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

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Authors and addresses

Yuka Iwahara[1*], Hokuto Shirakawa[1], Kazushi Miyashita[1], Yoko Mitani[1]

(1) Hokkaido University, 20-5 Benten-cho, Hakodate, Hokkaido 040-0051, JAPAN

*yuka.iw.irk@gmail.com

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) understand the potential prey distribution and environment.

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

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

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

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

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	$^{*}7.34 \times 10^{-14}$
	DP vs. HP	4.032	$^{*}1.64 \times 10^{-4}$
Distance from land			
	PWD vs. HP	3.977	$^{*}2.06 \times 10^{-4}$
	PWD vs. DP	1.189	4.60×10^{-1}
	DP vs. HP	4.202	$^{*}7.83 \times 10^{-5}$
Slope			
	PWD vs. HP	2.030	1.05×10^{-1}
	PWD vs. DP	7.706	$^{*}5.64 \times 10^{-14}$
	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

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	-

The lowest AIC model and models competing with the lowest AIC model (ΔAIC ≤ 2) are presented. Selected explanatory variables were indicated “+”. Dland indicated distance from the land.

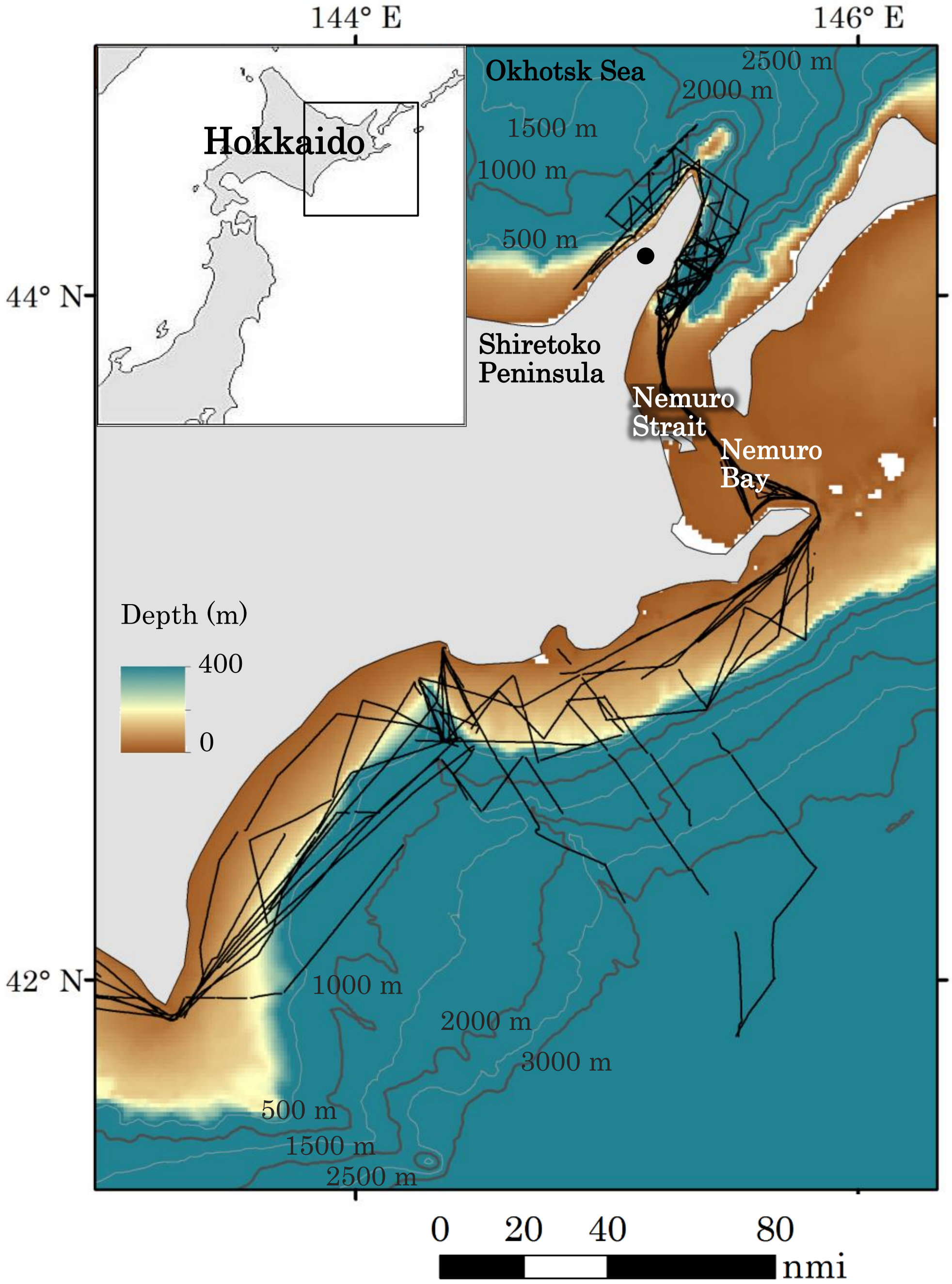

Fig. 1 Survey area of the eastern coastal waters of Hokkaido. The black lines indicate the survey lines and gray lines indicate isobaths.

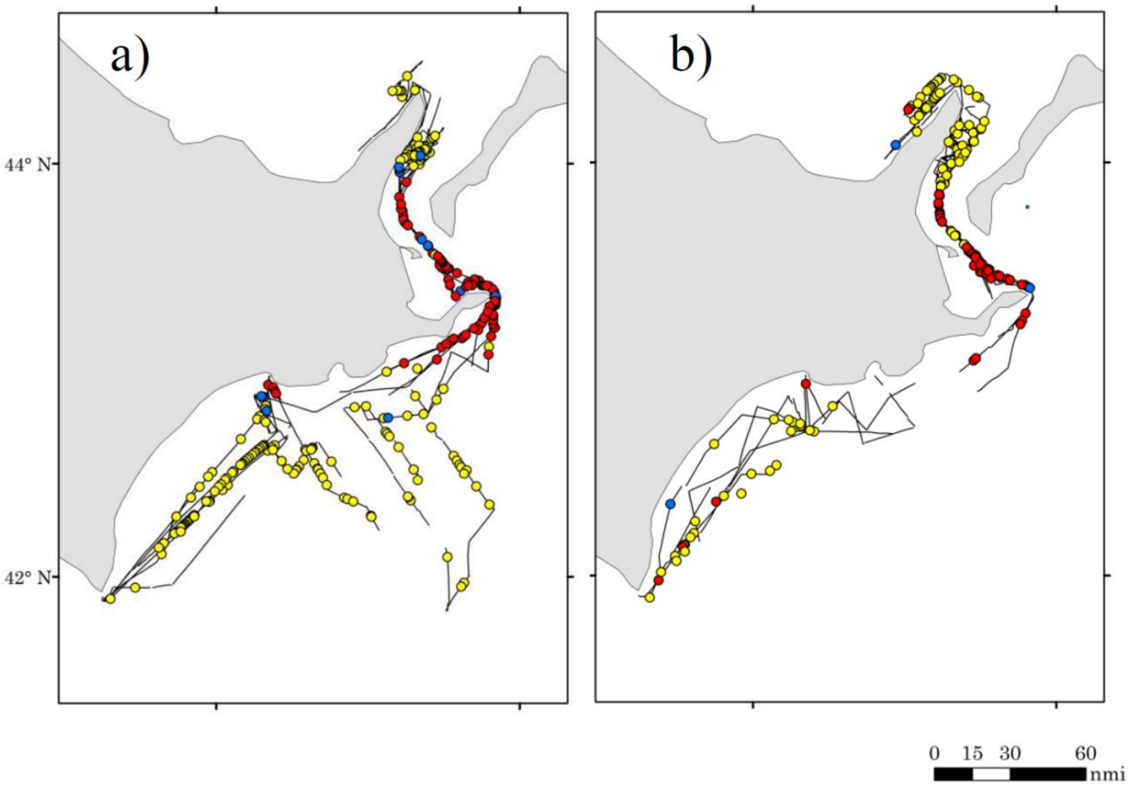

Fig. 2 Visual survey for small cetaceans in the eastern coastal area of Hokkaido in a) September in 2009, 2012, 2013 and 2014, and b) October in 2009, 2011, 2012, 2013 and 2015. The black line indicates the survey line; red circles indicate the Pacific white-sided dolphin; yellow circles indicate Dall's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

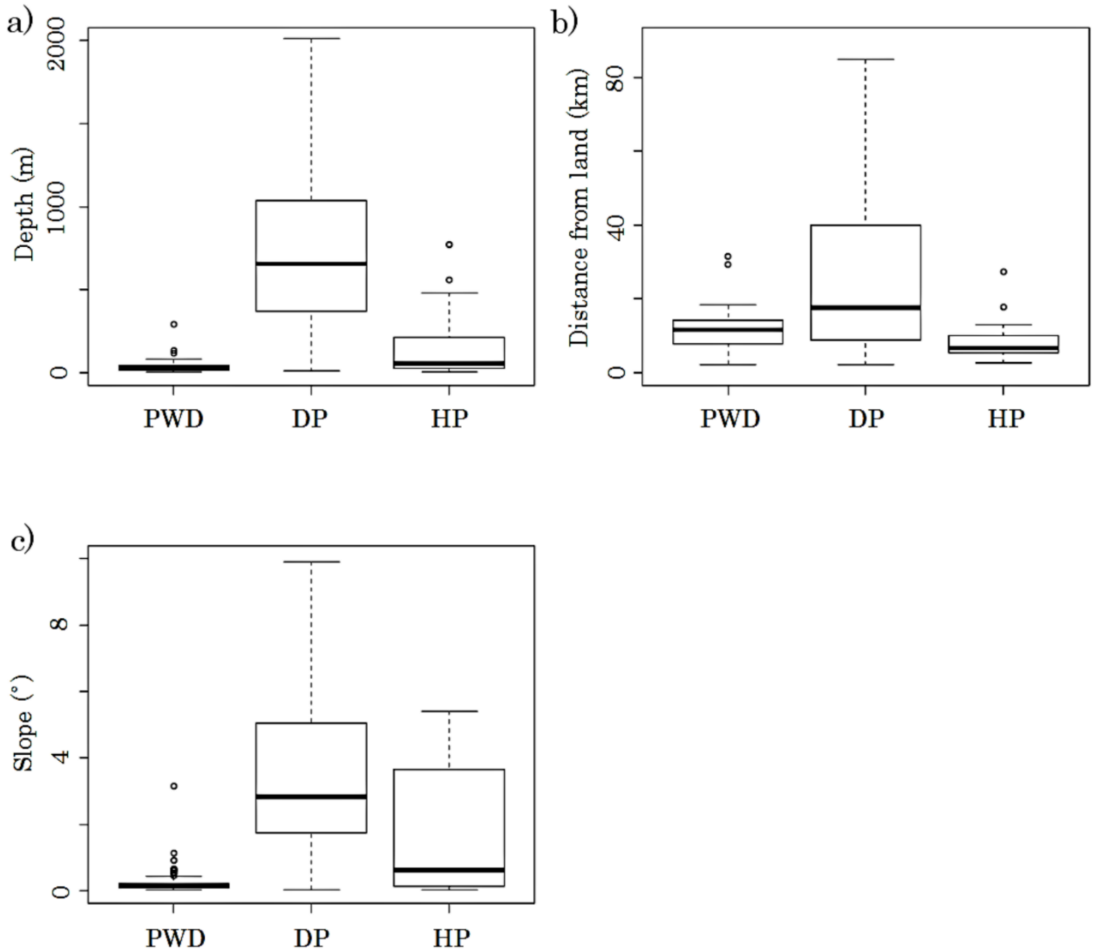

Fig. 3 Boxplot of the environmental data for the locations where each of the cetaceans were observed: a) water depth, b) distance from land, and c) slope. PWD, Pacific white-sided dolphin; DP, Dall's porpoise; and HP, Harbor porpoise. Upper and lower whisker indicate maximum and minimum value without 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.

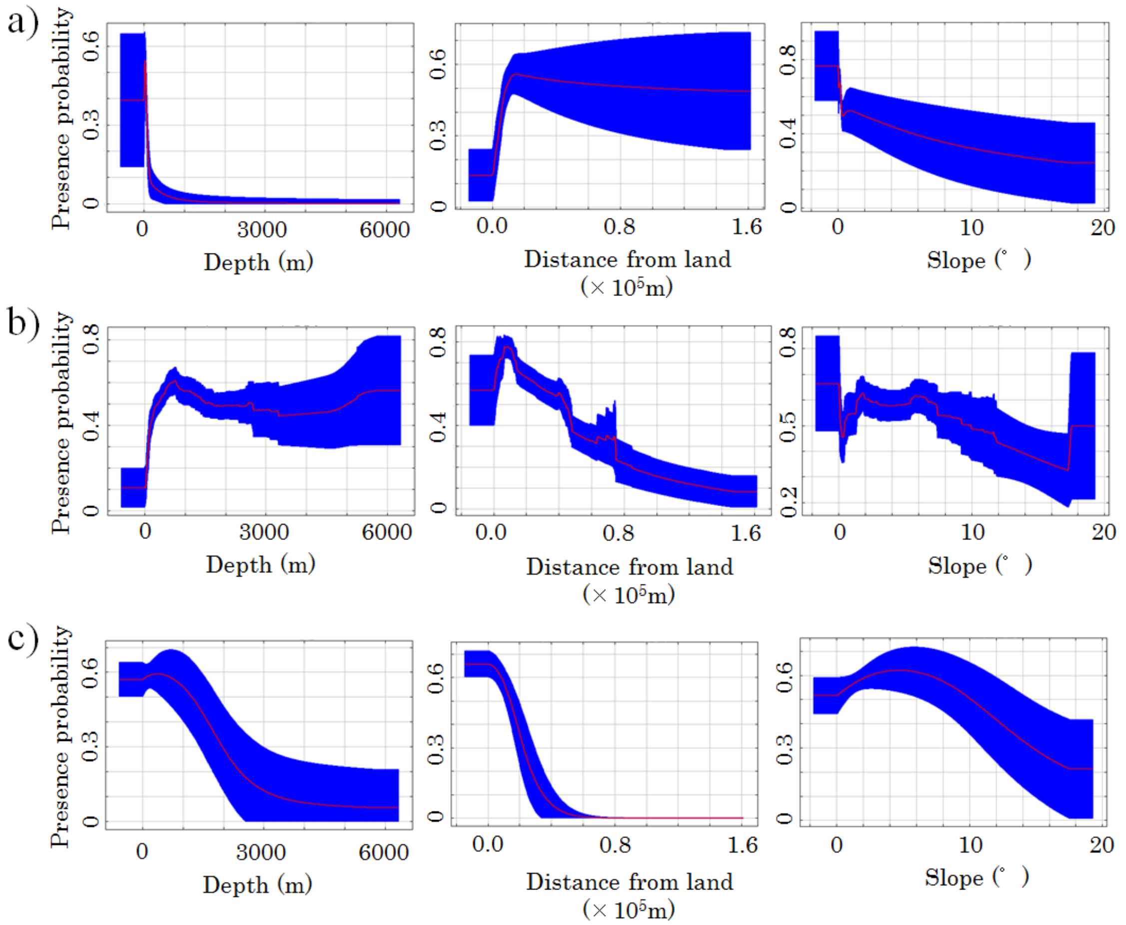

Fig. 4 Relationships between the presence probability of the cetaceans and environmental factors using Maxent software. a) Pacific white-sided dolphin, b) Dall's porpoise, and c) harbor porpoise. Red lines indicate average and blue ranges indicate one standard deviation of 100 Maxent models.

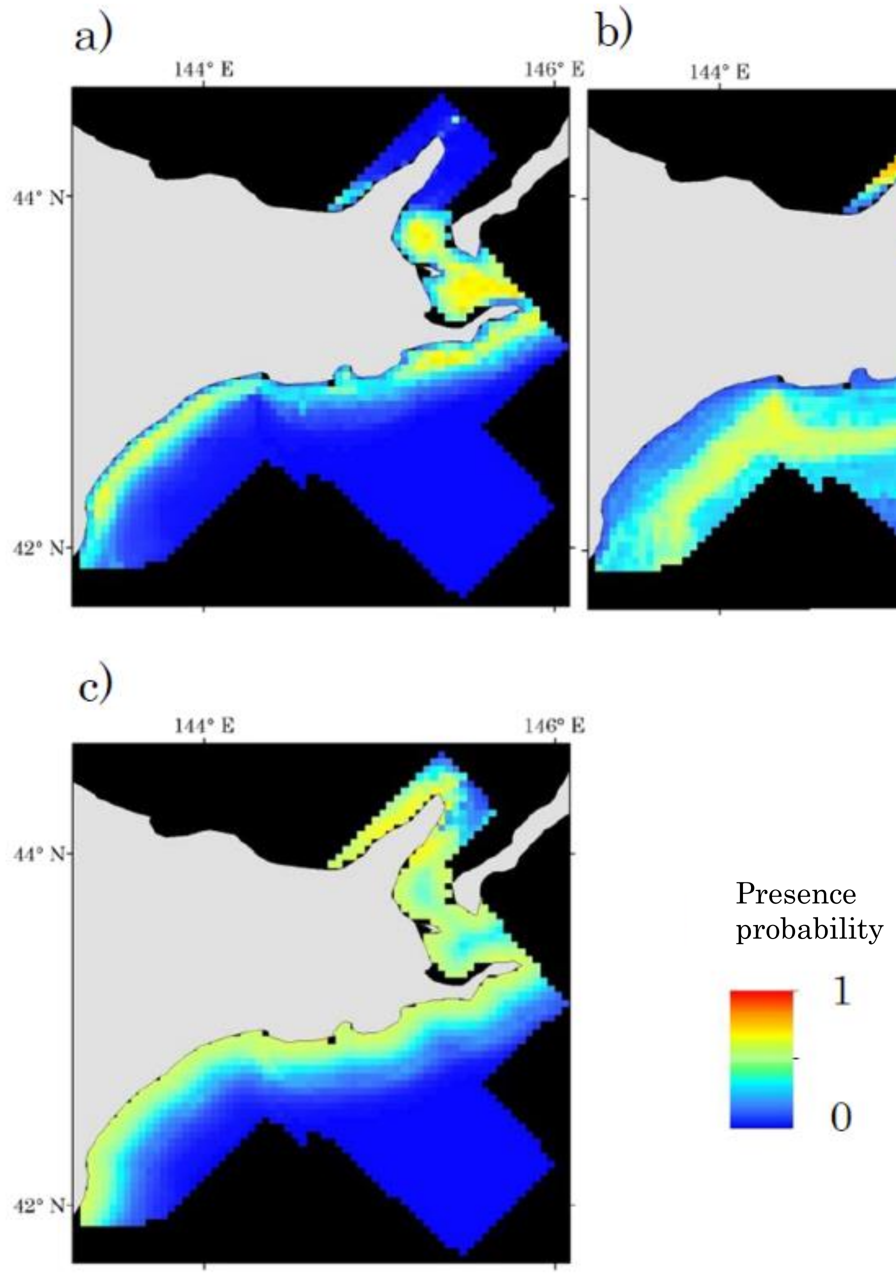

Fig. 5 Presence probability map of the three cetaceans predicted by Maxent software. a) Pacific white-sided dolphin, b) Dall's porpoise, and c) harbor porpoise. The black color indicates that the location is not in the survey area

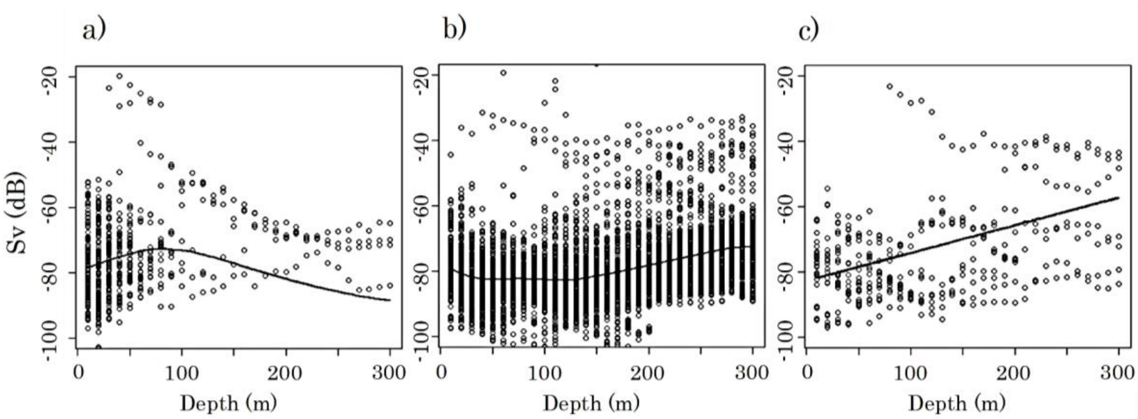

Fig. 6 Relationships between the volume backscatter strength (Sv: dB) and depth at the positions where each cetacean was observed. a) Pacific white-sided dolphin, b) Dall's porpoise, and c) harbor porpoise. Open circles indicate measured values and lines indicate the predictions made by the GAMM

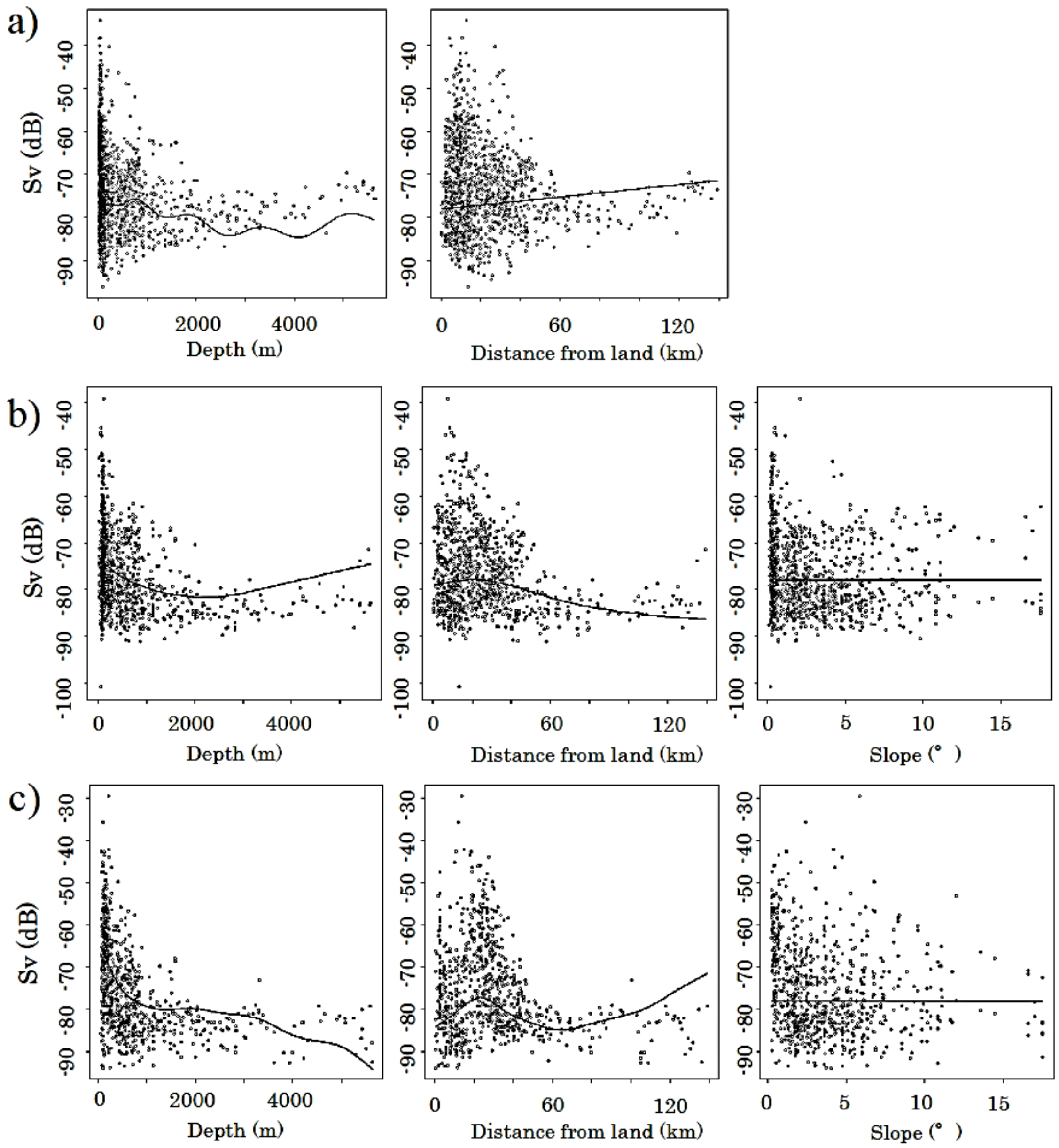

Fig. 7-1 Potential prey abundance (as volume backscatter strength; Sv) versus each environmental factor at different depth levels: (a) L1: 3-50 m, (b) L2: 50-100 m, (c) L3: 100-150 m, (d) L4: 150-200 m, (e) L5: 200-250 m, (f) L6: 250-300 m. Environmental factors were selected using Akaike's information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

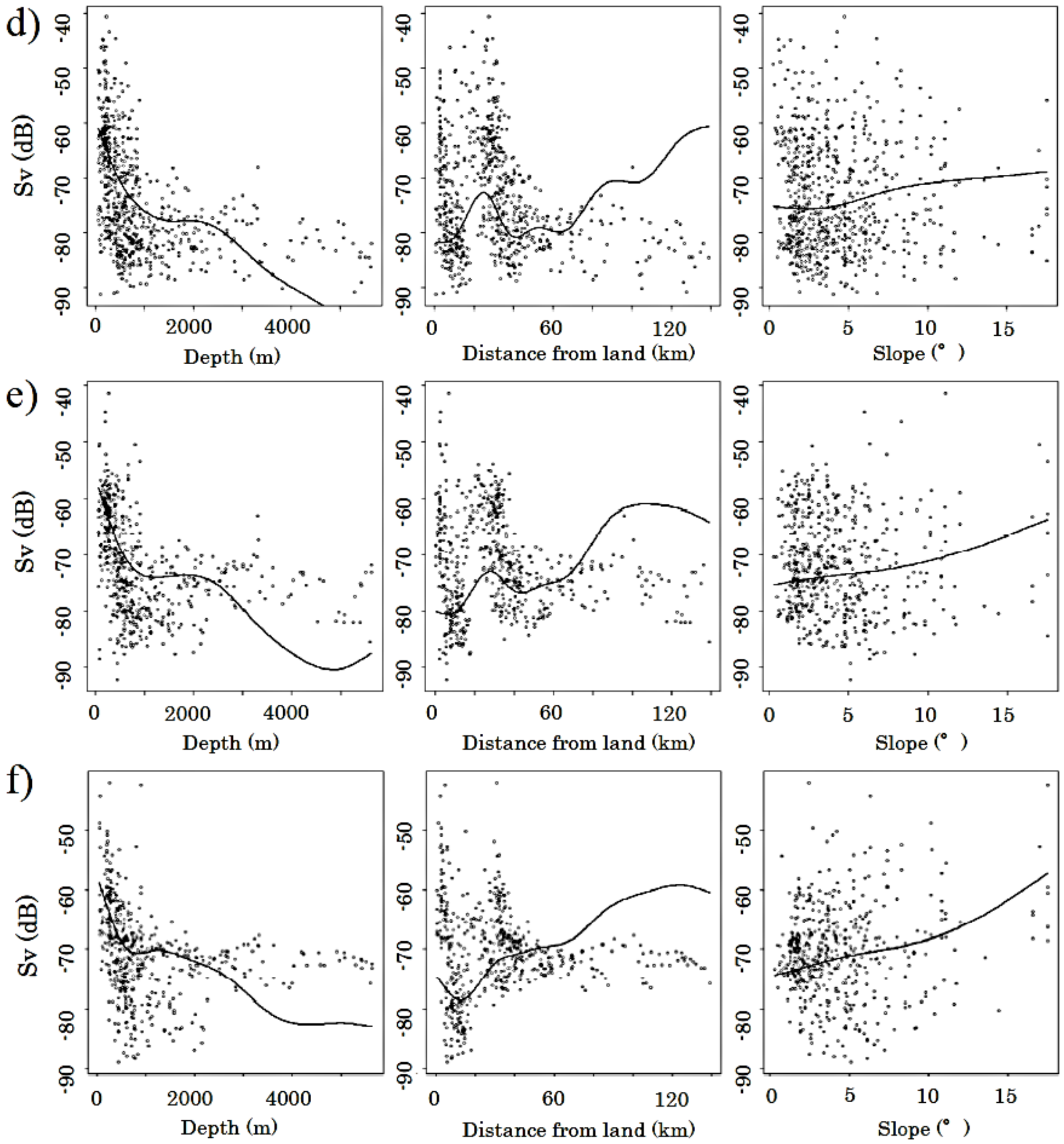

Fig. 7-2 Potential prey abundance (as volume backscatter strength; Sv) versus each environmental factor at different depth levels: (a) L1: 3-50 m, (b) L2: 50-100 m, (c) L3: 100-150 m, (d) L4: 150-200 m, (e) L5: 200-250 m, (f) L6: 250-300 m. Environmental factors were selected using Akaike's information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