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

B. Nishizawa[1, *], K. Matsuno[1,2], E.A. Labunski[3], K.J. Kuletz[3], A. Yamaguchi[1], Y. Watanuki[1]

[1]{Graduate School of Fisheries Sciences, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido, 041-8611, Japan}

[2]{National Institute of Polar Research, 10-3 Midori-cho, Tachikawa, Tokyo 190-8518, Japan}

[3]{US Fish and Wildlife Service, 1011 E. Tudor Road, Anchorage, AK 99503, USA}

[*]Correspondence to: B. Nishizawa (nishizawa@salmon.fish.hokudai.ac.jp)

Abstract

The short-tailed shearwater (*Ardenna tenuirostris*) is one of the abundant marine top predators in the Pacific; this seabird spends its non-breeding period in the northern North Pacific during May–October and many visit the southern Chukchi Sea in August–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 net tows in the southeastern Bering Sea/Aleutian Islands and in the Bering Strait/southern Chukchi Sea. Short-tailed shearwaters were mainly distributed in the southeastern Bering Sea/Aleutian Islands (60 ± 473 birds km^{-2}) in July 2013, and in the Bering Strait/southern Chukchi Sea (19 ± 91 birds km^{-2}) in September 2012. In the Bering Strait/southern Chukchi Sea krill size was greater in September 2012 (9.6 ± 5.0 mm in total length) than in July 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 × 50 km) where large size of krill were more abundant. These findings, and information previously collected in other studies, suggest that the seasonal northward movement of short-tailed shearwaters might be associated with the seasonal increase in krill size in the Bering Strait/southern Chukchi Sea. We could not, however, rule out the possibility that large interannual variation in krill abundance might influence the

seasonal distribution of shearwaters. This study highlights the importance of krill, which is advected from the Pacific, as an important 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). 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 an important role in trophic energy flow (Schneider et al., 1986; Piatt and Springer, 2003). As mobile predators that can respond quickly to shifts in prey distribution (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 have shown evidence of shifts in upper trophic level species composition, distribution, and abundance. For example, gray whales (*Eschrichtius robustus*) in the Chirikov Basin expanded their foraging range to the north as their prey biomass (amphipods) decreased from 1983 to 2000 (Moore et al., 2003). Similarly, dramatic declines in numbers of spectacled eiders (*Somateria fischeri*) coincided with declines in clam populations they feed on in the northern Bering Sea (Lovvorn et al., 2009). In addition, recent sea-ice loss and the concurrent increases in sea surface temperature (SST) in the western Beaufort Sea may have reduced availability of Arctic Cod (*Boreogadus saida*), which are primary prey of black guilmots (*Cepphus grylle mandtii*) breeding at Cooper Island in the western Beaufort Sea; these seabirds subsequently shifted to feeding their chicks sculpin (Cottidae), which led to lower nestling growth and survival compared to that in historical periods (1975–1984) (Divoky et al., 2015). Consistent with these examples, we propose that at-sea distributions of top predators in relation to their prey can provide useful information about large-scale ecosystem changes in these regions with seasonal sea-ice.

Short-tailed shearwaters (*Ardenna tenuirostris*) migrate annually from their breeding colonies in southeastern Australia and Tasmania to spend their non-breeding period of 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 amounts of krill, particularly the euphausiids *Thysanoessa raschii* and *T. inermis* (Schneider et al., 1986; Hunt et al., 1996, 2002; Toge et al., 2011). In the Bristol Bay area of the southeastern Bering Sea, krill consumption by 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).

Tracking studies using geolocaters revealed the large-scale migration of shearwater 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 north through the Bering Strait to feed in the Chukchi Sea during August and September. This northward shift of distribution was hypothesized to be related to the temperature driven changes in the abundance of their prey (krill), since 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 using vessel-based surveys in the Chukchi Sea in September 2012 and June–July 2013 in the Bering and Chukchi seas. We also examined the distribution of zooplankton (including krill) in the Bering and Chukchi seas.

2 Materials and Methods

2.1 Seabird surveys

At-sea seabird surveys were conducted onboard the *R/V Mirai* (Japan Agency for Marine-Earth Science and Technology) on 9 September–10 October 2012 and the *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 (Tasker et al., 1984), with surveys conducted at an average vessel speed of 10.7 knots. All birds (both flying and sitting on water) were counted continuously from the bridge (eye height above sea surface of 13.6 m on *R/V Mirai* and 8.5 m on *T/S Oshoro-Maru*). We used a 300-m transect window (from bow to 90° to port or starboard) for *T/S Oshoro-Maru* and a 500-m transect window for *R/V Mirai*, from 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 (*Ardenna 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 dark shearwaters that we identified to species were short-tailed shearwaters, therefore we assumed that all unidentified shearwaters were short-tailed shearwaters, and hereafter refer to total dark shearwaters as “shearwaters”.

We calculated the relative density (birds km^{-2}) of shearwaters over a 50 km × 50 km grid. We selected this grid size because foraging area fidelity of shearwaters was estimated to be 10 to 10^2 km in the southeastern Bering Sea (Baduini et al., 2006), and there is a strong correlation between density of shearwaters and an acoustic index of zooplankton abundance (including krill) at a scale of 10 km in the northern Sea of Japan (Kurasawa et al., 2011). To standardize for unequal survey effort among cells, the total number of birds in each grid cell was divided by km^2 surveyed in the cell.

An additional source of at-sea seabird data was obtained from the North Pacific Pelagic Seabird Database 2.0 (NPPSD; Drew et al., 2015). For this dataset, we excluded aerial surveys and surveys without a defined transect width. For additional information on the datasets and data collection methods used in the NPPSD, see Renner et al. (2013) and Kuletz et al. (2014). All NPPSD surveys used standard strip transect methodology, usually with a 300-m strip width, and counted all birds on the water or actively foraging (Tasker et al., 1984). Two different methods for counting flying birds were used. Most surveys in the 1970s and 1980s counted all flying birds observed within the transect strip. Beginning in the 1980s, many surveys used the snapshot method (Tasker et al., 1984), which was adopted by most investigators by the 2000s. The snapshot is a simple method for minimizing overestimation of flying birds and it allows calculation of densities (birds km^{-2}) without further manipulation of the data. To meld datasets collected using these different survey methods, we divided the number of flying birds in a sample by a correction factor λm when the snapshot method was not used. Lacking empirical data for short-tailed shearwater flight speeds, we used the value $\lambda m = 2.3$ reported by van Franeker (1994) for the southern fulmar (*Fulmarus glacialoides*), a bird of similar size and flying habits. To examine seasonal changes in the density of shearwaters in the Bering Sea and Chukchi Sea, we applied generalized additive models (GAMs) where the density of shearwaters was the response variable and Julian date (all sampling years, 1975 through 2012 were combined) was the explanatory variable. GAMs were fitted using the package mgcv in R software (version 3.1.0, R Development Core Team 2014).

2.2 Krill sampling

A total of 171 zooplankton samples were collected by the science crews 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 North Pacific Standard Net (NORPAC) (mouth diameter 45 cm, mesh size 335 μm) from 5 m above the bottom to the surface (depths of most stations were ~ 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 should not have affected 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 (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 (to the nearest 0.1 mm from the tip of the rostrum to the posterior end of the telson; Hanamura et al., 1989) usually on 20% of the specimens for each sample, and divided them into five growth stages (i.e., nauplius, calyptopis, furcilia, juvenile, and adult) following Brinton et al. (2000). We calculated the wet weight per individual krill using the length-weight relationship equation (wet weight = 0.009 × total length$^{3.02}$, R^2 = 0.95, p < 0.0001, for *T. raschii* (as per Harvey et al., 2012)); we 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 multiplied by abundance (ind. m^{-2}).

Krill samples collected by plankton net could be highly biased, because of the high net-avoidance ability of krill (Watkins, 2000), but they can provide a rough estimate of krill abundance across several orders of magnitude. Net avoidance can affect the absolute number of krill entering the net due to the advanced eye structures in both juveniles and adults

(Watkins, 2000). Furthermore, since large size of krill can swim faster than small size of krill, they may be able to avoid the net more successfully (Hovekamp, 1989). Thus, the absolute abundance of juvenile and adult krill may have been underestimated in this study. Nevertheless, we were able to compare the relative abundance of each size class (or growth stage) of krill between regions.

2.3 Analyses

To explore the factors affecting spatial patterns of shearwaters we used a habitat modelling approach using data collected in September 2012 in the Chukchi Sea and in July 2013 in the Bering and Chukchi seas, when both seabird and zooplankton surveys were conducted. Because shearwater densities 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 examined the factors affecting the presence or absence of shearwaters. We used generalized linear models (GLMs) where the occurrence (presence/absence in each 50-km grid cell) of 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 a 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 match the scale of the bird data. Krill sizes (total length in mm) were divided into two categories, "small" (< 8.0 mm in total length) and "large" (> 8.0 mm), since the length of krill found in shearwater diet during June–August in the southeastern Bering Sea was > 8.8 mm (Vlietstra et al., 2005). Then, the occurrence (presence or absence) and krill size (small or large) were treated as a categorical explanatory variable for each station. Each station with krill samples was linked to the closest seabird survey grid cell, with distance between krill and seabird cells averaging ~ 33 km. We defined two seasonal periods: summer (June–July) and fall (August–October), based on documented phytoplankton bloom in the southern Chukchi Sea (spring bloom occurs in May–July and fall bloom occurs in August–October; Nishino et al., 2016). The data for each season and year (fall 2012 and summer 2013) were pooled into a single dataset for constructing a GLM, because the sample size was small due to limited seabird surveys or missing environmental data (due to cloud cover) in remotely sensed data. Thus, to evaluate the effect of season we added "season" (summer or fall) as a second categorical explanatory variable. We did not have enough data (based on two cruises in fall 2012 and summer 2013) to examine interannual changes (2012 vs. 2013) in the size and abundance of krill (e.g., Pinchuk and Coyle, 2008; Bi et al., 2015).

Prior to modelling, the co-linearity of all continuous explanatory variables was evaluated using variance inflation factors (VIF). All VIF values were below 5, indicating that no co-linearity was assumed in this study (Zuur et al., 2009). We selected the best-performing models using Akaike Information Criterion (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 shearwaters and krill

In September 2012, shearwaters were widely distributed in both the Bering Sea and Chukchi Sea (Fig. 1a). Shearwater density (birds km^{-2} in each 50-km grid) was high in the Bering Strait (46.7 km^{-2}), the area off Point Hope (145.6 km^{-2}) and off Barrow (37.8 km^{-2}), with few birds in the Bering Sea basin (11.1 km^{-2}) (Fig. 1a). No shearwaters were found in the Chukchi Sea basin (Fig. 1a). In June–July 2013, shearwaters were distributed in the Bering Sea, while no birds were found in the Bering Strait and Chukchi Sea (Fig. 1b). Shearwater 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). NPPSD data indicated that shearwater density in the Bering Sea increases between mid-May and September, with the peak in early June (Fig. 2a). Shearwater density in the Chukchi Sea increases between mid-August and mid-October, with a peak in early September (Fig. 2b).

On the Bering Sea shelf in June–July, krill were collected throughout the study area (Figs. 3a–c). However, in June–July (2007, 2008, and 2013, combined), krill abundance (mean ± SD) and estimated biomass in the southeastern Bering Sea shelf (< 60 °N) (1,631 ± 2,972 m^{-2} for abundance, 3180 mg wet weight m^{-2} for biomass) were higher than those in the northwestern Bering Sea shelf (> 60 °N) (1,189 ± 3,981 m^{-2}, 535 mg wet weight m^{-2}). In September, no krill sampling was conducted in the Bering Sea. In the Chukchi Sea, krill were collected in both September 2012 and July 2013 (Figs 3d and e). Krill abundance in the Chukchi Sea in June–July 2013 (7,366 ± 16,420 m^{-2}) was much greater than that in September 2012 (133 ± 304 m^{-2}), while the krill 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}).

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 40 *T. raschii* and three *T. inermis*. In the Bering Sea, krill collected in June–July (2007, 2008, and 2013, combined) were larger in the southeastern shelf than those collected in the northwestern shelf (Mann-Whitney's *U* test, $p < 0.05$) (Fig. 4a). Krill 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 were larger than those in July 2013 (Mann-Whitney's *U* test, $p < 0.05$) (Fig. 4b). In July 2013, 90% of individuals were in the calyptopis stage, while in September 2012, 74% of individuals were furcilia, 7% juvenile, and 19% adult stage.

3.3 Occurrence of krill and shearwaters

Five better-fitting models (ΔAIC $\leq$ 2) were selected for explaining the occurrence of shearwaters (Table 3). *SST* was included in all better-fitting models and its effect was positive, indicating that the probability of the occurrence of shearwaters was higher in warmer waters in the Bering and Chukchi seas. The other explanatory variables such as *Chla*, *Slope* and *krill* were included in one or two better-fitting models, suggesting they had less influence (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* had a different effect 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 appeared to occur more often in grids with large size of krill in fall 2012 but this trend was not apparent in summer 2013 (Table 5). Shearwater density seemed to be greater in grids with large size of krill than in those without large size of krill in fall 2012 and summer 2013 (Table 6).

4 Discussion

4.1 Distribution and diets of shearwaters

Our surveys and the long-term NPPSD both showed similar seasonal changes in the distribution of shearwaters within the Bering and Chukchi seas. In May–July shearwaters mainly used the Bering Sea and Aleutian Islands, while in August–October they were widely distributed both in the Bering Sea and Chukchi Sea. Our results are consistent with previous studies from both 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 (2007–2012, pooled) by Wong et al. (2014) showed that high densities of shearwaters occurred in the Aleutian Islands, southern Bering Sea, and Bering Strait, but few birds were found in the Chukchi Sea. The other vesssel-based surveys in the northern Chukchi Sea occurred during August–October, 2008-2010; in this study, Gall et al. (2013) showed that shearwaters were found there from mid August to early October, with highest densities occurring in September in all 3 years. Overall, our study and previous studies show a similar pattern, with a substantial portion of shearwaters that are in the Bering Sea in summer moving into the Chukchi Sea in fall.

Information on the diets of shearwaters was not collected during this study, but previous studies have shown that krill comprise most of their diet in the northern North Pacific and Bering Sea (Table 7). Still the diets of shearwaters are highly variable across sub-regions, seasons, and years (Ogi et al., 1980; Hunt et al., 1996, 2002). Other prey species have 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, comprising 72–100% of diet for short-tailed shearwaters in the Bering Sea during the non-breeding season (Schneider et al., 1986; Hunt et al., 1996, 2002). Thus, in this study, we foucused on the linkage between distribution of krill and the seasonal movements of migrating shearwaters at a regional scale (Bering Sea vs. Chukchi Sea).

In the Aleutian Pass and southeastern Bering Sea, shearwaters ate large sizes of krill (11.5–16.9 mm) even when small sizes of krill (5.0–8.4 mm) were present, although they tended to feed on smaller krill at a tidal front (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 swarms of krill during daytime. Thus, short-tailed shearwaters tended to feed on larger and more mature krill, perhaps because larger krill contain more gross energy than smaller krill (Färber-Lorda et al., 2009). Additionaly, surface swarms of adult krill might 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 movement of shearwaters from the Bering Sea to Chukchi Sea in fall might be associated with the seasonal increase in krill size in the Chukchi Sea. In the Chukchi Sea, the size of krill collected during our survey period in September 2012 (9.6 ± 5.0 mm), was within the size range found in the stomach of short-tailed shearwaters in the southern Bering Sea (Vlietstra et al., 2005); they were also larger and older than those collected in July 2013 in the same region (1.9 ± 1.2 mm) (Fig. 4b).

In contrast to the Chukchi Sea, a study in the southeastern Bering Sea shelf, found that the mature *T. raschii* was abundant during May–June, while the smaller immature krill was abundant during August–September (Coyle and Pinchuk, 2002). Krill eggs and nauplii collected using CalVET net (CalCOFI vertical egg tow, 150-μm mesh) 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). This difference occurred 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). Earlier, Smith (1991) showed that high abundance of krill nauplii on the inner shelf of southeastern Bering Sea occurred in mid-May–June. Furthermore, 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 studies indicate that krill in the southeastern Bering Sea mainly spawns in May–June, and its size and density decreased seasonally. We should note here 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* (commonly 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. The presence of krill in various developmenetal stages is coincident with a portion of the short-tailed sherwaters staying in the southeastern Bering shelf until October, where they feed on adult *T. raschii* that continue spawning through August–September (Hunt et al., 1996).

In the Chukchi Sea in September 2012, the presence of large size of krill (> 8.0 mm) was associated with the occurrence and high density of shearwaters (Tables 5 and 6). Also, in the Bering Sea in July 2013, the density of shearwaters was higher in the southeastern shelf than in the northwestern shelf (Fig. 1b), which might be related to the higher abundance and the presence of larger sized krill there (Sigler et al., 2012; Bi et al., 2015; this study). These results also support our hypothesis that seasonal northward movement of shearwaters might be associated with the seasonal increase in krill size in the Chukchi Sea.

The interannual differences in krill abundance could have been due to the different seasons in which we sampled in the Chukchi Sea between years (September 2012 and July 2013). Previous studies showed that krill abundance in the eastern Bering Sea are not only seasonal but also variable from year to year (Stabeno et al., 2012; Hunt et al., 2015); krill abundance on the Bering Sea shelf is greater in years with cold, icy springs and cold summers versus years with warmer conditions (Coyle et al., 2008; Pinchuk and Coyle, 2008; Hunt et al., 2015). Stabeno et al. (2012) hypothesized that 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 predators such as walleye pollock (*Theragra chalcogramma*). In our study, the first day when sea-ice concentrations were below 10% in the southern Chukchi Sea (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°40N, 163°52W, Mooring

2) in both 2012 and 2013 (Fig. S1). Thus, the timing of sea-ice retreat did not differ substantially between 2012 and 2013. SST in 2013 was about 1 ºC higher than that in 2012 in the southeastern Bering Sea shelf and southern Chukchi Sea (Fig. S2). The surface chlorophyll *a* concentrations peaked on 14 May in 2012 and 10 May in 2013 in the southeastern Bering Sea shelf and on 20 June in 2012 and 12 June in 2013 in the southern Chukchi Sea (Fig S3). The timing of spring bloom in 2013 was therefore 4–8 days earlier than that in 2012. As a result, krill recruitment might have been poor in 2013 in the Bering and Chukchi Seas because of warmer SST and earlier spring bloom compared to 2012. One possibility we cannot exclude is that shearwater distribution differed between years because of interannual differences in krill abundance (not seasonal patterns); i.e., shearwaters were in the Chukchi Sea in September 2012, but not in July 2013 because there was a stronger krill recruitment (and high krill abundance) in 2012.

4.3 Environmental changes and trophic effects through krill

Our study indicates that one of the explanations for the seasonal movement of shearwaters is the spatial pattern of krill. Other top predators show a similar relationship with their prey. There are several examples among marine mammals: for example, bowhead whales (*Balaena mysticetus*) feed on subsurface patches of krill (*T. raschii*) in the western Chukchi Sea during fall (September–October; Moore et al., 1995). Gray whales that usually feed on benthic amphipods (Moore et al., 2003) feed on krill when and where abundance of amphipods decreased and/or that of krill increased (Bluhm et al., 2007). The arrival of migratory fin whales (*Balaenoptera physalus*) in the southern Chukchi Sea in August coincided with an increase in water temperature and abundance of zooplankton (including krill and large copepods) transported from the Bering Sea (Tsujii et al., 2016). Krill therefore serves as an important component of energy transfer from phytoplankton to top predators in the marine food webs of the northern Bering Sea and southern Chukchi Sea.

In the Bering Sea, spawning of krill (*T. raschii*) are influenced not only by seasonal change in ocean temperture (Smith, 1991) but also by elevated phytoplankton density (Paul et al., 1990; Hunt et al., 1996). *T. raschii* relies on its stored lipids to overwinter (Falk-Petersen et al., 2000), and has been observed foraging on under-ice algae, exhibiting higher feeding rates when feeding on large, ice-related algae in the laboratory (Lessard et al., 2010). 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). Indeed, krill abundance increased during a period of cold years when the extent of sea-ice was large, but krill decreased during the period with warm years (Coyle et al., 2008; Hunt et al., 2011; Ressler et al., 2012), although the mechanisms remain unclear.

The distribution and abundance of krill in the Chukchi Sea are believed to be affected by the advection of the Pacific water through the Bering Strait (Berline et al., 2008, Eisner et al., 2013). Our results showed that 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 interannual and regional variations in 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 krill reproduction 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°N) in the Russian Arctic (Timofeev, 2000). Further research on the potential recruitment of krill in the southern Chukchi Sea, and on mechanisms responsible for the seasonal and interannual variations in krill abundance usefull in interpreting shearwater migratory behavior.

In conclusion, krill is 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 affect the recruitment and development of krill in the Bering Sea, which via advection into the Chukchi Sea, transfers energy to predators such as short-tailed shearwaters which forage in the Arctic in late summer and fall.

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 analyzed all of the 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} in each 50-km^2 grid) of short-tailed shearwaters (*Ardenna tenuirostris*) in fall 2012 (a) and summer 2013 (b). Solid gray lines indicate the 200-m-depth contours.

Figure 2. Seasonal changes in the density (birds km^{-2}) of short-tailed shearwaters (*Ardenna tenuirostris*) in the Bering Sea (a) and Chukchi Sea (b). Densities were estimated using a generalized additive model (GAM). Gray shading indicates 95% confidence limits and thick marks on the *x*-axis indicate the locations of data points. Significance levels (*p*-values) are shown on each plot.

Figure 3. Densities (ind. m^{-2}) of krill in summer 2007 (a), 2008 (b), and 2013 (c) in the Bering Sea, and fall 2012 (d) and summer 2013 (e) in the Chukchi Sea. Solid gray lines indicate the 200-m-depth contours.

Figure 4. Regional changes (southern shelf <60°N, northern shelf >60°N) in the 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, and 2013 (pooled across years) (a), and in the Chukchi Sea during fall 2012 and summer 2013 (b).

Table 1. Summary of vessel-based short-tailed shearwater (*Ardenna tenuirostris*; STSH) surveys. The number of 50-km^2 grids with and without STSH, and the density of STSH (birds km^{-2} in each 50-km grid; 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 showing the abundance, total length, and estimated wet weight of krill in each sampling area. Values are means ± SD (min.– max.), and sample sizes are also shown.

Year	Area	Period	No. stations with krill	No. stations 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	0.7±3.9 (0.0-88.6), 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. The five better-fitting models explaining the occurrence (presence/absence) of short-tailed shearwaters (*Ardenna tenuirostris*) in fall 2012 and summer 2013. The occurrence and size of krill were categorized as “absent,” “small,” and “large.” Season was categorized as “summer” and “fall.” Parameter coefficients and standard errors (SE), Akaike’s information criterion (AIC), and the difference in AIC are shown. Only competing models (ΔAIC $\leq$ 2) are presented. SST: sea surface temperature; Chl*a*: sea surface chlorophyll *a* concentration. Plus marks indicate the categorical variables that were included 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 the explanatory variables between the 50-km^2 grids with and without short-tailed shearwaters (*Ardenna tenuirostris*) during fall (September) 2012 in the Chukchi Sea and summer (June–July) 2013 in the Bering and Chukchi Seas. Values are means ± SD, with sample sizes in parentheses. The results of Mann-Whitney *U* tests are also shown.

		Presence	Absence	*U* -test
SST (^oC)	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. The occurrence (and percentage occurrence) of short-tailed shearwaters (*Ardenna tenuirostris*; STSH) in 50-km^2 grids with and without large krill (>8.0 mm total length) in fall (September) 2012 and summer (June–July) 2013. The results of Fisher's exact tests are also 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. Relationship between the density of short-tailed shearwaters (*Ardenna tenuirostris*; STSH) (individuals km^{-2} in each 50-km^2 grid) and the size of krill in fall (September) 2012 and summer (June–July) 2013. Values are means ± SD with sample sizes in parentheses. The results of Mann-Whitney *U* tests are also 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 (*Ardenna tenuirostris*) during the non-breeding period.

Diet composition (%)								Sampling periods	Area	No. of birds	Unit	Reference
Fish	Squid	Krill	Copepods	Amphipods	Jellyfish	Crab larvae	Others					
5	0	83	0	0	0	11	0	July-Aug., 1973	Okhotsk Sea	18	Wet wight	Ogi et al., 1980
63	19	9	6	3	0	0	0	April-June, 1973-1977	North Pacific Ocean	125	Wet wight	Ogi et al., 1980
5	14	73	0	8	0	0	0	June-Aug., 1970-1978	Bering Sea (shelf and basin)	296	Wet wight	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 wight	Hunt et al., 1996
31	0	56	8	0	0	5	0	May-Sep., 1997-1999	Bering Sea (shelf)	288	Volume	Hunt et al., 2002
21	12	57	0	0	0	0	0	July, 2003-2008	Being Sea (basin)	159	Wet wight	Toge et al., 2011

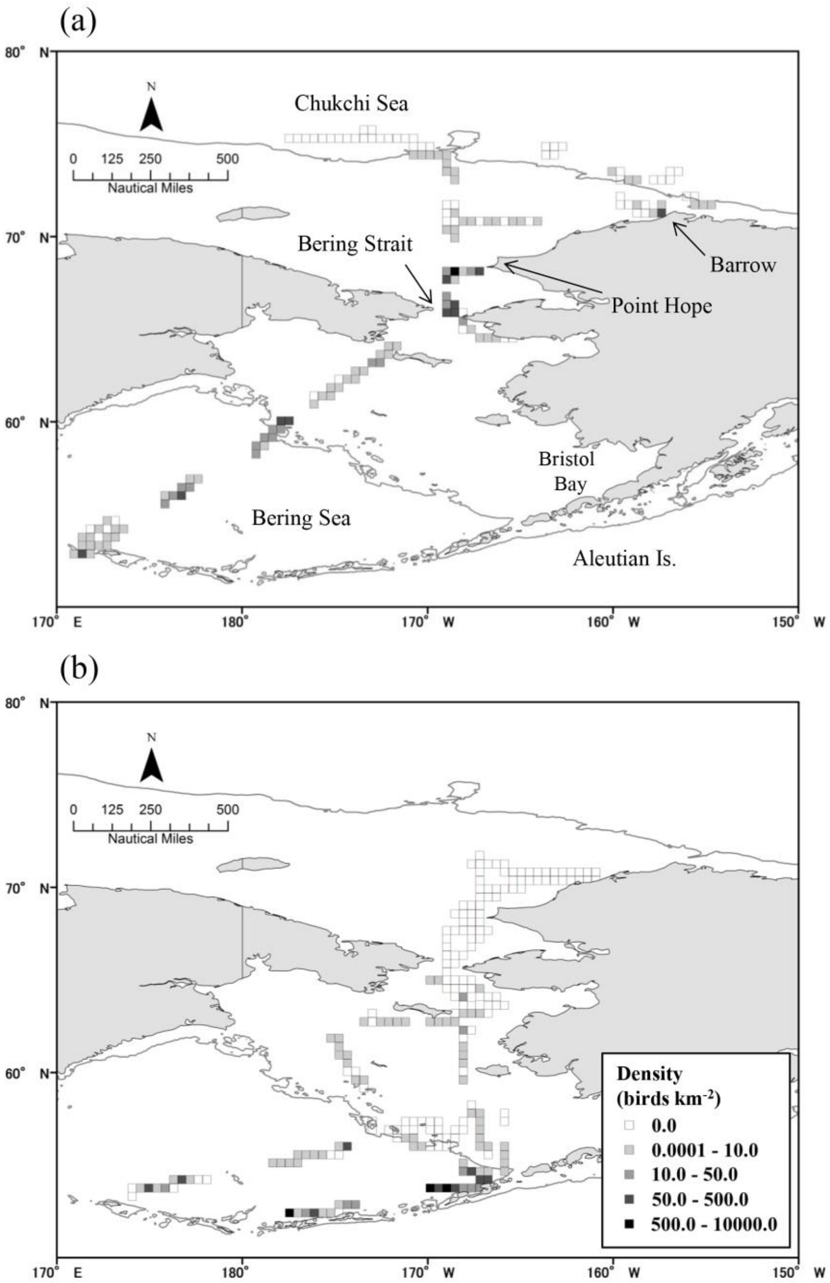
(a)
80° N
70° N
60° N
170° E
180°
170° W
160° W
150° W
N
0 125 250 500
Nautical Miles
Chukchi Sea
Bering Strait
Point Hope
Barrow
Bristol Bay
Bering Sea
Aleutian Is.
(b)
80° N
70° N
60° N
170° E
180°
170° W
160° W
150° W
N
0 125 250 500
Nautical Miles
Density (birds km^{-2})
0.0
0.0001 - 10.0
10.0 - 50.0
50.0 - 500.0
500.0 - 10000.0

Fig. 1

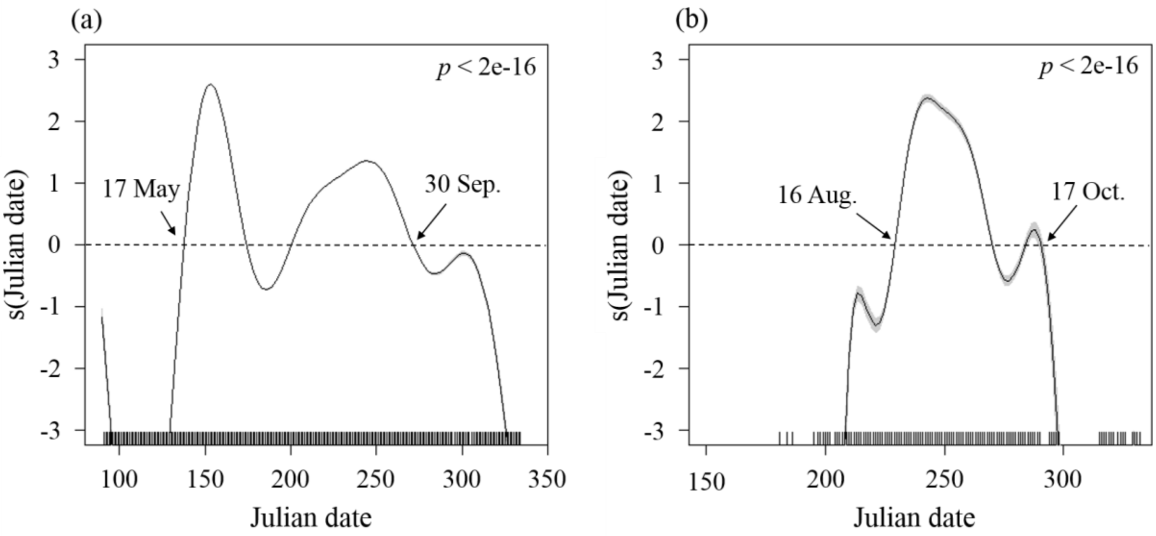
(a)
p < 2e-16
17 May
30 Sep.
s(Julian date)
Julian date
3
2
1
0
-1
-2
-3
100
150
200
250
300
350
(b)
p < 2e-16
16 Aug.
17 Oct.
s(Julian date)
Julian date
150
200
250
300

Fig. 2

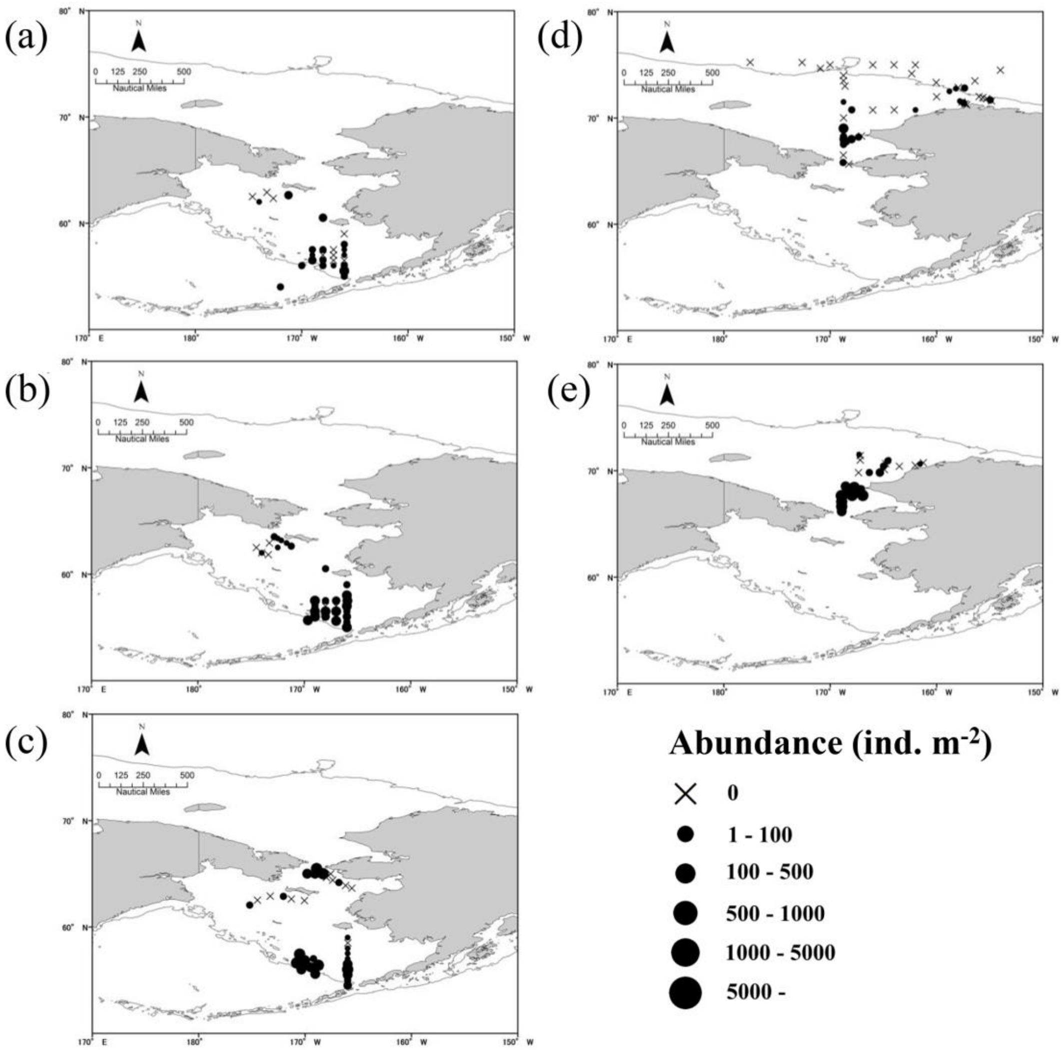

Fig. 3

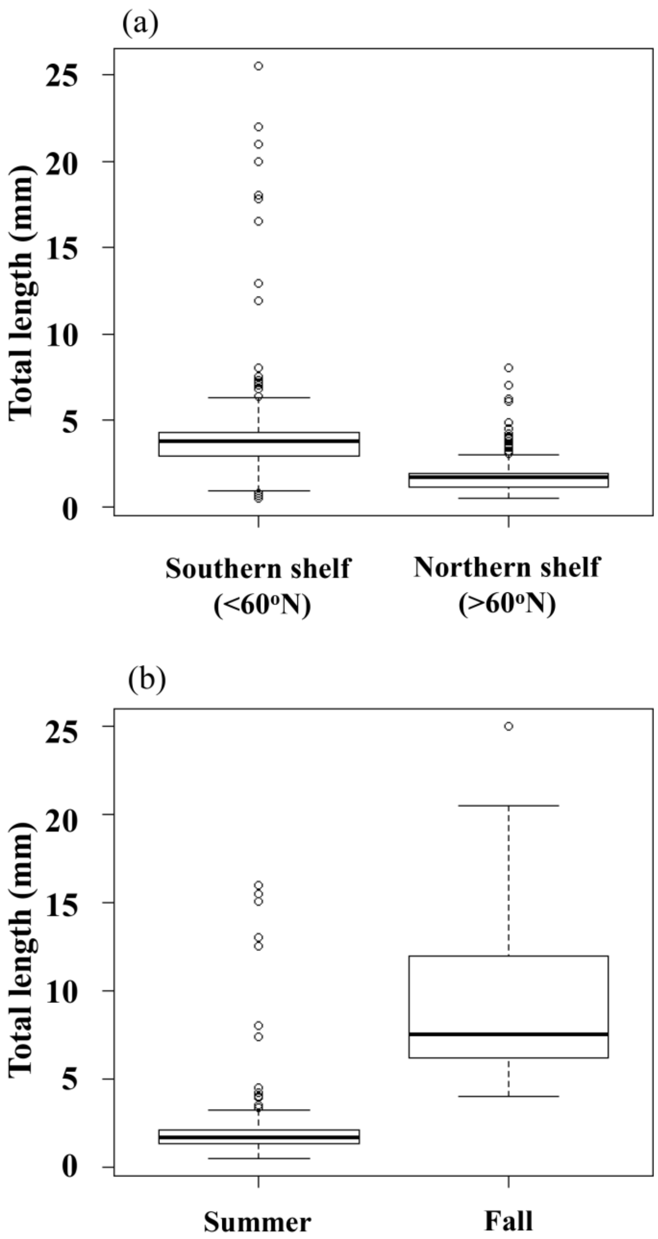
(a)
Total length (mm)
0
5
10
15
20
25
Southern shelf (<60ºN)
Northern shelf (>60ºN)
(b)
Total length (mm)
0
5
10
15
20
25
Summer
Fall

Fig. 4