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Habitat and prey selection of common minke, sei, and Bryde's whales in mesoscale during summer in the subarctic and transition regions of the western North Pacific

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Abstract This study represents the first quantitative analysis of the characteristics of the distribution areas and stomach contents of common minke whale *Balaenoptera acutorostrata*, sei whale *B. borealis*, and Bryde's whale *B. edeni* in relation to oceanographic and prey environments in mid summer in the western North Pacific. Common minke whales were distributed within subarctic regions and the northernmost region of the transitional domain, coinciding with the main habitat of their preferred prey, Pacific saury *Cololabis saira*. Sei whales were mainly found in the northernmost part of the transition zone and showed prey preference for Japanese anchovy *Engraulis japonica*, which was significantly more abundant in the main distribution area of the whale than in its adjacent areas. "Hot spots" of Bryde's whales were found in several regions of the transition zone between the subarctic boundary and the Kuroshio front. This whale species preferred Japanese anchovy as prey, for which the distribution density was significantly higher in the main distribution area of the whale than in the adjacent areas. These results indicate that the summer distributions of Pacific saury and Japanese anchovy greatly influence the distributions of these whale species, suggesting that the whales' habitat selection is closely related to their prey selection.

Keywords Common minke whale · Sei whale · Bryde's whale · Habitat selection · Prey selection · Prey environment · Oceanographic features · Western North Pacific

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Introduction

The common minke whale *Balaenoptera acutorostrata*, sei whale *B. borealis*, and Bryde's whale *B. edeni* are the major baleen whale species in the western North Pacific [1]. These species migrate into high latitudinal areas during spring and summer from the low latitudinal wintering area [2]. Previous studies have reported that these whale species frequently feed on small epipelagic fish species such as Japanese anchovy *Engraulis japonica*, Japanese sardine *Sardinops melanostictus*, mackerel *Scomber* spp., and/or Pacific saury *Cololabis saira*, and euphausiids from spring to summer [1, 3–6]. Subarctic copepod species such as *Neocalanus cristatus* and *N. plumchrus* can also be important prey for sei whales in regions east of 160–165°E, where Japanese sardine, anchovy, and mackerels, which are mainly distributed within Japanese waters, are less abundantly distributed [1, 3, 7, 8]. Furthermore, the stomach content compositions of these whales are known to fluctuate in relation to sea surface temperature (SST), latitude, and longitude [1]. However, quantitative information on the distribution patterns and feeding habits of these whale species in relation to oceanographic conditions and prey environments is extremely limited. Such knowledge is essential for estimating the feeding impact of these whales on various prey species, including commercially important small epipelagic fish species, for the sustainable use of marine resources, which is recognized worldwide as an important management issue for fisheries and is one of the major objectives of the second phase of Japanese Whale Research Program under the Special Permit in the western North Pacific (JARPN II) [1, 6, 9, 10]. Such knowledge is also important for single species management of whales given that the abundance of each whale species can be accurately measured using sighting surveys if their main distribution area is known. Furthermore, both extra- and interpolation methods of estimating whale abundance in areas where sighting surveys are not conducted could be established based on data of the habitat selections of each whale species.

Here, we aimed to quantitatively examine the habitat and prey selections of common minke, sei, and Bryde's whales in relation to oceanographic and prey environments by conducting concurrent oceanographic, prey species, whale sighting, and whale sampling surveys in the same area within 24 h in the subarctic, transition, and subtropical Kuroshio regions of the western North Pacific during mid summer. Prey selection of sei whale is firstly reported in this paper. Survey areas for each whale species were established based on previous knowledge of the latitudinal and SST ranges of their habitats in summer, i.e., 44–47°N (SST <15°C), 40–45°N (13–17°C), and 35–40°N (20–26°C) for common minke, sei, and Bryde's whales, respectively [1, 11, 12].

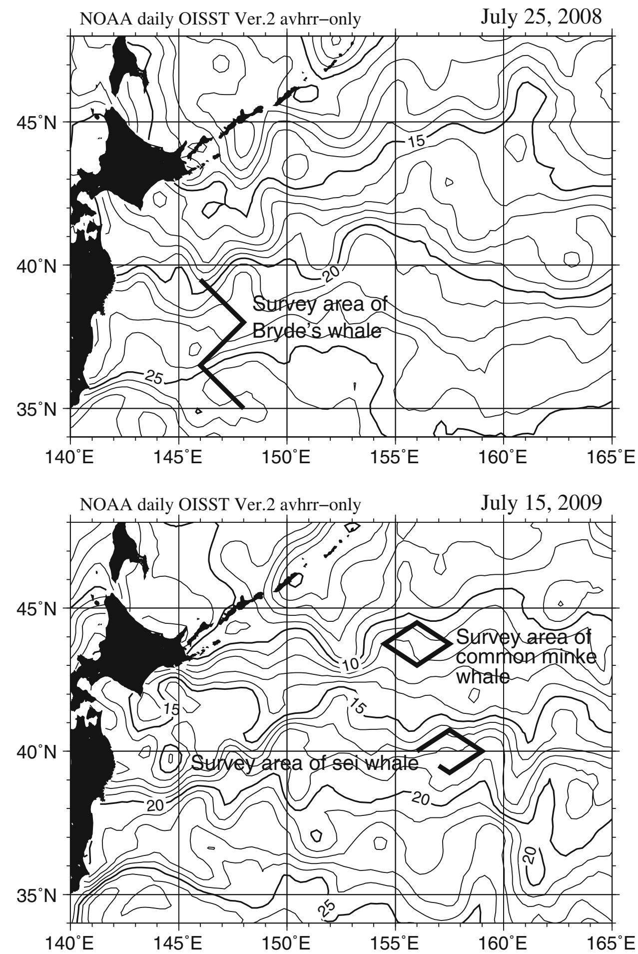

Fig. 1 Survey areas, survey track lines, and distributions of sea-surface isotherms in the western North Pacific in July 2008 and 2009

Materials and methods

Oceanographic and whale prey surveys

We conducted surveys of oceanographic observations and whale prey species from on board the R/V Shunyo Maru (887 GT, National Research Institute of Far Seas Fisheries) in the western North Pacific from 21–25 July 2008 and 10–22 July 2009 (Fig. 1). These surveys were conducted concurrently with whale sighting and sampling surveys as part of JARPN II by researchers on the Nisshin Maru (7575 GT, Kyodo-Senpaku Co., Ltd.) and two sighting/sampling vessels (Yushin Maru No. 2 and No. 3, 742–743 GT, Kyodo-Senpaku Co., Ltd.) on the same survey track lines during daylight periods from 1 h after sunrise to 1 h before sunset. In 2008, we conducted a survey of Bryde's whales within a survey area bounded by 35–39°30′N and 146–148°E, where the SST ranged from 17.5–27.6°C (Fig. 1). In 2009, surveys of common minke and sei whales were conducted within an area bounded by 43–45°N and 154°30′–157°30′E (SST 10.2–14.7°C), and 39–41°N and 156–160°E (SST 14.9–18.8°C), respectively (Fig. 1; Table 1). According to previous reports [1, 11, 12], these areas covered the southern part of the main distribution area of common minke and sei whales, as well as the main distribution area of Bryde's whales, in terms of both latitudinal and SST ranges.

The distribution and abundance of the whale prey species were investigated using a midwater trawl, Multiple Opening/Closing Net and Environment Sampling System (MOCNESS, Bess Co., Ltd.), North Pacific Standard net (NORPAC net), and quantitative echosounder with operating frequency of 38, 70, and 120 kHz (EK60, SIMRAD)

Table 1 Results of target trawlings in the survey area of Bryde's and sei whales and of predetermined trawlings in the survey area of common minke whales by midwater trawls

Stn.	Date	SST (°C)	Latitude (N)	Longitude (E)	Sampling depth (m)	Sampling duration (min)	CPUE (kg/h)				
							Japanese anchovy	Japanese sardine	Common mackerel	Pacific saury	Common squid
Survey area of Bryde's whale											
3	22 July 2008	25.6	36°12.4′	146°25.5′	0–30	60	1.9[a]	0	+	0	0
8	24 July 2008	23.2	38°35.5′	147°12.7′	0–30	60	0.8	0	0	0	0
Survey area of sei whale											
1	10 July 2009	16.7	40°11.7′	156°22.7′	0–30	60	62.5[a]	0.2	+	0	0
5	12 July 2009	18.8	40°00.0′	159°00.2′	0–30	60	28.2[a]	0.1	+	0	0
Survey area of common minke whale											
8	18 July 2009	12.0	44°06.8′	156°45.5′	0–30	60	0	0	0	163.9	0
10	19 July 2009	12.5	43°17.4′	156°34.7′	0–30	60	0.1	0	0	0	+
11	19 July 2009	13.0	43°12.3′	155°43.8′	0–90	60	0	0	0	156.9	0
12	20 July 2009	14.7	43°37.3′	155°10.7′	0–30	60	+	0	0	0	0.7
13	20 July 2009	12.7	44°09.2′	155°34.0′	0–30	60	0.1	0	0	268.3	0.4
14	21 July 2009	10.2	44°27.2′	155°56.4′	0–30	60	4.6[a]	0	0	210.8	+
15	22 July 2009	13.5	43°39.1′	156°01.4′	0–30	60	1.5[a]	0	0	244.5	0.3

+, 0.1 kg < catch per unit of effort (CPUE)

[a] Backscatters of Japanese anchovy were detected on the echogram during trawlings

on the track lines (Fig. 1). The midwater trawl used in this study had a mouth opening of 20 × 30 m with a 17.5-mm liner codend. The sampling depths and the height of the net mouth were monitored using a net monitor system (PI32, SIMRAD). Towing speed was 3–4 knots. Trawls were conducted to identify species and size compositions of acoustic backscatters in the echogram as well as to collect data on species such as Pacific saury, which are difficult to detect with the echosounder due to their distributions close to sea surface, generally shallower than the bottom of the ship. Within the survey area of the common minke whale, the SST was less than 15°C and Pacific saury were possibly distributed [13, 14]. Hence, all trawling stations of this area were predetermined, generally 20–30 nautical miles apart on the track lines, and acoustic backscatters for other small epipelagic fish species were identified based on predetermined trawling data (Fig. 1; Table 1). At each station, a trawl net was towed at depths of 0–100 m (oblique tow) or 0–30 m for 60 min (Table 1). All samples were identified to the lowest taxonomic level possible and the wet body weight of each species was measured. For the major species, individual body length was measured from 100 randomly selected samples. When the sample size for a species was less than 100 individuals, the body length was measured for all individuals collected.

We conducted MOCNESS samplings to confirm the taxonomic composition of euphausiid-like patchiness detected on the echogram as well as to confirm the distribution of euphausiids in each deep scattering layer in the epipelagic zone. The mouth opening and mesh size of MOCNESS were 1 m^2 and 0.33 × 0.33 mm, respectively. The net was towed at 2 knots at eight target depths (0–20, 20–40, 40–60, 60–80, 80–100, 100–150, 150–200, and 200–250 m) (Table 2). The volume of seawater filtered by each net was measured with a flow meter mounted at the net mouth. Samples were preserved in 5% formalin-buffered seawater, and size and abundances were analyzed in the laboratory. NORPAC net samplings were conducted in the 0–150-m layer at all sampling stations to estimate the biomasses of the copepod species *N. cristatus* and *N. plumchrus*, which are occasional prey of the sei whales [1]. The mouth opening and mesh size of the net were 0.16 m^2 and 0.33 × 0.33 mm, respectively. A flow meter was attached to the net to measure the volume of seawater

Table 2 Sampling dates and positions of the MOCNESS survey

Stn.	Date	SST (°C)	Latitude (N)	Longitude (E)	Sampling depth (m)
Survey area of Bryde's whale					
2	21 July 2008	26.9	35°52.5′	146°55.3′	0–250
5	23 July 2008	24.7	37°05.1′	146°46.8′	0–250
10	25 July 2008	19.2	39°31.7′	146°01.8′	0–250
Survey area of sei whale					
7	13 July 2009	18.7	39°18.9′	157°22.5′	0–250
Survey area of common minke whale					
14	21 July 2009	10.2	44°27.2′	155°56.4′	0–250

filtered. Samples were preserved in 5% formalin-buffered seawater.

A conductivity-temperature-depth (CTD, Sea-Bird Co., Ltd.) profiler cast was made to 500 m depth at each sampling station to determine the position of oceanographic fronts on the track lines. The distribution of oceanographic fronts around the track lines were estimated by 100-m and 200-m temperature and salinity maps by the North-East Asian Regional-Global Ocean Observing System (NEAR-GOOS) database and Fisheries Research Agency-Japan Coastal Ocean Predictability Experiment (FRA-JCOPE) system (Fisheries Research Agency of Japan: http://fj.dc.affrc.go.jp/; accessed 27 July 2011, Japan Oceanographic Data Center: http://near-goosl.jodc.go.jp/index.html; accessed 27 July 2011). The distribution of the SST isotherm was estimated using the NOAA Optimum Interpolation 1/4 Degree Daily Sea Surface Temperature Analysis database, version 2 (OISSTWeb: http://www.ncdc.noaa.gov/oa/climate/research/sst/papers/whats-new-v2.pdf; accessed 27 July 2011) [15].

Species identifications of backscatterings for euphausiids and epipelagic fish species except for Pacific saury were conducted based on MOCNESS and midwater trawl catches, respectively. The school shapes of euphausiids and Japanese anchovy recorded on the echogram were also taken into account, with reference to previous reports [16, 17]. For the epipelagic fish species except for Pacific saury, acoustic data collected at 38 kHz were used with the threshold set at −60 dB within 0–250 m. For euphausiids, data collected at −120 kHz were used with the threshold set at −80 dB within 0–250 m. The difference in the volume backscattering strength (SV) was also considered to identify euphausiids, because echoes could be identified as euphausiids when difference of SV between 120 and 38 kHz was between 10 and 15 dB [18]. When the difference in the SV was calculated, a threshold of 38 kHz was set at −80 dB. A biomass estimation for each species was conducted according to the method of Jolly and Hampson [19].

The mean backscattering area per square nautical mile of sea surface (S_A) by species for every one nautical mile of survey transect over defined depth interval was calculated using the following formula:

$$S_A = 4\pi r_0^2 1852^2 \int_{r_1}^{r_2} s_V \mathrm{d}r \left(\frac{\mathrm{m}^2}{\mathrm{n.mi}^2}\right),$$

where r is the depth from the sea surface, and $r_0 = 1$ m, representing the reference range for backscattering strength. The following length–target strength (TS) relationship for Japanese anchovy [20], which was the main component in the epipelagic fish community (see below), was used:

$$\mathrm{TS} = 20\log\mathrm{SL} - 64.0,$$

where SL is the scale length in centimeters. We estimated body wet weight of each individual from the SL values using the following equation [21]:

$$W = 0.010\mathrm{SL}^{3.00},$$

where W is weight in grams.

Because no length–TS relationship for euphausiids was available in this study area, we assumed that the TS of euphausiids was −83.3 dB, which was the value reported for *Euphausia pacifica* of 16.4 mm body length [22]. The average body length of euphausiids selected randomly from all samples was 16.0 mm ($n = 301$), suggesting that this assumption is suitable for this study. The average weight of euphausiids was calculated using a formula described by Odate [23]. The acoustic cross-section was converted from TS as follows:

$$\sigma = 4\pi 10^{0.1\mathrm{TS}}.$$

The average area biomass density ($\overline{\rho}$) for each species was calculated as

$$\overline{\rho} = \sum \frac{S_A}{\sigma} f_i W_i,$$

where f_i is the frequency distribution of the ith length class. The frequency distribution of each class (f_i), which represents the acoustical contribution to the area backscattering for each length class, was calculated as

$$f_i = \sum_{j=1}^{\infty} n_j L_j^2,$$

where n_j is the number of individuals in size class j and L is length (Ona E, unpubl. data, 1993).

The biomass of Pacific saury, which was one of the most abundant epipelagic fish species in the habitat of the common minke whale (Table 1), was estimated from midwater trawl sampling data. We assumed that the distribution depth of this species is 0–10 m, the area of mouth opening for the trawl net is 600 m^2, and the catching efficiency of the trawl we used is 14.4%, based on similar-sized trawl data [14]. To estimate the water volume filtered in each sampling, the average towing speed of midwater trawl in each sampling (approximately 4–5 knots) was adopted.

Whale sighting and sampling surveys

Whale sighting surveys were conducted mainly in a “closing” approach mode. In this mode, the vessels diverted from the track line by accelerating from the standard vessel speed to about 15 knots, and approached the detected animals in an attempt to identify the species and to count all animals in the group [24]. Because the survey track lines were established systematically in each study area, each sampling position for the whales could be considered to reflect their actual distribution patterns. Furthermore, because almost all target whale species found within a 3-nautical-mile radius from the track line were captured in this study, we deemed that the distribution density of the sampling position of each whale species generally reflected their relative abundance on the track line. However, some individuals of common minke whale could not be captured due to the dense distribution of commercial fishing vessels for Pacific saury in the northwestern part of the study area (Bando T, unpubl. data, 2009, see Fig. 2a). For this area, we also used whale sighting data obtained by sighting/sampling vessels to estimate the distribution patterns of the whales (Bando T, unpubl. data, 2009). We defined the main distribution area of sei and Bryde's whales as the area where whale individuals were continuously distributed within an interval of 5 nautical miles on the track line. Because all individuals of common minke whale were distributed continuously within an interval of 5 nautical miles in several parts of the study area, we divided the distribution area and other areas to estimate the distribution pattern of this whale (Bando T, unpubl. data, 2009, Fig. 2a).

In total, seven common minke, 23 sei, and 24 Bryde's whales were sampled in each sampling area. Body length, body wet weight, and wet weight of stomach contents in the first and second compartments of the stomachs, which were regarded as newly consumed prey [1], were measured. The prey species were identified by examining the whales' stomach contents. We collected subsamples by randomly selecting 2–4 and 0.5 kg of stomach contents from the first and second stomachs, respectively. The total number of each fish species in a subsample were determined by summing the number of undigested fish and half the total number of free otoliths. The total weight of each prey species before ingestion in the subsample was estimated by multiplying the average weight of fresh specimens by the number of individuals. Then, the total wet weight of each prey species in the first and second stomachs was estimated by applying the weight ratio in the subsamples to the total wet weight of the first and second stomach contents.

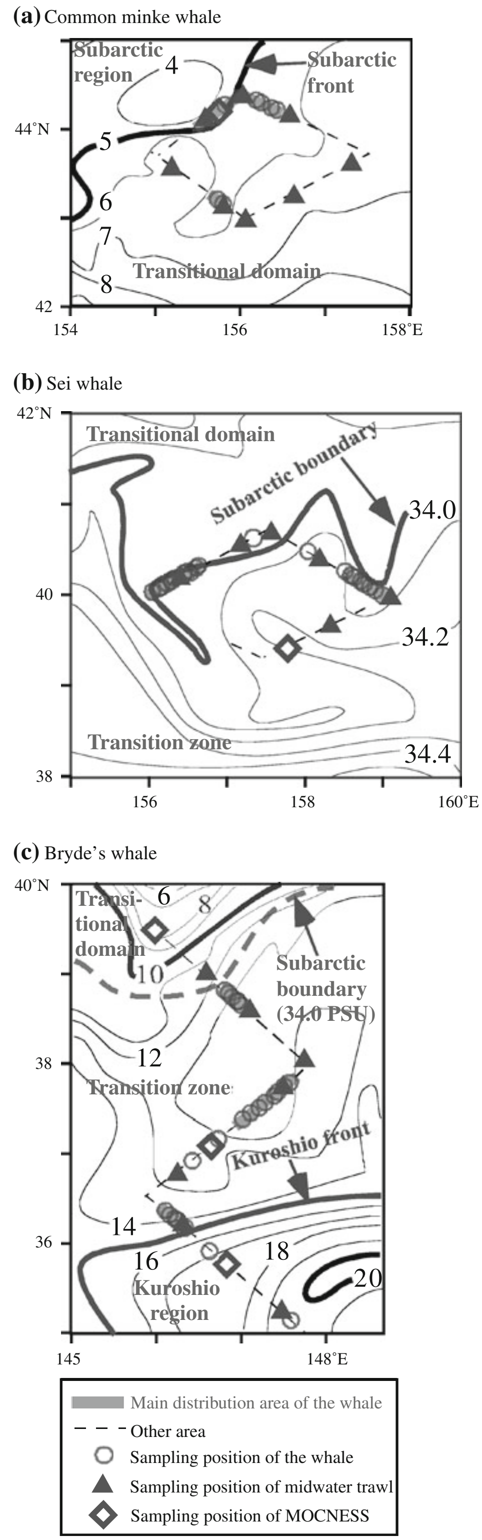

Fig. 2 **a** Distribution area of common minke whale and the distributions of isotherms at 100 m deep, **b** distribution area of sei whale and the distributions of the isohaline at 100 m deep, and **c** distribution area of Bryde's whale and the distributions of isotherms at 100 m deep as well as the subarctic boundary, on the survey track lines. The sampling positions of the midwater trawls and MOCNESS in each area are also indicated

Analysis of prey preferences

We used Manly's selection index to determine the prey preference of the whales in their main habitats [25], details of which was also described in Murase et al. [26]. The standardized form of the selection index, Manly's α [27], was applied to the North Atlantic stock of minke whales to reveal prey selectivity [28, 29]. Specifically, assuming that the jth stomach contents with the ith prey species are available, the total weight of prey species i used by all animals (u_{i+}) (kg) is

$$u_{i+} = \sum_{j=1}^{J} u_{ij},$$

where u_{ij} is the weight of prey species i used by animal j.

The total weight of prey species used by animal j (u_{+j}) is

$$u_{+j} = \sum_{i=1}^{I} u_{ij}.$$

The total weight of all prey species used by all animals (u_{++}) is $u_{++} = \sum_{i=1}^{I}\sum_{j=1}^{J} u_{ij}$.

The sample proportion of prey species i by weight used by all animals is $o_i = u_{i+}/u_{++}$.

The sample proportion of available units of prey species i is

$$\hat{\pi}_i = m_i \Big/ \sum_{i=1}^{I} m_i$$

where m_i is the amount of available units of prey species i in a sample of available resource units. Manly's selection indices are described as $\hat{w}_i = o_i/\hat{\pi}_i$.

Confidence intervals of the selection index were estimated as follows to determine the statistical significance level of whether whales randomly fed on prey species: The Bonferroni confidence interval of $\hat{w}_i$ is given by

$$\hat{w}_i \pm z_{\alpha/(2I)} se(\hat{w}_i).$$

If the confidence interval contains the value 1, whales feed on prey species randomly [25]. If $\hat{w}_i$ is greater or less than 1, species i is actively or negatively selected, respectively [25]. The value of α was set at 0.05.

Results

Oceanographic conditions

Two oceanographic fronts are distributed in the study area north of 38°N: the subarctic front between the subarctic region and the transitional domain, and the subarctic boundary between the transitional domain and the transition zone [30, 31]. According to Kawai [32] and Murakami [33], the subarctic front is defined by a water temperature of 5°C at 100 m. The subarctic boundary is defined by a vertical 34.0 PSU salinity front in the epipelagic zone [30]. In the survey area of common minke whales, the water temperature at 100 m was 4–7°C, indicating that this area was located in the subarctic region and the northern transitional domain close to the subarctic front (Fig. 2a). In the survey area of sei whale, surface salinity front of 34.0 PSU generally extended to 100 m depth, indicating that position of subarctic boundary could be estimated by the salinity at 100 m. The salinity at 100 m in the survey area of sei whales ranged from 33.9 to 34.2 PSU, indicating that this area was located in and around the subarctic boundary (Fig. 2b).

In the area west of approximately 152°E, another oceanographic front (the Kuroshio front) is defined as the area south of the 14.0°C isotherm at 200 m deep [32]. The temperature at 200 m at the survey area of Bryde's whales ranged from 15.1°C to 17.5°C in the area south of 36°N, indicating that this area was located in the subtropical Kuroshio region south of the Kuroshio front, which approximately corresponded to the 15°C isotherm at 100 m in this study (Fig. 2c). In the area north of 36°N within the survey area of Bryde's whales, the water temperatures at 100 and 200 m deep were >8°C and <14.0°C, respectively, and the salinities at 100 m deep were >34 PSU south of 39°N and <34 PSU north of 39°N (Fig. 2c). These data indicate that the southern area between 36°N and 39°N and the northern area north of 39°N were located in the transition zone and transitional domain, respectively.

Species composition of the small epipelagic fish community

The results of the target trawling showed that most of the small epipelagic fish-like acoustic backscatters were Japanese anchovy in the survey areas of both sei and Bryde's whales, indicating that Japanese anchovy was the most abundant species in the small epipelagic fish community in these regions (Table 1). In the survey area of common minke whales, acoustic backscatters of small epipelagic fish species were sometimes observed during predetermined trawl samplings, and we confirmed that these backscatters mostly represented Japanese anchovy (Table 1). In this area, however, Pacific saury was frequently detected and most abundantly captured by the predetermined trawl samplings (Table 1). In this study period, main distribution areas of Japanese anchovy and Pacific saury corresponded well to the northernmost region of the transition zone and the subarctic region, respectively (see below).

Distribution and diet composition of whales

Common minke whale

This species was distributed in the subarctic region and northernmost region of the transitional domain, where the temperature at 100 m deep was <6°C (Fig. 2a). Among the prey species, the abundances (mean ± standard deviation) of Pacific saury and Japanese anchovy were significantly higher in the habitat of the whales than in the adjacent area to the south (12.5 ± 3.2 versus 0 mg m^{-2} and 1.6 ± 0.5 versus 0.4 ± 0.2 mg m^{-2}, respectively, Mann–Whitney U test, $P < 0.05$, Fig. 3a). Conversely, euphausiids in the 0–250 m layer were less abundant in the distribution area of the whales than in the adjacent area (54.0 ± 8.8 versus 91.5 ± 10.3 mg m^{-2}, Mann–Whitney U test, $P < 0.05$, Fig. 3a). These data indicate that the distribution centers of the common minke whale, Pacific saury, and Japanese anchovy greatly overlapped. The results of stomach content analysis of the whales indicated that the most common prey item was Pacific saury, followed by Japanese anchovy, which reflected the prey species composition within the whales' habitat (Table 3).

Sei whale

Sei whales were mainly distributed in areas where the salinity at 100 m deep was 34.0–34.1 PSU, corresponding to the transition zone within or close to the subarctic boundary (Fig. 2b). Among the prey species examined, Japanese anchovy was significantly more abundant in the main distribution area of the whale (8.1 ± 3.5 mg m^{-2}) than in other areas both in the transition zone (0.4 ± 2.2 mg m^{-2}) and the transitional domain (0.3 ± 1.6 mg m^{-2}, Kruskal–Wallis test with Bonferroni-type adjustments, $P < 0.05$, Fig. 3b). However, euphausiids and two copepod species, *N. cristatus* and *N. plumchrus*, in the epipelagic zone were more abundant in the transitional domain than in the transition zone, including the main habitat of the whale (Kruskal–Wallis test with Bonferroni-type adjustments, $P < 0.05$, Fig. 3b). These results suggest that the main habitats of sei whale and Japanese anchovy greatly overlapped in the survey area. This whale species mostly fed on Japanese anchovy, and mean wet weight values of this prey in the whale stomachs (mean ± standard deviation) were

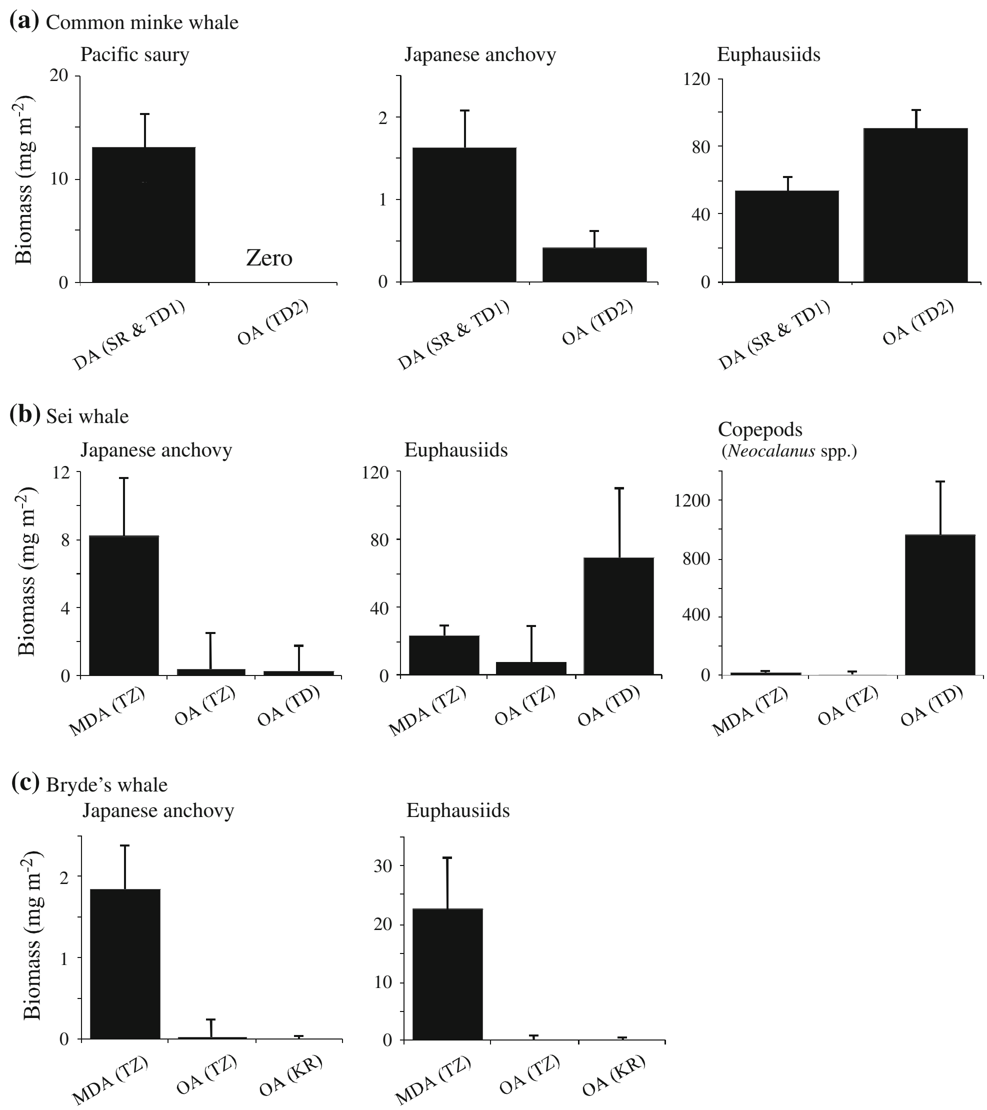

Fig. 3 Mean abundance of the prey species of common minke, sei, and Bryde's whales in their main distribution area and adjacent areas. Bars indicate standard deviation. *Neocalanus* spp. includes *N. cristatus* and *N. plumchrus*. *DA* distribution area of the whale, *MDA* main distribution area of the whale, *OA* other areas, *SR* subarctic region, *TD1* transitional domain close to the subarctic front where the temperature at 100 m was <6°C, *TD2* transitional domain where the temperature at 100 m was ≥6°C, *TZ* transition zone, *KR* Kuroshio region

significantly higher in its main distribution area than in the other two areas (Mann–Whitney *U* test, $P < 0.05$, Table 3; Fig. 4a).

Bryde's whale

This species was frequently found in several regions within the transition zone, whereas no and only a few individuals were distributed in the transitional domain and the Kuroshio region, respectively (Fig. 2c). Among the prey species examined, Japanese anchovy was significantly more abundant in the main distribution area of the whale than in other areas in the transition zone and in the Kuroshio region (Kruskal–Wallis test with Bonferroni-type adjustments, $P < 0.05$, Fig. 3c). Euphausiids at 0–250 m were also significantly more abundant in the main distribution area of the whale than in the other two areas (Kruskal–Wallis test with Bonferroni-type adjustments, $P < 0.05$, Fig. 3c). These data indicate that Bryde's whales mainly inhabit the distribution centers of Japanese anchovy and euphausiids. In the stomachs of the whales, Japanese anchovy and euphausiids ranked as the first and second most common preys (Table 3). The mean wet weight values of Japanese anchovy in the whale stomachs were significantly higher in the main distribution area than in the other two areas (80.6 ± 118.1 versus 7.4 ± 15.9 and 3.7 ± 5.0 kg, Kruskal–Wallis test with Bonferroni-type adjustments, $P < 0.05$, Fig. 4b). Furthermore, the mean wet weight of euphausiids in the stomachs of the whales was also significantly higher in the main Bryde's whale distribution area than in other areas in the transition zone (14.3 ± 35.0 versus 0.6 ± 1.4 kg, Mann–Whitney *U* test, $P < 0.05$, Fig. 4b). No euphausiids were found within the stomach contents of this whale in the Kuroshio region.

Table 3 Mean wet weight (kg) (mean ± standard deviation) of each prey species found in the stomachs of common minke, sei, and Bride's whales

Prey species	Common minke ($n = 7$)	Sei ($n = 23$)	Bryde's ($n = 24$)
Euphausiids	–	–	7.3 ± 25.2
Pacific saury	25.2 ± 7.4	–	–
Japanese anchovy	10.3 ± 7.7	255.8 ± 382.9	42.5 ± 106.0
Mackerels	–	4.2 ± 14.4	+
Japanese sardine	–	1.1 ± 3.7	+

n no. of whale stomachs examined, + average value was less than 0.1 kg

Prey preference

Manly's selection index ($\hat{w}_i$) [25] and analysis of the Bonferroni confidence interval of $\hat{w}_i$ indicated that the common minke whale showed positive selection for Pacific saury ($\hat{w}_i = 4.791$) and Japanese anchovy preys ($\hat{w}_i = 5.228$), and sei and Bryde's whales positively selected Japanese anchovy prey ($\hat{w}_i = 6.177$ and 11.368) (Table 4). The results of the selection index also indicated that Bryde's whales selected against euphausiid prey ($\hat{w}_i = 0.162$), although the whales frequently consumed this prey type. Furthermore, although euphausiids were abundantly distributed in the habitats of common minke and sei whales, these whales fed on any euphausiid prey (Table 3; Fig. 3). These results might indicate that it is difficult for these whale species to use euphausiid prey as their biomass.

Discussion

The distribution of common minke whales generally corresponded to the location of the subarctic front. Because common minke whale is mainly distributed in the subarctic region in summer [1, 6, 12], the survey area of this study was thought to be located at the southern limit of the main distribution area of the whale. The subarctic region and northern transitional domain close to the subarctic front constitute the main habitat of Pacific saury in the summer

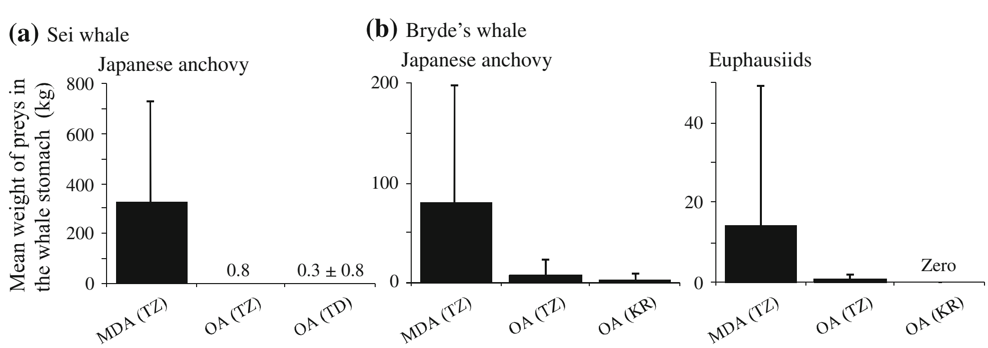

Fig. 4 Mean wet weight (kg) of prey species found in the stomachs of sei and Bryde's whales in their main distribution area and adjacent areas. Bars indicate standard deviation. *MDA* main distribution area of the whale, *OA* other areas, *TD* transitional domain, *TZ* transition zone, *KR* Kuroshio region

Table 4 Selection index ($\hat{w}_i$) and the results of the statistical test for common minke, sei, and Bryde's whales in their main habitat in the western North Pacific during mid summer

	Euphausiids	Japanese anchovy	Pacific saury
Common minke whale			
$\hat{w}_i$	0.000	5.228	4.791
Bonferroni CI (low)	–	2.447	4.443
Bonferroni CI (high)	–	8.010	5.138
Sei whale			
$\hat{w}_i$	0.000	6.177	–
Bonferroni CI (low)	–	6.148	–
Bonferroni CI (high)	–	6.207	–
Bryde's whale			
$\hat{w}_i$	0.162	11.368	–
Bonferroni CI (low)	0.132	11.000	–
Bonferroni CI (high)	0.191	11.736	–

[14], which was also demonstrated by our sampling data. In this study, Japanese anchovy was also more abundantly distributed in the minke whale habitat than in the transitional domain, probably due to high productivity of the former region in summer [34]. Common minke whales fed mainly on Pacific saury and secondarily on Japanese anchovy, suggesting that this whale species preferred the main distribution area of these fish prey for feeding. However, given that the main distribution area of Japanese anchovy in the summer is located in and around the transition zone chlorophyll front (TZCF) and south of the transitional domain, as discussed below [35, 36], Pacific saury appear to affect the distribution of common minke whales more significantly than do Japanese anchovy. This hypothesis is supported by the present result that common minke whales preferred Pacific saury prey, in combination with previous results that this whale species feeds mainly on Pacific saury in their main habitat in summer and early autumn in or close to the subarctic region [1]. According to Murase et al. [26], common minke whales positively select Japanese anchovy prey in the Kuroshio–Oyashio transition region south of the habitat of Pacific saury in August, suggesting that this whale species prefers small epipelagic fish species rather than zooplanktons, both in its main distribution area and in its southernmost distribution area during summer.

With respect to sei whales, the main distribution area was located in and around the subarctic boundary. According to Konishi et al. [1] and Fujise et al. [12], sei whale was mainly found in the transition zone south of 40°N in May and June and in the transitional domain of 40–45°N from July to September, suggesting that this species migrates into the transitional domain from the transition zone in July. Therefore, the present result that sei whale was mostly found in the northernmost part of transition zone likely indicates the distribution pattern of the whale in early July, when this survey was conducted. The subarctic boundary also corresponds to the summertime location of the TZCF, which migrates to the subarctic boundary from the subtropical region during spring and summer [35, 37–39]. The TZCF is a zone of surface convergence, where cool surface waters from the north, containing high levels of chlorophyll *a*, sink beneath warm, oligotrophic waters to the south. This indicates that the region of the TZCF and north of the TZCF is a productive area [35, 37, 38]. The present result that sei whales preferred and heavily fed on Japanese anchovy prey, which are mainly distributed in and around the TZCF in early summer [36, 37], suggests an enhanced feeding regime for the predator in the TZCF in this period. Conversely, euphausiids and two copepod species, *N. cristatus* and *N. plumchrus*, were less abundant in the transition zone, including the main habitat of the whale, than in the transitional domain, suggesting that these prey do not significantly affect the distribution of the whales in this study area. This whale species showed no prey preference for euphausiid prey and fed on any copepod prey, thus supporting this view. Such south–north distribution patterns of zooplankton are also shown in previous reports [34]. However, because we could not obtain adequate data in the transitional domain in this study, future surveys in this region are required to estimate distribution and migration pattern of sei whale in summer.

Main distribution area of Bryde's whale is located within an area bounded by 35–40°N in summer in the western North Pacific [1, 12], showing that survey area of this study was covered latitudinal distribution range of the whale. In this study, the main habitat of Bryde's whales was within the less productive transition zone south of the TZCF. However, from a trophic standpoint, the transition zone may be favorable over the wintering area of the subtropical region for the whale during the summer because the former area is an oligotrophic region in this season, whereas the latter area is more productive [40–42]. Given that Japanese anchovy and euphausiids greatly overlapped within the main habitat of Bryde's whale, this whale species appears to select the habitats where these prey are abundantly distributed. The present results that Bryde's whale feed mainly on Japanese anchovy and secondly on euphausiids, and that the feeding activity of the whale was significantly higher in its main habitat than in other areas, might support this view. However, positive prey selection of the whale was only shown for Japanese anchovy, suggesting that Japanese anchovy affects the distribution of the whale more significantly than euphausiids. Previous reports that Bryde's whale generally heavily feed on Japanese anchovy prey between the area of 35–40°N in the western North Pacific in summer might support this view [1, 12].

The present results indicated that the distributions of Pacific saury or Japanese anchovy preferred by common minke, sei, and Bryde's whales greatly affect the distributions of these whale species, which strongly suggests that the habitat selection of the whale species is closely related to their prey selection in summer in the western North Pacific. These prey species are known to undertake northward migration and migrate into subarctic regions or southern transitional domains from subtropical regions during spring and summer as the TZCF moves northward [8, 13, 37]. In spring in the western North Pacific, the main prey species of sei and Bryde's whales is also Japanese anchovy in the lower latitudinal areas between 38°N and 40°N, and 35°N and 38°N, respectively, which represent the main habitats of these whales in this season [1]. In summer, these whale species also mainly feed on Japanese anchovy in the higher latitudinal area as was shown in the present and previous studies [1, 12]. These observations suggest that the predator–prey relationship is almost maintained from spring to summer, since their seasonal migration patterns are spatiotemporally similar to one another. Therefore, these whales might exploit the distribution area of Japanese anchovy as a migration route and as a forage habitat from spring to summer. In case of common minke whales, the main prey species shifts from Japanese anchovy to Pacific saury from spring to summer during its northward migration period from subtropical to subarctic regions [1, 6]. This whale species continues to depend on Pacific saury during late summer and early autumn in or close to the subarctic region [1, 6]. Considering that Pacific saury migrate northward prior to Japanese anchovy from spring to summer, and that the summer distribution area of Pacific saury is the adjacent area north of the habitat of Japanese anchovy [43], common minke whales might migrate northward in the prey-rich area from spring to summer. Therefore, the summertime northward migrations of the three whale species are believed to be feeding migrations, like in many other predators such as swordfish *Xiphias gladius*, albacore *Thunnus alalunga*, and neon flying squid *Ommastrephes bartramii*, which also feed on seasonal south–north migratory prey like Japanese anchovy [35, 36, 42, 44–46].

The distribution of these whale species was also generally explained by the locations of the subarctic and Kuroshio fronts as well as the subarctic boundary, likely because the summer distributions of the preferred prey species are closely related to these oceanographic features [8, 23, 43, 44]. Although the present results were obtained from mesoscale data (i.e., a scale of several hundred kilometers), these fronts and boundaries are widely distributed in the western North Pacific [31, 32]. Because the whale species and their preferred prey species are widely distributed in the western North Pacific [1, 8, 23, 43, 44, 47], the present results could reflect the general mid summer distribution patterns of these whale species in relation to both physical oceanographic and prey environments in the western North Pacific. Therefore, information of the locations of these three fronts or boundaries is important for estimating the main distribution areas of these whales in this period. In this study area, SST has generally been used to estimate the distributions of baleen whale species [1, 11]. However, because these oceanographic fronts and boundaries could be recognized by the temperature at depths of 100 or 200 m or vertical salinity profiles in the epipelagic zone [31, 32], the mid summer distributions of these whale species might be more accurately estimated using prediction models of oceanographic conditions, including the positions of these fronts and boundaries.

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