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# EFFECT OF SEA SURFACE TEMPERATURE ON THE DISTRIBUTION OF COMMON MINKE WHALES OFF SOUTHEASTERN HOKKAIDO, JAPAN, BETWEEN 2002 AND 2006, WITH NOTES ON THE FORMATION OF PACIFIC SAURY FISHING GROUNDS

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## Abstract

The relationships between oceanographic conditions and the distribution of common minke whales off southeastern Hokkaido was investigated in this study. Sighting surveys of common minke whales in this region were conducted in September, in 2002 and from 2004 to 2006. The density index (DI, the number of schools per 100 n.miles) of the whales decreased from 5.6 schools in 2002 to 1.2 schools in 2006. During the 4 years in which surveys were conducted, the monthly mean sea surface temperature (SST) in the survey area increased from 16.6°C in 2002 to 19.5°C in 2006, while the mean SST recorded at sighting locations was 15.5°C. The proportions of surveyed areas with a monthly mean SST ≤16°C in 2002 and 2004 were 46.5% and 17.0% respectively, whereas in 2005 and 2006, none of these areas had a monthly mean SST of less than 16°C. Pacific saury are among the major prey items of the minke whales in this region, and the number of the fishing boats was used as an indicator of the presence of the species in the surveyed area. The 4 year mean SST at the locations of the boats was 15.1°C. A reduction in the local abundance of the saury from 2002 to 2006 was inferred from the number of the boats operating in the region. These findings suggested that the apparent decline in the abundance of whales in the study area was associated with changes in SST and the availability of Pacific saury.

**Key words:** *Balaenoptera acutorostrata*, *Cololabis saira*, habitat, North Pacific, Oyashio, spatial distribution.

## Introduction

The common minke whale (*Balaenoptera acutorostrata*, hereafter minke whale) is a small species of baleen whale with body length of approximately 8 m at physical maturity (Kato, 1992), and has been reported to live to ages of up to 49 years (Maeda *et al.*, 2017). Records of past commercial catches indicate that the waters off southeastern Hokkaido (also known as the Doto region), Japan, are among the most important summer feeding areas for the Okhotsk Sea–West Pacific Stock (O Stock) of the species, particularly for immature individuals and mature males (Hatanaka and Miyashita, 1997; Kasamatsu and Tanaka, 1992). The results of the Japanese Whale Research Program under Special Permit in the western North Pacific (JARPN) and its Phase II (JARPN II) between 1994 and 2016 showed that they fed on a variety of prey species, such as krill, Japanese common squid (*Todarodes pacificus*), Japanese anchovy (*Engraulis japonicus*), Pacific saury (*Cololabis saira*, hereafter saury) and walleye pollock (*Gadus chalcogrammus*) in the western North Pacific (Konishi *et al.*, 2009; Murase *et al.*, 2007; Tamura *et al.*, 2009). It has been suggested that the spatial distribution of minke whales off southwestern Hokkaido during September could be associated with the distribution of saury (Tamura and Fujise, 2002). Nevertheless, despite this conjecture, it has yet to be sufficiently established whether changes in the minke whale spatial distribution are associated with the distribution of saury and/or oceanographic conditions (e.g., sea surface temperature, SST).

The saury, along with other small pelagic fishes, such as Japanese sardine (*Sardinops melanostictus*), Japanese anchovy, and chub mackerel (*Scomber japonicus*), is regarded as an economically important species in Japan (Watari *et al.*, 2019). Since the 1900s, the commercial catches and biomass of these small pelagic fish have fluctuated, reflecting decadal changes in species composition (i.e., species replacement) (Yatsu, 2019). Fluctuations in the populations of small pelagic fish detected during the 20th century have been linked to cold and warm water temperature regimes, as indicated by the Pacific Decadal Oscillation (PDO) index. However, the regime around Japan from the 2000s to 2010s was now defined as an unconventional regime as the relationship did not follow previous ones (Kuroda *et al.*, 2020). It should be noted that the biomass of saury was high in the 2000s in the time series between 1980 and 2018 (4th Meeting of the Technical Working Group on Pacific Saury Stock Assessment, 2019).

Saury generally (1) spawn during the winter months in the Kuroshio (the subtropical western boundary current with warm high-salinity water) waters off the southern coastline of Japan, (2) migrate to the North Pacific subarctic–subtropical transition zone during summer to feed and (3) commence their southbound return migration to the spawning grounds (Fuji *et al.*, 2020; Fukushima, 1979; Kosaka, 2000; Watanabe and Lo, 1989). It is in September during this southbound migration that the saury is commercially fished in grounds off the southeastern coast of Hokkaido. With the transition of the seasons from summer to autumn, the first branch of the Oyashio (the subarctic western boundary current with cold low-salinity water) extends southward along the coast of Hokkaido and Honshu, showing annual variation in both pattern and extent. The location of these saury fishing grounds off Hokkaido is determined by the location of the Oyashio front (the 5°C water temperature isotherm at a depth of 100 m), and accordingly shifts from year to year, tracking the variable pattern of the Oyashio front (Yasuda and Kitagawa, 1996). The primary indicator determining the location of the saury fishing grounds is SST, and it has been reported that the mode of SST at the fishing grounds in this area is 15°C (Tseng *et al.*, 2011; Watanabe *et al.*, 2006). It can thus be speculated that the spatial distribution of minke whales off southeastern Hokkaido in September is associated with the seasonal extent of the Oyashio current and/or the southbound saury migration.

The findings of previous studies have provided evidence indicating that the spatial distribution of minke whales worldwide is associated with a diverse range of biotic and abiotic factors, including bottom depth, topography, seafloor substrate, oceanographic conditions (e.g., SST); and the distribution of prey species (Chavez-Rosales *et al.*, 2019; Doniol-Valcroze *et al.*, 2007; Hamazaki, 2002; Hooker *et al.*, 1999; Ingram *et al.*, 2007; Macleod *et al.*, 2004; Naud *et al.*, 2003; Skern-Mauritzen *et al.*, 2011; Tetley *et al.*, 2008; Waggitt *et al.*, 2020; Zerbini *et al.*, 2016). However, given that these associations tend to differ depending on location and season, it has hitherto not been possible to draw any general conclusions. Consequently, to gain a better understanding of minke whale ecology, the location and season-specific effects of biotic and abiotic factors on the spatial distribution of these whales warrant further investigation.

In this study, it was sought to determine the associations among oceanographic conditions, and the distribution of saury and minke whales off southeastern Hokkaido in September. Specifically, the aims were to investigate (1) whether the distribution of minke whales in this area in September is related to SST, and (2) whether the spatial distribution of minke whales is related to the presence of saury. An earlier version of this paper was submitted to the International Whaling Commission's Scientific Committee as Appendix 4 of paper SC/59/O7 in 2006.

## Materials and Methods

Sighting surveys of minke whales were conducted off the coast of southeastern Hokkaido, Japan, in 2002, 2004, 2005, and 2006, as a part of the coastal component of JARPN II (Hakamada *et al.*, 2009). The longitudinal boundaries of the survey area were set at 143°15′E and 146°00′E, whereas the latitudinal boundaries were set at the 50 m isobath and 41°N (Fig. 1). Surveys were conducted during the month of September in the aforementioned years (Fig. 2). The survey area between 143°15′E and 146°00′E was stratified into the following four strata: an Offshore (O) stratum and three coastal strata [coastal-Center (C), coastal-East (E), and coastal-West (W)], with the boundary between the offshore and coastal strata being set at a distance of 60 n.miles from the Hokkaido coastline. In 2005 and 2006, an additional stratum (H) was surveyed off Hidaka sub-prefecture (between 142°30′E and 143°15′E).

Sighting surveys were conducted from onboard the survey vessel (SV) *Kyoshin-Maru No. 2* (372 GT; Kyodo Senpaku Co., Ltd). Primary observers were allocated to the top barrel (3 observers) and the upper bridge (2 observers). Zigzag tracklines with randomly selected starting points were constructed in the survey area. The sighting survey (i.e., on-effort) was conducted during daylight hours from 1 hour after sunrise to 1 hour before sunset under acceptable weather conditions (i.e., the visibility was 2.0 nautical miles or more, the wind speed was 20 knots or less, and the Beaufort wind force scale was less than 6), and the nominal steaming speed along the tracklines was 10 knots. Sightings during the on-effort were treated as primary sightings.

There were two survey modes: Closing Mode and Passing Mode. Closing Mode was applied in 2002 and 2004 while Passing Mode was applied in 2005 and 2006 to increase survey coverages. When the sightings during Closing Mode (primary sightings) were likely to be minke whales, the SV approached them to confirm species and individuals within the schools. Sightings during the approaches to primary sightings were secondary sightings and were not included in the analysis. During Passing Mode, no approach was made to sightings. All sightings made in the Passing Mode were treated as

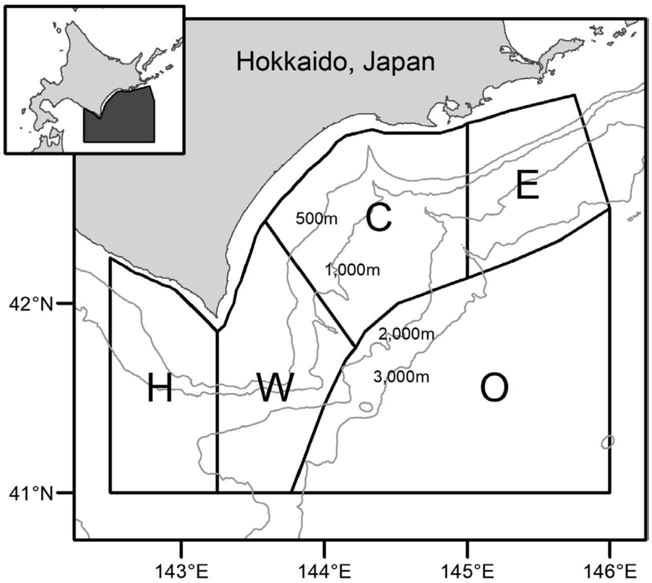


**Fig. 1.** Surveyed strata off the coast of southeastern Hokkaido, Japan [coastal-Center (C), coastal-East (E), coastal-West (W), Offshore (O)] and off Hidaka sub-prefecture (H). Black lines represent the boundaries between strata, and thin gray lines indicate isobaths.

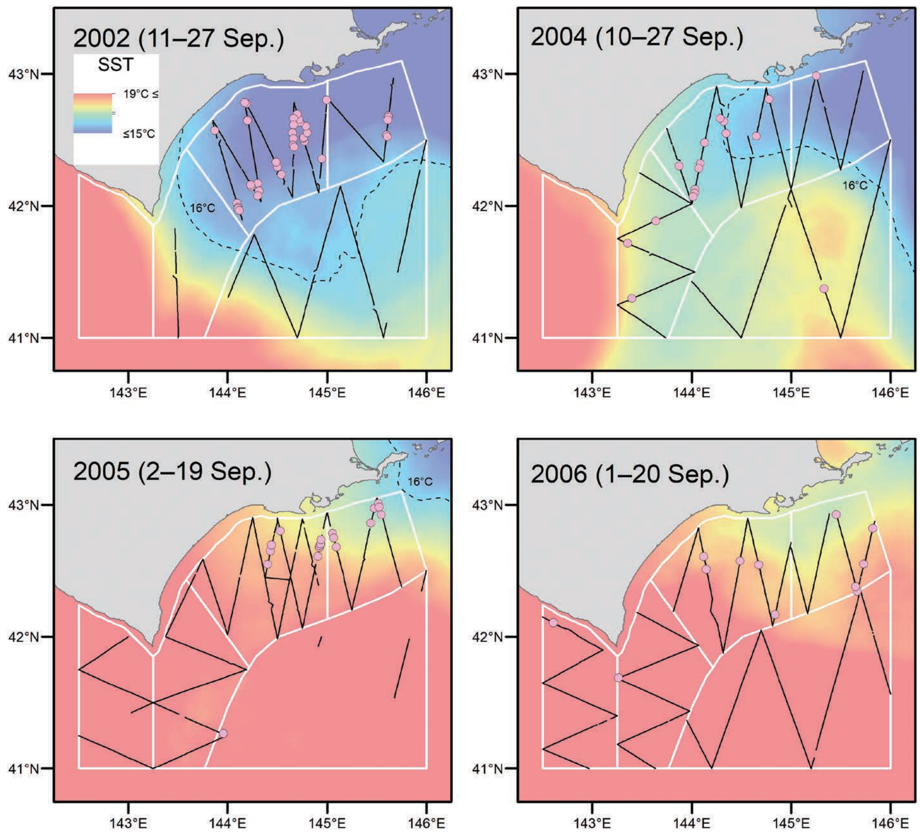


**Fig. 2.** Surveyed tracklines (black lines) and positions of common minke whale sightings (pink circles) off the coast of southeastern Hokkaido, Japan, in September 2002, 2004, 2005, and 2006. The monthly mean sea surface temperatures (SSTs) derived from GHRSST are also shown. Dashed black lines represent the 16°C isotherms, and white lines indicate the boundaries between strata.

primary sightings. However, if the identity of the species sighted was uncertain, abeam closing was conducted during Passing Mode. Given that the minke whales observed during the survey tended to occur individually rather than in schools, application of the Passing Mode is deemed adequate.

Density indices of schools and individuals (DI, the number of schools and individuals sighted per 100 n.miles) were calculated for each stratum in each survey year to show relative abundance of minke whales. Mean values of the SSTs recorded at the time of each sighting were obtained for each stratum in each of the survey years. Estimated abundance of minke whales based on the line transect sampling (Hakamada *et al.*, 2009) and amount of saury consumed by the whales (Tamura *et al.*, 2009) at the time of surveys were also used in this study.

As an indicator of the presence of saury, numbers of commercial saury fishing boats were summarized by each stratum in each survey year. Mean of SST recorded by the fishing boats was also summarized by each stratum in each survey year. The data of fishing positions of the boats and SST were provided by the Japan Fisheries Information Service Center (JAFIC).

SST data, A Group for High Resolution Sea Surface Temperature (GHRSST) Level 4 sea surface temperature analysis (JPL MUR MEaSUREs Project, 2010), were used to characterize oceanographic conditions at the time of the surveys. Monthly mean September SST data corresponding to the survey periods with a global 0.01 degrees grid spatial resolution were extracted using Marine Geospatial Ecology Tools 0.8a73 (Roberts *et al.*, 2010). Data pertaining to sightings, fishing boat locations, and SST were overlaid on maps using a geographic information system (GIS), ArcGIS Desktop 10.7 (ESRI, US). The area of sea surface classified by 1°C SST increments was also calculated using the GIS. ETOPO1 global relief model (Amante and Eakins, 2009) and A Global Self-consistent, Hierarchical, High-resolution Geography Database (GSHHG) (Wessel and Smith, 1996) data were also used in the maps. The UTM zone 55N projection was used for the mapping.

## Results

### All strata

The surveyed tracklines and the sighting positions of minke whales were overlaid on the SST maps (Fig. 2), as were the positions of the saury fishing boats (Fig. 3). These maps indicated an increase in the overall SST in the survey area during the course of the survey period from 2002 to 2006. Mean SST was found to have risen from 16.6°C in 2002 to 19.5°C in 2006 (Table 1). The frequency of the number of minke whale sightings with respect to SST (1°C increments) is shown in Fig. 4. During the four survey years, the mean SST at sightings positions was 15.5°C (CV=12.4%, n=87), whereas that in the years 2002, 2004, 2005, and 2006 was 14.3°C (CV=8.0%, n=38), 15.4°C (CV=4.5%, n=17), 15.6°C (CV=8.4%, n=20), 19.1°C (CV=6.0%, n=12), respectively (Table 1). Correspondingly reductions in the DIs, abundance, and saury consumption of minke whales were detected from 2002 to 2006. The frequency of the number of saury fishing boats with respect to SST (1°C increments) is shown in Fig. 5. Mean SST at the fishing positions of saury fishing boats over the four survey years was 15.1°C (CV=10.2%, n=2,646), whereas that in 2006 was 16.4°C (CV=10.3%, n=450) (Table 1). Notably, there were fewer boats fishing for saury in 2006. The frequency of area (n.mile$^2$) of SST ≤16°C and >16°C in all survey strata in September 2002, 2004, 2005, and 2006 is summarized in Table 1. Given that over the four survey years, the mean SST at the sighing positions of minke whales was 15.5°C, a temperature of 16°C was set as a cutoff point. From 2002 to 2006, a contraction

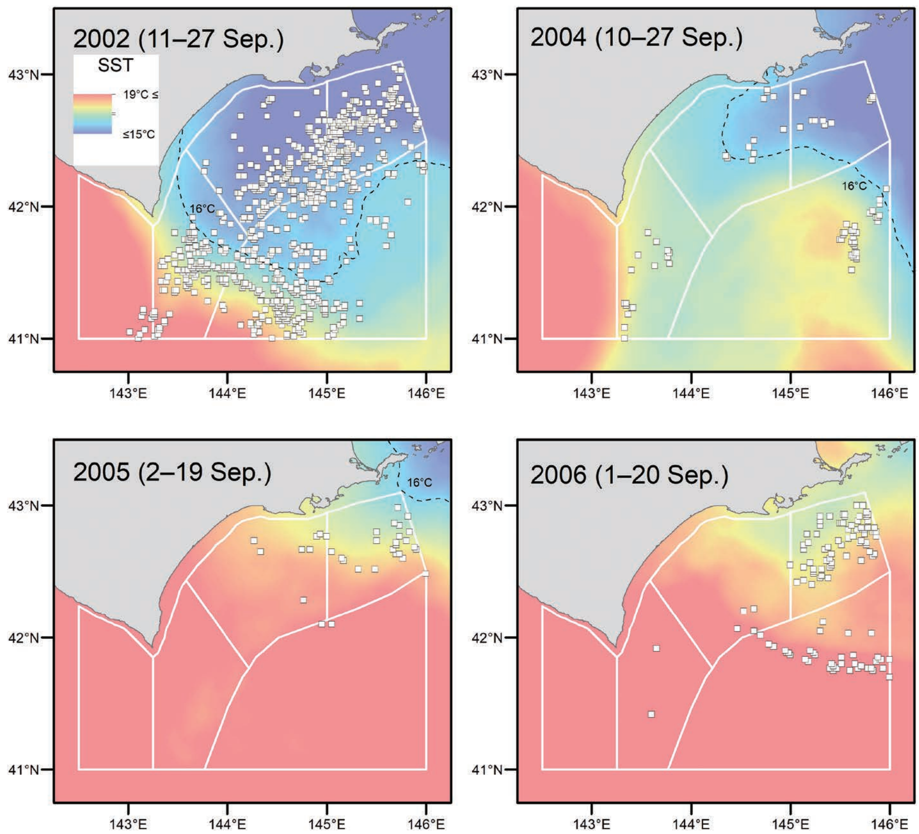


**Fig. 3.** The fishing positions of commercial Pacific saury fishing boats (open squares) off the coast of southeastern Hokkaido, Japan, in September 2002, 2004, 2005, and 2006. The monthly mean sea surface temperatures (SSTs) derived from GHRSST are also shown. Dashed black lines represent the 16°C isotherms, and white lines indicate the boundaries between strata.

**Table 1.** Summary of the September sightings and Pacific saury consumption of common minke whales, sea surface temperatures (SST) derived from GHRSST, and commercial Pacific saury fishing boats in the survey area. The density index (DI) indicates the number of schools/individuals per 100 n.miles. Values for the abundance and Pacific saury consumption of minke whales were obtained from Hakamada *et al.* (2009) and Tamura *et al.* (2009). Note that data for Pacific saury consumption are only available for “All strata”.

| Year | Common minke whale sightings & saury consumption | | | | | | | | | SST in survey blocks (GHRSST) | | | | Commercial Pacific saury boats | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Effort (n.miles) | Sch. | Ind. | Mean SST (°C) | DI (Sch.) | DI (Ind.) | Abundance | | Saury consumption (mt) | Mean | | Area ≤16°C (%) | Area 16°C< (%) | Number of boats | Mean SST (°C) |
| | | | | | | | Ind. | CV | | °C | CV | | | | |
| ***All strata*** | | | | | | | | | | | | | | | |
| 2002 | 681.5 | 38 | 40 | 14.3 | 5.6 | 5.9 | 601 | 0.4 | 861 | 16.6 | 9.8 | 46.5 | 53.5 | 1,815 | 14.8 |
| 2004 | 809.4 | 17 | 18 | 15.4 | 2.1 | 2.2 | 368 | 0.4 | 1,075 | 17.1 | 6.6 | 17.0 | 83.0 | 256 | 14.9 |
| 2005 | 827.1 | 20 | 21 | 15.6 | 2.4 | 2.5 | 316 | 0.4 | 39 | 19.1 | 4.6 | 0.0 | 100.0 | 125 | 15.5 |
| 2006 | 994.0 | 12 | 12 | 19.1 | 1.2 | 1.2 | 241 | 0.4 | 153 | 19.5 | 5.8 | 0.0 | 100.0 | 450 | 16.4 |
| ***C stratum*** | | | | | | | | | | | | | | | |
| 2002 | 272.6 | 33 | 34 | 14.4 | 12.1 | 12.5 | 323 | 0.2 | — | 15.1 | 2.3 | 100.0 | 0.0 | 403 | 14.6 |
| 2004 | 238.7 | 12 | 13 | 15.5 | 5.0 | 5.4 | 175 | 0.4 | — | 16.2 | 2.6 | 30.2 | 69.8 | 36 | 15.0 |
| 2005 | 365.3 | 10 | 11 | 15.4 | 2.7 | 3.0 | 81 | 0.7 | — | 18.5 | 2.0 | 0.0 | 100.0 | 47 | 15.0 |
| 2006 | 247.4 | 5 | 5 | 18.7 | 2.0 | 2.0 | 75 | 0.4 | — | 18.6 | 4.1 | 0.0 | 100.0 | 25 | 15.7 |
| ***E stratum*** | | | | | | | | | | | | | | | |
| 2002 | 73.5 | 5 | 6 | 13.8 | 6.8 | 8.2 | 117 | 1.1 | — | 15.0 | 3.4 | 100.0 | 0.0 | 431 | 14.2 |
| 2004 | 140.6 | 1 | 1 | 15.1 | 0.7 | 0.7 | 16 | 1.1 | — | 15.4 | 3.9 | 83.9 | 16.1 | 56 | 15.0 |
| 2005 | 127.7 | 9 | 9 | 15.3 | 7.0 | 7.0 | 135 | 0.3 | — | 17.8 | 4.3 | 0.0 | 100.0 | 81 | 15.5 |
| 2006 | 145.0 | 5 | 5 | 18.9 | 3.4 | 3.4 | 65 | 0.7 | — | 17.8 | 2.7 | 0.0 | 100.0 | 324 | 16.5 |
| ***W stratum*** | | | | | | | | | | | | | | | |
| 2002 | 48.2 | 0 | 0 | — | 0.0 | 0.0 | 0 | 0.0 | — | 17.1 | 7.1 | 28.2 | 71.8 | 305 | 15.2 |
| 2004 | 164.9 | 3 | 3 | 14.9 | 1.8 | 1.8 | 52 | 0.4 | — | 17.1 | 2.2 | 0.0 | 100.0 | 59 | 15.6 |
| 2005 | 180.3 | 1 | 1 | 20.7 | 0.6 | 0.6 | 15 | 1.1 | — | 19.1 | 1.5 | 0.0 | 100.0 | 0 | — |
| 2006 | 161.9 | 1 | 1 | 20.0 | 0.6 | 0.6 | 19 | 0.9 | — | 19.7 | 1.5 | 0.0 | 100.0 | 4 | 16.7 |
| ***O stratum*** | | | | | | | | | | | | | | | |
| 2002 | 287.2 | 0 | 0 | — | 0.0 | 0.0 | 0 | 0.0 | — | 16.5 | 4.7 | 29.2 | 70.8 | 664 | 15.0 |
| 2004 | 265.2 | 1 | 1 | 17.4 | 0.4 | 0.4 | 27 | 1.0 | — | 17.2 | 3.1 | 3.9 | 96.1 | 105 | 14.5 |
| 2005 | 41.7 | 0 | 0 | — | 0.0 | 0.0 | 0 | 0.0 | — | 19.3 | 1.1 | 0.0 | 100.0 | 7 | 18.1 |
| 2006 | 285.3 | 0 | 0 | — | 0.0 | 0.0 | 0 | 0.0 | — | 20.1 | 4.4 | 0.0 | 100.0 | 98 | 16.2 |
| ***H stratum*** | | | | | | | | | | | | | | | |
| 2002 | — | — | — | — | — | — | — | — | — | 19.6 | 3.2 | 0.0 | 100.0 | 17 | 16.9 |
| 2004 | — | — | — | — | — | — | — | — | — | 19.1 | 2.1 | 0.0 | 100.0 | 0 | — |
| 2005 | 112.1 | 0 | 0 | — | 0.0 | 0.0 | 0 | 0.0 | — | 20.7 | 2.1 | 0.0 | 100.0 | 0 | — |
| 2006 | 154.4 | 1 | 1 | 21.3 | 0.6 | 0.6 | 18 | 1.0 | — | 20.4 | 2.0 | 0.0 | 100.0 | 0 | — |

in the size of the area with an SST ≤16°C was recorded, with none of the areas having an SST of less 16°C in 2005 and 2006.

### Coastal-Center (C) stratum

Overall patterns of SST distribution, sightings of minke whales, and the positions of saury fishing boats in the C stratum were similar to those characterizing the entire survey area (Table 1). Most of sightings during surveys were found in this stratum. Over the four survey years, the mean SST recorded at the positions of minke whale sightings in this stratum was 15.1°C (CV=10.1%, n=60), whereas in 2006 it was 18.7°C (CV=3.9%, n=5). Comparatively, the mean SST at the fishing positions of commercial saury boats during these 4 years was 14.7°C (CV=7.4%, n=511), and that in 2006 was 15.7°C (CV=0.8%, n=25). The location of the 16.0°C isotherm SST front indicated that SST in the entire stratum was lower than 16.0°C in 2002, whereas in 2004, the temperature in only a small portion of the eastern part of the stratum was lower than this value (Fig. 2). Contrastingly, in 2005 and

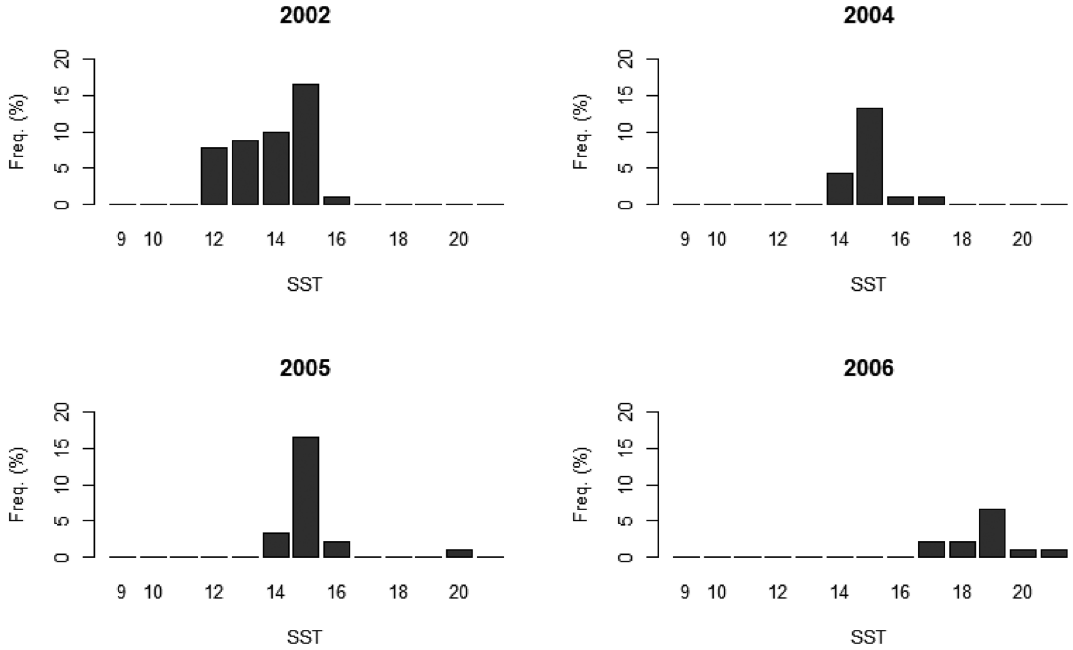


**Fig. 4.** Frequency of the number of common minke whale sightings according to sea surface temperature (SST: 1°C increments) in all surveyed strata off the coast of southeastern Hokkaido, Japan, in September 2002, 2004, 2005, and 2006. Data from all the years are pooled to calculate the frequency. SSTs recorded at sighting positions were used.

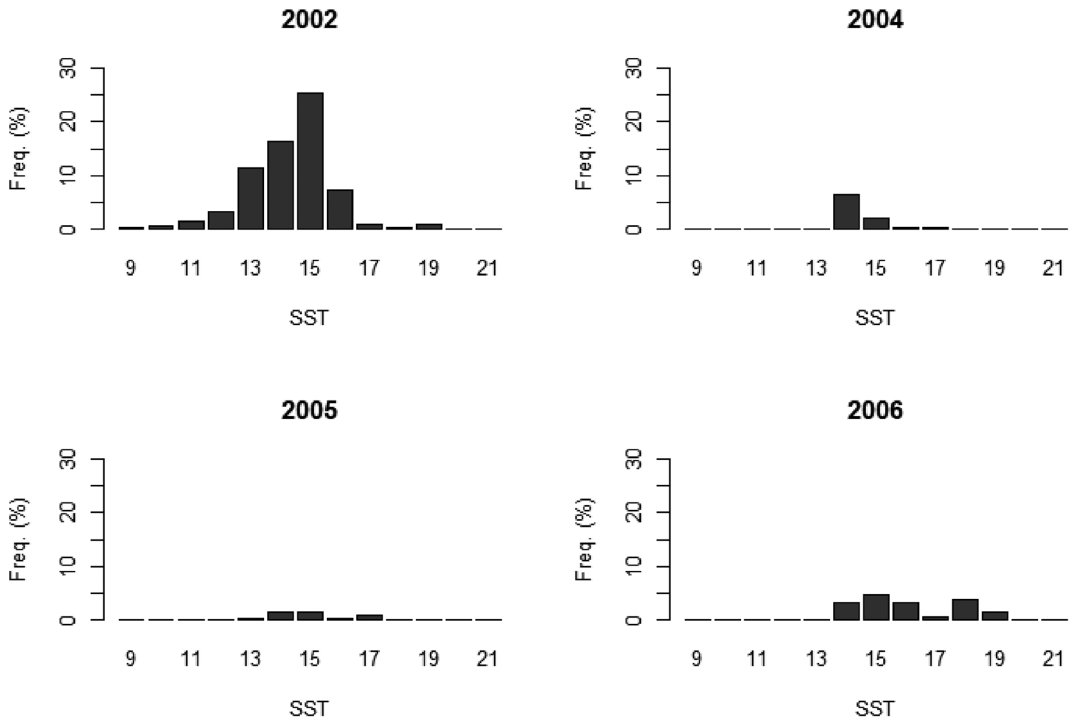


**Fig. 5.** Frequency of the number of commercial Pacific saury boats according to sea surface temperature (SST: 1°C increments) in all surveyed strata off the coast of southeastern Hokkaido, Japan, in September 2002, 2004, 2005, and 2006. Data from all the years are pooled to calculate the frequency. SSTs recorded at the positions of boats were used.

2006, no evidence of a 16.0°C isotherm SST front in this stratum was detected. Corresponding to an increase in the mean SST of this stratum from 2002 to 2006, a reduction in DI values was detected, and similarly a reduction in the frequency of SST ≤16°C during this period was recorded (Table 1).

**Strata other than the C stratum**

Compared with the C stratum, fewer sightings were made in the O and H strata, where mean SSTs were high regardless of the year of survey (Table 1). In the W stratum, the DIs and abundance were highest in 2004, coinciding with a period during which an area of relatively low SST extended over the stratum (Fig. 2), giving rise to the lowest (Table 1) and spatially homogeneous (Fig. 2) SST. Contrastingly, in the E stratum, DIs and abundance were the lowest in 2004. With respect to other survey years, the W stratum was found to be characterized by homogeneously high SSTs in 2005 and 2006 and a marked 16.0°C isotherm SST front in 2002, whereas in 2005 and 2006, DIs and abundance in the E stratum were higher than those in the C stratum.

## Discussion

The mean SST (15.1°C) recorded at the positions of minke whale sightings in the C stratum lies within the range of 7 to 17°C that has previously been reported for sightings of this species in the western North Pacific (Matsuoka *et al.*, 2000). Notably, relatively few minke whales were sighted in the C stratum when the SST was higher than 16.0°C, and thus it is conceivable that the distribution of minke whales is limited to within the SST range reported by Matsuoka *et al.* (2000). Consistent with findings in the present study, Watanabe *et al.* (2006) have reported that mode SST at the saury fishing boat positions was 15.0°C. Consequently, it would appear that minke and saury have a similar suitable range of SSTs. In this regard, it has been reported that the timing and route of the saury migration from northern waters to those off the southeastern coast of Hokkaido show considerable changes coinciding with annual fluctuation in oceanographic conditions (Fukushima, 1979; Yasuda and Kitagawa, 1996; Yasuda and Watanabe, 1994).

Historical commercial catch data indicate that the migration and spatial distribution of minke whales in the western North Pacific differ with respect to sex and maturation stage (Hatanaka and Miyashita, 1997; Ohsumi, 1983; Omura and Sakiura, 1956; Wada, 1989). The findings of JARPN II in the C stratum have revealed that immature individuals are generally distributed in coastal waters whereas mature males tend to be found at both coastal and offshore waters (Kishiro *et al.*, 2009). In this regard, it has been suggested that mature minke whale males showed prey preference for saury over other species, such as krill and walleye pollock (Kishiro *et al.*, 2009). The number of mature males in the C stratum during the period of the JARPN II survey declined from 2002 to 2006 (Kishiro *et al.*, 2009), coinciding with the decline of DIs and abundance reported in this study.

At least two different stocks of minke whales have been identified in the waters around Japan, namely the J and O stocks (Goto and Pastene, 1997; Kato, 1992; Ohsumi, 1977; Omura and Sakiura, 1956; Pastene *et al.*, 2007; Wada and Numachi, 1991). Of these, O stock is mainly distributed in the waters of the western North Pacific, whereas J stock is mainly distributed in the Sea of Japan, although it has been reported that a small proportion of this stock mixed with O stock off the southeastern coast of Hokkaido (Pastene *et al.*, 2016). Although the exact route whereby mature O stock males migrate is still under investigation, it is evident that during the summer months, at least a proportion of these individuals migrates northward in offshore regions of the western North Pacific (e.g., east of 150°E) (Zenitani *et al.*, 2000). Moreover, it seems probable that during autumn, they migrate southward along the coastal region of Japan, including waters off the southeastern coast of Hokkaido in autumn. The migration timing and route of mature male minke whales would thus appear to be similar to that of the saury, and indeed, these whales are known to feed on saury in both offshore regions and the waters off southeastern coast of Hokkaido (Lindstrøm *et al.*, 1998; Tamura *et al.*, 1998).

Findings in the present study provide evidence in support of the hypothesis that the migration route of mature male minke whales coincides with a suitable SST (approximately 15°C) and the migration of their primary prey species, the saury. In the C stratum, these mature males could make a high contribution to the observed changes in DIs and abundance. For example, in response to a suitable SST and an abundance of saury (as in 2002), many mature males could migrate into the stratum, whereas in contrast, when SSTs exceed a suitable level, and the availability of saury is low (as in 2006), there would be relatively few migrants in this stratum.

Collectively, the findings of this study indicate that the abundance of minke whales in a particular area is influenced to varying extents by changes in oceanographic conditions and the availability of prey. In this regard, abrupt changes in the abundance of minke whales have been reported in other regions of the world. For example, changes in abundance of this species in Icelandic waters have been linked to changes in oceanographic conditions and the patterns of prey species distribution (Víkingsson *et al.*, 2015). Consequently, to gain a reasonably clear understanding of the factors underlying such changes, analyses of whale sighting data should simultaneously take into consideration data obtained for a range of environmental variables, thereby enabling us to distinguish between apparent and absolute changes in abundance.

A stock assessment for a time series between 1980 and 2018, revealed that the overall abundance of saury was generally high during the period covered by the present study (2002–2006) (4th Meeting of the Technical Working Group on Pacific Saury Stock Assessment, 2019). Furthermore, the findings of a population dynamics study appear to indicate no abrupt change in abundance of the O stock of minke whales during the period between the 1990s and 2010s (Kitakado and Maeda, 2016). On the basis of these findings, it can be concluded that observed changes in the abundance of minke whales in waters off the southeastern coast of Hokkaido between 2002 and 2006 were apparent rather than actual changes, attributable to annual variations in oceanographic conditions. These variations similarly influence the route and timing of saury migrations. It seems probable that the apparent change in the abundance of minke whales coincided with changes in local oceanographic conditions and the availability of saury. It was reported that contractions in the size of potential saury fishing grounds off southeastern Hokkaido were associated with increases of SST and sea level anomaly, a reduction in chlorophyll concentration, an increase in the frequency of clockwise eddies, and a reduction in Oyashio transport (Kuroda and Yokouchi, 2017). It should be noted that the abundance index of saury in the present study area in August and September was high in 2002, although low between 2004 and 2006 in response to the environmental conditions (Kuroda and Yokouchi, 2017).

Nevertheless, given that minke whales also consume other prey items, such as Japanese anchovy, walleye pollock, and Japanese common squid (Tamura *et al.*, 2009), the interrelationships among minke whales, their prey, and oceanographic conditions in this region might be more complex than hitherto assumed. In this context, minke whales in the surveyed region have in the past fed on Japanese sardine and mackerel when the abundances of these prey were high (Kasamatsu and Tanaka, 1992). However, it has yet to be ascertained how the minke whale distribution changes in response to the replacement of pelagic fish species, along with changes in oceanographic conditions. Accordingly, long-term monitoring of both the whales and their prey, together with oceanographic conditions, will be necessary to gain a realistic insight into the factors underlying changes in the distribution of minke whales in the waters off southeastern Hokkaido.

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