

SC/F16/JR/8

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## Distribution of sei whales (*Balaenoptera borealis*) in the subarctic–subtropical transition area of the western North Pacific in relation to oceanic fronts



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## ARTICLE INFO

Available online 22 May 2014

## Keywords:

Baleen whale  
Cetacean  
Habitat  
Ocean front  
Oceanography  
Kuroshio Extension Front  
Kuroshio Bifurcation Front  
Subarctic Front  
Polar Front

## ABSTRACT

The subarctic–subtropical transition area of the western North Pacific is an important summer feeding grounds of sei whales. The oceanographic structure and circulation of this area are largely determined by strong oceanic fronts and associated geostrophic currents, namely the Polar Front (PF), Subarctic Front (SAF) and Kuroshio Extension Front (KEF). The relationship between the distribution of sei whales and oceanographic fronts was investigated using a generalized additive model (GAM), and the cetacean sighting survey data and oceanographic observations in July from 2000 to 2007 were used in the analysis. The number of individual sei whales was used as the response variable while the distances from the PF, SAF, and KEF to the whales were used as explanatory variables along with the longitude values. Sei whales were concentrated north and south of the SAF and the areas from 250 to 300 km north and from 100 to 200 km south of the SAF were estimated as high-density areas of sei whales. The entire inter-frontal zone between the PF and SAF featured an elevated concentration of sei whales, and the area south of the PF and along the SAF was identified as an important feeding ground of sei whales in July from 2000 to 2007.

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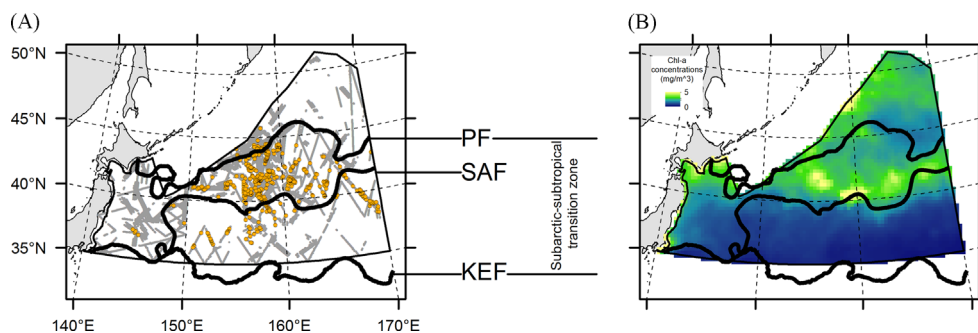
## 1. Introduction

An ocean front can be defined as a relatively narrow zone of enhanced horizontal gradients of physical, chemical and biological properties that separates broader areas of different vertical structures occurring at a variety of dimensional (hundreds of meters to thousands of kilometers) and time (short lived to year round) scales (Belkin et al., 2002). Many studies have quantitatively investigated the relationship between the spatial distribution of baleen whales and ocean fronts with the expectation that cetaceans were attracted to ocean fronts with high biological productivity to search for prey. Simultaneous recordings of the spatial distributions of baleen whales and their prey have been attempted (Murase et al., 2002; Tynan et al., 2005; Friedlaender et al., 2006; Laidre et al., 2010; Santora et al., 2010; Friedlaender et al., 2011; Skern-Mauritzen et al., 2011; Murase et al., 2013). However,

because such a practice faces logistical challenges, ocean fronts are used in other studies as indicators of the presence of prey. The relationship between the spatial distribution of baleen whales and sea surface thermal fronts detected by satellite remote sensing data (generally up to 10 km grid cell resolution) were widely investigated and included fin (*Balaenoptera physalus*), minke (*Balaenoptera acutorostrata*) and humpback whales (*Megaptera novaeangliae*) in the mid-western North Atlantic Ocean (Hamazaki, 2002), blue (*Balaenoptera musculus*), fin, humpback and minke whales in the Gulf of St. Lawrence (Doniol-Valcroze et al., 2007), blue whales off the Baja California Peninsula (Etnoyer et al., 2006), fin whales in the Mediterranean Sea (Cotté et al., 2011; Druon et al., 2012) and humpback whales in the coastal waters of British Columbia and adjacent areas (Dalla Rosa et al., 2012). The relationship with coastal upwelling fronts was also investigated and included humpback whales in the northern California Current System (Tynan et al., 2005) and bowhead whales (*Balaena mysticetus*) off Alaska (Okkonen et al., 2011). The relationship between the spatial distribution of grey whales (*Eschrichtius robustus*) and in-situ measured fronts was investigated in the south-central Chukchi Sea

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**Fig. 1.** The survey area (thin black line), surveyed tracklines (gray line) and sighting positions of sei whales (orange circle) from 2000 to 2007 (A). The mean sea surface chlorophyll a (Chl-a) concentrations in July from 2000 to 2007 (B). The locations of three major oceanic fronts – the Polar Front (PF), Subarctic Front (SAF) and Kuroshio Extension Front (KEF) – and the subarctic–subtropical transition zone are shown in (A) and (B). The Level 3 monthly mean Chl-a data (4 km resolution) obtained by SeaWiFS (Feldman and McClain, 2008) were used in (B).

(Bluhm et al., 2007). However, quantitative investigations of the relationship between the spatial distribution of baleen whales and basin scale oceanic fronts have rarely been conducted except in the Southern Ocean (Bost et al., 2009; Ainley et al., 2012; Santora and Veit, 2013).

In the Northwest Pacific Ocean east of Japan, three major oceanic fronts have been known for a long time: the Polar Front (PF), Subarctic Front (SAF), and Kuroshio Extension Front (KEF) (Science Council of Japan, 1960). This pattern has been confirmed by numerous studies (Kitano, 1972; Roden et al., 1982; Belkin and Mikhailichenko, 1986; Miyake, 1989; Belkin et al., 1992; Yoshida, 1993; Onishi, 2001; Belkin et al., 2002; Shotwell et al., 2014) (Fig. 1). The KEF tends to bifurcate in the vicinity of the Shatsky Rise, which is located at approximately 35°N and 160°E; its northern branch (sometimes called the Secondary Kuroshio Front, SKF) extends to approximately 40°N, where it joins the SAF. The SKF was noted in earlier studies as being related to the SAF (Kawai, 1972; Roden et al., 1982; Mizuno and White, 1983; Yoshida, 1993). Therefore, at least two bifurcations of the Kuroshio front have been reported: one at a short distance east of Japan (west of 150°E) and another upstream of the Shatsky Rise (at approximately 155°E) and the term “Kuroshio Bifurcation front (KBF)” is ambivalent and not used in this paper.

The area between the PF and KEF is called the subarctic–subtropical transition (interfrontal) area of the western North Pacific and is also called the Kuroshio–Oyashio transition area. The nutrients supplied by cyclonic eddies in the transition area support high primary production and high secondary production (Olson, 2001; Yatsu et al., 2013; also see Fig. 1). Small pelagic fish species such as the Japanese sardine (*Sardinops melanostictus*) and anchovy (*Engraulis japonicas*) in the transition area (Murase et al., 2012) are transported from the spawning ground on the coastal side of the Kuroshio by the Kuroshio extension (Itoh et al., 2009). Piscivore species such as skipjack tuna (*Katsuwonus pelamis*) (Nihira, 1996) and baleen whales (Murase et al., 2007) feed on the small pelagic fish in the area and a wide variety of species are distributed in the area (Percy et al., 1996).

Sei whales (*Balaenoptera borealis*) are the third largest baleen whales and typically reach 15 m of body length, weigh 20 t and are distributed in temperate and high-latitude oceanic waters of both hemispheres (Horwood, 1987; Horwood et al., 2009). In the western North Pacific, previous feeding ecology studies using stomach contents obtained by commercial whaling indicated that sei whales utilized the subarctic–subtropical transition area as their feeding grounds in the summer (Mizue, 1951; Nemoto, 1957; Kawamura, 1982). The distribution of commercial catch positions of sei whales in relation to the sea surface temperature (SST) fronts off the coast of Japan were also studied qualitatively (Uda, 1954; Uda and Dairokuno, 1957; Uda and Suzuki, 1958; Nasu, 1966). The

commercial harvesting of sei whales has been banned since 1976. The initial population level of sei whales in the North Pacific was estimated to be between 58,000 and 82,000 individuals (Ohsumi et al., 1971). These whales have been heavily exploited by commercial harvesting, and the population was depleted to 8,600 individuals in 1974 (Tilman, 1977). An assessment of the population has not been conducted since then. Studies on sei whales have rarely been conducted since the ban of commercial whaling because of data scarcity (Prieto et al., 2012).

Recently, results of studies on sei whales using data obtained by the second phase of the Japanese Whale Research Program under Special Permit in the western North Pacific (JARPNII) from 2000 to present have been reported. The survey area of JARPNII is located in the transition area. Konishi et al. (2009) and Watanabe et al. (2012) reported that sei whales mainly fed on euphausiids, copepods, and Japanese anchovy in the survey area. The distribution of sei whales in the survey area in relation to environmental variables that are derived from satellite remote sensing data such as the SST, chlorophyll-a concentration (Chl-a) and sea surface height anomaly (SSHa), and the depth were also investigated by a generalized linear model (GLM). The results suggested that the order of effective variables for the distribution of sei whales were SST, SSHA, Chl-a (Sasaki et al., 2013). The study reported that sei whales were distributed in an interquartile range of 13.1–16.8 °C with a mean value of 15.5 °C. The results of canonical correspondence analysis (CCA) analysis indicated that SST was one of the most significant variables for describing the distribution of sei whales (Konishi et al., 2009).

The relationship between the spatial distribution of sei whales and oceanographic conditions was also quantitatively investigated in other regions of the world. Long-term surface temperature data were used as a covariate in a GLM to predict the habitat of sei whales in the waters of coastal British Columbia (Gregg and Trites, 2001). Although temperature was selected in the model, the explicit relationship was not mentioned in the paper. The spatial distribution of sei whales at small scale (1–20 km<sup>2</sup>) along the Mid-Atlantic Ridge was related to the ocean flow gradients interacting with the steep topography (Skov et al., 2008), and a PLS regression and Ecological Niche Factor Analysis (ENFA) were used in the analysis. To date, however, the relationship between the distribution of sei whales and basin scale oceanic fronts has not been studied quantitatively.

In this paper, the current distribution of sei whales in the western North Pacific in relation to basin scale oceanic fronts is studied quantitatively. Specifically, the relationship between the number of sei whales and their distance to three subsurface fronts, the PF, SAF and KEF, is investigated by using a generalized additive model (GAM). Because the GAM is a non-parametric, regression technique not restricted by linear relationships, it is flexible enough to model relationships between the spatial distribution

of biological organisms and variables describing their environments (Murase et al., 2009).

The spatiotemporal scale of the feeding ecology of cetaceans can be defined as follows: at the macro scale, cetaceans migrate seasonally (months) between feeding and breeding grounds (> 1,000 km); at the meso scale, cetaceans move over days and weeks in search of a preferred local (> 100 km) abundance of food; at the micro scale, whales dive and search for food within localized areas (> 10 km) within hours (IWC, 2003) and at the nano scale, whales attack a prey patch in their proximity within minutes. The focus of this paper is from the macro to meso scales.

## 2. Materials and methods

### 2.1. Cetacean sighting survey data

The cetacean sighting surveys were conducted in the western North Pacific in July from 2000 to 2007 as part of JARPNII (Fig. 1). The southern, northern, eastern and western boundaries of the survey area were 35°N, the boundary of the economic exclusive zone (EEZ) claimed by countries other than Japan, 170°E and the eastern coast line of Japan, respectively. Six survey vessels were engaged in the cetacean sighting surveys from 2000 to 2007 and their specifications were similar. Their gross tonnages were approximately 1,000 GT with two main observation platforms: top barrels were set at 20 m above the sea surface and upper bridges were set at 10 m above the sea surface. Three observers at each observation platform using 7 × 50 binoculars were engaged in the sighting surveys. Sightings within 5.6 km ( $\approx 3$  nautical miles, nm) from the survey tracklines were counted. The survey vessels steamed at 19.5 km/h ( $\approx 10.5$  knots) along the survey tracklines during the survey hours and the survey was conducted during the daytime from 1 h after sunrise to 1 h before sunset. Surveying was stopped when the visibility was < 3.7 km ( $\approx 2$  nm) and/or sea state > 4 on the Beaufort wind force scale.

Activities aboard the ship were classified into two categories: on-effort and off-effort. On-effort activities were times when a full search effort was executed within acceptable conditions to conduct research. Off-effort activities were all times that were not on-effort and were not used in the analysis. All sightings recorded during on-effort activities were classified as primary-sightings. All other sightings were considered secondary sightings. On-effort surveys were conducted in the closing and passing mode; the survey vessels approached all sightings during the closing-mode to confirm the species and number of individuals in a school, and all sightings during the passing-mode were not approached although the species and estimated number of individuals in a school were recorded. As single year survey could not cover the entire survey area, so the data collected during on-effort activities in July from 2000 to 2007 were pooled in the analysis.

### 2.2. Oceanographic data

The subsurface water temperature and salinity data were obtained by conductivity-temperature-depth (CTD) profilers (CTD), expendable CTD (XCTD) and the Argo profiling floats. The CTD (SBE-19, Sea-Bird Electronics, USA) and XCTD (Tsurumi Seiki Co., Japan) data were obtained at 158 and 10 stations, respectively, in the JARPNII survey area from 2001 to 2007. The data from the Argo profiling floats that were prepared by Oka et al. (2007) and obtained at 3,913 locations north of 30°N from 2001 and 2007 were used. The data from 2001 to 2007 were pooled in the analysis because the oceanographic observations in a single year could not cover the entire survey area. The PF is defined as a 4 °C isotherm at 100 m depth (Favorite et al., 1976), the SAF is defined

as a 6 °C isotherm at 300 m depth (Mizuno and White, 1983), and the KEF is defined as a 14 °C isotherm at 200 m depth (Kawai, 1969). To locate the positions of the PF, SAF and KEF, water temperature maps at 100, 200 and 300 m depths were estimated by ordinary kriging with the aid of the geographic information system (GIS), ArcGIS 10.1 (ESRI, USA).

### 2.3. Modeling the relationships between whales and oceanic fronts

The relationship between the density of sei whales and distance from the oceanic fronts was investigated on a 30 × 30 km grid cell. The nearest distance from the oceanic fronts to the center of each grid cell within the survey area was calculated by using the “Near” tool of ArcGIS. The distance was a positive value if the grid cells were located north of the fronts and negative if the cells were located to south. Distances from the oceanic fronts to each grid cell were used as explanatory variables in the model. Longitude was also used as an explanatory variable under the premise that the oceanic fronts might not capture the longitudinal heterogeneity of the distribution of whales because they were located in a direction parallel with the lines of latitude.

The number of individual sei whales in each 30 × 30 km grid cell was used as a response variable, and the following procedures were conducted to estimate the number of individuals. Sighting effort data were divided first into 1 km segments, and then these segments were pooled in each grid cell ( $d$ ). Schools of sei whales were also pooled in each grid cell ( $n$ ). To estimate the number of sei whales in each grid cell, the effective search width ( $esw$ ) and mean school size ( $E(s)$ ) were estimated based on the multiple-covariate distance sampling method (Thomas et al., 2010). The  $esw$  and  $E(s)$  were estimated for the entire area (not just in each cell) using all sighting data because a sufficient number of sightings (e.g., more than 15 sightings) were generally required to obtain reliable estimates (Branch and Butterworth, 2001). A hazard rate model with no adjustment terms was used as a detection function model in the method. The surveyed years and the vessels were used as the covariates. It was assumed that the probability of detection of whales on the track line was 1 ( $g(0)=1$ ). Double-platform line transect data are widely used to estimate  $g(0)$  of whales (Okamura et al., 2003). However, because no such data were collected during the survey, the estimation of  $g(0)$  could not be carried out. It was reported that  $g(0)$  of Bryde’s (*Balaenoptera edeni*) and sei whales in the California Current ecosystem was 0.921 (Barlow and Forney, 2007). Therefore, the  $g(0)$  in this study could also be less than 1, but the effect on the estimated number of sei whales was not substantial. The number of individuals in a grid cell was first calculated by the density  $(n \times E(s))/(d \times 2 \times esw)$ , and then it was multiplied by area of a grid cell.

The relationship between the spatial distribution of sei whales and, the studied oceanographic fronts and longitude was modeled using GAM having a Tweedie error distribution with a logarithmic link function, which was similar to the method used by Williams et al. (2011). A Tweedie random variable with  $1 < p < 2$  is a sum of  $N$  gamma random variables in which  $N$  has a Poisson distribution (Wood, 2013). If  $p$  equals 1, then it is a generalization of a Poisson distribution and a discrete distribution supported on integer multiples of the scale parameter. If  $p$  is larger than 1 and smaller than 2 ( $1 < p < 2$ ), then the distribution is supported on the positive reals with a point mass at zero. If  $p$  equals 2, then it is a gamma distribution. In this analysis,  $p$  is set as 1.1. The smoothness parameters were estimated with the generalized cross-validation (GCV). For this analysis, the mgcv package (Wood, 2006) version 1.7–26 of the R software version 3.0.2 (R Development Core Team, 2013) was used. The shapes of the functional forms for the all covariates were also plotted by using the package. When the slopes of the functional forms were



positive, the covariates were related positively to the response variable, and vice versa. Collinearity among explanatory variables in the model could lead to the wrong identification of relevant predictors (Dormann et al., 2012). The collinearity was investigated by the variance inflated factor (VIF) using AED package (Zuur et al., 2009) working under R software version 2.15.0.

### 3. Results

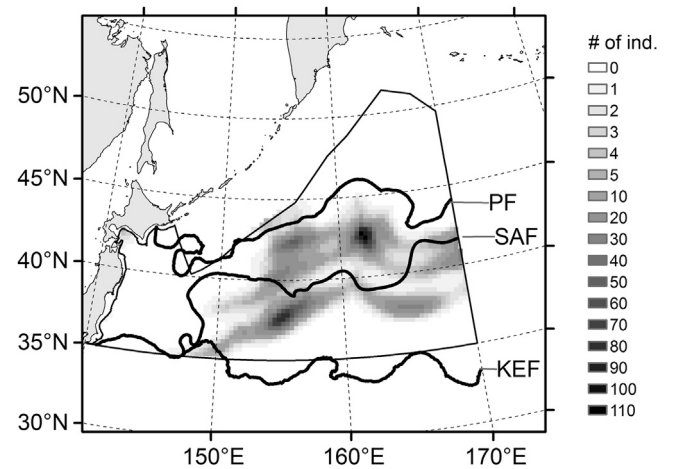
A total of 483 schools of sei whales during 56,450 km of sighting efforts recorded from 2000 to 2007 were used in the analysis. The number of grid cells used in the GAM was 1,441. The  $esw$  and  $E(s)$  were estimated as 3.39 km ( $\approx 1.83$  nm) and 1.83 individuals, respectively. The values of VIF and results of the GAM modeling are shown in Table 1. The collinearity among explanatory variables was considered minimal because the values of VIF were less than 10, although no specific rule to determine an acceptable level of collinearity based on the VIF has been reported. The approximate significance levels suggested that all covariates in the model were significant and had  $p$ -values lower than 0.01.

**Table 1**

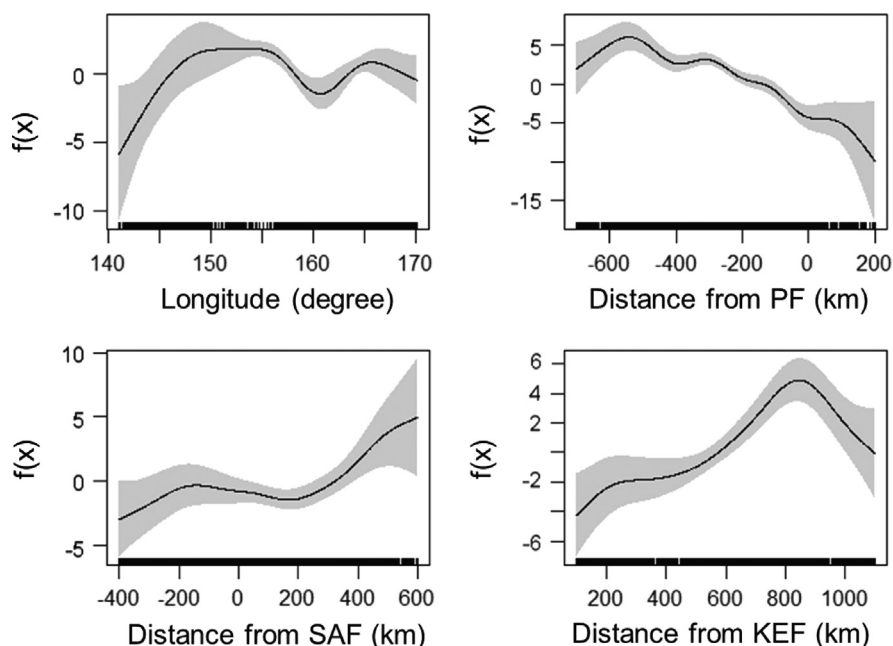
Results of a generalized additive model (GAM) to detect the relationship between the spatial distribution of sei whales and distance from oceanic fronts (PF=Polar Front, SAF=Subarctic Front and KEF=Kuroshio Extension Front) and longitude. The approximate significance levels ( $p$ -value),  $F$  statistics ( $F$ ) and estimated degrees of freedom (edf) are shown for each of the explanatory variables. The values of the variance inflated factor (VIF) for each explanatory variable are also shown.

Family	Tweedie			
Link function	Log			
Adjusted $R^2$	0.09			
Deviance explained (%)	44.9%			
GCV score	12.85			
	edf	$F$	$p$ -Value	VIF
<i>Explanatory variables</i>				
Longitude	7.18	17.20	< 0.01	3.16
Distance from PF	8.61	21.76	< 0.01	4.34
Distance from SAF	6.84	4.82	< 0.01	4.54
Distance from KEF	7.62	10.06	< 0.01	7.82

The shape of the functional response forms for the longitude indicated that the number of sei whales was low in the western part of the survey area (Fig. 2). The shape was relatively flat east of 150°E, except in a small depression at approximately 160°E. The shape of the functional response form for the distance from the PF indicated that the number of sei whales decreased from the south to north of the PF. The shape of the functional response form for the distance from the SAF indicated that the number of sei whales increased from the south to north of the SAF, with a small peak to the south at approximately 200 km from the SAF. The shape of the functional response form for the distance from the KEF indicated that the number of sei whales increased to north of the KEF. These results suggested that the number of sei whales was high in the area south of the PF and along the SAF west of 150°E. The results clearly depicted in the map of estimated spatial distributions of the sei whales using the model (Fig. 3). Specifically, the estimated number of sei whales was high in the areas from 250 to 300 km



**Fig. 3.** The estimated distribution patterns of the number of individual sei whales obtained by using a generalized additive model (GAM). The locations of the Polar Front (PF), Subarctic Front (SAF) and Kuroshio Extension Front (KEF) are also shown.



**Fig. 2.** Smoothed fits of selected covariates modeling the number of individuals of sei whales. Tick marks on the x-axis are the observed data points. The y-axis represents the contribution of the smoother to the fitted values, and shaded areas indicate the 95% confidence bounds. PF=Polar Front, SAF=Subarctic Front and KEF=Kuroshio Extension Front.

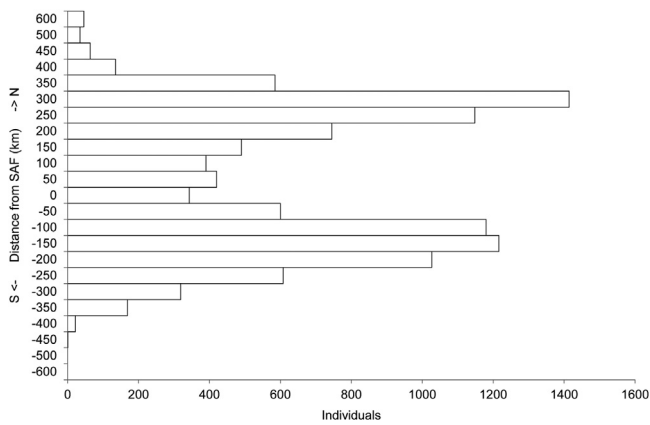


Fig. 4. The estimated number of individual sei whales in relation to the distance from the Subarctic Front (SAF).

north and 100 to 200 km south of the SAF (Fig. 4). Few sei whales were sighted north of the PF and west of the SAF.

#### 4. Discussion

This study revealed that the area south of the PF and along the SAF were important distribution areas of sei whales in the western North Pacific in July from 2000 to 2007. It was qualitatively reported that the distribution of sei whales and the sub-polar front (SPF) were related along the Mid-Atlantic Ridge (Skov et al., 2008). Similar relationships between baleen whales and oceanic fronts were reported in the Southern Ocean (Bost et al., 2009; Ainley et al., 2012; Santora and Veit, 2013). However, this is the first study that reports quantitative relationship between baleen whales and the basin scale oceanic fronts of the North Pacific. Interestingly, the abundance of sei whales was low near the SAF (i.e., within 100 km from the SAF), and a high abundance was observed in the areas from 250 to 300 km north and 100 to 200 km south of the SAF. We conducted the same analysis at the scale of a  $10 \times 10$  km grid cell and observed almost the same bimodal distribution pattern (not shown). The distribution pattern did not appear to be sensitive to the scale of the grid cells. It can be hypothesized that the bimodal distribution of sei whales along the SAF was linked to the distribution of their prey species. A study on the feeding ecology of sei whales that was conducted in the same area and time period (2000–2007) as this paper suggested that their main prey were copepods (*Neocalanus* spp.), euphausiids and Japanese anchovy and suggested that sei whales fed on Japanese anchovy in the western part of the survey area where the SST was higher and on copepods in the eastern part where the SST was lower (Konishi et al., 2009). Japanese anchovy spawn along the coastal side of the Kuroshio in spring and summer and the eggs and larvae are transported to the transition area by the Kuroshio extension (Aoki and Miyashita, 2000; Itoh et al., 2009), although it has been reported that Japanese anchovy also spawn offshore (Funamoto and Aoki, 2002). In contrast, high densities of krill (*Euphausia pacifica*) (Tojo et al., 2010) and *Neocalanus* spp. (Kobari, 1999) were observed south of the PF. Two high density areas of sei whales north and south of the SAF could reflect the distribution of their prey species. Although a high abundance of sei whales was observed bimodally across the SAF, their distribution was continuous. The result of the satellite tracking of a sei whale in the North Atlantic showed that the mean travelled distance per day was 90 km (Olsen et al., 2009) indicating that sei whales could move between the bimodal distribution areas within a few days. Furthermore, a study of the genetic characteristics of sei whales

conducted in the same area and within the same period of this paper showed that a single population of sei whales inhabited the western North Pacific (Kanda et al., 2006). These results precluded that the bimodal distribution of sei whales observed in this study could result from the existence of two distinct populations.

Both climatic and biological regime shifts have occurred in the North Pacific Ocean (Hare, 2000; Yatsu et al., 2001; Mantua, 2004; Overland et al., 2008). The relationship between the distribution of sei whales and oceanic fronts was investigated in this paper by using pooled data from 2000 to 2007. A regime shift was not reported as occurring during this period; therefore, the results of this paper can be considered fairly representative of the state of the ocean during this time at the macro to meso scale. However, it is obvious that the analysis overlooked the spatiotemporal relationship at the micro to nano scale. Furthermore, environmental factors other than distances from the oceanic fronts were not considered in this paper according to the editorial policy of this special issue. The observed bimodal distribution of the high abundance of sei whales across the SAF might reflect a year to year change of their environment at the micro and nano scales. Energetic jets (streamers) (Isoguchi et al., 2006) and meso scale eddies (Itoh and Yasuda, 2009) associated with the oceanic fronts in the transition area were reported. Sasaki et al. (2013) found that the spatial distribution of sei whales in the western North Pacific was related to the SST, Chl-a and SSHa at the 4 km grid cell resolution using monthly mean satellite remote sensing data. It was also well documented that the distribution of other baleen whale species were associated with meso to micro scale SST fronts (Hamazaki, 2002; Tynan et al., 2005; Doniol-Valcroze et al., 2007; Cotté et al., 2011; Dalla Rosa et al., 2012; Druon et al., 2012). A satellite tagging study of one sei whale indicated that its movement at the micro scale was associated with surface current patterns in the North Atlantic (Olsen et al., 2009). It was also reported that the distribution of sei whales was related to micro scale (1 to 20 km) frontal processes (Skov et al., 2008). The distribution of the prey of sei whales might be related to such meso to macro scale oceanographic conditions. For instance, the relationship between the vocalization rate of sei whales and vertical migration of copepods were reported in the southwestern Gulf of Maine at a scale of 10 km (Baumgartner and Fratantoni, 2008). The inclusion of prey data as an explanatory variable of the model might produce more insight into the spatial prey-predator relationship at the meso to micro scale. No nano scale behavior of sei whales has been reported. The observation of nano scale behavior of sei whales in relation to their environment using a data logger such as a high-resolution digital tag (Goldbogen et al., 2008) is warranted, and the integration of studies from the macro to nano scales is required to understand the detailed processes involved in the spatial distribution of sei whales.

In the past, the main whaling grounds of sei whales were located north of the survey area studied in this paper. In particular, high densities of sei whales were observed south of the Aleutian Islands and Gulf of Alaska (Masaki, 1977). The whaling grounds were in the Alaska and Subarctic Current System. Stomach contents analysis of commercially harvested animals revealed that sei whales mainly fed on copepods (*Neocalanus plumchrus* and *Neocalanus cristatus*) (Nemoto and Kawamura, 1977). It was suggested that the spatial distribution of copepods around the Aleutian Islands were linked to the Alaska Coastal Current and Alaska Stream (Coyle, 2005). The spatial distribution of sei whales south and north of the PF might be different because of the different oceanographic structures and circulations on the opposite sides of this front. The distribution patterns of sei whales north of the PF should be studied in the future and compared with the results of this paper.

## 5. Conclusion

The spatial distribution of sei whales in the subarctic–subtropical transition area of the western North Pacific was associated with three oceanic fronts (PF, SAF and KEF), and the whales were concentrated north and south of the SAF. The basin scale oceanic fronts can be considered indicators of their feeding ground at the macro to meso scale. It was reported that energetic jets (streamers) and meso scale eddies associated with these fronts were observed in the feeding ground. It can be assumed that the whales search for their prey using these oceanographic conditions at the meso to macro scale and then finally attack the prey at the nano scale. Further study should be designed to capture the linkage among these scales. An integration of data of oceanography, whales and their prey will enhance our understanding of the ecology of whales.

## Acknowledgements

The authors express their thanks to the crews and researchers who participated in the surveys to collect these valuable data. We thank Dr. Igor Belkin for his kind invitation to submit our manuscript to this special issue “Fronts, Fish, and Top Predators.” He also provided us the definitions of the oceanic fronts used in the paper. Drs. Igor Belkin and Rui Prieto as well as four other reviewers provided thoughtful comments to improve our manuscript. The study was supported by the Fisheries Agency of Japan, the Fisheries Research Agency of Japan and the Institute of Cetacean Research. We thank these institutions for their support.

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