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Title: Spatial niche partitioning among three small cetaceans in the eastern coastal area of Hokkaido, Japan

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Abstract

Spatial niche partitioning of marine mammals is thought to be caused by dietary differences. However, due to the difficulty of conducting simultaneous marine predator and prey distribution surveys at the same scale, marine mammals have not been studied alongside their prey distribution. To understand the spatial niche overlap between three small cetaceans observed in the eastern coastal waters of Hokkaido, Japan (Pacific white-sided dolphin *Lagenorhynchus obliquidens*, Dall's porpoise *Phocoenoides dalli*, and harbor porpoise *Phocoena phocoena*), and the mechanisms behind the differences in their distributions, visual and hydroacoustic surveys, using a quantitative echosounder, were concurrently conducted. A clear spatial niche overlap was observed between the Pacific

white-sided dolphin and Dall's porpoise, whereas the spatial overlap was moderate between the harbor porpoise and the other two species. In areas where Pacific white-sided dolphins were observed, potential prey was abundant in a shallower layer, at approximately 80-90 m depth. On the other hand, potential prey was more abundant in deeper layers in areas where Dall's and harbor porpoises were observed. Water depth affected the potential prey abundance at all depth layers (0-300 m), as potential prey were more abundant in areas with a shallower water depth. Additionally, potential prey were more abundant in shallower layers (3-200 m) than in deeper layers (200-300 m), where the maximum water depth was 3000 m. The differences in spatial niche among the Pacific white-sided dolphin, Dall's porpoise, and harbor porpoise might cause their dietary differences, as they are epipelagic feeders, midwater feeders, and both epipelagic and midwater feeders, respectively.

Keywords

Spatial niche partitioning, small cetaceans, prey distribution, echosounder, Pacific white-sided dolphin, Dall's porpoise, harbor porpoises

1. INTRODUCTION

1.1. Niche partitioning

When species that require similar resources occur in the same habitat, they must differ to some degree in their ecological requirements, or niches, to avoid interspecific competition (Roughgarden 1976, Friedlaender et al. 2009). Such niche partitioning affects the abundance and/or distribution of animals (e.g., Litvaitis & Harrison 1989, Arlettaz 1999, Nicholls & Racey 2006, Harrington et al. 2009, Stewart et al. 2010). Therefore, it is important to understand the mechanisms of niche partitioning among species. An example of spatial resource competition is reported between two barnacle species: *Balanus balanoides* and *Chthamalus stellatus*. When they occur sympatrically, *B. balanoides* occupies the lower zone of intertidal rocky shores, where both barnacles can survive, and force *C. stellatus* to the upper zone. However, once *B. balanoides* are removed, *C. stellatus* can expand to the lower zone (Connell 1961).

To understand the drivers of species coexistence, it is necessary to elucidate species-specific preferred conditions as well as the effects of interspecific interactions at various temporospatial scales (Kadowaki 2016). Some species have been observed to interact differently at different temporospatial scales, for example, the foraging ranges of seabird species show a large overlap at a regional scale (1000s km), but segregation in the environmental factors was found at a smaller scale (100s km) (Pinaud & Weimerskirch 2007).

1.2. Niche partitioning among top marine predators

One approach for understanding the mechanisms that allow the coexistence of multiple species is finding some order from their distribution patterns and analyzing the mechanisms behind those patterns (Kadowaki 2016). For apex predators in marine ecosystems, it is particularly difficult to reveal these mechanisms experimentally, as can be done in a laboratory, e.g. by changing the environmental conditions of two algal species (e.g. Tilman et al. 1981). Thus the distribution patterns of multiple species have been studied instead (e.g. Gowans & Whitehead 1995, Kasamatsu et al. 2000, Gross et al. 2009). Integrated analyses of the spatial distribution patterns and habitats of small cetacean species, some of the top marine predators, have revealed that they are linked with abiotic factors, such as water depth, slope, distance from land, and water temperature. These differences may be related to the different feeding habits of each species (Bearzi 2005, Parra 2006).

For example, white-beaked dolphins (*Lagenorhynchus albirostris*) occur further from the shore and in significantly deeper water than short-beaked common dolphins (*Delphinus delphis*) in the Minch, Scotland (Weir et al. 2009). Their habitat partitioning could be related to differences in their diets, as white-beaked dolphins are predominantly a demersal predator, while short-beaked common dolphins are epipelagic predators (Weir et al. 2009). However, in small cetaceans overlapping spatiotemporal niches are difficult to evaluate and discuss in terms of differences in diet, because to do this it is necessary to conduct cetacean sighting surveys simultaneously with direct prey sampling such as by net tows or fishing, in

a broad area, at the same fine scale. This may lead to a lack of scientific evidence supporting the hypothesis that cetacean habitat partitioning occurs due to prey distribution, which is affected by the marine environment. One possible solution is spatially surveying prey distributions using an echosounder and net sampling alongside cetacean visual surveys, as conducted by Friedlaender et al. (2009). This study made it possible to understand the relationship between whale distribution and krill abundance. Thus, echosounders can be used for a variety of studies on the distribution and ecology of cetaceans, because of the ability to estimate prey abundance concurrently with cetacean visual surveys (e.g., Tynan et al. 2005, Doksæter et al. 2008).

Most habitat partitioning studies evaluate what differences there are in parameters of habitats utilized by sympatric species, such as the distance from the shore, water depth, and sea surface temperature (e.g., Weir et al. 2009). However, few quantifiable studies have examined the extent to which the spatial niches of sympatric species overlap (Friedlaender et al. 2009). The quantitative evaluation of spatial niche overlap will provide information for the evaluation of regional and seasonal differences of interspecific relationships and allow us to forecast future dynamics in cetacean ecology.

1.3. Probability of niche overlap among the 3 small cetaceans in the eastern coastal area of Hokkaido

The eastern coast of Hokkaido is a highly productive feeding area for several top predators, such as killer whales (*Orcinus orca*) and minke whales

(*Balaenoptera acutorostrata*). Small cetaceans such as the Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) and Dall's porpoise (*Phocoenoides dalli*) migrate from the southern coast of Japan and are frequently observed on the eastern coast of Hokkaido in the fall. Harbor porpoises (*Phocoena phocoena*) are also observed in the fall, although compared to the former species, they are difficult to observe from ships. These three species are considered to feed in this area. They use a similar range of sea surface temperatures (7-22 °C, 7-18 °C, and 3-22 °C, respectively), and have a broad diet of surface and mesopelagic prey (Wilke et al. 1953, Miyazaki et al. 1991, Gaskin et al. 1993, Ohizumi et al. 2000, Matsuda & Matsuishi 2012, Matsuda 2017). Although the Pacific white-sided dolphin and Dall's porpoise were divided as a different habitat group at a broad scale (1° × 1° grid) in the north Pacific (Kanaji et al. 2016), they coexist in coastal areas, such as the eastern coast of Hokkaido, western coast of Canada, and Californian coast (Yen et al. 2004, Tynan et al. 2005, Miyashita 2013). Therefore, the spatiotemporal niches of these three species could potentially overlap in coastal areas.

1.4. Objectives

Our goal was to understand the mechanisms behind the distribution of the Pacific white-sided dolphin, Dall's porpoise, and harbor porpoise around the eastern coast of Hokkaido. In this study, we conducted on-board sightings and hydroacoustic monitoring surveys to (1) understand the habitat characteristics of the three cetaceans, (2) generate a presence probability map and calculate the spatial overlap index among the three species, and (3)

140 understand the potential prey distribution and environment.

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2. MATERIALS & METHODS

2.1. Field study

Visual surveys were conducted from the T/S Ushio-maru (Hokkaido University, 286 Gross tonnage) around the eastern coastal area of Hokkaido, in September and October of 2009 and 2011-2015 (Table 1, Fig. 1). The southern part of the survey area was the Pacific coast of southeast Hokkaido, which is an area with a gentle continental slope (Kagami 1990). The central part of the survey area was Nemuro Bay, which has a shallow water depth of less than 50 m. The northern part of the survey area was the coastal area of the Shiretoko Peninsula, a UNESCO World Heritage site, which has a submarine canyon with a water depth greater than 2000 m (Yamaji 1985).

Visual surveys were conducted from the vessel's upper bridge (approximately 6 m above sea level) while the vessel was moving, from one hour after sunrise until one hour before sunset, weather permitting (Beaufort scale <5 and visibility >1 km). During the survey, two observers, at least one of which had previous experience in identifying marine mammals, including the three study species, constantly scanned the ocean's surface using 8-power binoculars.

In the survey area, two color morphs of Dall's porpoise are present: *dalli* and *truei* types (Amano and Hayano 2007). However, we did not distinguish between these two types due to time constraints for identification purposes.

Positions in latitude and longitude were recorded whenever the visual

survey was started or stopped. When the observers detected cetaceans, the species name, time, position in latitude and longitude, distance from the ship, angle from the front of the ship, and number of individuals were recorded. Distance from the ship was estimated by eye. Each researcher trained to estimate distance using ship radar or laser rangefinder (NIKON, Laser 1200S) outside of survey hours. In principle, the ship did not approach any sightings.

Hydroacoustic data was recorded to estimate prey distribution, using a Simrad EK 60 quantitative echosounder (38 kHz, Simrad, Norway) (Table 2), concurrently with the visual survey. The echosounder transducer was installed on the bottom of the ship and the beam pointed downward. We used 38 kHz backscatter as an approximate measure of fish (Tynan et al. 2005). Although fish species were not identified in our study, acoustic studies of walleye pollock (*Gadus chalcogrammus*) and California headlightfish (*Diaphus theta*) have been previously conducted in this survey area (Honda et al. 2004, Yasuma et al. 2010). Additionally, Japanese anchovy (*Engraulis japonicus*), Japanese sardine (*Sardinops melanostictus*), chum salmon (*Oncorhynchus keta*), Pacific saury (*Colobabis saira*), walleye pollock, Pacific cod (*Gadus microcephalus*), and Japanese flying squid (*Todarodes pacificus*) were caught by a local fishery (Hokkaido Government Office 2015). All of these species, except chum salmon, were known to be detected by 38 kHz echosounder (Kawabata 1999, Fujino et al. 2010, Murase et. al. 2012, Weinberg et al. 2016). There are not published data describing the acoustic characteristics of chum salmon at 38 kHz, but unpublished data suggests they

can also be detected by 38 kHz echosounder (Minami et al. unpublished data) and previous studies demonstrate that salmonid fish can be detected at 28~70 kHz (Suzuki and Sonoda 1972, Anma and Sano 1975, Mukai and Iida 1996, Sawada et al. 2012). Therefore, these fishes were considered to be potential prey that the echosounder might detect.

In recent years, increasing levels of anthropogenic noise in the marine environment, including echosounders, have led to concern about the impact upon marine animals. The impact of echosounders upon Pacific white-sided dolphins and Dall's porpoises has not been studied, but we observed bow-riding in most groups of Pacific white-sided dolphins and some groups of Dall's porpoises while the acoustic surveys were conducted. Harbor porpoises seem to avoid ships due to ship noise, not due to the presence of an echosounder (Dyndo et al. 2015). The ship did not approach any sightings during sighting surveys, therefore the effect of the echosounder and ship noise upon the three cetaceans was considered to be minimal.

2.2. Measuring the spatial niche overlap

Presence probability maps were generated using Maxent software (Ver. 3.3.3, Philips et al. 2006). Presence-only modelling, such as Maxent and ecological niche factor analysis (Hirzel et al. 2002, Phillips et al. 2006), can estimate presence probability using presence-only data or using background data as pseudo-absence, and thus is suited for data in which absence data is not available or is of questionable value. Visual survey cannot observe all cetaceans perfectly even on the survey line because cetaceans spend almost

time underwater. Therefore, we used presence only modelling in this study. Additionally, Maxent performs better using smaller sample sizes than other algorithms (Wisz et al. 2008). Therefore, this algorithm is suitable for the harbor porpoise, which has a small sample size. Those contributed to our choice to use Maxent, a presence-only model. The positions of each species during the survey period were the response variables, with the water depth, slope, and distance from land included as the explanatory variables. Mesh bathymetric data from an average water depth of 500 m was obtained from the Japan Oceanographic Data Center (<http://www.jodc.go.jp>). The slope was calculated from the water depth using the Generic Mapping Tools software (Wessel and Smith 1998). Explanatory variables were averaged in 4 km grids using ArcGIS 10 (ESRI).

We repeated the bootstrapping and Maxent procedure 100 times for each species, with 25% of the presence data used as the test data. The results are presented as an average of the 100 Maxent models. The area under the curve (AUC) was used to evaluate the model performance (Manel et al. 2001). AUC values of 0.5–0.7 were interpreted as indicating low accuracy, while values of 0.7–0.9 indicated useful applications, and values >0.9 indicated a high accuracy (Swets 1988).

A spatial niche overlap index, Schoener's D (Schoener 1968), was calculated for the three species from each presence probability map, using the ENM tool (ver. 1. 3) (Warren et al. 2008). This index ranged from 0 to 1, with 0 indicating that species have completely discordant ecological niche models and 1 indicating that species have identical ecological niche models.

In addition to creating a presence probability map using Maxent, we compared the three environmental parameters among the cells in which the three species were present using the Steel-Dwass test. The Steel-Dwass test is used to verify the difference among values in three or more groups (e.g. Honda et al. 2013, Inoue et al. 2017).

2.3. Overlap between each small cetacean and their potential prey

The hydroacoustic data was analyzed with Echoview 5.0 software (Myriax, Australia). The volume backscatter strength (Sv·dB) was calculated every 50 m along the survey line, at depth intervals of 10 m, to estimate the potential prey abundance. Sv indicates the strength of backscatter per unit volume, so the higher the Sv value, the more fish are present.

Due to noise caused by waves near the sea surface and sea floor, only backscatter between 3 m below the sea surface and 2 m above the sea floor was used. The maximum depth of calculation was defined as 300 m, in accordance with the maximum diving depth of the three cetaceans (Hall 1970, Westgate et al. 1995, Otani et al. 1998). We then averaged the Sv for every 10 m depth within a 2 km radius from the positions where cetaceans were observed.

We generated statistical models to understand the relationships between prey abundance and depth for each cetacean species, using generalized additive mixed models (GAMM) with a smooth spline function. GAMMs were chosen because they can express non-linear relationships. For all models a Gaussian distribution was used for error structures and the link

function was identity. The response variable was the averaged Sv and the explanatory variable was the depth layer. Each observation as categorical data was included as a random effect.

2.4. Environmental factors influencing the potential prey distribution at each depth layer

The Sv data was partitioned into depth layers (L1-L6) as follows: L1: 3-<50 m; L2: 50-<100 m; L3: 100-<150 m; L4: 150-<200 m; L5: 200-<250 m; and L6: 250-<300 m. Layer thickness was defined as 50 m according to the most frequent diving depth layer of Dall's porpoises and harbor porpoises (Hanson and Baird 1998, Otani et al. 1998, Teilmann et al. 2007). The diving behavior of the Pacific white-sided dolphin has not been well-studied, but they were found at depths shallower than 50 m in this survey. This further supported our decision to choose 50 m bins. Environmental data, water depth, slope, and distance from land, were then obtained at every 50 m using ArcGIS v.10 (ESRI).

We generated statistical models to understand the relationships between prey abundance and each of the environmental factors, using GAMMs. GAMMs were chosen as they can express non-linear relationships and include the random effect of month. In all models a Gaussian distribution was used for error structures and the link function was identity link function. The response variable was the averaged Sv and the explanatory variables were water depth, slope, and distance from the land. Multicollinearity among the explanatory variables was checked using the variance inflation factor

286 before modelling. Variable selection was performed using the Akaike
287 information criterion (AIC).

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3. RESULTS

3.1. Visual survey

In total, we observed 230 Pacific white-sided dolphins in 147 schools, 1282 Dall's porpoises in 266 schools, and 55 harbor porpoises in 24 schools (Table 1, Fig. 2). Pacific white-sided dolphins were mainly observed in Nemuro Bay and the coastal waters of southeast Hokkaido, whereas Dall's porpoises were found off southeast Hokkaido and in the coastal waters of the Shiretoko Peninsula. Harbor porpoises were observed sparsely across the entire survey area.

3.2. Environmental factors influencing the three cetaceans

Pacific white-sided dolphins were observed in the shallowest areas, where the water depth was shallower than approximately 100 m, whereas Dall's porpoises were observed in the deepest areas (Fig. 3a). There were significant differences in the water depths at which the different species were observed, including between Dall's porpoise and Pacific white-sided dolphins (Steel-Dwass test, $P < 0.05$, Table 3) and between Dall's porpoise and the harbor porpoise (Steel-Dwass test, $P < 0.05$, Table 3).

Harbor porpoises were found significantly closest to land (Steel-Dwass test, $P < 0.05$, Table 3), whereas Dall's porpoises were found furthest from land (Fig. 3b). Pacific white-sided dolphins were observed in the areas with the shallowest slope, but no significant difference was found between the Pacific white-sided dolphin and harbor porpoise (Fig. 3a). Dall's porpoises were observed in the steepest areas (Fig. 3c), but there was no significant

difference between Dall's porpoise and the harbor porpoise.

The presence probability of the Pacific white-sided dolphin was high in areas that were close to land with shallow water (Table 4, Fig. 4-5). In particular, the presence probability was >0.6 in Nemuro Bay (Fig. 5a). On the other hand, the presence probability of Dall's porpoise was high in areas where the water depth was greater; for example, the presence probability was >0.7 in the coastal waters of the Shiretoko Peninsula (Fig. 5b). The presence probability of the harbor porpoise was approximately 0.5 in areas close to land (Fig. 5c). The AUC of all habitat models were higher than 0.8. The habitat model of the Pacific white-sided dolphin had the highest accuracy ($\text{AUC} > 0.9$, Table 4). The spatial niche overlap index, Schoener's D, was low between the Pacific white-sided dolphin and Dall's porpoise (0.32), higher between Dall's porpoise and the harbor porpoise (0.51), and highest between the Pacific white-sided dolphin and harbor porpoise (0.70).

3.3. Differences in depths of potential prey where the 3 cetaceans were observed

In areas where Pacific white-sided dolphins were observed, potential prey were abundant in the shallower layers, being most abundant at approximately 80-90 m depth (Fig. 6a). On the other hand, potential prey were more abundant in the deeper layers in areas where Dall's and harbor porpoises were observed (Fig. 6b, c).

3.4. Environmental factors influencing the distribution of potential prey at

each depth layer

Water depth was included in all models under model selection as were all depth layers (L1-L6) (Table 5). The potential prey were more abundant in areas with shallower water than in areas with deeper water (Fig. 7). Potential prey were more abundant in areas with shallower (<1000 m) and deeper (4500 m) water depth than middle (3000 m) water depth in the upper depth layers (L1-2) (Fig. 7a, 7b). Where the slope was steeper, the potential prey were detected more abundantly in the deeper depth layers (150-200, 200-250, and 250-300 m) (Fig. 7). Potential prey were more abundant in the shallower layers (L1-4: 3-200 m) than in the deeper layers (L5-6: 200-300 m).

4. DISCUSSION

4.1. Distribution of the three cetaceans

Although our study was conducted to understand the spatial niche overlap among three small cetacean species, their spatial distribution and habitat is essential information around Japan, where few studies on the habitats of small cetaceans have been conducted. Therefore, we also discussed the spatial distribution and habitat of the three cetaceans.

Our study revealed that Pacific white-sided dolphins used shallower areas. However, this tendency is rare in other regions. For example, in the Tsugaru Strait, which was previously the only area where the distribution and habitat of Pacific white-sided dolphins were studied around Japan, there was no clear relationship between water depth and dolphin distribution (Maezawa et al. 2014, Iwahara et al. 2017). On the West Coast of North America, in the California Current region, Pacific white-sided dolphins were observed at a depth of 200-1000 m or on the continental slope, rather than at shallower depths (Gowans & Whitehead 1995, Yen et al. 2004, Tynan et al. 2005). In this region, deeper waters are also areas of high productivity due to upwelling (Tynan et al. 2005). Therefore, Pacific white-sided dolphins were considered to use greater depths in the western coastal area of North America, compared with our survey area.

In addition to prey availability, breeding might be another reason why Pacific white-sided dolphins use shallower depths in our study area. The reproductive success of female Indian Ocean bottlenose dolphins (*Tursiops* sp.) in Australia can be predicted by water depth (Mann et al. 2000).

Shallower depths might allow mothers and calves to detect and avoid predatory sharks. The birth period of Pacific white-sided dolphins is thought to be from May to September (Black 1994, Ferrero & Walker 1996, Ishikawa et al. 2013), and a group including a mother-calf pair was observed in this area (Iwahara personal observation). Killer whales, a potential predator of the Pacific white-sided dolphin, were also observed in this area, especially in the 200 m isobath and at depths of 300-500 m (Sato et al. 2006, Sasamori et al. 2013, Miyamoto et al. 2017). Therefore, Pacific white-sided dolphins might use shallower areas to avoid predatory killer whales. Our results that Pacific white-sided dolphins use shallower areas also suggest that they could be impacted by human activity, such as coastal fisheries.

Dall's porpoises were observed in deeper areas, but they were found near the coastal area of the Shiretoko Peninsula. The coastal area is steep, with a water depth of more than 3000 m. Dall's porpoise was likely observed here as it is mainly a mesopelagic predator.

The breeding area of Dall's porpoise is considered to be the Okhotsk Sea, which is located north of our study area (Amano & Kuramochi 1992, Amano & Hayano 2007, Fig. 1), and mother-calf pairs are rarely observed in our survey area (Kasuya 2011). Therefore, Dall's porpoise may not need to remain in shallower areas for breeding.

The distribution and habitat of harbor porpoises is critically important information, because harbor porpoises are frequently bycaught by fisheries (e.g., Barlow & Hanan 1995, Vinther & Larsen 2004). Whilst their abundance has been estimated in the North Atlantic Ocean and Northeast

Pacific Ocean (e.g., Stenson 2003, Hobbs & Waite 2010), their abundance and habitat use have not been well studied around Japan. Their seasonal migration around Japan was presumed from stranding data (Taguchi et al. 2010), because they were rarely observed from ferries or dolphin-watching tour boats aimed at the study of cetacean distributions (Ichimori et al. 2013). Therefore, our study provides valuable information for understanding the distribution and habitat of harbor porpoises around Japan. Our study reports that harbor porpoises were observed in areas close to land. The results indicate that harbor porpoises could be impacted by human activity, such as coastal fisheries (Taguchi et al. 2010).

4.2. Spatial niche overlap among the three species

Our results show that the spatial niche overlap between the Pacific white-sided dolphin and the Dall's porpoise was comparatively low, with Pacific white-sided dolphins observed in shallower waters (< 100 m), while Dall's porpoises were found in deeper waters. Although the diets of the two species have not been studied in the eastern coastal area of Hokkaido in recent years, Pacific white-sided dolphins mainly feed on epipelagic prey and Dall's porpoises mainly feed on mesopelagic prey in the western and southwestern coastal areas of Hokkaido (Matsuda 2017). Ohizumi et al. (2000) also reported that Dall's porpoises feed on mesopelagic prey, like the walleye pollock and magistrate armhook squid (*Berryteuthis magister*), in the northwestern and northeastern coastal areas of Hokkaido where epipelagic prey is not abundant. However, Dall's porpoises also feed on epipelagic prey

if they are available (Ohizumi et al. 2000).

The shallow water depths, where Pacific white-sided dolphins were observed, had higher prey abundance than greater depths, where Dall's porpoises were observed. In areas with deep water, where Dall's porpoises were observed, potential prey were more abundant in the shallower layers (L1-3) than the deeper layers (L4-6). Therefore, differences in Pacific white-sided dolphin and Dall's porpoise diet may explain the difference in spatial niche.

Potential prey were more abundant in shallower areas than deeper areas in all depth layers (L1-L6). Potential prey were more abundant in the surface layers (L1-2) in areas where the water depth reached deeper than 3000 m, than in the areas where water depth was approximately 2000 m. In areas where the water depth was 2000 m, the potential prey in the shallower layers (L1-4) was more abundant than in the deeper layers (L5-6). Therefore, our results suggested that Dall's porpoises use deep water areas where epipelagic and mesopelagic prey are available. In terms of physiology, Dall's porpoises can dive for a longer duration than Pacific white-sided dolphins due to the differences in their blood volume, hemoglobin, heart weight, and hematocrit (Ridgway & Johnston 1966, Reed et al. 2000). Therefore, Dall's porpoises may feed on prey in deeper layers where there is less competitive with large groups of Pacific white-sided dolphins. Dall's porpoises may even avoid Pacific white-sided dolphins in shallow areas, although potential prey are abundant. However, further study is needed to validate this hypothesis.

The spatial overlap between the harbor porpoise and both the other

two species was moderate. Harbor porpoises were observed in areas close to the shore and their distribution was mostly not influenced by water depth, while the distribution of the other two species was. Although harbor porpoises have a varied diet, they have a higher tendency to feed on benthic prey compared to the other two species (Otani 1999, Matsuda 2017). The distribution and abundance of benthic animals are difficult to measure using an echosounder; therefore, the relationship between harbor porpoises and their prey might not have been assessed properly if they feed on benthic prey in shallower areas. A varied diet including benthic prey probably allows harbor porpoises to coexist with the other two species.

In addition to diet partitioning, the eastern coast of Hokkaido is a highly productive area (Yasuma et al. 2010); therefore, this potential abundance of prey might allow them to coexist in the same areas. Additionally, a low number of harbor porpoises might explain why their spatial niche overlapped more with the other two species. Although the distribution of harbor porpoises is not well-understood, Kanaji et al. (2017) reported that harbor porpoises were more abundant in the Okhotsk Sea than in our survey area from July to September. In the northwest Atlantic Ocean, seasonal movement of harbor porpoises has been observed; harbor porpoises are usually observed in shallow nearshore waters, but they migrate offshore in winter (Read et al. 1996). Therefore, our study area might not be the primary distribution area of harbor porpoises in the fall, which may be why a low number of harbor porpoises were observed.

In this study, we examined the distribution of three cetacean species

and their potential prey only during daylight hours. Differences in behavior and depth between day and night have been observed in many cetaceans (e.g. Henderson et al. 2011, Ishii et al. 2017), and potential prey fishes also conduct vertical migration (e.g. Yasuma et al. 2010, Honda et al. 2004). Therefore, to understand the entire mechanism behind the distribution of these three small cetacean species we must study the distribution and diving depth of cetaceans at night, for example by using satellite tracking and bio-logging methods (e.g. Saijo et al. 2017, Ishii et al. 2017).

Acoustic surveys are the standard method to estimate the distribution and abundance of fish and zooplankton and are valuable in estimating the occurrence of potential prey at the same time as visual surveys from ships. However, the impact of echosounders upon marine mammals is not well understood. The vocalization behavior of beaked whales did not differ in periods before, during, or after echosounder deployment (Vires 2011). On the other hand, short-finned pilot whales (*Globicephala macrorhynchus*) changed their heading more frequently when an echosounder was active (Quick et al. 2016). Although echosounders usually generate lower-level sound than military sonar or airguns used in marine geological surveys, which stranding events have been linked with (Taylor et al. 2004, Filadelfo et al. 2009, Lurton and DeRuiter 2011), the impact upon marine mammals, such as the risk of auditory system damage or interference with their echolocation, must be studied. In addition, whether echosounders attract or repulse marine mammals is not understood (Doksæter et al. 2009, Quick et al. 2016). Future research should investigate the effect of echosounders on the detection of

marine mammals when conducting visual and acoustic surveys simultaneously.

Our study investigated the distribution of three small cetaceans with overlapping spatial niches, by quantification of the spatial niche overlap and comparing the potential prey distribution and habitat using an echosounder. Based on our findings we postulated that despite broad spatial overlap, habitat partitioning is evident with respect to distance to shore, bottom depth, slope, and vertical prey distribution, likely reflecting differences in foraging strategies and diet. Our study also provided important information relevant to the conservation and management of three small cetaceans in the eastern coastal area of Hokkaido, where fisheries are thriving.

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518 Reference

- 519 Amano M, Kuramochi T (1992) Segregative migration of Dall's porpoise
520 (Phocoenoides dalli) in the Sea of Japan and Sea of Okhotsk. Mar
521 Mamm Sci 8:143-151.
- 522 Amano M, Hayano A (2007) Intermingling of Dall-Type Dall's Porpoises into
523 a Wintering Truei-Type Population Off Japan: Implications from Color
524 Patterns. Mar Mamm Sci 23:1-14.
- 525 Anna G, Sano N (1975) Study for Estimating the Existent Amount of Salmon
526 Resources by Means of Echo Sounding Techniques I. On a preparative
527 experiment for the use of the vertical echo sounder in the Bering Sea.
528 Bull Fac Fish, Hokkaido Univ 26:137-153. (In Japanese with English
529 abstract)
- 530 Arlettaz R (1999) Habitat selection as a major resource partitioning
531 mechanism between the two sympatric sibling bat species Myotis
532 myotis and Myotis blythii. J Anim Ecol 68:460-471.
- 533 Barlow J, Hanan D (1995) An assessment of the status of harbour porpoise in
534 central California (SC/42/SM6). Rep Int Whal Comm Spec Issue
535 16:123-140.

536 Bearzi M (2005) Habitat partitioning by three species of dolphins in Santa
537 Monica Bay, California. *Bull South Calif Acad Sci* 104:113-124.

538 Black NA (1994) Behavior and ecology of Pacific white-sided dolphins
539 (*Lagenorhynchus obliquidens*) in Monterey Bay, California. MSc
540 dissertation, San Francisco State University, San Francisco, CA.

541 Connell JH (1961) The influence of interspecific competition and other factors
542 on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*
543 42:710-723.

544 Doksæter L, Olsen E, Nøttestad L, Fernö A (2008) Distribution and feeding
545 ecology of dolphins along the Mid-Atlantic Ridge between Iceland and
546 the Azores. *Deep Sea Res II* 55:243-253.

547 Doksæter L, Godø OR, Olsen E, Nøttestad L, Patel R (2009) Ecological studies
548 of marine mammals using a seabed-mounted echosounder. *ICES J Mar*
549 *Sci* 66:1029-1036.

550 Dyndo M, Wisniewska DM, Rojano-Doñate L, Madsen PT (2015) Harbour
551 porpoises react to low levels of high frequency vessel noise. *Sci Rep* 5:
552 11083.

553 Ferrero RC, Walker WA (1996) Age, growth, and reproductive patterns of the

554 Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) taken in
 555 high seas drift nets in the central North Pacific Ocean. Can J Zool 74:
 556 1673-1687.

557 Filadelfo R, Mintz J, Michlovich E, D'Amico A, Tyack PL, Ketten DR (2009)
 558 Correlating military sonar use with beaked whale mass strandings:
 559 what do the historical data show? Aquat Mamm 35:435-444.

560 Friedlaender AS, Lawson GL, Halpin PN (2009) Evidence of resource
 561 partitioning between humpback and minke whales around the western
 562 Antarctic Peninsula. Mar Mamm Sci 25:402-415.

563 Fujino T, Kawabata A, Kidokoro H (2010) Echograms of aquatic organisms
 564 observed by a quantitative echosounder around Japan. Japan Sea
 565 National Fisheries Research Institute, Niigata, pp.1-216 (In Japanese)

566 Gaskin D, Yamamoto S, Kawamura A (1993) Harbor porpoise, *Phocoena* -
 567 *phocoena* (L.), in the coastal waters of northern Japan. Fish Bull
 568 91:440-454.

569 Gowans S, Whitehead H (1995) Distribution and habitat partitioning by small
 570 odontocetes in the Gully, a submarine canyon on the Scotian Shelf. Can
 571 J Zool 73:1599-1608.

572 Gross A, Kiszka J, Van Canneyt O, Richard P, Ridoux V (2009) A preliminary
573 study of habitat and resource partitioning among co-occurring tropical
574 dolphins around Mayotte, southwest Indian Ocean. *Estuar Coast Shelf*
575 *Sci* 84:367-374.

576 Hall J (1970). Conditioning Pacific White-Striped Dolphins, *Lagenorhynchus*
577 *obliquidens*, for Open-Ocean Release. Technical Paper No. 200. Naval
578 Undersea Research and Development Center, San Deigo, CA.

579 Hanson MB, Baird RW (1998) Dall's porpoise reactions to tagging attempts
580 using a remotely-deployed suction-cup tag. *Mar Technol Soc J* 32:18-23.

581 Harrington LA, Harrington AL, Yamaguchi N, Thom MD, Ferreras P,
582 Windham TR, Macdonald DW (2009) The impact of native competitors
583 on an alien invasive: temporal niche shifts to avoid interspecific
584 aggression. *Ecology* 90:1207-1216.

585 Henderson EE, Hildebrand JA, Smith MH (2011) Classification of behavior
586 using vocalizations of Pacific white-sided dolphins (*Lagenorhynchus*
587 *obliquidens*). *J Acoust Soc Am* 130:557-567.

588 Hirzel AH, Hausser J, Chessel D, Perrin N (2002) Ecological - niche factor
589 analysis: how to compute habitat - suitability maps without absence

590 data? Ecology 83:2027-2036.

591 Hobbs RC, Waite JM (2010) Abundance of harbor porpoise (*Phocoena*
592 *phocoena*) in three Alaskan regions, corrected for observer errors due
593 to perception bias and species misidentification, and corrected for
594 animals submerged from view. Fish Bull 108:251-267.

595 Hokkaido Government Office (2015) “Hokkaido Suisan Gensei, Heisei 27
596 nendo”; literally, Fisheries status in Hokkaido Prefecture,
597 http://www.pref.hokkaido.lg.jp/sr/sum/03kanrig/sui_toukei/H27gensei.pdf
598 i.pdf” Accessed 7 July 2019” (in Japanese)

599 Honda S, Oshima T, Nishimura A, Hattori T (2004) Movement of juvenile
600 walleye pollock, *Theragra chalcogramma*, from a spawning ground to
601 a nursery ground along the Pacific coast of Hokkaido, Japan. Fish
602 Oceanogr 13:84-98.

603 Honda K, Nakamura Y, Nakaoka M, Uy WH, Fortes MD (2013) Habitat Use
604 by Fishes in Coral Reefs, Seagrass Beds and Mangrove Habitats in the
605 Philippines. PLOS ONE 8:e65735.

606 Ichimori D, Suzuki S, Kojima S, Ishimori K, Sugitani M, Matsuda A, Ono Y,
607 Matsuishi T (2013) Seasonal variability and yearly trend of cetacean
608 encounters in decadal sighting survey in the Tsugaru Strait, Japan.

609 Jpn Cetol 23: 29 -33. (In Japanese with English abstract.)

610 Inoue K, Terashima Y, Shirakihara M, Shirakihara K (2017) Habitat use by

611 Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Amakusa,

612 Japan. *Aquat Mamm* 43:127-138.

613 Ishii M, Murase H, Fukuda Y, Sawada K, Sasakura T, Tamura T, Bando T,

614 Matsuoka K, Shinohara A, Nakatsuka S (2017) Diving behavior of sei

615 whales *Balaenoptera borealis* relative to the vertical distribution of

616 their potential prey. *Mammal study* 42:1-10.

617 Ishikawa H, Goto M, Mogoe T (2013) Stranding records in Japan (1901-2012).

618 Report No. 1. Shimonoseki Academy of Marine Science, Shimonoseki.

619 (In Japanese)

620 Iwahara Y, Mitani Y, Miyashita K (2017) Estimation of Environmental

621 Factors That Influence Migration Timing and Distribution of Pacific

622 White-Sided Dolphins around Hokkaido, Japan. *Pac Sci* 71:303-318.

623 Kadowaki K (2016) The mechanisms of maintenance of biodiversity in patchy

624 environments. *Jap J Ecol* 66: 1-23.

625 Kagami H (1990) Chapter 29 Eastern and southern coastal area of

626 Hokkaido. I Topography. In: *Coastal Oceanography Research*

627 Committee, The Oceanographical Society of Japan. (ed) Coastal
628 Oceanography of Japanese Islands • Supplementary Volume. Tokai
629 University Press, Tokyo, p463-472.

630 Kanaji Y, Okazaki M, Watanabe H, Miyashita T (2016) Biogeography of small
631 odontocetes in relation to wide - scale oceanographic structure in the
632 North Pacific Ocean. *Fish Oceanogr* 25:119-132.

633 Kanaji Y, Okazaki M, Miyashita T (2017) Spatial patterns of distribution,
634 abundance, and species diversity of small odontocetes estimated using
635 density surface modeling with line transect sampling. *Deep Sea Res II*
636 140: 151-162.

637 Kasamatsu F, Matsuoka K, Hakamada T (2000) Interspecific relationships in
638 density among the whale community in the Antarctic. *Polar Biol*
639 23:466-473.

640 Kasuya T (2011). Conservation biology of small cetaceans around Japan,
641 University of Tokyo University Press, Tokyo.

642 Kawabata A (1999) Measurement of the target strength of Japanese flying
643 squid, *Todarodes pacificus* Steenstrup. *Bull Tohoku Natl Fish Res Inst*
644 61:29-40 (In Japanese with English abstract).

645 Litvaitis J, Harrison D (1989) Bobcat-coyote niche relationships during a
646 period of coyote population increase. *Can J Zool* 67:1180-1188.

647 Lurton X, DeRuiter S (2011) Sound radiation of seafloor-mapping
648 echosounders in the water column, in relation to the risks posed to
649 marine mammals. *Int Hydrogr Rev* 6:7-17.

650 Maezawa T, Higashisaka H, Ishii M, Tashiro G, Kuroda M, Matsuda A,
651 Matsuishi T (2014) Environmental preference of Pacific white-sided
652 dolphin in Tsugaru Strait. *Jpn Cetol* 24: 27-32. (In Japanese with
653 English abstract.)

654 Manel S, Williams HC, Ormerod SJ (2001) Evaluating presence–absence
655 models in ecology: the need to account for prevalence. *J appl Ecol*
656 38:921-931.

657 Mann J, Connor RC, Barre LM, Heithaus MR (2000) Female reproductive
658 success in bottlenose dolphins (*Tursiops* sp.): life history, habitat,
659 provisioning, and group-size effects. *Behav Ecol* 11:210-219.

660 Matsuda A, Matsuishi T (2012) Stomach contents of Dall's porpoise
661 *Phocoenoides dalli* stranded in Hokkaido. *Jpn Cetol* 22: 9-13. (In
662 Japanese with English abstract.)

663 Matsuda A (2017) Diet study on small toothed whales around Japan. PhD
 664 dissertation, Hokkaido University, Sapporo (In Japanese)
 665 Miyamoto H, Iwahara Y, Haba S, Nakahara F, Ohizumi H, Saino S,
 666 Yamamoto Y, Yoshioka M, Mitani Y (2017) Distribution and Habitat
 667 Conditions of Killer Whales in Eastern Hokkaido. Bull Shiretoko Mus
 668 39:37-48.
 669 Miyashita T (2013) Studies on population and population dynamics of Dall's
 670 porpoises. PhD dissertation, TokyoUniversity of Marine Science and
 671 Technology, Tokyo (in Japanese).
 672 Miyazaki N, Kuramochi T, Amano M (1991) Pacific white-sided dolphins
 673 (*Lagenorhynchus obliquidens*) off northern Hokkaido. Mem Natn Sci
 674 Mus 24:131-139.
 675 Mukai T, Iida K (1996) Depth dependence of target strength of live kokanee
 676 salmon in accordance with Boyle's law. ICES J Mar Sci 53:245-248.
 677 Murase H, Kawabata A, Kubota H, Nakagami M, Amakasu K, Abe K,
 678 Miyashita K, Oozeki Y (2012) Basin-scale distribution pattern and
 679 biomass estimation of Japanese anchovy *Engraulis japonicus* in the
 680 western North Pacific. Fish Sci 78:761-773.

681 Nicholls B, Racey P (2006) Contrasting home-range size and spatial
 682 partitioning in cryptic and sympatric pipistrelle bats. *Behav Ecol*
 683 *Sociobiol* 61:131-142.

684 Ohizumi H, Kuramochi T, Amano M, Miyazaki N (2000) Prey switching of
 685 Dall's porpoise *Phocoenoides dalli* with population decline of Japanese
 686 pilchard *Sardinops melanostictus* around Hokkaido, Japan. *Mar Ecol*
 687 *Prog Ser* 200:265-275.

688 Otani S, Naito Y, Kawamura A, Kawasaki M, Nishiwaki S, Kato A (1998)
 689 Diving behavior and performance of harbor porpoises, *Phocoena*
 690 *phocoena*, in Funka Bay, Hokkaido, Japan. *Mar Mamm Sci* 14:209-220.

691 Otani S (1999) Behavioral and physiological study on continuous diving
 692 behavior of harbor porpoise. PhD dissertation, Sokendai, Hayama (In
 693 Japanese)

694 Parra GJ (2006) Resource partitioning in sympatric delphinids: space use and
 695 habitat preferences of Australian snubfin and Indo - Pacific humpback
 696 dolphins. *J Anim Ecol* 75:862-874.

697 Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of
 698 species geographic distributions. *Ecol Model* 190:231-259.

699 Pinaud D, Weimerskirch H (2007) At - sea distribution and scale - dependent
700 foraging behaviour of petrels and albatrosses: a comparative study. J
701 Anim Ecol 76:9-19.

702 Quick N, Scott-Hayward L, Sadykova D, Nowacek D, Read A (2017) Effects of
703 a scientific echo sounder on the behavior of short-finned pilot whales
704 (*Globicephala macrorhynchus*). Can J Fish Aquat Sci 74:716-726.

705 Read AJ, Nicolas JR, Craddock JE (1996) Winter capture of a harbor porpoise
706 in a pelagic drift net off North Carolina. Fish Bull 94:381-383.

707 Reed JZ, Chambers C, Hunter C, Lockyer C, Kastelein R, Fedak M, Boutilier
708 R (2000) Gas exchange and heart rate in the harbour porpoise,
709 *Phocoena phocoena*. J Comp Physiol B 170:1-10.

710 Ridgway SH, Johnston DG (1966) Blood oxygen and ecology of porpoises of
711 three genera. Science 151:456-458.

712 Roughgarden J (1976) Resource partitioning among competing species—a
713 coevolutionary approach. Theor Popul Biol 9:388-424.

714 Saijo D, Mitani Y, Abe T, Sasaki H, Goetsch C, Costa DP, Miyashita K (2017)
715 Linking mesopelagic prey abundance and distribution to the foraging
716 behavior of a deep-diving predator, the northern elephant seal. Deep

717 Sea Res Part II 140:163-170.

718 Sasamori K, Takahashi M, Josha S, Kondo S, Shimoda A, Kobayashi B (2013)

719 Movement of killer whales in eastern Hokkaido ocean and northern

720 territories. In: Sakurai Y, Ohshima K, Ohtaishi N (eds) Ecosystem and

721 its conservation in the Sea of Okhotsk. Hokkaido University Press,

722 Sapporo, p.175-185 (In Japanese).

723 Sato H, Ishikawa S, Ezaki I, Sasamori K, Takahashi T, Masuda Y, Yoshida T

724 (2006) Opportunistic Sighting-basis Trend of Occurrence of *Orcinus*

725 orca, and Their Photographic Identification Catalog in Shiretoko-

726 Nemuro Strait Water, Eastern Hokkaido, Japan, 1990-2005. Bull

727 Shiretoko Mus 27:9-36.

728 Sawada K, Matsuura T, Aono H, Hashiba A (2012) Target strength pattern

729 measurement of juvenile chum salmon (*Oncorhynchus keta*) in a tank

730 by the controlled method. IEICE Tech Rep. Ultrasonics 112:105-110.

731 (In Japanese with English abstract)

732 Schoener TW (1968) The *Anolis* lizards of Bimini: resource partitioning in a

733 complex fauna. Ecology 49:704-726.

734 Stenson G (2003) Harbour porpoise (*Phocoena phocoena*) in the North

735 Atlantic: Abundance, removals, and sustainability of removals.
 736 NAMMCO Sci Publ 5:271-302.

737 Stewart KM, Bowyer RT, Kie JG, Hurley MA (2010) Spatial distributions of
 738 mule deer and North American elk: resource partitioning in a sage-
 739 steppe environment. *Am Midl Nat* 163:400-412.

740 Suzuki T, Sonoda H (1972) On a Trial Fish Finder for Salmon and its
 741 Experimental Results. *Bull Jpn Soc Sci Fish* 38:463-469. (In Japanese
 742 with English abstract)

743 Swets JA (1988) Measuring the accuracy of diagnostic systems. *Science*
 744 240:1285-1293.

745 Taguchi M, Ishikawa H, Matsuishi T (2010) Seasonal distribution of harbour
 746 porpoise (*Phocoena phocoena*) in Japanese waters inferred from
 747 stranding and bycatch records. *Mammal study* 35:133-138.

748 Taylor B, Barlow J, Pitman R, Ballance L, Klinger T, DeMaster D, Hildebrand
 749 J, Urban J, Palacios D, Mead J (2004). A call for research to assess risk
 750 of acoustic impact on beaked whale populations. Paper presented to the
 751 Scientific Committee at the 56th Meeting of the International Whaling
 752 Commission, 29 June-10 July 2004, Sorrento, Italy, SC/56/E36.

753 Teilmann J, Larsen F, Desportes G (2007) Time allocation and diving
 754 behaviour of harbour porpoises (*Phocoena phocoena*) in Danish and
 755 adjacent waters. *J Cetacean Res Manage* 9:201-210.

756 Tilman D, Mattson M, Langer S (1981) Competition and nutrient kinetics
 757 along a temperature gradient: an experimental test of a mechanistic
 758 approach to niche theory. *Limnol Oceanogr* 26: 1020–1033.

759 Tynan CT, Ainley DG, Barth JA, Cowles TJ, Pierce SD, Spear LB (2005)
 760 Cetacean distributions relative to ocean processes in the northern
 761 California Current System. *Deep Sea Res II* 52:145-167.

762 Vinther M, Larsen F (2004) Updated estimates of harbour porpoise (*Phocoena*
 763 *phocoena*) bycatch in the Danish North Sea bottom-set gillnet fishery.
 764 *J Cetacean Res Manag* 6:19-24.

765 Vires G (2011) Echosounder effects on beaked whales in the Tongue of the
 766 Ocean, Bahamas. MSc thesis, Duke University, Durham, NC.

767 Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency
 768 versus conservatism: quantitative approaches to niche evolution.
 769 *Evolution* 62:2868-2883.

770 Weinberg KL, Yeung C, Somerton DA, Thompson GG, Ressler PH (2016) Is

771 the survey selectivity curve for Pacific cod (*Gadus macrocephalus*)
 772 dome-shaped? Direct evidence from trawl studies. *Fish Bull* 114:360-
 773 370.

774 Weir CR, Macleod CD, Calderan SV (2009) Fine-scale habitat selection by
 775 white-beaked and common dolphins in the Minch (Scotland, UK):
 776 evidence for interspecific competition or coexistence? *J Mar Biol Assoc*
 777 UK 89:951-960.

778 Wessel P, Smith W (1998) The generic mapping tools. School of ocean and
 779 earth science and technology, University of Hawaii at Manoa, Honolulu,
 780 HI.

781 Westgate AJ, Head AJ, Berggren P, Koopman HN, Gaskin DE (1995) Diving
 782 behaviour of harbour porpoises, *Phocoena phocoena*. *Can J Fish Aquat*
 783 *Sci* 52:1064-1073.

784 Wilke F, Taniwaki T, Kuroda N (1953) *Phocoenoides* and *Lagenorhynchus* in
 785 Japan, with notes on hunting. *J Mammal* 34: 488-497.

786 Wisz MS, Hijmans R, Li J, Peterson AT, Graham C, Guisan A (2008) Effects
 787 of sample size on the performance of species distribution models.
 788 *Divers Distrib* 14:763-773.

789 Yamaji H (1985) Chapter 1 Coastal area of the Okhotsk Sea. I Topography.
 790 In: Coastal Oceanography Research Committee, The Oceanographical
 791 Society of Japan. (ed) Coastal Oceanography of Japanese Islands. Tokai
 792 University Press, Tokyo, p.1-6.

793 Yasuma H, Ohshima T, Honda S, Miyashita K, Aoki I (2010) Acoustic biomass
 794 estimate of California headlightfish *Diaphus theta*, off eastern
 795 Hokkaido, Japan. *Nippon Suisan Gakkai Shi* 76: 362-369.

796 Yen PP, Sydeman WJ, Hyrenbach KD (2004) Marine bird and cetacean
 797 associations with bathymetric habitats and shallow-water
 798 topographies: implications for trophic transfer and conservation. *J Mar*
 799 *Syst* 50:79-99.

800

801 Table 1. Details of the surveys for the 3 small cetaceans around Hokkaido, and the results of the visual survey

802

Year	Month	Days	Period (day)	Distance (km)	Time (hr:min)	Pacific white- sided dolphin	Dall's porpoise	Harbor porpoise
						(Individuals/Groups) (Individuals per100 km/Groups per 100 km)		
2009	9	5-6, 8-11, 14-17	10	1028	65:42	230/25 22.37/2.43	735/131 71.50/12.74	6/4 0.58/0.39
2009	10	1-7	7	776	39:25	492/27 63.40/3.48	207/59 26.68/7.60	3/1 0.39/0.13
2011	10	4-10	7	502	19:46	- -	111/25 22.11/4.98	- -
2012	9	19-23, 26	6	726	38:25	166/21 22.87/2.89	88/19 12.12/2.62	1/1 0.14/0.14
2012	10	10, 12-14	4	233	12:05	200/1 85.84/0.43	16/7 6.87/3.00	- -
2013	9	15, 18-23	7	552	29:36	145/8 26.27/1.45	35/9 6.34/1.63	10/4 1.81/0.72
2013	10	19-20, 23, 26	4	108	11:55	- -	1/1 0.93/0.93	- -
2014	9	13-19	7	746	41:05	363/39 48.66/5.23	20/2 2.68/0.27	25/9 3.35/1.21
2015	10	14-17, 19	5	695	36:11	402/26 57.84/3.74	69/13 9.93/1.87	10/5 1.44/0.72
Total						1998/147 37.23/2.74	1282/266 23.89/4.96	55/24 1.02/0.45

803 Table 2. Parameters of the quantitative echosounder (EK60)

Parameter	Value
Frequency (kHz)	38
Pulse duration (ms)	1.024
Minor axis beam width (°)	7.40
Major axis beam width (°)	7.65

804

805

806

Table 3. Results of the Steel-Dwass tests for the three species and each of the environmental factors. PWD: Pacific white-sided dolphin; HP: harbor porpoise; DP: Dall's porpoise. *p < 0.05

Combination	t value	p value
Depth		
PWD vs. HP	0.615	8.11×10^{-1}
PWD vs. DP	7.661	* 7.34×10^{-14}
DP vs. HP	4.032	* 1.64×10^{-4}
Distance from land		
PWD vs. HP	3.977	* 2.06×10^{-4}
PWD vs. DP	1.189	4.60×10^{-1}
DP vs. HP	4.202	* 7.83×10^{-5}
Slope		
PWD vs. HP	2.030	1.05×10^{-1}
PWD vs. DP	7.706	* 5.64×10^{-14}
DP vs. HP	2.096	9.07×10^{-2}

Table 4. Results of the Maxent mapping. AUC: Area under the curve, PC: Percent contribution, and PI: Permutation importance. Dland indicates distance from the land.

	Dall's porpoise (AUC 0.820)		Pacific white-sided dolphin (AUC 0.912)		Harbor porpoise (AUC 0.826)	
	PC	PI	PC	PI	PC	PI
Depth	40.2	45.3	70.7	84.8	12.2	12.6
Slope	37.2	42.0	22.9	7.3	4.7	13.5
Dland	22.6	12.7	6.5	7.9	83.1	73.9

818 Table 5. Model selection results of the GAMM.

Layers	Depth	Dland	Slope	AIC	Delta AIC
L1 (3~50m)					
	+	+		10640.31	-
L2 (50~100m)					
	+		+	7543.36	-
	+	+	+	7543.45	0.09
L3 (100~150m)					
	+	+	+	6201.19	-
L4 (150~200m)					
	+	+	+	5031.99	-
L5 (200~250m)					
	+	+	+	3861.12	-
L6 (250~300m)					
	+	+	+	3410.19	-

819
820 The lowest AIC model and models competing with the lowest AIC model
821 ($\Delta AIC \leq 2$) are presented. Selected explanatory variables were indicated “+”.
822 Dland indicated distance from the land.

824 Fig. 1 Survey area of the eastern coastal waters of Hokkaido. The black lines
825 indicate the survey lines and gray lines indicate isobaths.

Fig. 2 Visual survey for small cetaceans in the eastern coastal area of Hokkaido in a) September in 2009, 2012, 2013 and 2014, and b) October in 2009, 2011, 2012, 2013 and 2015. The black line indicates the survey line; red circles indicate the Pacific white-sided dolphin; yellow circles indicate Dall's porpoise; blue circles indicate harbor porpoises.

Fig. 3 Boxplot of the environmental data for the locations where each of the cetaceans were observed: a) water depth, b) distance from land, and c) slope. PWD, Pacific white-sided dolphin; DP, Dall's porpoise; and HP, Harbor porpoise. Upper and lower whisker indicate maximum and minimum value without outliers. Top and bottom of box indicate upper and lower quartile. Heavy line in the box indicate median. Open circles out of whisker range indicate outliers.

Fig. 4 Relationships between the presence probability of the cetaceans and environmental factors using Maxent software. a) Pacific white-sided dolphin, b) Dall's porpoise, and c) harbor porpoise. Red lines indicate average and blue ranges indicate one standard deviation of 100 Maxent models.

Fig. 5 Presence probability map of the three cetaceans predicted by Maxent software. a) Pacific white-sided dolphin, b) Dall's porpoise, and c) harbor porpoise. The black color indicates that the location is not in the survey area

Fig. 6 Relationships between the volume backscatter strength (S_v : dB) and depth at the positions where each cetacean was observed. a) Pacific white-sided dolphin, b) Dall's porpoise, and c) harbor porpoise. Open circles indicate measured values and lines indicate the predictions made by the GAMM

Fig. 7-1 Potential prey abundance (as volume backscatter strength; Sv) versus each environmental factor at different depth levels: (a) L1: 3-50 m, (b) L2: 50-100 m, (c) L3: 100-150 m, (d) L4: 150-200 m, (e) L5: 200-250 m, (f) L6: 250-300 m. Environmental factors were selected using Akaike's information criterion. Circles: measured values; lines: predictions made by the generalized additive mixed model.

Fig. 7-2 Potential prey abundance (as volume backscatter strength; Sv) versus each environmental factor at different depth levels: (a) L1: 3-50 m, (b) L2: 50-100 m, (c) L3: 100-150 m, (d) L4: 150-200 m, (e) L5: 200-250 m, (f) L6: 250-300 m. Environmental factors were selected using Akaike's information criterion. Circles: measured values; lines: predictions made by the generalized additive mixed model.