental care and sociality. Old animals too may benefit from care-giving behaviour. The only mechanism remaining to increase mortality among adolescents is aggressiveness of older animals, and this mechanism disappears within the most social species.

A population however must expand slowly if it is to maintain itself. Eventually it will come up against an environmental barrier which will limit its continued growth. Such barriers must in some way involve either food or space. Mass strandings represent a high proportion of the total mortality of the social species and must therefore constitute the main mechanism by which populations of these species are limited.

It is just possible that the true Delphinidae can be divided into two groups: the Delphininae with about a year's gestation, and a normally long lactation period which can be shortened in the way described; and the Orcininae with a long pregnancy, and a long lactation not susceptible to being shortened. This dichotomy, if real, would fit with the subdivision into frequent mass-stranders and others. Unfortunately there are not yet enough data on pregnancy length or on density-dependence in lactation length to know if the suggested division is real. For instance, the lengths of pregnancy and of lactation of *Orcinus orca* seem to be unknown. The same is true for *Pseudorca crassidens* and *Peponocephala electra* though it should be only a matter of time before a sufficient number of animals are examined in mass strandings of these species.

PROXIMATE CAUSES OF STRANDINGS

Examination of mass-stranded Cetacea has shown no obvious bacteriological, helminthological or other pathological findings including those of neuropathology (Hall, Gilmartin and Mattson 1971, Hall and Schimpff 1979). Yet single-stranded animals are frequently highly infected either with trematodes in the liver and brain (Ridgway and Dailey 1972), or with nematodes in lung alveoli or head air sinuses (Delyamure 1955, Dailey and Perrin 1973, Dailey and Stroud 1978). Since many delphinds are known to have heavy infections of nematodes in air-sinuses or lungs, it is important to obtain quantitative information on numbers of parasites in normal and stranded animals. The only such data known to me are due to Delyamure (1955), who examined *D. delphis* from the Black Sea. Seven naturally-stranded animals had heavy infections of the nematode *Skjrabinalius cryptocephalus* in their tracheae and bronchi with pus blocking the small respiratory passages, together with hyperemia, and destruction of the bronchial mucosa. Examination of the lungs of 604 *D. delphis* caught in the fishery showed that 175 (28.9%) had *S. cryptocephalus* infections with from 3 to 227 nematodes present. Infections increased with age, though a few adults were self-cured with healed lesions. Evidence for acute bacterial infections tends to come more from captive animals where the water must have high concentration, *e.g.* of *Staphylococcus aureus* (Colgrove and Migaki 1976). In summary, nearly all singly-stranded animals are diseased or highly parasitised, but mass-stranded animals are not. Geraci and St. Aubin (1979) found that the adrenal cortex of mass-stranded adult female *Lagenorhynchus acutus* showed cysts characteristic of prolonged stress. This interesting observation needs to be followed up, and it is particularly important to examine the cortex from free-living controls to compare with those of the stranded animals.

Most authors (*e.g.* Dudok van Heel 1962) have placed emphasis on the immediate circumstances of mass-strandings, such as the configuration of the coastline, but I do not believe these features to be important. Certainly, many strandings occur on shoaling coasts. Thus Maigret (1979) notes a concentration of mass strandings of *Globicephala macrorhyncha*, *Delphinus delphis*, *Tursiops truncatus* and *Steno bredanensis* on the north side of the Cap-Vert peninsula, Senegal. Six of seven strandings occurred in May and June when there are trade winds from the northwest and a surface current setting from the northeast on to the shore. Another such region may be the neighbourhood of Wellfleet, Cape Cod, where, according to SEAN reports, *Lagenorhynchus acutus* strand repeatedly as well as other species such as *Globicephala melaena* occasionally. I believe that the animals can best be regarded as " drift bottles " which will inevitably tend to arrive on such sites. Passivity of the animals is stressed in many observations, e.g. the pilot whales *G. macrorhyncha* which stranded repeatedly along the west coast of Florida in August 1971 (Fehring and Wells, 1976); and the 30 *Pseudorca crassidens* which were filmed coming ashore at the Dry Tortugas, Florida in June 1976 (Porter, 1977). Moreover, as is well known, a herd once so stranded is likely, if taken out to sea, to strand again (Fehring and Wells, 1976). I therefore judge it more important to examine the internal causes of the observed passivity.

MASS STRANDINGS AS EMIGRATIONS

Considering the extralimital occurrences of mass-stranding *Pseudorca crassidens* at Britain and probably also in south temperate seas one would expect mass-strandings within an increasing population to be accompanied by some range expansion. This does not seem to have occurred as yet with *Lagenorhynchus acutus* which has merely increased within its known range in the northwest Atlantic, there being no evidence of a concomitant increase of the same species within the northeast Atlantic (Evans, 1980, 1981). Thus for this species, the scope of a population increase so far been has quite restricted. It will be worthwhile to continue to monitor it.

PRACTICAL APPLICATIONS

Sergeant (1977) used the frequency of singleton strandings of fin whales on the coasts of Britain over time, expressed as an order of rank within all Cetacean strandings, in order to determine changes of the population as a result of commercial whaling.

If frequency of mass and singleton strandings varies directly with the abundance of an Odontocete species, prone to mass strand, then occurrence of mass strandings could give additional evidence on the state of such a stock. This could be of practical value for a species such as the sperm whale.

In the *eastern North Atlantic,* Fairlie (1981) notes that there has been no decline in recent years in the (singleton) stranding rate of sperm whales in Ireland, though all Mysticetes have declined in their stranding rate at Britain, this correlating well with the reduction of their populations by hunting (Sergeant 1977, 1979). From the evidence given I would deduce that sperm whales have not declined in the eastern North Atlantic. Mitchell (1975b) demonstrated a cross-over from Nova Scotia to Spain from tagging, showing that eastern and western North atlantic sperm whales are not isolated from one another. Allen, Compton-Bishop and Gordon (1979) demonstrated a reduction in catch and increase in catch per unit effort of sperm whales at the Azores between the 1950's and 1970's, due to massive human emigration and reduction in number of whaling stations. Catches there in the 1950's were about 400 per annum; in the 1970's about 200 and falling. The main catch of sperm whales is now at Iceland (about 200 per annum) where only adult males are available. I conclude that the North Atlantic population of sperm whales is probably not reduced nor are present catches excessive. The main concern appears to be whether the falling mean size of males due to selective catching of them(Martin 1981) could affect reproductive success.

In the *eastern North Pacific* there have been 4 recent mass strandings: in the Gulf of California in 1953 and 1954 (Gilmore 1957, 1959) and in 1979 (Byrant 1979; SEAN Bull., January 1979), and on the coast of Oregon in June, 1979 (Anon, 1979, SEAN Bull. June 1979). The Mexican strandings were all or mainly of males; the Oregon stranding was of a harem herd. Pike and MacAskie (1979) show that harem herds normally extend as far north as off the coast of British Columbia between spring and autumn. Knowledge of stock identity of sperm whales in the North Pacific Ocean is still incomplete, but Bannister and Mitchell (1980), basing themselves partly on unpublished tagging recoveries due to D. W. Rice, and partly on discontinuous distributions of sperm whales at sea, accept the existence of an eastern North Pacific or American stock. Horwood and Garrod (1980), examining the state of this stock from catch per unit of effort and comparisons of pregancy rate over time, conclude it is in a healthy state.

At *New Zealand*, there were mass strandings of sperm whales in 1970 (Robson and Van Bree 1970), 1972 (Robson 1978) and 1974 (Stephenson 1975)with apparently none subsequently (*fide* SEAN Bulls. to December 1981). Best (1976), table 2) shows that stock reductions of sperm whales in the southern hemisphere generally and the New Zealand area in particular (Best's division VII) were severe for exploitable males, reducing them to about half initial stock size by 1972. However it had been computed that the stock of mature females was reduced only to ca 90% of initial sock. Clearly, the females are the main animals which appear in strandings of harem herds.

I conclude that analysis of mass and single strandings of sperm whales may throw light on the status of stocks additional to that which may be obtained by other methods, and that this finding makes important the widespread dcoumentation of their strandings.

SUMMARY

1. In eastern Newfoundland from 1950 to 1971 an abundant oceanic population of pilot whales *Globicephala melaena* was hunted down to low catch levels. Its cumulative catch gave an initital population estimate of 54,000. It was protected in 1972. The population was estimated in 1980 to number at least 14,000 animals. Recovery of the population was presumably accelerated by immigration from areas where the species had remained common. From 1975, mass-strandings began at Newfoundland and neighbouring areas and continue at the rate of between 100 and 200 animals a year.

In the area of the northwest Atlantic extending from the Gulf of Maine to the Gulf of St. Lawrence, white-sided dolphins *Lagenorhynchus acutus* have become very common since about 1970 with at least 10,000 individuals present in the U.S. sector of this range. During the 1970's there were two mass strandings and many singleton strandings of this species.

At North Island, New Zealand, harem herds of sperm whales have mass-stranded on many occasions, and this area contains one of the highest densities of sperm whales and especially females in the southern hemisphere.

From these examples, mass strandings can be associated with dense populations of Odontocetes.

2. From an examination of the literature, mass strandings are the main source of coastal mortality (perhaps exceeding 90% of deaths) in a group of species (*Globicephala* spp., *Pseudorca crassidens*, *Peponocephala electra*) belonging to the subfamily Orcininae of the family Delphinidae. Mass strandings represent a lower percentage of deaths in typical dolphins of the subfamily Delphininae.

3. The frequency of mass strandings can vary geographically, whatever the rate of overall incidence. A study of the incidence of mass strandings by latitude in the allopatric species *Globicephala melaena* and *G. macrorhyncha* along the eastern North American seaboard showed that each species has a wide " core " area where

both mass and singleton strandings occur, located to the northward in *G. melaena* and southward in *G. macrorhyncha*. At the edges of the respective ranges, where the two species are in contact, only singleton strandings occur in both species. This evidence is taken to mean that mass strandings occur in that part of the range where the species is abundant.

4. A comparison of life histories shows that *Globicephala melaena* among the Orcininae exhibits greater sociality, expressed by greater homogeneity of herds, than do *Tursiops truncatus* and *Lagenorhynchus acutus* among the Delphininae. Pilot whales also show absence of aggression by adult to immature animals. This greater sociality occurs among member species of the Orcininae in spite of a greater sexual dimorphism, delayed sexual maturity and higher male mortality rate, features typical of territorial marine mammals of other groups.

Physeter catodon exhibits mass mortality among harem herds, but solitary stranding mortality of subadult and adult males at high latitudes, consistent with the known aggressive behaviour of harem bulls.

5. No evidence exists for emigration among mass-stranding populations of Odontoceti, except for the examples of *Pseudorca crassidens* stranding in cool seas.

6. In Mysticetes, high mortality occurs among young animals just after weaning, and at extreme old ages. This pattern remains among Odontoceti in the weakly social *Phocoena phocoena*, but is not observed from length frequencies of stranded *Delphinus*, *Tursiops* and *Globicephala*. However high adolescent mortality remains due to aggression in *Lagenorhynchus acutus* and *Stenella attenuata* at least. It is argued that sociality reduces the mortality of juveniles of the social Odontoceti, probably through such features as the long lactation and other features of parental care such as succorant behaviour. Since length of lactation has been demonstrated to be density-dependent among members of the Delphininae and among sperm whales, social behaviour must be important in reducing calf mortality. When other sources of mortality are reduced, social mortality expressed in mass strandings becomes the major source.

7. The main purpose of the study has been to emphasise internal factors and especially population density as responsible for mass strandings and to discount immediate external factors such as coastal configuration. What the internal factors might be leading to morbidity of herds is unknown but it is suggested that studies of stress might be valuable, with the need to study controls from among normal animals at sea.

ACKNOWLEDGMENTS

I am greatly indebted to Jon Lien, Memorial University of Newfoundland, and to Keith Hay, Department of Fisheries and Oceans of Canada in St. Jonh's for unpublished information on mass strandings and on net catches of humpback whales. Michael Moore and Paul Brodie also provided useful observations. Especially I wish to thank the compilers of the Scientific Event Alert Network (SEAN) of the Smithsonian Institution, Washington, D. C. and many observers on the United

States east coast for the opportunity to analyse their carefully documented observations of Cetacea.

M. Didier Marchessaux, Aix-en-Provence, France, recently a visitor to Ste. Anne de Bellevue, Hr. Chr. Hysing-Dahl, Bergen, Norway and especially Dr. Margaret Klinowska, Department of Anatomy, Cambridge University, provided me with many valuable references. Robin Allen and Michael Scott of the Inter-tropical Tuna Commission, William F. Perrin and Douglas DeMaster of Southwest Fisheries Center, La Jolla, and James Mead and Aleta Hohn of the National Museum of Natural History, Washington, criticised earlier versions of the paper; Dr. A. W. Mansfield—a later draft. They are not responsible for its imperfections.

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THE MANDIBLE OF BOWHEAD IN KATHMANDU

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ABSTRACT

The huge mandibular bones which I unexpectedly found at National Museum of Nepal, Kathmandu, was compared with a mandibular specimen of the bowhead whale in Taiji Whale Museum and those of the Pacific right whales in Tokyo University of Fisheries and National Science Museum, Tokyo. It was cleared that the owner of the huge bones was a *Balaena mysticetus*, and from their size, the whale must have been about 16 m in body length. It is still a matter of investigation that when and how they came up to Kathmandu.

INTRODUCTION

It was quite unexpeced encounter of myself with huge mandibular bones of whale at a dark corridor of the National Museum of Nepal, Kathmandu, in my second visit to the city in July 1974 on the wayback from USSR. As I had been to Kathmandu in the investigation on the Ganges river dolphin in Pakistan (now Bangradesh) in times between 1970 and 1974, trying to know if distribution of the dolphin was extended to the upper Ganges in Himalayan out-skirts, but had least imagined that such a thing was in the museum.

Instantly after I saw the bones, I tried to inquire about them and asked to take photographs, but there was only an attendant of the museum who did not speak English, and he only shook his head. Unfortunately it was Sunday and I had no time to stay for another inquiry.

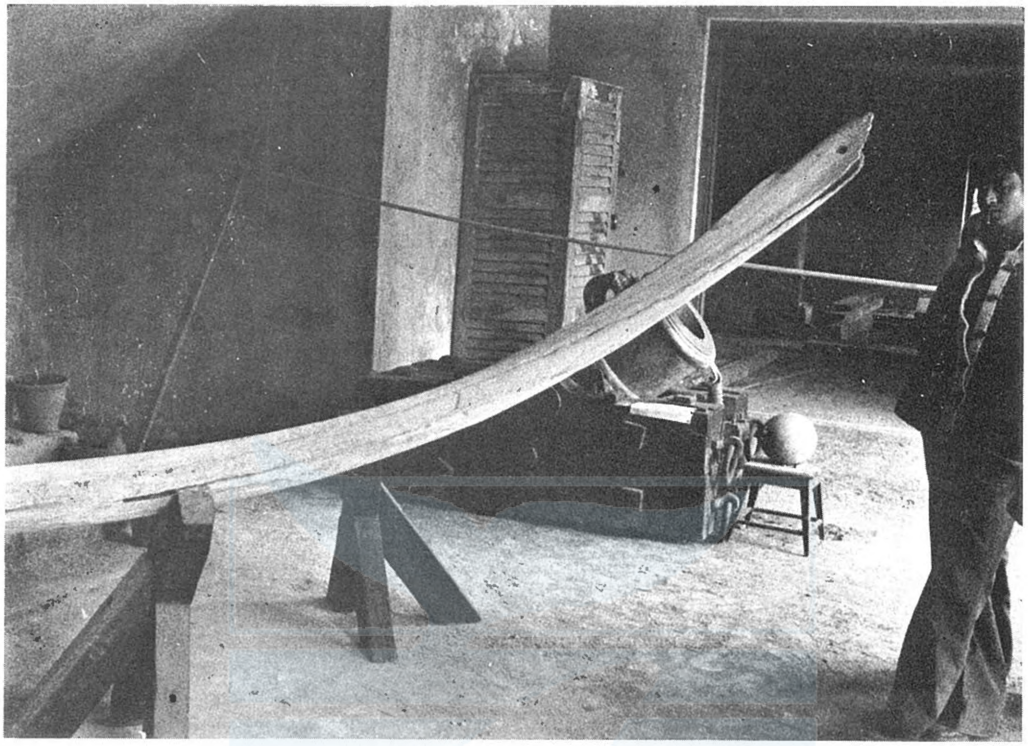
Since then, I tried to make contact with the museum to get permission for investigation and photograph on them. My asking had been in vain for a few years, but through introduction of many kind people, permission came from Dr. R. J. Thapa, Director General of the Department of Archaeology, Kathmandu, Nepal, in 1979. With great expectation, I visited Kathmandu again on my way to west Africa in Jan. 1980. As shown in Fig. 1, photographs of the bones were taken by having them taken out to the hall from the dark corridor. Measurements were also taken.

INVESTIGATION AND DISCUSSION

The mandible was a pair of bulky bones of about five meter in length. Species of whales who have such a big mandible, are the blue whale (*Balaenoptera musculus*), the fin whale (*Balaenoptera physalus*), the right whale (*Eubalaena glacialis*) and the bowhead whale (*Balaena mysticetus*). As I saw the indistinct coronid processes of

Fig. 1. A huge whale mandible found in

the mandible of Kathmandu, the owner of it must have been a species of *Balaenidae*, never of a *Balaenopteridae*, (Fig. 2). Trying to clear the species of whale, mandibular bones of Kathmandu were compared with other specimens of *Balaenidae*. Data value were collected from the mandible of the skeletons of bowhead in Taiji Whale Museum (*TWM*) and those of the two Pacific right whales in Tokyo University of Fisheries (*TUF*) and National Science Museum (*NSM*), Tokyo. In measurement of Kathmandu specimen, (Table 1) girth and height (depth) of the bones were measured at Point 1 (one meter from the front tip along the dorsal surface of curved line), Point 2 (two meters from the tip), Point 3 (three meters from the tip), and at the center of the coronoid process. However, the coronoid process was so indistinct that I managed to reach the highest point at a susceptible center. Other specimens were also marked at three points fit to those in Kathmandu specimen in equal percentage against the mandibular length. The length of right bone of Kathmandu speimen was made to be a standard, because there were rat bites in the specimen and damage in the left condyle was serious, and length of right and left bones became varied. Compared Kathmandu specimen with the mandible of *E. glacialis* of *TUF* in Table 1, together with their lateral view in Fig. 3, it is understood that length of the two are similar, shape is more monotonus in Kathmandu specimen, but in *TUF* specimen the posterior part is apparently thicker than the anterior part of it. Naturally, girth and height of



the National Museum of Nepal, Kathmandu.

Fig. 2. Showing coronoid process of mandibles:
distant: North Pacific blue whale,
near: East China Sea fin whale. (National Science Museum, Tokyo)

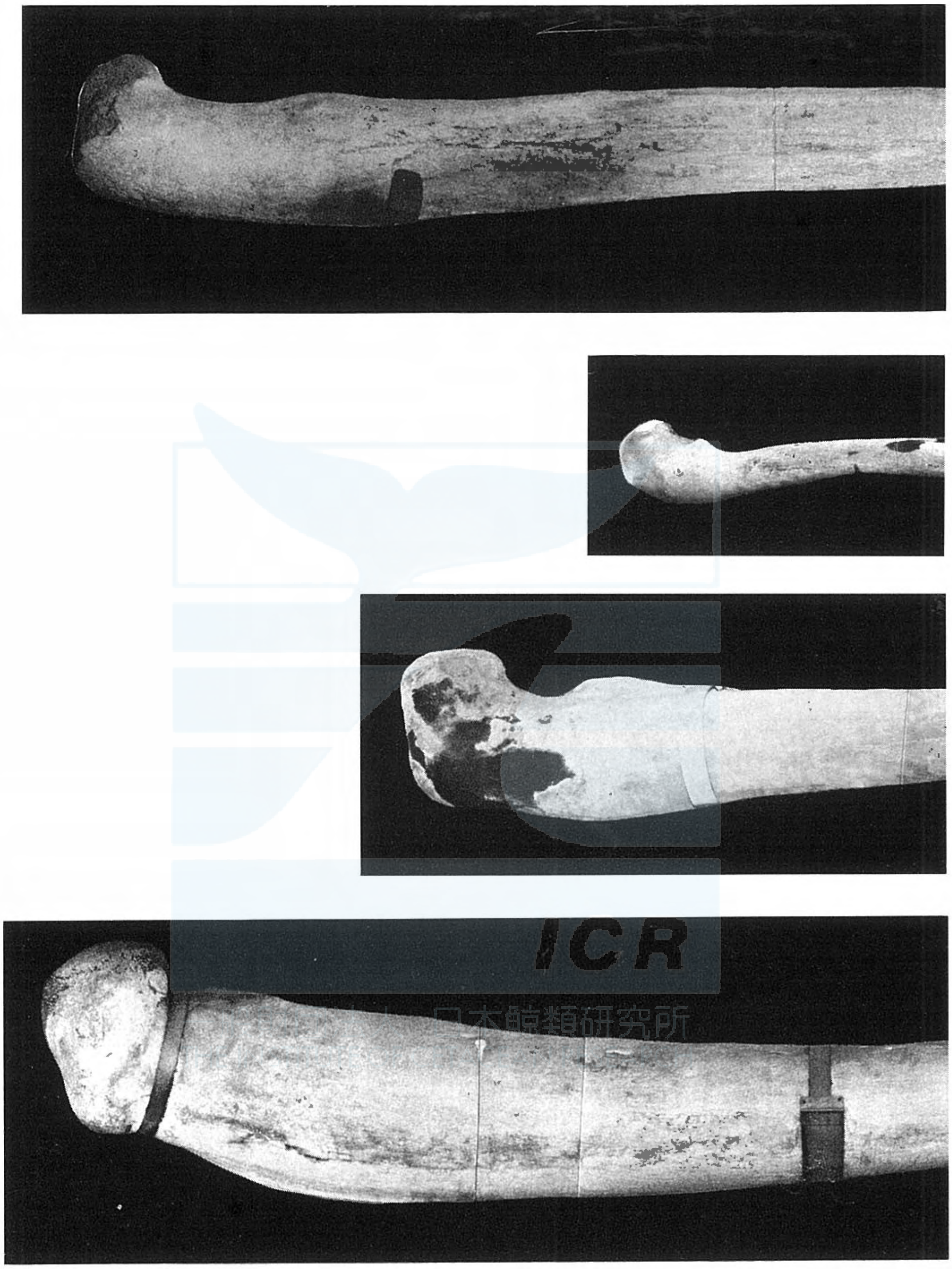


Fig. 3. Mandible specimen in Kathmandu compared with other known specimens. From (young *E. glacialis*) and *TUF* specimen (*E. glacialis*).

upper to lower: Kathmandu specimen, *TWM* specimen (young *B. mysticetus*), *NSM* specimen

TABLE 1. MANDIBLE MEASUREMENT OF THE KATHMANDU SPECIMEN COMPARED WITH OTHER KNOWN SPECIMENS. (in cm)

Name of specimen Species of whale	Natiomal Museum of Nepal, Kathmandu			Taiji Whale Museum		TokyoUniversity of Fisheries		National Science Museum, Tokyo	
				Balaena mysticetus		*Eubalaena glacialis*		*Eubalaena glacialis*	
Body length of whale				640		1710		1165	
Straight length of mandible	left	right		right		right		right	
between tip and condyle	480+	491		184		510		296	
Curved length of mandible			%		%		%		%
along mid-dorsal surface	509+	514	100.0	189	100.0	526	100.0	318	100.0
Height of mandible									
at point1 1(19.5% of curved length from the tip)	23	23	4.5	9.4	5.0	32	6.1	15	4.7
at point 2 (39.0% of curved length from the tip)	21	22	4.3	9.5	5.0	34	6.5	16	5.0
at point 3 (58.5% of curved length from the tip)	31	30	5.8	9.8	5.2	37	7.0	19	6.0
at coronoid process (highest)	39	39	7.6	19.6	10.4	68	12.9	39	12.3
at condyle (biggest)	40+	45	8.7	25.4	13.4	57	10.8	39	12.3
Length of condyle	—	28	5.5	18	9.5	50	9.5	28	8.8
Breadth of condyle	53	30+	10.3(L)	22.5	11.9	55	10.5	38	11.9
Girth at point 1	68	67	13.0	25	13.2	77	14.6	41	12.9
at point 2	81	81	15.8	27	14.3	96	18.3	50	15.7
at point 3	86	87	16.9	31	16.4	108	20.5	62	19.5
at coronoid process	96	97	18.9	36	19.0	145	27.6	78	24.5
Length between coronoid process and rear end of condyle	87	88	17.1	33	17.5	58	11.0	34	10.7

Fig. 4. Shape of anterior part of the mandibles, Kathmandu specimen (top), *TWM* specimen, *Balaena mysticetus* (middle) and *TUF* specimen, *Eubalaena glacialis* (bottom).

anterior and posterior parts show less differences in Kathmandu specimen, but some variety in *TUF* specimen. In Kathmandu specimen there is a little unusual value, height at Point 2 is lesser than that in Point 1, which can be seen in Fig. 3 in shape. In all the four specimens, the coronoid process is indistinctly developed. In *TWM* specimen, the whale is presumed as the youngest of the four, (1+1/3 years old), the process is recognized, but in Kathmandu speimen (presumably very old), the process is hardly recognized. The coronoid process in the Kathmandu specimen must be relatively under-developed in accordance with growth. The coronoid processes in both *Eubalaena* specimen of *TUF* and *NSM* are, however, located 6% more posterior against the length than in Kathmandu and *TWM* specimens. In the photograph of Fig. 3, both *TUF* and *NSM* specimens have a swell at the ventral side just under the coronoid process. The feature can not be perceived in the Table 1. While, the swell is less distinct in Kathmandu and *TWM* specimens. The shapes of the anterior-most of the three specimens are compared in Fig. 4. The anterior tip of Kathmandu specimen might have worn a little, but the shape resembles well *TWM* specimen. After those comparison in shape and mesaurement values, it may be safe to say that the Kathmandu specimen is a pair of mandibles of a bowhead whale (*Balaena mysticetus*).

Estimation of body length from a mandible is not so difficult. The young individual of *TWM* specimen was 640 cm in body length, and the mandibular bones are 184 cm (right) and 185 cm (left) respectively, and the head portion of this species of whale becomes bigger proportionally and reach 1/3 of the body length in adult animals. This is not a presumption at this moment, but this phenomenal tendency is generally known among whalers and scientists. Then, if 30–33% is the adult head length rate against the total length, the whale, owner of Kathmandu mandible (419 cm), must have been more or less 16 m in body length. Although Eskimo people might have some huge specimens, this Kathmandu mandibular bones is one of the biggest specimens of *B. mysticetus* known among museums at present.

PROCESS TO KATHMANDU

As I have studied and discussed the huge mandibular bones in the National Museum of Nepal, Kathmandu, and presumed the species of it as the bowhead whale (*Balaena mysticetus*) and the body length as about 16 m, though sex can not be identified. It may be natural to wonder, from where and how the bulky heavy bones were transported to such a long distant and high place of Kathmandu. If it was in an old time, transportation might have been without machinary. Inquiry was made to many people in the museum and those who kindly opened a road to this investigation, but nobody knew the process of delivery or history of the specimen. Only Dr. Badri Prasad Shrestha, Ambassador of Napel to Japan, presumed that the mandible bones were thought to be there since about 100 years before. Many royal people of Nepal Kingdom have studied in England since old times. Presumably, one of those royal people might have seen the bones at the

British Museum (Natural History) or somewhere else, and wanted to have it and was transported to Kathmandu as a present. His story is one of the presumptions, and I asked the National Museum of Nepal to investigate the process.

ACKNOWLEDGMENT

I should like to extend my sincere gratitude to Mrs. Sushuma Omata, Nepal princess in Japan, and Dr. Badri Prasad Shrestha, Ambassador of Nepal to Japan, who helped me in contact to the National Museum of Nepal, and Dr. R. J. Thapa, Director General of the Department of Archaeology who gave me permission to study on the mandibular bones through Mr. J. L. Sharma of the same Department, and Mr. J. K. Shrestha of National Msueum of Nepal who helped my investigation in the museum. My gratitudes are also to Mr. M. Kumazawa of the Museum of Tokyo University of Fisheries, Mr. Masami Shoji of Taiji Whale Museum and Mrs. Haruka Ito, postgraduate student of the Department of Fisheries, University of Tokyo, for their good assistance in taking measurements and photographs of the comparable specimens at home. At the end, I cannot omit Dr. Hiroo Kanai of the National Science Museum, Tokyo, who made effort to have me contact with the National Museum of Nepal.

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FOOD HABITS AND PREY DISTRIBUTIONS OF THREE RORQUAL SPECIES IN THE NORTH PACIFIC OCEAN

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ABSTRACT

Stomach conditions and a total of 1675 stomach samples of fin, sei and Bryde's whales caught in the North Pacific during the seasons of 1969–1979 were examined. The percent of filled stomach to all animals examined was about 60% with varying fullness; and this figure was considered to be very high notwithstanding the fact that large number of whales were caught in the subartic to subtropical waters where the zooplankton distribution is poorer than the northern North Pacific region. Due to southerly shifted whaling ground there found many warm water prey species in the stomach samples. Of more than 40 prey species occurred, however, very few number of the species actually comprised principal prey items, *i.e.*, *Calanus cristatus*, *C. plumchrus*, *C. pacificus*, *Euphausia pacifica*, *E. similis*, *Thysanoessa longipes*, *T. spinifera*, *T. inermis*, *Nematoscelis difficilis*, *Sergestes similis*, *Vinciguerria nimbaria*, *Scomber japonicus*, *Cololabis saira* and *Pseudopentaceros richardsoni*. The composition of stomach contents by whale species revealed that the fin, sei and Bryde's whales eat mainly euphausiid, copepods, and small gregarious fish species in this order. From the characteristics of geographical distributions of the major prey items by each whale species, it was suggested that the North Pacific rorqual whales share a possible food species among them by selecting different prey items. There also suggested that the feeding conditions in the pelagic waters of the North Pacific region differ from those in the marginal sea regions such as the Kurile Islands and/or the Bering Sea in the composition of prey fish species.

INTRODUCTION

Since the establishment of the Whales Research Institute in 1947, one of main study areas was to know the food habits of baleen whales of both northern and southern species. In the North Pacific region including Japanese coastal waters, Mizue (1951) was the first who dealt with the food habits of larger whales caught by the land-based whaling around Japanese waters during 1946–1948, and pointed out an extreme importance of krill for fin whales, whilst squid and/or Japanese sardine may contribute as main food items in sei whales. In accordance with the development of the North Pacific pelagic whaling since 1952, the whaling ground geographically expanded year after year towards more northern latitudes of the Bering Sea (Omura, 1955; Nasu, 1957; Nemoto, 1957), which caused the shift of main study area from the coastal regions to the pelagic catches of whales. Studies of the food habits of baleen whales by Nemoto (1957, 1959, 1963) con-

Sci. Rep. Whales Res. Inst.,
No. 34, 1982, 59–91.

tributed to clarify the feeding conditions of baleen whales over the North Pacific and Bering Sea, and the prey items of baleen whales by whale species bacame clear in detail, although some more earlier Russian works in this field have been reported (e.g. Zenkovitch, 1937). Nemoto (1959) finally compiled large amount of data that came from a total of 9,270 animals caught in the North Pacific, Bering Sea, and Okhotsk Sea during 1952–1958. Later, Nemoto (1963) discussed distribution characteristics and importance of two major *Calanus* species as the prey of whales using additional materials obtained up to the 1961 season.

After a pause of effort to collect the stomach contents of the North Pacific baleen whales during the 1962–1968 seasons, activity of material collection by the Whales Research Institute was restored again in 1969, and the effort was continued until 1979 except 1978 season, while the geographical occupation of whaling ground along with the composition of exploitable whale species changed considerably during these periods. However, stomach samples of whales covering last 10 years have not been examined nor reported todate except several short articles of limited subjects (Omori *et al.*, 1972; Kawamura, 1973; Nemoto & Kawamura, 1977; Kawamura, 1978; Kawamura & Hamaoka, 1981; Kawaguchi & Kawamura, 1981). Among these reports, Omori *et al.* (1972) reported the mass occurrence of the sergestiid shrimp, *Sergestes similis* Hansen, and pointed out its importance as whales food particularly in the eastern half of the northern North Pacific, while Kawamura (1973) focussed his discussion on the food conditions of whales in the southern part of the subarctic North Pacific region, and he (Kawamura, 1973) pointed out a possible significant ecological role of several commercially important fish species as food of sei whales.

The long-lasted Japanese activity in the North Pacific pelagic whaling ceased its 18-year operations in 1979 as it was the final expedition. This report aims to provide a knowledge about the food habits of the North Pacific baleen whales, fin, sei, and Bryde's that were caught largely in the southern waters from subarctic to subtropical regions. In this point of view, this report can be regarded as a supplement of our earlier knowledge that was obtained in the boreal to arctic regions.

MATERIALS AND METHODS

The stomach contents of whales were collected randomly from the cut opened first stomach that was found to be containing fresh enough food for the identification of each prey item. Usually, several hundred grams (wet weight) of stomach contents were collected, and they were preserved in plastic bottles with 10% formalin solution. The number of samples should be collected by each season and by the fleet was basically guide lined to take one stomach sample per every ten animals processed, but actually it varied considerably by situations in the field and by the fleet participated. However, being independent of the sampling scheme above mentioned, the materials were collected to meet with the necessity of data analysis, *i.e.*, to collect the materials so as to totally represent the geographical expansion of whaling ground and the month (=season) occupied. Sampling was

TABLE 1. NUMBER OF STOMACH SAMPLES COLLECTED IN THE NORTH PACIFIC AND BERING SEA WHALING DURING THE SEASONS OF 1969—1979.*

( ): Number of whales caught

Season	Fin	Sei	Bryde's
1969	56	316	—
	(576)	(3,591)	—
1970	32	258	—
	(518)	(3,235)	—
1971	62	181	1
	(542)	(2,431)	(98)
1972	14	70	—
	(426)	(2,041)	(5)
1973	24	98**	—
	(256)	(1,710)	(2)
1974	46	100	46
	(216)	(1,190)	(522)
1975	31	52	51
	(118)	(454)	(688)
1976	—	—	56
	—	—	(578)
1977	—	—	97
	—	—	(424)
1978	No sampling		(200)
1979	—	—	94
	—	—	(175)
Total	265	1,075	345
	(2,652)	(14,641)	(2,694)

* A catch of ten minke whales in 1970 was excluded

** One unknown stomach sample probably belongs to sei whale stomach was included

also conducted whenever the species of prey items seemed to have changed by a visual observations. Several number of stomach samples were damaged by a leakage and evaporation of preserving solution under an unfavourable conditions of storage during the past 13 years.

During the summer period of 1969–1979 a total of 19,992 baleen whales were harvested by the Japanese pelagic whaling in the North Pacific and Bering Sea regions. The number of materials actually examined in this study was 1,685 stomachs in all as given in Table 1. The whale species treated were fin, sei and Bryde's. During the study period there were several number of pelagic catches of minke whales but they were excluded in this study due to small number in the available amount of materials.

The traditional catch records (*Geirui Hokaku Daicho*) on each animal processed along with some results of biological observations *in situ* by fleet and whaling season that were compiled by the Far Seas Fisheries Research Laboratory of the Fisheries Agency were available, and these statistical data were referred or quoted whenever it was felt necessary. To construct an approximate expansion of the whaling ground occupied in the past seasons, I consulted a report series (The reports on the biological investigations of the North Pacific whale stocks) published by the Japan Whaling Association or the Whales Research Institute, Tokyo. Since the general methods and items of observations in recording the stomach conditions of whales in the field have been reported elsewhere (*e.g.* Nemoto, 1957; Kawamura, 1974), no details were mentioned in this report.

RESULT

1. Whaling ground

Geographical occupation

As it was reported earlier (*e.g.* Nemoto, 1957, 1959), the fin whales occur more larger numbers in the Bering Sea and higher latitudes of the northern North Pacific regions from May to August. Due to reduced catch quotas for fin whales year after year the catches of this whale species during study period were confined in small local areas closer to the Pribilof Islands, whereas in the North Pacific the majority of fin whales were caught in the southeast region off Kamchatka and in the Gulf of Alaska. However, the trends of their catches on the whole were somewhat sporadic during the 1960's. In contrast to fin, the sei whales, a major exploitable species during the study period, were found to be distributed over a wide range of the subarctic North Pacific region of north of 40°N. With the change in exploitable whale species from sei to Bryde's along with the opening of warmer temperate/subtropical region down to 20°N as a possible whaling ground in the western North Pacific, the Bryde's became a major species of pelagic whaling since 1971 (Kawamura, 1973).

In order to show approximate trend of the changes in geographical occupations of whaling ground, Fig. 1 was constructed by selecting several representative whaling seasons. During the 1950's the expansion of whaling ground was confined in geographically smaller area of higher latitudes of the North Pacific. The major whaling ground was established both in the eastern/southeastern waters off Kamchatka Penninsula and in the eastern North Pacific/Bering Sea regions. With the developments of whaling activity along with the change in exploitable whale species from fin to sei the whaling ground during the first half of the 1970's became wide ranged occupation where the southern most whaling ground extended to 40°N such the case as shown in 1971. The trend of more southerly shift of whaling ground in 1972 indicates that the movements of whaling fleet were intense in pursuit of more profitable whaling ground in accordance with lifting of the banned area, and this along with covering the catch quotas for fin and sei resulted a largest occupation of whaling ground during the first half of the 1970's throughout the whole North Pacific whaling.

Since the close of hunting fin and sei whales in 1976, there left the Bryde's alone, a warm water species that inhabits widely the temperate to subtropical waters in the North Pacific (Omura & Nemoto, 1955; Kawamura & Satake, 1976). In order to catch the Bryde's whales there found a new whaling ground in far southern waters down to 20°N particularly in the western North Pacific. The

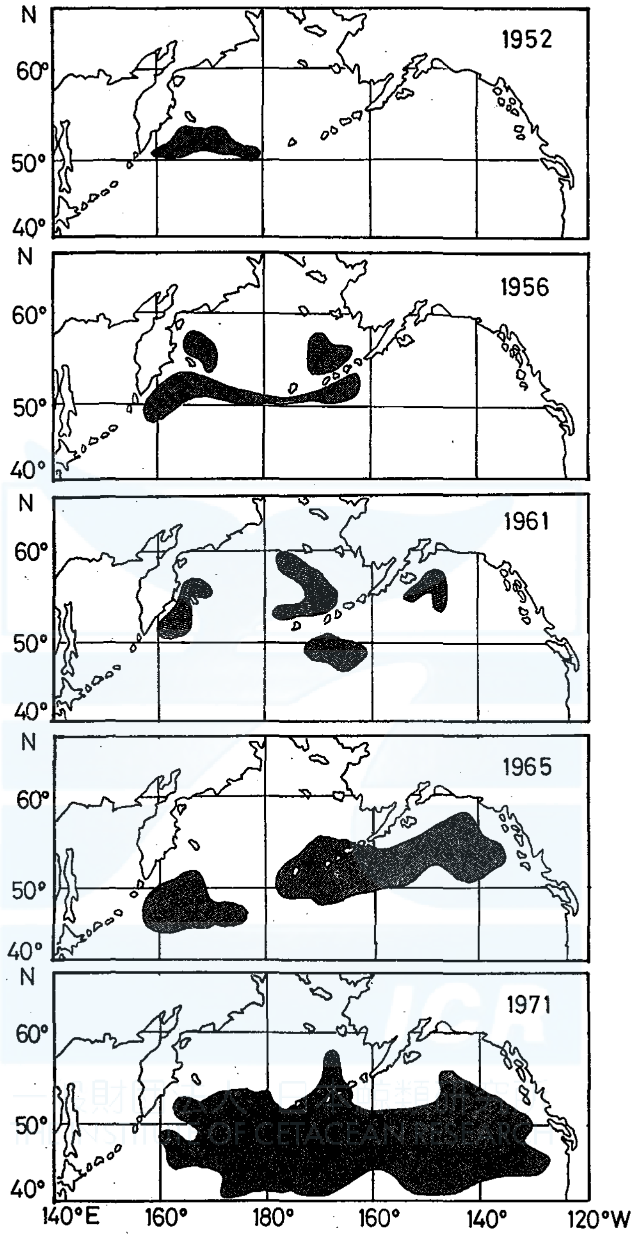
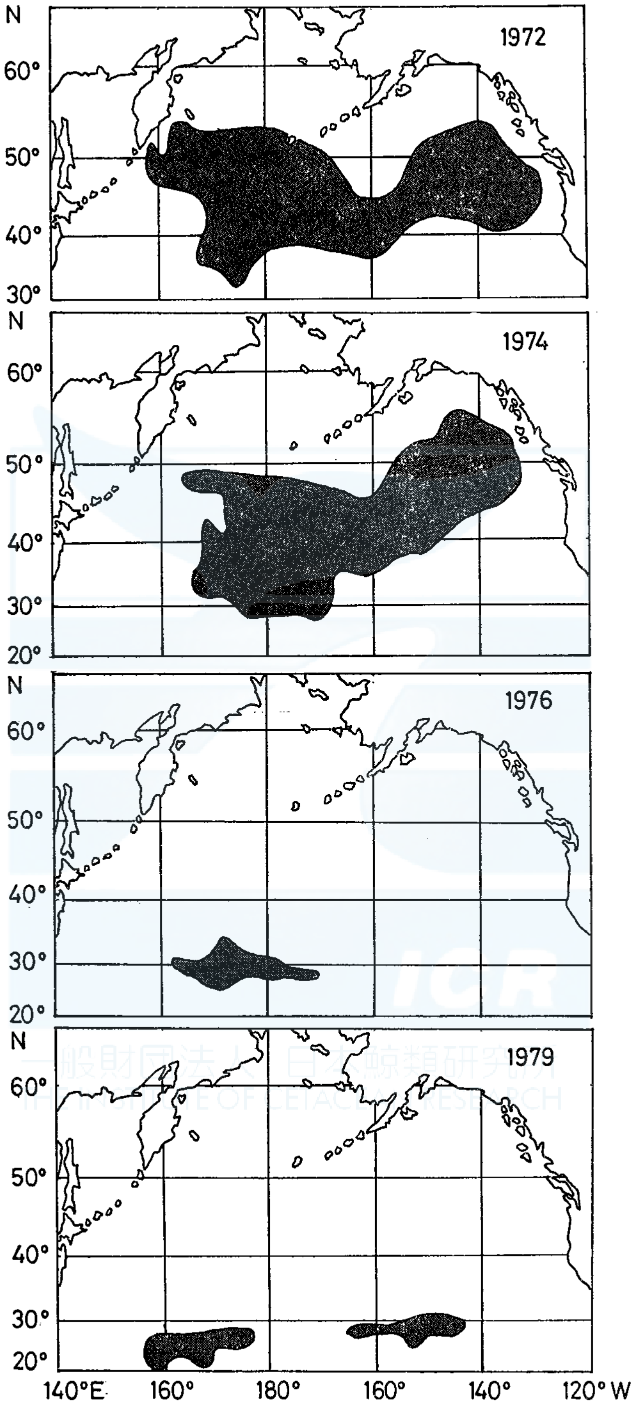


Fig. 1. Geographical occupations of the North Pacific whaling grounds in the past nine seasons.

geographical changes in the occupation of whaling ground can be comparable with the changes in the composition of exploited whale species; the fin and blue were the main species during 1952–1962 when they were hunted in somewhat geographically

(Fig. 1 continued)



smaller local regions. With larger increase in the number of sei whale catch from the 1962–1963 seasons onwards (*e.g.* 4–945 animals in 1955 vs 1398–3819 animals in 1963–1975, IWS, 1967–1972), the whaling ground began to occupy more larger sea area into all horizontal directions until 1975. The very small geographical occupation of whaling ground in the southern North Pacific came from hunting a relatively smaller number of Bryde's whales since 1976, and similar situation continued until 1979, the final whaling season of the long-lasted pelagic whaling in the North Pacific Ocean.

Monthly changes in geographical occupation

Since pelagic whaling in the North Pacific is usually operated for four months or more, the main whaling ground changes in its geographical occupation in accordance with the proceeding of seasons and catch conditions by whale species. Fig. 2 demonstrates such example of changes as shown by monthly occupation through the whaling years of 1969–1973. To see the figures, there observed different monthly occupations from one year to another. In some years such the case as in August of 1970, there were two or more geographically separated whaling grounds occupied within the same month due to difference in accomplished catch conditions by each whaling fleet.

2. Stomach conditions of whales in general

Monthly changes in prey item

Examination of stomach conditions of whales that were processed on the factory ship is one of the items of biological observations in the field. Due to visual observations on the ship each prey item was recorded by the larger taxonomical groups such as the Euphausiacea, Copepoda, Amphipoda, Pisces, and Cephalopoda. One of these available data is found in the catch records of whales by the Fisheries Agency, and a related part of the records were modified to show a monthly changes of prey items in Figs. 3–4, and in appended table, where all data obtained during the 1969–1979 seasons were combined altogether.

It is observed in Figs. 3–4 that there were no significant monthly changes in the percent figure of animals with filled stomach to the total catches, where about 60% of stomachs were found to be filled with variable amount of food over the three whale species and whaling seasons. In the prey items, however, there observed a considerable difference between each whale species. More than 65% of fin whales feed on the Euphausiacea from May through August without notable monthly changes in percent figures. The Euphausiacea along with the Copepoda comprise major food items of the North Pacific fin whales. Towards mid summer, however, the Cephalopoda (=squid) become to share a similar percent to the Copepoda. Sei whales, on the other hand, feed almost exclusively on the Copepoda, and this prey alone accounts for about 75.8% of the animals with filled stomach. Different from the case found in fin whales, relative importance of the Pisces and Euphausiacea is a characteristic food habits of sei whales. In both fin and sei whales the major prey item showed a quite high and less varibale percent fugures

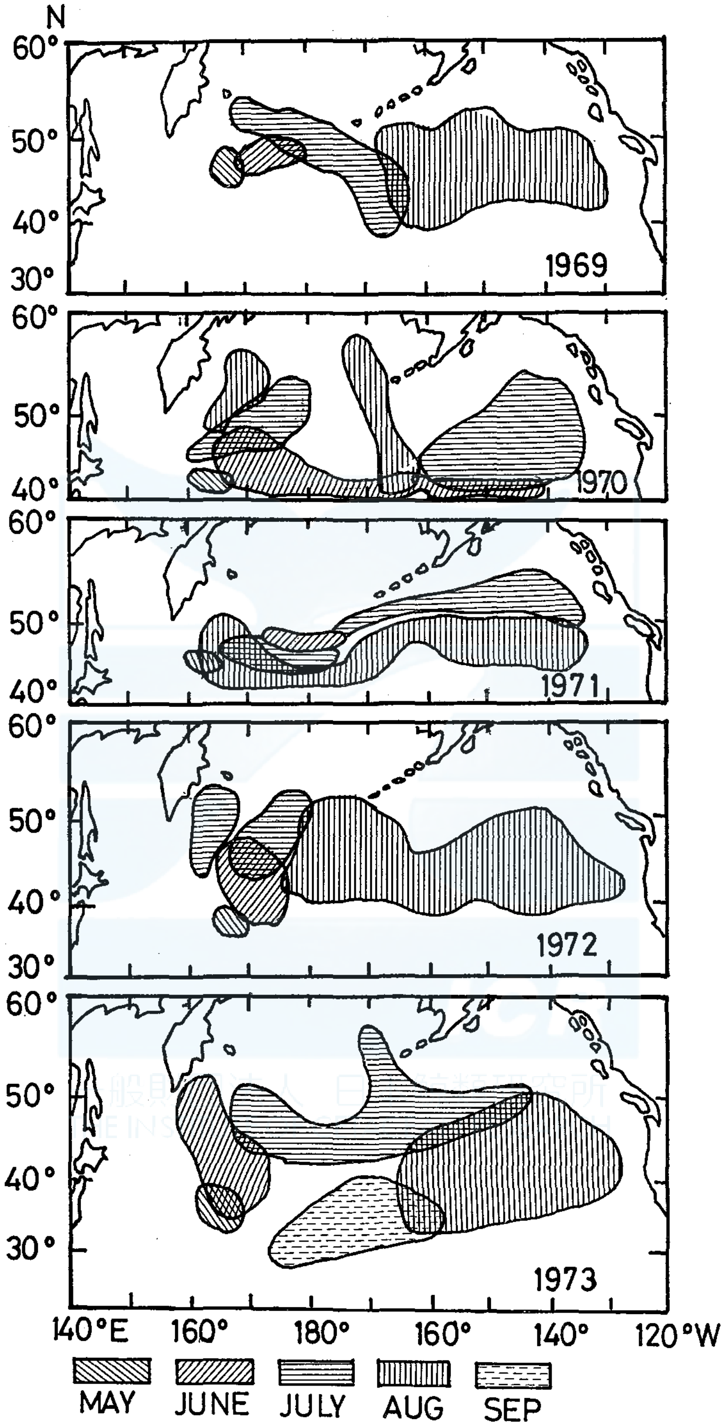


Fig. 2. Monthly occupation of the whaling grounds.

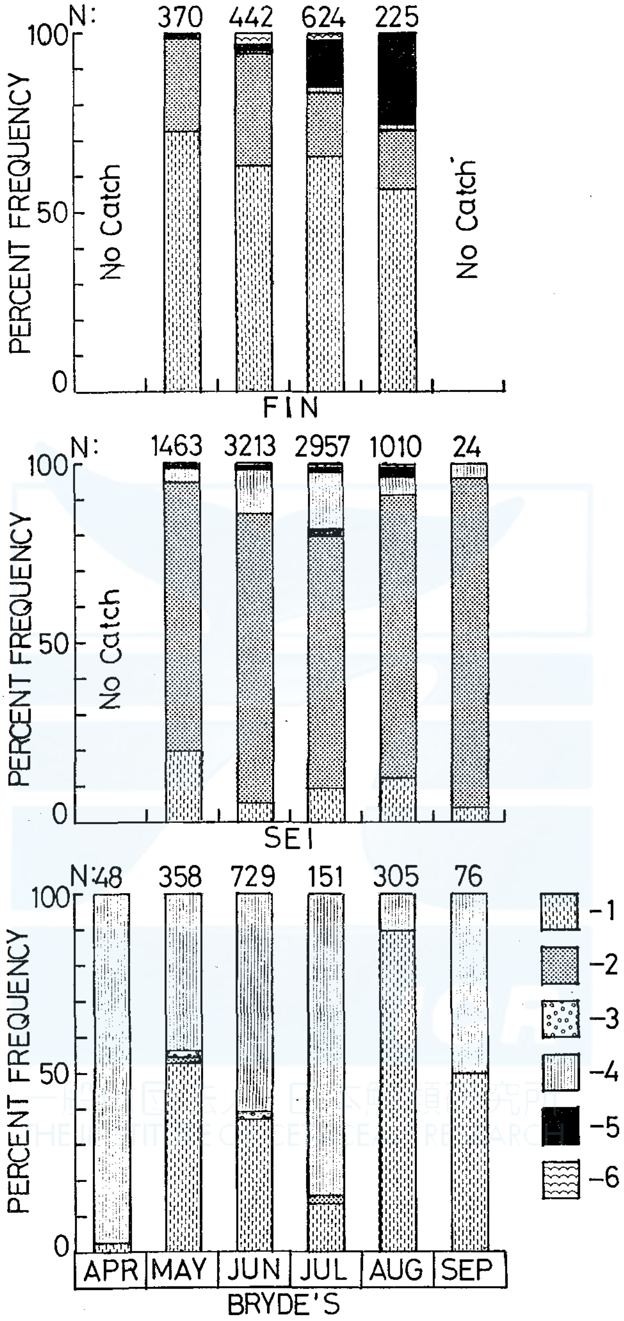


Fig. 3. Composition of stomach contents by the larger prey taxa in fin, sei and Bryde's whales caught during the seasons of 1969–1979.

1-Euphausiacea 2-Copepoda 3-Amphipoda 4-Pisces 5-Cephalopoda(decapoda) 6-Cephalopoda(octopoda)

N: Number of filled stomach

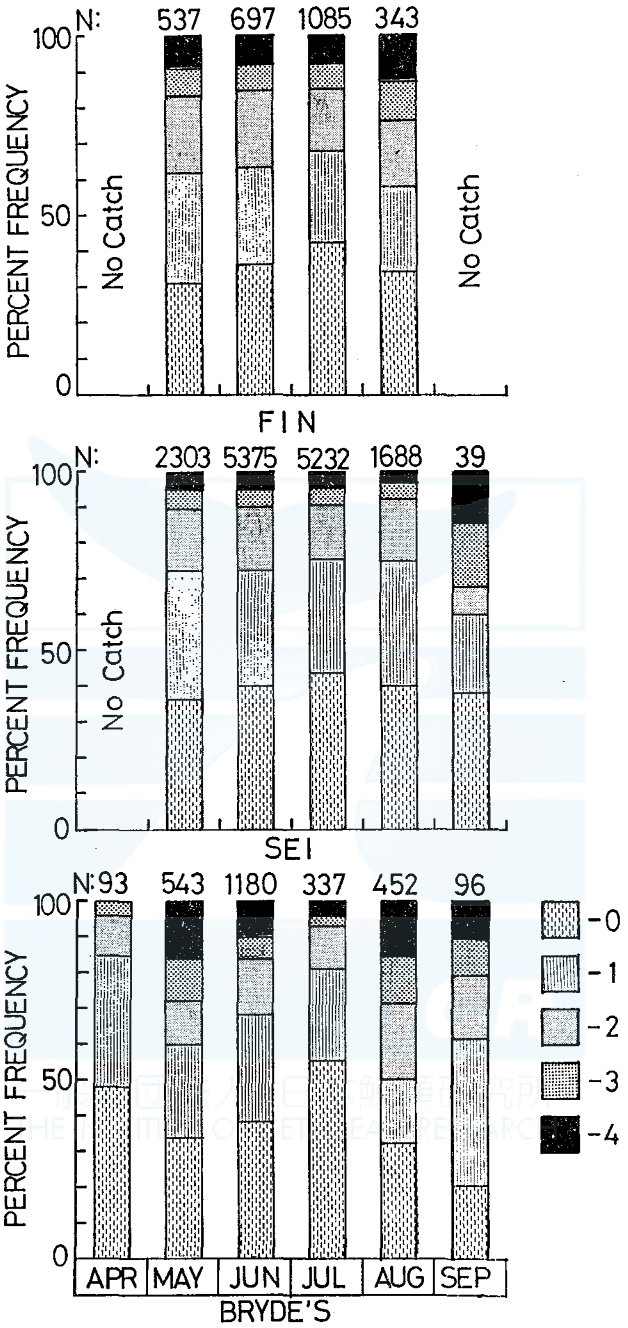


Fig. 4. Stomach fullness in fin, sei and Bryde's whales caught during the seasons of 1969–1979.

0-Empty 1-Few 2-Moderate 3-Rich 4-Full

N: Number of whales

throughout the whaling season. In contrast to this, there observed considerable seasonal changes in the major prey items in Bryde's whales, where both the Euphausiacea and Pisces comprised most important prey items. The Copepoda occurred only in 0.12% of animals with filled stomach, and this prey item along with the Amphipoda and Cephalopoda was unlikely to keep any importance in the food habits of the Bryde's whales. During April the Bryde's feed exclusively on the Pisces, but the Euphausiacea becomes very important food towards mid summer, then fish shares 50% again in September. Although there found the occurrence of ' Octopus ' as one of prey items in the catch records of whales, its occurrence seems to be doubtful since none of this prey was collected as the stomach samples. The overall figures in Fig. 3 clearly show that the major prey items of fin, sei and Bryde's whales in the North Pacific region including a part of the Bering Sea are quite different by each whale species. Dominancy of the Euphausiacea in fin, and the Copepoda in sei whales was seasonally unchanged while that of the Euphausiacea and Pisces in Bryde's whales showed distinct seasonal changes. These characteristics of possible selection in prey items by the whale species have been pointed out elsewhere (*e.g.* Nemoto, 1959; Nemoto & Kawamura, 1977, Kawamura, 1981).

Monthly changes in stomach fullness

The stomach fullness of killed animal was also available in the catch records of whales. Usually, it is recorded in the field by classifying the fullness of stomach into five different categories, being based on approximate volume of stomach contents against a whole stomach volume, *i.e.*, few (less than 25%), moderate (25–50%), rich (50–75%) and full (more than 75%). To see Fig. 4 and appended table the fullness of stomach by each volume category does not seem to change seasonally over the three whale species concerned, but there was slightly higher percent of empty stomach in July. The percentages of empty stomach throughout the whaling months in the order of fin, sei and Bryde's were 31.1–42.5%, 38.5–43.5%, and 20.8–55.2% respectively. Both fin and sei whales showed nearly constant fullness during the whole whaling season whereas the Bryde's alone showed seasonally variable figures. This is probably due to the difference in major prey items of Bryde's whales from fin and sei whales, that is, the Bryde's whales feed mainly on both the Euphausiacea and Pisces, while the latter two feed almost exclusively on one of the Euphausiacea and Copepoda.

The categories of both ' rich ' and ' full ' among filled stomachs were relatively fewer than that of ' few ' and/or ' moderate '. It can be observed over the three whale species that both ' rich ' and ' full ' stomach generally increase in their percentage figures when the ' empty ' stomach decreases, but no clear relationship was observed between the principal prey items and the stomach fullness (Figs. 3–4). An unusual high percentage of filled stomach of Bryde's whales in September came largely from the catches in both the 1974 and 1975 seasons when a vast amount of the gonostomatid fish, *Vinciguerria nimbaria* and euphausiids, *Nematoscelis difficilis* comprised major prey items.

3. Species of prey item

Prey item in general

Because of wider geographical and longer seasonal occupation of whaling ground, there occurred a considerable large number of prey species throughout this study. However, some zooplankton and fish species as whales food known from the animals caught during past seasons in the waters of higher latitudes did not occur completely throughout the present study due to very little effort to catch whales in such regions as reported by Nemoto (1957, 1959). They were: *Metridia lucens, Gnathophausia gigas*, cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), Atka mackerel (*Pleurogrammus monopterygius*) Pacific sandlance (*Ammodytes hexapterus hexapterus*), capelin (*Mallotus villosus*), rockfish (*Sebastes polyspinis*), Pacific herring (*Clupea harengus pallasi*) and sea lamprey (*Entosphenus tridentatus*) (Nemoto, 1957).

Instead of these northern fish species there found the occurrence of more variable prey items of warm temperate species in the southern whaling ground. Some of them composed major prey item but some others were considered to be occasional or even accidental occurrence. Table 2 shows all prey items found in the stomach samples taken from fin, sei and Bryde's whales during the 1969–1979 seasons. One of characteristics in the composition of prey items is an occurrence of so variable fish species as whales food, among which a mass occurrence of the gonostomatid fish, *Vinciguerria nimbaria* (see Kawamura & Hamaoka, 1981) and relative importance of the clupeid, scombrid, pentacerotid, scomberesocid, and engraulid fish species are noteworthy. Some of these characteristics found in southerly shifted whaling ground were reported earlier by Kawamura (1973), and he pointed out the ecological significance of the juvenile forms of commercially important fish species for sei whales. The mass occurrence of pelagic armorhead as prey item of sei whales was another interesting evidence that was firstly reported by Chikuni (1970). Although relatively large number of fish species were found in the present study, nine species out of 18 occurred with small number of individuals, and were considered to be an occasional or accidental occurrence.

In crustaceans there occurred four species of calanid copepods, *Calanus plumchrus, C. cristatus, C. marshallae* and *C. pacificus*, and natantia shrimp, *Sergestes similis* (see Omori *et al.*, 1972). All these five crustacean species were considered very important prey items except *C. marshallae* that was found in one stomach collected in the Alaskan shelf waters in the Bering Sea. In the Euphausiacea, however, the 14 species of euphausiids, which cover such northern temperate species as *Thysanoessa* group to the southern temperate or even subtropical species as *Euphausia similis* and *Nematoscelis difficilis* were found to be another important prey items for fin and Bryde's whales. The luxuarious species composition in euphausiids can be regarded as one of another characteristics that came from the southerly shift of whaling ground during the last decade. It was noticed that there were no other taxonomical groups to be noted as whales food, but locally limited occurrence of the larvae of a squid, *Berryteuthis anonychus*.

TABLE 2. PREY ITEMS OCCURRED IN THE STOMACHS OF FIN, SEI AND BRYDE'S WHALES

COPEPODA
  Calanus plumchrus MARUKAWA
  Calanus cristatus KRÖYER
  Calanus pacificus BRODSKY*
  Calanus marshallae FROST
EUPHAUSIACEA
  Euphausia pacifica HANSEN
  Euphausia similis G. O. SARS
  Euphausia recurva HANSEN
  Euphausia tenera HANSEN
  Euphausia gibboides ORTMANN
  Euphausia diomedeae ORTMANN
  Thysanoessa inermis (KRÖYER)
  Thysanoessa raschii (M. SARS)
  Thysanoessa longipes BRANDT
  Thysanoessa gregaria G. O. SARS
  Thysanoessa spinifera HOLMES
  Nematoscelis difficilis HANSEN
  Nematoscelis gracilis HANSEN
  Thysanopoda monacantha ORTMANN
DECAPODA
  Sergestes similis HANSEN
AMPHIPODA
  Themisto sp.
MOLLUSCA
  Berryteuthis anonychus (PEARCY & VOSS)**
  Gonatus sp.**
  Limacina helicina helicina (PHIPPS)
COELENTHELATA
    Velella sp.
PISCES
  Scomber japonicus HOUTTUYN
  Maurolicus muelleri (GMERIN)
  Tarletonbeania taylori MEAD
  Sardinops melanosticta (TEMMINCK & SCHLEGEL)
  Engraulis japonica HOUTTUYN
  Cololabis saira (BREVOORT)
  Pseudopentaceros richardsoni (SMITH)
  Exocoetus volitans LINNAEUS***
  Decapterus lajang BLEEKER
  Argyropelecus aculeatus CUVIER ET VALENCINNES****
  Myctophum asperum (RICHARDSON)****
  Diaphus bertelseni NAFPAKTITIS*****
  Polypnus matsubarai SCHLUTZ****
  Ranzania laevis makua JENKINS
  Pleurogrammus azonus JORDAN & METZ
  Gasterosteus aculeatus LINNAEUS
  Sebastes sp.
  Vinciguerria nimbaria (JORDAN & WILLIAMS)

* During discussions about this result with Dr A. Fleminger of the Scripps Institute of Oceanography, it was suggested that there must be some occurrence of *Calanus orientalis* among *C. pacificus* occurred in the northern waters.

** Identified by T. Kubodera
*** " " K. Amaoka
**** " " H. Nakaya
***** " " K. Kawaguchi

Some biological notes of the major prey species

Copepoda

C. cristatus: Occurrence of copepodid stage V (CV) alone. The body length was recorded up to 7.7 mm.

C. plumchrus: Occurrence of CV with occasional occurrence of CIV. The former was 41–50 mm with major body size of 41–43 mm, and the latter was about 30 mm.

C. pacificus: CIII-CV, and both adult male and female. Usually CV of 33–36 mm was predominated among all. The prey composition by the developmental stages was usually CV alone, but there were also the case of adult male and female with a dominancy of male, CV+male+female, CV+female, CV+male+female, and CIII+CIV+CV+female. CIII was about 25 mm.

Euphausiacea

E. pacificus: Both adult male and female of 21–22 mm with occasional occurrence of juveniles of 12–17 mm and 6.8–9.3 mm size classes. There was no clear trend in the dominancy of one of two sexes. Some male and female carried a single spermatophore.

E. similis: Adult female alone or juveniles of 17–21 mm.

T. longipes: Both male and female of ordinal and spine forms (12–13 mm) were found. Most example of prey comprised female alone, but sometimes mixture of very few number of adolescent males, or juveniles of furcilia stages. No spermatophore was observed.

T. inermis: Both male and female of ordinal and 2-spined forms. Very strongly biassed in sex composition. Usually, male or female predominates from another.

T. spinifera: Female alone, but occassional mixture with very few number of males. Body size was 23–30 mm. Two spermatophores were found in both sexes.

T. raschii: Male alone or both sexes with considerable predominancy in females.

T. gregaria: Male and female of about equal number. Sometimes juveniles of 9–10 mm were found among adult forms, but lesser extent in quantity. Some adults of both sexes carried one spermatophore.

N. difficilis: Both male and female with variable predominancy of one of two sexes.

T'poda monacantha: Recorded in one sample collected in the northern waters of Hawaii Islands in April 9, 1979.

Decapoda

S. similis: Usually matured adult forms (49–50 mm) and juveniles composed the prey. Occasionally, adolescent forms of 27–35 mm formed the principal prey composition. (see also Omori *et al.*, 1972).

Amphipoda

Only unidentifiable small hyperiids including *Themisto* sp. (4–5 mm). There was no occurrence of adult forms of any amphipod species.

Pisces

V. nimbaria: Most individual was 46–60 mm (T.L.). Details of this fish and its food habits were reported by Kawamura and Hamaoka (1981).

T. taylori: Recorded body length (T.L.) was 46–75 mm. The prey item found in 6 individuals (49–60 mm) was very small hyperiids, Ostracoda, young euphausiids and Copepoda including *Euchirella* sp.

M. muelleri: Recorded body length was 34–58 mm (T.L.) with dominancy of 42–48 mm individuals. Prey items found in 42–58 mm individuals were hyperiids, *Conchoecia* sp., *Pareuchaeta* sp., *Candacia* sp. and micro-calanoida.

G. aculeatus: 36–48 mm (T.L.)

P. azonus: 83–115 mm (T.L.).

E. japonica: 60–125 mm (T.L.), but 60–70 mm was the main body length. Prey item of this fish in June were CV and adult female of *C. pacificus*, furcilia of eupahusiids, *Oikopleura* sp. and micro-calanoida.

S. japonicus: 99–188 mm (T.L.). Very variable prey items were found; *C. pacificus* (CV), *Candacia bipinnata*, *Candacia* sp. *Pseudocalanus* sp., *Oncaea* sp., unidentifiable micro-calanoida, *Phronima pacifica*, *Salpa* sp., *Muggiaea* sp. and fish scale.

S. melanosticta: 75–106 mm (T.L.). Prey item was furcilia of euphausiids, *Clausocalanus arcuicornis*, *Corycaeus* sp. and other micro-calanoida.

C. saira: 98–133 mm (T.L.). Prey item was simply composed of CV of *C. plumchrus*.

*R. laevis makua**: 89–147 mm (T.L.)

*E. monicirrhus**: 98 mm (T.L.)

*D. lajang**: 118 mm (T.L.)

*A. aculeatus**: 56 mm (T.L.)

*D. bertelseni**: 100.5 mm (S.L.) Very rare occurrence as reported by Kawaguchi and Kawamura (1981).

Cephalopoda

B. anonychus: 10–52 mm

4. Geographical distribution of prey organisms

Copepoda

Figure 5 demonstrates the distribution of three copepod species that were preyed upon by fin, sei and Bryde's whales during the summer seasons of 1969–1977 and 1979. Since the stomach samples collected were combined together all through the fishing season and month, the geographical distribution of prey organisms by species showed somewhat complicated features. For example, northern boundaries of *Calanus pacificus* distributions in the eastern half of the North Pacific showed local irregularity, that is, there were several tongue like intrusions of distribution range and/or even an isolated patches in the region occupied by another prey species. The southern boundaries of *C. plumchrus* was the case of similar pattern to *C. pacificus*. As it was mentioned in Table 2, copepods were

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* The number of specimens was single or very few, and their occurrence in whale stomachs was considered to be accidental.

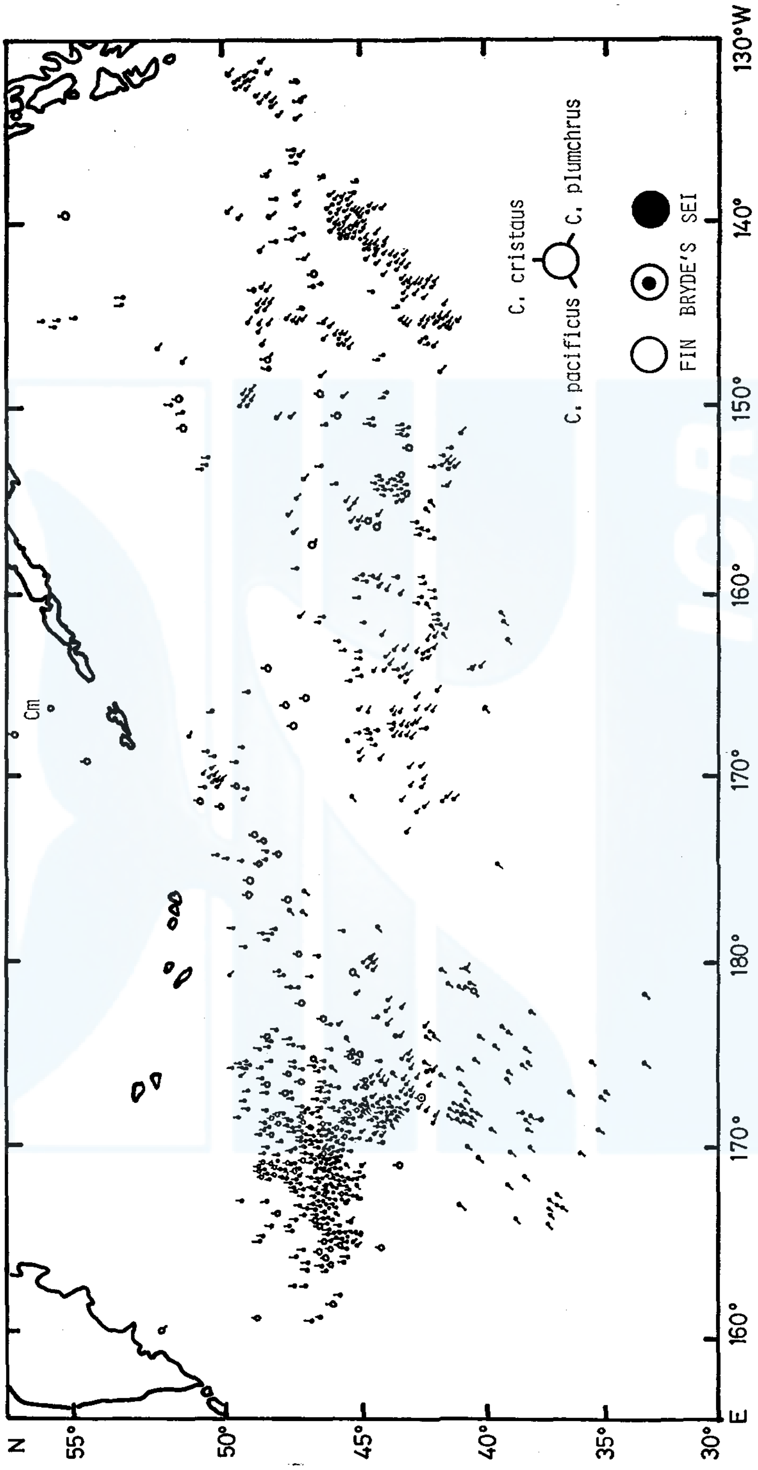


Fig. 5. Distributions of prey copepods. Cm: *Calamus marshallae*.

largely preyed upon by the sei whales, and this resulted to show an absence of any copepod food in the Bering Sea, because the sei usually does not enter this region (Nemoto, 1959). One of copepod samples collected at the slope region of the Alaskan Continental Shelf consisted of *Calanus marshallae*. This evidence is perhaps the first record of the species as whales food from this region. To see the general distribution pattern over the whole North Pacific, it is clearly observed that the major occurrence region of *Calanus pacificus* is concentrated in the western half of the subarctic North Pacific with two eastern most occurrences in 155°W. *C. cristatus*, one of another major prey item was found to be the most important food copepods both for fin and sei whales in the western half region. *C. cristatus*, however, may possibly become important prey item in the northern latitudes in the Gulf of Alaska.

C. plumchrus, on the other hand, began to occur frequently towards the eastern half region with most prominent occurrence in the pelagic region of the mid latitudes in the east of 150°W. In the central region of the North Pacific the distributions of *C. plumchrus* became very scarce or almost absent between 180° and 170°W, but this species occurred at 37°N as the southern most record throughout this study. Due to somewhat sporadic whaling effort in the Gulf of Alaska, information of this region is very limited but suggesting a possible importance of *C. cristatus* both for fin and sei whales.

In general the characteristics of copepod prey in its distributions are summerized as that *C. cristatus*+*C. pacificus* dominate in the western half but they change to *C. cristatus* alone or *C. cristatus*+*C. plumchrus* community in the middle. Towards more east, *C. cristatus* occurs again but it finally changes to *C. plumchrus*.

Euphausiacea

In contrast to copepod, the prey species of the Euphausiacea comprised at least 14 species (Fig. 6). Due to smaller number in the catch of fin whales that feed mainly on euphausiids, spots of distributions in Fig. 6 showed more dispersed occurrence than the copepod food. In the northern waters north of 50°N there occurred only fin whales except a very few sei whales, but the fin also occurred considerably in the southern waters down to 35°N in the western half region. In the shelf region of the Bering Sea there were five collections from fin whales, and *Thysanoessa rashii* was the major prey item. In the higher latitudes of the North Pacific, *T. spinifera*, *T. inermis* and *T. longipes* were found to be the most important prey items, of which *T. spinifera* showed its importance in the offshore region of British Columbia, while the latter two species frequented in the pelagic regions. In the middle latitudes between 40°–50°N, *Euphausia pacifica* was exceptionally occurred both in fin and sei whales along with two *Thysanoessa* species. Towards southern waters, however, the composition of prey became to show more complexity by the local and sporadic occurrence of many rare species such as *Thysanopoda monacantha*, *Nematoscelis difficilis*, *Euphausia gibboides*, *E. tenera*, *E. recurva* and *E. diomedeae*. Apart from fin and sei whales, the catch of Bryde's whales was clearly confined in the southwestern region down to 25°N, where *E. similis*, *N. difficilis* and *T. gregaria* were found to be most important as the prey items.

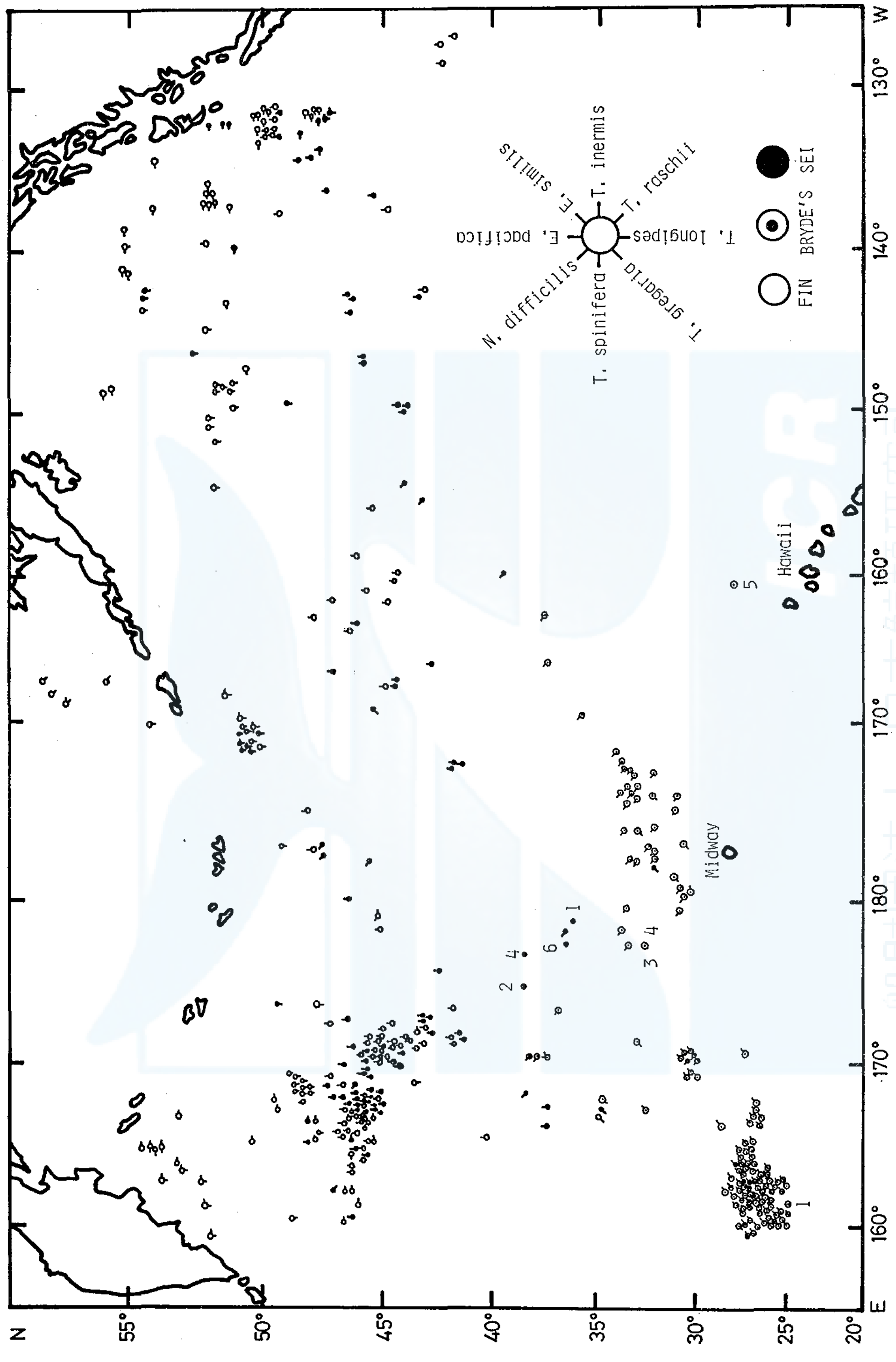


Fig. 6. Distributions of prey euphausiids.

1-*Euphausia recurva* 2-*Euphausia similis* 3-*Euphausia gibboides* 4-*Nematoscelis gracilis* 5-*Thysanopoda monacantha* 6-*Euphausia diomedeae*

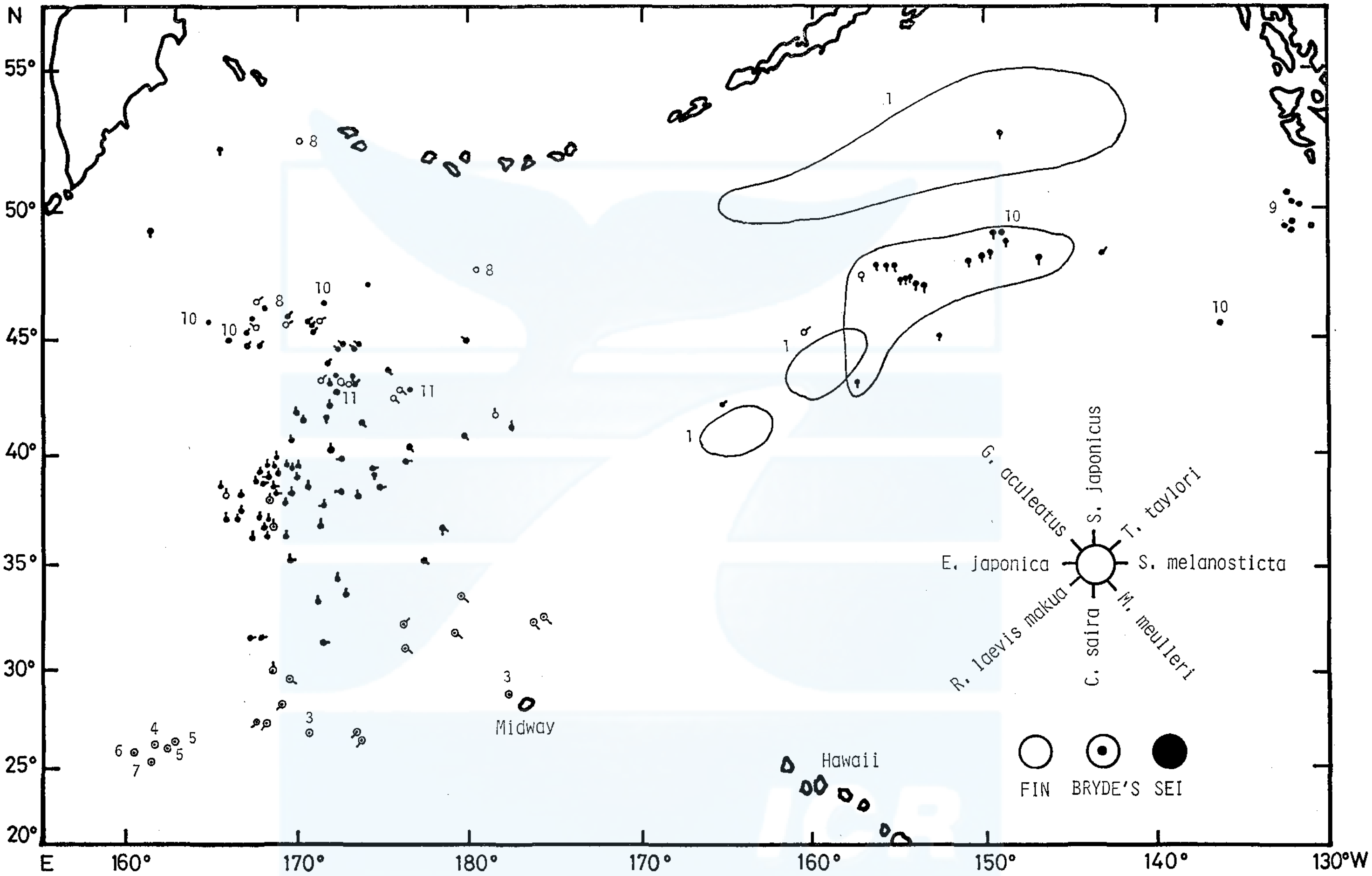


Fig. 7. Distributions of prey fish. The encircled areas show approximate range of the occurrences of pelagic armorhead and Pacific saury that found in the catch records of whales compiled by the Fisheries Agency.
1-*Pseudopentaceros richardsoni* 2-*Exocoetus volitans* 3-*Decapterus lajang* 4-*Argyropelecus aculeatus* 5-*Myctophum asperum* 6-*Diaphus bertelseni* 7-*Polypnus matsubarai* 8-*Pleurogrammus azonus* 9-*Sebastes* sp. 10-Myctophids(unidentified) 11-Trigger fish(unidentifed)

Pisces

There were very few stomach samples of fin that preyed upon fish, but both sei and Bryde's whales fed largely on such various kind of fish species as pointed out by Nemoto & Kawamura (1977). To see Fig. 7 there observed very clear difference in major prey items between western and eastern halves of the North Pacific. The fin and sei occurring in the western half region of the mid latitudes ate pre-

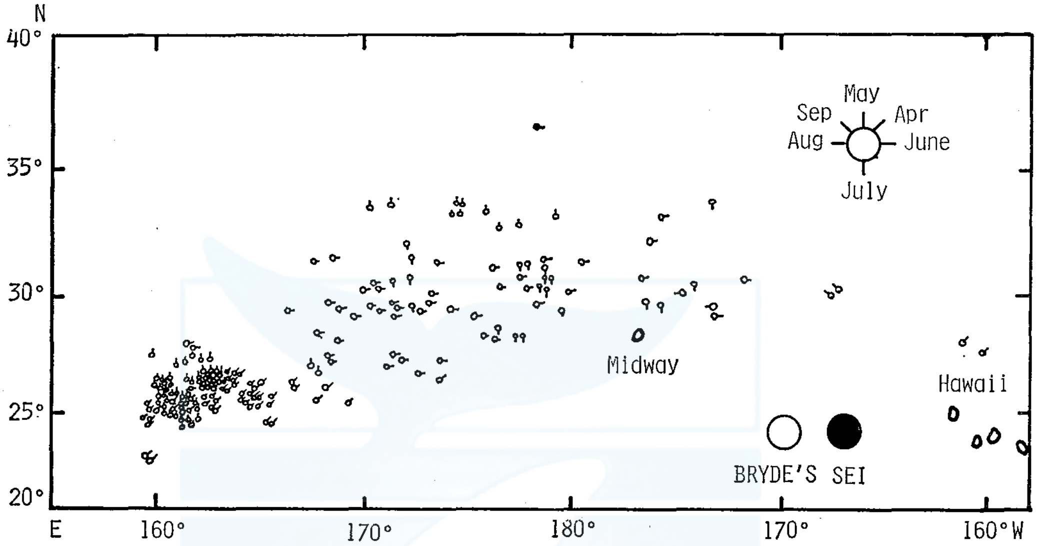


Fig. 8. Monthly distribution of *Vinciguerria nimbaria* eaten by the sei and Bryde's whales.

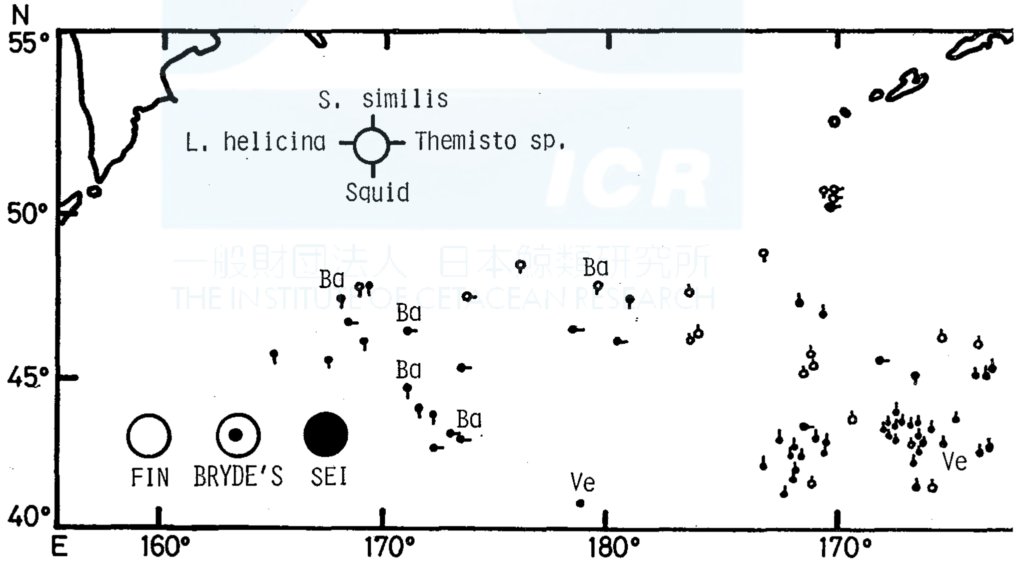


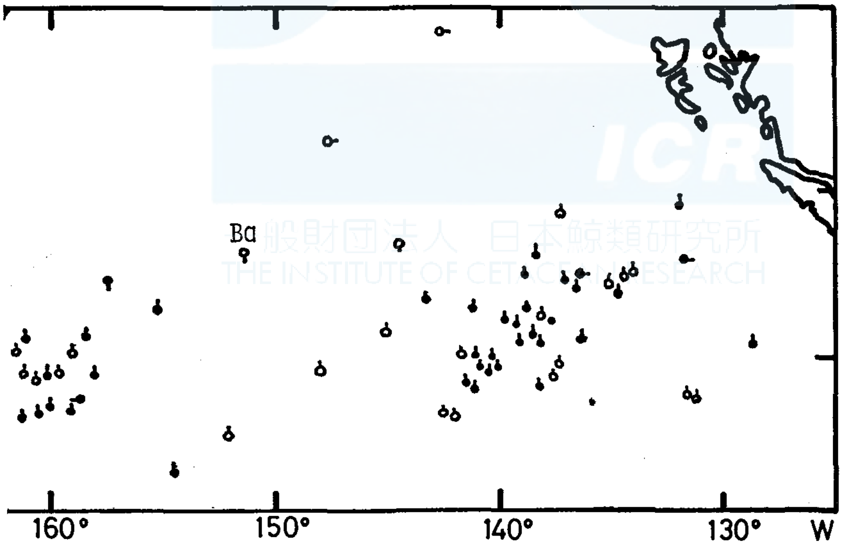
Fig. 9. Distribution of shrimp, *Sergestes*
Ba: *Berryteuthis*

dominantly on mackerel (*S. japonicus*) among all and both anchovy (*E. japonica*) and Japanese sardine (*S. melanosticta*) came to the next. Towards more northern waters, however, the major prey item changed to a myctophid fish (*T. taylori*) and three spine stickleback (*G. aculeatus*) while gonostomatid fish (*V. nimbaria*), *M. muelleri*, *R. laevis makua* and myctophids (*M. asperum* and *Diaphus bertelseni*) may become important prey for the Bryde's whales (see also Fig. 8, and Kawamura & Hamaoka, 1981). Among various species of fish prey *V. nimbaria* is considered most important item for the Bryde's whales occurring in the subtropical regions of the North Pacific during April through September (Fig. 8).

In the eastern North Pacific the collection of stomach samples was fewer than the western region due to difficulty in collecting and preserving such large-sized fish prey as the pelagic armorhead (*P. richardsoni*). Being based on the catch records of whales by the Fisheries Agency, it was proved that the sei eat mainly Pacific saury (*C. saira*) during July to August in the pelagic waters of the eastern half region. One of another important fish species was pelagic armorhead in the Gulf of Alaska region. Because of its large-sized body length and easiness in identification in the field, no *P. richardsoni* was collected as stomach samples, but their occurrence in the catch records of whales was indicated by the encircles in Fig. 7. Closer to waters off Vancouver Island, there were another possible important prey item, the larval forms of rock fish (*Sebastes* sp.).

Others

Among several other prey items the sergestid shrimp, *S. similis* was most important prey both for fin and sei whales in the midst towards eastern region of the northern latitudes between 40°–50°N as it was reported previously (Omori *et al.*, 1972). To see Fig. 9 along with Figs 5–7 it can be observed that *S. similis* was



similis and other prey species.
anonychus, Ve: *Vellela*

one of very few prey items that was available in the midst of the northern North Pacific. Towards west, however, larval forms of squid (*B. anonychus* and *Gonatus* sp.) and hyperiid amphipods were considered to be moderately important. However, amphipods represented largely by *Themisto* sp. never showed such importance of appreciable extent as the case known in the southern counter part, *Parathemisto gaudichaudii* (Kawamura, 1970, 1974).

5. Species composition of stomach contents

Fin whales

It was indicated in Table 3 that the euphausiids were relatively more important than the copepods as food of fin whales. However, the detailed composition of prey species being based on the collected material shows that very limited number of euphausiid species actually comprise a major food of fin whales. The matrix of prey composition clearly shows a predominant occurrence of three euphausiid species, *i.e.*, *E. pacifica*, *T. longipes*, *T. spinifera*, and *T. inermis* (Table 3). Although there were several examples of mixture with other prey species in both the case of *E. pacifica* and *T. inermis*, most stomach contents were found to be monospecific in the composition.

In copepods, *C. cristatus* was a major prey item, and this species along with sergestid shrimp, *S. similis* formed additional important prey items. The very clear monospecific composition in *T. spinifera* was noteworthy, while there were many examples of mixed composition in *T. inermis*. The major prey species that composed a stomach contents was usually monospecific. In three examples, however, there found mixed compositon of food with three species such as *C. cristatus*+*T. longipes*+*T. spinifera*, *T. inermis*+*N. difficilis*+*C. pacificus* and *T. inermis*+*T. longipes*+*C. cristatus*. There were only four stomachs that were filled with fish. Although there occurred a considerable number of prey species on the whole, it can be said that the fin whales in the North Pacific region mainly live on by eating six species of crustaceans where euphausiids account for a largest part of the prey composition.

Sei whales

In contrast to somewhat simple or poor composition of prey species in fin whales, a total of 27 prey items were found to be important in sei whales. As mentioned before, copepod food was found in quite large part of the sei whale stomachs, and *C. cristatus*, *C. plumchrus* and *C. pacificus* accounted for more than 79% among all stomachs examined (Table 4). One of the characteristics in the copepod food was a frequent occurrence of mixed composition with different prey items such as with euphausiids particularly the case in *C. plumchrus*. To see the frequency in the number of stomachs, relative importance of euphausiid food reduced largely in sei whales except the case in *E. pacifica*, but sergestid shrimp, *S. similis* that was a very important prey item in fin whales also showed considerable importance again in sei whales. One of characteristic compositions was the relative importance of commercially important fish species as a major prey com-

TABLE 3. COMPOSITION OF THE STOMACH CONTENTS IN FIN WHALES (NUMBER OF STOMACHS)

Major components	Minor components																							Total	Percent
	C. cristatus	*C. plumchrus*	*C. marshallae*	*C. pacificus*	*E. pacifica*	*T. longipes*	*T. spinifera*	*T. inermis*	*T. raschii*	*T. gregaria*	*N. difficilis*	*S. similis*	*V. nimbaria*	*S. japonicus*	*G. aculeatus*	*P. azomus*	*T. taylori*	Squid	*C. pacificus* + *N. difficilis*	*C. cristatus* + *T. raschii*	*C. cristatus* + *T. longipes*	*T. longipes* + *T. spinifera*	*T. inermis* + *T. spinifera*		
C. cristatus	52	1			3	5										1	1	3				1		67	25.9
C. plumchrus	1	7																						8	3.08
C. marshallae			1																					1	0.39
E. pacifica	8				40		1					1					2							52	20.07
T. longipes	7					19		2															1	29	11.20
T. spinifera							29																	29	11.20
T. inermis	1					4	2	18											1	1	1			28	10.81
T. raschii	1			1					1															3	1.16
T. gregaria										1			1											2	0.77
N. difficilis											1													1	0.39
S. similis					2							25					2							29	11.20
M. muelleri													1											1	0.39
S. japonicus														2										2	0.77
G. aculeatus															1									1	0.39
Squid																		5						5	1.93

TABLE 4. COMPOSITION OF THE STOMACH

Major components	Minor *C. cristatus*	*C. plumchrus*	*C. pacificus*	*E. pacifica*	*E. diomedeae*	*E. recurva*	*E. tenera*	*T. longipes*	*T. spinifera*	*T. inermis*	*T. gregaria*	*N. difficilis*	*N. glacilis*	*S. similis*	*G. aculeatus*	*P. azonus*	*C. saira*	*S. japonicus*	*S. melanosticta*	*E. japonica*	*Sebastes* sp.	*M. muelleri*
C. cristatus	398	3		9						1		1		1								
C. plumchrus	10	270	3	5				3		1				11	3		1				1	
C. pacificus		3	89	2		1				2	1	4										
E. pacifica	5	5	4	37					1									1				
E. diomedeae					1																	
E. recurva						1																
E. tenera							1															
T. longipes								4		3												
T. spinifera									7													
T. inermis										1												
T. gregaria											2											
N. difficilis												2										
N. glacilis													1									
S. similis		4												48								
G. aculeatus															2							
P. azonus																1						
C. saira																	5					
S. japonicus		1	2															33	2	1		
S. melanosticta																			5			
E. japonica																				3		
Sebastes sp.																	1				5	
M. muelleri																						5
T. taylori																						
myctophido																						
P. richardsoni (?)																						
Squid				1																		
L. helicina																						

* Since the occurrence of the pelagic armorhead, *P. richardsoni* was based on the catch records of whales excluded from this table.

ponent. They were, Japanese mackerel, *Sebastes* sp., Pacific saury, Japanese sardine, Japanese anchovy, and lanternfish, *M. muelleri*. These greater variety of prey composition in sei whales is the reflexion of larger geographical occupation of whaling ground along with longer duration in sei whale catches. There were several records of mixed stomachs composed of more than three prey items; they were, *E. pacifica*+*C. cristatus*+*T. taylori*, *E. pacifica*+*S. similis*+*Vellela* sp., *T. longipes*+*C. plumchrus*+*T. inermis*, *T. longipes*+*T. inermis*+*T. spinifera*, *E. pacifica*+*C. pacificus*+*C. cristatus*, *C. plumchrus*+*C. pacificus*+*C. cristatus*, and *S. similis*+*C. plumchrus*+*C. cristatus*. Although prey composition showed greater variety in sei whales, but it can be said that the sei in general feeds largely on three species of copepods, one species of euphausiids, sergestid shrimp, and scombrid fish.

CONTENTS IN SEI WHALES* (NUMBER OF STOMACHS)

components

T. taylori	myctophids	*P. richardsoni* (?)	Squid	*L. helicina*	hyperiids	*C. pacificus* + *C. plumchrus*	*C. pacificus* + *C. cristatus*	*C. plumchrus* + *C. cristatus*	*C. cristatus* + *T. taylori*	*T. inermis* + *T. spinifera*	*C. plumchrus* + *T. inermis*	*S. similis* + myctophids	*T. taylori* + myctophids	*S. similis* + *Velella* sp.	*C. saira* + squid	*Velella* sp.	Total	Percent
6	2		5		5								1				427	39.8
1	1		2				1										318	29.7
																1	103	9.6
3						1			1			1		1			60	5.6
																	1	0.09
																	1	0.09
																	1	0.09
					2					1	1						12	1.1
																	7	0.6
																	1	0.09
																	2	0.18
																	2	0.18
																	1	0.09
								1									53	4.9
																	2	0.18
																	1	0.09
																	5	0.47
																	39	3.6
																	5	0.47
																	3	0.28
																	6	0.56
															1		6	0.56
1																	1	0.09
	1																1	0.09
		1															1	0.09
3			8														12	1.11
				1													1	0.09

alone, the actual composition of stomach contents was unknown, and consequently this fish species was

Bryde's whales

Due to different geographical occupation of whaling ground in the case of the Bryde's whales, the composition of major prey item for this whale species was far different from that in fin and sei whales (Table 5). Most important prey item was a gonostomatid fish, *V. nimbaria* which accounted for more than 55% among all instance, and *E. similis* came to the next (25.2%). *N. difficilis* was also important member of the prey composition (10.8%). Except a single record of multispecific prey composition (*V. nimbaria*+*E. gibboides*+*N. gracilis*), the food of Bryde's whales can be considered quite monospecific with stronger trends of eating small and gregarious fish species in the pelagic waters.

TABLE 5. COMPOSITION OF THE STOMACH CONTENTS IN BRYDE'S WHALES (NUMBER OF STOMACHS)

	Minor components																						
Major components	*C. cristatus*	*E. similis*	*E. recurva*	*T. gregaria*	*T. inermis*	*N. difficilis*	*E. gibboides* + *N. glacilis*	*S. similis*	*V. nimbaria*	*M. muelleri*	*S. japonicus*	*S. melanosticta*	*T. taylori*	*L. laevis makua*	*E. volitans*	*D. lajang*	*P. matsubarai*	*A. aculeatus*	*M. asperum*	*D. bertelseni*	Fish bones	Total	Percent
C. cristatus	1																					1	0.03
E. pacifica		1																				1	0.03
E. similis		80							2										2			84	25.2
E. recurva			1																			1	0.03
T. gregaria				5																		5	1.5
T. inermis					1																	1	0.03
Thysanoessa sp.		1																				1	0.03
N. difficilis						35			1													36	10.8
T'da monacantha									1													1	0.03
S. similis								1														1	0.03
V. nimbaria		3		1			1		175			1					1	1		1		184	55.1
M. muelleri									1	3												4	1.2
S. japonicus											4											4	1.2
S. melanosticta												1										1	0.03
T. taylori													1									1	0.03
L. laevis makua									1					4								5	1.5
E. volitans															1							1	0.03
D. lajang																1						1	0.03
Fish bones																					1	1	0.03
																						334	

DISCUSSION

The whaling ground during the seasons of 1969–1979 was occupied in the more southern sea regions than that occupied during the 1950's to early 1960's. This geographical difference along with somewhat seasonally longer whaling operation resulted to show a wide ranged variety in the taxon of prey items, particularly in species composition of the Euphausiacea and Pisces. The conditions of surface sea temperature in general over the whaling ground is considered to be somewhere between about 26°C and 10°C in August (Sverdrup *et al.* 1942), and from the zoogeographical point of view in zooplankton communities, the whaling ground of under consideration includes the region of boreal complex, zone of mixing and even tropical complex (Zenkevitch, 1963).

The stomach condition of whales in general revealed that about 60% or more stomachs of fin, sei and Bryde's were filled with variable amount of food without showing any notable seasonal changes in the percent figures of filled stomach. According to Nemoto (1957), 52% of fin and 44% of sei caught in the northern North Pacific during the 1952–1956 seasons were found to be filled stomachs. These percentages seem to be considerably lower than the above mentioned figures (ca.

60%) found in this study. During the years of 1952–1971 when the whaling ground began to expand southwards, the corresponding percentages for fin and sei were 60% and 55.5% respectively (Nemoto & Kawamura, 1977), while it was 94% and 81% respectively in the Kurile region (after Sleptsov, 1955). These figures seem to be high enough when it is compared with that found in the present study and also in the Antarctic feeding grounds (Kawamura, 1978). Usually the distribution of zooplankton biomass in the boreal region of the northwestern North Pacific decreases to about 1/5 or 20% towards the tropical region (Zenkevitch, 1963). According to Odate (1966), the wet zooplankton biomass in the south of 40°N of the western North Pacific was 20–30 gr/1000 m^3 while it was 200–400 gr/1000 m^3 in the boreal regions of the North Pacific and Bering Sea. Notwithstanding these facts the comparisons mentioned above strongly suggest that the boreal or subarctic North Pacific to the subtropical or even tropical regions may provide very important feeding ground for the baleen whales as well as the northern North Pacific region. One of possible, but important explanations for this is the local and extremely biassed patchy distributions of prey species (e.g. Brodie et al. 1978; Kawamura, 1979). The occurrence of fish prey in the southwestern North Pacific may come from the scarceness of patch-forming zooplankton species in this region since those fish species can eat and survive on such variable zoo plankton species as studied in *Vinciguerria nimbaria* (Kawamura & Hamaoka, 1981).

As it was shown in Fig. 4 the stomach fullness by the quantity of contents did not change seasonally in its general pattern over the three whale species. However, stomachs combined both ‘ full ’ and ‘ rich ’ showed relatively higher figures in fin and Bryde’s than sei whales. This evidence seems to be related to the difference of major prey items between whale species as shown in Fig. 3, where it was suggested that the larger the size of prey organisms, the larger percent of well filled stomachs were expected (Nemoto, 1963). Similarly, the smaller percent figures of ‘ full ’ and ‘ rich ’ stomach in sei whales that feeds mainly on copepods are resulted from more smaller size of prey, since the biomass of prey organisms may become smaller in accordance with the reduction of their body size (Nemoto & Kawamura, 1977). The prey items which occurred in boreal regions of the North Pacific were agreed on the whole to those known previously in the pelagic waters (e.g. Nemoto, 1959), and distributions of *Thysanoessa* species and copepods were agreed well to that found in the Olyutorsky and Commandorsky regions (Ponomareva, 1949). However, when each prey item is compared with the case found in marginal seas such as the Kuril or Bering Sea regions, there were considerable difference in the composition of prey fish species. As mentioned before, there occurred no common fish species between the results from the Bering Sea and the present study (see Kawamura, 1980, Table 17), while only two species, Pacific saury and anchovy were common with the Kurile region (Betesheva, 1954, 1955). In the Far Eastern Seas, of 14 prey fish species only Pacific sardine and Pacific saury were common with the present study (Sleptsov, 1955; Tomilin, 1967). These characteristics in the prey composition suggest that the feeding conditions of whales in the North Pacific may differ considerably from place to place especially in the marginal sea regions, but they also differ in several prey taxa even in the pelagic waters.

Distributions of each prey species showed very interesting results (Figs. 5–9). Since stomach samples obtained during 1969–1977 and 1979 seasons were plotted altogether simply by separating each major prey species, the number of plots do not agree with the number of stomachs sampled because there were many examples of mixed stomach composition of two or more species. Figures 5–9 however, demonstrate a zoogeographical pattern of ditribution of each prey item during April to September, where variable density of plot distribution suggests relative abundance of whale distribution by sea regions. To see through Figs. 5–9 the overall distribution pattern of each prey species agrees well with the generally known zoogeography of planktonic animals such as the distribution boundary of *Calanus* species (e.g. Minoda, 1958; Omori, 1965 Frost, 1974), euphausiids (e.g. Boden *et al.*, 1955; Mauchline and Fisher, 1969) and lanternfishes (e.g. Wisner, 1974; Gjosaeter and Kawaguchi, 1980). However, important evidence is that the plotted region indicates more possible area of frequent occurrence of plankton aggregations that are preferable food condition for baleen whales, and a vacancy of the plots never means negative distribution of each corresponding prey species. In this connection, the lack of amphipods as whales food in the North Pacific must be noteworthy, while *Parathemisto gaudichaudii* constitutes important prey item in the southern sei whales (Kawamura, 1974). Actually several number of *Themisto* species are known to form dense swarms, but they were not eaten by the whales.

The characteristic of the stomach contents as shown in Tables 3–5 is such an extremely predominant occurrence of monospecific composition over the stomachs of three whale species as it was reported by Kawamura (1974, 1980) for the southern sei and Bryde's whales. Although data on the freshness of stomach contents by each prey species were not shown in this study, it was observed that the freshness of prey species which occurred together in a stomach such as the case of *C. plumchrus* and *C. pacificus*, was different from one to another. Similarly the different freshness can be observed in many stomachs when their contents were composed of more than two prey species. As it was discussed on the mixed prey with *C. cristatus* and *C. plumchrus* (Nemoto, 1963), these phenomenon was perhaps caused by the time-lag in picking up each prey species due to horizontal and vertical differences in the distribution of prey organisms. Occurrence of the Siphonophora, *Velella* sp., however, indicates that the whales often feed in the very surface waters. The plot in Figs. 5–9 consequently, suggests that how frequently each prey organism occurs patchily in the region by forming dense monospecific swarms, aggregations, and/or schools. After analysing a small scale of distributions of whales and their stomach contents observed within a short enough period, Kawamura (1978) estimated a spacial scale of patchiness of prey species as less than 5–6 km as an estimated diameter of patches in *C. cristatus*, *C. plumchrus* and *C. pacificus* complex whereas it was slightly larger in *E. pacifica*, *T. inermis*, *T. raschii*, *T. longipes*, *T. spinifera* and possibly in *N. difficilis*.

To conclude the geographical distributions of prey species that form dense swarms or aggregations, it can be summerized that the North Pacific fin, sei and

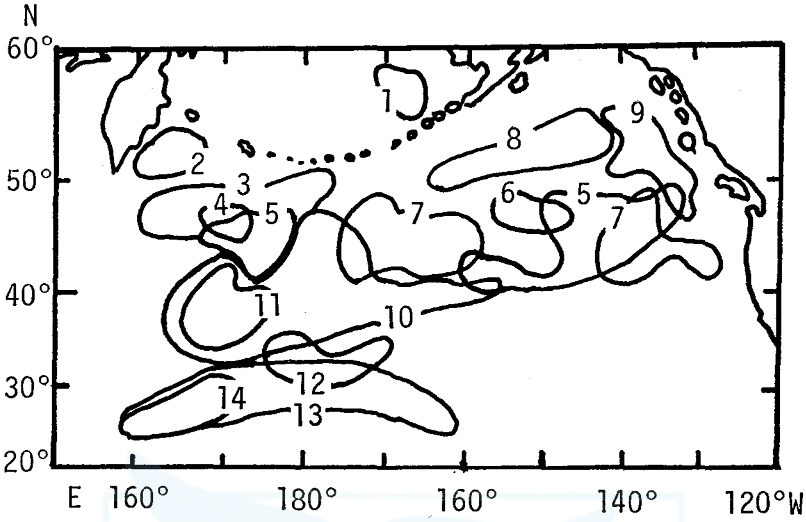


Fig. 10. Approximate geographical occupations of the principal prey species. 1-*Calanus marshallae* 2-*Thysanoessa inermis / T. longipes* 3-*Calanus cristatus* 4-*Tarletonbeania taylori* 5-*Calanus plumchrus* 6-*Cololabis saira* 7-*Sergestes similis* 8-*Pseudopentaceros richardsoni* 9-*Thysanoessa spinifera* 10-*Euphausia pacifica* 11-*Calanus pacificus* 12-*Nematoscelis difficilis* 13-*Vinciguerria nimbaria* 14-*Euphausia similis*

Bryde's whales share a possible prey species each other by selecting euphausiids, copepods and fish communities respectively. Among so many variable prey items, the distribution ranges of major prey species over the whole North Pacific can be demonstrated in schema (Fig. 10). Although *C. cristatus*, *C. plumchrus* and *C. pacificus* are known to distribute widely over the whole North Pacific, the main occurrence of their patchy swarms show different geographical distributions, i.e., both *C. cristatus* and *C. pacificus* predominantly form their patches more frequently or intensively in the northwestern to western North Pacific whereas *C. plumchrus* does in the eastern North Pacific. Although physical and chemical conditions of the sea surface in the northern North Pacific shows very homogeneous features from the west to the east in general, the distributions of many prey species on the whole suggest that there seems to exist geographically discontinuous region somewehere between 160°–170°W where the variety of prey species is very poor.

ACKNOWLEDGMENTS

I am very grateful to Dr. H. Omura and his staff of the Whales Research Institute for their support and encouragement throughout my 10-year sampling scheme. Thanks are also due to Dr. S. Ohsumi and his colleagues of the Far Seas Fisheries Research Laboratory for their welltimed supervision and advice through which the collection of stomach samples was implemented. Data in the Catch Records of Whales by the Fisheries Agency become also available by their courtesy, and all these support that facilitated the present study is greatly acknowledged. I am grateful, as well, to all personnel who belonged to whaling division of the Nippon Suisan K.K., Taiyo Gyogyo K.K., K.K. Kyokuyo and Nippon Kyodo Hogei K.K. for their long-term cooperation in collecting a large part of the stomach materials during the seasons of 1969–1979.

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APPENDIX I. STOMACH CONDITIONS OF FIN, SEI AND BRYDE'S WHALES CATCH RECORDS OF WHALES COMPILED BY THE FAR SEAS

		Catch	Food item				
			Euphausiacea	Copepoda	Amphipoda	Pisces	Squid
Fin	May	537	268 (72.4)	101 (27.3)	—	—	1 (0.3)
	June	697	281 (63.6)	139 (31.4)	—	6 (1.4)	1 (0.2)
	July	1,085	410 (65.7)	115 (18.4)	—	5 (0.8)	92 (14.7)
	August	343	128 (56.9)	35 (15.6)	—	1 (0.4)	61 (27.1)
	Total	2,662	1,080	388	—	12	154
	% to total		65.4	23.5	—	0.7	9.32
Sei	May	2,303	293 (20.0)	1,092 (74.6)	—	69 (4.7)	9 (0.6)
	June	5,375	169 (5.3)	2,574 (80.1)	—	456 (14.2)	8 (0.3)
	July	5,232	278 (9.4)	2,080 (70.3)	2 (0.07)	523 (17.7)	65 (2.2)
	August	1,688	123 (12.2)	800 (79.2)	—	48 (4.8)	38 (3.8)
	September	39	1 (4.2)	22 (91.7)	—	1 (4.2)	—
	Total	14,637	864	6,568	—	1,097	120
	% to total		9.97	75.8	—	12.66	1.38
Bryde's	April	93	1 (2.1)	—	—	47 (97.9)	—
	May	543	191 (53.4)	1 (0.3)	1 (0.3)	165 (46.1)	—
	June	1,180	274 (37.6)	—	1 (0.3)	454 (62.3)	—
	July	337	22 (14.6)	1 (0.7)	—	128 (84.8)	—
	August	452	274 (89.8)	—	—	31 (10.2)	—
	September	96	38 (50.0)	—	—	38 (50.0)	—
	Total	2,703*	800	2	2	863	—
	% to total		47.99	0.12	0.12	51.76	—

* Two Bryde's whales that were unknown their catch month were excluded

CAUGHT DURING THE SEASONS OF 1969–1979. (CONSTRUCTED USING FISHERIES RESEARCH LABORATORY OF THE FISHERIES AGENCY)

			Stomach fullness				
Octopus	Total of filled stomach	% of filled stomach to total	Few	Moderate	Rich	Full	Empty
—	370	68.90	167 (31.1)	115 (21.4)	39 (7.3)	49 (9.1)	167 (31.1)
15 (3.4)	442	63.41	188 (27.0)	146 (20.9)	55 (7.9)	53 (7.6)	255 (36.6)
2 (0.3)	624	57.51	265 (24.4)	190 (17.5)	84 (7.7)	85 (7.8)	461 (42.5)
—	225	65.60	83 (24.2)	64 (18.7)	35(10.2)	43(12.5)	118 (34.4)
17	1,661	62.39	703 (26.4)	515 (19.3)	213 (8.0)	230 (8.6)	1,001 (37.6)
1.02	62.39						
—	1,463	63.53	824 (35.8)	393 (17.1)	128 (5.6)	118 (5.1)	840 (36.5)
6 (0.2)	3,213	59.78	1,731 (32.2)	974 (18.1)	265 (4.9)	243 (4.5)	2,162 (40.2)
9 (0.3)	2,957	56.52	1,625 (31.1)	834 (15.9)	254 (4.9)	244 (4.7)	2,275 (43.5)
1 (0.1)	1,010	59.83	587 (34.8)	297 (17.6)	72 (4.3)	54 (3.2)	678 (40.2)
—	24	61.54	8 (20.5)	3 (7.7)	7(17.9)	6(15.4)	15 (38.5)
16	8,667	59.21	4,775 (32.6)	2,501 (17.1)	726 (4.9)	665 (4.5)	5,970 (40.8)
0.18	59.21						
—	48	51.61	34 (36.6)	10 (10.8)	4 (4.3)	—	45 (48.4)
—	358	65.93	141 (26.0)	66 (12.2)	66(12.2)	85 (15.7)	185 (34.1)
—	729	61.78	361 (30.6)	181 (15.3)	68 (5.8)	119 (10.1)	451 (38.2)
—	151	44.81	88 (26.1)	43 (12.8)	7 (2.1)	13 (3.9)	186 (55.2)
—	305	67.48	80 (17.7)	99 (21.9)	57(12.6)	69 (15.3)	147 (32.5)
—	76	79.17	39 (40.6)	17 (17.7)	10(10.4)	10 (10.4)	20 (20.8)
—	1,667	61.67	743 (27.5)	416 (15.4)	212 (7.8)	296 (11.0)	1,034 (38.3)
—							


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CLASSIFICATION AND PHYLOGENY OF THE SUPERFAMILY PLATANISTOIDEA, WITH NOTES ON EVIDENCE OF THE MONOPHYLY OF THE CETACEA

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ABSTRACT

Important basis provided by the morphological studies on the skeleton, digestive and respiratory organs of the Platanistoidea have further proved that this group can be divided into four families. Considering the characteristics of the skeleton and other morphological features, the phylogenetic relationships among the four families are discussed. The systematic sequence of the families should be Iniidae, Lipotidae, Pontoporiidae and Platanistidae. Some characters noticed in the investigations are evidence in favour of the monophyly of the cetacea.

INTRODUCTION

The superfamily Platanistoidea possesses a number of primitive characters similar to the Oligocene-Miocene Squalodontoidea, some characters similar to the primitive forms of the higher cetacean families and some specialized structures. Two different opinions advocating divide or combination concerning the classification of the Platanistoidea have been held over a long period of time.

In the middle of the 19th century, Gray (1863, 1866) first divided the Platanistoid dolphins into groups. In his catalogue, *Platanista* constitutes the fourth family of Cetacea—Platanistidae; *Inia* constitutes the fifth family—Iniidae; *Pontoporia* was placed into the sixth family—Delphinidae. Flower (1869) gave another opinion before long, put together the above mentioned three genera into the Platanistidae. He made *Platanista* and *Inia* belong to the subfamily Platanistinae and Iniinae respectively and placed *Pontoporia* into the subfamily Iniinae provisionally.

At the beginning of the 20th century, Miller (1918) named *Lipotes*, the fourth genus of the modern Platanistoids, and referred it to the Iniidae. In another paper published in 1923, he followed Gray in recognizing Platanistidae and Iniidae and still considering *Pontoporia* a member of the Delphinidae. Nevertheless, he has placed *Pontoporia* into the subfamily Stenodelphininae to differ from other groups of the Delphinidae. Kellogg (1928) held the same opinion as Miller did, whereas Winge (1918) maintained to put *Platanista, Inia, Pontoporia* and the newly discovered *Lipotes* together into the Platanistidae. In this period, argument concerning divide or combination of the Platanistoids was continued and different opinion was set in whether *Pontoporia* belongs to Platanistoids.

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In 1936 Slijper adopted the concept in favour of combination and placed all the living genera of Platanistoids into the family Platanistidae. Following Slijper's opinion, Simpson (1945) recognized Platanistidae but retained three subfamilies and, moreover, established superfamily Platanistoidea in the higher category. This taxonomical system has been accepted by most cetologists ever since. Slijper's system has been adopted by Norman and Fraser (1948), Slijper (1962), Nishiwaki (1965, 1972), Tomilin (1974), Matthews (1978), Lockley (1979), and others. Simpson's system has been followed by Fraser and Purves (1960), Carvalho (1961), Marcuzzi and Pilleri (1971), Brownell and Herald (1972), Mead (1975), Rice (1977), and others. The single family system was also adopted by Hershkovitz (1966), but a new name Susuidae which he proposed has not been accepted by other cetologists. Authors studying fossil Platanistoids such as Kellogg (1944, 1955), Rensberger (1969) have continued to recognize the iniid as a distinct family. Gaskin (1976) who is studying modern cetaceans has followed their opinion.

The investigations of Platanistoid dolphins have gained great attention again since 1960s. Kasuya (1973) recognized the Platanistidae, Iniidae and Pontoporiidae of the Platanistoidea on the basis of the study of the tympano-periotic bone. In a paper on the study of *Lipotes*, van Bree and Purves (1975) put it in the Iniidae. Pilleri et al. (1976) proposed to separate *Inia*, *Lipotes* and *Pontoporia* from the Platanistidae and put them in the Iniidae. The coexistence of the one family system (Slijper, 1936; Simpson, 1945) with the two and three family systems (Pilleri *et al.*, 1976; Kasuya, 1973) occured. In 1978, Zhou *et al.* proved that *Lipotes* is not closely related to *Inia* and the differences between the two genera exceed those between the Delphinidae and Phocoenidae, and placed *Lipotes* into a separate family—Lipotidae. After this, Pilleri and Gihr (1980) have turned to use a four family system, but no argument has been given.

The present paper summarizes the important basis provided by the morphological studies of the skeleton, digestive and respiratory organs of *Inia* (Flower, 1869; Mead, 1975; Lönnberg, 1928; Pilleri and Gihr, 1976c, 1977; Yamasaki and Kamiya, 1981; Zhou, Li and Pilleri, 1982), *Lipotes* (Miller, 1918; Chen and Chen, 1975; Zhou *et al.*, 1978, 1979a, b; Chen *et al.*, 1980; Liu and Lin, 1980; Zhou and Li, 1981), *Pontoporia* (Burmeister, 1867; Flower, 1869; Carvalho, 1961; Schenkkan, 1972; Yamasaki *et al.*, 1974, 1975, 1977; Mead, 1975; Pilleri and Gihr, 1976b; Yamasaki and Satomi, 1976) and *Platanista* (Eschricht, 1852; Anderson, 1879; Arvy and Pilleri, 1970; Yamasaki and Takahashi, 1971; Takahashi and Yamasaki, 1972; Yamasaki *et al.*, 1972; Purves and Pilleri, 1973; Pilleri and Gihr, 1976a; Yamasaki, Komatsu and Kamiya, 1977) and further proves that the Platanistoids can be divided into four families. The phylogenetic relationships among the four families and the evidence in favour of the monophyly of the cetacea are also discussed.

BASIS OF THE CLASSIFICATION OF THE SUPERFAMILY

An uniform understanding of the genera of Platanistoids has been acquired early

TABLE 1. COMPARISON OF THE COMPARTMENTS OF THE STOMACH OF CETACEA

	Fore-stomach	Main stomach	Connecting channel	Pyloric stomach
Iniidae	1	1	1	1
Lipotidae	0	3	0	1
Pontoporiidae	0	1	1	1
Platanistidae	1	2	1	1
Ziphiidae	0	1	0	many compartments
Physeteridae	1	1	0	1
Monodontidae	1	1	1	1
Delphinidae	1	1	1	1
Phocoenidae	1	1	1	1
Balaenopteridae	1	1	0	1

in the third decade of the twentieth century. However, no identical result on the classification in family rank has been obtained so far. The materials studied which were mostly confined to skulls have something to do with the matter. When studying the affinity between *Lipotes* and *Inia*, Zhou *et al.* (1978, 1979a) compared attentively the vertebrae, sternums, flipper skeletons and other available materials of external and internal structures in addition to the careful comparison of the structure of the skulls. As a result of these studies, the close relationship between *Lipotes* and *Inia* was refuted. In recent decade, the studies of the skeleton and digestive tract of Platanistoids by Yamasaki *et al.*, Pilleri *et al.* and Zhou *et al.* have provided important basis for the classification of the modern Platanistoids.

Table 1 indicates that the stomachs of other modern cetaceans consist of fore-stomach, main stomach and pyloric stomach except those of the Ziphiidae in which the fore-stomach is absent. They differ from each other only in the present (Delphinidae, Monodontidae, Phocoenidae) or absent (Physeteridae, Balaenopteridae) of the connecting channel. The stomachs of different groups of Platanistoids differ from each other not only in the above mentioned characters, but also in the subdividing of the main stomach or not (Fig. 1). Both *Inia* and *Platanista* possess fore-stomach, but the main stomach is single chambered in the former and divides into two compartments in the latter. In *Lipotes* and *Pontoporia* the fore-stomach is lacking. The main stomach divides into three compartments and the connecting channel is absent in the former, while the latter possesses single chambered main stomach and the connecting channel. The differences between the stomach of any two groups of Platanistoids go beyond the mutual differences between the stomach of most of the odontocetes. Refer to the Artiodactyla, the number of compartments of the stomach goes so far as to be the main character in distinguishing Infraorder Tragulina (3 compartments) and Infraorder Pecora (4 compartments). Thus the structure of the stomach is one of the key characters in weighing the degree of separation among different groups of Platanistoids.

The structure of the skeleton is still important basis in classifying the Platanistoids. Attention should be paid first of all to four note-worthy differences between *Inia* and three other groups of Platanistoids. 1. The palatal portion of the two

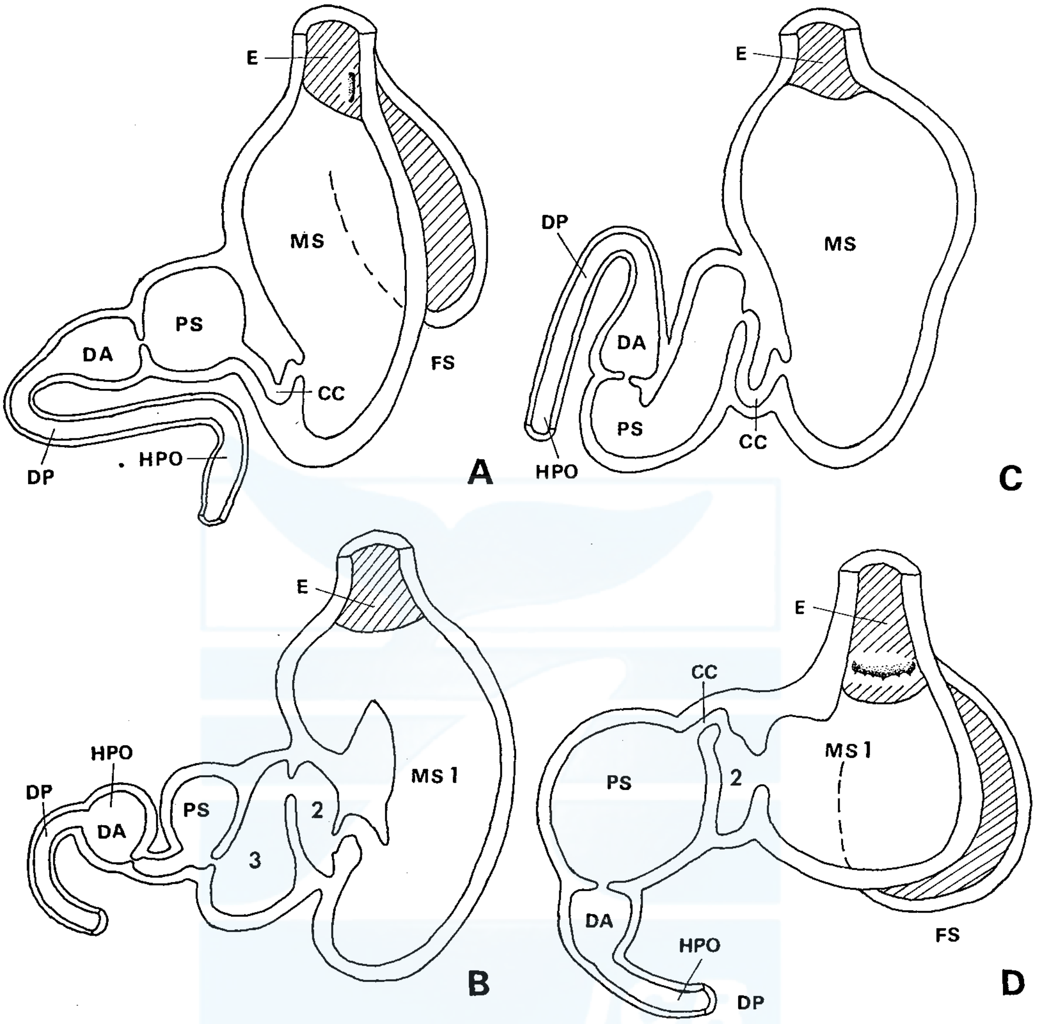
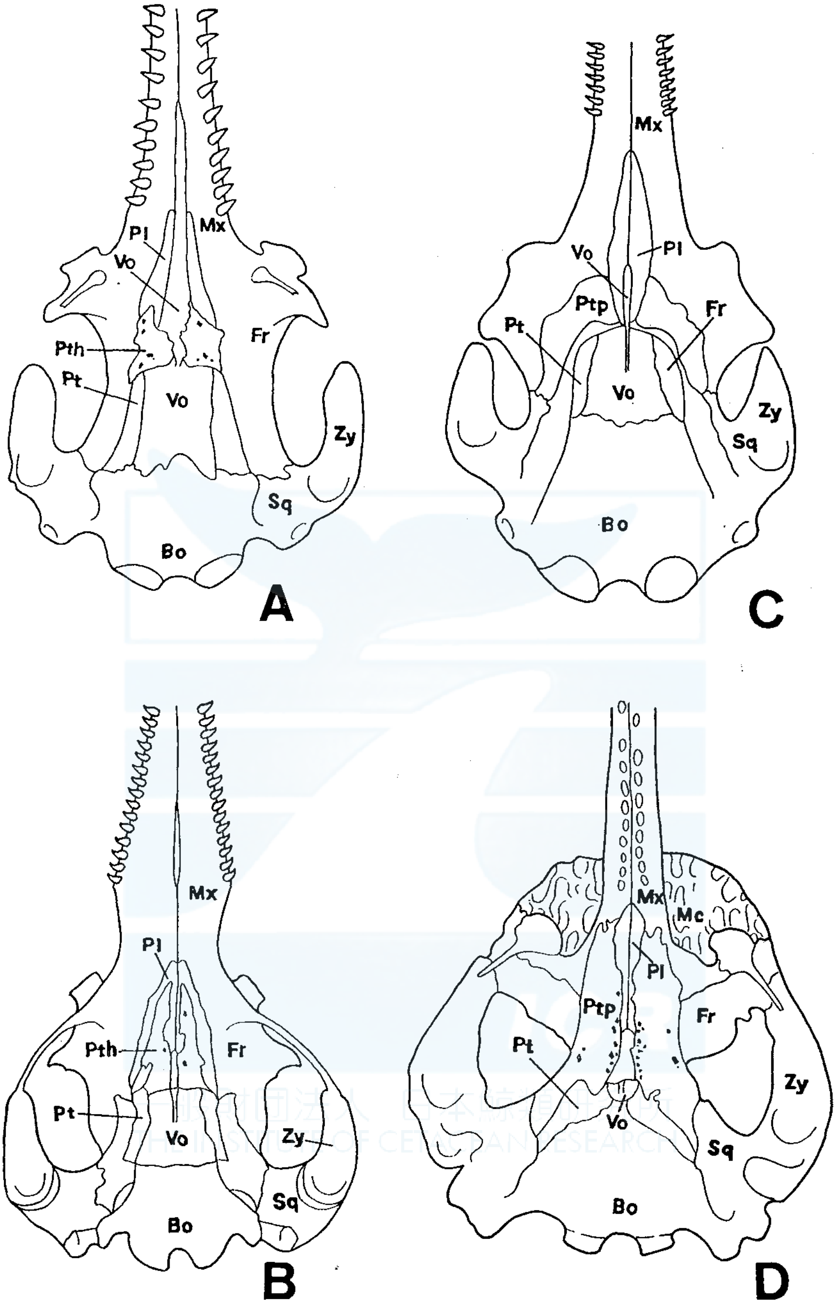


Fig. 1. Diagram of the stomach of (A) *Inia geoffrensis*, (B) *Lipotes vexillifer*, (C) *Pontoporia blainvillei*, (D) *Platanista gangetica*.
CC. connecting channel; DA. duodenal ampulla; DP. duodenum proper; E. esophagus; FS. fore-stomach; MS. main stomach; MS1. first compartment of main stomach; 2. second compartment of main stomach; 3. third compartment of main stomach; PS. pyloric stomach; HPO. opening of hepato-pancreatic duct.

→Fig. 2. Ventral aspect of skull of (A) *Inia geoffrensis*, (B) *Lipotes vexillifer*, (C) *Pontoporia blainvillei*, (D) *Platanista gangetica*.
Bo. basioccipital; Fr. frontal; Mc. maxillary crest; Mx. maxilla; Pl. palatine; Pt. pterygoid; Pth. pterygoid hamulus; Ptp. lateral plate of pterygoid; Sq. squamosal; Vo. vomer; Zy. zygomatic process of squamosal.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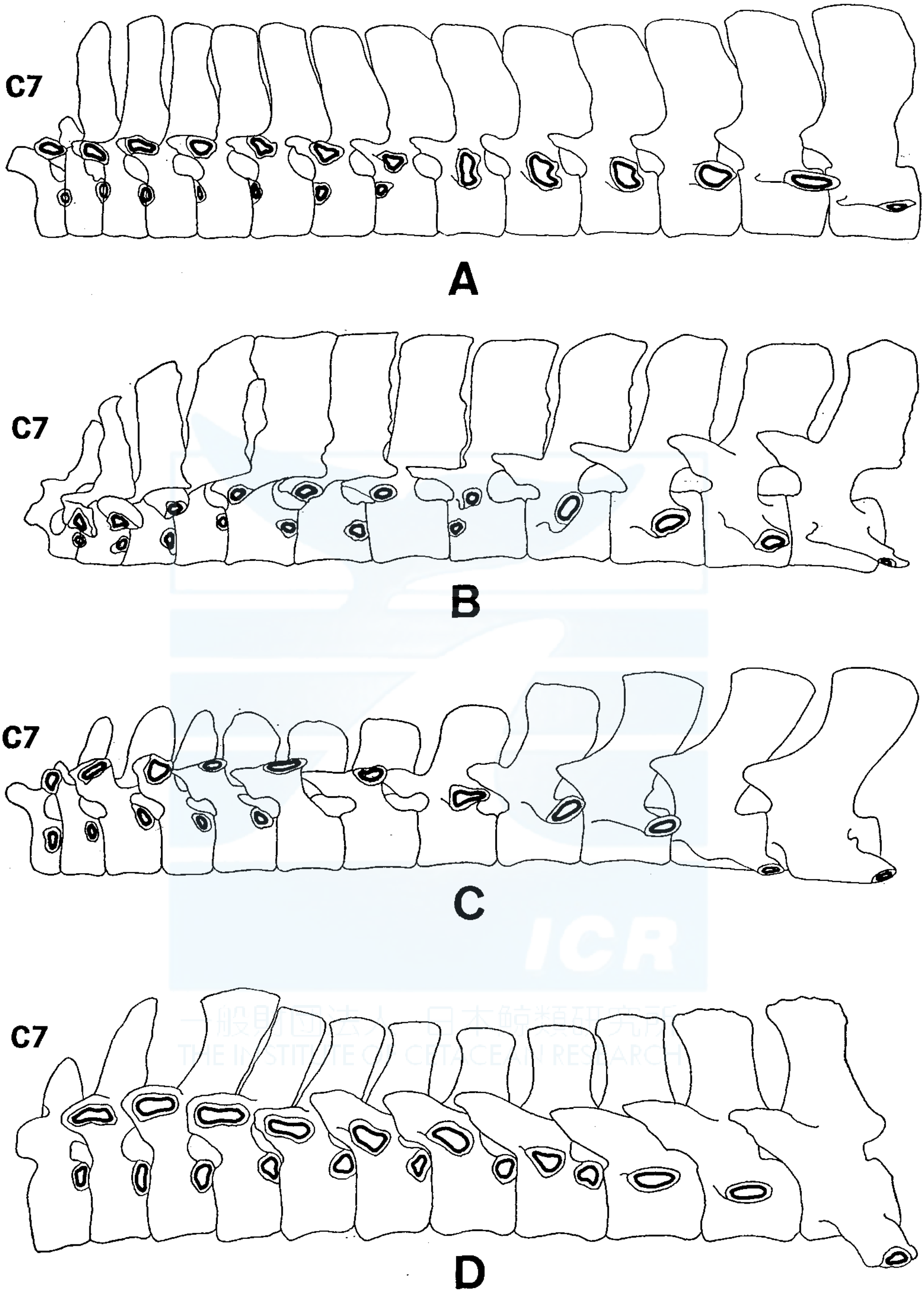

Fig. 3. Thoracic vertebrae of (A) *Inia geoffrensis*, (B) *Lipotes vexillifer*, (C) *Pontoporia blainvillei*, (D) *Platanista gangetica* showing costal facets (bold line).

maxillas and palatines of *Inia* is separated by the vomer. In three other groups of Platanistoid, the palatal portion of maxilla contacts that of the opposite side (Fig. 2). 2. Only irregular tubercles are found on the ventral aspect of the pterygoid hamuli of *Inia*, whereas the pterygoid hamuli of *Lipotes* possess a thin plate which recurves dorsally. This portion enlarges to form the lateral plate of pterygoid in *Pontoporia* and *Platanista*. 3. In *Inia*, the costal facets are located at the

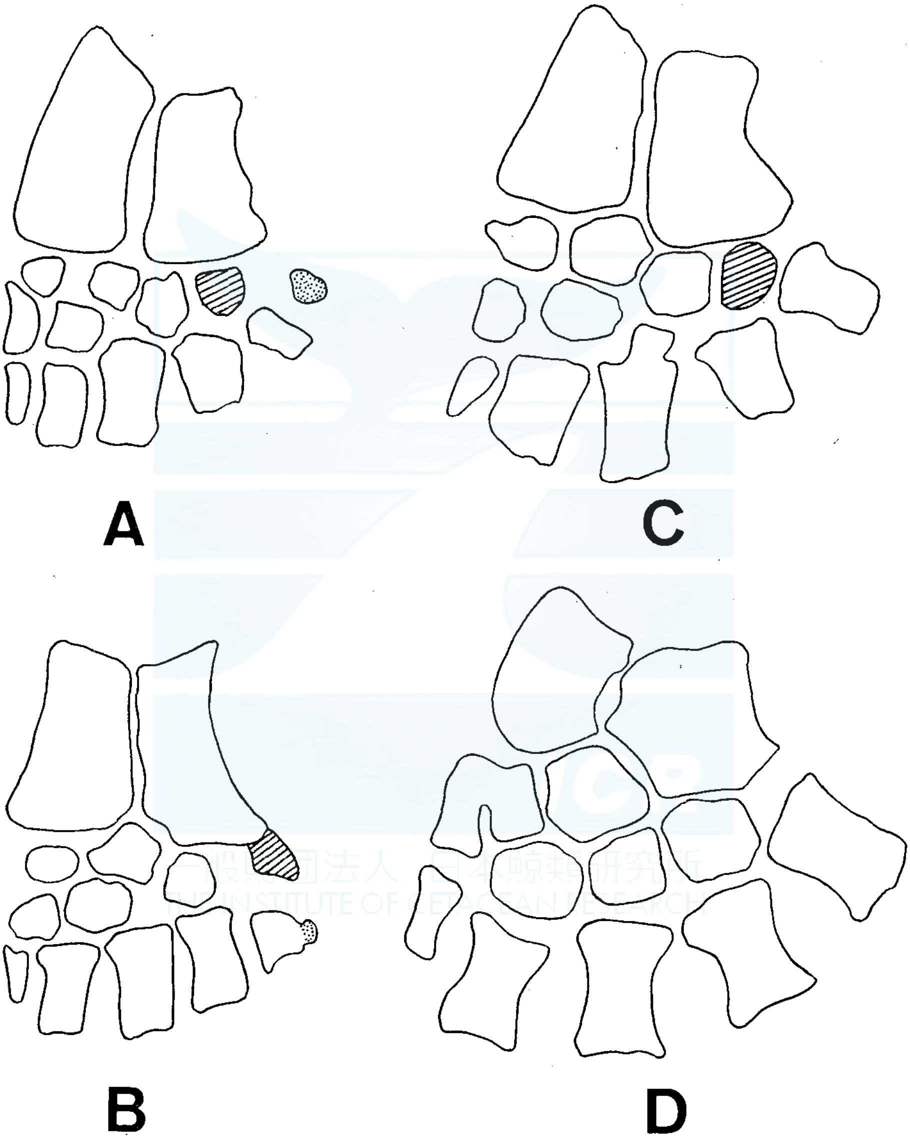

Fig. 4. Flipper skeleton (not including phalanges) of (A) *Inia geoffrensis*, (B) *Lipotes vexillifer*, (C) *Pontoporia blainvillei*, (D) *Platanista gangetica*. Ulnare hatched; pisiform stippled.

anterior and posterior edges on each centrum of the first two thoracic vertebrae and occured at the anterior edge only in the hinder thoracic vertebrae. In *Lipotes*, they are located both at the anterior and posterior edges of the centrum of the first vertebra and occured at the posterior edge only on the centrum of the 2nd—5th thoracic vertebrae. In the 7th thoracic vertebra, the facet occurs on the anterior edge only. The costal facets are located at the hind edge on the centrum of the thoracic vertebrae in most individuals of *Pontoporia*. In few individuals, those of 5th or 4th—5th thoracic vertebrae are situated at the front edge of the centrum. All costal facets of the thoracic vertebrae of *Platanista* are situated at the hind edge of the centrum (Fig. 3). 4. According to the radiograph published by Pilleri and Gihr (1976a, b, c), the ulnare and pisiform are free in *Inia*; the ulnare is free but the pisiform is missing in *Pontoporia*; both bones are missing in *Platanista*. According to our specimens, although the ulnare and pisiform of *Lipotes* are fused to the ulna and 5th metacarpal respectively, they are still distinguishable (Fig. 4).

The tympano-periotic of the cetacea has moved ventrally and lost the direct

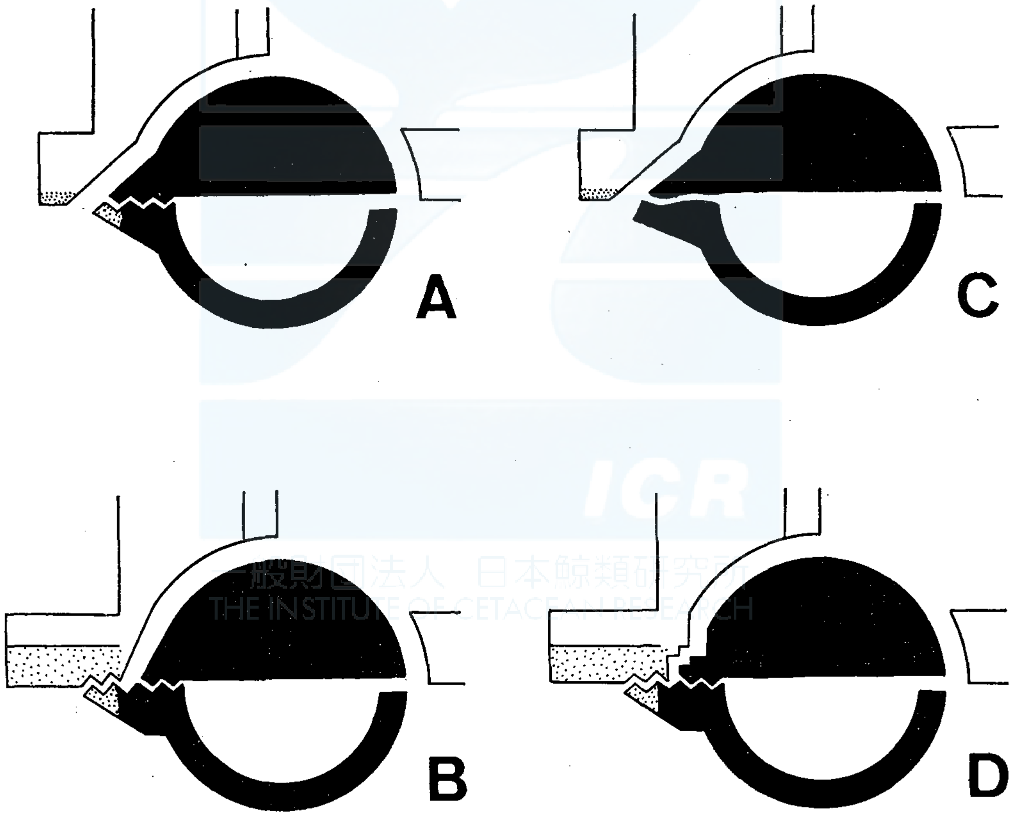

Fig. 5. Connection between tympano-periotic and skull in (A) *Inia geoffrensis*, (B) *Lipotes vexillifer*, (C) *Pontoporia blainvillei*, (D) *Platanista gangetica*, Waved edge indicates suture of bones and dotted are the laminated structure. (A) and (C): fixed with ligament; (B) and (D): direct joining. (Modified from Kasuya, 1973,)

TABLE 2. COMPARISON OF THE MAIN CHARACTERS OF THE FAMILIES OF THE SUPERFAMILY PLATANISTOIDEA

Characters	Iniidae	Lipotidae	Pontoporiidae	Platanistidae
Hairs	sparsely on snout	absent	absent	absent
Blow hole	transverse, crescentic	longitudinal, elliptic	transverse, crescentic	longitudinal, slitlike
Apical bronchus	arising from trachea slightly higher than bifurcation of right and left bronchi	arising from trachea markedly higher than bifurcation of right and left bronchi	arising from trachea just above bifurcation of right and left bronchi	arising from trachea markedly higher than bifurcation of right and left bronchi
Stomach	fore-stomach, single main stomach, connecting channel and pyloric stomach present	fore-stomach absent, three compartments of main stomach and pyloric stomach present	fore-stomach absent, single main stomach, connecting channel and pyloric stomach present	fore-stomach, two compartments of main stomach, connecting channel and pyloric stomach present
Opening of hepato-pancreatic duct	located at duodenum proper	located at duodenal ampulla	located at duodenum proper	located at duodenum proper
Caecum	absent	absent	absent	present
Ratio of intestinal length to body length	19—20	12.5—14.9	24.0—37.3	3.6—4.9
Maxillary crest	absent	absent	absent	very well developed
Zygomatic process of squamosal	not reaching supraorbital process of frontal	not reaching supraorbital process of frontal	reaching supraorbital process of frontal	reaching orbital plate of frontal from which a supra-orbital process is usually developed
Palatal portion of two maxillas	separated by vomer	in contact	in contact	in contact
Bony plate of pterygoid hamulus	small tubercles on ventral aspect of pterygoid hamulus	thin bony plate recurves dorsally	enlarges to form lateral plate of pterygoid	enlarges to form lateral plate of pterygoid
Connection between tympano-periotic and skull	fixed with ligament	posterior process of tympanic bulla loosely sutured to squamosal	fixed with ligament	posterior process of tympanic bulla loosely sutured to squamosal
Teeth	crown with nodular enamel rugosity	crown with reticulate enamel rugosity	crown simple	crown simple, upper tooth rows merged together and almost in contact
Costal facet of thoracic vertebrae	located mostly at anterior edge of centrum	located mostly at posterior edge of centrum	located at posterior edge of centrum in most individuals	located at posterior edge of centrum
Carpals	7, ulnare and pisiform present	4—5, ulnare fused to ulna and pisiform fused mostly to 5th metacarpal	6, ulnare present, pisiform missing	5—6, ulnare and pisiform missing

joining to the skull in various degrees in the course of the adaptations to the aquatic life. In *Lipotes* and *Platanista* the posterior process of tympanic bulla is still loosely sutured to the skull (Kasuya, 1973; Zhou *et al.*, 1979a). The tympano-periotic of *Inia* and *Pontoporia* is fixed with ligament to the skull (Fig. 5). Besides, *Inia* and *Lipotes* differ from *Pontoporia* and *Platanista* in having the zygomatic process of squamosal not reaching the supraorbital process of frontal. The distinction between the teeth of different Platanistoids is as follows: The crown of the teeth of *Inia* and *Lipotes* is covered with nodular and reticulate enamel rugosity respectively and that of *Pontoporia* and *Platanista* is simple. The upper tooth rows of *Platanista* merge together and are almost in contact with each other. *Platanista* also differs from three other Platanistoids and all other living odontocetes in having the curious maxillary crest.

The morphological distinctions between different Platanistoids showing in Table 2 are far more than those between different families of most mammals. This fact proves that each of the four Platanistoid dolphins represents a separate lineage derived from the primitive ancestor at an early stage of the evolutionary process. Their taxonomic categories should be referred to family rank.

PHYLOGENY

The traditional view concerning the relationship of different Platanistoid dolphins is that *Lipotes* is closely related to *Inia* and that *Pontoporia* is close to them. The systematic sequence of these groups has been arranged as A and B by most authors (Simpson, 1945; Carvalho, 1961; Marcuzzi and Pilleri, 1971; Kasuya, 1973; Tomilin, 1974; Mead, 1975; Matthews, 1978 other). It has been arranged as C by Slijper (1936, 1962) and some authors (Norman and Fraser, 1948; Nishiwaki, 1965, 1972) according to the sequence of naming. There are still few other sequences (Fraser and Purves, 1960; Hershkovitz, 1966; Rice, 1977). According to the informations now understood, these arrangements can not express the natural relationships of Platanistoids.

A

subfamily Platanistinae
  (or family Platanistidae)
  genus *Platanista*
subfamily Iniinae
  (or family Iniidae)
  genus *Inia*
  genus *Lipotes*
subfamily Pontoporiinae
  (or family Pontoporiidae)
  genus Pontoporia

B

family Platanistidae
  genus *Platanista*
  genus *Inia*
  genus *Lipotes*
  genus *Pontoporia*

C

family Platanistidae
  genus *Platanista*
  genus *Inia*
  genus *Pontoporia*
  genus *Lipotes*

By inference from the analysis of the characters, the phylogenetic relationships among the families of Platanistoids may be expressed as Fig. 6. The Iniidae is a side branch diverged from primitive Platanistoids. This family is characterized

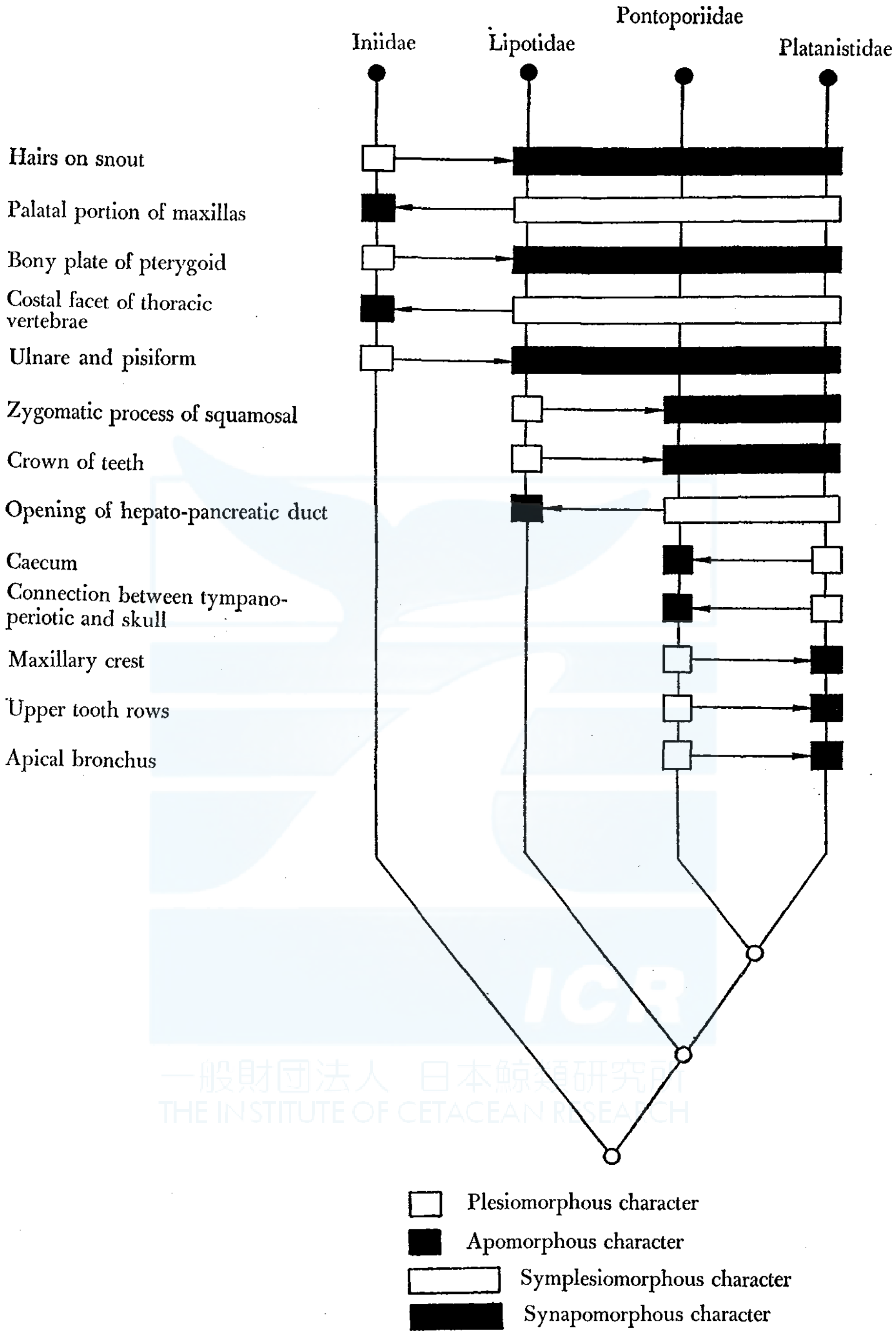

Fig. 6. Diagram of the phylogeny of the superfamily Platanistoidea.

by apomorphous characters, i.e. the separation of the palatines by the vomer and the location of most of the costal facets at the anterior edge of the centrum of the thoracic vertebrae, which differentiate Iniidae from other Platanistoids. The position of the head of the ribs articulating to the centrum of the thoracic vertebrae indicated by the costal facets is features differentiated during the early stage of adaptation to the aquatic life. In view of the fact that the costal facets of the thoracic vertebrae of Delphinoidea and Physeteroidea locates on the posterior edge of the centrum, the position of that of Iniidae probably situates opposite that of all other living odontocetes. The synapomorphous characters of Lipotidae, Pontoporiidae and Platanistidae are the development of the bony plate of pterygoid hamuli and the reduction of the carpals. Through the development of the recurved thin plate from the irregular small tubercles of pterygoid hamulus and the formation of the former to the well-developed lateral plate of pterygoid, the evolutionary sequences of this feature can be seen. The evolutionary trend of the carpals is the fusion of the ulnare and pisiform to adjacent bones or missing of both bones.

The Lipotidae is the second branch descended from the primitive Platanistoids. A series of features of the Lipotidae such as the bony plate of pterygoid hamuli, costal facet of thoracic vertebrae, carpals, zygomatic process of squamosal and crown of teeth is relatively more primitive than those of Pontoporiidae and Platanistidae. The Lipotidae also differs from these two families by the apomorphous character in having the hepato-pancreatic duct opens into the duodenal ampulla.

The Pontoporiidae and Platanistidae have diverged from the primitive Platanistoids slightly later than the Lipotidae. The maxillary crest, upper tooth rows, carpals and apical bronchus of Platanistidae are characters more specialized than those of the Pontoporiidae, whereas the caecum and the direct joining of the tympano-periotic to the skull in the same family are primitive characters as compared with those of the Pontoporiidae. The mosaic distribution of the Plesiomorphous characters and apomorphous characters between Pontoporiidae and Platanistidae also has been formed.

The structure of the digestive tract of Iniidae remains relatively close to the ancestor. In Lipotidae and Pontoporiidae the fore-stomach is absent, the stomach of the former is most specialized in the losing of the fore-stomach and the dividing of the main stomach into three compartments. The digestive tract of Platanistidae is characterized by the differentiation of the main stomach and notable shortening of the intestine on the one hand, and is unique among odontocetes in retaining the caecum on the other hand. The transverse crescent shaped blow hole of Iniidae and Pontoporiidae is similar to that of most of the recent odontocetes, whereas the shape of the blow hole of Lipotidae and Platanistidae has been changed separately. The process of moving of the apical bronchus from the right bronchus to trachea hasoccured in the course of phylogenetical development. The degree of forward shift of the apical bronchus varies in different group of Platanistoids. The reduction of the visual apparatus has taken place in relation to the increase of the turbidity of the water and the weakening of the light. The eyes of the

Pontoporiidae are comparatively well-developed and those of the fresh water Platanistoid species exhibit a marked regression. The eyes of the Platanistidae are almost completely blind. The degree of reduction of the eyes is in order of Pontoporiidae, Lipotidae, Iniidae, then Platanistidae (Zhou, Pilleri and Li, 1980). The orbit of Platanistoids is reduced in correspondence with the regression of the eye. In the case of Iniidae and Lipotidae, the zygomatic process of the squamosal is not lengthened in correspondence with the reduction of the orbit and is not in contact with the supra orbital process of the frontal. The unique maxillary crest of the Platanistidae functions together with the air sinuses in the reflection of the sound signals. It was probably developed parallel with regression of the eye to compensate for the loss of vision (Pilleri, 1979). The development of the brain of the Platanistoid families is comparatively low as compared with that of other living odontocetes. In totality, the Iniidae is the family keeping relatively more primitive characters and the Platanistidae is the most specialized one. The systematic sequence of the families in accordance with their evolution should be Iniidae, Lipotidae, Pontoporiidae and Platanistidae.

According to the fossils of the primitive Platanistoids discovered, these four families probably diverged during the Miocene from the marine ancestor originated from the Squalodontoidea. Three of the recent families of Platanistoids have entered fresh-water rivers secondarily, whereas Pontoporiidae has remained in coastal waters. Although the structures of Platanistoids have been differentiated during the long period of evolution, their development level is still lower than that of other recent odontocetes. Further studies on fossil groups of the Platanistoids are needed.

EVIDENCE OF THE MONOPHYLY OF THE CETACEA

Whether the cetacea originated from a common ancestor or two or several ancestors is a disputed problem. Slijper (1962) and some Soviet investigators have reached a conclusion in favour of polyphyly that the three suborders of the cetacea probably originated separatly from respective terrestrial ancestors. On the contray, Gaskin (1976) and van Valen consider that the cetacea as a whole are probably monophyletic. The basis of their argument is a series of morphological characters which are common to mysticetes and odontocetes such as the loss of the pelage, the lacking of the true vocal cord, the similarity in the structure of the tympanic bulla and the shape of the lung, the oblique position of the diaphragm and the moving of the blow hole to the dorsal aspect of the head, etc. The cytogenetic studies of Arnason (1969, 1972, 1974) and Kulu (1972) are also quoted by them to indicate the close agreement of mysticetes and odontocetes in the number and shape of the chromosomes as well as the distribution of C-heterochromatin in the chromosomes. No reasonable explanation would be obtained if the cetaceans were not of common ancestry.

A character common to mysticetes and odontocetes, which has not been brought to great attention yet, has been noticed during the studies on the phylogeny of the Platanistoids. That is, the stomach of most cetaceans is composed of three compartments, the fore-stomach, main stomach and pyloric stomach. The fore-stomach covered with esophageal epithelium is not subdivided further and the glandular stomach is divided into two or more compartments. The cetacean stomach composed of single chambered fore-stomach and subdivided glandular stomach is different from that of any other mammals. This fact makes me to come over to the side of the monophyly.

The mysticetes are grazers and the odontocetes are predators. Since they differ not only in feeding methods but also in food, the similarity of the stomach could not be explained by parallel adaptations. If the cetaceans were not of common origin, it would be impossible for majority of them to possess the fore-stomach formed by the esophagus and the subdivided glandular stomach. It is reasonable to infer that such basic structure was developed before the differentiation of the mysticetes and odontocetes. It is the symplesiomorphous character of the two groups and another evidence of the monophyly of the cetacea.

Certain characters which were thought to be found in mysticetes only still remain in some Platanistoids, such as the hair on the snout of Iniidae and the caecum of Platanistidae. These features add evidence to support the monophyly of the cetacea. It should be stated that the unique musculus palpebrales of the cetaceans (Hosokawa, 1951) is also a proof which has not been cited by previous authors.

ACKNOWLEDGEMENTS

The present paper was completed after I had examined the Platanistoid skeletons deposited in the Ocean Research Institute of the University of Tokyo. I am greatly indebted to Dr. M. Nishiwaki, Professor Emeritus of the University of Ryukyus, for his kind invitation made my studies in Japan possible, and to Dr. T. Kasuya of the Ocean Research Institute of the University of Tokyo who provided the above mentioned specimens in his collection. Thanks are also due to Xu Xinrong for drawing.

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MORPHOLOGICAL STUDY ON THE HYBRID BETWEEN *TURSIOPS* AND *PSEUDORCA*

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ABSTRACT

A hybrid calf born in Kamogawa Sea World, Chiba, on May 3, 1981 was supposedly between mother *Tursiops truncatus gilli* and a male *Pseudorca crassidens.* It lived 277 days. In the past record of Kamogawa Sea World, there were three abortively born fetuses of hybrid in different degree of growth. External observation and comparison of osteological examinations on the calf, the fetuses and parents species cleared that the calf was an offspring of the above two species. Situation of the pool and relation between the mother dolphin and males of variety of species, and the process of growing and death of the particular individual were studied.

INTRODUCTION

The first report on the interspecies hybrid of cetaceans is the three anomalous dolphins stranded at the Blacksod Bay, Ireland. The specimens were presumed as hybrids between *Tursiops truncatus* and *Grampus griseus* (Fraser, 1940). It is well known that a hybrid individual was born in Sea Life Park, Hawaii in Oct. 1971 between male *Tursiops truncatus* and *Steno bredanensis* (Shallenberger and King, 1977; Nishiwaki, 1978). The present hybrid was born in Kamogawa Sea World in 1981. From morphological aspects and also from the situation in the pool, in which the mother and males were living together, we presumed that it was a hybrid between *Tursiops truncatus gilli* and *Pseudorca crassidens.* The senior author spoke on the hybrid calf while it was living, at Symposium on Cetacean Reproduction, La Jolla, California at the end of 1981. Cromozome study was desired on the hybrid in the symposium in case if the individual should have died, and was to be carried out in cooperation with Dr. Deborah S. Duffield of the Portland State University. The death of the individual was a big disappointment, but the study became available, undesirablly soon. The senior author carried a fresh blood sample from the dead calf to USA on his way to Silver Bank, a breeding area of humpback whales. A result of examination has not yet appeared, morphological aspects of the hybrid calf in comparison with data of other hybrid fetuses and those of parents species are in this report.

Sci. Rep. Whales Res. Inst.,
No. 34, 1982, 109–121

Fig. 1. The hybrid calf with her parents.

PROCESS OF GROWING AND DEATH OF THE CALF

Parturition was observed at 16:45 on May 3, 1981. The first sucking of the new-born calf was recognized after five hours. The mother and the calf were swimming closely for the first couple of weeks, and the calf was growing in very good health, which had been known as female till then. Individual swimming apart from mother was increasingly frequent after 19 days or so. She showed her attracted to food after 74 days and she bit a hand of caretaker after 85 days, so he gave her a smelt (*Mallotus villosus*). She touched the fish by her snout tip, bit it and swallowed it. This first food taking was about a month earlier than that of the calves of general *Tursiops*. She had four errupted teeth in the central part of each upper tooth row at that time. Since then, the calf continued to take boneless smelts and mackerel (*Scomber japonicus*) as well as sucking milk, while she was often seen with her tongue-tip showing out of mouth. Number of fish indidivual taken by the calf in each month in average per day was 0.19 kg in Aug., 0.5 kg in Sept., 1.3 kg in Dec. and 1.4 kg in Jan, 1982.

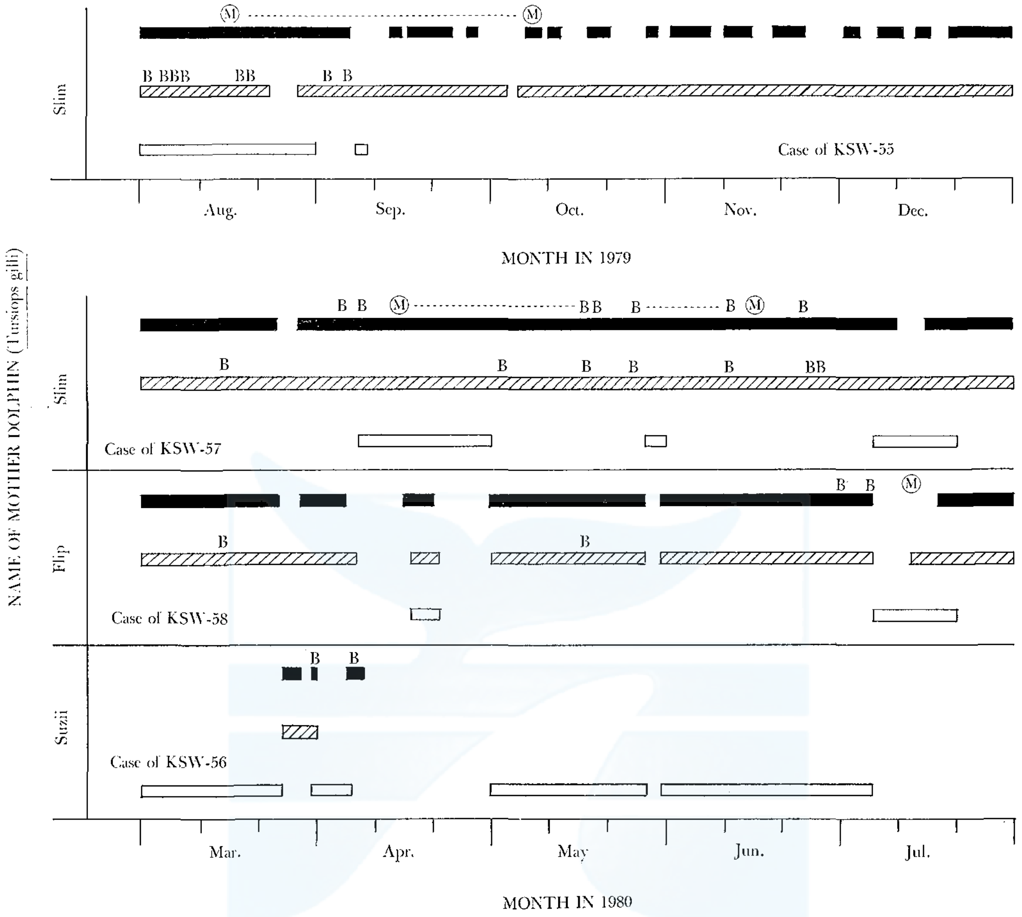

Fig. 2. Situation of the mother dolphins live together with each male in the pool.
Periods of each males in the mothers' pool.
■ *Pseudorca crassidens* ▨ *Lagenorhynchus obliquidens* ☐ *Tursiops gilli* (immature)
B Witnesses of chasing Ⓜ Witnesses of copulation

On the late afternoon of the 273rd days after birth, calf's appetite decreased, and without serious disorder seen in appearence, she died three days later, Feb. 2, 1982. The sudden death of the calf was a shock to whole Kamogawa Sea World and related scientists. Examination after death made it clear that the cause was acute-pneumonia. Body length was 190 cm and weight was 81.6 kg at its death.

INCIDENTS OF HYBRID BETWEEN *TURSIOPS* AND *PSEUDORCA*

When the two abortive fetuses occurred, it was considered each time that a hybrid from so divergent parents would never grow normally to reach parturition and was not a matter of serious report. However, after one successful birth of KSW-57,

TABLE 1. LIST OF HYBRIDS BETWEEN *TURSIOPS GILLI* AND *PSEUDORCA CRASSIDENS* AND THEIR MOTHER DOLPHINS

Hybrids					Mother dolphins			
Specimen No.	Sex	Body length in cm	Date of birth		Species	Name	Body length in cm	Period in captivity
KSW-55	F	74.0	Jan. 29 1980	Deadborn	*Tursiops gilli*	Slim	289	10 years
KSW-56	M	116.0	Apr. 30 1981	Deadborn	*Tursiops gilli*	Suzii	284	5 years
KSW-57	F	190.6*	May 03 1981	Live born	*Tursiops gilli*	Slim	289	10 years
KSW-58	M	121.5	Jul. 07 1981	Deadborn	*Tursiops gilli*	Flip	278	10 years

* measured at her death on Feb. 02 1982.

TABLE 2. LIST OF MALE DOLPHINS KEPT IN THE POOL WITH MOTHER DOLPHINS

Species	Name	Body length in cm	Period of captivity
Pseudorca crassidens	Leo	409	10 years
Lagenorhynchus obliquidens	Billy	185	6 years
Tursiops gilli	Ace	250	4 years

another abortive delivery occurred, and the fetus was nearly parturient.

In the pool of Kamogawa Sea World, in which all those incidents of hybrid occurred, there happened to be no mature male *Tursiops*, but one *Pseudorca*, one *Lagenorhynchus* and one immature male *Tursiops*, less than four years old. Observation on mating behavior in the pool is shown in Fig. 2, in which mark " B " is chasing behaviors and " M " is copulations. From Fig. 2, we can tell that mating between the female *Tursiops* (by the name of Slim) and a male, *Pseudorca* (Leo) in August or that in October 1979 delivered abortive fetus KSW-55 74 cm in length, which may have been in mother's womb for about 4 months. Similarly, mating between female *Tursiops* (Flip) and Leo in July 1980 delivered the abortive KSW-58. Again, mating between the third female *Tursiops* Suzii and Leo in April 1980 delivered abortive KSW-56. The present specimen KSW-57 was an offspring of mother Slim, her mating with Leo had been seen from April to June 1980. Other male *Lagenorhynchus* in the pool was also chasing females, but his lesser sized body may not have been strong enough, no mating mark of him is recorded. The only male *Tursiops* in the pool was a young son of Slim and a male *Tursiops*, his father died before those incidents. The young *Tursiops* was four years old (fifth year from birth) reaching an age of sexual maturity, he only showed some chasings.

MORPHOLOGICAL FEATURE OF THE FOUR HYBRID SPECIMENS

To compare the body proportion of the three hybrid fetuses and that of general *T. t. gilli* in similar stage of growth, external measurement in the certain parts of the body is shown in Table 3, in which values are indicated in parcentage against the total length. As a reference, measurements from parents species in respec-

TABLE 3. COMPARISON OF FOETAL AND CALF BODY PROPORTION BETWEEN *TURSIOPS-PSEUDORCA* HYBRIDS AND NORMAL *T. GILLI*.

Specimen No.	KSW-55	*T. gilli*	KSW-56	*T. gilli*	KSW-57*	*T. gille**	KSW-58	*T. gilli*
Sex	F	M	M	F	F	M	M	F
Body weight in kg.	4.4	—	16.8	15.6	81.6	68.8	17.2	22.8
Point of measurement								
1. Total body length in cm.	74.0	73.0	116.0	113.0	190.6	188.0	121.5	127.0
2. Tip of upper jaw to apex melon	1.8	3.4	1.9	4.0	1.4	4.3	1.8	3.7
3. Tip of upper jaw to angle of gape	11.5	13.0	14.6	13.4	11.0	13.6	12.7	13.7
4. Tip of upper jaw to blowhole	12.9	16.4	16.3	14.2	13.1	20.2	13.9	15.1
5. Tip of upper jaw to center of eye	14.2	17.1	16.7	16.1	15.0	16.5	15.0	17.3
6. Tip of upper jaw to anterior insertion of flipper	23.7	—	21.0	26.0	20.0	22.9	23.8	24.8
7. Center of eye to external auditory meatus	3.6	4.7	4.5	3.5	3.5	3.5	4.5	3.9
8. Tip of upper jaw to tip of dorsal fin	62.2	58.9	62.9	63.9	63.4	61.7	61.3	68.0
9. Tip of upper jaw to center of anus	72.7	73.9	72.4	70.3	70.1	71.8	71.3	71.4
10. Tip of upper jaw to midpoint of umbilicus	51.4	52.0	52.7	49.5	46.5	48.7	50.1	49.7
11. Maximum height of body	18.6	28.7	21.6	21.0	24.1	27.4	19.1	23.2
12. Length of flipper, anterior insertion to tip	17.3	16.4	18.7	18.9	17.1	18.4	17.4	15.2
13. Length of flipper, axilla to tip	11.9	10.9	13.3	13.4	12.5	13.3	12.5	12.9
14. Width of flipper, maximum	6.1	6.8	6.9	6.7	6.3	6.4	5.9	6.4
15. Length of dorsal fin (base)	13.5	14.3	12.5	15.0	16.4	17.0	15.2	16.6
16. Height of dorsal fin	9.7	10.9	7.8	7.7	8.5	8.5	9.6	9.4
17. Width of flukes, tip to tip	21.6	21.9	15.5	20.7	23.6	21.0	17.0	19.0
18. Anterior insertion of tail flukes to notch	10.2	8.9	8.2	8.7	7.3	8.5	7.9	8.0
19. Anterior insertion of tail flukes to tip	18.9	16.4	15.7	18.0	15.8	15.4	16.5	17.6

* calf

TABLE 4. ADULT BODY PROPORTION ON EXTERNAL MEASUREMENT OF A MALE *PSEUDORCA CRASSIDENS* AND FIVE FEMALES *TURSIOPS GILLI*.

Species	*Pseudorca crassidens*	*Tursiops gilli*	*Tursiops gilli*	*Tursiops gilli*	*Tursiops gilli*	*Tursiops gilli*
Sex	M	F	F	F	F	F
Pint of measurement						
1. Total length in cm	465	272	292.5	283.5	290	316
2. Tip of upper jaw to apex melon	—	3.7%	3.4%	3.0%	3.8%	3.7%
3. Tip of upper jaw to angle of gape	6.6%	10.7	12.1	10.4	10.7	10.1
4. Tip of upper jaw to blowhole	10.1	11.4	11.4	11.1	13.8	10.6
5. Tip of upper jaw to center of eye	9.2	12.9	11.6	12.2	12.4	11.9
6. Tip of upper jaw to anterior insertion of flipper	13.9	18.9	19.5	20.3	19.6	20.9
7. Center of eye to extermal auditory meatus	1.9	2.7	4.0	3.0	2.7	3.0
8. Tip of upper jaw to tip of dorsal fin	49.2	57.7	61.9	60.8	57.2	59.5
9. Central notch of tail flukes to center of anus	65.5	67.3	72.0	70.4	70.9	65.2
10. Central notch of tail flukes to midpoint of umblicus	39.1	48.7	45.6	44.3	45.2	44.9
11. Girth on anterior insertion of flipper	—	46.3	35.9	39.1	34.5	38.3
12. Girth on anterior insertion of dorsal fin (maximum)	—	54.8	47.9	48.0	43.1	40.8
16. Maximum height of body	24.0	32.3	32.8	—	21.0	23.7
17. Length of flipper, anterior insertion to tip (curved)	13.7	16.9	16.1	15.2	14.1	17.0
18. Length of flipper, anterior insertion to tip (straight)	10.1	12.1	10.6	10.9	10.1	15.7
19. Width of flipper, maximum	5.3	6.2	5.9	5.1	5.2	5.7
20. Length of dorsal fin (base)	10.7	15.8	17.4	18.3	14.8	19.0
21. Height of dorsal fin	7.0	10.1	10.2	8.8	8.3	9.2
22. Total spread of tail flukes	21.0	27.5	21.0	20.1	18.3	25.9
23. Anterior insertion of tail flukes to notch	5.5	8.7	6.8	7.4	6.5	8.5
24. Anterior insertion of tail flukes to tip	12.9	18.0	16.7	16.2	14.8	18.2

tive parts of body are shown together, specimens are one adult male *P. crassidens* and five adult females of *T. t. gilli*, in Table 4.

As seen in Point 2 of Table 3, namely from the tip of upper jaw to the apex of melon, the beak of the hybrid specimens is apparently shorter than that of normal *T. t. gilli*.

Body colour of the hybrid calf and other three still born specimens are altogether darker than that of normal *T. t. gilli* fetuses and living calves of similar stage in growth. Specimen KSW-55, 56 and 58 are still darker than the calf KSW-57.

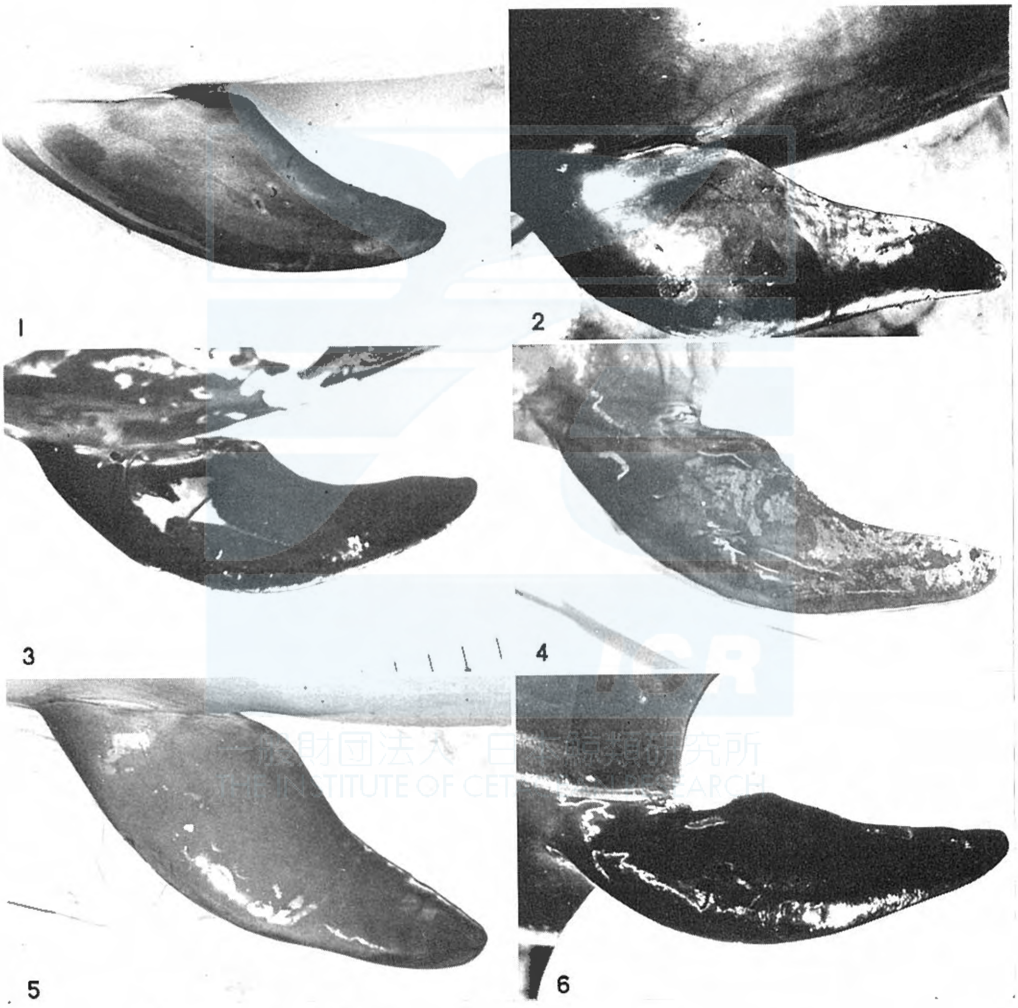

Fig. 3. Shape of flippers.

1: Adult *Tursiops gilli*.
2: Adult *Pseudorca crassidens*.
3: 74.0 cm foetus (KSW-55).
4: 116.0 cm foetus (KSW-56).
5: Living calf (KSW-57).
6: 121.5 cm foetus (KSW-58).

TABLE 5. VERTEBRAL, DENTAL AND PHALANGEAL FORMULAE OF THE HYBRIDS BETWEEN *TURSIOPS* AND *PSEUDORCA* COMPARED WITH THOSE OF STANDARD FORMULAE OF *TURSIOPS GILLI* AND *PSEUDORCA CRASSIDENS*.

Specimen			KSW-55		KSW-56		KSW-57		KSW-58		*Tursiops gilli*	*Pseudorca crassidens*
Body length			74.0		116.0		190.6		121.5			
Vertebral formula		C	7		7		7		7		7	7
		D	11		11		12		12		14	10
		L	10		11		13		11		15	10
		Ca	24		25		25		25		29	23
		Sum	52		54		57		55		65	50
Dental formula	Upper	Left Right	17	16	15	16	17	17	15	16	20–25*	8–11*
	Lower	Left Right	17	16	15	16	17	17	15	16	20–25*	8–11*
		Sum	66		62		68		62		80–100	32–44
			L	R	L	R	L	R	L	R	*	*
Phalangeal formula		I	1	1	2	2	2	2	2	2	2	2
		II	7	7	8	8	9	9	8	8	9	8
		III	5	5	6	6	7	7	6	6	7	6
		IV	2	2	3	3	4	4	4	4	4	4
		V	1	1	1	1	3	3	2	2	2	2

* Number is equal in left and right side.

Osteological X-ray survey was done on the hybrid fetuses. Naturally, there are no big variation in the standard phalangeal formulae between adult *Tursiops* and *Pseudorca*, however, there are considerable varieties in the number of pharanges in KSW 55 and 56, but in 58. Varieties may because of preparturient stages. Specimen KSW-58, 128 cm in length, has the same phalangeal formula as in the standard *Pseudorca*. So, if KSW-55 and 56 had lived longer, they would grow one more finger bone in II and III. Although the phalangeal formulae do not suggest a clear trace to *Pseudorca*, the external shape of flippers are showing more visible characteristics of *Pseudorca*. Shape of flipper in *Pseudorca* has distinct peculiarity among all cetacean species. As seen in Fig. 3, all the fetuses have similar shape of flippers which is descended from father. On the other hand the calf specimen KSW-57 has same numbers as in *T. t. gilli* in pharange I, II, III, and IV except V which shows one more finger bone than in general *Tursiops*. But shape of the flippers is more similar to the flippers in the father species of *Pseudorca*.

In X-ray examination, number of teeth is 15–17 in each fetus specimen. The senior author spoke in the Symposium in La Jolla that the dental number in the calf KSW-57 was 15 in counting on the clear photographs, and that the calf would grow one or two more teeth according to its growth. Actual counting at its death cleared that the dental number was 17. The dental formulae of those hybrid specimens are just inbetween *Tursiops* and *Pseudorca*.

In the vertebral formulae, thoracic, lumber and caudal, of the all hybrid specimens are altogether just inbetween the two species. Table 5 shows all those number and formulae of bones and teeth with the standard of adult *T. t. gilli* and *Pseudorca*. Tables may explain more clearly than words that there is little doubt that all the four specimens are hybrid between the two species.

SKULL MEASUREMENT OF THE HYBRID CALF

The skull and other bones of the hybrid calf was made to be skeletal specimens and preserved in Kamogawa Sea World. The measurement values on the skull are in Table 6. Photographs of them are in Fig. 4 and 5. The tympanic bones are in Fig. 6. Table 6. also indicates that the calf is inbetween *T. t. gilli* and *Pseudorca* in values.

EXPECTATION IN FUTURE

Among land animals, the first interspecies hybrids, between the lion and the tiger for an example, must have been born accidentally, however, it became somehow intentional experiments in some zoos. "The liger" or "the tyon" by intentional hybridization has been seen in many places. But those hybrid animals have never had following generations. The fact is considered as a proof that each parent species is independent.

All the four specimens in this report were born accidentally. In this rare

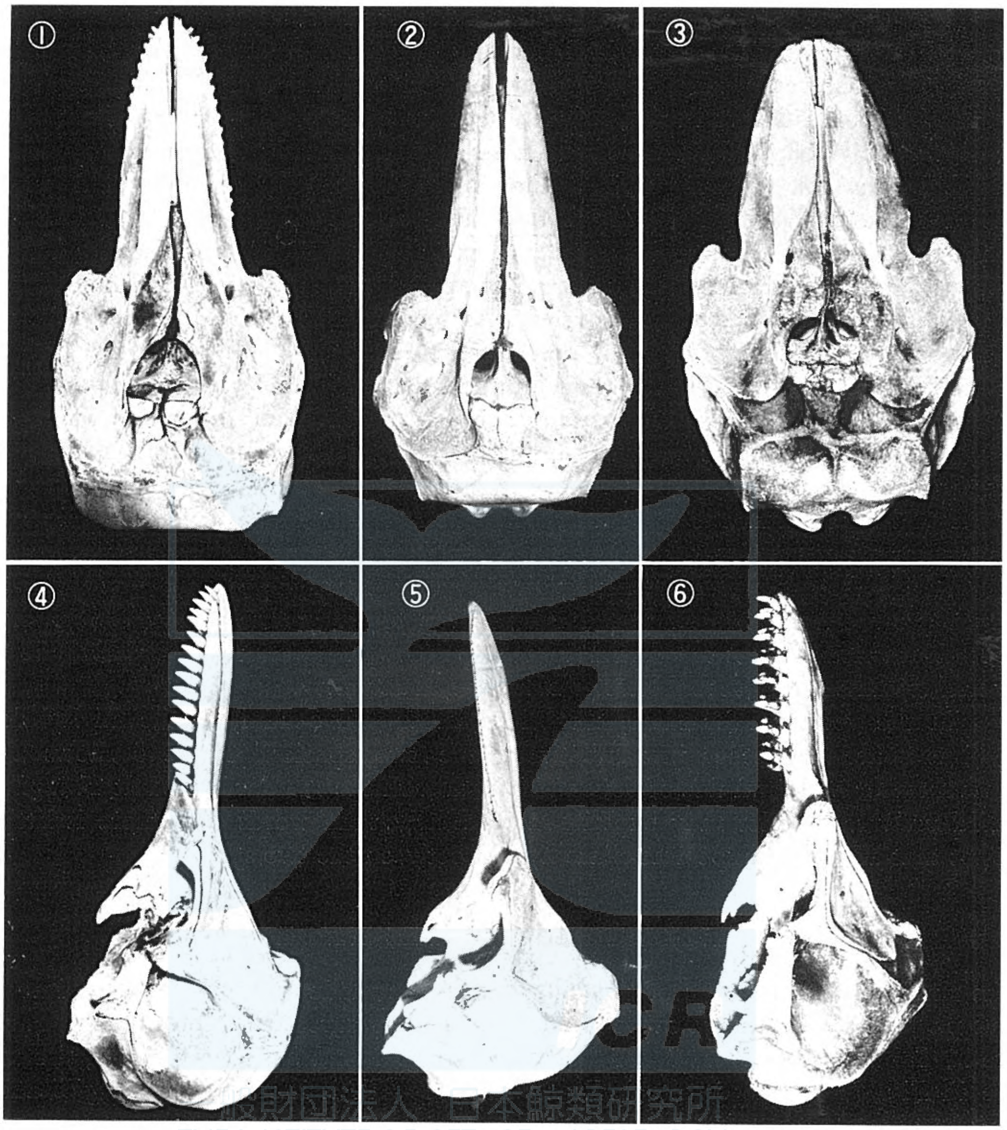

Fig. 4. Skull of the Hybrid between *Tursiops* and *Pseudorca*, *Tursiops gilli* and *Pseudorca crassidens*.
Top to bottom: Dorsal and lateral view.
Left, Hybrid (KSW-57) between *Tursiops* and *Pseudorca*.
Middle, *Tursiops gilli* (B. L. 270 cm).
Right, *Pseudorca crassidens* (B. L. 415 cm).

case, examination on their chromosome number, blood type, electrophoretic pattern of protein (analysis of blood component) etc. were desired, but only a chromosome study is going on in cooperation by Dr. Duffield. In future, based on those genetic studies, we might reach to a point that if there are possibilities of a third

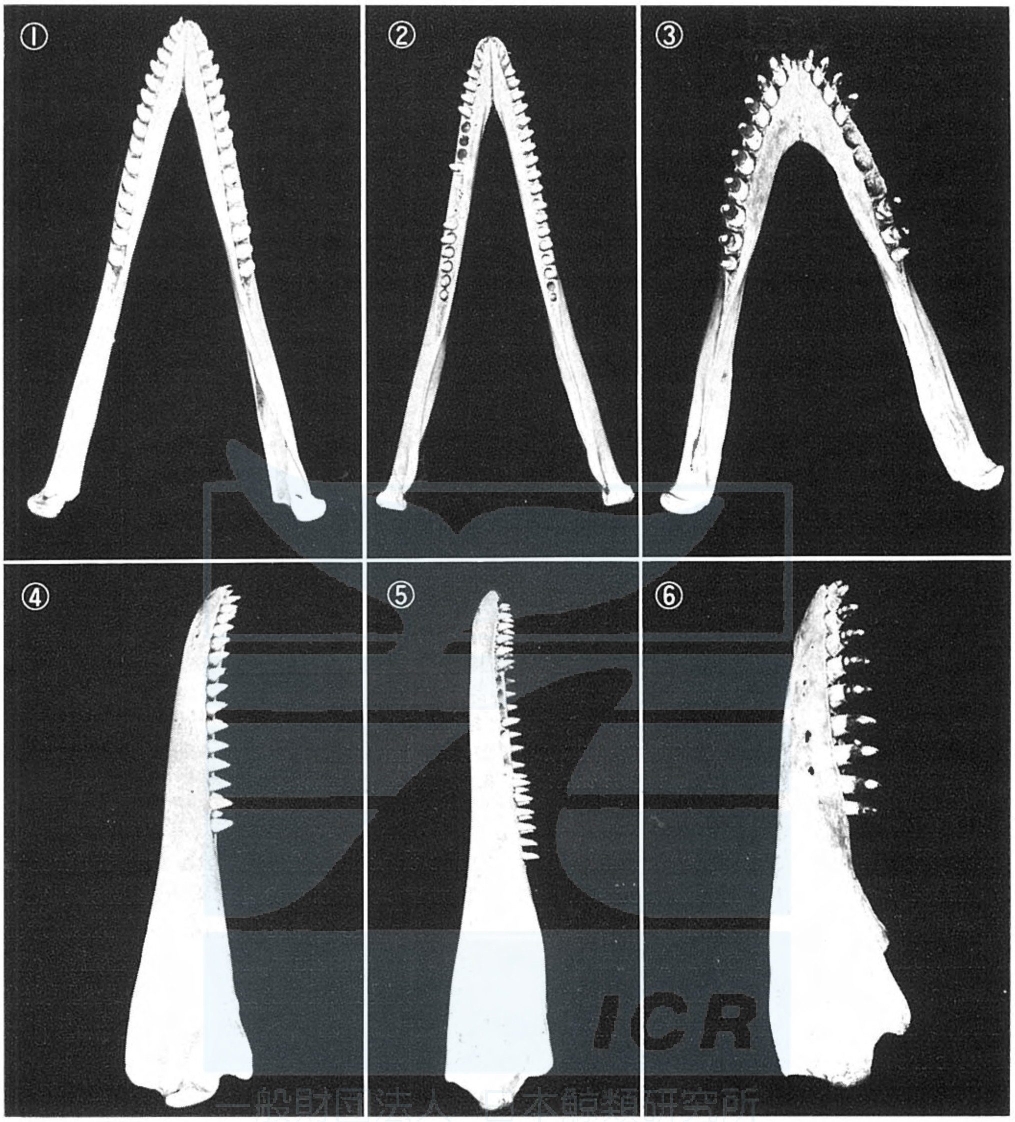

Fig. 5. Mandible of the Hybrid between *Tursiops* and *Pseudorca, Tursiops gilli* and *Pseudorca crassidens*.
Top to bottom: Dorsal and lateral view.
Left, Hybrid (KSW-57) between *Tursiops* and *Pseudorca*.
Middle, *Tursiops gilli* (B. L. 270 cm).
Right, *Pseudorca crassidens* (B. L. 415 cm).

generation hybrid of smaller cetacean species.

In the case of Kamogawa Sea World, all available cares were given to the calf born with so divergent blood. As expectation for her growing was great, her death was a disappointment and sadness. Cause of death was diagnosed as

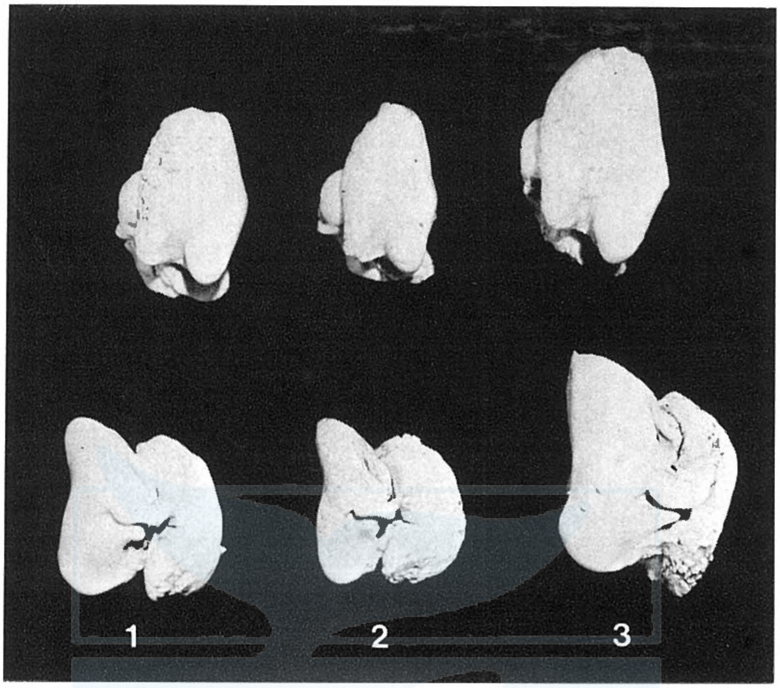

Fig. 6. Shape of Tympano-periotic bones.
1. Hybrid calf, KSW-57, left side.
2. *Tursiops gilli*, B. L. 270 cm, left side.
3. *Pseudorca crassidens*, B. L. 415 cm, left side.

acute-pneumonia, but there remained a doubt that whether death was indirectly or directly caused by her abnormal blood from parents species so different each other. We have no intention in cultivating interspecie-hybrid animals. However, in limited number of pools in an oceanarium or aquarium, in which males and females of variety of species are kept together, accidental interspecies hybrid birth will be seen again in furure. If we would have such cases again, we will give more cares to save calves.

ACKNOWLEDGMENT

This study started from unexpected birth of the hybrid calf. In Kamogawa Sea World, generous care was given to the calf after its birth by veterinarians and caretakers. Owing to the help by those number of people attended to the dolphin pool, in observation, recording and photographs taken and so on, this study was possible. We are deeply indebted to all those people and particularly to Mr. Yoshiaki Maeda of Kamogawa Sea World, who helped us in collecting data and taking skull photographs.

TABLE 6. SKULL MEASUREMENTS OF THE CALF HYBRID BETWEEN *TURSIOPS* AND *PSEUDORCA* COMPARED WITH ADULTS *TURSIOPS GILLI* AND *PSEUDORCA CRASSIDENS*

Specimen	KSW-57		T. gilli		P. crassidens	
Sex	F		F		M	
Body length in cm.	190.6		270.0		415.0	
Point of measurement						
Condylobasal length	422 mm	(100%)	505 mm	(100%)	624 mm	(100%)
Length of rostrum	208	(49.3)	278	(55.0)	294	(47.1)
Width of rostrum at base	117	(27.7)	142	(28.1)	225	(36.1)
Width of rostrum at midlength	79	(18.7)	95	(18.8)	182	(29.2)
Length of premaxillae, L.	297	(70.4)	373	(73.9)	429	(68.8)
R.	318	(75.4)	394	(78.0)	448	(71.8)
Maximum width of premaxillae	85	(20.1)	95	(18.8)	151	(24.2)
Maximum breadth of superior nares	58	(13.7)	57	(11.3)	86	(13.8)
Tip rostrum to anterior margin of superior nares	258	(61.1)	328	(65.0)	363	(58.2)
Tip rostrum to center of eye	259	(61.4)	345	(68.3)	340	(54.5)
Preorbital width	190	(45.0)	246	(48.7)	332	(53.2)
Postorbital width	214	(50.7)	273	(54.1)	363	(58.2)
Parietal width	191	(75.3)	202	(40.0)	262	(42.0)
Length of temporal fossae, L.	105	(24.9)	112	(22.2)	196	(31.4)
Depth of temporal forssae, L.	79	(18.7)	86	(17.0)	143	(22.9)
Length of maxillary toothrow, L.	180	(42.7)	236	(46.7)	232	(37.2)
R.	182	(43.1)	233	(46.1)	236	(37.8)
Length of mandibular rami, L.	351	(83.2)	432	(85.5)	489	(78.4)
R.	353	(83.6)	432	(85.5)	489	(78.4)
Breadth across mandibular condyles	203	(48.1)	268	(53.1)	356	(57.1)
Length of symphsis	59	(14.0)	67	(13.3)	87	(13.9)
Coronoid height of ramus, L.	82	(19.4)	89	(17.6)	133	(21.3)
R.	84	(19.9)	88	(17.4)	135	(21.6)
Length of mandibular toothrow, L.	184	(43.6)	238	(47.1)	243	(38.9)
R.	189	(44.8)	238	(47.1)	243	(38.9)

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FOOD HABITS OF LARGHA SEAL PUPS IN THE PACK ICE AREA

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ABSTRACT

The stomach contents from largha seal (ice-breeding harbor seals) collected in the pack ice areas off the eastern Hokkaido and the east coast of Sakhalin were examined. Analyses revealed that fishes, cephalopods, euphausiids and decapods were principal foods. Among them, fishes were primary foods as well as *Theragra chalcogramma*, secondary cephalopods as well as squids and octopus. The result of stomach contents analyses suggested that this seal used many organisms of wide range as foods in the pack ice areas.

Although there are no definite trends of changes in foods by age among the older seals, specialized feeding on euphausiids was found in newly weaned pups. Euphausiids appeare to be not only available but also indispensable foods for pups after the weaning, this would be evolved feeding adapted to the pack ice condition.

INTRODUCTION

Ice-breeding harbor seals (largha seal), *Phoca largha*, is relatively frequent species in the pack ice areas off the Western Hokkaido and Southern Okhotsk Sea occurring in early spring (Inukai, 1942; Wilke, 1954; Tikhomirov, 1968; Naito and Nishiwaki, 1972; Naito and Konno, 1980). In these days, the informations related to the reproduction and distribution have been reported (Naito and Nishiwaki, 1972; Naito and Konno, 1980). However, no studies on food of this species have been made except the fragmental informations.

Fay (1974) reviewed the relations between sea ice and marine mammals, and he pointed out that one of the roles of sea ice for pagophilic seals was food supply. In this connection, the investigations on food of largha seals would be meaningful so as to consider the relations between sea ice and this seal.

In the present study, stomach contents of largha seals collected in the open pack ice area of the east coast of Sakhalin and Nemuro Strait were examined. The sampling was carried out in the early to mid spring of post-breeding season for largha seals. Then, changes in food with age, especially for pups after the weaninng, were examined.

MATERIALS AND METHODS

Sampling areas and seasons

During this study, some parts of stomachs were collected from the carcase

Sci. Rep. Whales Res. Inst.,
No. 34, 1982, 123–136

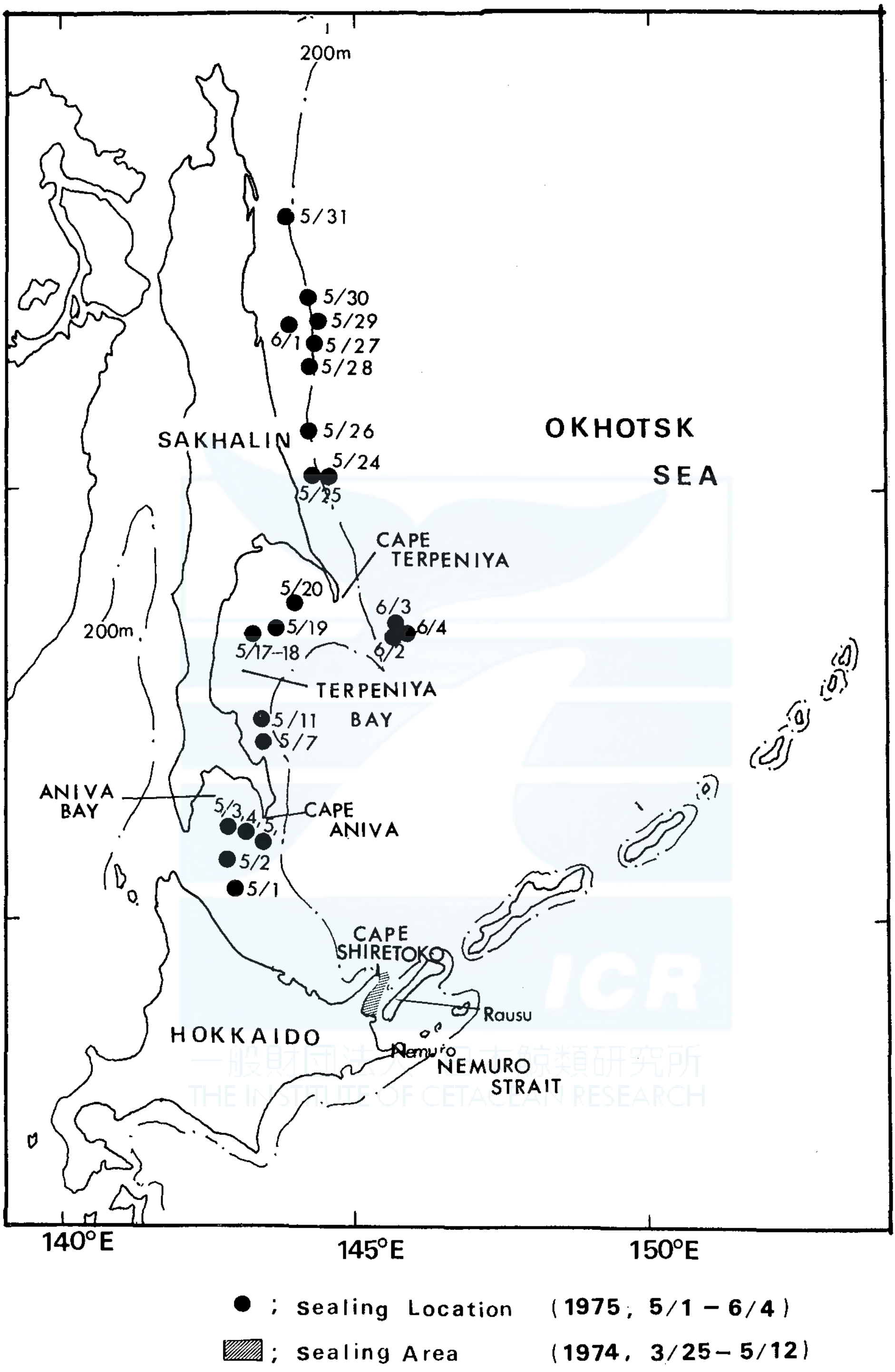

Fig. 1. Catch locations of the largha seal.

accumulated in Kanazawa Fur Co., Nemuro, Hokkaido. Those seals were hunted in the pack ice area of Nemuro Strait during 25 March and 12 May 1974. Others were obtained in the pack ice area off the east of Sakhalin from the operation of *Dairin maru No. 5* (75.00 gross ton.), which is floating factory sealing type, in the early spring during 4 March and 2 July 1975 with chasing to " front " of pack ice area. Both of sampling areas are shown in Fig. 1.

Stomach contents and data collection

All seals used in the present study were killed by shot guns or rifles. Initially, for the convenience of sampling stomach contents, all stomachs which were supposed to contain foods were reserved, but empty stomachs were not sampled after checking of contents. The stomachs were removed from the carcase bound at acrdiac orfice and pylorus with strings to avoid flowing out of contents. Sampled stomachs were reserved in 20% of formalin solution. The details of samples are summarized in Table 1. At the same time, body length and sex data follow on the all samples in both areas.

For the ageing carnine teeth were taken from under jaws, the growth layers were counted based on the same methods as reported in Naito and Nishiwaki (1972). Among the Sakhalion samples, 43 animals with stomach contents were aged by above methods, however, no ageing materials were collected in Nemuro Strait.

Identification of food species

Stomach contents were examined at the laboratory after the sampling works. If the contents are found under the very fresh condition in the stomach, food species was identified based on the outside characters, whereas in the case of contents heavily digested identification was aided by several collections of fish skelton, otolith and beak of cephalopods obtained in the adjacent waters of Hokkaido, as well as following publications; Hotta (1961), Matsubara (1955) and Watanabe (1958).

However, I was not able to succeed in satisfactorily identifying most of squids and octopus which consisted of only beak.

TABLE 1. SAMPLING SAMMARY ON STOMACHS OF LARGHA SEALS IN THE PRESENT STUDY

Sampling Area & periods	No. stomach examined	No. stomach with age and length data	No. stomach with length data
Nemuro Strait			
25 March—9 May 1974	47	—	47
15 March—15 May 1970	26*	26*	26*
Sakhalin			
1 May—4 July 1975	43	43	18

* Samples collected by Mr T. Itoh in 1970, these were used in only examination of changes in food with age.

Index of food composition

Several problems have been devoted in index of stomach contents analysis, therefore following two methods similar to the indices used in Spalding (1964) were considered for the present study.

Weight index: The stomach contents were weighed in each 5 g scale under the wet condition separately by food species. Small amounts of heavily digested materials less than 5 g which should not be regarded as food were recorded as " trace " in weight. Weights of each food species in each stomach are summed and index was represented as a percentage of summed weight against combined weight of each item of the total stomachs examined.

Occurrence index: Regardless of number of individuals, if at least one food species occurred in a stomach, this species was recorded as " one occurrence ". This index is expressed as a percentage of number of occurrence against the total number of stomach examined.

STOMACH CONTENTS

As shown in Table 2, the analyses of largha seal stomach contents revealed that fishes, cephalopods were the primary food in the Nemuro Strait and waters off the east coast of Sakhalin.

Among the Nemuro strait samples, fishes was the primary food item for largha seals, comprising 78.9% and 91.7% in occurrence and weight indices, respectively. Among them, *Theragra chalcogramma* was the dominant species at 48.9% of occurence index and 47.0% of weight index, Pleuronectidae and *Hypomesus japonicus* seemed to be also major species.

Cephalopods was secondary item, comprising 42.6% and 6.3% in occurrence and weight indices, respectively. It should be taken in account of under-representation in weight index of this item, because the remainder of cephalopods in stomachs usually consisted of beaks, eye lenses and pens. Concerning the identification, most of cephalopods were found under the heavily digested condition, it was considerably difficult, therefore, to identify species among the squid's beaks, although octopus was identified to be *Paraoctopus dofleini* by the chracteristic their beaks.

Euphausiids including *Thysanoessa inermis* were found in the ten stomachs comprising 21.3% and 2.0% in occurrence and weight indices, respectively. There were clearly two types in occurrence of this item; one case was very small amount of fragments of euphausiids occurred, the other was large amounts of euphausiids occupied the most portions of the stomach contents. The latter type feeding seemed to be more frequent in younger animals. This will be examined in the latter chapter.

The results of stomach contents analyses in the Sakhalin samples, were almost similar to that in the Nemuro samples. *T. chalcogramma* was also the most important food far from the others, comprising 72.1% and 82.5% in occurrence and weight indices, respectively. *Clupea pallasi*, which is abundant species in sea ice

TABLE 2. FOOD COMPOSITIONS OF LARGHA SEALS IN NEMURO STRAIT AND OFF THE EAST COAST OF SAKHALIN

Food species	Nemuro Strait n=47				Sakhalin n=43			
	Occurrence index		Weight index		Occurrence index		Weight index	
	Number Oc-curred	%	g	%	Number Oc-curred	%	g	%
Fishes	37	78.9	24,495	91.7	31	72.1	13,560	82.5
Theragra chalcogramma	23	48.9	12,645	47.0	23	53.5	7,710	46.9
Pleuronectidae	10	21.3	1,020	3.8	1	2.3	trace	0.0
Eleginus gracilis	2	4.3	435	1.6	3	7.0	1,585	9.6
Pleurogrammus sp.	1	2.1	70	0.3	2	4.7	1,460	8.9
Hypomesus japonocus	5	10.6	4,180	15.5	—	—	—	—
Osmerus dentex	2	4.3	465	1.7	1	2.3	70	0.4
Sebastolobus macrochir	2	4.3	1,735	6.5	—	—	—	—
Sebastes schleigeli	1	2.1	300	1.1	—	—	—	—
Ammodytes sp.	1	2.1	10	0.0	—	—	—	—
Aptocyclus ventricosus	1	2.1	300	1.1	—	—	—	—
Gymnocanthus sp.	1	2.1	950	3.5	—	—	—	—
Gadus macrocephalius	1	2.1	310	1.2	—	—	—	—
Lycogramma zesta	1	2.1	2,140	8.0	—	—	—	—
Clupea pallasi	—	—	—	—	6	14.0	2,665	16.2
Cottidae	—	—	—	—	2	4.7	70	0.4
Unidentified fish	2	4.3	100	0.4	5	11.6	trace	0.0
Cephalopods	20	42.6	1,710	6.3	15	34.9	720	4.3
Octopus, *Paraoctopus dofleini*	3	6.4	225	0.8	12	27.9	90	0.2
Squids	17	36.2	1,485	5.5	3	7.0	630	3.8
Euphausiids	10	21.3	530	2.0	12	27.9	2,035	12.4
Thysanoessa inermis	2	4.3	390	1.5	4	9.3	290	1.8
T. raschii	—	—	—	—	5	11.6	1,505	9.2
Decapods	—	—	—	—	7	16.3	130	0.7
Pandalus borealis	—	—	—	—	3	7.0	130	0.7
Chionoecetes opitio	—	—	—	—	1	2.3	trsce	0.0

area in Okhotsk Sea, was ranked in second species among fishes.

It was notable, among the item of cephalopods, that octopus were more frequent than squids in contrast with that in Nemuro samples.

Euphausiids revealed two species, *T. inermis* and *T. raschii* indicating almost same occurrence. Two species of decapods, *Pandalus borealis* and *Chionoecetes opitio* were found, but these were minor item as foods for largha seals.

The analyses show that *T. chalcogramma* are heavily used as a most important food for largha seals in the early spring of both areas. This fish is also important foods for land-breeding harbor seal, *P. richardi*, in the northwestern region of North Pacific (Imer and Sarber, 1947; Wilke, 1954; Kenyon, 1965), furthermore Pitcher (1977) found that this fish was most dominant prey for *P. richardi* throughout the year in Prince William Sound.

Table 3 shows the fishing yields statistics in the Nemuro Strait during March

TABLE 3. FISHING YIELD STATISTICS FOR 1973 MARCH-MAY FROM NEMURO STRAIT AND FOR 1975 MAY FROM ANIVA AND TERPENIYA BAY

Species	Nemuro Strait March-May, 1973		Aniva and Terpeniya Bay May, 1975	
	tons	(%)	tons	(%)
Gadus macrocephalus	4,455.3	(13.3)	2.2	(0.1)
Theragra chalcogramma	18,029.1	(55.8)	1,425.3	(81.5)
Eleginus gracilis	—	—	17.9	(1.0)
Pleurogrammus sp.	773.6	(0.2)	0.1	(0.0)
Clupea pallasi	5.1	(0.0)	0.1	(0.0)
Pleuronec tidae	1,872.1	(5.6)	205.4	(11.4)
Hypomesus sp.	—	—	0.1	(0.0)
Sebastolobus sp.	177.5	(0.5)	—	—
Other fishes	8,269.5	(24.6)	—	—
Octopus	10.0	(0.0)	0.4	(0.0)
Squid	1.5	(0.0)	—	—
Shrimp	—		9.0	(0.5)
Others	—	—	98.5	(5.5)

and May 1973 and in the waters off the east coast of Sakhalin in May 1975 (Hokkaido suisanbu, 1974; 1976), approximately coinciding with the sampling seasons and areas in the present study. The catch of *T. chalcogramma* was also dominant far from those of others. Although there are still several problems, assuming the fisheries catch shows fish-fauna in the both of two waters, largha seals feed primarily on abundant species. This suggests no preference on species if the organisms are available size and behavior for seals as foods. Generally speaking in the trends of stomach contents, most of food species which occurs in stomachs are basically in the category of coastal species in this season inhabiting from the surface to the bottom, moreover, schooling fishes such as *T. chalcogramma*, *Hypomesus japonocus* contributed as major food species for this seal. The only few informations of fishes, cephalopods and others are available in the ice areas, but largha seals can possibly use the most of nekton inhabiting ice areas as their foods.

CHANGES IN FOOD WITH AGE

Spalding (1964) pointed out an increase in food size and suggested changes in food species with age in northern fur seals, *Callorhinus ursinus*. Moreover specialized feeding habits of newly weaned pups in *P. richardi* has been reported by Havinga (1933), Fisher (1952), Bigg (1973) and Pitcher (1977). Therefore, substantial changes in food with age would be expected in the samples of the present study.

For the convenience of this examination, " growth stage " which was classified into four categories, pups, youngs, maturings and adults, based on primarily ages was adopted instead of age classes due to small sample size. Among the samples of no age data, however, growth stages were classified tentatively by their body length based on age-length relations in Tikhomilov (1964) and Naito and

Nishiwaki (1972). As a result, following criteria were used in this examination:

Stage	Age	Body length (cm) Male	Female
Pups	0	distinguishable from other stages	
Youngs	1-2	-130	-127
Maturings	3-4	131-145	128-141
Adults	5-	146-	142-

The 26 stomach samples with age data obtained in Nemuro Strait in 1970 were added to the present study examined in previous section, then the total of 116 stomachs were available in this examination.

Food compositions

Food compositions in each growth stage are indicated in Table 4.

Pups: 16 stomachs were examined in this stage, revealing fishes, cephalopods, euphausiids and decapods. Among them, euphausiids are the dominant

TABLE 4. COMPOSITION OF FOOD ITEMS IN RELATION TO THE GROWTH STAGE IN HARBOUR SEAL

Food items	Pups Oc.%	N=16 W.%	Young Oc.%	N=35 W.%	Maturing Oc.%	N=16 W.%	Adult Oc.%	N=49 W.%
Fishes	18.8	1.0	74.3	90.9	75.0	88.7	91.8	95.8
Theragra chalcogramma	6.3	0.2	34.3	36.4	56.3	58.7	65.3	53.7
Clupea pallasi	—	—	8.6	3.5	6.3	0.7	6.1	7.2
Pleuronectidae	6.3	0.0	8.6	9.4	31.3	8.7	12.2	3.5
Eleginus gracilis	—	—	11.4	4.5	—	—	4.1	8.2
Pleurogrammus sp.	—	—	—	—	6.3	0.9	2.0	0.2
Hypomesus japonicus	—	—	—	—	—	—	2.1	1.6
Osmerus dentex	—	—	8.6	18.7	—	—	6.1	1.7
Sebastolobus macrochior	—	—	5.7	8.9	—	—	4.1	0.4
Sebastes schleigeli	—	—	8.6	7.8	—	—	4.1	3.7
Sebastes sp.	—	—	—	—	—	—	8.2	4.4
Ammodytes sp.	—	—	2.9	0.1	—	—	—	—
Aptocyclus ventricosus	—	—	—	—	—	—	4.1	1.3
Gymnocanthus sp.	—	—	—	—	12.5	19.7	6.1	1.0
Lycogramma zesta	—	—	—	—	—	—	2.0	6.9
Unidentified fish	6.3	0.8	5.7	1.6	—	—	2.0	1.0
Cephalopods	6.3	0.8	54.2	6.7	75.0	9.6	50.0	4.0
Octopus	—	—	22.9	0.2	25.0	4.7	30.6	1.2
Squid	6.3	0.8	31.4	6.5	50.0	4.9	24.5	2.8
Euphausiids	81.3	95.5	25.7	2.4	18.8	1.7	6.1	0.0
Thysanoessa inermis	25.0	24.0	—	—	—	—	—	—
Thysanoessa raschii	31.3	67.8	—	—	—	—	—	—
Decapods	12.5	2.7	—	—	—	—	12.2	0.2
Pandalus borealis	6.3	1.2	—	—	—	—	—	—
Chionoecetes opitio	—	—	—	—	—	—	2.0	0.0

Oc.% = percentages of frequency of occurrence
W.% = Percentages of weight composition

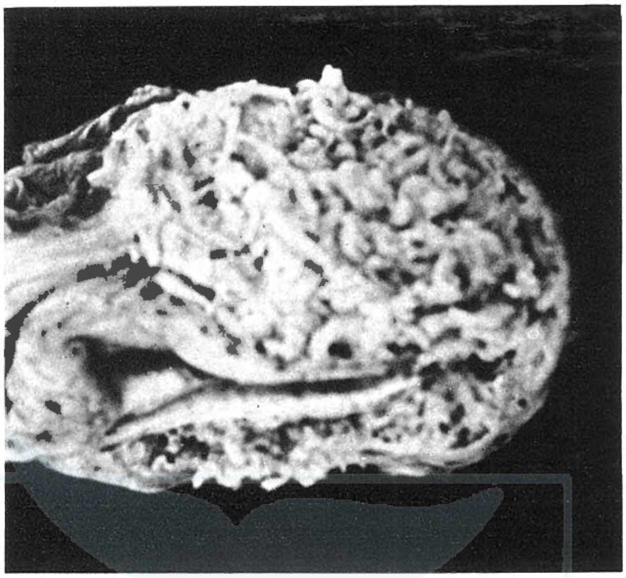

Fig. 2. Stomach contents of pups containing *Thysanesas inermis*.

item in both indices (81.3% and 95.5% in occurrence and weight indices, respectively), *T. inermis* and *T. raschii* were identified in this item. It was notable that 13 out of 16 pups fed on only euphausiids, showing clearly " true foods " rather than " accidental foods " as shown in Fig. 2. On the other hand, fish (*T. chalcogramma*) and cephalopods were minor item in this stage, and these were found in only one stomach collected in 17 May.

Young: 35 stomachs were available in this stage. Fish was primary item comprising 74.3% and 90.9% in occurrence and weights indices, however, *T. chalcogramma* of dominant species showed only 34.5% and 36.4% in occurrence and weight indices, respectively, indicating considrably lower value than that in older stages. On the other hand, indices of euphausiids revealed lower value than pups stage and these are seemed to be not " true food " in this stage, although two seals fed on relatively large amounts of euphausiids.

Maturing: Fish was primary item in the 16 stomachs, indicating almost same value as previous stage. It was notable that cephalopods occurred frequently (75.0%) among the all growth stages.

Adult: Fish contributed as more important foods indicating 91.8% and 95.8% in occurrence and weight indices, respectively. At least 13 species as well as *T. chalcogramma* were identified. The segments of euphausiids occurred in three stomachs, but these were cleary accidental foods.

Summarizing above, euphausiids were mainly used as a substantial food for pups, whereas this item was minor as " accidental food " in the other older stages, although few seals in young stage fed on relatively large amounts of euphausiids. These suggested specialized feeding on euphausiids in pups. On the other hand, fishes and cephalopods much contributed as major items in older three

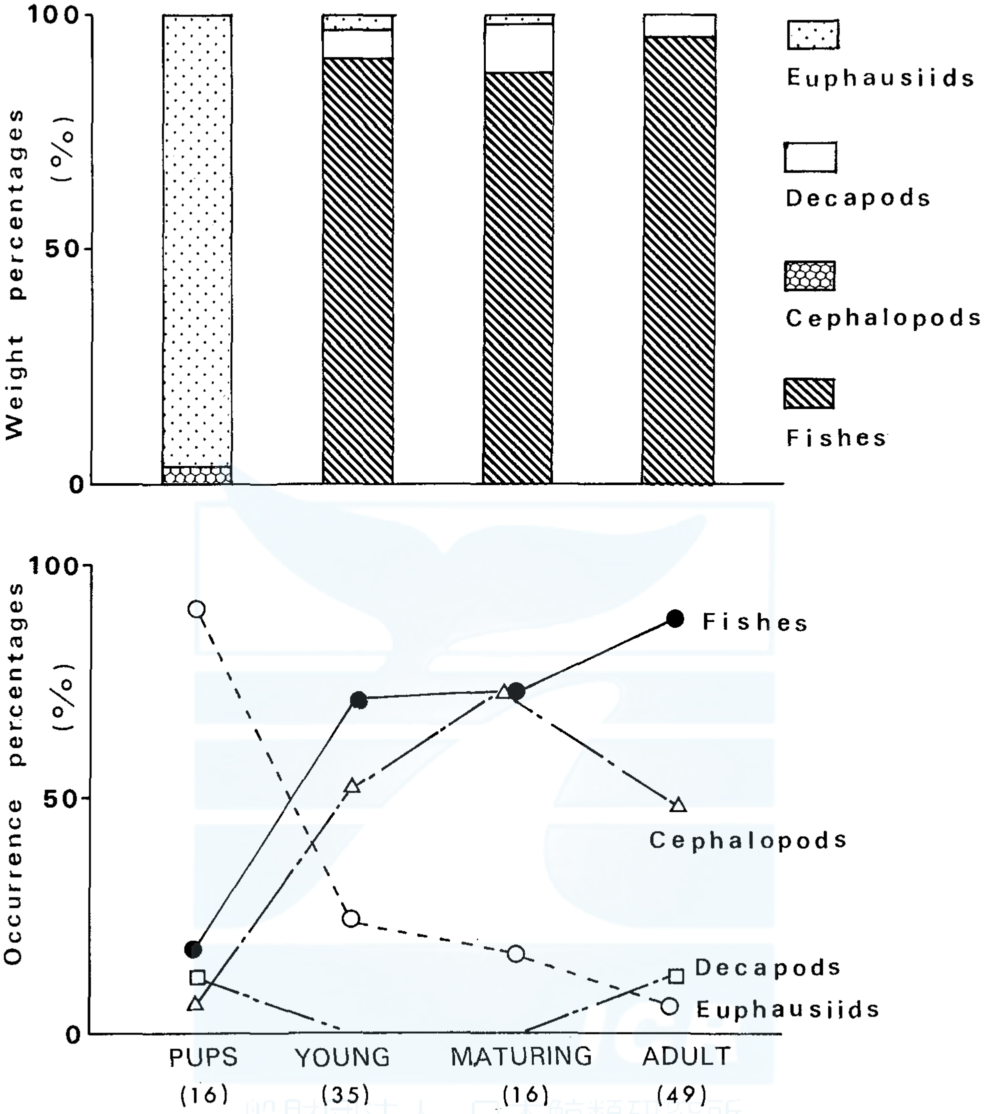

Fig. 3. Changes of food composition in relation to the growth stages in largha seal. upper: weight index, below: occurrence index.

stages. It was notable that the values in both indices of *T. chalcogramma* seem to increase with growth stages. Fig. 3 shows changes in foods composition based on food items with growth stages. These changes were confirmed by the statistical test in both indices. In the case of weight index, 2-n test utilizing χ^2 values was adopted so as to examine changes between nearest two growth stages. The test revealed the significant difference between pups and young stages ($\chi^2_{cal}=26.26>\chi^2=(0.05, 3)$), whereas any differences were not detected between the other stages. For the convenience of statistical test in occurrence index, 2-2 test utilizing χ^2

values was adopted. The test revealed significant differences between pups and youngs stages in items of euphausiids ($\chi^2_{cal}=13.81>\chi^2$ (0.05, 1)), fishes ($\chi^2_{cal}=13.81>\chi^2$ (0.05, 1)) and cephalopods ($\chi^2_{cal}=10.63>\chi^2$ (0.05, 1)).

Both of tests confirmed different food composition between pups and other stages, that is, pups preferred euphausiids to fishes and cephalopods.

Food size

It seems that food size probably changed with growth stages with changes in food species. However, it is slightly difficult to measure food size directly utilizing stomach contents. *T. chalocogramma* was dominant food species in the stomach contents examination of this seal, and occurred in all growth stages. Then, assuming that this fish is the representative food item, food size was examined. The subopercle of this fish has very unique shape as shown in Fig. 4, and it often contributed to the identification of this fish in the stomach contents. Moreover,

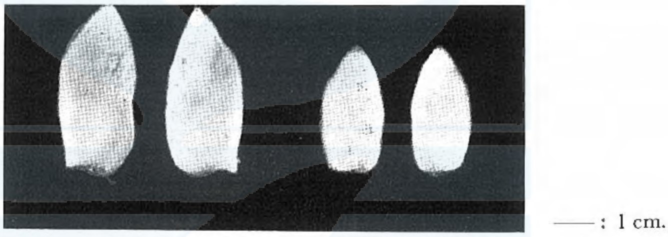

Fig. 4. Subopercle of *Theragra chalcogramma* found in stomach of largha seals.

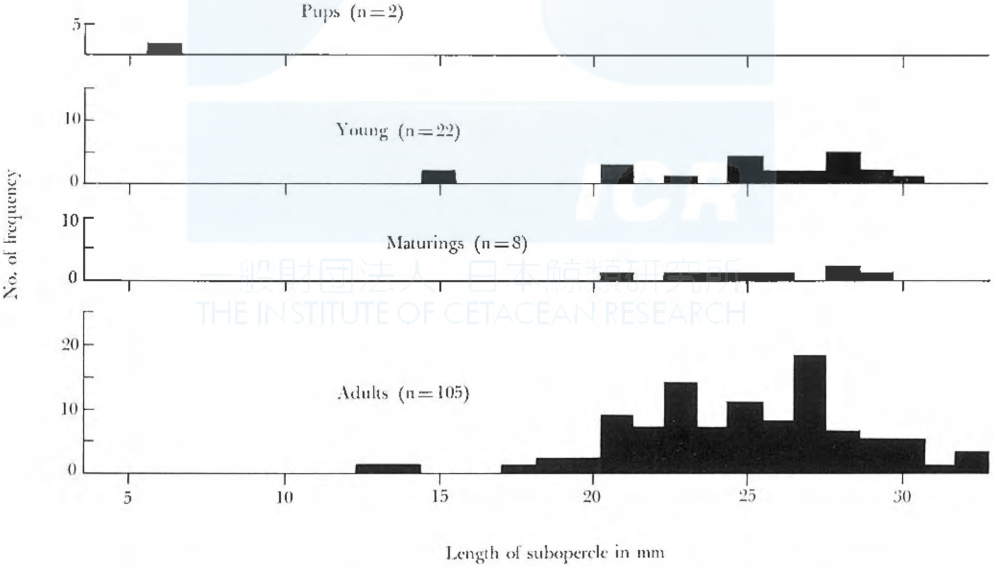

Fig. 5. Size distributions of subopercles of *Theragra chalcogramma* found in the stomach contents in each growth stage.

at the counts of number of individuals, this character appears to be better than that of otolith.

The length distributions of undamaged subopercles in each growth stage are shown in Fig. 5. The means and variances (95% confidence limits) of those in each stage were:

pups,	7.00 (mm)
youngs,	25.09±7.55
maturing,	25.50±5.10
adult,	25.15±6.96

The differences of mean length of subopercles between stages were examined utilizing t-values. The test revealed no significant difference between three older stages. Yoshida and Kato (1981) examined the relation between length of subopercle and standard length of *T. chalcogramma*, following relation was made:

$$Y=0.0936\ X^{0.958}$$

where, X=length of fish and Y=length of subopercle.
Utilizing above relation, stnadard length of *T. chalcogramma* can be reproduced as follows:

pups	90.35 (mm)
youngs	342.51±97.78
maturing	348.36±64.93
adults	343.37±89.82

From the above estimations, it is clear that pups fed on smaller size of *T. chalcogramma* compared with older animals in other three stages.

Taking account of sizes of other food organisms, *T. chalcogramma* was in the largest category of food size in each older three stage. It was notable that all food species found under the fresh condition retained whole body. These suggest swallowing feeding type rather than gnawing. Therefore, there is no difference in available food size among the three older stages.

DISCUSSION

As mentioned previously, sample collections in the present study were carried out during the post breeding seasons, where is front of sea ice area when sea ice were melting and retreating toward the north. The chronological reproductive behavior of largha seal in this period have been reported by Naito and Nishiwaki (1972). According to their reports, the parturition took place between middle and end of March, moulting of the white coat and weaning occurred 2–3 weeks after birth. It is also notable in their report that independence of pups from their mothers occurred suddenly compared with land-breeding harbour seal, suggesting no mother's care of feeding to pups. Although the behavior of pups of early stage of life after weaning is still not known, even for such pups as never experienced and learned diving and feeding, available food would be only euphausiids which is stational and smaller organisms in the ice area. Moreover, *T. inermis* and

T. raschii found in stomachs of pups usually formed patch distribution near the surface (Ponomareva, 1963), these would be also convenient for pups. Furthermore, Naito and Nishiwaki (1972) found the decreasing in the thickness of blubber among the after weaning pups compared with suckling animals. If the euphausiids or similar organisms were absent in the pack ice area, most of pups would not be able to survive in such a critical period above. It appears, therefore, that the presence of euphausiids in the area and zone in which newly weaned pups can swim and dive guarantees survival of pups in the early life stage of this species.

Fay (1974) pointed out that one of the major role of sea ice for pagophilic seals was food supply. In this connection, generally speaking, specialized ice community of organisms are formed under inner parts of ice floes (McRoy, 1974; Horner, 1976), and the zoo plankton such as euphausiids which used organisms above as food are concentrated in the pack ice area (Fukushima and Meguro, 1966). Therefore, specialized feeding on euphausiids of pups seems to utilize fully above phenomena.

However, specialized feeding of pups would be only continued during limited periods in post breeding season, that is, this feeding may be transitional feeding, until pups can feed on fishes and cephalopods with increasing of feeding experience. This would be supported by the result of stomach contents of pup collected in latest periods among the stomach samples from pups, and also would be closely related to the behavior of sea ice in this season. Moreover, considerably short suckling periods of this seal reported by Naito and Nishiwaki (1972) possibly related to the specialized feeding on euphausiids of pups. After the specialized feeding in pups, it appears that young seals forage over a larger feeding area with development and increasing in feeding experience, select a greater number of food species and take prey of larger size. As a result, throughout their life, largha seals use organisms in very wide range inhabiting the pack ice area.

Finally, the pack ice served not only reproductive grounds but also food supply for largha seals, especially in early stage of their life. In other words, largha seals have evolved feeding habits adapted to the ice condition.

ACKNOWLEDGMENTS

This paper originally consisted some parts of a thesis which was submitted for an M. A. degree in Fisheries at Hokkaido University. It has been slightly modified for the present publication.

During the course of above thesis, Drs T. Tsujita, S. Mishima, K. Shimazaki, T. Nishiyama (present, University of Alaska) and H. Ogi of RINPF of Faculty Fisheries, Hokkaido University made helpful suggestions and gave facilities. Drs T. Igarashi and A. Kawamura of Hokkaido University also made valuable suggestions in draft of thesis.

I wish to express my thanks to Dr Y. Naito of National Polor Research Institute for his valuable instructions in the treatment of seal's materials and suggestion in making draft. My sincere thanks also are due to Mr T. Itoh of Gifu dental college for the permission to use his stomach collections and valuable suggestion. Dr K. Wada of Kyoto University and member of Marine Mammal Research Group encouraged to develop my thesis.

Finally, I was not able to carry out sample collecting without the co-operation of those mentioned below: Mr K. Shibuta of Shibuta Kaijyu Gyogyo Co. Ltd., crew of *Dairin maru* No. 5, and Messrs N. Kanazawa and S. Sasamori of Kanazawa fur skin Co. Ltd.

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RECENT SURVEY ON THE DISTRIBUTION OF THE AFRICAN MANATEE

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ABSTRACT

The survey was made in travelling west African countries in 1980 and 1981 mainly on the distribution of African manatee, *Trichechus senegalensis*.

It was confirmed that the manatees were inhabiting the Senegal River system.

Manatees were distributed sparsely between Guinea-Bissau and Liberia through Sierra Leone and abundantly from Ivory Coast to Nigeria extending to Mali. Considerable numbers were in Cameroon and Gabon. The most abundant area was in the Niger River and its tributaries with connected swamps.

According to the literature, the southern limit of the distribution is in Angola, but we were not able to enter the country to confirm it.

INTRODUCTION

A fundamental thing for the study of an animal distribution is to determine whether only one or more than one species are present. In an attempt to answer the species question, the senior author examined the sirenia collection at the British Museum (Natural History) in 1973. Also, through the kind cooperation of Dr. Chales Roux (Museum Nationale d'Histoire Naturelle, Paris), the senior author studied the skeleton of a male manatee in Abidjan, Ivory Coast and found no evidence that more than a single species of African manatee exists. This agrees with previous findings (Hatt, 1934; Kaiser, 1974; Rice, 1977; Husar, 1978).

Since then, the senior author has visited Dakar and Abidjan twice for preparatory survey on the status of the animals. In the summer (July-August) of 1980 and the winter (January-March) of 1981, the present authors shared in area to perform extensive field survey.

Brief report on the survey was aurally presented by the senior author at the marine mammal symposium, International Theriological Congress III on 17 August 1982 in Helsinki. The present report was rewritten with some corrections, particularly the estimation of living numbers were to be left to the future studies.

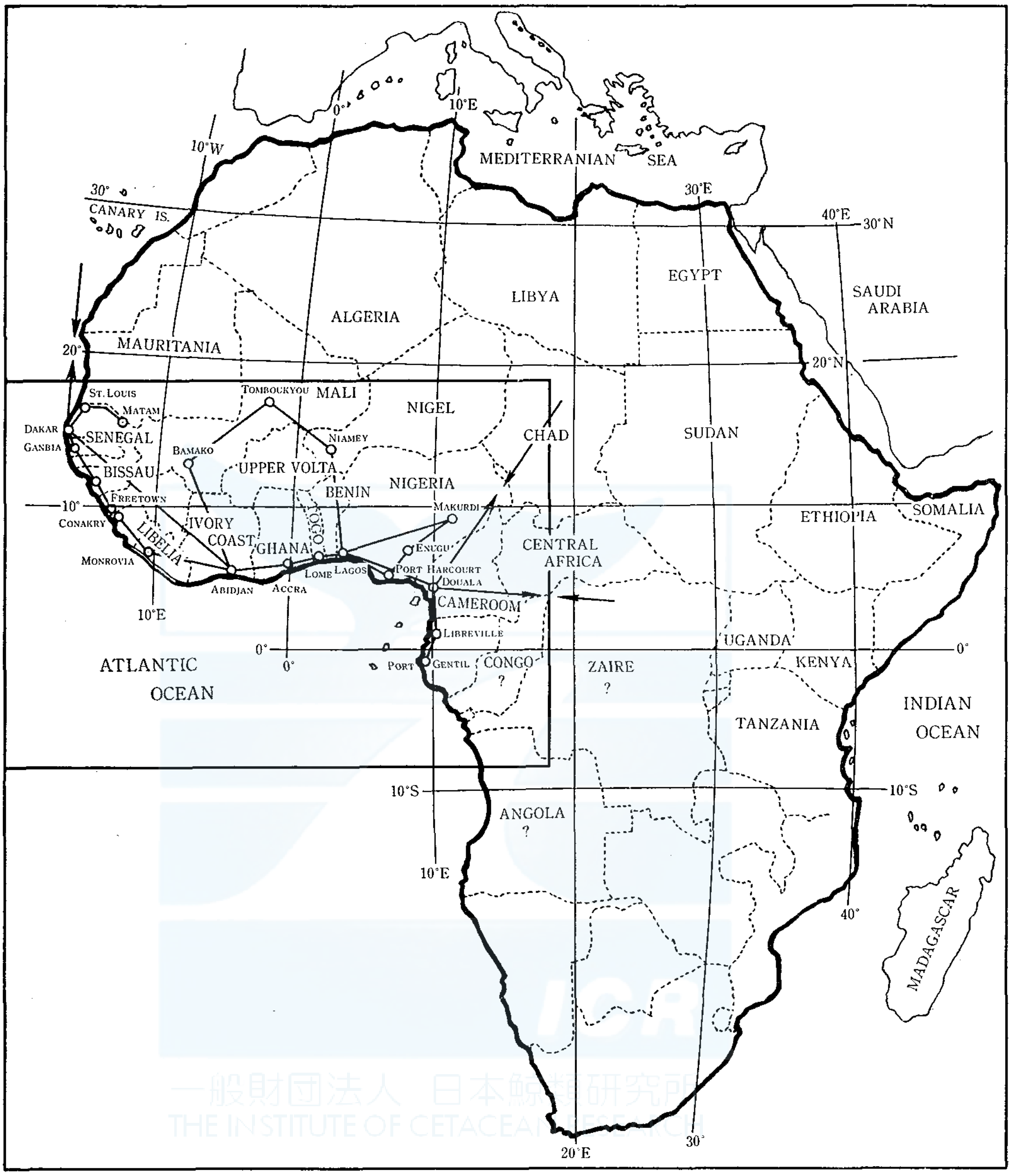


Fig. 1. Traveling route of the survey.

METHOD

The principal method of survey was to collect information through interviewing local zoologists or biologists, fishermen at market places and general inhabitants by showing photographs of the animal. Information on the climate and other environmental conditions were also recorded. The group members often walked into the river valley, swamps or other places where manatees might occure. One of the most difficult problem was to identify the animals in muddy colour who quietly submerged in the water for most of the day and surfaced to breathe by exposing only a small portion of the muzzle tip.

DATA COLLECTION

Senegal (Republique du Senegal)

Investigation on geographical and environmental conditions along the Senegal River was made to determine the northern and western limit of the distribution of the manatee. Two group members flew from Dakar to Saint Louis and one of them further proceeded to Richard Toll, Podor, Matan along the border between Senegal and Mauritania.

The Senegal River is very broad at its mouth where sand bar stretches to the sea and blocks high waves, so the water around the estuary is calm. Since the area (Saint Louis as its center) is heavily industrialized, it seemed difficult for manatees to inhabit. Naturally no report of manatee sightings were obtained in this area. Similarly, we were unable to collect data of recent years in Dakar district.

This area which used to be a quiet lagoon has now turned to dry land. Recent extreme dry weather apparently affected the river and subsequently the manatee habitat.

Survey at Richard Toll was greatly facilitated by Dr. Morel, French ornithologist stationed there, through the cooperation of Dr. Alioune Ndiaye of Dakar. According to Dr. Morel's information, manatees are decreasing, but a considerable number of animals are still inhabiting Lac de Cuiers. At Matan, no report was obtained to indicate the existence of manatee.

The Senegal River meets a flow from Lac de Cuiers and winds widely on its way to Podor. The river is incredibly dark brown in colour and flowing further to the vast land of savannah. There seemed to be little possibilities of the animals feeding on water grass, because no forage would be available in this area. Therefore it seemed that manatees were not able to live there, at least from Lac de Cuiers to Matan except in the secluded parts of Lake Lac de Cuiers and swamps. Native people of Matan gave us no report of living manatees. Matan is so hot in July that even Dakar people feel it too hard. Environmental condition seemed to be too severe for manatees to survive in summer. However since the head waters of Senegal River is said to be connected with that of the Niger River in the vicinity of Bamako during rainy seasons, there is possibility of some manatees are recruited from the Niger to the Senegal. Based on what we have heard and on the examination of local conditions, a rough estimate of the manatee population in Senegal, would be a few hundred.

Gambia (Republic of the Gambia)—Liberia (Republic of Liberia)

We only collected data that manatees were inhabiting the Gambia River. To collect clear evidences of manatees existance there, our stay was too limited in

Bissau (*Republica da Guine-Bissau*), Conarkry (*Republique Populaire Revolutionaire de Guinee*), Freetown (*Republic of Sierra Leone*) and Monrovia (*Republic of Liberia*).

Ivory Coast (Republique de Cote D'Ivoire)

In the Ivory Coast geographical feature altered during August under influence of tropical rainbelt which shifts to the north in summer in the northern hemisphere (Beadle, 1978). In Abidjan, we exchanged all available information and knowledge on manatees with Dr. Francis Laugine, French veterinarian and director of the Abidjan Zoo. With his assistance, we used cars and a small plane of Cesna type for survey. We sighted considerable number of manatees in various rivers, swamps and lagoons. This area holds a large population of manatees as well as the Niger does. The number of the animals in this country may amount to several thousands. There were some suspicions that manatees were caught and eaten by native people. Catch of manatees had been prohibited since the time of French domination and was still in effect. But poachers catch and eat manatees without leaving any evidence of carcass or bones and keep the fact secret for long time. So there is no effective procedure of conservation. The situations are similar to dugong catch regulation in Indo-Pacific (Nishiwaki et al., 1981). Dr. Laugine plans a project of manatee research which may start in near future.

Ghana (Republic of Ghana) with information about *Togo (Republique Togolais)* and *Bennin (Republique Populaire du Bennin)*

Investigation in Ghana was enhanced through the cooperation of Dr. Kazumori Minami of the Noguchi Memorial Institute for Medical Research, University of Ghana, and Dr. R. Kumar, Indian entomologist, of the Department of Zoology, University of Ghana. Survey in the Lake Volta area was carried out under their guidance. According to Dr. J. Vanderpuye, Ghanian researcher of Volta Basin Research Project, no manatee inhabits the Akosombo dam area. Mr. A. K. Opoku of the Volta River Development Authority, informed us that he heard a few years ago that there had been abundant manatees in Asukawkaw River Arm, east coast of Lake Volta, about 9 km north to Akosombo. Dr. E.Q.A. Asibey of the Department of Game and Wildlife, Ministry of Forestry, told us that manatee catch was prohibited by law, and because of that, reports of local manatee catches hardly reached to the government officer. However, one catch was reported in the West Arm of Lake Volta in 1964 and another in Central Three Corner area in 1980, and some animals were seen in the River Tano (west Ghana) sometime before, but none at present. During the construction of Akosombo dam which was completed in 1965, (Obeng, 1969), series of manatee skeletons were excavated, which are kept at the Department of Zoology, University of Ghana: photographs of them were taken.

In the former description (Happold, 1975), the manatee distribution was reported along the coast line of Ghana, but no fisherman in Cape Three Point, Elmina, Cape Coast, Accra, and of Tema, reported occurences of the animal in the sea. Although someone told us that an individual or individuals of such animal were caught by fishing net in Angola, there was no dependable evidence of the incident. It was suspected, therefore, that the report might have been of dolphins or sharks. Togo and Bennin seemed to be quite different in political, economic and other features. There is little possibility of the manatee distribution, partly because there is no big river such as the Niger or the Congo (Zaire) Rivers in their territories.

Through the assistance of Japan International Cooperation Agency (JICA), we were able to obtain some information in a relatively short period of time.

Mali (*Republique du Mali*) and *Niger* (*Republique de Niger*)

In the vast desert area of extremely dry Mouritania (*Republique Islamique du Mouritanie*), northern Mali and the major land of Niger, exceptional green patches can be seen in Mandingo Plateau in the up stream of the Senegal River. The upper Niger River also reaches to this high plateau area with its central town named Bamako, Mali. Although the river is not very wide at Bamako area, volume of the river water fluctuates largely between dry and rainy seasons. The Niger River flows to northeast and continues into the wilder area, forming Inland Niger Delta, and reaches to Tombouctou (Timbuktu). After Tombouctou, the river gradually turns to southeast and crosses the border to Niger.

Collected data in the area indicate that considerable number of manatees are in the Inland Niger Delta, and some are inhabiting the lower stream neigbouring to Neamey, but the population size is scarcely known. The river basin is the only place in the dry desert area for manatees to survive.

Nigeria (*Federal Republic of Nigeria*)

Investigation in this country resulted us something through the help of local scientists. Dr. C. B. Powell of the School of Biological Sciences, University of Port Harcourt, gave us a valuable report that abundant population of manatees had been in Lake Kainji located in the middle flow of the Niger River and its tributary of the Benue River. However, over killing caused the manatees to decrease in number and now there may be a few hundred in the lake.

An important and reliable information was provided to us by Mr. A. B. Wilson of the Nigerian Institute for Oceanography and Marine Research. He told us that there were still many manatees in the Benue River. Although Dr. Powell spoke as a few hundred, his estimation was likely a few thousand. Dr. Akihiro Takihara, Medical Officer of the Embassy of Japan to Nigeria, told us that he saw some manatees kept alive by local people near by Makurde located on the side of the Benue River.

People said that occurrences of manatees had been counted before (Happold, 1975), but the number has been decreasing. Mr. Wilson informed us that an animal was tangled in a fisherman's net at Port Harcourt. He identified the animal as a manatee by seeing our photographs. If it is true, his report sounds like a manatee was taken from the sea, but the fact was that, Port Harcourt is located on the river side, a little up stream from the mouth. Brackish waters may be flowing in from time to time, but salinity of waters is low in the very wide estuary. Some individuals might be washed out to the sea with strong current, against the animal's swimming effort.

Cameroon (*Republique Unie du Cameroun*)

The coastline of Cameroon faces the Gulf of Guinea, and it may be divided geographically into two sections; high rocky coast of volcanic lava in the northwest and low swampy and sandy coasts in the south (Ngwa, 1967). Because of this difference in topography, the west section (former British Cameroon) appears to have no manatees in small and rapid rivers flowing down from the Mount Cameroon (altitude 4070 m, active volcano). A small Zoo (Zoological Garden) has been established at Victoria, but its caretakers knew nothing about manatees in the district (South-West Cameroon). Fishermen in this town had some knowledge of the animal, called " Maiga ", but they denied its occurrences.

There is a well-developed estuary, near the commercial capital of Douala, into which two rivers (R. Mungo and R. Wouri) are flowing, and the local residents informed us that there were manatees in the upstream of the River Mungo. However, the littoral district is heavily populated and urbanized, so it is hardly considered that there are large number of manatees. The Museum of Douala has a pictorial display of a manatee as one of the significant components of the local fauna.

There may remain a considerable number of manatees in the Sanaga River System, which is the largest in the country. Local residents interviewed at a riverside market at Edea described that the animal, called " Maga ", lived along the entire river except in the rapids, and that the manatees were eating grasses in the river. Although it is prohibited to kill manatees by law, they occasionally catch them for meat in order to entertain visiting dignitaries, with special permissions. It appeared that, from what the people described, there were wide-spread incidents of poaching activities, at least near the population centers. It is also told that there was a licensed manatee hunter, Mr. Ngoye Samuel, at Mal Jeown near Mouanko village, south of Douala, who possessed a special permit for manatee hunting, which might be for local festivity.

Gabon (*Republique Gabonaise*)

In the vicinities of Libreville, the capital of Gabon, manatees had been caught very rarely from Baie de Mondah and Estuaire du Gabon. This report is based on personal communication between the group members and the missionary people at Donguila, and Dr. Domart, Direction des Chasses et Piches, Ministerie de l'Agriculture. The manatee is called as " Manga " in Gabon.

Approximately 150 km south to Libreville lies the city of Port-Gentil which is located at the mouth of River Ogoué, the largest river in Gabon. Mr. Bayona of Ogoué Marine Service, who regularly commute between the city and off-shore oil-rigs for servicing, informed us that he had not seen any manatee at sea, although seen large number of whales and dolphins passing in dry seasons. The local fishermen at Port-Gentil and also those at the neighbouring place of Ntchengue village mentioned that manatees were common in the River Ogoué and in the several connected lakes located between Port-Gentil and Lambaréné. Several individual persons informed equally that the manatees were also common in the southern coastal lagoons, such as Lagune Nkomi or Fernan Vaz. near Omboué and Lagune Ndogo, near Sette Cama. According to Mr. Jean Wack of Libreville, who worked as a timber merchant soon after the World War II and travelled frequently along the River Ogoué, manatees were abundant there before. He described that some experienced fishermen would lie in ambush for the animals in the river because manatees had moved onto a certain particular route every time in search of the food, species of aquatic plants.

Since Gabon is less extensively developed, it holds vast rain-forest area and river basins with relatively smaller population of about 1.3 million people in about 270,000 km^2 (density about 5/km^2) (Hancock, 1978), there may be large population of manatee in some of the above-mentioned localities. One of the group member went into the wilder swampy Ivendo River area where manatees may inhabit abundantly. One of our problems was that though experienced scientists may find the muzzle tip or a part of the body in muddy water and estimate abundance in the area, it is very difficult for them to count number of the animals. Relatively dense distribution of animals was presumed. A rough estimate of manatees may be several thousands.

The government has prohibited manatee hunting, but the situation was the same as everywhere, there seemed to have no efficient measures to prevent local poachings.

Angola (*Republica Populare de Angola*) *and Congo* (*Republique Populaire du Congo*)

As we were refused to enter into Angola and Congo because of political unstability due to the civil war, no survey was carried out in those two countries. Only information collected through Dr. Akihiro Takihara was that manatees were seen in Stanley Pool, a lake nearby Kinshasa, Zaire (*Republique du Zaire*). No manatee was said to be seen in the Ubangi River, a big tributary of the Congo (or Zaire) River, which flows from the territory of Central African Republic (*Enpire Centrafricain*), passing through Bangui, crossing the border to Congo and flowing into Stanley Pool.

The town of Lubumbashi is located near the border of Zambia (*Republic of Zambia*). A report came from the area that manatees, called " Manga " were seen in remote rivers and swamps. However, since the body length of the animals reported were 30–150 cm, it was so doubtful that we concluded the report was false.

The southern and the eastern limit of manatee distribution is still unconfirmed.

DISCUSSION AND SUMMARY

As a result of the recent survey in the west African countries, it is clear that the most abundant distribution of manatee is in the Niger River and its tributaries and associated swamps. The rivers which hold secondarily abundant populations are the Sanaga and the Ivindo Rivers, in Cameroon and Gabon, respectively. The nor-

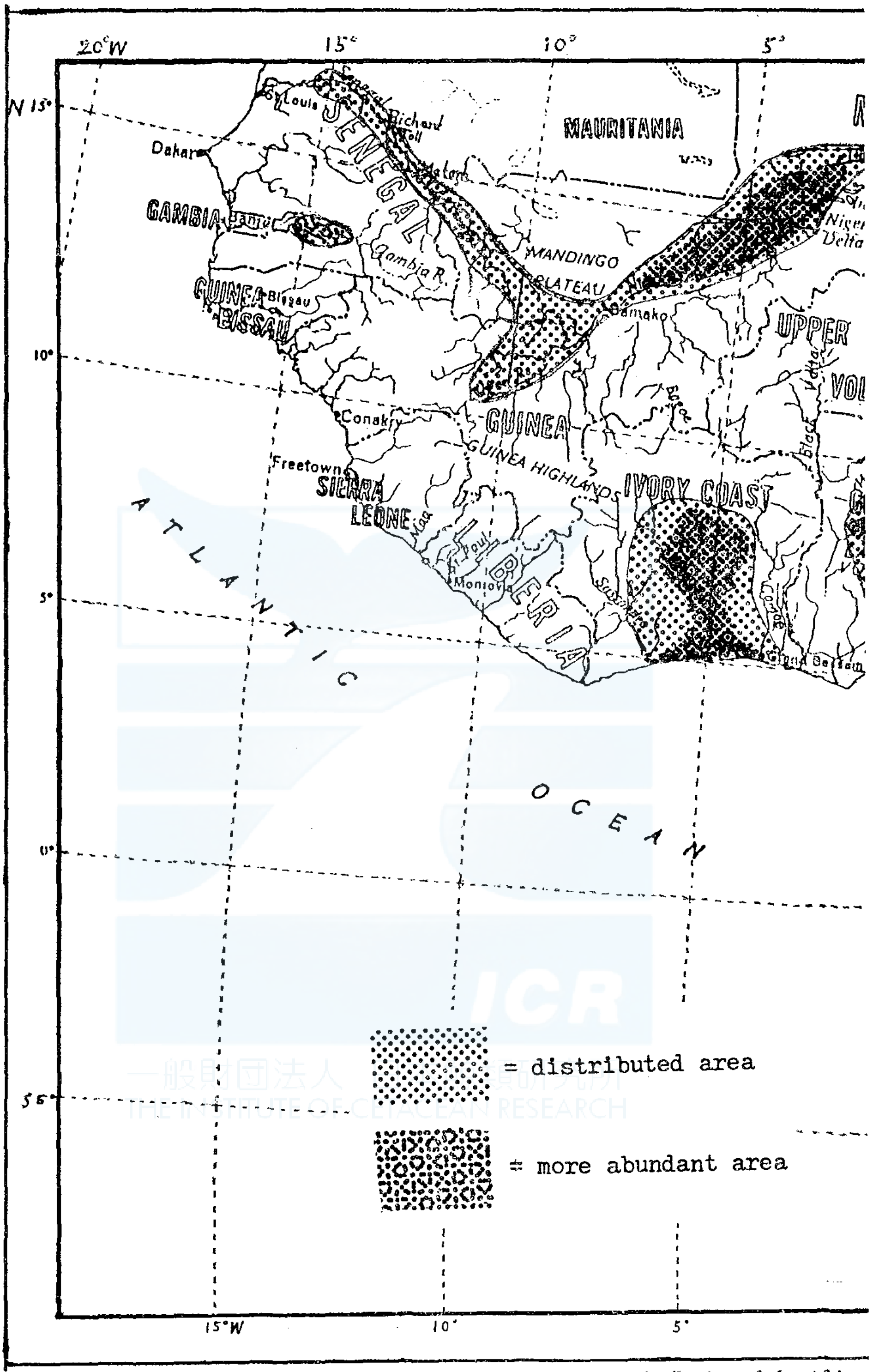
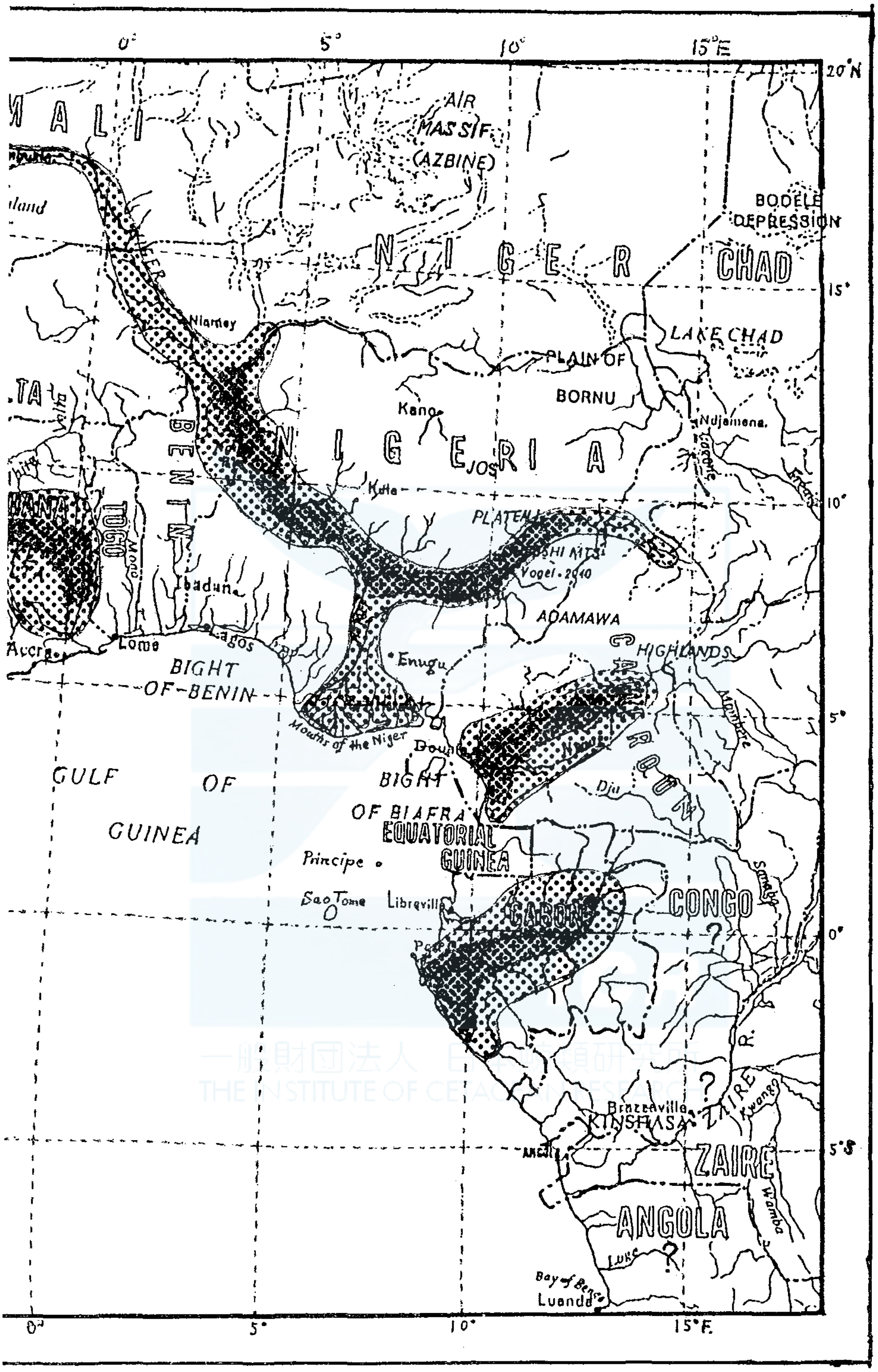


Fig. 1. Distribution of the African



manatee (*Trichechus senegalensis*).

thern and the western limit of distribution is in the Senegal River system. However, dispersing and fading distribution in both the western and the northern parts of the river were so scarce that we had once thought that it might be better to report the Inland Niger Delta in Mali as the northern limit and the Gambia River as the western limit.

The African manatee was proved to have a delicate sense to avoid salt water, which unlike the American manatee, *Trichechus manatus*, which inhabits marine environment as well as estuarine and freshwater habitat (Odel et al., 1978; Erdman, 1970; Hartman, 1979). Some local reports telling manatees were observed at sea were supposedly false and disregarded in our records. We thought that dolphins, whales or sharks might have been mistaken for manatees in those cases.

Based on the all collected data, we drew a distribution map of the African manatee in west Africa trying to show recent status of the animal and hoping that it would be a reference to some conservation measures.

The Niger River flows through extensive areas crossing the borders of countries, merges with other rivers, and is very long. If conservation of the African manatee would be planned, conservation strategy by a single country would not be effective. A conserved population in one country may be poached in other territories. Only properly organized extensive and long standing project would work for this purpose. Almost every country we visited, prohibits the manatee hunting by law. But we were informed in many places that the actual status and condition of manatees and poaching incidents had scarcely reached Government Officials because of people's fear of punishment. It should be noted that research projects by scientists stationing in the field for long periods, and who are able to establish good terms with tribal chiefs and general local people of the district, are most desirable, Dr. Laugini in Abidjan is a good example. Sufficient collection of local reports and workable conservation plans would be available by those people.

While travelling many lands of severe natural conditions where many people were nearly starved, we realized that the conservation of this species must be very difficult because of delicious meat and easy hunting by local people. Saving those people from poor status by developing agricultural and other improvement and progress must have superior priority than establishment of conservation measures on manatee. However if we wait until these conditions are fulfilled, it should be too late for conservation of the African manatee.

ACKNOWLEDGMENT

We should like to express our sincere gratitude to the number of people, scientists, local residents, fishermen and so on, who gave us help in collecting information as the greater part of study was based on those hearings. We specially appreciate following people who kindly gave us particular helps and were able to have names during the survey; Dr. Alioune Ndiaye, Director du Projet P.N.U.D. R.A.F., Senegal, Dr. G. J. Morel, Orstom, Richard-Toll, Senegal, Dr. F. Laugine, Zoo D'Abidjan, Cote D'Ivoire, Dr. K. Minami and Dr. K. Minakami, Noguchi Memorial Institute for Medical Research, Accra, Ghana, Dr. R. Kumar, Department of Zoology, University of Ghana, Legon, Ghana, Dr. E.Q.A. Asibey and Mr. C. K. Manu, Department of Game and Wildlife, Ministry of Forestry, Ghana, Dr. J. N. Raybould, Volta Lake Research and Development Project, Akosombo, Ghana, Mr. D. N. Quaynor, Fishery Research Unit, Tema, Ghana, Dr. C. B. Powell, School of Biological Science, University of Port Harcourt, Mr. A. B. Wilson, Nigerian Institute for Oceanography and Marine Research, Nigeria, Dr. Akihiro Takihara, Messers Akikazu Nakamura, Norihiro Kobayashi, Daiko Okura, the Embassy of Japan to Nigeria, Mr. James B. Ndeffo, Douala, Cameroon (guide, taxi-driver), Dr. Domart, Ministerie de l'Agriculture, des Eaux et Forets, Gabon, Dr. Jean Wack, Libreville Gabon, Mr. Jean-Pirre Bayona, Port-Gentil, Gabon, Dr. Jean L. Deval, IRAF, Gabon, Prof. T. Kano and Mr. T. Takeda, University of the Ryukyus, Japan, and from the preparatory survey by the senior author, till the end of this study, Miss Marie-Jeanne Ndiaye of the Broad Casting Station, Dakar, Senegal, has given us generous help in collecting information, contact among group members while travelling and valuable advices for our survival in the countries quite different from home, who has understandings in Japan and Japanese since she has been in Japan for technical study.

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THE SCIENTIFIC REPORTS OF THE WHALES RESEARCH INSTITUTE

昭和57年12月15日 印刷
昭和57年12月30日 発行

財団法人 日本捕鯨協会
編輯者 鯨類研究所
東京都江東区大島3丁目32番11号

編輯責任者 大村秀雄

印刷者 研究社印刷株式会社
東京都新宿区神楽坂1丁目2番地

Printed by
Kenkyusha Printing Co.
Shinjuku-ku, Tokyo

定価 4,000 円

Obtainable from Japan Publication Trading Co. Ltd.,
Sarugakucho, Chiyoda-ku, 1-2-1, Tokyo **101**