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 potential 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 July in 2013 but in the Bering Strait/southern Chukchi Sea (19 ± 91 birds km^{-2}) in September in 2012. In the Bering Strait/southern Chukchi Sea size of krill was greater in September in 2012 (9.6 ± 5.0 mm in total length) than in July in 2013 (1.9 ± 1.2 mm). Within the Bering Strait/southern Chukchi Sea in September 2012, short-tailed shearwaters occurred more frequently in cells (50 x 50 km) where large krill was more abundant. These findings and the information previously collected in other studies suggest that the seasonal northward movement of short-tailed shearwaters might be associated with the seasonal increase of large krill in the Bering Strait/southern Chukchi Sea. We could not, however, rule out the possibility of large interannual variation in the krill abundance might influence the seasonal distribution of the shearwaters. This study indicates 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 (Mueter and Litzow, 2008; Steel et al., 2008; Li et al., 2009; Hunt et al., 2011; 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). In addition, recent sea-ice loss and the concurrent increases in SST in the western Beaufort Sea have reduced availability of Arctic Cod (*Boreogadus saida*), primary prey of the black guilmots (*Cepphus grylle mandtii*) breeding at Cooper Island in the western Beaufort Sea, which leads to their diet shifts to sculpin (Cottidae) with decrease in nesting growth and survival compared to that in the historical periods (1975–1984) (Divoky et al., 2015). Thus, 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, 2002a; 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).

Recent tracking studies using geolocaters revealed large scale migration of sherawater species (e.g., Shaffer et al., 2006). A geolocater-based study by Yamamoto et al. (2015) showed that short-tailed shearwaters in the Bering Sea move through the Bering Strait to feed in the Chukchi Sea during August and September. 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 the Chukchi Sea in September 2012 and June–July 2013 in the Bering and Chukchi seas and that of the zooplankton (including krill) by vertical tows of NORPAC net in June–July of 2007 and 2008 in the Bering Sea, September 2012 in the Chukchi Sea, and June–July 2013 in the Bering and Chukchi seas. Krill samples collected by plankton net should be highly biased, because of the high net-avoidance ability of krill (Watkins, 2000), but provide a rough estimate of krill abundance across several orders of magnitude.

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 and *T/S Oshoro-Maru* (Department of Fisheries Sciences, Hokkaido University) on 19 June–28 July 2013 in the

Bering and Chukchi seas (50–78^{o}N, 170^{o}E–150^{o}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 an average speed 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). 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. This grid size was selected because foraging area fidelity of short-tailed shearwaters was suggested at a scale of 10 to 10^2 km in the southeastern Bering Sea (Baduini et al., 2006) and strong correlation between density of short-tailed shearwaters and 200 kHz back-scattering strength of acousitics, i.e., the index of zooplankton abundance including krill, was observed at a scale of 10 km in northern Japan Sea (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 collected by the science crew of *T/S Oshoro-Maru* and *R/V Mirai* for the Bering Sea during 20–31 July 2007 (n = 27), 24 June–2 July 2008 (n = 33) and 22 June–7 July 2013 (n = 34), and for the Chukchi Sea during 13 September–3 October 2012 (n = 50) and 8–17 July 2013 (n = 27) (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 ((wet weight) = 0.009 x (total length) $^{(3.02)}$, $R^2 = 0.95$, $p < 0.0001$, for krill of *T. raschii* (as per Harvey et al., 2012)), 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.

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 September 2012 in the Chukchi Sea and during July 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.: 0–5,601.1 birds km^{-2}), and the sample size was relatively small (20 grid cells in September 2012 and 52 in July 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 link function. Explanatory variables included three continuous oceanographic data - sea surface temperature (*SST*; ^{o}C), sea surface chlorophyll *a* concentrations (*Chla*; mg m^{-3}) and ocean bottom slope (*Slope*; ^{o}), and categorical krill data on their occurrence and size.

Monthly *SST* and *Chla* 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 to fit the scale of the bird's data. 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 June–August 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. We defined our survey periods of June–July as "summer" and August–September as "fall" respectively, considering that seasonality of phytoplankton bloom in the southern Chukchi Sea (i.e., spring bloom occur in May–July and fall bloom occur in August–October) (Nishino et al., 2016). 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 *Chla*. Thus, to evaluate effect of season we added "season" (summer or fall) as a second categorical explanatory variable. Unfortunately, we did not have enough data (based on two cruises in fall 2012 and summer 2013) so could not include the "year" as a categorical explanatory variable to examine interannual changes (2012 vs. 2013) in the size and abundance of krill (e.g., Pinchuk and Coyle, 2008; Bi et al., 2015) which could potentially influence shearwater's distribution.

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 $\Delta\text{AIC} \leq 2$ 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 September 2012, short-tailed shearwaters were distributed in the Bering Strait and Chukchi Sea. Density (birds km^{-2} at each 50-km grid) 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 June–July 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). Density 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 (Figs. 2a, b and c). In June–July of 2007, 2008, and 2013, krill abundance (mean ± SD) and estimated biomassin the southeastern Bering Sea shelf (< 60 ^{o}N) (1,631 ± 2,972 m^{-2} for abundance, 1,468 mg wet weight m^{-2} for biomass) were higher than those in the northwestern Bering Sea shelf (> 60 ^{o}N) (1,189 ± 3,981 m^{-2}, 119 mg wet weight m^{-2}). In September, no krill sampling occurred in the Bering Sea. In the Chukchi Sea, krill abundance in June–July 2013 (7,366 ± 16,420 m^{-2}) was greater than that in September 2012 (133 ± 304 m^{-2}), while the biomass in June–July 2013 (1,473 mg wet weight m^{-2}) was similar to that in September 2012 (2,190 mg wet weight m^{-2}). No krill were collected in the Chukchi basin in both July 2013 or September 2012 (Figs. 2d and e).

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, krill collected in September 2012 was larger than that in July 2013 (Mann-Whitney's *U* test, $p < 0.05$) (Fig. 3b). In July 2013, 90% of individuals were in the calyptopis stage while in September 2012, 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 *Chla,* 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 2013 or fall 2012 separately. *SST* was higher in grids with shearwaters than in those without shearwaters both in summer 2013 and fall 2012 (Table 4). *Chla* was not different between grids with or without shearwaters in summer 2013 or fall 2012 (Table 4). *Slope* was different between seasons; *Slope* was steeper in grids with shearwaters than in grids without shearwaters in summer 2013, but the opposite trend occurred in fall 2012 (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 2013 (Table 5). Density of shearwaters was greater in grids with large krill than in those without large krill in fall 2012 and summer 2013 (Table 6).

4 Discussion

4.1 Distribution and diets of short-tailed shearwaters

Our study indicated that short-tailed shearwaters stay in the Bering Sea and Aleutian Islands in June–July and in the Bering Strait and Chukchi Sea in September. Our surveys, however, were based on two cruises carried out in different season in different years and did not include August surveys. Nevertheless the seasonal difference in distribution of short-tailed shearwaters is consistent with previous results from vessel-based surveys and tracking studies of individual birds, which also show interannual variation in their abundance. Tracked short-tailed shearwaters concentrated in the southeastern Bering Sea in July 2010 and 68% of them (13 of 19 birds) moved into the Chukchi Sea in September 2010 (Yamamoto et al., 2015). In contrast, only 38% of tracked shearwaters (9 of 24 birds) moved into the Chukchi Sea from the Bering Sea in September 2011 (Yamamoto et al., 2015). Boat surveys in the Bering and Chukchi seas during early-July to early-August (the data were pooled in 2007–2012) 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 birds were found in the Chukchi Sea. The other boat surveys in the northern Chukchi Sea during August–October, 2008-2010 by Gall et al. (2013) showed that short-tailed shearwaters were found there from mid-August to early-October, and the highest densities in September were common in all 3 years, though the densities of short-tailed shearwaters fluctuated by four orders of magnitude among years (the highest density was found in 2009 and lowest densities in 2008). All these indicate the seasonal movement of the short-tailed sheawaters from the Bering Sea in June–August to the Chukchi Sea in August–October with extensive interannual variation.

Information on the diets of short-tailed shearwaters was not collected in this study. Previous studies have shown that krill comprised most of their diet in the northern North Pacific and Bering Sea (Table 7), although the diet of short-tailed shearwaters are highly variable across areas at a small scale, seasons, and years (e.g, Ogi et al., 1980; Hunt et al., 1996, 2002a). 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, 2002a). Thus, in this study, we foucused on the linkage between distribution of krill and the seasonal movements of migrating shearwaters at a reginal scale (Bering Sea vs. Chukchi Sea).

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, although 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 during daytime. 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 trend of northward movement of short-tailed shearwaters in September from Bering Sea to Chukchi Sea might be associated with the seasonal increase in the abundance of larger size of krill in the Chukchi Sea. In the Chukchi Sea, the size of krill collected during this study in September (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 collected in June–July in the same region (1.9 ± 1.2 mm) (Fig. 3b). In contrast, in the southeastern Bering shelf, previous study based on MOCNESS sampling showed that the mature *T. raschii* was abundant during May–June, while the smaller immature was abundant during August–September (Coyle and Pinchuk, 2002). Krill eggs and nauplii collected using CalVET net (CalCOFI vertical egg tow) in the southeastern Bering Sea shelf were more abundant during May–June (56 m^{-3} in 1997, 133 m^{-3} in 1998 and 306 m^{-3} in1999) than during August–September (0.2 m^{-3} in 1997, 11 m^{-3} in 1998 and 3.5 m^{-3} in 1999) in all three sampling years (1997–1999), indicating that the most of the krill spawning might occur in May–June in the southeastern Bering shelf (Coyle and Pinchuk, 2002). The other study using MOCNESS tows also showed that high abundance of krill nauplii on the inner shelf of southeastern Bering Sea occurred in mid-May to June (Smith 1991). Continuous echo data collected by the mooring system in the southeastern Bering Sea in 2006 showed that the densities of krill were high in July and decreased in August-September (Stafford et al., 2010). These indicate that krill spawns in May–June and its the size and density decreased seasonally in the southeastern Bering Sea. Krill in the Bering Sea is known to live 3–4 years (Hunt et al., 2015), and they are likely to decend to deep and cold water except when spawning (e.g., Hanamura et al. 1989; Coyle and Pinchuk, 2002).

Some short-tailed shearwaters stay in the southeastern Bering shelf in August–September, and they feed on alternative prey, such as copepod, crab zoea and 0-age walleye Pollack or *T. raschii* that continued spawning until August–September (Hunt et al., 1996, 2002a). Note that timing of krill spawning varies between species; *T. inermis* (commonly found in middle and outer shelf domain) spawns in early spring (April–May) at the onset of the phytoplankton bloom and relies on lipid reserves to produce eggs, while *T. raschii* (commnly found in the middle and inner shelf domains) reproduces for a more prolonged period through August–September with main spawning during May–June (Smith, 1991;

Coyle and Pinchuk, 2002), apparently utilizing ambient food supplies.

Within the Chukchi Sea in September, the density of short-tailed shearwaters was high in areas off Point Hope and off Point Barrow. The latter also remained a “hotspots” of shearwater activity in 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), though there might be the effects of interannual changes of krill abundance and distribution. Within the Bering Sea in July, 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; Bi et al., 2015; this study).

Previous studies in the eastern Bering Sea showed that abundance of krill are not only seasonal but also variable from year to year (Stabeno et al., 2012; Hunt et al., 2015). There is recent evidence that the abundance of krill on the Bering Sea shelf is greater in years with cold, icy spring and cold summers versus years with warmer conditions (Coyle et al., 2008; Pinchuk and Coyle, 2008; Hunt et al., 2015). The dramartic decline in *T. inermis* and *T. raschii* abundance of eastern Bering shelf in August 2004 as compared to August 1999 coincided with a warmer summer accompanied by weak winds, which resulted in 4–5^{o}C higher temperatures in the upper-mixed layer and strong stratification of the water column (Coyle et al., 2008). In this study, we could not directly compare the abundance of krill between 2012 and 2013 due to different sampling season (September 2012 and July 2013) in the Chukchi Sea. The first day when sea-ice concentrations were below 10% in the southern Chukchi Sea hotspot (68°03N, 168°50W) were 9 June in 2012 and 10 June in 2013. No sea-ice was found in the southeastern Bering Sea shelf (56^{o}40N, 163^{o}52W, location of Mooring 2) in both 2012 and 2013 (Figure S1). Thus this timing of sea-ice retreat did not differ largely between 2012 and 2013. SST in the southeastern Bering Sea shelf during April–October in 2012 and 2013 were 4.6 ± 3.2 ^{o}C and 5.7 ± 3.8 ^{o}C respectively, and SST in the southern Chukchi Sea during May–October in 2012 and 2013 were 2.3 ± 2.6 ^{o}C and 3.6 ± 2.7 ^{o}C respectively (Figure S2). Thus SST in 2013 was 1.1–1.3 ^{o}C higher than that in 2012 in the southeastern Bering Sea shelf and southern Chukchi Sea. The surface Chla peaked on 14 May in 2012 and 10 May in 2013 in the southeastern Bering Sea shelf (56^{o}40N, 163^{o}52W) and on 20 June in 2012 and 12 June in 2013 in the southern Chukchi Sea (68^{o}03N, 168^{o}50W) (Figure S3). Thus the timing of spring bloom in 2013 was 4–8 days earlier than that in 2012. The growth and survival of krill are poor in the warm water years because of lack of food, i.e., ice-associated bloom, and high predation pressure due to the increase and range expansion of predator, i.e., walleye pollack (Stabeno et al., 2012). Therefore, recruitment of krill might be poor in 2013 because of warmer SST and earlier spring bloom compared to 2012. Thus, we could not exclude the possibility that short-tailed shearwaters were found in the Chukchi Sea in September 2012 and were not found there in July 2013, which might be related to presumable stronger recruitments of krill (i.e., high krill abundance) in 2012 than in 2013.

4.3 Environmental change and trophic effects through krill

Our study indicates that the one of explanations of the seasonal movement of short-tailed shearwaters may be spatial pattern of krill. 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 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). The arrival of migratory fin whales (*Balaenoptera physalus*) in the southern Chukchi Sea in August coincided with an increase of the water temperature and that of the abundance of zooplankton including krill and copepods transported from the Bering Sea (Tsujii et al., 2016). All these indicate that the seasonal and regional patterns of the abundance of krill affect diets and distributions of top predators in the nothern North Pacific and Arctic Ocean. Our study further indicate that the size of krill might affect the distribution of top predators. Therefore, krill could be an important component of energy transfer from phytoplankton to top predators in the marine food webs in the northern Bering Sea and southern Chukchi 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., 2002b). Further, the timing of sea-ice retreat can influence primary producers by modifying light availability which could in turn affect krill abundance (Stabeno et al., 2012). Late ice retreat (late March or later) leads to an early, ice-associated bloom in cold water, whereas no ice or early ice retreat before mid-March, leads to an open-water bloom in May or June in warm water. Krill abundance increased during the cold period when the extent of sea ice was large and decreased during the warm period (Coyle et al., 2008; Hunt et al., 2011; Ressler et al., 2012), though the mechanisms responsible for this are not clear. One possibility is bottom-up controls. A failure of food availability at a critical time (mismatch) may reduce the growth and survival of krill during the warm years. *T. raschii* relies on its stored lipids to overwinter (Falk-Petersen et al., 2000), and has been observed foraging on under-ice algae (ice-associated bloom) in the Bering Sea and feeding rates were enhanced when they were allowed to feed on large cells of ice related algae in the laboratory (Lessard et al., 2010). Or the warmer conditions with reduced ice coverage, early ice retreat, greater spring and summer solar radiation, and reduced wind mixing leading to smaller “cold pools” and warmer, stratified surface temperatures in summer are somehow unfavorable for krill. Because strong stratification in summer depresses post-bloom new production, therefore, the krill, lacking appropriate food resources, leave the water column when the surface layer warms (Coyle et al., 2008). Another possibility that high predation pressure due to the increase in predator (walleye pollock) abundance and the expansion of predator distribution (top-down control). However, a recent study by Ressler et al. (2014) suggested that the spatial distribution of krill did not show significant relationship with the abundance of walleye pollock.

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 ^{o}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 ^{o}C; Bering Shelf Water and Anadyr Water, 0–10 ^{o}C, Coachman et al., 1975; Eisner et al., 2013). There are interannual 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 (75^{o}N) in part of the Arctic Ocean (Timofeev, 2000). Thus, careful researches have to be carried out on the potential of the recruitment of krill in the southern Chukchi Sea, and on the seasonal and interannual variations in abundance of this important prey.

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 water temperature, 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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Figure captions

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.

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.

Figure 3. Reginal changes (Southern shelf < 60 ^{o}N, Northern shelf > 60 ^{o}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).

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 June - 28 July	Summer	24	84	62	59.6 ± 472.5 (0 - 5601.1)	10.5
2013	Chukchi	8 July - 18 July	Summer	11	0	66	0	9.3

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	6.2±24.1 (0.0-159.2), 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	0.8±4.9 (0.0-55.6), 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	16.5±24.9 (0.6-150.0), n=106
2013	Bering	22 Jun-7 Jul	24	10	3059.5±5137.7 (0-20785.0)	3.3±1.5 (0.7-21.0), n=1253	4.3±8.8 (0.0-88.0), n=1253
2013	Chukchi	8 Jul-17 Jul	18	9	7366.4±16419.9 (0-69949.0)	1.9±1.2 (0.5-16.0), n=884	0.2±2.3 (0.0-39.0), n=884

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 (ΔAIC ≤ 2) are presented. SST; sea surface temperature, Chla; sea surface chlorophyll a concentration. Plus marks in the categorical variables show the selected variables in the model.

Model ID.	SST	Chla	Bottom Slope	Krill	Season	AIC	ΔAIC
1	+0.54 (0.24)				+	62.2	0.00
2	+0.47 (0.24)		+0.54 (0.61)		+	63.4	1.20
3	+0.62 (0.24)			+	+	63.5	1.30
4	+0.64 (0.25)	-2.32 (1.90)		+	+	63.9	1.65
5	+0.54 (0.24)	-0.92 (1.65)			+	63.9	1.68

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 (^{o}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)	$U = 527, p < 0.05$
Chla (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)	$U = 480, p < 0.05$

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)	

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	July-Aug., 1973	Okhotsk Sea	18	Wet weight	Ogi et al. 1980
63	19	9	6	3	0	0	0	April-June, 1973-1977	North Pacific Ocean	125	Wet weight	Ogi et al. 1980
5	14	73	0	8	0	0	0	June-Aug., 1970-1978	Bering Sea (shelf and basin)	296	Wet weight	Ogi et al. 1980
19	13	73	3	9	11	7	17	June-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	July, 2003-2008	Bering Sea (Basin)	159	Wet weight	Toge et al. 2011