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Distribution of Dall's Porpoise, *Phocoenoides dalli*, in the North Pacific and Bering Sea, Based on T/S Oshoro Maru 2012 Summer Cruise Data

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Dall's porpoise (*Phocoenoides dalli*) is a small toothed cetacean, widely inhabiting the North Pacific Ocean and adjacent seas, between about 30 and 62°N; however, only limited studies of its ecology have been made in nearshore areas. A cetacean sighting survey lasting 60 days was conducted during the 2012 summer cruise of the T/S Oshoro Maru (Hokkaido University, Japan) in the North Pacific Ocean and Bering Sea. Based on this data, the distribution of Dall's porpoises and the factors controlling it in the pelagic habitat were investigated. A total of 808 individual Dall's porpoises in 166 groups were sighted during a total of 469.6 hr and 4946.6 nm observations. The cruise consisted of three legs and the average porpoise group size was significantly larger in Leg 1. The sightings were concentrated at water depths of less than 1000 m and near eastern Aleutian passes. Sighting clusters were found on the 200 m isobath of the southeastern Bering Sea continental slope. There was a peak in sightings where the sea surface temperature (SST) was relatively cold, between 5 and 7°C. Although similar track routes were taken in Leg 1 and Leg 3, the number of sightings per unit effort was larger in Leg 1. This difference may have arisen from the significant rise in SST as the season progressed. Relatively large group size found in this study might relate with prey abundance along the Aleutian Islands.

Key words: Dall's porpoises, *Phocoenoides dalli*, North Pacific Ocean, Bering Sea, distribution, sighting survey

INTRODUCTION

Dall's porpoise (*Phocoenoides dalli*) is a small odontocete species of the family Phocoenidae, which is widely distributed across the North Pacific Ocean and the adjacent seas, between about 30 and 62°N (Houck and Jefferson, 1999; Jefferson et al., 2008). It is distributed over a broad range from the shallow continental sea shelf (Friday et al., 2013) to the deep central North Pacific Ocean (Ohizumi et al., 2003).

Because of their wide-ranging habitat, Dall's porpoises occur in the highly variable marine environment of the northern North Pacific and Bering Sea (Fig. 1). The Subarctic Gyre in the North Pacific causes mixing of warm subtropical and cold Bering Sea waters (Ladd et al., 2005). The series of passes along the Aleutian Islands allows water exchange between the North Pacific and the highly productive Bering

Sea (Springer et al., 1999). The geographic and oceanographic features along the Aleutian Islands change at Samalga Pass, one of the major passes in the eastern Aleutian Islands. To the east of this pass, the continental shelf is wider and shallower, and the surface water is warmer and less nitrogen rich (Springer et al., 1999).

Sea surface temperature (SST) is considered to be an important factor in determining cetacean distribution of Dall's porpoise. The SST of its habitat is cold, ranging from 3 to 25°C (Jefferson, 1988), but this species is rarely found in areas where the water is warmer than 18–19°C (Kasuya and Jones, 1984; Jefferson, 1988; Miyashita and Kasuya, 1988). In the eastern Bering Sea shelf, Friday et al. (2013) reported westward shifts in Dall's porpoise distribution and to deeper waters in colder SST years compared to a warmer SST year. They concluded that porpoises may shift habitats in response to changes in SST.

Dall's porpoise's main diets are small fishes and squids, but they may change their feeding strategies depending on their habitat. According to previous studies, Dall's porpoises primarily feed on mesopelagic prey at night in the pelagic

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zone (Ohizumi et al., 2003) and the continental slope off the Sanriku coast of Japan (Okamoto et al., 2010), and on epipelagic Japanese pilchard (*Sardinops sagax melanostictus*) in the southern Sea of Okhotsk during daytime (Walker, 1996). Thus, Amano et al. (1998) concluded that Dall's porpoises were not necessarily nocturnal feeders but fed opportunistically depending on prey behavior and distribution.

Although Dall's porpoises are well-distributed animals and probably an important key species in the entire northern North Pacific ecosystem, previous studies on this species have been restricted to near-shore waters. In the present study, we used the cetacean sighting survey data from the T/S Oshoro Maru 2012 summer cruise to the North Pacific and Bering Sea. The survey track line of the T/S Oshoro Maru cruise was not designed for determining cetacean abundance; however, the track line covered vast areas in the northern North Pacific and Bering Sea, and thus the survey data are unique and valuable. Here, we attempt to investigate the general distribution and ecology of Dall's porpoises in pelagic waters and the potential factors affecting porpoise distribution were examined. The effects of prey abundance and water temperature on the distribution are discussed.

MATERIALS AND METHODS

Dall's porpoise sighting data for this study were collected during the cetacean sighting survey on the summer cruise of the T/S Oshoro Maru (72.85 m length and 1792 gross tonnage, belonging to Hokkaido University, Japan) from June to August 2012. The cruise track was divided into three legs: Leg 1 (8–28 June, from Hakodate to Dutch Harbor), Leg 2 (2–19 July, from Dutch Harbor to Kodiak), and Leg 3 (23 July–5 August, from Kodiak to Hakodate). The track lines are shown in Fig. 2. The sighting survey was conducted when the vessel was moving between survey stations during daylight hours, from one hour after sunrise until one hour before sunset, from either the upper bridge or bridge, depending on the weather and oceanic conditions. A total of six (Legs 1 and 3) or eight (Leg 2) observers rotated observation hourly. The detailed survey method was described in Sekiguchi et al. (2014). The water depth and SST data were obtained

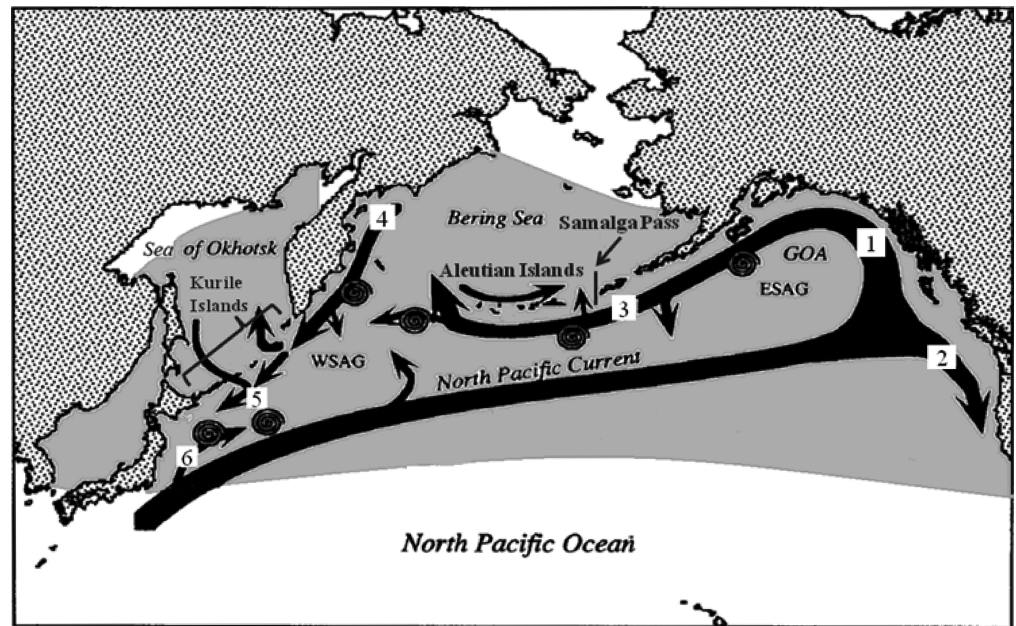


Fig. 1. Oceanographic features of northern North Pacific and Bering Sea. The map was modified from Springer et al. (1999), indicating the habitat range of Dall's porpoise (Houck and Jefferson, 1999) in light gray-colored area. The abbreviations on the figure indicate: Gulf of Alaska (GOA); Eastern Subarctic Gyre (ESAG); Western Subarctic Gyre (WSAG); Alaska Current (1); California Current (2); Alaska Stream (3); East Kamchatka Current (4); Oyashio Current (5); Kuroshio Current extension (6). Spirals indicate locations of turbulent rings.

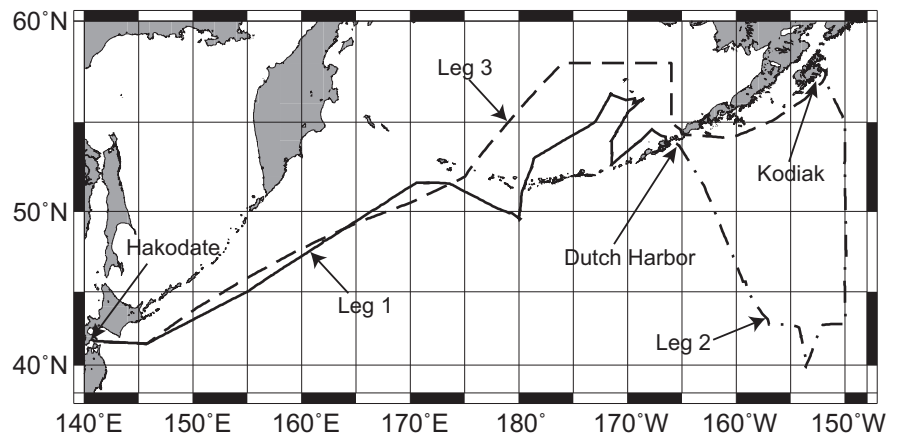


Fig. 2. Track lines of the T/S Oshoro Maru 2012 summer cruise, consisting of three Legs. Leg 1 (solid line; from Hakodate to Dutch Harbor on 8–28 June), Leg 2 (dash and dotted line; from Dutch Harbor to Kodiak on 2–19 July) and Leg 3 (dashed line; from Kodiak to Hakodate on 23 July–5 August).

from the vessel when sightings were made.

All Dall's porpoise on-effort sighting data (166 data points) were used for this study. Sighting locations were plotted on the chart to investigate porpoise distribution. Group size, water depth and SST at the sighting were examined. Because the track line of T/S Oshoro Maru was not designed for a cetacean sighting survey and the vessel sailed vast oceanic areas, the track line sampled a variety of depths non-uniformly. A large number of sightings in shallow waters might be caused by an excess of effort spent surveying in shallow water. Therefore we had to smooth out this bias derived from unevenly surveyed depth to examine porpoise distribution relating to water depth. We calculated on-effort time for every 500 m water depth and then calculated sighting number per on-effort

time in each 500 m depth range for each Leg. The on-effort hours at each water depth were calculated proportionally from the hourly position record of the vessel and ETOPO1 depth data (<http://www.ngdc.noaa.gov/mgg/global/global.html>) (Supplementary Table S1 online).

In order to examine the effect of SST on the distribution, SSTs at the porpoise sighting locations were compared between Legs 1 and 3, which covered similar survey areas. Because the total effort (i.e. observation times and distances) varied between the legs, the number of sightings of groups and individuals per unit effort (1 hour or 10 nautical miles) were calculated and compared between Legs 1 and 3. T-tests were performed for statistical analyses for original observation data of group size and SST. Here we assumed that observations within each leg are independently and identically distributed as a normal distribution, as follows:

$$Y_{ij} = \text{the } j^{\text{th}} \text{ observation of } i^{\text{th}} \text{ leg such as group size and SST}$$

$$Y_{11}, Y_{12}, Y_{13}, \dots \sim (\text{iid}) N(\mu_1, \sigma_1^2)$$

$$Y_{21}, Y_{22}, Y_{23}, \dots \sim (\text{iid}) N(\mu_2, \sigma_2^2)$$

$$Y_{31}, Y_{32}, Y_{33}, \dots \sim (\text{iid}) N(\mu_3, \sigma_3^2)$$

In this study, our interest is to test homogeneity at μ_1 , μ_2 and μ_3 .

RESULTS

In total, 469.6 hours (hr) of observations were made over 4946.6 nautical miles (nm) during the 60-day T/S Oshoro Maru 2012 summer cruise (Table 1). The overall survey effort from the upper bridge was 2256.9 nm (45.6% of the total surveyed distance) and 203.6 hr (43.4% of the

Table 1. The effort summary for the cetacean survey during the T/S Oshoro Maru 2012 summer cruise.

		Observation from		Total
		Upper	Bridge	
Leg 1	Distance (nm)	911.1	734.6	1645.7
	Time (hr:min)	82:15	83:17	165:32
Leg 2	Distance (nm)	658.2	895.5	1553.7
	Time (hr:min)	62:14	84:24	146:38
Leg 3	Distance (nm)	687.6	1059.6	1747.2
	Time (hr:min)	59:07	98:19	157:26
Total	Distance (nm)	2256.9	2689.7	4946.6
	Time (hr:min)	203:36	266:00	469:36

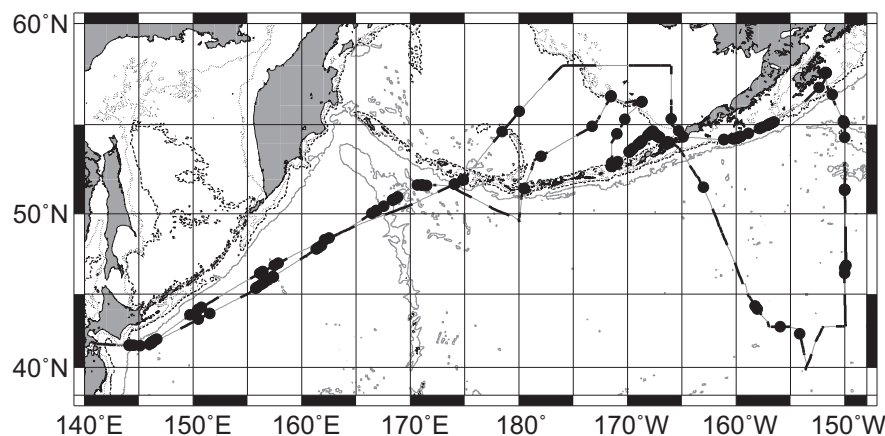


Fig. 3. On-effort sighting locations of Dall's porpoises during T/S Oshoro Maru 2012 summer cruise (black circles). On-effort sections of track lines are indicated by thicker line, and off-effort sections are thinner lines. Thinner gray lines indicate contour lines; the areas of 200 m (dotted line), 1000 m (dashed line) and 4000 m (straight line) deep.

total surveyed time). By leg, the upper bridge observational effort was 911.1 nm (55.4%) and 82.3 hr. (49.7%) in Leg 1, 658.2 nm (42.4%) and 62.2 hr (42.4%) in Leg 2, and 687.6 nm (39.4%) and 59.1 hr (37.6%) in Leg 3. The remaining effort was made from the bridge. The effort ratio of the upper bridge observations to the whole leg observations was lower in later legs due to the bad weather/oceanic conditions. Bad weather (rain, fog, patchy thin fog, and drizzle) during on-effort time made up 30.8% (56 times out of 182 hourly records) in Leg 1, 42.4% (70 out of 165) in Leg 2 and 48.2% (82 out of 170) in Leg 3. Overall, these wet conditions made up 40.2% of the total record. The oceanic conditions were recorded by wind speed and the Beaufort wind force scale, and the average wind speed was 14.8 ± 0.5 knots (kt) in Leg 1, 13.0 ± 0.4 kt in Leg 2, and 13.5 ± 0.5 kt in Leg 3.

During the survey, Dall's porpoises were sighted over the entire track line (Fig. 3), and 808 animals in 166 groups were recorded as on-effort sightings (Table 2). The total sighting number was 521 individuals in 87 groups for Leg 1, 84 individuals in 26 groups for Leg 2, and 203 individuals in 53 groups for Leg 3. Many porpoises were sighted along the Aleutian Islands, especially near and east of Samalga Pass ($52.5^\circ\text{N } 169.5^\circ\text{W}$). Strongly clustered sightings were made over the continental slope of the southeastern Bering Sea (around $54^\circ\text{N } 167^\circ\text{W}$ and $54^\circ\text{N } 159^\circ\text{W}$).

The average group size was significantly larger in Leg 1 (6.0 ± 0.5 ; Table 2) than in Leg 2 (3.2 ± 0.4 ; *t*-test, $P < 0.001$, $F_{\text{leg } 1, \text{leg } 2} = 4.1$) and in Leg 3 (3.8 ± 0.3 ; *t*-test, $P < 0.001$, $F_{\text{leg } 1, \text{leg } 3} = 4.0$). It did not differ significantly between Legs 2 and 3 (*t*-test, $P = 0.25$, $F_{\text{leg } 3, \text{leg } 2} = 1.0$). The mean group size throughout the survey was 4.9 ± 0.3 , and 91.0% of the sighted groups consisted of 8 or fewer animals ($n = 151$ groups; Fig. 4A). Many large sized groups were sighted in Leg 1, including the largest group of 28 animals at $54.6^\circ\text{N } 167.7^\circ\text{W}$.

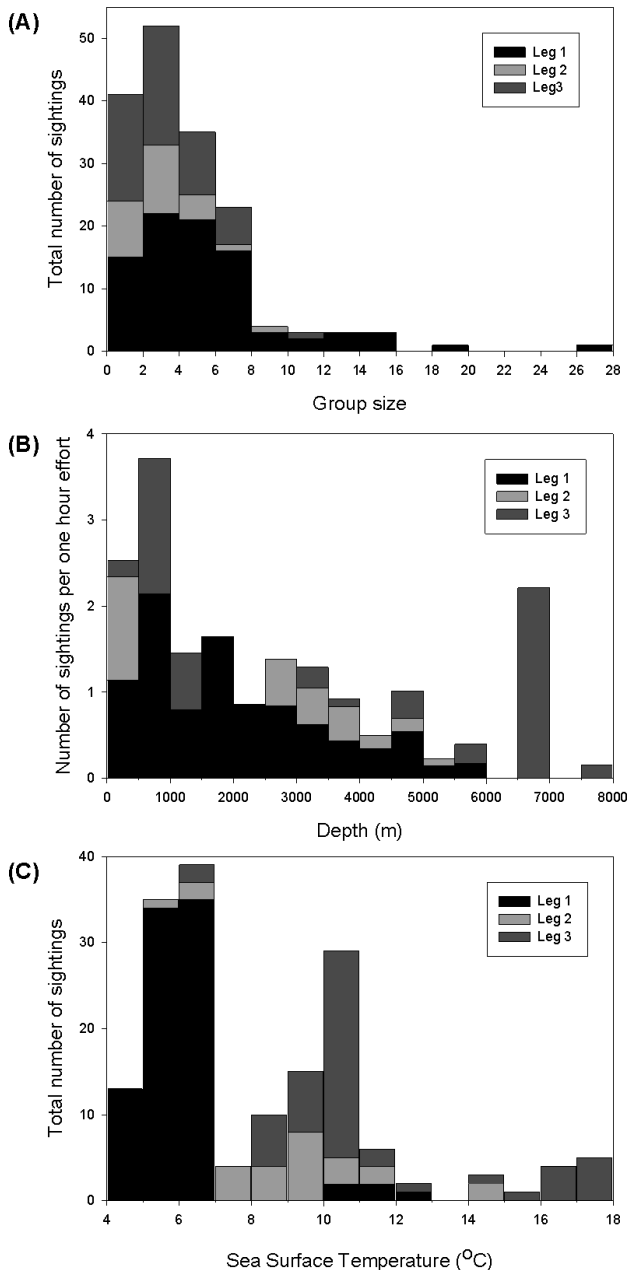
Water depths at the porpoise sighting locations were varied, and ranged from 66.0 m (one sighting in Leg 2) to 8,250.0 m (in Leg 3). The shallowest record, 66.0 m, was at $57.7^\circ\text{N } 151.8^\circ\text{W}$, where a group of three animals was sighted on the continental slope near Kodiak Island. The

deepest record, 8,250.0 m, was of a group of five animals located in the Kuril Trench at $44.1^\circ\text{N } 150.8^\circ\text{E}$. A large proportion of sightings was made at water depths less than 1,000 m and 42.8% of sightings ($n = 71$) fell in this range. The number of sightings per effort hour in each leg was calculated for every 500 m depth range to normalize the data. Although the normalized frequency histogram (Fig. 4B) shows a decline after the peak at 500–1000 m, there was another peak at 6500–7000 m, which included Leg 3 sightings only. Despite similar surveyed track lines, sightings in Leg 1 generally occurred in shallower areas than in Leg 3. Locations of Leg 2 sightings were divided into shallow (0–500 m) and middle (2500–5500 m) depth ranges.

The SST at locations of Dall's por-

Table 2. Sighting results of Dall's porpoises during the T/S Oshoro Maru 2012 summer cruise.

	Total sighting number		Sighting numbers per hr		Sighting numbers per 10 nm		Average \pm SE		
	Groups	Individuals	Groups	Individuals	Groups	Individuals	Water depth (m)	SST ($^{\circ}$ C)	Group size
Leg 1	87	521	0.53	3.1	0.53	3.2	2287.2 \pm 192.1	6.2 \pm 0.2	6.0 \pm 0.5
Leg 2	26	84	0.18	0.57	0.17	0.54	2697.9 \pm 460.5	9.4 \pm 0.4	3.2 \pm 0.4
Leg 3	53	203	0.34	1.3	0.30	1.2	2872.1 \pm 384.4	11.4 \pm 0.4	3.8 \pm 0.3
Total	166	808					2538.3 \pm 174.4	8.4 \pm 0.2	4.9 \pm 0.3

**Fig. 4.** Frequency histograms of Dall's porpoise sighting numbers from the T/S Oshoro Maru 2012 summer cruise. Sighting numbers (groups) were plotted against (A) group size, (B) water depth (m), and (C) Sea surface temperature (SST, $^{\circ}$ C). For (B), to smooth the depth bias, sighting numbers were divided by on-effort hours in each 500 m depth range, calculated from hourly position data of the vessel. Each bar is totaled by original/normalized sighting numbers for each legs; black color for Leg 1, white for Leg 2 and gray for Leg 3.

poise sighting was between 4.8 $^{\circ}$ C and 17.1 $^{\circ}$ C. The highest number of porpoises were sighted in the SST 5–7 $^{\circ}$ C range (44.6%, $n = 74$; Fig. 4C), which mostly consisted of sightings in Leg 1 ($n = 69$). There was another sighting peak between 10 and 11 $^{\circ}$ C (29 sightings), which mostly consisted of Leg 3 sightings ($n = 24$). The average SST became higher in the later legs as the summer season progressed (6.2 \pm 0.2 $^{\circ}$ C in Leg 1, 9.4 \pm 0.4 $^{\circ}$ C in Leg 2 and 11.4 \pm 0.4 $^{\circ}$ C in Leg 3; Table 2). Relatively high SSTs (10–14 $^{\circ}$ C) were also recorded when the vessel headed south during Leg 2 (Fig. 2). The average SST was significantly lower in Leg 1 (6.2 \pm 0.2 $^{\circ}$ C) than Leg 3 (11.4 \pm 0.4 $^{\circ}$ C; t -test, $P < 0.001$, $F_{\text{leg 3, leg 1}} = 3.9$).

The number of sightings per unit effort (per hr or per 10 nm) was calculated to minimize the bias of uneven survey effort in each leg (Table 2). Comparing Legs 1 and 3, the number of sightings per unit effort (time or distance) was larger in Leg 1 than in Leg 3 for both groups and individuals. The average sighting number per hour was 0.53 groups and 3.1 animals in Leg 1, while that of Leg 3 was 0.34 groups and 1.3 animals. The same tendency was observed per unit distance (10 nm): 0.53 groups and 3.2 animals in Leg 1 and 0.30 groups and 1.2 animals in Leg 3. No statistical comparison was made for Leg 2 because the Leg 2 surveyed area was very different from that of Legs 1 and 3.

DISCUSSION

The results indicate that Dall's porpoises were distributed over the entire surveyed portion of the North Pacific and Bering Sea. Animals were sighted at a wide range of depths (66.0–8250.0 m) and sea surface temperatures (4.8–17.1 $^{\circ}$ C). These results agree with the general ecology of Dall's porpoises described by Jefferson et al. (2008).

Our sightings were concentrated in the area with depths of 0–1000 m (Fig. 4B), where 42.8% of the total sightings ($n = 71$) were made. The decrease in sightings beyond the peak at 500–1000 m supports the view that Dall's porpoise is primarily a continental shelf and slope species (Jefferson, 2012), and a shallow water habitat may be advantageous for feeding because of abundant prey species. There was another peak at 6500–7000 m comprising the eight groups sighted at the end of Leg 3 (41.6–41.9 $^{\circ}$ N, 146.0–146.5 $^{\circ}$ E). This area is a part of the Japan Trench and is continuous with the continental slope off Hokkaido. These deep-sea sightings thus may not contradict the general distributional trend over the continental shelf and slope.

Our survey results agree with other regional studies concerning the relatively shallow-water distribution of Dall's porpoises. In the central-eastern Bering Sea, Moore et al. (2002) reported that in summer clusters of Dall's porpoises were found along the 200 m isobaths. Our survey also found a sighting concentration in a similar area, around 54 $^{\circ}$ N

167°W (Fig. 3). In our study, there were no sightings when the vessel crossed the continental slope at about 58°N 174°W, where frequent sightings occurred in former studies (Moore et al., 2002; Friday et al., 2012, 2013). This lack of sightings may have been due to the bad weather/oceanic conditions when we crossed the area (foggy with some drizzle; Beaufort scale = 5). In our survey, frequent sightings occurred near and east of Samalga Pass (Fig. 3). As the passes in the Aleutian Island chain are important areas where nutrients and plankton aggregate (Sinclair et al., 2005), this concentration of Dall's porpoise sightings may arise from the high productivity and the abundance of prey in this region.

The SST at locations of Dall's porpoise sightings throughout our survey ranged between 4.8 and 17.1°C, and this range agrees with the porpoises' preferred temperature range described in previous studies (3–18°C) (Norris and Prescott, 1961; Kasuya and Jones, 1984; Miyashita and Kasuya, 1988; Houck and Jefferson, 1999). Within that range, this study showed a cold water preference, and 44.6% of sightings ($n = 74$) were between 5 and 7°C (Fig. 4C). This peak range was lower than the peaks of 8–13°C in June and 12–16°C in July, recorded by Miyashita and Kasuya (1988) for the Sea of Japan-Okhotsk Sea stock.

SST might affect the total sighting numbers. Comparing the number of sightings per unit effort between Legs 1 and 3, Leg 3 sightings (about one animal per hr or per 10 nm) were lower than in Leg 1 (about three animals per hr or per 10 nm) (Table 2). The average SST in Leg 3 ($11.4 \pm 0.4^\circ\text{C}$) was significantly higher than in Leg 1 ($6.2 \pm 0.2^\circ\text{C}$; $P < 0.001$, $F_{\text{leg } 3, \text{leg } 1} = 3.9$). This may suggest that the lower number of sightings in Leg 3 was related to the rise in SST due to seasonal progress, although the bad weather and oceanic conditions in Leg 3 may have inhibited the sightings as well. Kasuya and Jones (1984) suggested possible seasonal migration around Japanese waters. Seasonal change of SST might cause some kind of movement in offshore water as well.

In total, 91.0% of sighted groups ($n = 151$) consisted of eight or fewer individuals (Fig. 4A), and the mean group size was 4.9 ± 0.3 (Table 2). Houck and Jefferson (1999) reported a general group size of 2–12 animals, and our result fits in this range. In previous studies, the mean group size was 2.6 in summer off British Columbia (Jefferson, 1987), 2.77 in the inland waters of southeast Alaska (Dahlheim et al., 2009), and 3.4 in the eastern Bering Sea outer-shelf (Friday et al., 2013). Our mean size was slightly larger than those records. Our surveyed area was over the deep pelagic waters, where some species of porpoise prey have patchy distribution (Ohizumi et al., 2003). Group-living animals have the benefit of finding and capturing prey through co-operative hunting strategies (Acevedo-Gutiérrez, 2002). A large group size may be advantageous for feeding on such patchy prey. On the other hand, larger groups were sighted during Leg 1, in which many sightings occurred in relatively shallow areas and near passes (Figs. 3, 4A and B). Therefore, large groups can also be formed in the nutrient rich and prey abundant shallow areas. The large average group size over the entire study may have been caused by a combination of such factors.

Further shipboard surveys are desired to understand the

ecology of Dall's porpoises in their pelagic habitat.

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