



# Two species of seabirds foraged in contrasting marine habitats across the cold-water belt along the coast of northern Hokkaido in the southwestern Okhotsk Sea

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## Abstract

To understand the environmental factors affecting the density of foraging seabirds across the cold-water belt in the southwestern Okhotsk Sea, we conducted a 1-day (180-km transect length) shipboard seabird survey off the northeastern coast of Hokkaido during summer in 2019, along with acoustic observations of potential prey (zooplankton and fish) biomass, thermosalinograph measurements, and CTD observations. Planktivorous short-tailed shearwaters *Ardenna tenuirostris* (66% of total seabirds) and piscivorous rhinoceros auklets *Cerorhinca monocerata* (28%) were predominant, but foraged in contrasting habitats. A large foraging flock of shearwaters was observed in the cold-water belt zone, including its front with coastal Soya Warm Current Water and the offshore Fresh Surface Okhotsk Sea Water, where surface chlorophyll *a* concentrations were the highest but not related to their prey (zooplankton) biomass at any spatial scale between 4.6 and 9.2 km. In contrast, the density of auklets was high in the coastal Soya Warm Current Water, where the acoustically determined fish biomass was large, and showed a positive relationship with the fish biomass especially in the lower layer (29–104 m depth) at any spatial scale. This species-specific difference in response to prey biomass might be related to prey-searching behaviors; i.e., rhinoceros auklets search prey underwater visually, but short-tailed shearwater can use both visual and olfactory cues to locate zooplankton patches from the air.

**Keywords** Rhinoceros auklets · Short-tailed shearwater · Acoustics · Spatial scale · Biophysical interaction · Foraging behavior

## Introduction

Many marine apex predators often rely on small- to meso-scale oceanographic features such as fronts, seamounts, and canyons where prey is highly available as a result of upwelling, convergence, or other mechanisms (Hunt and Schneider 1987; Sims and Quayle 1998; Bost et al. 2009). Consequently, regions of the ocean with these features are characterized by elevated energy transfer rates from lower trophic levels to the top predators and are known as biological hotspots (Sydeman et al. 2006; Hazen et al. 2013). It is important to identify biological hotspots and understand the biophysical processes driving high trophic energy transfer, particularly those connecting oceanographic features with mid- and upper trophic levels, for the conservation of biodiversity and management of marine

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protected areas (Hooker and Gerber 2004; Sydeman et al. 2006).

In the southwestern Okhotsk Sea off Hokkaido, Japan, there is a unique oceanographic system characterized by a cold-water belt (CWB) in the summer. The CWB extends from the southwest coast of Sakhalin to the offshore side of the Soya Warm Current Water (SWCW), flowing to the south along the northeastern coast of Hokkaido, and is characterized by a temperature lower than that of the SWCW or the offshore Fresh Surface Okhotsk Sea Water (FSOSW) (Ishizu et al. 2006, 2008) (Fig. 1). Thus, well-developed temperature fronts are formed on both the coastal and offshore sides of CWB (Iida et al. 2018). The CWB region shows higher chlorophyll *a* concentrations in the spring and summer due to the nutrient supply associated with upwelling (Ishizu et al. 2006, 2008).

Observation and tracking studies of seabirds and marine mammals in the southwestern Okhotsk Sea off Hokkaido suggest that this region provides important foraging habitats for marine top predators (Tanaka and Kajihara 1979; Yamamoto et al. 2015; Nakanowatari et al. 2017; Kazama et al. 2018). However, studies investigating the links between oceanographic environments and the upper trophic levels are lacking in this region, and the underlying mechanisms that form these foraging habitats of the top predators are unknown. Information on the distribution and abundance of seabirds at sea, and their spatial associations with oceanographic environments and prey

abundance is necessary to improve our understanding of the mechanisms involved.

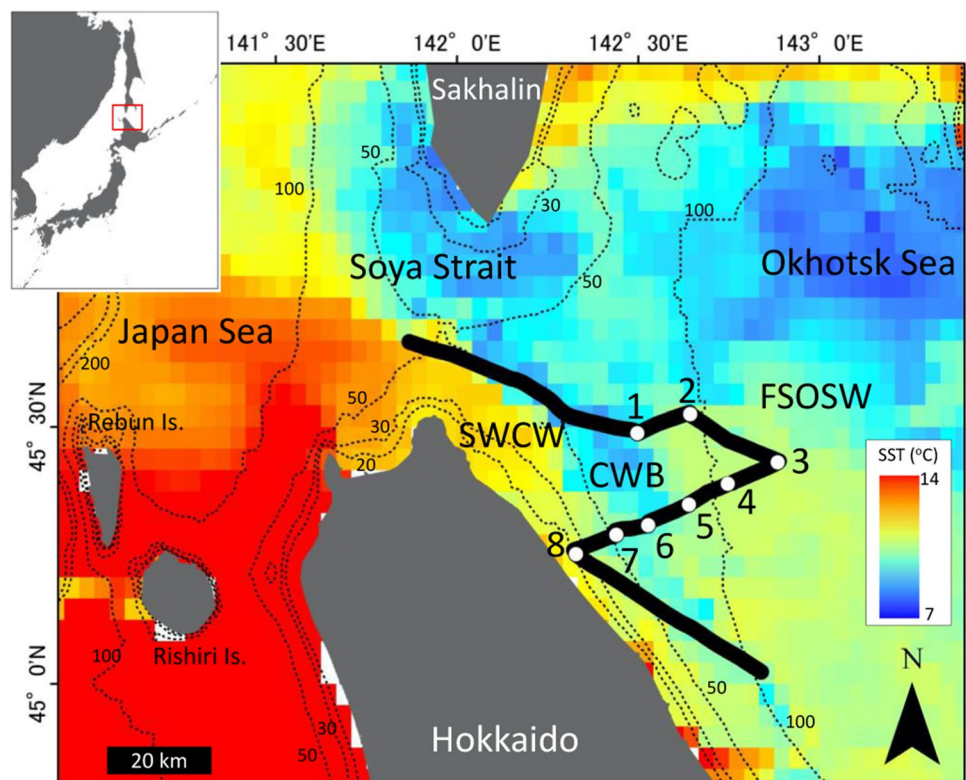
We conducted a ship-based observation of seabirds, acoustic surveys of potential prey biomass, and thermosalinograph and conductivity-temperature-depth (CTD) profiler measurements around the CWB in the southwestern Okhotsk Sea in the summer to examine spatial relationships between seabirds, prey, and oceanographic environments. Specifically, we expected that foraging seabirds would aggregate in or near the CWB where high chlorophyll *a* concentrations and frontal systems can enhance prey (zooplankton and fish) availability (Hunt and Schneider 1987; Suryan et al. 2006; Bost et al. 2009).

## Materials and methods

### Study site and oceanographic measurements

This research was conducted in the Okhotsk Sea off northeastern Hokkaido (Fig. 1) on 27 June 2019 onboard the T/S *Oshoro-Maru* (Faculty of Fisheries Sciences, Hokkaido University). Surface water (4-m depth) environments including sea surface temperature (SST), salinity (SSS), and chlorophyll (SSC) were continuously recorded using a thermosalinograph (JFE Advantech Co., Ltd., Hyogo, Japan) installed in the vessel's sea chest when the seabird observations were made. The 180-km-long

**Fig. 1** The study site in the Okhotsk Sea off northeastern Hokkaido. Seabird, acoustic, and thermosalinograph survey transect shown by the black line are overlaid on the 8-day average SST image from 25 June to 2 July 2019, derived from moderate-resolution spectroradiometer/Aqua standard mapped images with a spatial resolution of approximately 4 km provided by the Ocean Color website (<http://ocean.color.gsfc.nasa.gov>). CTD and NORPAC net sampling stations are shown as white circles with the station number. Isobaths are represented in meters by dotted lines. Soya Warm Current Water (SWCW), Fresh Surface Okhotsk Sea Water (FSOSW), and cold-water belt (CWB) are shown



transect was classified into three areas based on SST and SSS: the coastal Soya Warm Current Water (SWCW,  $T > 7\text{ }^{\circ}\text{C}$ ,  $S > 33.6$ ), offshore Fresh Surface Okhotsk Sea Water (FSOSW,  $T < 18\text{ }^{\circ}\text{C}$ ,  $S < 32.5$ ) (Takizawa 1982; Ishizu et al. 2008), and the cold-water belt zone (CWBZ) (Fig. 2, Online Resource, Fig. S1). The CWBZ included the CWB that is at a lower temperature ( $8\text{--}10\text{ }^{\circ}\text{C}$ ) near the sea surface (Ishizu et al. 2006, 2008) and its boundary with the SWCW and FSOSW (Fig. 2, Online Resource, Fig. S1). Vertical distributions of temperature, salinity, and chlorophyll (a proxy for primary production) were measured at 8 stations (3 stations in SWCW, 2 in CWBZ, and 3 in FSOSW) along the transect using a CTD probe (SBE 911plus, Sea-Bird Electronics, Bellevue, WA) (Fig. 1).

### Seabird observations

We used a standard strip transect methodology (Tasker et al. 1984) while the vessel was underway at speeds of  $9.9 \pm 1.4$  knots. An observer continuously recorded the number and behaviors (flying, sitting on water, foraging) of all seabirds using  $8\times$  binoculars from the ship's bridge (10 m above the water) within a 300-m survey window (from the bow to  $90^{\circ}$  to port or to starboard), from the side of the vessel that offered the best observation conditions (i.e., lowest sun glare) during daylight hours. Ship-following birds were recorded when they first entered the survey range and were ignored thereafter. We defined seabirds sitting on the water or foraging as “foraging seabirds” (Hunt et al. 1998; Kokubun et al. 2008) and flying seabirds (other than actively foraging from the air) as “non-foraging.” The total area surveyed was  $54\text{ km}^2$ .

Short-tailed shearwaters *Ardenna tenuirostris* (66% by number) and rhinoceros auklets *Cerorhinca monocerata* (28%), which accounted for 94% of total seabirds observed (Table 1), were used in the analysis. Short-tailed shearwaters migrate annually from their breeding colonies in southeastern Australia and Tasmania to spend their non-breeding period in the northern North Pacific during May–October. They feed mainly on euphausiids by surface-seizing and pursuit-diving in the Okhotsk Sea and the northern North Pacific (Ogi et al. 1980; Hunt et al. 1996, 2002). Rhinoceros auklets are a diving seabird breeding in the middle latitude of the North Pacific between early spring and late summer (Gaston and Jones 1998). Rhinoceros auklets breeding on Teuri Island ( $44^{\circ}25'\text{N}$ ,  $141^{\circ}52'\text{E}$ ), northern Hokkaido, Japan, deliver forage fish such as arabesque greenling *Pleurogrammus azonus*, sand lance *Ammodytes* spp., and Japanese anchovy *Engraulis japonicus* to their chicks during the chick-rearing periods between May and July (Watanuki 1987; Takahashi et al. 2001; Ito et al. 2009).

### Prey biomass estimation using acoustic and net sampling

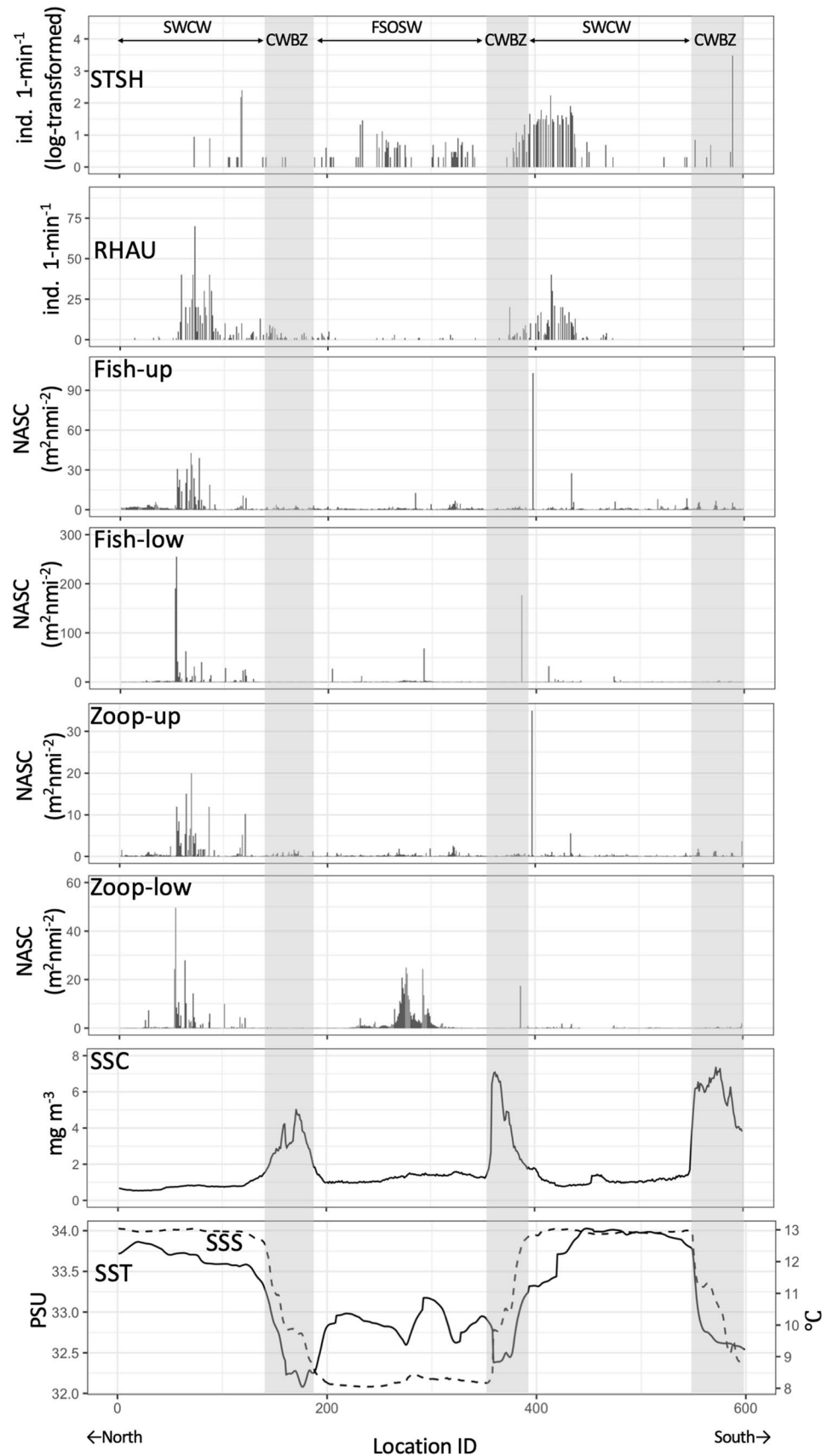
For analyses on acoustic data, we used Echoview (version 10.0; Echoview Software Pty Ltd.) following Nishizawa et al. (2020). We measured the biomass of potential seabird prey using acoustic surveys (Fig. 1). Acoustic volume backscattering strength (SV) data were collected along the transects where seabird observations were made, using a SIMRAD EK80 scientific echosounder at 38 and 120 kHz. The transducers were mounted on the bottom of the vessel (4 m below the sea surface). The echosounder was calibrated using the standard sphere method (Foote et al. 1987) with a 38.1 mm tungsten carbide sphere. The SV data from the upper 5-m layer (i.e., 9-m depth from the surface) and the 2-m layer above the bottom were excluded because of the surface turbulence and bottom echo integration. Fish and zooplankton were identified using a “dB-difference” method (De Robertis et al. 2010; Korneliussen 2018). The differences between backscatter at 120 and 38 kHz ( $\text{SV}_{120\text{ kHz}} - \text{SV}_{38\text{ kHz}}$ ) in the range of  $-12$  to  $10$  dB were assigned to the fish category, and those in the range of  $10$  to  $30$  dB were assigned to the zooplankton category (De Robertis et al. 2010). To compare the regional differences in the biomass of potential prey, the nautical area scattering coefficient (NASC,  $\text{m}^2\text{nmi}^{-2}$ , hereafter acoustically determined biomass) of fish and zooplankton was calculated at a 1-min (ca. 300 m) horizontal resolution and a 5-m vertical resolution (Reiss et al. 2008; Santora et al. 2011). As different seabird species forage at different depths, we present acoustically determined prey biomass at two different water layers: an upper layer (9–29 m depth) and a lower layer (29–104 m depth).

Zooplankton samples were collected during daylight hours at the CTD stations using vertical tows with a North Pacific standard net (NORPAC; mouth diameter 45 cm, mesh size  $335\text{ }\mu\text{m}$ ) from 5 m above the bottom to the surface (depths of stations ranged between 20 to 121 m). The zooplankton samples were immediately preserved with v/v 5% borax-buffered formalin-seawater on the vessel. The filtered water volumes were estimated from the readings of a flowmeter (Rigo Co. Ltd., Tokyo) mounted in the mouth of the net. The total zooplankton biomass ( $\text{mg wet weight m}^{-3}$ ) at each station was measured in the laboratory.

### Statistical analyses

Before statistical analysis, it is necessary to confirm the spatial independence of seabird densities and acoustically determined biomass of fish and zooplankton. In clumped distributions, such as seabird flocks, adjacent observations are often more similar than would be expected in randomly distributed data, indicating a positive autocorrelation (Schneider 1990).

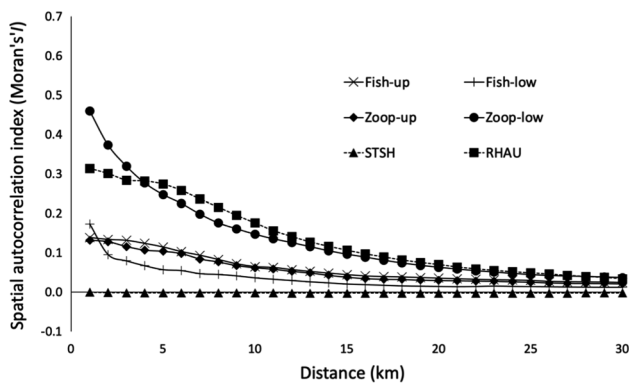
**Fig. 2** Changes in sea surface salinity (SSS), sea surface temperature (SST), sea surface chlorophyll (SSC), acoustically determined zooplankton biomass in the upper layer (9–29 m depth) (Zoop-up) and lower layer (29–104 m depth) (Zoop-low), acoustically determined fish biomass in the upper layer (9–29 m depth) (Fish-up) and lower layer (29–104 m depth) (Fish-low), and densities of short-tailed shearwaters (STSH, log-transformed) and rhinoceros auklets (RHAU) at 1-min interval along the transect. Defined areas based on water mass properties; Soya Warm Current Water (SWCW) and Fresh Surface Okhotsk Sea Water (FSOSW) are shown on the top of panels and the cold-water belt zone (CWBZ) between SWCW and FSOSW are shaded in grey



**Table 1** Seabird density (ind. km<sup>-2</sup>) observed during our surveys

Species	Latin name	Density (ind. km <sup>-2</sup> )	%density
Short-tailed shearwater	<i>Ardenna tenuirostris</i>	103.75	65.70
Rhinoceros auklet	<i>Cerorhinca monocerata</i>	44.64	28.27
Fork-tailed storm-petrel	<i>Oceanodroma furcata</i>	4.19	2.66
Northern fulmar	<i>Fulmarus glacialis</i>	2.43	1.54
Black-tailed gull	<i>Larus crassirostris</i>	2.26	1.43
Flesh-footed shearwater	<i>Ardenna carneipes</i>	0.35	0.22
Slaty-backed gull	<i>Larus schistisagus</i>	0.11	0.07
Parakeet auklet	<i>Aethia psittacula</i>	0.06	0.04
Spectacled guillemot	<i>Cephus carbo</i>	0.04	0.02
Ancient murrelet	<i>Synthliboramphus antiquus</i>	0.02	0.01
Leach's storm-petrel	<i>Oceanodroma leucorhoa</i>	0.02	0.01
Pomarine jaeger	<i>Stercorarius pomarinus</i>	0.02	0.01
Thick-billed murre	<i>Uria lomvia</i>	0.02	0.01
Unidentified murre	<i>Uria</i> spp.	0.02	0.01
Total seabirds		157.92	100.00

All individuals (foraging and non-foraging) were included



**Fig. 3** Spatial variability (Moran's *I* correlogram) for acoustically determined zooplankton biomass in the upper layer (9–29 m depth) (Zoop-up) and lower layer (29–104 m depth) (Zoop-low), acoustically determined fish biomass in the upper layer (9–29 m depth) (Fish-up) and lower layer (29–104 m depth) (Fish-low), and densities of short-tailed shearwaters (STSH) and rhinoceros auklets (RHAU)

Moran's *I* correlograms were calculated to examine the spatial autocorrelation of the seabird densities and of the acoustically determined biomass of fish and zooplankton (Santora et al. 2011; Nishizawa et al. 2020). Lag size was defined as an interval of 1 km. Moran's *I* statistics range from -1 (negative autocorrelation) to +1 (positive autocorrelation), with null values being indicative of a lack of spatial structure (Sokal and Oden 1978). In the preliminary analyses, the densities of rhinoceros auklets and acoustically determined zooplankton biomass in the lower layer showed positive spatial autocorrelations ( $0.28 < \text{Moran's } I < 0.46$ ) at 1–3-km scales and reduced spatial autocorrelation (Moran's  $I < 0.28$ ) at larger scales ( $> 3$  km) (Fig. 3). Therefore, we divided the transects into 15-min (= 4.6 km long) intervals and used

them as the smallest sampling unit for statistical analysis. We compared the seabird density, acoustically determined prey biomass, net-sampled zooplankton biomass, and oceanographic variables among three areas (i.e., SWCW, FSOSW, and CWBZ) using the Steel–Dwass pairwise non-parametric test, because these data were not normally distributed (Shapiro–Wilk normality test,  $p < 0.05$ ). The spatial relationships between seabird density, acoustically determined prey biomass, and surface oceanographic variables were assessed using Spearman's correlation matrix. Further, spatial relationships between the density of foraging seabirds and acoustically determined biomass of fish and zooplankton were evaluated using Spearman's correlation coefficient at four spatial scales (4.6-, 6.1-, 7.6-, and 9.2-km bin sizes), as seabird–prey relationships are typically scale-dependent (e.g., Hunt and Schneider 1987; Hunt et al. 1992; Fauchald et al. 2002). All statistical analyses were done using R software (v.4.0.2, R Development Core Team 2020).

## Results

### Oceanographic parameters and lower trophic levels

SST was highest in SWCW and lowest in the CWBZ (Table 2). SSS was highest in SWSW and lowest in FSOSW (Table 2). For the entire study region, there was a positive relationship between SST and SSS (Table 3). The lowest SST and highest SSC occurred within the CWBZ, indicating the upwelling of the CWB (Table 2, Fig. 2). Within the CWBZ, SST and SSS showed steep gradients, especially at the boundary of the SWCW (Fig. 2). Acoustically determined zooplankton biomass was higher in both



**Table 2** Mean ( $\pm$ SD) values, with the range in parentheses, for foraging seabird density (ind. km<sup>-2</sup>), acoustically determined biomass of fish and zooplankton (m<sup>2</sup>nmi<sup>-2</sup>), and surface oceanographic variables between areas

Variable	Area			Steel–Dwass test ( <i>t</i> -statistics, <i>p</i> -value)		
	SWCW	CWBZ	FSOSW	SWCW vs. CWBZ	SWCW vs. FSOSW	CWBZ vs. FSOSW
SST (°C)	12.58 $\pm$ 0.58 (11.28–13.23), <i>n</i> = 18	9.90 $\pm$ 1.26 (8.09–12.08), <i>n</i> = 11	9.91 $\pm$ 0.58 (8.54–10.66), <i>n</i> = 11	4.18, <i>p</i> < 0.01	4.45, <i>p</i> < 0.01	0.62, <i>p</i> = 0.81
SSS	33.99 $\pm$ 0.02 (33.95–34.02), <i>n</i> = 18	33.13 $\pm$ 0.56 (32.24–33.94), <i>n</i> = 11	32.15 $\pm$ 0.06 (32.08–32.31), <i>n</i> = 11	4.45, <i>p</i> < 0.01	4.45, <i>p</i> < 0.01	3.91, <i>p</i> < 0.01
SSC (mg m <sup>-3</sup> )	0.93 $\pm$ 0.29 (0.55–1.70), <i>n</i> = 18	3.76 $\pm$ 1.87 (1.06–6.50), <i>n</i> = 11	1.31 $\pm$ 0.32 (1.00–2.07), <i>n</i> = 11	4.22, <i>p</i> < 0.01	2.92, <i>p</i> < 0.01	4.44, <i>p</i> < 0.01
Zooplankton biomass via net (mg wet weight m <sup>-3</sup> )	227.92 $\pm$ 53.52 (185.18–287.96), <i>n</i> = 3	219.62 $\pm$ 14.6 (209.30–229.94), <i>n</i> = 2	229.81 $\pm$ 37.04 (187.39–255.74), <i>n</i> = 3	0.00, <i>p</i> = 1.00	0.22, <i>p</i> = 0.97	0.58, <i>p</i> = 0.83
Zoop-up (9–29 m depth)	0.82 $\pm$ 1.20 (0.09–4.61), <i>n</i> = 18	0.34 $\pm$ 0.19 (0.11–0.77), <i>n</i> = 11	0.29 $\pm$ 0.19 (0.13–0.77), <i>n</i> = 11	0.04, <i>p</i> = 0.99	0.58, <i>p</i> = 0.83	0.76, <i>p</i> = 0.73
Zoop-low (29–104 m depth)	0.91 $\pm$ 1.88 (0.00–7.14), <i>n</i> = 18	0.23 $\pm$ 0.35 (0.04–1.25), <i>n</i> = 11	2.24 $\pm$ 3.77 (0.05–12.16), <i>n</i> = 11	1.21, <i>p</i> = 0.45	1.17, <i>p</i> = 0.47	1.87, <i>p</i> = 0.15
Fish-up (9–29 m depth)	2.70 $\pm$ 3.32 (0.26–13.15), <i>n</i> = 18	1.00 $\pm$ 0.33 (0.41–1.53), <i>n</i> = 11	1.01 $\pm$ 0.64 (0.44–2.63), <i>n</i> = 11	1.26, <i>p</i> = 0.42	1.30, <i>p</i> = 0.39	0.69, <i>p</i> = 0.77
Fish-low (29–104 m depth)	3.70 $\pm$ 8.40 (0.00–36.05), <i>n</i> = 18	1.52 $\pm$ 3.53 (0.13–12.10), <i>n</i> = 11	1.44 $\pm$ 1.81 (0.11–6.35), <i>n</i> = 11	1.17, <i>p</i> = 0.47	0.09, <i>p</i> = 0.99	1.35, <i>p</i> = 0.37
Foraging STSH density (ind. km <sup>-2</sup> )	56.08 $\pm$ 105.14 (0–294.52), <i>n</i> = 18	203.42 $\pm$ 656.70 (0–2183.10), <i>n</i> = 11	11.04 $\pm$ 11.67 (0–36.36), <i>n</i> = 11	0.19, <i>p</i> = 0.98	0.78, <i>p</i> = 0.72	1.26, <i>p</i> = 0.42
Foraging RHAU density (ind. km <sup>-2</sup> )	35.51 $\pm$ 50.58 (0–167.26), <i>n</i> = 18	10.45 $\pm$ 11.94 (0–32.00), <i>n</i> = 11	2.64 $\pm$ 3.00 (0–8.73), <i>n</i> = 11	1.15, <i>p</i> = 0.48	1.50, <i>p</i> = 0.29	0.60, <i>p</i> = 0.82

SWCW: Soya Warm Current Water, FSOSW: Fresh Surface Okhotsk Sea Water, CWBZ: cold-water belt zone between SWCW and FSOSW

The results of the Steel–Dwass test (*t*-statistics and *p*-value) are also shown. SST: sea surface temperature, SSS: sea surface salinity, SSC: sea surface chlorophyll, Zoop-up (low): acoustically determined biomass of zooplankton in the upper (lower) layers, Fish-up (low): acoustically determined biomass of fish in the upper (lower) layers, STSH: short-tailed shearwater, RHAU: rhinoceros auklets

the SWCW and FSOSW than in the CWBZ on average, although these trends were not statistically significant (Table 2, Fig. 2). No strong signal of acoustically determined zooplankton biomass was observed in the CWBZ (Fig. 2). Similarly, net-sampled zooplankton showed lower biomass in the CWBZ (Table 2). Acoustically determined fish biomass was higher in SWCW than in FSOSW or CWBZ (Table 2; Fig. 2). Acoustically determined biomass

of zooplankton and fish was not correlated with SST or SSC (Table 3).

### Seabirds

We observed 13 seabird species (Table 1). Short-tailed shearwaters were the most abundant (66% by number), followed by rhinoceros auklets (28%) (Table 1). The density

**Table 3** Spearman’s correlation matrix for surface oceanographic variables, acoustically determined biomass of zooplankton and fish, and seabird densities at 4.6-km scale ( $n = 40$ )

Variables	SST	SSS	SSC	Zoop-up	Zoop-low	Fish-up	Fish-low	STSH	RHAU
SST	1								
SSS	0.69**	1							
SSC	-0.67**	-0.54**	1						
Zoop-up	-0.16	0.23	-0.13	1					
Zoop-low	-0.02	-0.02	-0.29	0.52**	1				
Fish-up	0.06	0.39*	-0.19	0.78**	0.32*	1			
Fish-low	0.08	0.15	-0.38	0.55**	0.82**	0.34*	1		
STSH	-0.17	-0.11	0.08	0.23	0.24	0.17	0.23	1	
RHAU	0.04	0.40**	-0.20	0.47**	0.23	0.28	0.34*	0.37*	1

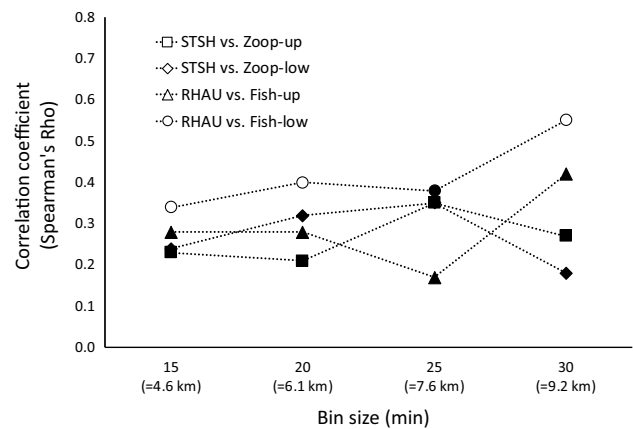
\*\*Correlation is significant at the 0.01 level. \*Correlation is significant at the 0.05 level. SST: sea surface temperature, SSS: sea surface salinity, SSC: sea surface chlorophyll, Zoop-up (low): acoustically determined biomass of zooplankton in the upper (lower) layers, Fish-up (low): acoustically determined biomass of fish in the upper (lower) layers, STSH: short-tailed shearwater density, RHAU: rhinoceros auklets density



**Fig. 4** A rhinoceros auklet holding an adult (> 1-year-old) sand lance in the Soya Warm Current Water in the southwestern Okhotsk Sea on 27 June 2019 (photo by B. Nishizawa)

of foraging short-tailed shearwaters seemed to be higher in CWBZ than in SWCW or FSOSW, although the trends were not statistically significant (Table 2). In CWBZ, we observed a dense flock (up to 3300 ind. km<sup>-2</sup>, Fig. 2) of short-tailed shearwaters where individuals showed head-dipping foraging behavior. In contrast, higher density of foraging rhinoceros auklet was observed in SWCW than in FSOSW or CWBZ, although the trend was not statistically significant (Table 2, Fig. 2). In SWCW, we observed ~ 10 individuals of the rhinoceros auklets capturing adult (> 1-year-old) sand lance (Fig. 4). The densities of short-tailed shearwaters and rhinoceros auklets were low in FSOSW (Table 2, Fig. 2).

The density of foraging short-tailed shearwaters was not correlated with oceanographic environments (Table 3) or prey (i.e., acoustically determined zooplankton biomass) at any spatial scale between 4.6 and 9.2 km ( $p > 0.05$ , Fig. 5). In contrast, positive relationships (0.34–0.55 of Spearman’s



**Fig. 5** Spearman’s correlation coefficient between the densities of foraging seabirds and acoustically determined prey biomass at four different spatial scales (4.6-, 6.1-, 7.6-, and 9.2-km bin sizes). Squares = short-tailed shearwater (STSH) vs. zooplankton in the upper layer (9–29 m depth) (Zoop-up); diamonds = short-tailed shearwater (STSH) vs. zooplankton in the lower layer (29–104 m depth) (Zoop-low); triangles = rhinoceros auklets (RHAU) vs. fish in the upper layer (9–29 m) (Fish-up); circles = rhinoceros auklets (RHAU) vs. fish in the lower layer (29–104 m) (Fish-low). Filled symbols represent statistically non-significant ( $p > 0.05$ )

correlation coefficient) were found between the densities of foraging rhinoceros auklets and their prey (i.e., acoustically determined fish biomass) in the lower layer at scales between 4.6 and 9.2 km (Fig. 5).

### Discussion

This is the first study to provide detailed information on the links between hydrographic features and top predators (i.e., seabirds) at a unique oceanographic system characterized by a cold-water belt in the southwestern Okhotsk Sea off

Hokkaido, Japan. We found that two seabird species, planktivorous short-tailed shearwaters and piscivorous rhinoceros auklets, mainly used our study region for their foraging habitats. However, both seabirds and prey were not always associated with the CWB.

The CWBZ between the coastal SWCW and offshore FSOSW showed elevated chlorophyll *a* concentration, as in previous studies (Ishizu et al. 2006, 2008). This high primary production may be explained by the supply of nutrients associated with upwelling (Ishizu et al. 2006, 2008). This elevated surface chlorophyll *a* concentration, however, was not always related to the acoustically determined zooplankton biomass. Our continuous recording of surface (4-m depth) chlorophyll *a* often overlooks subsurface chlorophyll *a* maximum, which can occur at depths > 20 m, as it did at a CTD station in FSOSW (Online Resource, Fig. S1). A variety of zooplankton species are associated with these subsurface chlorophyll *a* maxima (Townsend et al. 1984; Harris 1988; Moeller et al. 2019). Consequently, the limited overlap of phytoplankton and zooplankton indicated in our study may only be an apparent mismatch. Another possible explanation is a temporal lag between phytoplankton and zooplankton abundance. Continuous echo data collected by the mooring system in the southeastern Bering Sea showed that peak measures of copepod biovolume occurred in advance of the springtime bloom, while the highest euphausiid aggregations occurred in mid-summer (Stafford et al. 2010). Further, the herbivorous zooplankton biomass dynamics in the Barents Sea followed that of spring phytoplankton with a lag of about 1 month (Dalpadado et al. 2020).

During the summer months, short-tailed shearwaters feed on euphausiids and small fish (such as juvenile *Pleurogrammus* sp.) in the Okhotsk Sea and the northern North Pacific (Ogi et al. 1980). Therefore, it was expected that short-tailed shearwaters in our study region would feed on macroplankton that could be detected acoustically (e.g., Korneliusson and Ona 2002). However, there was no association between the density of foraging short-tailed shearwaters and the zooplankton biomass at any spatial scale between 4.6 and 9.2 km. The average prey availability at larger scales (i.e., 10–100 km) might be more important in determining the shearwater density, although our study area was too small (20 sample size at 9.2-km scale) for testing the association at larger scales. The short-tailed shearwaters in the southeastern Bering Sea were assumed to stay in foraging within a 10- to 100-km area for several weeks (Baduini et al. 2006). The density of short-tailed shearwaters in the Japan Sea was correlated with an acoustic index of zooplankton biomass at a scale of 10 km (Kurasawa et al. 2011). The density of these birds in the northern Bering Sea was greater in 50-km grids with euphausiids than in those without (Nishizawa et al. 2017).

Rhinoceros auklets tended to feed in coastal SWCW and were likely to feed in regions where the fish biomass was high in the lower layer (29–104 m depth). The acoustically determined fish biomass likely reflects the presence of forage fish in this region, including sandlance (Safrudin 2013; Hokkaido National Fisheries Research Institute 2017). In the northern Japan Sea, rhinoceros auklets dive up to 50-m depth and feed on these forage fish (Watanuki 1987; Takahashi et al. 2001; Kuroki et al. 2003). We found rhinoceros auklets feeding on sandlance in SWCW (Fig. 3). Shallower water (< 80 m seabed depth) with coarse sand sediments (Wright et al. 2000; Holland et al. 2005) is the preferred habitat for sandlance and presents an important fishing ground for the fisheries targeting this species (Hokkaido National Fisheries Research Institute 2017) as well as for rhinoceros auklets. This area is likely to be a more stable and predictable foraging ground for rhinoceros auklets feeding sandlance compared to those in Japan Sea feeding mainly on pelagic fish including Japanese anchovy, where a weak relationship between the auklets and their prey was reported (Kurasawa et al. 2011).

In this study, piscivorous rhinoceros auklets foraged mainly in the coastal SWCW and planktivorous short-tailed shearwaters did not show a distinct habitat preference. In addition, while the rhinoceros auklet density was sensitive to changes in fish biomass, short-tailed shearwaters were unlinked to zooplankton biomass. These species-specific differences might be related to their prey-searching behaviors. Alcids, including rhinoceros auklets, search visually for the fish school itself underwater (Burger et al. 1993), while tubenosed Procellariiformes, including short-tailed shearwaters, can use both visual and olfactory cues to locate prey patches from the air and therefore search broader areas (Nevitt et al. 1995; Savoca and Nevitt 2014). Another explanation for the species-specific response to their prey might be differences in life-history stages. In the study area and period, short-tailed shearwaters were in the non-breeding stage in which they were not restricted by energy requirements from chicks. On the other hand, observed rhinoceros auklets were likely in the chick-rearing stage, since our study site was located within the foraging range (~ 164 km from the colony, Kato et al. 2003) of the auklets rearing chicks in Teuri, Rebun, and Moneron islands (Watanuki 1987; Kondratyev et al. 2000; Hasebe and Senzaki 2016; Biodiversity Center of Japan 2017). Therefore, the prey-searching area of those breeding auklets may have been restricted to a smaller space than that for non-breeding shearwaters and may have shown clearer concordance with underwater prey biomass. Since our result showed that the spatial autocorrelations of auklets were higher in the smaller spatial scale whereas those of shearwaters were consistently low (Fig. 3), this result may, in part, support the above hypotheses.



Our study suggests that different seabird species use the environment in different ways, and that the heterogeneous marine environment is an important factor for creating various foraging hotspots of top predators.

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