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Diving behavior of sei whales *Balaenoptera borealis* relative to the vertical distribution of their potential prey

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Abstract. In this study, we investigated the diving behavior of sei whales relative to the vertical distribution of their potential prey in the western North Pacific during the summer of 2013. Acoustic time-depth transmitters were attached to two sei whales for 10.2 and 32.0 h, respectively. The vertical distribution and density (expressed as the volume backscattering strength, SV) of their potential prey were recorded by an echosounder. Diving behavior was classified into two shapes: U-shaped and V-shaped. For both individuals, U-shaped diving was associated with higher SV values than V-shaped diving and the frequency of U-shaped diving increased from late afternoon until sunset. During the daytime, dense scattering layers (presumably zooplankton) were distributed at approximately 40 m and they then migrated toward the surface around sunset. The diving depth of the whales followed the diel migration of the scattering layers and the diving was concentrated in these layers when the density became high. The results of this study indicate that sei whales change their diving depth and shapes in response to the diel vertical migration of their potential prey.

Key words: baleen whales, biologging, cetacean, foraging, habitat.

Observations of the diving behaviors of baleen whales have been reported widely and have developed in parallel with advances in biologging and underwater biotelemetry (e.g., acoustic transmitter) devices. These devices have been applied to several species, including the blue whale (*Balaenoptera musculus*; Fiedler et al. 1998; Croll et al. 2001; Calambokidis et al. 2008; Goldbogen et al. 2013; Friedlaender et al. 2015; Goldbogen et al. 2015), the fin whale (*B. physalus*; Croll et al. 2001; Goldbogen et al. 2006; Friedlaender et al. 2015), the Bryde's whale (*B. brydei*; Alves et al. 2010), the Antarctic minke (*B. bonaerensis*; Friedlaender et al. 2014), and the humpback whale (*Megaptera novaeangliae*; Goldbogen et al. 2008; Friedlaender et al. 2009; Nowacek et al. 2011). Simultaneous monitoring of the diving profiles of humpback and fin whales as well as the vertical distributions of their prey was attempted to elucidate their feeding behaviors relative to prey availability (Witteveen et al. 2008, 2015). In the latter two studies, small acoustic time-depth transmitters (pingers) were used to follow the swimming paths of individuals based on their acoustic signals while the vertical distribution of their prey was recorded by echosounders.

The food habits of baleen whales have been investi-

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gated using their stomach contents (e.g., Konishi et al. 2009), while their prey selections have been investigated using the proportions of prey in their stomachs with those in the environment (e.g., Murase et al. 2007). These traditional methods provide important baseline information about the feeding habits of whales, but they do not consider individual feeding behavior. Recent developments in biologging and underwater biotelemetry devices now allow us to obtain such detailed data.

Sei whale (*Balaenoptera borealis*) is the third largest baleen whales (typically 15 m in length) after the blue (*B. musculus*) and fin (*B. physalus*) whales, and they are distributed in the temperate waters of both hemispheres, including the North Pacific (Horwood 2009). Their feeding behavior in the North Atlantic was inferred from horizontal movements based on geographical locations obtained by satellite-based biotelemetry (Olsen et al. 2009; Prieto et al. 2014), but their diving behaviors relative to the vertical distribution of their prey have not been investigated.

Thus, in this study, we investigated the diving behavior of sei whales relative to the vertical distribution of their potential prey by using acoustic time-depth transmitters and an echosounder simultaneously.

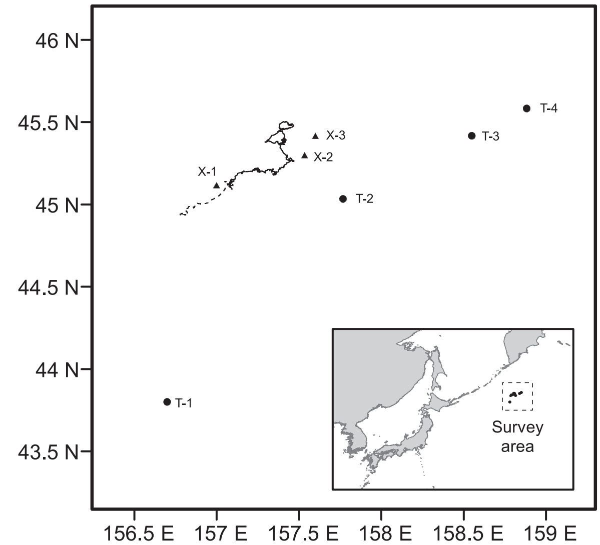

Fig. 1. Map of the area in the western North Pacific surveyed in August 2013. Lines indicate cruise tracks by the survey vessel while tracking the first (S-1; dotted line) and second (S-2; thick line) tagged sei whales. Circles indicate the positions of trawl and plankton net sampling stations (T-1, 2, 3, and 4). Triangles indicate expandable conductivity, temperature, and depth probe (XCTD) stations (X-1, 2, and 3).

Materials and methods

The survey was conducted in the subarctic-subtropical transition area of the western North Pacific in the summer of 2013 (Fig. 1). The bottom depth in the area is around 5000 m. Two survey vessels called *Yushin-Maru* (YS1; 724 gross tons (GT); cetacean sighting survey vessel) and *Shunyo-maru* (SHU; 887 GT; trawler type fisheries survey vessel) were engaged to deploy transmitters on August 13 and 14, 2013, respectively. The length of each vessel was roughly 70 m and the height of the bow deck from the sea surface was roughly 8 m. Compound crossbows were used to attach transmitters to the dorsal surfaces of sei whales from the bow decks of the survey vessels. The transmitters were tethered to small titanium spearheads (3.8 cm in length, 1.45 cm maximum head width, and 4 g in air) by polyethylene (Dyneema) fishing line with a linear strength of 55 kg. The spearheads were loosely attached to titanium shafts (12.15 cm in length) with the expectation that the transmitters and spearheads would detach from the shafts upon contact with a whale. The shafts were attached to carbon bolt arrows. The spearheads and shafts were manufactured by Koreisangyo (Yokohama, Japan). The spearheads were employed to secure rigid attachment to whales so we could obtain data about their diurnal diving behavior (i.e., more than 24 h). Acoustic time-depth transmitters (FPXG-1040-60P500T30, Fusion Inc., Tokyo, Japan) were used, which sent pulses (62.5 kHz) every second and encoded the depth data (0.01 m resolution with ± 0.2% accuracy). The transmitters measured 43 mm in length, 9.5 mm in diameter, and 6 g in air. The maximum duration of the batteries was 48 h and the maximum detection range was 800 m. The transmitted signals were received by a directional hydrophone (VH170, Vemco, Nova Scotia, Canada). The hydrophone was hull-mounted on SHU at a depth of 4.3 m below the sea surface. Four (bow, port, starboard, and bottom sides) out of the 17 hydrophone channels were used because the receiver could only handle four channels. The received signals were processed by a receiver (FRX-4001, Fusion Inc., Tokyo, Japan) onboard SHU. SHU followed the tagged individuals based on their relative swimming direction according to the signals received.

A calibrated quantitative echosounder (Simrad EK60; Simrad, Horten, Norway), with a 120 kHz transducer was used to record the volume backscattering strength (SV, dB; an index of prey density) while tracking the whales. The transducer was hull-mounted on SHU at a depth of 4.3 m below the sea surface. Acoustic backscatter deeper than 7.5 m was processed using Echoview 4.9 (Myriax, Hobart, Australia). Trawl (NBT-2P-SY, Nitto Seimo Co., Tokyo, Japan) and plankton net, i.e., the North Pacific standard net (NORPAC; mouth opening = 45 cm, mesh size = 0.33 mm) sampling were conducted by SHU at four stations prior to the diving behavior observations (August 10–12, 2013) in order to obtain qualitative information about the potential prey species around the area (Fig. 1). The midwater trawl net was 84.9 m long with a mouth opening of 42.4 × 42.4 m and a cod end of 8.0 m. The sampling depth and height of the net's mouth were monitored with the Scanmar system (Scanmar, Åsgårdstrand, Norway). The mouth opening was set to 30 × 30 m while the net was towed. The towing speed of the trawl net was 4–5 knots. The sampling depth was either midwater (0–90 m; T-1 in Fig. 1) or surface (0–30 m; T-2, T-3, and T-4 in Fig. 1). Surface trawls were conducted using midwater trawls with the floats attached to the bridle so the trawl could be towed at the surface. Both daytime and nighttime tows were conducted at T-1 to compare the species compositions during the day and night. It has been well documented that myctophids undergo diel vertical migration between epipelagic layer (shallower than 200 m) during night and the mesopelagic layer during daytime (Yatsu et al. 2005 and the references therein). The purpose of the nighttime tow in this study was to obtain qualitative information on species compositions in water column. Because myctophids is not main diet of sei whales (Konishi et al. 2009), only one nighttime tow was conducted during the survey. Only daytime tows were conducted at the rest of sampling stations because small pelagic fish, which are main diet of sei whales in the western North Pacific (Konishi et al. 2009), are mostly distributed at shallow depths according to our previous studies (Murase et al. 2007, 2009, 2011, and 2012) as well as other studies (Fujino et al. 2010). Trawl samplings were conducted at predetermined sites (approximately 93 km [≈ 50 nautical miles] apart) rather than targeting specific acoustic backscatters. The NORPAC net was towed vertically from 150 to 0 m. Expandable conductivity, temperature, and depth probe (XCTD; Tsurumi Seiki Co., Yokohama, Japan) casts were made at three stations (X-1, 2, and 3; Fig. 1) from August 13–16, 2013 in order to measure the oceanographic conditions around the tracking area. A continuous recording of the near-surface temperature obtained by SHU was used to investigate the oceanographic conditions encountered by the tagged individuals, although the exact geolocations of whales and the vessel could differ by up to 800 m (maximum detection range of the transmitters).

Diving depth profiles were analyzed using the Ethographer package version 2.01 (Sakamoto et al. 2009) with Igor Pro version 6.12 (WaveMatrics, Oregon, US). The start and end points of each diving behavior were set at 3 m from the surface. Individuals were considered to be "diving" when they remained deeper than 5 m in the water column for longer than 5 s, considering the maximum diving depths of the sei whales observed in this study. The nonparametric Mann–Whitney *U* test was used to test whether the maximum depth in each dive and the duration of each dive showed diel pattern. Daytime hours (from sunrise to sunset) were defined as 5:00 to 19:00 (local time), whereas all other hours were defined as nighttime. The time allocation at depth index (TAD) was calculated according to Fedak et al. (2001). TAD is a dimensionless index of dive shape, which was designed to utilize relevant information from dive profiles and highlight where the diver centers its activity with respect to depth during a dive. TAD varies from zero to one and it represents the differences between dive shapes. Diving behavior deeper than 10 m was classified according to two shapes based on TAD: U-shaped (TAD ≥ 0.7) and V-shaped (TAD < 0.7). In general, the dive shapes reflected the bottom time portion of the total dive time. SV values were divided by 500 m intervals along the cruise tracks. Next, the SV values were extracted in the range of ± 2.5 m from the maximum depth in each dive. The data were averaged and compared using the Mann–Whitney *U* test to determine differences between U- and V-shapes.

Results

Observations of the diving behavior of one individual sei whale (S-1) started from 44.93°N, 156.78°E on August 13, 2013, while those of the other (S-2) started from 45.10°N, 157.08°E on August 14, 2013. The body lengths of S-1 and S-2 were visually estimated at 13 and 14 m, respectively. The initial group sizes for S-1 and S-2 were five and three individuals, respectively. During the tracking surveys, we observed changes in the group sizes and the number of other schools surrounding the target individuals within sighting distance (approximately 5.6 km), although we could not record these changes appropriately because they were not expected before the study. No calves were observed in the groups.

The diving behavior of S-1 was observed for 10 h 11 min from 10:16 to 20:27 on August 13, 2013, while that

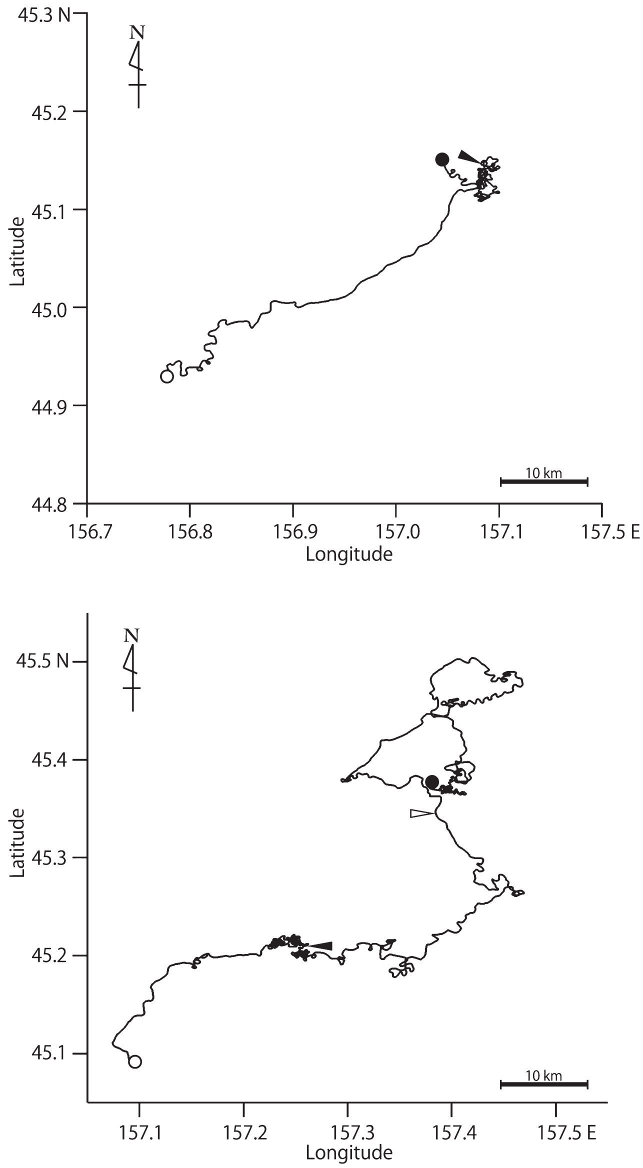

Fig. 2. Cruise tracks of the survey vessel during tracking of sei whales (upper panel, S-1; lower panel, S-2). White and black circles indicate the start and end points of tracking, respectively. Black and white arrows indicate the survey vessel position at sunset and sunrise, respectively.

of S-2 was observed for 31 h 59 min from 10:37 on August 14 to 18:36 on August 15, 2013. Due to data recording technical problems, one (21 min) and two (1 h 11 min and 1 h 10 min) long gaps without signals existed for S-1 and S-2, respectively, and these were excluded from the analysis. The remaining signal gaps were less than 4 min. The steaming distances for SHU while tracking each individual were 101.4 and 259.0 km, and the mean vessel steaming speeds during these observations were 10.0 and 8.1 km/h, respectively (Fig. 2). It should be noted that the distances and speeds of the vessel should not be translated directly into those of the tagged individuals.

The total numbers of dives for S-1 and S-2 were 119 and 387, respectively, while the overall mean dive depths and standard deviations (*SD*) were 17.9 ± 12.6 m (deepest depth = 57 m) and 14.2 ± 9.6 m (deepest depth = 48 m). The overall mean dive durations for S-1 and S-2 were 3.2 ± 2.3 min (maximum duration = 12.2 min) and 3.0 ± 2.5 min (maximum duration = 11.0 min), respectively. The results of the Mann–Whitney *U* test revealed that the mean dive durations were significantly longer in the daytime than the nighttime for both individuals ($P < 0.01$) (Table 1). Maximum diving depth of S-2 in daytime was deeper than nighttime ($P < 0.01$). Although that of S-1 was not statistically significant ($P = 0.08$), the individual also dove deeper in the daytime than nighttime. The diving depths of both individuals coincided with changes in the dense scattering layers observed in shallow water (Fig. 3). Two prominent dense scattering layers were observed while tracking the individuals. One shallow layer was observed at approximately 40 m in the daytime and it then migrated toward the surface around sunset. The other deep layer was observed deeper than 60 m in the daytime and it then migrated toward 30 m in the nighttime. The maximum SV values in the daytime and nighttime were approximately –80 and –72 dB,

Table 1. Comparison of diving depths (m) and durations (min) during the day and night

Whale ID		Day Mean ± *SD* (Max)	Night Mean ± *SD* (Max)	Mann–Whitney *U* test	
S-1	No. of dives	94	25		
	Max depth (m)	19 ± 14 (57)	12.2 ± 5.4 (26)	$U = 1437.5$	$P = 0.08$
	Duration (min)	3.5 ± 2.4 (12.2)	2.2 ± 2.1 (9.1)	$U = 1640$	$P < 0.01$
S-2	No. of dives	275	112		
	Max depth (m)	16 ± 10 (48)	9.5 ± 5.1 (31)	$U = 21852$	$P < 0.01$
	Duration (min)	3.4 ± 2.7 (11.0)	2.0 ± 1.6 (7.7)	$U = 20306$	$P < 0.01$

Means and standard deviations (*SD*) of the maximum depth in each dive and the diving durations for two tagged sei whales (S-1 and S-2). Maximum values and the results of Mann–Whitney *U* tests are also shown.

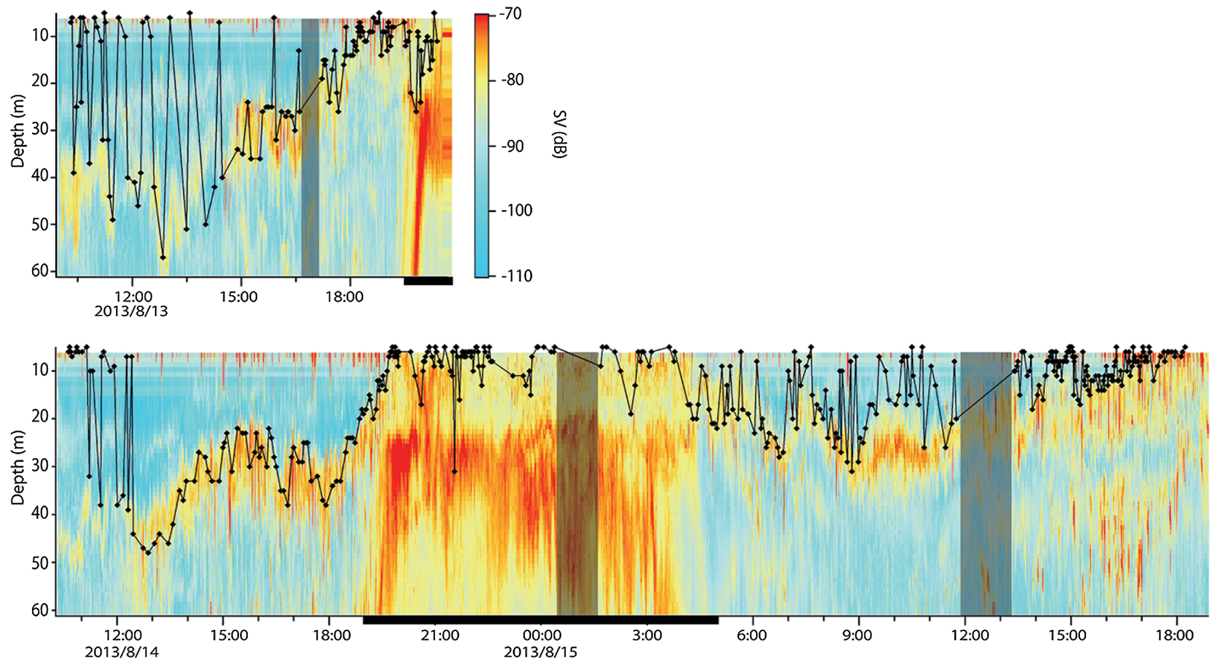

Fig. 3. Maximum depth in each dive (filled circle) by sei whales (upper panel, S-1; lower panel, S-2) overlaid on the echogram. Nighttime is indicated by black horizontal bars. Gray shadows indicate hours with long signal gaps (more than 21 min).

Table 2. Species compositions by wet weight (kg) in the catch of trawl net samplings

Station	T-1	T-1	T-2	T-3	T-4
Day/night	Day	Night	Day	Day	Day
Date	10 Aug 2013	10 Aug 2013	11 Aug 2013	12 Aug 2013	12 Aug 2013
Latitude (N)	43°45'	43°45'	44°58'	45°24'	45°33'
Longitude (E)	156°38'	156°38'	157°42'	158°33'	158°52'
Sampling depth (m)	0–90	0–90	0–30	0–30	0–30
Tow duration (miniute)	45	45	30	30	30
Japanese anchovy (*Engraulis japonicus*)	0.55 [100.0]	226.49 [67.4]	0.10 [62.5]	–	
Japanese anchovy (larva) (*Engraulis japonicus*)	–	–	–	–	0.01 [14.3]
Chub mackerel (*Scomber japonicus*)	–	7.17 [2.1]	–	–	–
Spotted mackerel (*Scomber australasicus*)	–	–	0.06 [37.5]	–	–
California headlightfish (*Diaphus theta*)	–	22.32 [6.6]	–	–	–
Reinhardt's lantern fish (*Hygophum reinhardti*)	–	39.88 [11.9]	–	–	–
Myctophidae spp.	–	1.88 [0.6]	–	–	–
Northern smoothtongue (*Leuroglossus schmidti*)	–	20.67 [6.1]	–	–	–
Unidentified fish	–	0.43 [0.1]	–	–	–
Japanese flying squid (*Todarodes pacificus*)	–	–	–	0.23 [100.0]	0.06 [85.7]
Boreal clubhook squid (*Onychoteuthis borealijaponica*)	–	1.25 [0.4]	–	–	–
Firefly squid (*Watasenia scintillans*)	–	16.08 [4.8]	–	–	–
Total	0.55 [100.0]	336.17 [100.0]	0.16 [100.0]	0.23 [100.0]	0.07 [100.0]

Compositions in percentage are shown in square brackets.

respectively.

The results of trawl sampling were summarized in Table 2. Mesopelagic species, especially myctophids, were only sampled in the nighttime tow. Dense schools were recorded near surface by the echosounder during the nighttime tow while no such school was recorded during the daytime tows. The dense schools observed during the nighttime tow were assumed to be mainly consisting of

Table 3. Means and standard deviations (*SD*) of the volume backscattering strength (SV, dB) for each diving type (V- and U-shaped) by two tagged sei whales (S-1 and S-2)

Whale ID		V-shaped Mean ± *SD*	U-shaped Mean ± *SD*	Mann–Whitney *U* test	
S-1	No. of dives	42	37		
	SV (dB)	–84.1 ± 5.2	–81.7 ± 5.1	$U = 1003$	$P < 0.03$
S-2	No. of dives	78	132		
	SV (dB)	–81.2 ± 5.0	–79.8 ± 4.8	$U = 5986$	$P < 0.05$

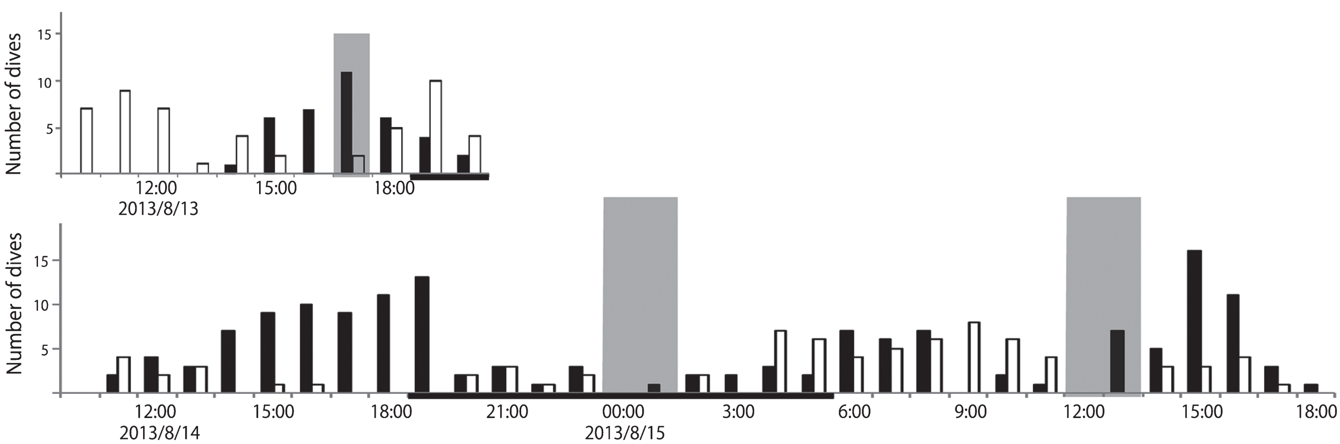

Fig. 4. Temporal changes in number of U-shaped and V-shaped dives (black and white vertical bars, respectively) of sei whales (top, S-1; bottom, S-2). Data are aggregated hourly. Nighttime is indicated by black horizontal bars. Grey shadows indicate hours with long signal gaps (more than 21 min).

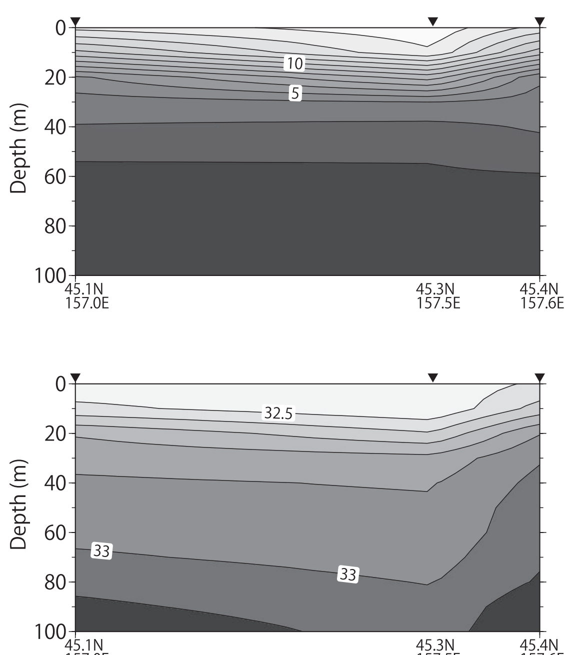

Fig. 5. Vertical cross-sections of the water temperature (°C) (top) and salinity (bottom) around the area where the tagged sei whales were observed. Arrows indicate the positions of expandable conductivity, temperature, and depth probe (XCTD) stations.

the Japanese anchovy (*Engraulis japonicus*) based on the results of the trawl sampling as well as past surveys conducted in the western North Pacific as shown in Fujino et al. (2010) and Murase et al. (2012). Presence and absence of dense schools during sampling were reflected in amount of sampled Japanese anchovies. Wet weight proportions of *Neocalanus* spp. in the plankton net samples at T-1, T-2, T-3, and T-4 were 64.0, 16.4, 53.2, and 49.2%, respectively. *Neocalanus* spp. were dominated in these samples except T-2.

U-shaped diving was associated with a higher SV value than V-shaped diving for both individuals ($P < 0.05$) (Table 3). The frequencies of each dive shape varied over time. U-shaped diving increased from late afternoon (approximately 15:00) until sunset (Fig. 4). Means and *SD*s of the near-surface temperatures encountered by S-1 and S-2 were 15.1 ± 0.1 and 15.0 ± 0.1°C, respectively. The vertical cross-sections of the water temperature and salinity around the area were relatively stable, although the subsurface salinity increased slightly toward the east (Fig. 5).

Discussion

Both individuals dove repeatedly to the shallow scattering layers in the daytime, although the diving depths varied greatly (from 50 to 30 m). However, both individuals dove sequentially once the density became high and the diving depths were concentrated in the dense scattering layers, especially in the late afternoon. After sunset, the swimming depth became shallower at approximately 10 m. *Neocalanus* spp. are recognized as one of the important prey species for sei whales in the western North Pacific (Konishi et al. 2009). It has been reported that *Neocalanus* spp. occurs in such shallow scattering layers (e.g., Murase et al. 2009). It can be assumed that *Neocalanus* spp. occurred in the shallow scattering layers observed in our study because *Neocalanus* spp. were dominated in the plankton net samples. However, the inference was limited because exact distribution depth could not be investigated by the net. It has also been reported that *Neocalanus* spp. are distributed at approximately 30 m in the daytime and that they migrate to approximately 10 m in the nighttime (Seki and Shimizu 1998). It has been observed that *Neocalanus* spp. form dispersed small-dense patches at dawn, whereas they form large patches from dusk until midnight (Tsuda et al. 1993). Therefore, similar to other baleen whale species, such as fin (Friedlaender et al. 2015) and Bryde's whales (Alves et al. 2010), sei whales may change their diving depth in response to changes in the distribution depth of their prey in order to maximize their feeding efficiency.

The results of trawl sampling indicated that the Japanese anchovy was distributed near the surface in the daytime, while both anchovy and myctophids were distributed in the sampled water column although the inference was qualitative. Nevertheless, it is reasonable to assume that the deep scattering layers observed in the nighttime mainly comprised myctophids. Our results indicate that the observed sei whales swam near the surface and dove rarely to the depth of the deep scattering layers, which were distributed around 30 m at night where the myctophids were located. Myctophids are not recognized as a main dietary source for sei whales (Konishi et al. 2009). However, these observations cannot preclude the possibility that sei whales feed near the surface at night because the behavior and prey distribution near the surface could not be recorded by the acoustic devices (acoustic transmitter and echosounder) used in this study. In the southwestern Gulf of Maine, the calling rates of sei whales are reduced at nighttime (Baumgartner and Fratantoni 2008). Calls are probably used for communication with other individuals, so it is hypothesized that the reduced call rates in the nighttime may indicate that sei whales allocate more time to foraging and feeding on copepods, i.e., *Calanus finmarchicus*, near the surface rather than social behavior.

Small pelagic fish, such as the Japanese anchovy and mackerels (*Scomber* spp.) are also important prey of sei whales in the western North Pacific (Konishi et al. 2009). However, relationship between diving behavior of sei whales and their vertical distributions could not be investigated in this study. These species tend to occur as schools rather than layers. However, few schools were recorded by the echosounder during diving behavior observations. The relationship could be investigated in future if sufficient number of schools are recorded during behavior observations. The same is true for krill which is also known as diet of sei whales. Although Pacific saury (*Cololabis saira*) is also fed by sei whales, investigation on the relationship is difficult because Pacific saury is mainly distributed just beneath of sea surface that cannot be detected by echosounder.

The water temperatures encountered by the individuals in this study were stable along the horizontal movement paths. Previous studies suggest that the spatial distribution of sei whales in the western North Pacific is determined largely by oceanographic conditions such as the sea surface temperature (SST) and oceanic fronts (Sasaki et al. 2013; Murase et al. 2014). Previous results and those obtained in the present study indicate that the spatial distribution of sei whales at the meso-scale (> 100 km) is determined largely by oceanographic conditions such as the SST rather than prey availability. Sei whales then search for their prey within the optimal oceanographic conditions at the micro-scale (> 10 km). This hypothesis should be tested in a future study.

The mean swimming speed of sei whales estimated by satellite tracking data is in the range of 3.7 to 7.4 km/h (Olsen et al. 2009; Prieto et al. 2014). It appears that the swimming speeds of sei whales inferred based on the vessel steaming speeds in the present study (10.0 and 8.1 km/h) were fast in the feeding area. However, the swimming speed calculated based on the distance between two consecutive positions obtained by satellite tags can be considered as the minimum speed. This is because the swimming path between these points might not be the actual path as the two consecutive points obtained by satellite tags generally have long time durations. The linear distance calculated between two points separated by an hour during our behavior observations rather than the actual steaming distances gave mean swimming speeds for S-1 and S-2 of 5.0 and 3.6 km/h, respectively. Thus, caution is necessary when comparing the swimming speeds obtained using different devises.

Based on visual observations in our survey, the tagged individuals exhibited no obvious behavioral reactions during transmitter deployment or in subsequent observations. Witteveen et al. (2008) tracked humpback whales using acoustic transmitters within close proximity (less than 1 km) of the survey vessel but it appeared that they had no effect on their behavior. Watkins et al. (1981) reported that a tanker passing within 800 m did not disrupt the feeding of humpback whales. This range corresponds to the maximum detection range for the acoustic transmitters used in our survey. Nevertheless, it was difficult to preclude the possibility of effects on whales due to the close proximity of the vessel in our study. An independent survey using biologging devices with a careful design might be necessary to assess this effect quantitatively.

This study provides new insights into the foraging behaviors of sei whales in the western North Pacific. However, general conclusions cannot be made at this stage because of the limited sample size (two individuals) and survey methods. It may be assumed that U-shaped dives are related to underwater foraging behavior, whereas V-shaped dives are related to other behaviors such as traveling or searching for prey. However, the distinction is not clear-cut. For example, blue whales exhibit foraging behavior while ascending (Goldbogen et al. 2015). Recording more detailed data using archival tags with accelerometers may be necessary to elucidate the behavior of sei whales more fully. In our study, the results obtained by net sampling were used as qualitative information to understand the distributions of potential prey species. Species identification based on a multi-frequency echosounder data and sampling using multiple opening and closing net system may help to understand the prey-predator relationship at a fine scale.

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