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

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ABSTRACT

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

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

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INTRODUCTION

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

MATERIALS AND METHOD

1. *Outline of Cruise*

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

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

2. *Method of Sighting*

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

The observation range was 180° in the direction of travel (90° port and starboard). Any changes of weather, visibility and wind force were recorded, regardless of sighting of marine mammals. The surface water temperature was recorded

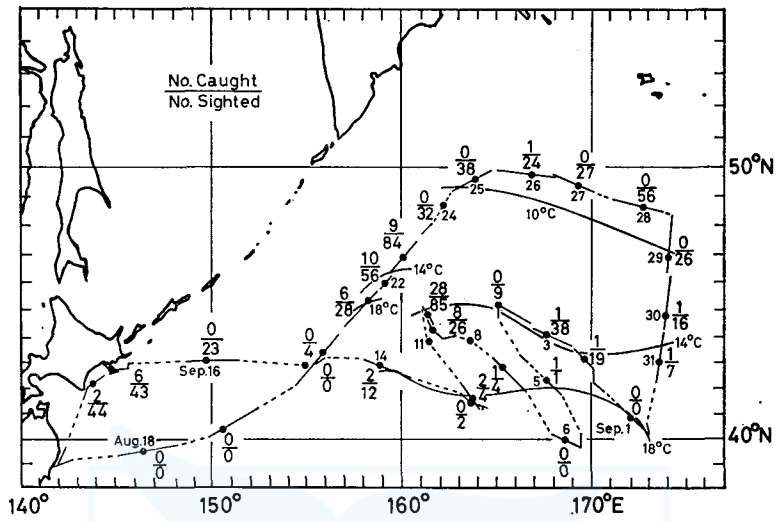

Fig. 1. Cruise track of the *Hoyomaru No. 12* (solid lines), noon position (closed circle, JST), surface water temperature, and number of Dall's porpoises sighted and caught during the cruise. The dotted lines indicate area where the sighting survey was not conducted. There was no chase or catch of porpoise on 16 September.

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

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

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

3. *Capture and Shipboard Processing of Porpoise*

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

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

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

4. *Laboratory Procedures*

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

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

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

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

RESULTS

1. *Segregation between Dall's Porpoise and Other Delphinids*

During the cruise, Dall's porpoises were sighted during the period from 20 August to 18 September, with the exception of 6 days (17–19 August, 1, 6 and 19 September) when the ship cruised south of 41°N (Table 1 and Fig. 1). Therefore it is concluded that the southern limit of this species in the northwestern North Pacific Ocean during this season is about 41°N.

To determine the distribution of the species, it is desirable to analyse the segregation between Dall's porpoise and other delphinids. As shown in Tables 1, 2 and 3, nine delphinid species were observed during the cruise. There was a correlation between surface water temperature and the occurrence of certain species. Sightings of Dall's porpoise were limited to surface water temperatures below 20°C.

Warm water delphinids, such as *Delphinus*, *Tursiops*, *Globicephala*, and *Stenella*, were sighted in waters above 17°C. Dall's porpoise accounted for about half of all the schools sighted in surface water temperatures of 18°C to 19°C, and since the size of Dall's porpoise schools was small, we conclude this species will be dominant in August-September in the waters below 18°C. This temperature is slightly higher than the figure obtained by Kasuya (1982) but agrees with data obtained by Ohsumi and Takaki (unpublished manuscript) for this season. The lower limit of the water temperature for Dall's porpoise was not determined in the present study. They have been sighted in this area in temperatures to 2°C (NMML unpublished data).

Two boreal species, *Lissodelphis* and *Lagenorhynchus*, were sighted at surface water temperatures between 12°C and 19°C. Near the southern limit of the range of the Dall's porpoise, the distribution of these three species overlaps. Although *Phocoena phocoena* also occur in this temperature range, they inhabit coastal waters, and were only sighted on the continental shelf off the east coast of Hokkaido.

2. *Segregation between the Two Colour Types*

The two major colour types, *dalli*-type and *truei*-type, are not currently distinguishable by characteristics other than pigmentation. Geographically *dalli*-type lives in the northern North Pacific and waters adjacent to it, and the *truei*-type lives off the Pacific coast of the southern Kuril Islands and northern Japan. Although it is clear that there are at least two stocks of Dall's porpoise in the northwestern North Pacific (Kasuya, 1978), little is known about the taxonomic relationship of the two color types or about the variation in color pattern in these stocks.

On the northbound offshore route, Dall's porpoise first appeared at 43°20′N and 155°54′E, and were the *truei*-type. On the return, the *truei*-type appeared at

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

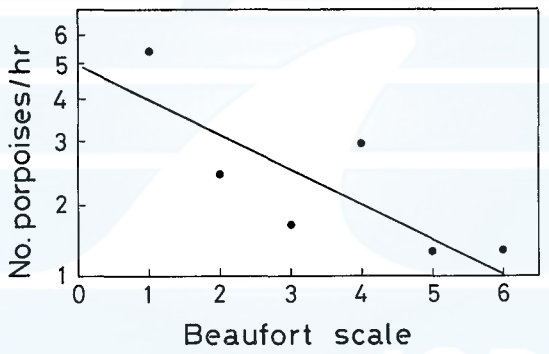

Fig. 2. The relationship between the number of Dall's porpoise sighted per sighting hour (y) and Beaufort wind force (x) during cruise of *Hoyomaru No. 12*. The y-axis is in a logarithmic scale. The solid line is the least squares regression, $\ln y = \ln 4.98 - 2.253x$, $r = 0.8$.

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

$$\ln y = -2.253x + \ln 4.98, \quad r = 0.8$$

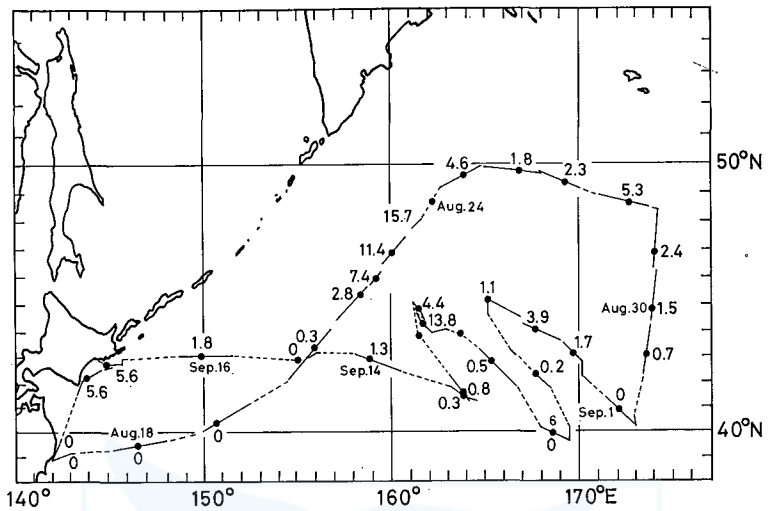

Fig. 3. Number of Dall's porpoise sighted per sighting hour with the correction for wind force, during cruise of *Hoyomaru No. 12* (17 August-19 September, 1982). The closed circles are noon positions (JST). The solid lines are the ship's track and dotted lines are tracks on which there was no sighting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

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

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

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

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

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

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

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

4. *Geographical Difference in the Wave Riding Behavior*

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

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

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

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

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

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

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

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

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

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

5. *Segregation of Mother-Calf Pairs*

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

Out of 41 mother-calf pairs sighted in the offshore area where *dalli*-type

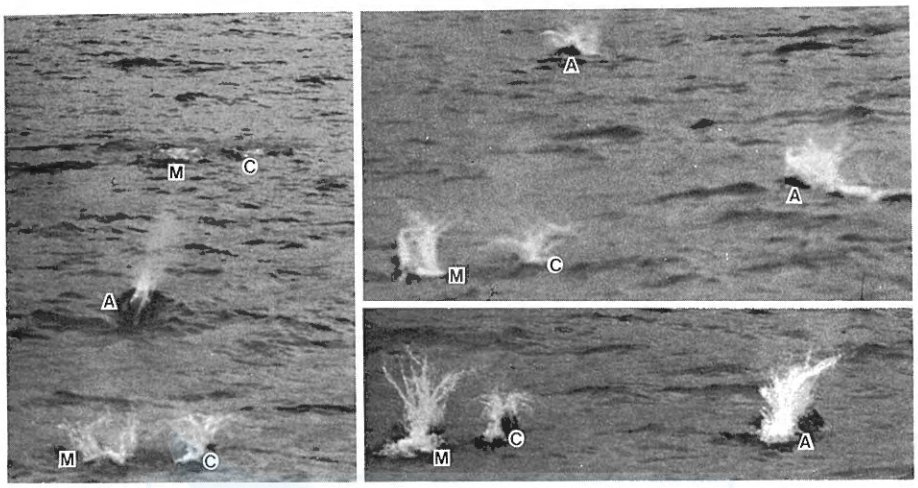

Fig. 4. Dall's porpoise school (School No. 118, 28 August 1982, 48°53′N, 171°10′E). When sighted initially at 0352 (JST), this group consisted of 2 mother-calf pairs and 2 adults, but during the chase (at 0403), another mother-calf pair joined the group. At 0405, they escaped from the vessel. All 8 were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

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

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

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

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

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

1 mother-calf pair and 1 adult: 3 schools
2 mother-calf pairs and 1 adult: 1 school

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

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

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

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

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

The following inferences can be drawn from the above data:

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

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

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

6. *School Structure*

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

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

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

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

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

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

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

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

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

7. *Analyses of the Catch*

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

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

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

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

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

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

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

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

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

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

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

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

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

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

For male *dalli*-type, the ages of the youngest mature individual and oldest

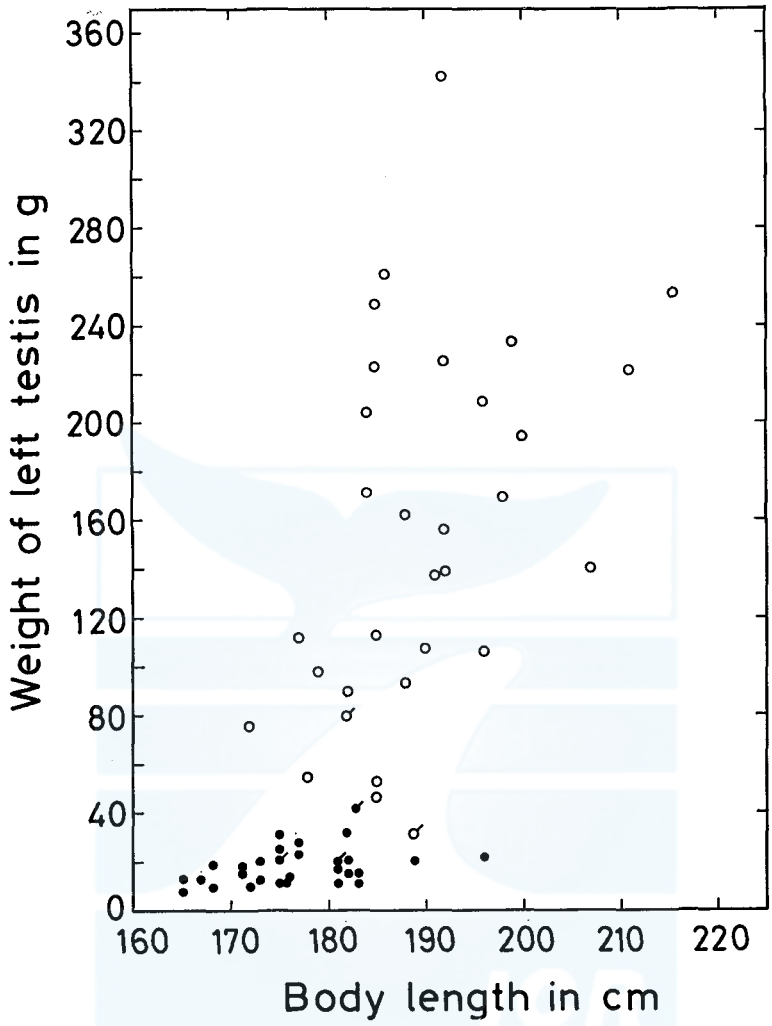

Fig. 6. Relationship between body lengths and left testis weights of Dall's porpoise caught with hand harpoons during the cruise of *Hoyomaru No. 12* (17 August—19 September, 1982). Open circle without bar: Mature. Open circle with bar: Late maturing. Closed circle with bar: Early maturing. Closed circle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

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

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

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

The data on the *dalli*-type obtained in the present study was biased towards males (male 60: female 12). In the southern area, the proportion of individuals that did not ride the ship's wave was 30% of the total number of Dall's porpoises sighted. If all of them are assumed to be females, the sex ratio of Dall's porpoise in the area would be $(12+72\times0.3\div0.7)/(12+72\times0.3\div0.7+60)=0.42$. Even with such an extreme assumption, it is difficult to explain the unbalanced sex ratio of the catch. One interpretation is that more males live in the southern area. The fact that there are fewer females than males in all age groups (Table 9) may indicate that sexual segregation is present in all age groups over 2 years.

DISCUSSION

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

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

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

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

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

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

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

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