Dear Editor and Reviewer, Prof. George Hunt,

We deeply appreciate you for reviewing our manuscript carefully. We carefully revised the manuscript following the reviewer comments, and the manuscript has been edited for English grammar, clarity and structure by co-author Kathy Kuletz. We analyzed North Pacific Pelagic Seabird Database and added a new Figure using this dataset in the revised MS. We hope that our responses and revise MS will be acceptable.

The comments by the referee highlighted with "Q" with the number, and our answers to comments highlighted with "A".

Response to Prof. George Hunt

Nishizawa et al document the distribution and abundance of short-tailed shearwaters in the southeastern Bering Sea and the Chukchi Sea in summer and fall. They also document the size and abundance of euphausiids available to the shearwaters. They find that the shearwaters are most abundant in the Bering in summer, but more abundant in the Chukchi in fall. They also find that euphausiid sizes in the Chukchi Sea were greater in fall than in summer. They conclude that shearwaters remain in the Bering in summer because the krill there are larger, and then only move to the Chukchi when the krill there have increased in size. The paper is potentially an important contribution, but needs some substantial revision before publication.

[Q1] I liked this paper in that it began with a hypothesis and then set about testing it. That said, the test is a bit less robust than it might have been. In their comparisons, they are forced to compare summer in the Bering in year 1 with summer or fall in the Chukchi in year 2 (except in 2013, when they looked at the summer in both the Bering and the Chukchi). There is now considerable evidence that krill recruitment was depressed from 2001- 2005, that an increasing biomass of pollock further depressed krill abundance until about 2008, after which krill abundance increased until about 2009, then declined (see Ressler et al., 2012, 2014; Hunt et al., In Press Deep-Sea res. II). As a result, there may be aliasing of the krill biomass by other factors that are unique to the different years. Thus, in the models of explanatory variables (Table 3), it would be good to include year. In Table 4, there is a spatial component (Bering vs Chukchi) as well as SST, Chl a, and slope. How much of the effects of slope or temperature is because of location? I do not think that this is a problem in tables 5, 6 and 7. What happens with krill size in fall in the Bering Sea (Table 2 suggests no fall samples in the Bering)?

[A] We appreciate the critical and helpful comments. Yes. There are many studies showing that the composition of krill species and their biomass varied between warm and cold years (Coyle et al., 2008; Pinchuk and Coyle, 2008), and also varied across years during the cold period (2008–2010) in the southeastern Bering Sea (Bi et al., 2015). This interannual variation of species composition and biomass during the recent cold period can be partially attributed to the changes in water temperature and salinity and also the changes in other physical and biological factors (Bi et al., 2015). These other factors include ocean currents, stratification (Buchholz et al., 2010), predation from walleye Pollock (Hunt et al., 2011; Ressler et al., 2012). These large interannual variation of krill biomass can be one of reasons explaining larger krill size in September 2012 in the Chukchi Sea than that in July 2013. Unfortunately, we did not have enough data (2 years sample in the Chukchi Sea during summer or fall with no fall samples in the Bering Sea) to examine the interannual changes (2012 vs. 2013) in the size and abundance of krill so could not put the “Year” as fixed effect factor in the model explaining changes in krill size and biomass (this sentence was described in P7, L7-L10). Thus, we would like to discuss the possibility that the interannual variation in the abundance of krill might explain the change of distribution of short-tailed shearwaters in the DISCUSSION (P11, L22-P12, L12).

It is interesting to examine whether effects of slope or temperature on shearwaters occurrence differ between sampling locations, but our objective is to investigate seasonal shifts in shearwater’s distribution from Bering Sea to Chukchi Sea and factors affecting them. So I pooled each sampling locations within the region (Bering Sea and Chukchi Sea) for our statistical analysis.

I responded to your all comments as below.

[Q2] You suggest that the increase of shearwaters in fall in the Chukchi is related to an increase in large krill there. Could it be due to a decrease in krill in the Bering? Could you have detected that?

[A] Thanks for the comment. Unfortunately, we do not have data on the size and abundance of krill in the Bering Sea in September. So we do not know if krill availability decrease in the Bering Sea in September. However, according to the previous studies based on the data collected by the mooring-buoy furnished with continuous echo sounder, ship-based acoustics, and net samplings in the Bering Sea shelf, the size and abundance of krill decreased seasonally. I added following explanations in the DISCUSSION (P10, L24-P11, L5).

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.

[Q3] You might be able to test whether there is a general pattern of decreasing numbers of shearwaters in the se Bering Sea by using the data available in the North Pacific Pelagic Seabird Database available at the USGS. Co-author Kuletz should be able to develop a nice set of figures from that.

[A] Thanks for the helpful suggestion. We examined seasonal changes in the short-tailed shearwaters in both the Bering Sea and Chukchi Sea using NPPSD from 1975 through 2012. This result indicated that the density of short-tailed shearwaters in the Bering Sea increased between mid-May and September, with the greatest peak in early June (Fig. 2a), while that in the Chukchi Sea increased between mid-August and mid-October, with the greatest peak in early September (Fig. 2b). Also previous tracking- and boat-based studies indicate that the magnitude of interannual variation in the abundance of short-tailed shearwaters and reported seasonal pattern of distribution seemed to be consistent among years. So, we believe that the seasonal shifts in the distributions of shearwaters might be a general pattern. I added following explanations in the DISCUSSION (P9, L11-L28).

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.

[Q4] Page 17723, line 1: Hunt 2011 would be better than Hunt 2002a

[A] Changed as you suggested.

[Q5] Page 17724, lines 16-19: the lack of observations in both places in the same year or in the same place, summer and fall complicates the analysis, as there may be considerable interannual differences in both the availability of krill, and in the numbers of shearwaters in the Bering.

[A] See reply Q2 and Q3. In the Chukchi Sea, information on seasonal and interannual variation in size and abundance of krill was very limited in our study. We did krill sampling in Chukchi Sea in July 2013 and September 2012. We found that krill size in July 2013 was much smaller than that in September 2012 and that the short-tailed shearwaters were more abundant in the area where large size of krill were abundant in September 2012 in the Chukchi Sea.

As in answer to Q2, and Q3, one possible explanation is that the seasonal northward shifts in short-tailed shearwaters distribution might be likely associated with decrease of the abundance of large size of krill especially mating swarm in the surface layer in September in the southeastern Bering Sea and increasing in large size of krill availability in September in the Chukchi Sea. However, considering large interannual variation in the abundance and distribution of krill and shearwaters found in the references, the other explanation is 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 that strong recruitments of krill (i.e., high krill abundance) occurred in 2012 and poor recruitments of krill (i.e., low krill abundance) occurred in 2013. This is now described in the DISCUSSION part (P11, L22-P12, L12) (See also reply to Q7).

[Q6] Page 17724, lines 24 -26. These were apparently continuous counts of flying birds, rather than snapshot counts. This can complicate comparisons if in some places you encountered large flock of flying shearwaters, but in others most shearwaters were feeding or on the water.

[A] As pointed out, continuous counts of flying birds overestimate the density of flying birds (Tasker et al., 1984). Continuous count data will give information on relative density. We aimed to find environmental factors affecting the changes in seasonal distribution between the Bering Sea and Chukchi Sea. So, relative density could meet our objective. In GLM we used presence and absence of shearwaters as a dependent variable.

[Q7] Page 17725, lines 15 – 18: 2012 was a cold year with late ice retreat, 2013 was a warm year with early ice retreat. The timing of the spring bloom and the recruitment of krill in these two years were likely VERY different.

[A] Thanks for helpful comments. We could not directly compare the abundance of krill between 2012 and 2013 due to different sampling season (i.e., September 2012 vs. July 2013). Thus, we could not exclude the possibility that short-tailed shearwaters were found in the Chukchi Sea in September 2012 but were not found there in July 2013 due to the greater krill abundance in 2012 than in 2013. I added following explanations in the DISCUSSION part (P11, L22-P12, L12)

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^{o}40N, 163^{o}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 ^{o}C 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.

[Q8] Page 17726, lines 5-8: Why not use length weight relationships for the species of krill in the SE Bering? They are available in several publications (see Hunt et al., In Press). There are considerable interspecific differences in mass and in lipid content, and presumably both wet and dry weights per unit length.

[A] Thank you for the helpful comments. We used length weight relationships for the species of *T. raschii* ($WW = 0.009 \times TL^{(3.02)}$, $R^2 = 0.95$, $p < 0.0001$, provided by Harvey et al. (2012) Deep Sea Res II) which predominate in the Bering Sea shelf to show biomass of krill collected in this study. I added the explanation in the MATERIALS and METHODS part (described in P5, L24-L28). The biomass data were shown in the RESULT section (described in P7, L30-P8, L8).

[Q9] Page 17726, line 17-18: Is there a way to test this assumption? Are there not some small-scale differences in where krill are found? Anadyr water versus Bering Shelf Water in the northern Bering Sea?

[A] We used incorrect sentences, so removed it from the manuscript. We are very sorry for that.

[Q10] Page 17727, line 3 -4: I do not think that you can assume that slope is a good proxy for upwelling, but it may be. Can you check this?

[A] Thanks. Yes, we could not say that the slope is a good proxy for upwelling. Many previous studies showed that slope may be an important habitat of seabird (e.g., Yen et al. 2004 J of Marine Systems, Suryan et al. 2006 Deep Sea Res II, Zydelis et al. 2011 Proc R Soc Lond B). In this study, however, slope was not important factor explaining the distributions of short-tailed shearwater (Table 3). We removed the sentence “slope is a proxy for upwelling” from the manuscript.

[Q11] Page 17729, lines 8 – 10. Here you are contrasting not only the Bering and the Chukchi seas, but also, 2012 (cold and early bloom, likely strong krill recruitment) and 2013, (Warm and late bloom, likely very poor krill recruitment). In 2013, many of the krill may have been adults rather than first year recruits (Bering Sea *T. raschii* live 3-4 years).

[A] Thank you for the helpful comments. Please see the answer of [Q7].

[Q12] Page 17730, line 7: In view of no fall SE Bering Sea data, I think that “substantiate” is too strong. Perhaps “is in line with”?

[A] Changed from “substantiated” to “showed” following your suggestion.

[Q13] Page 17730, lines 10 – 20: This is a very good point about seasons vs months. Even months may be misleading. Late August is “fall” in the SE Bering, as most birds leave the colonies in August, and migrant phalaropes and other species appear. Perhaps fall also begins in August in the Chukchi?

[A] I agreed with your opinion. The acoustic monitoring systems that was deployed in the southern Chukchi Sea showed that fin whale (*Balaenoptera physalus*) calls and the highest abundance of zooplankton were detected from August to October in both during 2012 and 2013 (Tsujii et al., 2016 ICES Journal of Marine Science). Further, mooring deployed in Hope valley of the southern Chukchi Sea from 16 July 2012 to 19 July 2014 showed that Chla concentration (45-53 m depth) increased sharply in May (2013 and 2014), when sea-ice still remained in this area, and high concentration continued until July, which is a spring bloom. In addition, relatively high Chla concentration (> 1 mg m^{-3}) were found in September-October 2012 and August-Octobor 2013, which is a fall bloom (Nishino et al., 2016 Biogeoscience). Thus, “fall” probably begins in August in the Chukchi Sea. I add the following explanations in the in the MATERIALS AND METHODS section (P6, L32-P7, L3).

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).

[Q14] Page 17731, lines 3 – 7: You need to be a bit more explicit about the mechanisms for a temperature- driven impact on the availability of krill. Remember, T. raschii is apparently breeding until at least mid-August in the SE Bering Sea and shearwaters are foraging at breeding swarms then (Hunt et al., 1996). The main bloom in the Bering Sea is done in May or June. I am not certain that Yamamoto et al. (2015) put enough emphasis on the breeding chronology of T. raschii rather than on temperature.

[A] Thank you for the helpful comment. I modified the DISCUSSION part as follows (P11, L5-L14).

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).

[Q15] Page 17731 lines 10 – 14: What they are eating may depend, in part, on where they were collected. Also, amphipods (*Thermisto libellula*) may be important only after a series of very cold years (Pinchuk et al., 2013).

[A] As suggested, the diet of short-tailed shearwaters are highly variable across sub-regions, seasons, and years (Ogi et al., 1980, Schneider et al., 1986; Hunt et al., 1996, 2002a). However, major diet of short-tailed shearwater was krill. Thus, we were looking for the linkage between krill and the seasonal movements of migrating shearwaters. I add these explanations in DISCUSSION part as follows (P9, L29-P10, L6).

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).

[Q16] Page 17731, line 27: size, and or abundance??

[A] Changed from “size of krill” to “abundance of larger size of krill” to become more clearly.

[Q17] Page 17732, line 5 – 8: May depend where one is sampling- remember Hunt et al. (1996) had lots of adult T. raschii at the surface in mid-August near the Pribilofs. See also the paper by Vleitstra et al.2005, where shearwaters were taking adult T raschii just north and east of Unimak Pass.

[A] See reply Q14.

[Q18] Page 17733, line 19: There are a number of papers specific to the SE Bering Sea summarizes in Coyle et al., 2011, Hunt et al. 2011, In Press).

[A] Thank you for the helpful comment. I modified DISCUSSION as following (P12, L26-P13, L3).

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.

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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~~The short-tailed shearwater ~~*Puffinus*~~(*Ardenna tenuirostris*) is one of the ~~of~~ abundant marine top predators in the Pacific; this seabird ~~spend~~spends its non-breeding period in the northern North Pacific during May–~~September~~October and many visit the southern Chukchi Sea in ~~July~~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 ~~NORPAC~~ 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 ~~in~~ 2013 ~~but~~, and 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 size 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 size of krill ~~was~~were 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~~in krill size in the Bering Strait/southern Chukchi Sea. We could not, however, rule out

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the possibility ~~of~~that large interannual variation in ~~the~~ krill abundance might influence the seasonal distribution of ~~the~~ shearwaters. This study ~~indicates~~highlights the importance of krill, which is advected from the Pacific, as ~~a~~an important prey of top predators in the Arctic marine ecosystem.

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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~~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~~an important 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~~prey 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 upper trophic level 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~~Similarly, dramatic declines in numbers of spectacled eiders (*Somateria fischeri*) ~~that consume the clams~~ 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 ~~the~~ black guilmots (*Cepphus grylle mandtii*) breeding at Cooper Island in the western Beaufort Sea~~,~~

~~which leads~~; these seabirds subsequently shifted to feeding their ~~diet shifts to~~ chicks sculpin (Cottidae~~) with decrease in nesting~~), which led to lower nestling growth and survival compared to that in ~~the~~ historical periods (1975–1984) (Divoky et al., 2015). ~~Thus, knowledge of recent changes in the~~Consistent with these examples, we propose that at-sea distributions of top predators ~~and~~in relation to their prey ~~should~~can provide useful information about large-scale ecosystem changes in these regions with seasonal sea-ice.

Short-tailed shearwaters (~~*Puffinus*~~*Ardenna tenuirostris*) migrate annually from their breeding colonies in southeastern Australia and Tasmania to spend their non-breeding period ~~for~~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 ~~amount~~amounts of krill, ~~in particular~~particularly the euphausiids *Thysanoessa raschii* and *T. inermis* (Schneider et al., 1986; Hunt et al., 1996, ~~2002a~~2002; Toge et al., 2011). In the Bristol Bay area of the 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~~Tracking studies using geolocaters revealed the large~~-~~-scale migration of ~~sherawaters~~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 ~~relate~~be related to the temperature-driven changes in the abundance of their prey~~, –~~ (krill~~, as~~), 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 ~~by~~using vessel-based surveys in the Chukchi Sea in September 2012 and June–July 2013 in the Bering and Chukchi seas~~ and that~~. We also examined the distribution 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~~

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~~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~~.

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2 Materials and Methods

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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°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~~), 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* ~~above sea surface) within~~). We used 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~~, 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 (~~*Puffinus*~~*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~~). 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".

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We calculated the relative density (~~number of~~ birds ~~per km^2~~km^{-2}) of ~~short-tailed~~ shearwaters ~~and used bird densities within~~ over a 50- km × 50 km grid ~~for the survey area. This~~. We selected this grid size ~~was selected~~ because foraging area fidelity of ~~short-tailed~~ shearwaters was ~~suggested at a scale of~~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 ~~short-tailed~~ shearwaters and ~~200 kHz back-scattering strength of acousitics, i.e., the~~ an acoustic index of zooplankton abundance (including krill~~, was observed~~) at a scale of 10 km in the northern Sea of Japan ~~Sea~~ (Kurasawa et al., 2011). ~~Moreover, owing to~~ To standardize for unequal ~~total length of the distance in each grid cell~~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 ~~area. Thus,~~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 ~~short-tailed~~ shearwaters ~~at each 50-km grid cell was given as the number per km^{2}.~~ 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 ~~crew~~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 ~~NORPAC (~~North Pacific Standard Net~~) net~~ (NORPAC) (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

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range of krill, which undertake a diurnal vertical migration (Watkins, 2000). Thus, the diurnal vertical migration of krill ~~did~~should not ~~affect~~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 (~~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 (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). ~~Moreover, we~~We calculated the wet weight per individual krill using the length-weight relationship equation ~~((~~(wet weight~~)~~ = 0.009 ~~x (~~× total ~~length)~~ ~~$^{(3}$~~length$^{3.02}$~~$^{)}$~~ ~~,~~, $R^2 = 0.95$, $p < 0.0001$, for ~~krill of~~ *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~~. Juveniles and adults of krill with progressed~~ due to the advanced eye structures ~~may be able to avoid the nets more successfully~~in both juveniles and adults (Watkins, 2000). ~~Large~~Furthermore, since large size of krill~~, which~~ can swim faster than small size of krill, they may be able to avoid the net more successfully ~~than small krill~~ (Hovekamp, 1989). Thus, the absolute abundance of ~~juveniles~~juvenile and ~~adults of~~adult krill ~~might be~~may have been underestimated in this study. Nevertheless, we ~~could~~were able to compare the relative abundance ~~at~~of each size ~~of krill~~class (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~~in September 2012 in the Chukchi Sea and ~~during~~in July 2013 in the Bering and Chukchi seas, when both seabird and zooplankton surveys were conducted. Because shearwater densities ~~of short-tailed shearwaters~~ among 50-

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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~~examined the factors affecting the ~~occurrence~~ presence or absence of ~~short-tailed~~ shearwaters. We used generalized linear models (~~GLM~~GLMs) 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*; °C), sea surface chlorophyll *a* concentrations (*Chla*; mg m^{-3}~~)~~), and ocean bottom slope (*Slope*; °), 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 ~~fit~~match 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 (presence or absence) and ~~size of~~ krill size (small or large) were treated as a categorical explanatory variable~~, "absence", "small" or "large"~~ for each station. Each station ~~of~~with krill samples was ~~related~~linked to the closest seabird survey grid cell~~ that had by vessel-based short-tailed shearwater surveys. Distance~~, with distance between ~~the cells (each station of~~ krill ~~samples~~, and ~~the closest grid cell with short-tailed shearwater surveys) averaged approximately~~seabird cells averaging ~ 33 km. We defined ~~our survey~~two seasonal periods~~ of~~: summer (June–July~~ as "summer"~~) and ~~August–September as "~~fall~~" respectively, considering that seasonality of~~ (August–October), based on documented phytoplankton bloom in the southern Chukchi Sea (~~i.e.,~~ spring bloom ~~occur~~occurs in May–July and fall bloom ~~occur~~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 ~~data set~~dataset for constructing a GLM, because the sample size was small ~~owing~~due to ~~the~~ limited ~~survey periods and~~ seabird

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surveys or missing environmental data (~~resulting from~~due to cloud cover) in ~~satellite images of *SST* and *Chla*.~~remotely sensed data. Thus, to evaluate the effect of season we added “season” (summer or fall) as a second categorical explanatory variable. ~~Unfortunately, we~~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 5, 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 Akaike Information Criterion (AIC) values, assuming that models having $\Delta\mathrm{AIC} \leq 2$ 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 widely distributed in both the Bering ~~Strait~~Sea and Chukchi Sea~~. Density~~ (Fig. 1a). Shearwater density (birds km^{-2} ~~at~~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}), ~~and a~~with few birds in the Bering Sea basin (11.1 km^{-2}) (Fig. 1a). No ~~short-tailed~~ shearwaters were found in the Chukchi Sea basin (Fig. 1a). In June–July 2013, ~~however, short-tailed~~ shearwaters were ~~widely~~ distributed in the Bering Sea, while no ~~short-tailed shearwaters~~birds were found in the Bering Strait and Chukchi Sea (Fig. 1b). ~~Density~~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).

~~In~~On the Bering Sea shelf in June–July, krill were collected throughout the study area (Figs. ~~2a, b and~~ 3a–c). ~~In~~However, in June–July ~~of~~ (2007, 2008, and 2013, combined), krill abundance (mean±SD) and estimated ~~biomassin~~biomass in the southeastern Bering Sea shelf (< 60 °N) (1,631±2,972 m^{-2} for abundance, ~~1,468~~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}, ~~119~~535 mg wet weight m^{-2}). In September, no krill sampling ~~occurred~~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}). ~~No krill were collected in the Chukchi basin in both July 2013 or September 2012 (Figs. 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~~40 *T. raschii* and three *T. inermis*. In the Bering Sea, krill collected in ~~summer~~June–July (2007, 2008, and 2013~~ samples were pooled~~, combined) were larger in the southeastern shelf than those collected in the northwestern shelf (Mann-Whitney's *U* test, $p < 0.05$) (Fig. ~~3a). Samples~~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%)).

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In the Chukchi Sea, krill collected in September 2012 ~~was~~were larger than ~~that~~those in July 2013 (Mann-Whitney's *U* test, $p < 0.05$) (Fig. ~~3b~~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 ~~shearwater~~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 ~~within each of~~in the ~~two regions.~~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 ~~were~~had less ~~important. Shearwaters appeared to occur more frequently in grids with lower *Chla*, steeper *slope*, and larger krill~~ 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* ~~was~~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 ~~tended~~appeared to occur more often in grids with large size of krill in fall 2012 but this trend was not apparent ~~(or possibly was opposite)~~ in summer 2013 (Table 5). ~~Density of shearwaters was~~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 ~~short-tailed~~ shearwaters

~~Our study indicated that short-tailed~~ Our surveys and the long-term NPPSD both showed similar seasonal changes in the distribution of shearwaters ~~stay in~~within the Bering and Chukchi seas. In May–July shearwaters mainly used the Bering Sea and Aleutian Islands, while in ~~June–July and~~August–October they were widely distributed both in the Bering ~~Strait and Chukchi~~ Sea ~~in September.~~and Chukchi Sea. 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~~results are consistent with previous ~~results~~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 (~~the data were pooled in~~ 2007–2012, pooled) by Wong et al. (2014) showed that high densities of ~~short-tailed~~ shearwaters occurred in the

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Aleutian Islands, ~~south~~southern Bering Sea, and Bering Strait, but few birds were found in the Chukchi Sea. The other ~~boat~~vesssel-based surveys in the northern Chukchi Sea occurred during August–October, 2008-2010~~ by~~; in this study, Gall et al. (2013) showed that ~~short-tailed~~ shearwaters were found there from mid~~-~~ August to early~~-~~ October, ~~and the~~with highest densities occurring in September ~~were common~~ in all 3 years~~, though the densities~~. Overall, our study and previous studies show a similar pattern, with a substantial portion 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~~ that are in the Bering Sea in ~~June–August to~~summer moving into the Chukchi Sea in ~~August–October with extensive interannual variation~~fall.

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Information on the diets of ~~short-tailed~~ shearwaters was not collected ~~in~~during this study~~. Previous~~, but previous studies have shown that krill ~~comprised~~comprise most of their diet in the northern North Pacific and Bering Sea (Table 7~~), although~~). Still the ~~diet~~diets of ~~short-tailed~~ shearwaters are highly variable across ~~areas at a small scale~~sub-regions, seasons, and years (~~e.g,~~ Ogi et al., 1980; Hunt et al., 1996, ~~2002a~~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 ~~periods~~season (Schneider et al., 1986; Hunt et al., 1996, ~~2002a~~2002). Thus, in this study, we foucused on the linkage between distribution of krill and the seasonal movements of migrating shearwaters at a ~~reginal~~regional scale (Bering Sea vs. Chukchi Sea).

In the Aleutian Pass and southeastern Bering Sea, ~~short-tailed~~ shearwaters ate large size of krill (11.5–16.9 mm) even when small size of krill (5.0–8.4 mm) were present, although ~~short-tailed shearwaters associating with a tidal front~~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 swarm of krill during daytime. Thus, short-tailed shearwaters ~~fed~~tended to feed on larger and more mature krill, perhaps because larger krill contain more gross energy than ~~small~~smaller krill (Färber-Lorda et al., 2009). Additionaly, surface swarms of ~~adults may~~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 ~~trend of northward ~~movement of ~~short-tailed ~~shearwaters ~~in September ~~from the Bering Sea to Chukchi Sea in fall might be associated with the seasonal increase in ~~the abundance of larger size of ~~krill size in the Chukchi Sea. In the Chukchi Sea, the size of krill collected during ~~this study~~our survey period in September 2012 (9.6 ± 5.0 mm), ~~which ~~was within the ~~ranges of ~~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 ~~June–~~July 2013 in the same region (1.9 ± 1.2 mm) (Fig. ~~3b).~~ 4b).

In contrast~~,~~ to the Chukchi Sea, a study in the southeastern Bering Sea shelf, ~~previous study based on MOCNESS sampling showed~~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). ~~The other study using MOCNESS tows also~~Earlier, Smith (1991) showed that high abundance of krill nauplii on the inner shelf of southeastern Bering Sea occurred in mid-May~~ to ~~–June~~ (Smith 1991). Continuous~~. 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 ~~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~~. 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,

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while *T. raschii* (~~commnly~~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).

~~Within~~In the Chukchi Sea in September 2012, 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 size of 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~~). Also, in the Bering Sea in July 2013, the density of ~~short-tailed~~ shearwaters was higher in the southeastern shelf than ~~that~~ in the northwestern shelf (Fig. 1b), which might ~~also reflect~~ be related to the higher abundance and the presence of larger ~~size of krill in the southeastern shelf than northwestern shelf~~ sized krill there (Sigler et al., 2012; Bi et al., ~~2015; this study).~~ 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 ~~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~~); krill abundance ~~of krill~~ on the Bering Sea shelf is greater in years with cold, icy ~~spring~~springs 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~~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 ~~compared to August 1999 coincided with a warmer summer accompanied by weak winds, which resulted in 4–5°C higher temperatures in the upper-mixed layer and strong stratification of the water~~

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~~column (Coyle et al., 2008). In this~~walleye pollock (*Theragra chalcogramma*). In our 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~~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°40N, 163°52W, ~~location of~~ Mooring 2) in both 2012 and 2013 (~~Figure~~Fig. S1). Thus~~ this~~, the timing of sea-ice retreat did not differ ~~largely~~substantially between 2012 and 2013. SST in ~~the southeastern Bering Sea shelf during April–October in 2012 and~~ 2013 ~~were 4.6 ± 3.2 °C and 5.7 ± 3.8 °C respectively, and SST in the southern Chukchi Sea during May–October in 2012 and 2013 were 2.3 ± 2.6 °C and 3.6 ± 2.7 °C respectively (Figure S2). Thus SST in 2013 was~~was about 1~~.1–1.3~~ °C higher than that in 2012 in the southeastern Bering Sea shelf and southern Chukchi Sea~~.~~ (Fig. S2). The surface ~~Chla~~chlorophyll *a* concentrations peaked on 14 May in 2012 and 10 May in 2013 in the southeastern Bering Sea shelf ~~(56°40N, 163°52W)~~ and on 20 June in 2012 and 12 June in 2013 in the southern Chukchi Sea (~~68°03N, 168°50W) (Figure~~Fig S3). ~~Thus the~~The timing of spring bloom in 2013 was therefore 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,~~ As a result, krill recruitment ~~of krill~~ might ~~be~~have been poor in 2013 in the Bering and Chukchi Seas because of warmer SST and earlier spring bloom compared to 2012. ~~Thus, we could not exclude the possibility that short-tailed~~ 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 ~~found~~ in the Chukchi Sea in September 2012~~ and were~~, but not ~~found there~~ in July 2013~~, which might be related to presumable~~ because there was a stronger ~~recruitments of~~ krill ~~(i.e.,~~ recruitment (and high krill abundance) in 2012~~ than in 2013.~~.

4.3 Environmental ~~change~~changes and trophic effects through krill

Our study indicates that ~~the~~ one of the explanations ~~of~~for the seasonal movement of ~~short-tailed~~ shearwaters ~~may be~~is the spatial pattern of krill. Other top predators show a similar relationship~~. For~~ with their prey. There are several examples among marine mammals: for example, bowhead whales (*Balaena mysticetus*) feed on ~~aggregated~~subsurface patches of krill

(*T. raschii*) in the ~~northern North Pacific and Arctic Ocean in~~western Chukchi Sea during fall (September–October; Moore et al., 1995~~; Lowry et al., 2004).~~). Gray whales that usually feed on benthic amphipods (Moore et al., 2003) ~~fed~~feed 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).~~2007). The arrival of migratory fin whales (*Balaenoptera physalus*) in the southern Chukchi Sea in August coincided with an increase ~~of the~~in water temperature and ~~that of the~~ abundance of zooplankton (including krill and large 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~~Krill therefore serves as an important component of energy transfer from phytoplankton to top predators in the marine food webs ~~in~~of 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~~spawning of krill (*T. raschii*) ~~appears to occur~~are influenced not only by seasonal change in ~~the presence of~~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 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~~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~~ Indeed, krill abundance increased during ~~the cold~~a period of cold years when the extent of sea~~-~~ice was large~~ and~~, but krill decreased during the ~~warm~~ period with warm years (Coyle et al., 2008; Hunt et al., 2011; Ressler et al., 2012), ~~though~~although the mechanisms ~~responsible for this are not clear. One~~

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~~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.~~ remain unclear. ~~*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.~~

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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 ~~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 interannual and regional variations ~~of~~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 ~~the~~krill 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°N) in ~~part of~~ the Russian Arctic ~~Ocean~~ (Timofeev, 2000). ~~Thus, careful researches have to be carried out~~Further research on the potential ~~of the~~ recruitment of krill in the southern Chukchi Sea, and on mechanisms responsible for the seasonal and interannual variations in krill abundance ~~of this important prey~~, be usefull in interpreting shearwater migratory behavior.

In conclusion, krill ~~could be~~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 ~~might~~ affect the recruitment and ~~deveropment~~development of krill in the Bering Sea, which via advection ~~influences~~into the ~~transfer of~~Chukchi Sea, transfers energy to ~~top~~ predators ~~like~~such as short-tailed shearwaters which forage in the ~~Chukchi Sea~~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 ~~analysed~~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} ~~by~~in each 50-~~km~~km^2 grid) of short-tailed ~~shearwaters~~shearwaters (*Ardenna tenuirostris*) in fall ~~of~~ 2012 (a) and summer ~~of~~ 2013 (b). ~~Gray solid~~Solid gray lines ~~in each map~~ indicate the 200~~—~~-m-depth ~~contour~~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 ~~summers of~~summer 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~~Solid gray lines ~~in each map~~ indicate the 200~~—~~-m-depth ~~contour~~contours.

Figure ~~3. Reginal~~**4.** Regional changes (~~Southern~~southern shelf <~~-~~60~~°~~~~N, Northern~~°N, northern shelf >~~-~~60~~°~~~~N~~°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 ~~seasonal changes in total length of krill~~ in the Chukchi Sea during fall ~~of~~ 2012 and summer ~~of~~ 2013 (b).

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Table 1. ~~—~~Summary of vessel-based short-tailed ~~shearwater's~~ shearwater (*Ardenna tenuirostris*; STSH) surveys. The number of 50-~~km~~km^2 grids with and without ~~short-tailed shearwaters (~~STSH~~)~~, and the density of STSH (~~ind.~~birds km^{-2} ~~at~~in each 50-km ~~grids) (~~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

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Table 2. ~~–~~Summary of krill surveys~~. krill~~ showing the abundance, total length~~ of kirll~~, and estimated wet weight ~~at~~of krill in each sampling area. ~~Mean~~Values are means ± SD (min~~. –~~.– max~~.)~~.), and sample ~~size~~sizes are also 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

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
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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
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Table 3. ~~Better~~The five better-fitting models explaining ~~-~~the occurrence (presence/absence) of short-tailed shearwaters *(Ardenna tenuirostris)* in ~~the~~ fall ~~of~~ 2012 and summer ~~of~~ 2013. ~~Occurrence~~ The occurrence and size of krill were categorized as ~~"~~“absent~~", "~~,” “small~~"~~,” and ~~"~~“large~~".~~.” Season was categorized as ~~"~~“summer~~"~~” and ~~"~~“fall~~".~~.” Parameter coefficients~~, their~~ and standard errors (~~S.E.) of each explanatory variables, Akaike's~~SE), Akaike’s information criterion (AIC~~)~~), and the difference in AIC are shown. Only competing models (ΔAIC ≤ 2) are presented. SST~~;~~: sea surface temperature~~,~~; Chl*a*~~;~~: sea surface chlorophyll *a* concentration. Plus marks ~~in~~indicate the categorical variables ~~show the selected variables~~that were included in the model.

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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~~km^2 grids with and without short-tailed shearwaters (*Ardenna tenuirostris*) during ~~the~~ fall ~~of~~(September) 2012 in the Chukchi Sea and ~~the~~ summer ~~of~~(June–July) 2013 in the Bering and Chukchi Seas. ~~Mean±~~Values are means ± SD, with sample ~~size~~sizes in parentheses ~~and the~~. The results of Mann-Whitney *U* ~~test~~tests are also 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~~ 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 ~~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~~) in fall (September) 2012 and summer (June–July) 2013. The results of Fisher's exact ~~test~~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. ~~Rerationship~~Relationship between the density of short-tailed shearwaters (*Ardenna tenuirostris*; STSH) ~~(ind.~~(individuals km^{-2} ~~at~~in each 50-~~km grids~~km^2 grid) and the size of krill in ~~the~~ fall ~~of~~(September) 2012 and summer ~~of~~(June–July) 2013. ~~Mean±~~Values are means ± SD~~,~~ with sample ~~size~~sizes in parentheses~~ and the~~. The results of Mann-Whitney *U* ~~test~~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)	$U = 339.5, p = 0.28$

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 ~~periods~~period.

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

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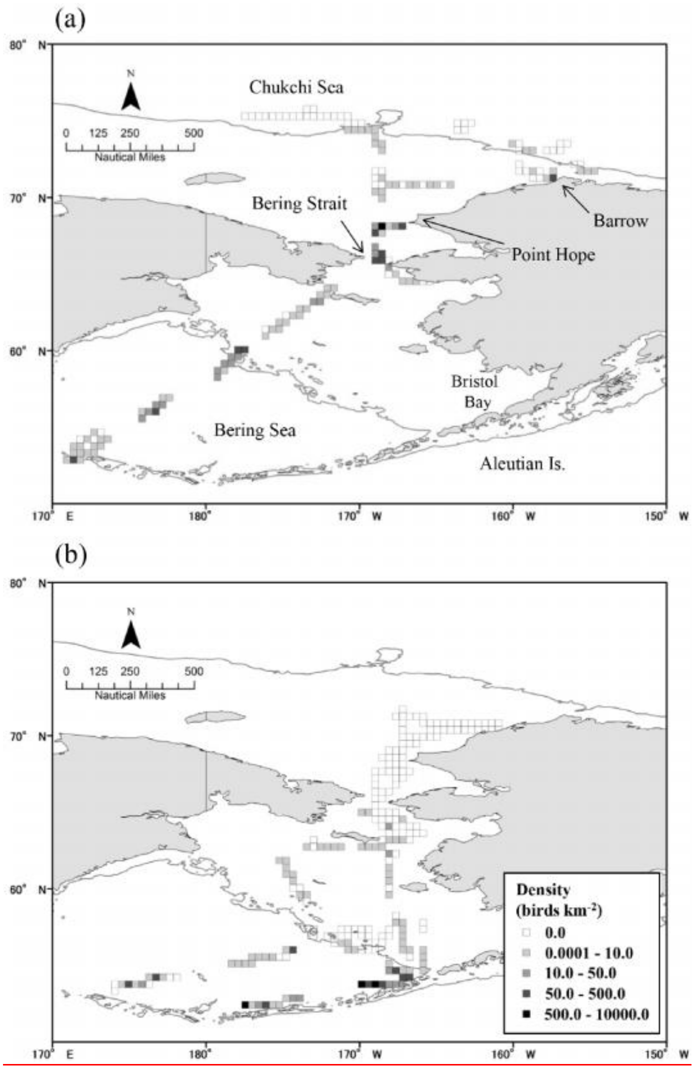

(a)
Chukchi Sea
N
0 125 250 500
Nautical Miles
Bering Strait
Barrow
Point Hope
Bristol Bay
Bering Sea
Aleutian Is.
80° N
70° N
60° N
170° E
180°
170° W
160° W
150° W
(b)
Density (birds km-2)
0.0
0.0001 - 10.0
10.0 - 50.0
50.0 - 500.0
500.0 - 10000.0

Fig. 1

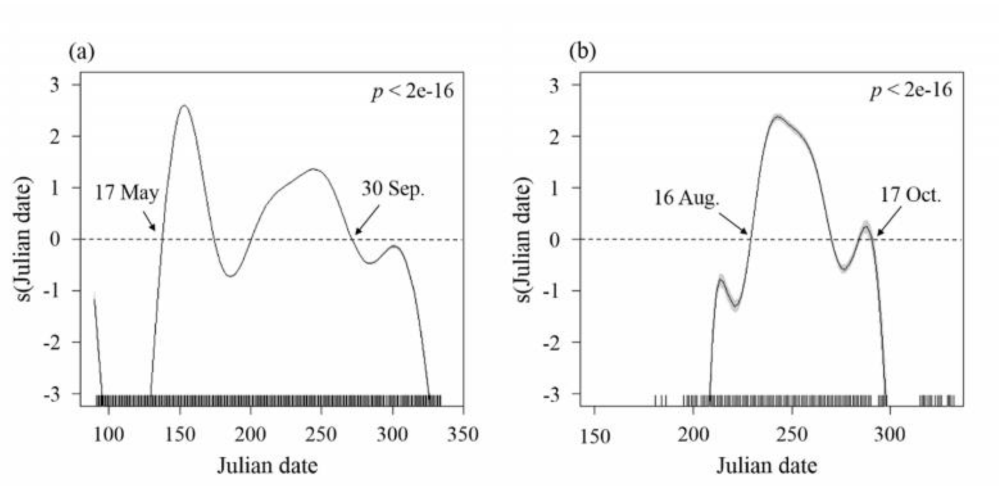
(a)
p < 2e-16
17 May
30 Sep.
s(Julian date)
3
2
1
0
-1
-2
-3
100
150
200
250
300
350
Julian date
(b)
p < 2e-16
16 Aug.
17 Oct.
s(Julian date)
3
2
1
0
-1
-2
-3
150
200
250
300
Julian date

Fig. 2

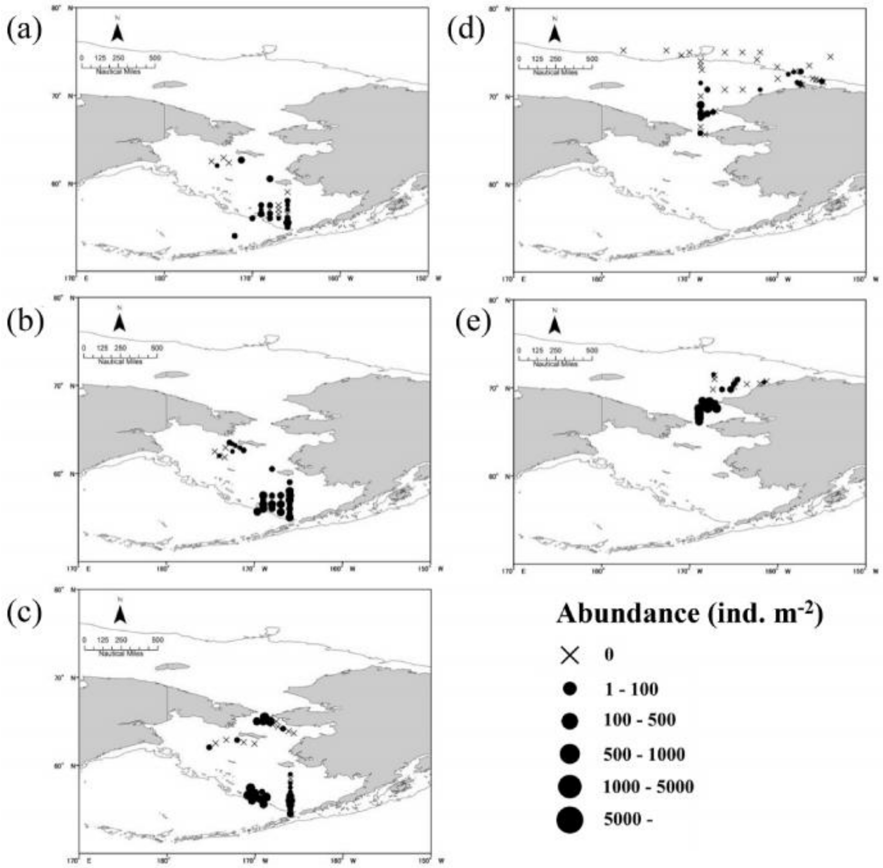
(a)
(b)
(c)
(d)
(e)
0 125 250 500
Nautical Miles
Abundance (ind. m⁻²)
× 0
● 1 - 100
● 100 - 500
● 500 - 1000
● 1000 - 5000
● 5000 -

Fig. 3

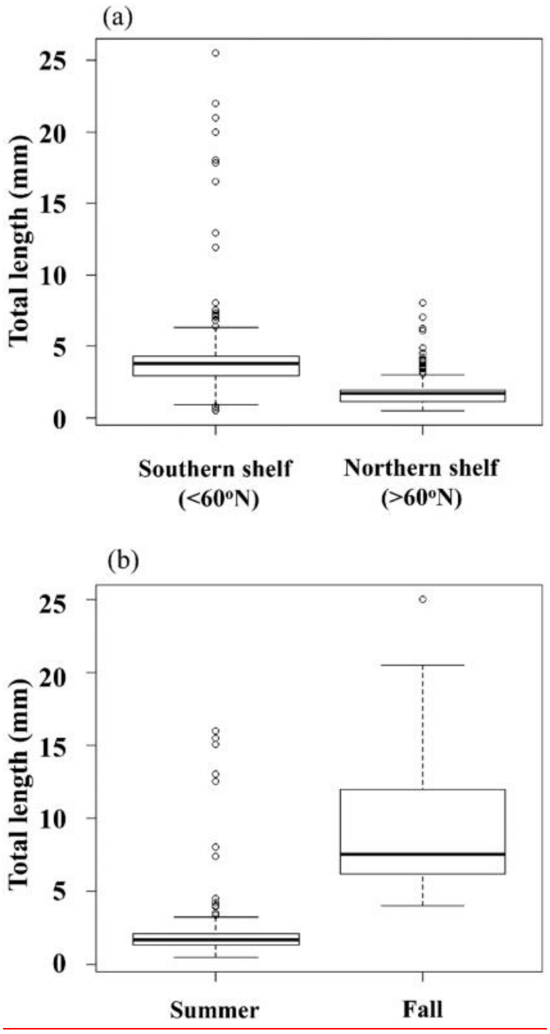

Fig. 4

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