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Seasonal distribution of short-tailed shearwaters and their prey in the Bering and Chukchi Seas

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Abstract

Short-tailed shearwater *Puffinus tenuirostris* is one the of abundant marine top predators in the Pacific; this seabird spend its non-breeding period in the northern North Pacific during May–September and many visit the southern Chukchi Sea in July–September. We examined factors affecting this seasonal pattern of distribution by counting short-tailed shearwaters from boats. Their main prey, krill was sampled by NORPAC net in the southeastern Bering Sea/Aleutian Islands and in the Bering Strait/southern Chukchi Sea. Short-tailed shearwaters mainly distributed in the southeastern Bering Sea/Aleutian Islands (60 ± 473 birds km^{-2}) in summer (July) but in the Bering Strait/southern Chukchi Sea (19 ± 91 birds km^{-2}) in fall (September). In the Bering Strait/southern Chukchi Sea size of krill was greater in fall (9.6 ± 5.0 mm in total length) than in summer (1.9 ± 1.2 mm). Within the Bering Strait/southern Chukchi Sea in fall, short-tailed shearwaters occurred more frequently in cells (50 km × 50 km) where large krill was more abundant. Our results suggest that the seasonal northward movement of short-tailed shearwaters could be associated with the seasonal increase of large krill in the Bering Strait/southern Chukchi Sea. This study substantiates the importance of krill, which is advected from the Pacific, as a prey of top predators in the Arctic marine ecosystem.

1 Introduction

The shelf region in the Bering and Chukchi seas harbors one of the most productive marine ecosystems in the world (Grebmeier et al., 2006; Hunt et al., 2013). These areas are also among the regions where recent reductions of sea-ice coverage have been particularly significant (e.g., Perovich and Richter-Menge, 2009). The changes in the timing of sea-ice formation and retreat, along with increasing seawater temperatures and freshwater content, determine the timing, intensity, and locations of phytoplankton bloom, and hence affect the distribution and abundance of primary and secondary consumers (Hunt et al., 2002a; Mueter and Litzow, 2008; Steel et al., 2008; Li et al., 2009; Kahru et al., 2011; Matsuno et al., 2012).

In the Bering Sea and Chukchi Sea shelf regions, marine mammals and seabirds, as homoeothermic top predators, play a significant role in the trophic energy flow (Schneider et al., 1986; Piatt and Springer, 2003). As mobile predators that can respond quickly to shifts in the distribution of prey (i.e., by switching foraging areas or prey species), changes in their distribution can potentially serve as indicators of fluctuations of trophic relationships (Sydeman et al., 2006; Iverson et al., 2007; Piatt et al., 2007). Recently, the northern Bering and Chukchi shelf region have shown evidence of shifts in species composition, distribution and abundance of top predators. For example, gray whales (*Eschrichtius robustus*) in the Chirikov Basin expanded their foraging range to the north as their prey biomass (amphipods) has decreased from 1983 to 2000 (Moore et al., 2003). Also, the decline in the dominant clam populations in the northern Bering Sea has been consistent with dramatic declines in numbers of spectacled eiders (*Somateria fischeri*) that consume the clams (Lovvorn et al., 2009). Knowledge of recent changes in the distributions of top predators and their prey should provide useful information about large-scale ecosystem changes in these regions with seasonal sea-ice.

Short-tailed shearwaters (*Puffinus tenuirostris*) migrate annually from their breeding colonies in southeastern Australia and Tasmania to spend their non-breeding period for ca. 5 months in the northern North Pacific. Up to 16 million birds stay in the Bering Sea between April and October (Schneider and Shuntov, 1993), where they consume substantial amount of krill, in particular the euphausiids *Thysanoessa raschii* and *T. inermis* (Schneider et al., 1986; Hunt et al., 1996, 2002b; Toge et al., 2011). In the Bristol Bay area of southeastern Bering Sea, krill consumption by the short-tailed shearwaters from April to June was estimated to be 30 000 tons (Ogi et al., 1980), a consumption roughly equivalent to that (32 280 tons) by sockeye salmon (*Oncorhynchus nerka*) (Nishiyama, 1974). Thus, the trophic linkage between short-tailed shearwaters and krill can be one important pathway of energy flow in the Bering Sea ecosystem (Schneider et al., 1986).

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A recent tracking study revealed that short-tailed shearwaters in the Bering Sea move through the Bering Strait to feed in the Chukchi Sea during late summer and fall (Yamamoto et al., 2015). This northward shift of distribution was hypothesized to relate to the temperature-driven changes in the abundance of their prey, krill, as the timing of krill spawning coincides with the seasonal increase in water temperature (Smith, 1991). However, large scale (Bering Sea and Chukchi Sea) relationships between the distribution of short-tailed shearwaters and that of krill have not been explored. In this study, we investigated at-sea distribution of short-tailed shearwaters by vessel-based surveys in fall (September 2012) and summer (June–July 2013) and that of the zooplankton (including krill) by vertical tows of NORPAC net in July of 2007 and 2008, September 2012, and June–July 2013. Krill samples collected by plankton net should be highly biased, because of high net-avoidance ability of krill (Watkins, 2000), but will give useful information within a limit.

2 Materials and methods

2.1 Seabird surveys

At-sea seabird surveys were conducted onboard R/V *Mirai* (Japan Agency for Marine-Earth Science and Technology) on 9 September–10 October 2012 (fall) and T/S *Oshoro-Maru* (Department of Fisheries Sciences, Hokkaido University) on 19 June–28 July 2013 (summer) in the Bering and Chukchi seas (50–78° N, 170° E–150° W, Fig. 1 and Table 1). We used standard strip transect methodology to estimate the distribution and abundance of seabirds (Tasker et al., 1984) when the vessel was at averaged speeds of 10.7 knots. All birds (both flying and sitting on water) were counted continuously from the bridge (eye height 13.6 m on R/V *Mirai* and 8.5 m on T/S *Oshoro-Maru* above sea surface) within a 300 m transect window (from bow to 90° to port or to starboard) for T/S *Oshoro-Maru* and within a 500 m transect window for R/V *Mirai* on the side of the vessel that offered the best observation conditions (i.e., lowest sun glare).

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Birds following the vessel were recorded when they first entered the transect and were ignored thereafter. Sooty shearwater (*Puffinus griseus*) and short-tailed shearwater are difficult to distinguish in the field and sooty shearwaters are rare north of the Aleutian Islands (Howell, 2012); all shearwaters that we identified to species were short-tailed shearwaters.

We calculated relative density (number of birds per km^2) of short-tailed shearwaters and used bird densities within a 50 km grid for the survey area; the grid size was based on short-tailed shearwater foraging area fidelity at a scale of 10 to 10^2 km in the southeastern Bering Sea and north Pacific (Baduini et al., 2006; Kurasawa et al., 2011). Moreover, owing to unequal total length of the distance in each grid cell, the total number of birds in each grid cell was divided by survey area. Thus, the density of short-tailed shearwaters at each 50 km grid cell was given as the number per km^2.

2.2 Krill sampling

A total of 171 zooplankton samples were corrected by the science crew of T/S *Oshoro-Maru* and R/V *Mirai* for the Bering Sea during 20–31 July 2007 ($n = 27$, summer), 24 June–2 July 2008 ($n = 33$, summer) and 22 June–7 July 2013 ($n = 34$, summer), and for the Chukchi Sea during 13 September–3 October 2012 ($n = 50$, fall) and 8–17 July 2013 ($n = 27$, summer) (Table 2). Zooplankton samples were collected at day or night by vertical tows with a NORPAC (North Pacific Standard Net) net (mouth diameter 45 cm, mesh size 335 µm) from 5 m above the bottom to the surface (depths of most stations were about 50 m); covering the entire vertical distribution range of krill, which undertake a diurnal vertical migration (Watkins, 2000). Thus, the diurnal vertical migration of krill did not affect our samples. The volume of water filtered through the net was estimated using a flow-meter mounted in the mouth of the net. Zooplankton samples were immediately preserved with 5 % v/v borax buffered formalin. In the laboratory (in Hokkaido University), samples were split using a Motoda box splitter (Motoda, 1959). Krill in the half aliquots were identified and enumerated under a dissecting microscope. We accordingly measured the total length of krill (0.1 mm) (from the tip of the rostrum to the posterior end of the telson, Hanamura et al., 1989) usually on 20 % specimens for each sample, and divided them into five growth stages (i.e., nauplius, calyptopis, furcilia, juvenile, and adult) following Brinton et al. (2000). Moreover, we calculated the wet weight per individual krill using the length–weight relationship equation (ln(wet weight) = −4.71 + 2.91 × ln(total length), $r = 0.97$, $n = 376$, for krill of *Euphausia pacifica* (as per Heath, 1977)), then, estimated the biomass of krill (mg m^{-2}) for each region (i.e., Bering Sea and Chukchi Sea) as mean wet weight (mg) per individual by abundance (ind. m^{-2}).

Net avoidance can affect the absolute number of krill entering the net. Juveniles and adults of krill with progressed eye structures may be able to avoid the nets more successfully (Watkins, 2000). Large krill, which can swim faster than small krill, may be able to avoid the net more successfully than small krill (Hovekamp, 1989). Thus, the absolute abundance of juveniles and adults of krill might be underestimated in this study. Nevertheless, we could compare the relative abundance at each size of krill (or each growth stage of krill) between regions. Our goal was to clarify the relationship between the seasonal distribution of short-tailed shearwaters and availability of krill at a regional scale, thus the potential sampling bias between stations did not affect our analysis.

2.3 Analyses

To explore the factors affecting spatial patterns of the short-tailed shearwaters we used a habitat modelling approach using data collected during fall of 2012 in the Chukchi Sea and during summer of 2013 when both seabird and zooplankton surveys were conducted. Because densities of short-tailed shearwaters among 50 km grid cells were highly variable (Min.–Max.: 0–5601.1 birds km^{-2}), and the sample size was relatively small (20 grid cells in fall 2012 and 52 in summer 2013), we assessed the factors affecting the occurrence of short-tailed shearwaters. We used generalized linear models (GLM) where the occurrence (presence/absence in each 50 km grid cell) of short-tailed shearwaters was the response variable, assuming a binomial distribution with the logit

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link function. Explanatory variables included three continuous oceanographic data – sea surface temperature (SST; °C), sea surface chlorophyll *a* concentrations (Chl *a*; mg m^{-3}) and ocean bottom slope (Slope; °) (as a proxy for upwelling), and categorical krill data on their occurrence and size.

Monthly SST and Chl *a* data were obtained from moderate-resolution spectroradiometer/Aqua standard mapped images with a spatial resolution of approximately 9 km provided by Ocean Color website (http://oceancolor.gsfc.nasa.gov). The Slope was calculated from ETOPO 1 min gridded data provided by NOAA's National Geospatial Data Center, using the slope function package in the Spatial Analyst tool (ArcGIS 10.0). These oceanographic parameters were spatially resampled to 50 km scales (the Slope was calculated after ETOPO 1 min were spatially resampled to 50 km scales) using the SeaWiFS Data Analysis System version 6.2 software. Krill sizes (total length in mm) were divided into two categories, i.e., "small" (< 8.0 mm in total length) and "large" (> 8.0 mm), since the length of krill found in short-tailed shearwater's diet during summer in the southeastern Bering Sea was > 8.8 mm (Vlietstra et al., 2005). Then, the occurrence and size of krill were treated as a categorical explanatory variable, "absence", "small" or "large" for each station. Each station of krill samples was related to the closest grid cell that had by vessel-based short-tailed shearwater surveys. Distance between the cells (each station of krill samples and the closest grid cell with short-tailed shearwater surveys) averaged approximately 33 km. The data for each season and year (fall 2012 and summer 2013) were pooled into a single data set for constructing GLM because the sample size was small owing to the limited survey periods and missing data (resulting from cloud cover) in satellite images of SST and Chl *a*. Thus, to evaluate effect of season we added "season" (summer or fall) as a second categorical explanatory variable.

Prior to modelling, the co-linearity of all continuous explanatory variables was evaluated using variance inflation factors (VIF). All VIF values were below 2, indicating that no co-linearity was assumed in this study (Zuur et al., 2009). We selected the best-performing models for each species at the three spatial scales using AIC values, assuming that models having ΔAIC ≤ 2 were better-fitting models (Burnham and Anderson, 2010). All statistical analyses were carried out in R software (version 3.1.0, R Development Core Team, 2014).

3 Results

3.1 Distribution of short-tailed shearwaters and krill

In fall (September) of 2012, short-tailed shearwaters were distributed in the Bering Strait and Chukchi Sea. Density was high in the Bering Strait (46.7 km^{-2}), area off Point Hope (145.6 km^{-2}) and off Barrow (37.8 km^{-2}), and a few in the Bering basin (11.1 km^{-2}) (Fig. 1a). No short-tailed shearwaters were found in the Chukchi basin (Fig. 1a). In summer (June–July) of 2013, however, short-tailed shearwaters were widely distributed in the Bering Sea while no short-tailed shearwaters were found in the Bering Strait and Chukchi Sea (Fig. 1b). Mean density (birds km^{-2} at each 50 km grid) in the northwestern Bering shelf (1.1 km^{-2}) was lower than that in the southeastern Bering shelf (4.4 km^{-2}) and around the Aleutian Islands (425.6 km^{-2}) (Fig. 1b).

In the Bering Sea shelf, krill were collected throughout the study area (Fig. 2a, b and c). In summer of 2007, 2008, and 2013, krill abundance and estimated biomass (mean ± SD) in the southeastern Bering Sea shelf (< 60° N) (1631 ± 2972 m^{-2} for abundance, 1468 mg wet weight m^{-2} for biomass) were higher than those in the northwestern Bering Sea shelf (> 60° N) (1189 ± 3981 m^{-2}, 119 mg wet weight m^{-2}). In fall, no krill sampling occurred in the Bering Sea. In the Chukchi Sea, krill abundance in summer of 2013 (7366 ± 16 420 m^{-2}) was greater than that in fall of 2012 (133 ± 304 m^{-2}), while the biomass in summer (1473 mg wet weight m^{-2}) was similar to that in fall of 2012 (1579 mg wet weight m^{-2}). No krill were collected in the Chukchi basin in summer or fall (Fig. 2d and e).

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3.2 Size of krill

Identified krill specimens in the Bering Sea ($n = 10$) included four *T. raschii*, three *T. longipes*, two *T. inermis* and a single *T. spinifera*, and those in the Chukchi Sea ($n = 43$) included forty *T. raschii* and three *T. inermis*. In the Bering Sea, krill collected in summer (2007, 2008, and 2013 samples were pooled) were larger in the southeastern shelf than those collected in the northwestern shelf (Mann–Whitney's U test, $p < 0.05$) (Fig. 3a). Samples collected in the southeastern shelf were comprised of nauplius (1 %), calyptopis (27 %), furcilia (71 %) and adult (1 %) stage, while those collected in the northwestern shelf were comprised of slightly younger stages (nauplius (2 %), calyptopis (88 %), and furcilia (30 %)).

In the Chukchi Sea, mean total length of krill collected in fall 2012 was larger than that in summer 2013 (Mann–Whitney's U test, $p < 0.05$) (Fig. 3b). In summer, 90 % of individuals were in the calyptopis stage while in fall, 74 % were furcilia, 7 % juvenile, and 19 % adult stage.

3.3 Occurrence of krill and shearwater

Five better-fitting models (ΔAIC ≤ 2) were selected for explaining the occurrence of shearwaters (Table 3). SST was included in all models and effect was positive; the probability of the occurrence of shearwaters was higher in warmer waters within each of the two regions. The other explanatory variables were included in one or two better-fitting models, suggesting they were less important. Shearwaters appeared to occur more frequently in grids with lower Chl *a*, steeper *slope*, and larger krill (Table 3).

Since all better-fitting models included *season* as an explanatory variable, values of other explanatory variables were compared between grids with and without shearwaters during summer or fall separately. SST was higher in grids with shearwaters than in those without shearwaters both in summer and fall (Table 4). Chl *a* was not different between grids with or without shearwaters in summer or fall (Table 4). Slope was different between seasons; Slope was steeper in grids with shearwaters than in grids without

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shearwaters in summer, but the opposite trend occurred in fall (Table 4). Shearwaters tended to occur more often in grids with large krill in fall but this trend was not apparent (or possibly was opposite) in summer (Table 5). Density of shearwaters was greater in grids with large krill than in those without large krill in fall and summer (Table 6).

4 Discussion

4.1 Distribution and diets of short-tailed shearwaters

Our study substantiated that short-tailed shearwaters stay in the Bering Sea and Aleutian Islands in summer (June–July) and they move to the Bering Strait and Chukchi Sea in fall (September). Our surveys were based on two cruises carried out in different years and did not include August surveys, but the seasonal difference in distribution of short-tailed shearwaters is consistent with previous results from vessel-based surveys and tracking studies of individual birds. Studies differ in whether shearwaters occur in the Chukchi Sea in summer, but this appears to be due to how they define summer, in patucular whether August is included with summer counts. For example, boat surveys by Wong et al. (2014) showed that high densities of short-tailed shearwaters occurred in the Aleutian Islands, south Bering Sea and Bering Strait, but few were found in the Chukchi Sea during summer, however this study transited the Chukchi Sea in July and possibly early fall. Gall et al. (2013) noted that shearwaters were abundant in early fall (August–September) in the northern Chukchi Sea and Kuletz et al. (2015) identified "hotspots" of shearwater densities in the Chukchi Sea in "summer", which included mid-june through August in that study.

Observations of geolocator-tracked short-tailed shearwaters confirm a similar pattern of seasonal movement from the Bering Sea to the Chukchi Sea. Individual birds spent summer (May–July) in the Aleutian Islands and Bering Sea, then moved into the southern Chukchi Sea in August and September (Carey et al., 2014). The other geolocator-based study showed that a substantial proportion (22 of 43 birds) of individuals moved to the Chukchi Sea through the Bering Strait where they spend ca. one month before their return migration, presumably to utilize the relatively high food concentrations available after the main bloom in the southern Bering Sea had passed (Yamamoto et al., 2015). The northward shift in the distribution of short-tailed shearwaters may be related to temperature-driven changes in the availability of krill, although the relationship between the distribution of short-tailed shearwaters and that of krill were unexplored by Yamamoto et al. (2015).

Information on the diets of short-tailed shearwaters was not collected during this study. Previous studies have shown that krill comprised most of their diet in the northern North Pacific and Bering Sea (Table 7). Other prey species included fish (19 % in wet weight), squid (9 %), copepods (1 %) and crab larvae (2 %) (Table 7). Within the krill prey items, *T. raschii* was the primary species (72–100 %) for short-tailed shearwaters in the Bering Sea during the non-breeding periods (Schneider et al., 1986; Hunt et al., 1996, 2002b).

In the Aleutian Pass and southeastern Bering Sea, short-tailed shearwaters ate large krill (11.5–16.9 mm) even when small krill (5.0–8.4 mm) were present, though short-tailed shearwaters associating with a tidal front tended to feed on smaller krill (Vlietstra et al., 2005). In the southeastern Bering Sea, short-tailed shearwaters consumed almost exclusively the mature females of *T. raschii* carrying spermatophores (Hunt et al., 1996; Baduini et al., 2001), indicating that they fed on the mating swarm of krill. Thus, short-tailed shearwaters fed on larger and mature krill perhaps because larger krill contain more gross energy than small krill (Färber-Lorda et al., 2009). Additionaly, surface swarms of adults may be more easily available for diurnal surface feeders such as short-tailed shearwaters (Hunt et al., 1996).

4.2 Krill and short-tailed shearwaters

The northward movement of short-tailed shearwaters in late summer or fall might be associated with the seasonal increase in the size of krill in the Chukchi Sea. In the Chukchi Sea, the size of krill sampled during this study in fall (September)

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(9.6 ± 5.0 mm), which was within the ranges of size found in the stomach of short-tailed shearwaters in the southern Bering Sea (Vlietstra et al., 2005), were larger and older than those sampled in summer (June–July) (1.9 ± 1.2 mm) (Fig. 3b). In contrast, in the southeastern Bering Sea it is reported that the size and density of krill decreased seasonally. Previous studies based on MOCNESS sampling showed that in the southeastern Bering shelf, the mature *T. raschii* was abundant during spring (May–June) when the phytoplankton bloom occurs, while the immature was abundant during fall (August–September) (Smith, 1991; Coyle and Pinchuk, 2002). Continuous echo data collected by the mooring system in the southeastern Bering Sea showed that the densities of krill were high in mid-summer (July–August) and decreased in fall (September) (Stafford et al., 2010). Some short-tailed shearwaters stayed in the southeastern Bering shelf in fall and used alternative prey, such as copepod, crab zoea and 0-age walleye pollack, or fed on *T. inermis* in the productive shelf slope where nutrients-rich water are consistently upwelled (Hunt et al., 1996, 2002b).

Within the Chukchi Sea in fall, the density of short-tailed shearwaters was high in areas off Point Hope and off Point Barrow. The latter remained a "hotspots" of shearwater activity into late fall (September–October) during 2007–2012 (Kuletz et al., 2015). Our results indicated that the presence of large krill (> 8.0 mm) was associated with the occurrence and the high density of short-tailed shearwaters (Tables 5 and 6). Within the Bering Sea in summer, the density of short-tailed shearwaters was higher in the southeastern shelf than that in the northwestern shelf (Fig. 1b), which might also reflect the higher abundance and larger size of krill in the southeastern shelf than northwestern shelf (Sigler et al., 2012; this study).

4.3 Environmental change and trophic effects through krill

Our study indicates that the spatial pattern of krill influenced the movement of short-tailed shearwaters. Other top predators show a similar relationship. For example, bowhead whales (*Balaena mysticetus*) feed on aggregated krill in the northern North Pacific and Arctic Ocean in fall (Moore et al., 1995; Lowry et al., 2004). Gray whales that

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usually feed on benthic amphipods (Moore et al., 2003) fed on krill when and where abundance of amphipods decreased and/or that of krill increased (Bluhm et al., 2007). Species diversity of whales in the Chukchi Sea was highest in areas of high krill density and migration of whales might be affected by availability of krill (Clarke et al., 2013). All these results indicate that the seasonal and regional patterns of the abundance and size of krill affect diets and distributions of top predators in the nothern North Pacific and Arctioc Ocean. Therefore, krill is an important component of energy transfer from phytoplankton to top predators in the marine food webs in the southern Chukchi Sea and northern Bering Sea, in addition to major zooplankton in this region, i.e., copepods (Hopcroft et al., 2005; Hop and Gjøsæter, 2013; McBride et al., 2014).

In the Bering Sea, swarming of krill (*T. raschii*) appears to occur in the presence of elevated phytoplankton density (Paul et al., 1990; Hunt et al., 1996). The seasonal progression in the spawning of krill, as indicated by the seasonal increase in abundance of naupliar in the Chukchi Sea, follows the seasonal development of temperature (Smith, 1991) which consequently leads to a phytoplankton bloom (Hunt et al., 2002a). The reduction of sea-ice coverage influences the water masses, temperature, and salinity of seawater and seasonal changes of these, ultimately affecting timing of the phytoplankton bloom (Steele et al., 2008; Yamamoto-Kawai et al., 2009; Kahru et al., 2011).

The distribution and abundance of krill in the Chukchi Sea are believed to be affected by advection of the Pacific water through the Bering Strait (Berline et al., 2008). Our results showed that short-tailed shearwaters occurred more frequently in waters of 3–9 °C SST in the Bering Strait and southern Chukchi Sea, which is within the ranges of SST of Pacific water masses in the Chukchi Sea (Alaskan Coastal Water, 2–13 °C; Bering Shelf Water and Anadyr Water, 0–10 °C, Coachman et al., 1975; Eisner et al., 2013). There are inter-annual and regional variations of the advection of krill from the Bering Sea to the Chukchi Sea (Berline et al., 2008) and the volume of Pacific water advection is known to be associated with seasonality of sea-ice coverage (Woodgate et al., 2006, 2010). Although the reproduction of krill has not been confirmed in the Chukchi Sea (Siegel, 2000; Berline et al., 2008), spawning of *T. raschii* has been reported in the Laptev Sea in part of the Arctic Ocean (Timofeev, 2000). Thus, careful attention should be paid to potential recruitment of krill inthe southern Chukchi Sea, and how seasonal abundance of this important prey affects top predators.

In conclusion, krill could be one of the key prey species driving distribution of top predators in the Arctic Ocean. Sea-ice dynamics, increases in SST, and timing of phytoplankton bloom might affect the recruitment and deveropment of krill in the Bering Sea, which via advection influences the transfer of energy to top predators like short-tailed shearwaters in the Chukchi Sea.

Author contributions. Y. Watanuki and K.J. Kuletz designed and coordinated the vessel-based seabird surveys. B. Nishizawa, E.A. Labunski and Y. Watanuki measured the distribution of short-tailed shearwaters during the cruise. K. Matsuno and A. Yamaguchi collected the zooplankton samples during the cruise. B. Nishizawa performed species identification and enumeration of the zooplankton samples in the laboratory and analysed all of data used in this study. B. Nishizawa and Y. Watanuki wrote the manuscript, with contributions from all of the co-authors.

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Table 1. Summary of vessel-based short-tailed shearwater's surveys. The number of 50 km grids with and without short-tailed shearwaters (STSH) and the density of STSH (ind. km^{-2} at each 50 km grids) (mean ± SD (min.–max.)) are shown.

Year	Area	Period	Season	Survey period (days)	No. grids with STSH	No. grids without STSH	Density of STHS (ind. km^{-2})	Ship speed (kt)
2012	Bering	9 Sep–10 Oct	Fall	12	52	8	16.1 ± 38.4 (0–200.0)	11.6
2012	Chukchi	13 Sep–4 Oct	Fall	21	42	50	18.9 ± 91.1 (0–778.2)	11.5
2013	Bering	19 Jun–28 Jul	Summer	24	84	62	59.6 ± 472.5 (0–5601.1)	10.5
2013	Chukchi	8 Jul–18 Jul	Summer	11	0	66	0	9.3

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Table 2. Summary of krill surveys. krill abundance, total length of kirll and estimated wet weight at each sampling area. Mean ± SD (min.–max.) and sample size are shown.

Year	Area	Period	No. station with krill	No. station without krill	Krill abundance (ind. m^{-2})	Total length of krill (mm)	Wet weight (mg $ind.^{-1}$)
2007	Bering	20 Jul–31 Jul	18	9	176.0 ± 270.3 (0–1157.2)	5.5 ± 4.0 (0.6–25.5) $n = 75$	4.4 ± 16.6 (0.0–108.0) $n = 75$
2008	Bering	24 Jun–2 Jul	27	6	929.1 ± 1227.1 (0–4334.3)	3.0 ± 1.9 (0.5–18.0) $n = 343$	0.7 ± 3.5 (0.0–39.3) $n = 343$
2012	Chukchi	13 Sep–3 Oct	19	31	132.7 ± 304.4 (0 – 1845.3)	9.6 ± 5.0 (4.0–25.0) $n = 106$	11.9 ± 17.4 (0.5–102.0) $n = 106$
2013	Bering	22 Jun–7 Jul	24	10	3059.5 ± 5137.7 (0–20 785.0)	3.3 ± 1.5 (0.7–21.0) $n = 1253$	0.5 ± 2.8 (0.0–61.5) $n = 1253$
2013	Chukchi	8 Jul–17 Jul	18	9	7366.4 ± 16 419.9 (0–69 949.0)	1.9 ± 1.2 (0.5–16.0) $n = 884$	0.2 ± 1.7 (0.0–28.0) $n = 884$

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Table 3. Better-fitting models explaining the occurrence (presence/absence) of short-tailed shearwaters in the fall of 2012 and summer of 2013. Occurrence and size of krill were categorized as "absent", "small" and "large". Season was categorized as "summer" and "fall". Parameter coefficients, their standard errors (S.E.) of each explanatory variables, Akaike's information criterion (AIC) and difference in AIC are shown. Only competing models ($\Delta AIC \leq 2$) are presented. SST; sea surface temperature, Chl *a*; sea surface chlorophyll *a* concentration. Plus marks in the categorical variables show the selected variables in the model.

Model ID.	SST	Chl *a*	Bottom Slope	Krill	Season	AIC	ΔAIC
1	+0.54				+	62.2	0.00
2	+0.47		+0.54		+	63.4	1.20
3	+0.62			+	+	63.5	1.30
4	+0.64	−2.32 (1.90)		+	+	63.9	1.65
5	+0.54	−0.92 (1.65)			+	63.9	1.68

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Table 4. Differences in explanatory variables between the 50 km grids with and without short-tailed shearwaters during the fall of 2012 in the Chukchi Sea and the summer of 2013 in the Bering and Chukchi Seas. Mean ± SD, sample size in parentheses and the results of Mann–Whitney *U* test are shown.

		Presence	Absence	*U* test
SST (°C)	2012 (Fall)	2.65 ± 1.12 (28)	1.59 ± 1.83 (11)	$U = 253$, $p < 0.05$
	2013 (Summer)	8.80 ± 0.97 (15)	6.77 ± 2.35 (46)	$U = 527$, $p < 0.05$
Chl *a* ($mg\,m^{-3}$)	2012 (Fall)	2.14 ± 0.81 (19)	1.79 ± 1.92 (2)	$U = 20$, $p = 0.95$
	2013 (Summer)	0.64 ± 0.44 (10)	0.97 ± 0.93 (42)	$U = 137$, $p = 0.09$
Slope (°)	2012 (Fall)	0.13 ± 0.31 (31)	0.63 ± 0.52 (19)	$U = 105$, $p < 0.05$
	2013 (Summer)	0.21 ± 0.50 (15)	0.07 ± 0.24 (46)	$U = 480$, $p < 0.05$

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Table 5. For the occurrence (presence/absence) of large krill (> 8.0 mm in total length), the number of 50 km grids where the short-tailed shearwaters (STSH) occurred or not are presented. Percentages in parentheses and the result of Fisher's exact test are shown.

Year	Season	Grid type	Occurrence of STSH		Total	Fisher's exact test
			Presence	Absence		
2012	Fall	with large krill	14 (87.5)	2 (12.5)	16 (100)	$p < 0.05$
		without large krill	17 (50)	17 (50)	34 (100)	
2013	Summer	with large krill	4 (33.3)	8 (66.7)	12 (100)	$p = 0.46$
		without large krill	11 (22.4)	38 (77.6)	49 (100)	

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Table 6. Rerationship between the density of short-tailed shearwaters (STSH) (ind. km^{-2} at each 50 km grids) and the size of krill in the fall of 2012 and summer of 2013. Mean ± SD, sample size in parentheses and the results of Mann–Whitney *U* test are shown.

Year	Season	Density of STSH		*U* test
		with large krill	without large krill	
2012	Fall	179.8 ± 311.1 (16)	52.2 ± 155.6 (34)	$U = 384.5$, $p < 0.05$
2013	Summer	1.7 ± 3.2 (12)	0.5 ± 1.5 (49)	$U = 339.5$, $p = 0.28$

Table 7. Diet composition of short-tailed shearwaters during non-breeding periods.

Diet composition (%)								Sampling periods	Area	No. of birds	Unit	Reference
Fish	Squid	Krill	Copepods	Amphipods	Jelly fish	Crab larvae	Others					
5	0	83	0	0	0	11	0	Jul–Aug 1973	Okhotsk Sea	18	Wet weight	Ogi et al., 1980
63	19	9	6	3	0	0	0	Apr–Jun 1973–1977	North Pacific Ocean	125	Wet weight	Ogi et al., 1980
5	14	73	0	8	0	0	0	Jun–Aug 1970–1978	Bering Sea (shelf and basin)	296	Wet weight	Ogi et al., 1980
19	13	73	3	9	11	7	17	Jun–Aug 1981–1982	Bering Sea (Shelf)	46	Frequency	Schneider et al., 1986
0	0	100	0	0	0	0	0	Aug 1989	Bering Sea (Shelf)	23	Wet weight	Hunt et al., 1996
31	0	56	8	0	0	5	0	May–Sep 1997–1999	Bering Sea (Shelf)	288	Volume	Hunt et al., 2002b
21	12	57	0	0	0	0	0	Jul 2003–2008	Bering Sea (Basin)	159	Wet weight	Toge et al., 2011

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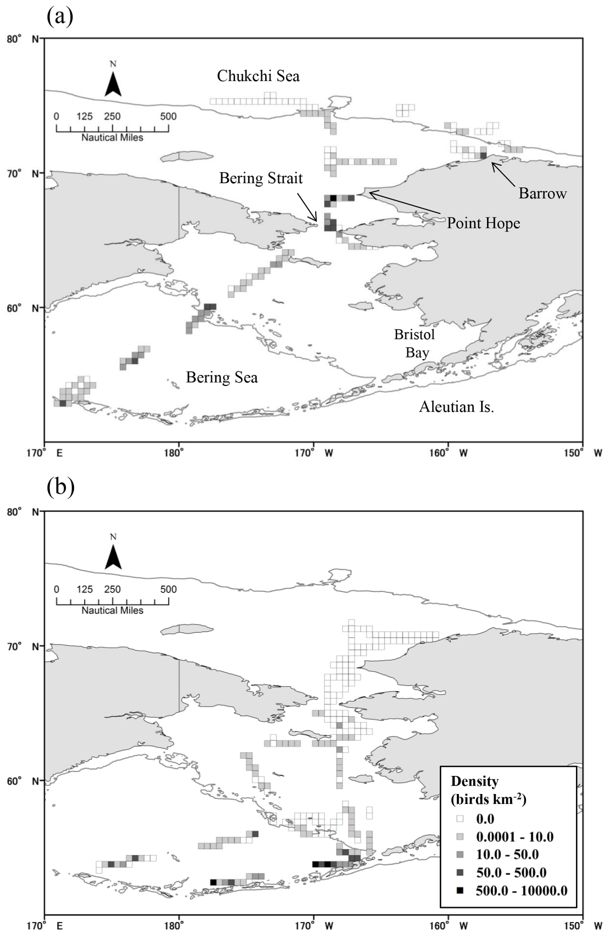

Figure 1. Study area and densities (birds km^{-2} by 50 km grid) of short-tailed shearwater in fall of 2012 **(a)** and summer of 2013 **(b)**. Gray solid lines in each map indicate 200 m-depth contour.

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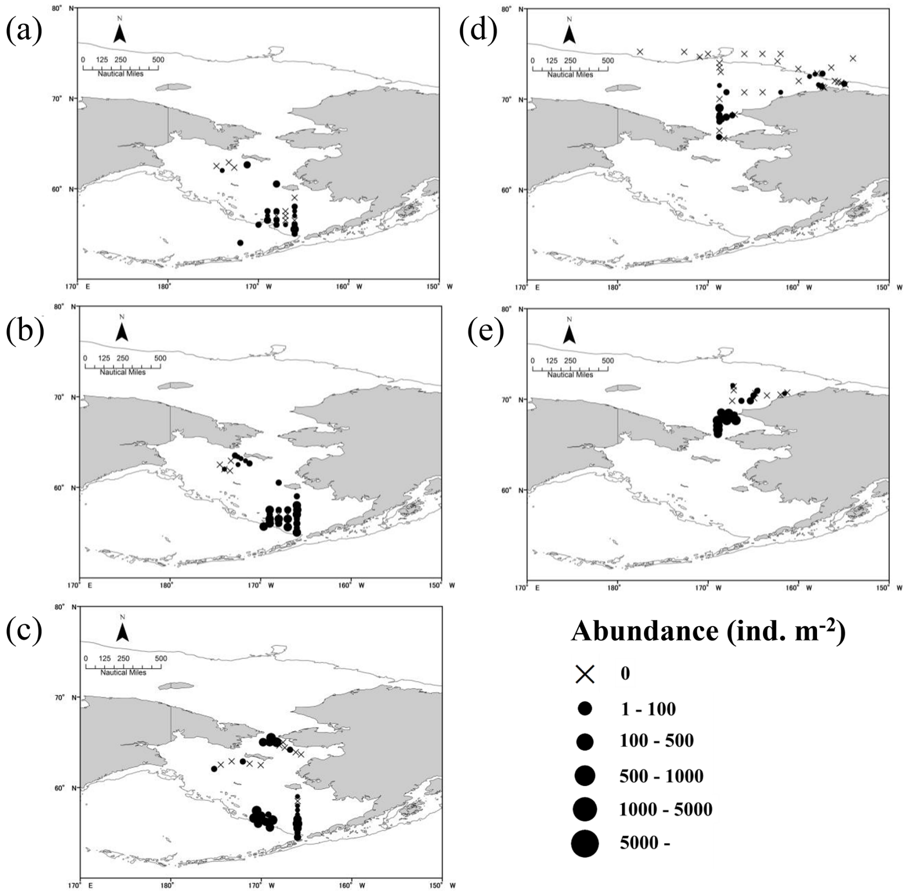

Figure 2. Densities (ind. m^{-2}) of krill in summers of 2007 **(a)**, 2008 **(b)** and 2013 **(c)** in the Bering Sea, and fall of 2012 **(d)** and summer of 2013 **(e)** in the Chukchi Sea. Gray solid lines in each map indicate 200 m-depth contour.

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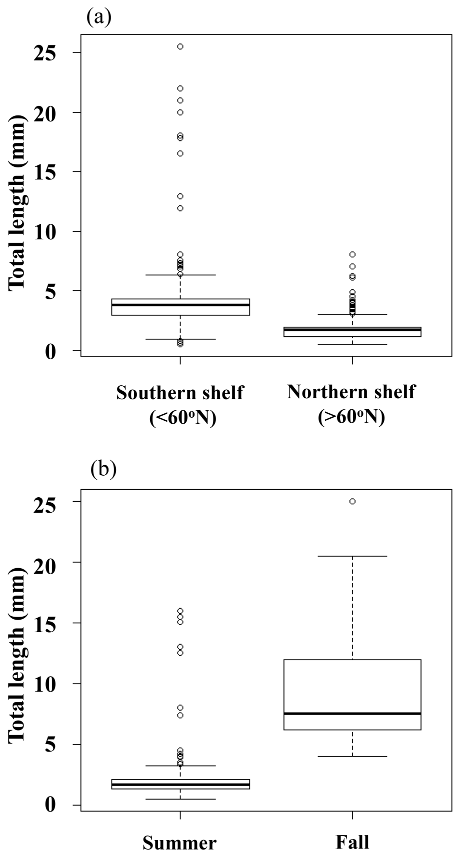

Figure 3. Reginal changes (Southern shelf $< 60^\circ$ N, Northern shelf $> 60^\circ$ N) in total length (from the tip of the rostrum to the posterior end of the telson) of krill in the Bering Sea during summer, 2007, 2008, 2013 (pooled across years) **(a)**, and seasonal changes in total length of krill in the Chukchi Sea during fall of 2012 and summer of 2013 **(b)**.

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