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Habitat differentiation between sei (*Balaenoptera borealis*) and Bryde's whales (*B. brydei*) in the western North Pacific

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ABSTRACT

Two closely related baleen whale species, sei and Bryde's whales, in the western North Pacific were studied to identify differences in habitat use. Data were obtained from May to August 2004 and 2005. This study examined the relationship between oceanographic features derived from satellite data and the distribution of sei and Bryde's whales using basic statistics. We investigated oceanographic features including sea surface temperature (SST), sea surface chlorophyll *a* (Chl-*a*), sea surface height anomalies (SSHAs), and depth of the habitat. These two whale species used habitats with different SST, Chl-*a*, and SSHA ranges. The 0.25 mg m^{-3} Chl-*a* contour (similar to the definition of the Transition Zone Chlorophyll Front) was a good indicator that separated the habitats of sei and Bryde's whales. Then generalized linear models were used to model the probabilities that the whale species would be present in a habitat and to estimate their habitat distribution throughout the study area as a function of environmental variables. The potential habitats of the two species were clearly divided, and the boundary moved north with seasonal progression. The habitat partitioning results indicated that SST contributed to the patterns of habitat-use and might reflect differences in prey species between the two whales. This study showed that the habitats of the sei and Bryde's whales were clearly divided and their potential habitat-use changed seasonally.

Key words: Bryde's whale, generalized linear models, habitat partitioning, oceanographic features, sei whale, western North Pacific

INTRODUCTION

Marine mammals play important roles in marine ecosystems as top predators (Bowen, 1997; Hunt *et al.*, 2000). The amount of food consumed by cetaceans is not negligible, and they can cause top-down effects by foraging on large amounts of prey, such as zooplankton and fishes (Tamura, 2003). Cetaceans are affected by environmental changes attributable to the dynamics of complex physical and biological processes. Identification of the habitats used by cetaceans is fundamental to understanding the interactions between cetaceans and marine ecosystems.

Marine mammals also experience bottom-up effects from environmental changes. Atmospheric and climate-related processes drive changes in marine ecosystems on different timescales. Accordingly, understanding climate patterns and ecosystems, and connections between the two, is important (Overland *et al.*, 2008). Interannual variation in climate is now widely recognized to affect fish production (Baumgartner *et al.*, 1992; Mantua *et al.*, 1997; Bakun and Broad, 2003). Changes in fish populations are related to changes in the amount and timing of primary production (Hunt, 2006), and temperature-related changes in the growth and maturation of zooplankton (Mackas *et al.*, 1998). Hunt and McKinnell (2006) indicated that decadal-scale changes in atmospheric forcing (climatic regime shifts) are associated with changes in the distribution and population size of a wide variety of fishes in the North Pacific. Marine mammals, which feed on zooplankton and fishes, would be susceptible to such bottom-up effects. Longer-term climate changes could affect marine

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mammals, but the extent to which they will be impacted is not yet certain (Simmonds and Eliott, 2009). To investigate the responses of marine mammals to climate and ecosystem changes at various timescales, understanding current habitat-use patterns in relation to oceanographic conditions is critically important. Recent improvements in satellite remote sensing techniques allow us to conduct such analyses.

In the past, habitat-use by cetaceans in the western North Pacific was generally studied qualitatively using commercial catch data. Uda (1954) and Nasu (1966) suggested that the distribution of baleen whales was closely related to the locations of eddies and fronts, in addition to topography. Kawamura (1973) reported that sei whales were distributed around the Emperor seamount (Fig. 1) and that they preyed almost exclusively on copepods. Nemoto (1959) found that the distributions of prey species were related to the distributions of baleen whales. Such studies have rarely been conducted since 1987, when a moratorium on commercial whaling was imposed by the International Whaling Commission. Medium-sized baleen whales, the sei (*Balaenoptera borealis*) and Bryde's (*Balaenoptera brydei*) whales, are distributed in the western North Pacific. The two species are closely related in terms of genetics and morphology. Until 1955, they were collectively recorded as 'sei whales' in Japanese whaling statistics because of their morphological similarity, although sei and Bryde's whales were recognized as northern and southern types of 'sei whales', respectively (Omura and Fujino, 1954; Omura, 1959). An examination of 901 aligned sites of the control region sequence of mtDNA suggested that the smallest interspecific nucleotide difference in congeners was between sei and Bryde's whales (Wada *et al.*, 2003). Wada *et al.* (2003) also indicated that three species of Bryde's-like whales occur worldwide, namely, Bryde's whale (*Balaenoptera brydei*), Eden's whale (*Balaenoptera edeni*), and Omura's whale (*Balaenoptera omurai*). However, some scientists consider the former two forms to be subspecies rather than species (Kato and Perrin, 2009; Committee on Taxonomy, 2011). These Bryde's-like whales are still treated as *B. edeni* by the International Whaling Commission, with recognition that the designation contains more than one species (International Whaling Commission, 2001). In a genetic study, Kanda *et al.* (2007) identified Bryde's-like whales distributed in the western North Pacific as Bryde's whales. In this paper, we assume Bryde's whale as *B. brydei* following the nomenclature proposed by Wada *et al.* (2003). Sei and Bryde's whales mainly feed on zooplankton and small pelagic fishes in the western North Pacific, although their dominant prey species differ geographically, seasonally, and annually (Nemoto, 1959; Kawamura, 1980; Horwood, 1987; Murase *et al.*, 2007; Konishi *et al.*, 2009; Watanabe *et al.*, 2012). Sei whales remain in low-latitude areas for breeding in the winter and move to higher latitudes for feeding in the summer (Horwood, 1987), whereas Bryde's whales show little seasonal movement and remain at low latitudes throughout the year (Kato and Perrin, 2009). The distributions of sei and Bryde's whales differ in relation to sea surface temperature (Omura and Nemoto, 1955; Nemoto, 1959; Horwood, 1987). For example, Ohsumi (1977) reported that sea surface temperature ranges for sei and Bryde's whales at catch positions were 5–25°C and >18°C, respectively. Previous reports have indicated that these two species are found in different areas in the western North Pacific. However, little quantitative information is available regarding their spatial and temporal habitats. Seasonal and annual shifts in the habitats of

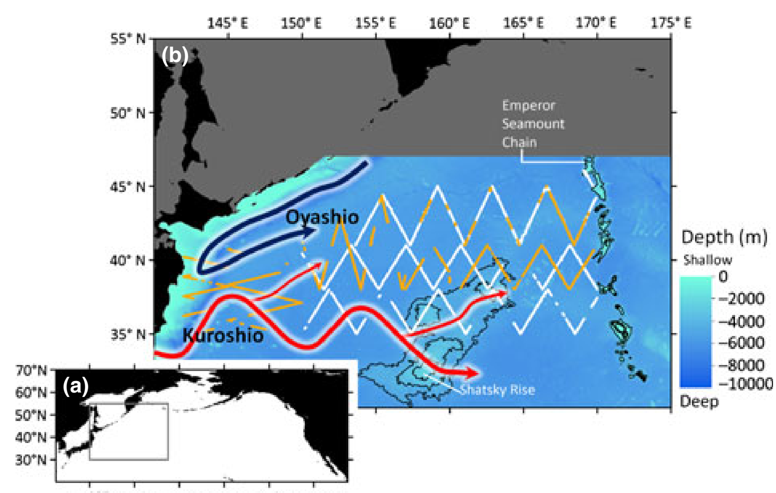

Figure 1. Map of the North Pacific showing (a) location of the study area identified by black box and (b) enlarged map depicting the tracklines covered. The orange line indicates the JARPN II research trackline in 2004 and the white line shows the trackline in 2005.

other marine life, such as albacore tuna (*Thunnus alalunga*) and loggerhead turtles (*Caretta caretta*), have been characterized by specific oceanographic conditions in the western North Pacific (Polovina *et al.*, 2001; Polovina *et al.*, 2004; Zainuddin *et al.*, 2004, 2008). Many marine animals utilize the transition zone between subarctic and subtropical waters in the western North Pacific as feeding grounds and migration corridors between these waters.

Generalized linear models (GLMs) are widely used to predict cetacean distributions and understand the ecological processes determining these distributions (Waring *et al.*, 2001; Hamazaki, 2002; Macleod *et al.*, 2004; MacLeod *et al.*, 2008; Praca *et al.*, 2009; Anderwald *et al.*, 2011). In these studies, the presence/absence of animals was used as a binary response variable.

To determine how whale habitats differ with respect to environmental conditions, we first examined relationships between environmental conditions, which were mainly determined using satellites, and the distribution patterns of sei and Bryde's whales using basic statistics. In contrast to previous studies, the presence of sei and Bryde's whales was used as a binary response variable to differentiate their habitats. Finally, suitable and potential habitats for the two whale species in the study area were estimated using the selected habitat models.

MATERIALS AND METHODS

Study area

The study area was located in the western North Pacific, between 35° and 48°N, and between the eastern coast of Japan and 175°E, excluding waters that are claimed by countries other than Japan (Fig. 1). Most regions in the study area had depths >4000 m. Topographic features in the area included the Kuril Trench in the northwest of the basin, the Japan trench on the west, and the Emperor seamount at around 170°E, which runs in a north–south direction (Fig. 1). The Shatsky Rise is located at the center of the basin and divides the Kuroshio Extension. The Kuroshio south of Japan and the Kuroshio Extension east of Japan are the western boundary currents of the North Pacific subtropical gyre, and they transport warm saline surface water (Yasuda, 2003). Subarctic currents, including the south-flowing Oyashio (Yasuda *et al.*, 1996, 2001; Okuda *et al.*, 2001), represent other major currents in the western North Pacific. Our study area was part of the Kuroshio-Subarctic transition zone (Kawai and Saitoh, 1986; Kawamura *et al.*, 1986; Yasuda *et al.*, 1992), which is one of the world's major fishing grounds.

Whale sighting data

Surveys were conducted as part of the second phase of the Japanese Whale Research Program under a Special Permit in the North Pacific (JARPN II). Surveys were conducted in the summers (May–September) of 2004 and 2005 (Table 1, Fig. 2). From these surveys, we only utilized the subset data from May to August. Sighting data for sei and Bryde's whales were collected during the day by a sighting survey vessel, the *Kyoshin Maru* No. 2 (KS2: 368GT). The vessel traveled at a speed of 10.5 knots ($\approx$19.5 km h^{-1}). The survey was only conducted when the wind speed did not exceed 16 knots ($\approx$7.9 m s^{-1}) and the visibility was >2 nautical miles ($\approx$3.7 km). Primary observers were allocated to the top barrel (three observers) and the upper bridge (two observers). The barrel and upper bridge were 17 and 8 m above the water surface, respectively. The observers searched for whales within 3 nautical (n.) miles ($\approx$5.6 km, perpendicular distance) within 3 n.miles boundary either side of the constructed trackline using 7 × 50 binoculars with a reticule. Zigzag tracklines were constructed within the survey area. The starting points of the tracklines were randomly selected. The sighting survey was conducted during daylight hours from 1 h after sunrise to 1 h before sunset. The dates and positions of sightings of sei and Bryde's whales recorded during the survey were used in this study. It was assumed that all the schools of sei and Bryde's whale within the 3 n.miles boundaries were sighted. We evaluated the pattern of spatial autocorrelation for each species using Moran's I. Moran's I provides a measure of similarity of 'presence' as a function of spatial distance between consecutive segments (in this case 4 km spatial resolution). Values of index range from −1 to +1, and indices close to zero suggest a random distribution (not be spatial autocorrelated).

Table 1. Summary of survey details for sighting data of sei whales and Bryde's whales.

Period	Total distance (n. miles)	Survey effort (n. miles)	No. of sightings (groups)	
			Sei whales	Bryde's whales
2004 May–August	10 609.54	3939.42	80 (53)	40 (35)
2005 May–August	9763.13	5082.41	360 (181)	15 (12)

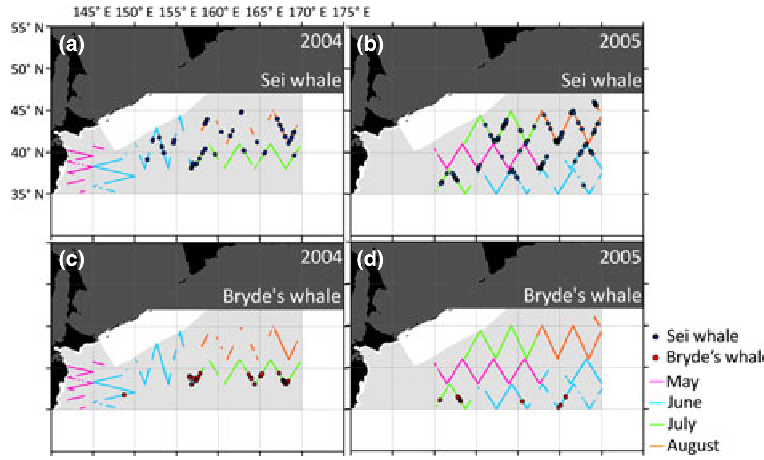

Figure 2. Tracklines and sighting points of the survey. (a) 2004 sei whales, (b) 2005 sei whales, (c) 2004 Bryde's whales, (d) 2005 Bryde's whales. Colored lines indicate the trackline for each month. Colored circles indicate locations of sighting points for each species.

Environmental data

Four types of environmental data were used to model the habitats of sei and Bryde's whales: sea surface temperature (SST; °C), sea surface chlorophyll *a* concentration (Chl-*a*; mg m^{-3}), sea surface height anomalies (SSHAs; cm), and depth (m) (Table 2).

Satellite-derived monthly mean SST data sets, NOAA/Advanced Very High Resolution Radiometer (AVHRR) Pathfinder version 5.0, were used in this analysis. The data were provided by the National Aeronautics and Space Administration (NASA)/Jet Propulsion Laboratory (JPL) Physical Oceanography Distributed Active Archive Center (PO-DAAC).

Monthly mean Chl-*a* data sets were derived from a satellite sensor Orbview-2/ Sea-viewing Wide Field-of-View Sensor (SeaWiFS), and used as an indicator of the concentration of primary producers. Specifically, global area coverage, monthly composite level-3 standard mapped image data were used.

The SSHA data were provided by the Maps of Sea Level Anomalies (MSLA)/Archiving, Validation and Interpretation of Satellite Oceanographic Data (AVISO) scientific team of Collecte, Localisation, Satellite (CLS)/Center National d'Etudes Spatiales (CNES) data center. The SSHA data were originally derived from the satellite sensors Topex/Poseidon, Jason-1, ENVISAT, and ERS altimeter. Because monthly mean SSHA data were not provided by the data center, monthly mean data were calculated using data from 7-day periods.

A depth data set, 2-minute Worldwide Bathymetry/Topography (ETOPO2), was provided by the NOAA/National Geophysical Data Center (NGDC). The data had a cylindrical projection and a spatial resolution of 2 min. Because the spatial resolutions and map projections of the four data sets were different, they were standardized using ARCGIS 9.2 (ESRI, Redlands, CA, USA). First, all data were converted to an equidistant cylindrical projection. Secondly, each data set was interpolated within ordinary kriging using the Geostatistical Analyst extension of ARCGIS. Finally, each data set was converted to a raster data set that had a spatial resolution of 4 km.

Table 2. Parameters for the generalized linear model (GLM).

Type	Parameter	Explanation	Unit
Dependent	$\pi(x_i)$	Probability of the presence of sei whales	
Independent	SST	Sea surface temperature	°C
	Chl-*a*	Chlorophyll *a* concentration	mg m^{-3}
	SSHA	Sea surface height anomaly	cm
	Depth	Depth	m

Summary statistics of selected environmental variables

To elucidate the distribution ranges of sei and Bryde's whales in response to four environmental variables (SST, Chl-*a*, SSHAs, and depth), summary statistics (mean, standard deviation, median, and interquartile range, IQR) were calculated. Environmental variables corresponding to sighting positions per month were extracted using ARCGIS.

Spatial modeling of potential habitats

A GLM was used to identify potential habitats of sei and Bryde's whales in the western North Pacific. In the model, a binary response variable *Y* (presence of sei whale equal to 1 and presence of Bryde's whale equal to 0) was estimated using four environmental variables (SST, Chl-*a*, SSHAs, and depth) as explanatory variables. As a prerequisite for our approach, when a sei or Bryde's whale was found, the presence of sei whales was defined as [$P(Y = 1)$] and that of Bryde's whale was defined as [$P(Y = 0)$]. The binary response variable is assumed to follow a binomial error distribution in the model. Formulae for the model were as follows:

$$\begin{aligned}\mathrm{logit}[P(Y=1)] &= \frac{P(Y=1)}{1-P(Y=1)} \\ &= \alpha + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 \end{aligned} \quad (1)$$

where $P(Y = 1)$ is the probability of presence of sei whales varying between 0 and 1; α is the intercept; x_i is the *i*-th explanatory variables, namely SST, Chl-*a*, SSHAs, and depth; and βi is the coefficient term for *i*-th explanatory variables.

The probability of occurrence for Bryde's whales was defined as:

$$P(Y = 0) = 1 - P(Y = 1) \quad (2)$$

Model selection was based on Akaike's information criterion (AIC; Akaike, 1974; Burnham and Anderson, 2010). The model with the lowest AIC value was taken to be the best model. We calculated AIC differences (ΔAIC) defined by the difference in AIC values between the best and other models. A ΔAIC of 0–2 is considered to demonstrate substantial empirical support and values of 4–7 indicate considerably less empirical support (Burnham and Anderson, 2010). For cases in which multiple models have ΔAIC of 0–2, substantial uncertainty exists in terms of which model is truly the best model. Therefore, we compared pairs of models from among the models that have ΔAIC of 0–2 using likelihood-ratio tests. The potential habitats of sei and Bryde's whales in each month from May to August were estimated using the selected best model. Maps of the estimated habitats were drawn using ARCGIS.

Identification of suitable habitats

Mean values for each environmental variable at the sighting positions of sei and Bryde's whales, with standard deviations, were calculated as suitable habitat ranges (Zainuddin *et al.*, 2008). If the selected environmental variables were within the suitable habitat range in a 4-km grid, the grid was defined as containing suitable habitat. In addition, we overlaid the 0.25 mg m^{-3} Chl-*a* contour as an indicator of the Transition Zone Chlorophyll Front (TZCF) in the western North Pacific. The TZCF is important for the migrations and foraging of large pelagic species (Polovina *et al.*, 2001; Polovina and Howell, 2005; Zainuddin *et al.*, 2008). We also investigated the probabilities that sei and Bryde's whales occurred in each suitable habitat area by overlaying the potential habitat map onto the suitable habitat map.

RESULTS

Summary statistics of environmental variables

Sei whales were distributed in areas with lower SST values and an IQR range of 13.1–16.8°C (mean: 15.5°C), whereas Bryde's whales were distributed in higher SST areas with an IQR range of 19.7–22.2°C (mean: 21.5°C) (*U*-test: $P < 0.001$; Fig. 3). Sei whales were distributed in higher Chl-*a* areas with an IQR range of 0.26–0.57 mg m^{-3} (mean: 0.50 mg m^{-3}) and Bryde's whales were distributed in lower Chl-*a* areas with an IQR range of 0.15–0.25 mg m^{-3} (mean: 0.22 mg m^{-3}) ($P < 0.001$; Fig. 3). These results show that sei whales tended to be distributed in areas with lower SST and higher Chl-*a* compared with Bryde's whales. IQR ranges for SSHA were narrower for sei whales (–3.00 to 3.59 cm, mean: –1.35 cm) than for Bryde's whales (–17.8 to 18.9 cm, mean: 3.85 cm, $P < 0.001$; Fig. 3). The distributions of sei and Bryde's whales were not different with respect to depth.

Spatial modeling of potential habitats

The result of Moran's I shows no evidence for significant autocorrelation for either of the species (Moran's I < 0.5). Therefore, we took no account of spatial autocorrelation in our approach. The model that included SST, SSHAs, and Chl-*a* had the lowest AIC value (Table 3, Model-1). However, Model-1 and Model-2 had similar AIC values, and they did not significantly differ based on the likelihood-ratio test. The only difference between the two models was whether the variable 'depth' was included (Model-2) or not (Model-1). A comparison of the depth between the two models using a *U*-test indicated no significant difference ($P > 0.05$). Furthermore, 'depth' was not significant in Model-2 ($P > 0.05$). Therefore, we selected Model-1 as the best model.

The order of significance for the variables in the model was [P(SST) < 0.0001, P(SSHA) < 0.05, P(Chl-*a*) = 0.07]. According to the AIC value, the best model with SST, SSHAs, and Chl-*a* was 110.9, whereas Model-3 (without Chl-*a*), Model-4 (without SSHAs), and Model-5 (without SST) were 2.60, 10.71, and 31.47 units higher, respectively (Table 3).

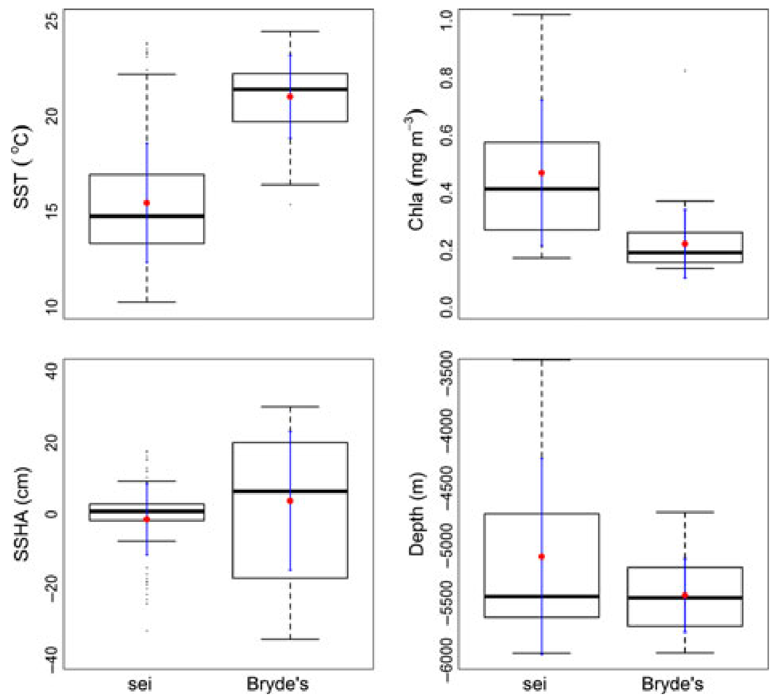

Figure 3. Boxplots of occurrences of sei and Bryde's whales as a function of sea surface temperature (SST; °C), sea surface chlorophyll *a* concentration (SSC; mg m^{-3}), sea surface height anomalies (SSHA; cm), and depth (m). The box is 25% and 75% quantile range, the upper and lower horizontal lines the 95% confidence limits, the center horizontal line the median, the red dot the mean, and the blue line the mean ± one standard deviation.

The order of effective variables, based on the AIC values, was SST, SSHAs, and then Chl-*a*.

The coefficients of the selected model indicated that SST and SSHAs had significant negative effects, whereas Chl-*a* had a significant positive effect on the spatial distribution of sei whales.

The potential habitats of sei and Bryde's whales were estimated spatially using the selected model (Fig. 4). The isoline for a 50% probability of occurrence is also provided in the figure as a habitat partitioning line (HPL) between sei and Bryde's whales. The HPL moved northward through the summer. In May, the HPL was around 35°N, and it moved to 40°–45°N in August in both 2004 and 2005.

Identification of suitable habitats

Suitable habitats for sei whales were located north of the suitable habitats for Bryde's whales throughout the survey season in both years (Fig. 5). The suitable habitats of both sei and Bryde's whales shifted northward as the season progressed. The rate of the shift was faster in 2004 than in 2005. Although suitable habitats for Bryde's whales were apparent regardless of month, suitable habitats for sei whales were obscure in May and June. In general, the boundary between the suitable habitats for the two species was wider in May and June and narrower in July and August, and sei whales were distributed north of the TZCF, whereas Bryde's whales were distributed south of it regardless of the month.

Probabilities of occurrence for sei and Bryde's whales within their suitable habitats are shown in Figure 6. Relatively high probabilities of occurrence were observed for sei whales in their suitable habitats. In contrast, probabilities of occurrence for Bryde's whales were relatively low within their suitable habitats, especially in May (Table 4). Probabilities of occurrence for Bryde's whales were high in the southern portion of their suitable habitat range in May, but the range moved northward as the season progressed. As a result, areas that had high probabilities of occurrence for sei and Bryde's whales were in close proximity in August.

DISCUSSION

The results of the GLM and basic statistics demonstrated that the habitats of sei and Bryde's whales are clearly separated with respect to oceanographic conditions. The habitats of sei whales were distributed to the north relative to the habitats used by Bryde's whales during the summer season in the western North Pacific. As suggested by Slijper (1965), habitat-use and migrations of cetaceans are limited by the supply of prey species. Gaskin (1982) also indicated the importance of cetacean foraging areas having continuous biological production and short timescale food chains. Some attempts were made to relate spatial distributions of cetaceans and their prey in the world (e.g. Friedlaender *et al.*, 2006; Laidre *et al.*, 2007; Torres, 2009; Skern-Mauritzen *et al.*, 2011; Murase *et al.*,

Table 3. Results of Akaike's information criterion (AIC)-based model selection for associations between the environmental variables and species (sei or Bryde's whales) with the value of coefficients. Models with substantial empirical support by AIC < 3.

Model	Coefficients (SE)									
	Intercept	SST	SSC	SSHA	Depth	*K*	AIC	ΔAIC	LRT	Residual deviance
1	+8.76 (2.58)***	−0.47 (0.11)***	+4.25 (2.36)*	−0.059 (0.018)***		3	110.90	0.00	–	102.90
2	+7.87 (3.06)**	−0.49 (0.12)***	+4.23 (2.32)*	−0.058 (0.018)***	−0.24 E–05 (−0.54 E–05)	4	112.70	1.80	0.66	102.70
3	+13.17 (1.89)***	−0.62 (0.095)***		−0.068 (0.018)***		3	113.50	2.60	0.03	107.50
4	+5.41 (2.03)**	−0.32 (0.080)***	+6.35(2.56)*			2	121.61	10.71	<0.001	115.61
5	−2.28 (0.70)**		+13.25 (2.77)***	−0.021 (0.014)		2	142.37	31.47	<0.001	136.37

SST, sea surface temperature; SSC, sea surface chlorophyll *a* concentration; SSHA, sea surface height anomaly; Depth, depth; *K*, number of variables in the model; ΔAIC, AIC difference; LRT, *P*-value of likelihood ratio tests. $*P < 0.1$, $**P < 0.05$, $***P < 0.01$.

2013). However, when prey data are not available at the time of a cetacean survey (as in the case of this study), statistical estimates of cetacean habitat suitability can be carried out using environmental data obtained from satellites and assuming relationships between prey species distributions and these environmental variables.

The sei whale IQR range for SST (13.1–16.8°C) was lower than that of the Bryde's whale (19.7–22.2°C) in this study. Based on the results of summer sighting surveys conducted in the western North Pacific from 1994 to 2003, sei whales were reportedly distributed in areas where the SST ranged between 8.0 and 25.0°C, whereas Bryde's whales were distributed in areas where the SST was higher than 20°C, although their distributions overlapped in areas where the SST was 20–25°C (Fujise *et al.*, 2004). Previously reported SST ranges (Ohsumi, 1977; Fujise *et al.*, 2004) largely overlap with the results of this study, although the SST ranges were narrower in the current results. The suitable SST ranges for sei and Bryde's whales could be related to the distributions of their prey species. Nemoto (1959) reported the prey species of these whales in order of preference (i.e., sei whale: copepods–krill–pelagic fishes–squids, Bryde's whale: krill–pelagic fishes–copepods) and classified the sei whale as a copepod feeder and Bryde's whale as a krill and fish feeder. Konishi *et al.* (2009) also indicated that the composition of prey in the stomachs of sei and Bryde's whales varied geographically. Based on the same survey during 2000–2007, 56.4% of the stomach contents of sei whales consisted of copepods and krill. On the other hand, 54.7% of the stomach contents of Bryde's whales consisted of Japanese anchovy (*Engraulis japonicus*) (Konishi *et al.*, 2009). Small anchovy tended to occur in areas with high SST, whereas large individuals tended to occur in low-SST areas (Murase *et al.*, 2012). Sei whales tend to feed on large anchovy individuals, whereas Bryde's whales tend to feed on smaller individuals (Konishi *et al.*, 2009). In our study, the SST IQR ranges of sei and Bryde's whales were clearly divided, with the SST range for Bryde's whales being higher (median: 21.4°C) than that of sei whales. The difference in the body length of Japanese anchovies in the stomachs of sei and Bryde's whales reflects the difference in their spatial distributions with respect to SST.

The difference in the SSHA range between sei and Bryde's whales could also indicate differences in their prey. SSHA is an index of water mass and current. The Kuroshio Extension region has the highest level of eddy variability in the North Pacific Ocean, whereas the Oyashio area has a low level (Qiu, 2001). Sei

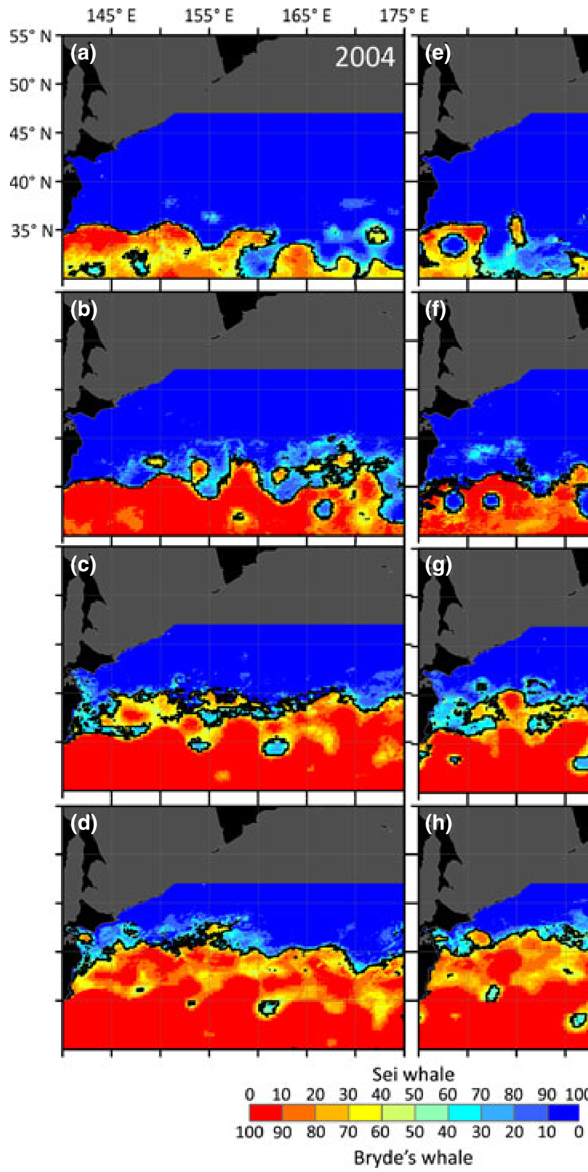

Figure 4. Probabilities of cetacean occurrence in 2004 and 2005. (a) 2004 May, (b) 2004 June, (c) 2004 July, (d) 2004 August, (e) 2005 May, (f) 2005 June, (g) 2005 July, and (h) 2005 August. Colors from blue to red indicate the probability of occurrence and which species can be found (sei or Bryde's whales). The black line indicates a probability of 50%.

whales tended to be distributed in areas within a narrow SSHA range (Fig. 3) where low variability in SSHAs was observed. Bryde's whales tended to occur in areas with large anomalies (Fig. 3) and were distributed throughout the Kuroshio and Kuroshio Extension areas. The Kuroshio and the Kuroshio Extension carry eggs and larvae of small pelagic fishes, such as Japanese sardine and anchovy, into the offshore transition area, where biological productivity is high (Odate, 1994). In contrast, zooplankton, such as krill and copepods, tend to concentrate just outside of eddies, such as in areas with low variability in SSHAs. Sei and Bryde's whales fed on krill in the western North Pacific regardless of location and SST (Konishi *et al.*, 2009). Many krill species are distributed in the western North Pacific (Brinton, 1962) and their distribution patterns are related to oceanographic conditions (Letessier *et al.*, 2011). Copepodite stage 5 (C5) of *Neocalanus* spp. is the most common copepod in sei whale stomachs (Konishi *et al.*, 2009). *Neocalanus* spp. is distributed around the subarctic North Pacific (Mackas and Tsuda, 1999). Nagasawa *et al.* (2001) reported that the highest abundance of *Neocalanus* spp. was found at around 40°–45°N in the southern subarctic North Pacific in summer. Differences in habitat-use by prey species partially explain why sei and Bryde's whale were distributed in areas with different SSHA conditions.

Sei and Bryde's whales were found in areas with Chl-*a* ranges of 0.26–0.57 and 0.15–0.25 mg m^{-3}

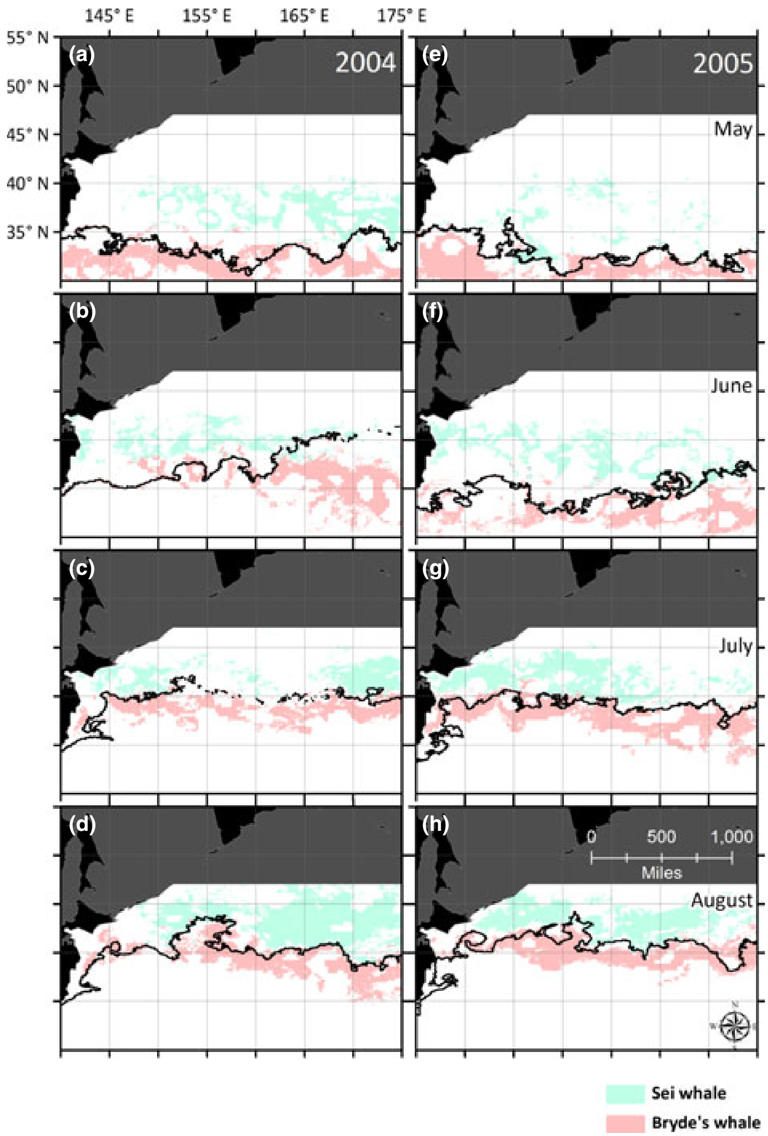

Figure 5. Suitable habitats calculated using boxplots and Transition Zone Chlorophyll Front in 2004 and 2005. (a) 2004 May, (b) 2004 June, (c) 2004 July, (d) 2004 August, (e) 2005 May, (f) 2005 June, (g) 2005 July, and (h) 2005 August. The green area indicates suitable habitats for sei whales and the pink area denotes suitable habitats for Bryde's whales. The black line represents the Transition Zone Chlorophyll Front.

Table 4. Averaged probabilities of the occurrence (%) of each species in areas of suitable habitat.

		Probability (SD)			
Species	Year	May	June	July	August
Sei whales	2004	95 (4.8)	94 (5.9)	95 (4.4)	96 (4.5)
	2005	94 (6.5)	96 (5.0)	96 (4.3)	95 (4.8)
Bryde's whales	2004	59 (16)	55 (19)	61 (20)	64 (19)
	2005	56 (15)	68 (18)	57 (18)	60 (20)

(Fig. 3), respectively. The boundary between their habitats was around 0.25 mg m^{-3} Chl-*a*. Polovina *et al.* (2001) reported that Chl-*a* values for the subarctic gyre and the Transition Zone, and the subtropical gyre, were >0.25 and <0.15 mg m^{-3}, respectively. Accordingly, at the study site, sei whales were mainly distributed in the subarctic gyre and the Transition Zone, whereas Bryde's whales were mainly found in the subtropical gyre. These two water masses were separated by a sharp chlorophyll front with a Chl-*a* of 0.25 mg m^{-3} that spans the North Pacific. The chlorophyll front is well known and is termed the TZCF (Polovina *et al.*, 2001; Polovina and Howell, 2005) and is important for the migration and foraging habitats of large pelagic species. The TZCF is defined by a 0.2 mg m^{-3} Chl-*a* contour in the eastern North Pacific, and Zainuddin *et al.* (2004, 2008) suggested that a Chl-*a* of 0.3 mg m^{-3} is an important proxy for albacore (*Thunnus alalunga*) in the western North Pacific. The TZCF can be assumed to be located around these

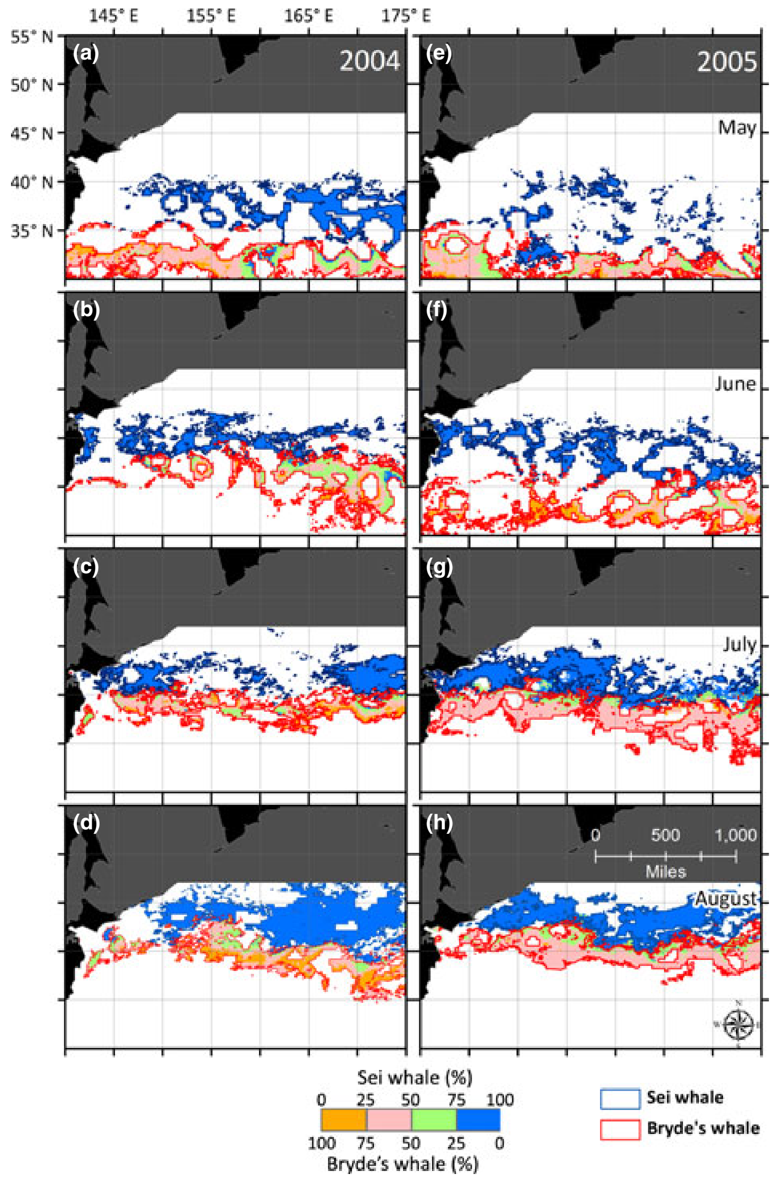

Figure 6. Probabilities of cetacean occurrence by species in suitable habitats in 2004 and 2005. (a) 2004 May, (b) 2004 June, (c) 2004 July, (d) 2004 August, (e) 2005 May, (f) 2005 June, (g) 2005 July, and (h) 2005 August. Colors indicate the probability pattern of cetacean occurrence. The blue line represents the form of suitable habitat for sei whales, and the red line represents suitable habitat for Bryde's whales.

values. In this study, a 0.25 mg m^{-3} Chl-*a* contour (similar to the definition of the TZCF) provided a good indicator that separated the habitats of sei and Bryde's whales. TZCF may also play a role as a proxy for cetacean habitats.

Ocean depth was not selected as a covariate based on AIC values in this study. In the past, important relationships have been found between cetacean habitats and topography (Gaskin, 1982; Keiper *et al.*, 2005; Morato *et al.*, 2008). The data used in this study were recorded offshore, at depths of 4000–5000 m. The magnitude of the relationship between depth and cetacean distribution could depend on the area of interest. The exception in this study area was the Emperor Seamount. Although no quantitative analysis was conducted, observed densities of sei whales were high around the Emperor Seamount compared with other regions in the study area. The relationship between sei whales and depth might be important if one focused on the area around the Emperor Seamount.

As already discussed, we deduced the oceanographic conditions in whale habitats and found a clear division between the suitable habitats that were determined for the two whale species (Fig. 3). Although the extent of suitable habitat differed depending on the season, the suitable habitats of sei whales were located north of the habitats of Bryde's whales

(Fig. 5). The potential habitat map also indicated that the northern area had a high probability of occurrence for sei whales and the southern area had a high probability of occurrence for Bryde's whales. The habitats of sei and Bryde's whales were distributed in different environments and clear habitat partitioning was observed in the western North Pacific during the summer (May–August) in 2004–2005. Although the magnitude of the difference changed depending on the season, the HPL moved northward as the summer progressed. Therefore, we could quantitatively determine that their habitats moved northward with seasonal changes in oceanographic conditions. Because the SST contributed strongly to the habitat-use patterns, this transition was mainly coupled with the SST. Furthermore, our results support a previous hypothesis that the SST plays an important role in defining whale habitats (Kaschner *et al.*, 2006, 2011; MacLeod, 2009).

Sei whales had higher probabilities of occurrence in their suitable habitats compared with Bryde's whales (Table 4, Fig. 6). Early in the summer, Bryde's whales could still be found in the southern portion of the survey area because the oceanographic conditions in the survey area were not suitable. After overlaying the survey tracklines on the potential habitat map, most of the tracklines were clearly set around the area of highest probability for the occurrence of sei whales (Figs 2 and 4). In contrast, little survey effort was allocated to areas with a high probability of occurrence for Bryde's whales. In 2004–2005, quantifying the primary habitat of Bryde's whales was difficult due to the lack of appropriate data for modeling. Consequently, the probability of sighting a Bryde's whale was low. Originally, Bryde's whales were distributed in lower-latitude areas, but almost all of them migrated seasonally (Fujise *et al.*, 2004; Kato and Perrin, 2009). The addition of data from the southern portion of the survey area in the early summer could improve the modeling results.

In our analysis, it was assumed that all the schools of sei and Bryde's whales were sighted (perfect detection). Imperfect detection (not all animals are sighted) is a common problem in wildlife sampling, although it has only recently been considered in the studies of species occurrence (Royle and Dorazio, 2008). It is expected that detection probability decreases with increasing distance from the trackline (Thomas *et al.*, 2010). Double-platform line transect data are widely used to estimate the probability of detection on the trackline g(0) of cetaceans (Okamura *et al.*, 2003). However, because no such data were collected during our survey, estimation of g(0) could not be carried out. Consideration of imperfect detection in modeling of occurrence of cetacean is required in future studies.

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