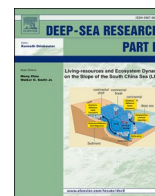




Contents lists available at ScienceDirect

Deep-Sea Research Part II

journal homepage: <http://www.elsevier.com/locate/dsr2>

Timing of spring sea-ice retreat and summer seabird-prey associations in the northern Bering Sea

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ARTICLE INFO

Keywords:

Arctic
Sea ice
Seabird distribution
Acoustic
Water mass
Zooplankton
Fish
Northern bering sea

ABSTRACT

To understand the effect of an unusually early sea-ice retreat in the northern Bering Sea in the spring of 2018 on the marine ecosystem of the northern Bering Sea, we compared at-sea observations of seabird density and acoustic observations of prey (fish and zooplankton) biomass during shipboard surveys around St. Lawrence Island in the summers of 2017 and 2018. Densities of foraging seabirds in 2018 (piscivorous divers: 4.7 birds km⁻², planktivorous divers: 5.1, shearwaters: 0.7, surface feeders: 6.6) were lower than those in 2017 (piscivorous divers: 14.7 birds km⁻², planktivorous divers: 10.3, shearwaters: 11.9, surface feeders: 11.9). Acoustically-determined prey biomass in 2018 (fish: 6.4 m²nmi⁻², zooplankton: 2.3) was also lower than in 2017 (fish: 18.4 m²nmi⁻², zooplankton: 5.5). Similarly, biomass of macrozooplankton (amphipods, euphausiids, *Neocalanus* spp. and *Calanus marshallae*) sampled using bongo nets was smaller in 2018. At scales of 5–30 km, correlations between the seabird density and prey biomass were weaker (–0.2–0.3 of Pearson's *r*) in 2018 than those in 2017 (0.4–0.9) for all seabirds except planktivorous divers. We suggest that the lack of sea ice, and the resulting lack of ice-edge phytoplankton blooms, may weaken trophic linkages by causing a low biomass of secondary consumers and hence a reduced density of seabirds.

1. Introduction

The Bering Sea shelf is one of the most productive marine ecosystems in the world (Grebmeier et al., 2006; Hunt et al., 2013). This area is experiencing a decline in seasonal sea-ice extent and earlier sea-ice retreat, but with large interannual variations (Perovich and Richter-Menge, 2009; Stabeno et al., 2012). Changes in the timing of sea-ice retreat, along with increasing seawater temperatures and freshwater content, affect the timing, magnitude, and location of phytoplankton blooms, and thereby affect the distribution and abundance of higher trophic levels (Li et al., 2009; Hunt et al., 2011; Renner et al., 2016; Sigler et al., 2016; Alabia et al., 2018).

In the northern Bering Sea, sea-ice extent during the winter of 2017/2018 was the lowest since satellite monitoring began in 1978 (Cornwall, 2019; Stabeno and Bell, 2019; Appendix A). The lack of sea-ice cover in the northern Bering Sea shelf in 2018 caused an absence of ice algae and ice-edge phytoplankton blooms (Siddon and Zador, 2018; Duffy-Anderson et al., 2019). As a result, the abundance of large copepods and

juvenile euphausiids, which feed on these ice-associated blooms, could have been reduced (Sigler et al., 2016; Siddon and Zador, 2018; Duffy-Anderson et al., 2019).

Other notable events in the northern Bering Sea ecosystem during 2018 included mass mortality of seabirds. In June 2018, a thousand dead murre (common *Uria aalge* and thick-billed *U. lomvia*) washed ashore along the coasts of St. Lawrence Island and around Norton Sound (Siddon and Zador, 2018; Duffy-Anderson et al., 2019; Romano et al., 2020 (this issue)). Reproductive failures, low reproductive success, and delayed breeding were also observed in murre, black-legged kittiwakes (*Rissa tridactyla*), and auklets (least *Aethia pusilla* and crested *A. cristata*) breeding on the islands of the northern Bering Sea in 2018 (Siddon and Zador, 2018; Dragoo et al., 2019; Romano et al., 2020 (this issue)).

This unusual mass mortality of marine top-predators might have been caused by food shortage because of anomalous oceanic conditions (Jones et al., 2019; Duffy-Anderson et al., 2019) and avian influenza (Will et al., 2020a (this issue)). However, the mechanism causing these mass mortalities of seabirds in the northern Bering Sea is not fully

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<https://doi.org/10.1016/j.dsr2.2020.104898>

Received 16 January 2020; Received in revised form 10 October 2020; Accepted 2 November 2020

Available online 9 November 2020

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known. Information on the distribution and abundance of seabirds at-sea, their foraging behavior, and spatial associations between seabirds and prey is necessary to improve our understanding of the mechanisms involved.

We used shipboard surveys around St. Lawrence Island in the northern Bering Sea during the summers of 2017 and 2018 to examine spatial relationships between seabirds and prey at various spatial scales. We compared these variables between the two study years, which had different sea ice conditions, to better understand the linkages between sea-ice coverage and marine top-predators in the northern Bering Sea ecosystem. Specifically, we predicted that the lack of sea ice and its associated phytoplankton blooms may alter trophic linkages through a reduced biomass of secondary consumers and hence a reduced density of seabirds.

2. Methods

2.1. Study area and oceanography

Research cruises onboard the T/S *Oshoro-Maru* (Faculty of Fisheries Sciences, Hokkaido University) were conducted around St. Lawrence Island (ca. 63°30'N, 170°30'W) in the northern Bering Sea in July of 2017 and 2018 (Fig. 1). The northern Bering Sea shelf is shallow, with a sea depth of approximately 50 m (Fig. 1). Large, mixed-species colonies support up to 12 million breeding seabirds in the region, along the mainland coast, on St. Lawrence Island, and on other smaller islands

(USFWS, 2014). The waters north of St Lawrence Island to the Bering Strait, known as the Chirikov Basin, are shallow and nutrient rich, particularly on the western side through which the Anadyr Water passes. In the study area, three distinct water masses can be discerned, which are known to impact the distribution of zooplankton, fish, and seabirds (Elphick and Hunt, 1993; Piatt and Springer, 2003; Eisner et al., 2013), namely Alaska Coastal Water (ACW), Bering Shelf Water (BSW), and Anadyr Water (AW). These water masses have a north-south orientation, with ACW on the east, BSW in the middle, and AW on the west (Coachman et al., 1975). The ACW is less saline, warmer, and has lower concentrations of nutrients and chlorophyll *a* than BSW and AW (Coachman et al., 1975; Walsh et al., 1989). In contrast, BSW and AW are cooler, more saline, and have substantially higher chlorophyll *a* and nutrient concentrations (Coachman et al., 1975; Walsh et al., 1989).

To determine the positions of the boundaries between water masses, we conducted CTD (SBE 911 Plus, Sea-Bird Electronics, Bellevue, WA) or expendable CTD (XCTD, Tsurumi-Seiki, Yokohama Kanagawa, Japan) measurements (23 stations in 2017, 24 stations in 2018, Fig. 1 a and b). The positions of the boundaries between water masses were determined using salinity (Coachman et al., 1975). The ACW was defined as having salinity below 31.8, BSW as between 31.8 and 32.5, and AW as over 32.5 (Walsh et al., 1989; Hunt and Harrison, 1990). Based on our salinity profiles, we defined the water mass that dominated the water column at each station (Fig. 1). The water around St Lawrence Island was stratified, especially in the Anadyr Water in 2017, and well-mixed in 2018 (Fig. 1 c and d, see Ueno et al., 2020 (this issue)).

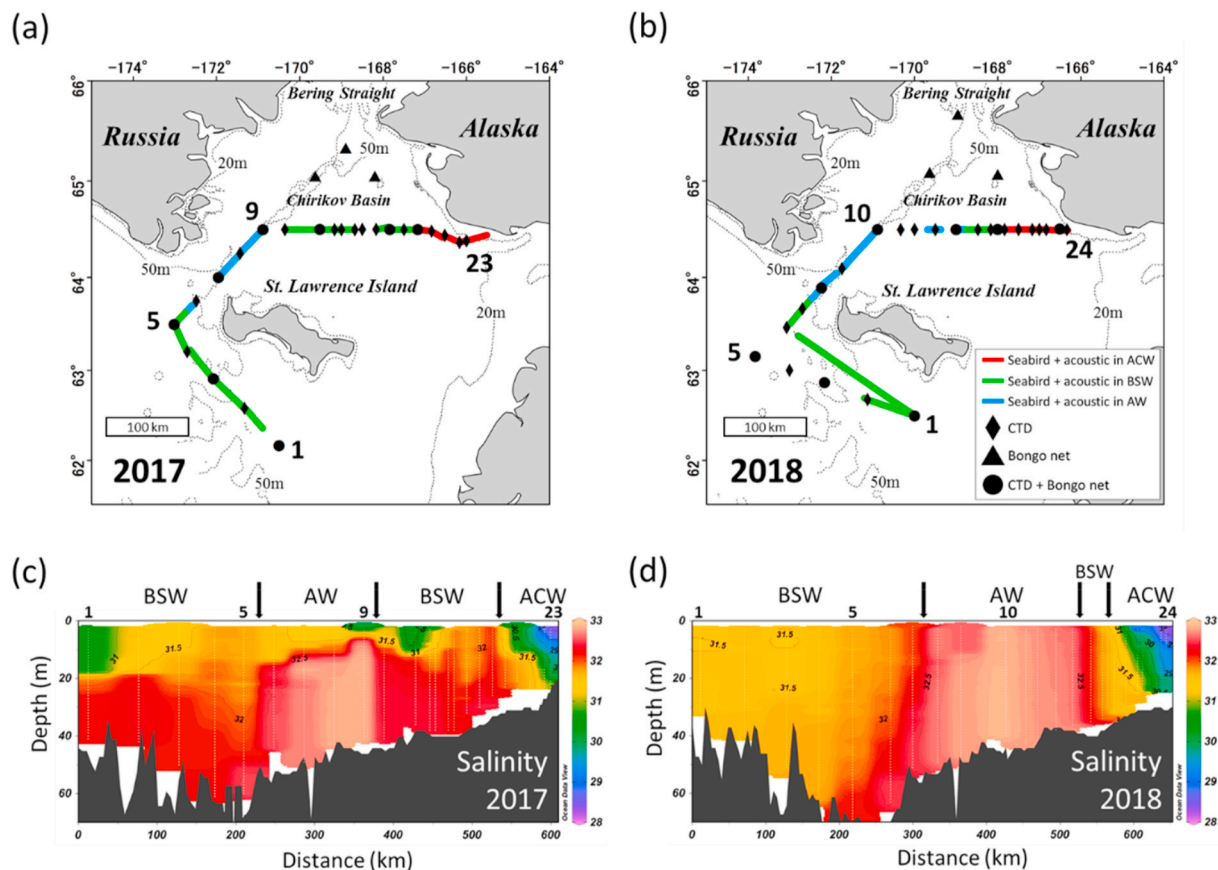


Fig. 1. The study area around St. Lawrence Island in the northern Bering Sea showing locations of seabird and acoustic survey lines [red = Alaska Coastal Water (ACW), green = Bering Shelf Water (BSW), blue = Anadyr Water (AW)], CTD stations (diamonds) with the number of stations, bongo net sampling stations (triangles), CTD and bongo net sampling stations (circles), and the 20- and 50-m isobath (dotted lines), for 2017 (a) and 2018 (b). The positions of the boundaries between water masses were determined using salinity (see methods). Vertical cross section of salinity around St. Lawrence Island for 2017 (c) and 2018 (d). White vertical lines in the cross sections indicate where CTD/XCTD measurements were conducted. The station number was also shown on the cross sections. Black arrows on the cross sections indicate the positions of the boundaries between water masses. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.2. Seabird observations

At-sea seabird observations were made on 16–21 July 2017 and 3–6 July 2018 around St. Lawrence Island (within 200 km from the island) in the northern Bering Sea (Table 1, Fig. 1). We used standard strip transect methodology (Tasker et al., 1984) while the vessel was underway at speeds of 8.8–10.3 knots (Table 1). An observer continuously recorded the number and behaviors (flying, sitting on water, foraging) of all seabirds using 8 × binoculars from the ship's bridge (10 m above the water) within a 300-m survey window (from the bow to 90° 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 observed 25 seabird species and classified them into four groups (piscivorous divers, planktivorous divers, shearwaters, surface feeders) according to their foraging modes (Table 2). Although we observed four benthic-feeding seabirds (eiders and other seaducks), we did not include them in the analyses, since we did not measure the benthos on which they feed, nor did we record any foraging among birds in this foraging guild. Seabird species were sometimes combined for analysis. Piscivorous divers included puffins (*Fratrercula*, 2 spp), murres (common *Uria aagle* and thick-billed *U. lomvia* were combined), pigeon guillemot (*Cepphus columba*), ancient murrelet (*Synthliboramphus antiquus*), loons (*Gavia*, 2 spp), and pelagic cormorant (*Phalacrocorax pelagicus*) (Table 2). Planktivorous divers included auklets (*Aethia*, 3 spp) (Table 2). Surface feeders included northern fulmars (*Fulmarus glacialis*), fork-tailed storm-petrel (*Oceanodroma furcata*), red phalarope (*Phalaropus fulicarius*), jaegers (*Stercorarius*, 3 spp), black-legged kittiwake (*Rissa tridactyla*), and gulls (Laridae, 5 spp) (Table 2). Short-tailed shearwaters (*Ardenna tenuirostris*) feed mainly on euphausiids by both surface seizing and pursuit diving (Ogi et al., 1980; Hunt et al., 1996; Hunt et al., 2002), and therefore they were classified as their own group (Table 2). We defined seabirds sitting on the water or foraging as “foraging seabirds” (Hunt et al., 1996; Hunt et al., 1998; Kokubun et al., 2008) and flying seabirds (other than actively foraging from the air) as “non-foraging”. We calculated seabirds counts as densities (birds km⁻²) for all analyses.

2.3. Prey biomass estimation using acoustics and net samplings

We measured the biomass of potential seabird prey using acoustic surveys (Fig. 1). Acoustic volume backscattering strength (S_V) data were collected along the transects where seabird observations were conducted, 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 once in 2016 and in 2018 using the standard sphere method (Foote et al., 1987) with a 38.1 mm tungsten carbide sphere. Calibration results were applied in the post-processing of acoustic data. The S_V 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 integrations. Fish and zooplankton were identified using a “dB-difference” method (De Robertis et al., 2010; Korneliussen, 2018). The differences between

Table 1

Summary of at-sea seabirds surveys in 2017 and 2018 around St. Lawrence Island in the northern Bering Sea. Date surveyed (Coordinated universal time: UTC), total survey length (km), area surveyed (km²), and ship speed (knots) are shown.

Year	2017	2018
Date surveyed (UTC)	16 July - 21 July	3 July - 6 July
Total survey length (km)	453.56	513.71
Area surveyed (km ²)	136.07	154.11
Ship speed (mean ± SD) (knots)	8.8 ± 1.5	10.3 ± 0.6

backscatter at 120 and 38 kHz ($S_{V\ 120\ \text{kHz}} - S_{V\ 38\ \text{kHz}}$) in the range of -12 to 10 dB were assigned to the fish category, and those in the range of 10–30 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 (S_A , m²nmi⁻², hereafter acoustically-determined biomass) of fish and zooplankton were calculated at a 1-min (ca. 300 m) horizontal resolution and a 5-m vertical resolution (Reiss et al., 2008; Santora et al., 2011; Nishizawa et al., 2019). Because seabirds forage at different depths among foraging guilds, we present acoustically-determined prey biomass at two different water layers: an upper layer (9–24 m depth) and a lower layer (24–59 m depth). For analyses on acoustic data, we used Echoview (version 10.0; Echoview Software Pty Ltd.).

Zooplankton samples were collected at 11 stations in each year using a bongo net (505 μm mesh size, 0.7 m mouth diameter) (Fig. 1). The net was obliquely towed from 5 m above the bottom to the surface at a ship's speed of 2 knots. 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 flow-meter (Rigo Co. Ltd., Tokyo) mounted in the mouth of the net. In the laboratory, species identification and enumeration were performed under a stereomicroscope. Zooplankton was classified into six taxonomic groups (amphipods, euphausiids, *Neocalanus cristatus*, *N. flemingeri*, *Calanus marshallae*, others) following studies on the diet of two abundant auklets (least and crested) breeding on St. Lawrence Island (Gall et al., 2006; Sheffield Guy et al., 2009). Subsequently, we measured the wet weight (WW) of each taxonomic group with a precision of 0.1 μg using an electronic balance (Mettler AE-100). The zooplankton biomass (X: mg WW m⁻³) was calculated based on the WW and volume of water filtered through the net.

2.4. Statistical analyses

Before statistical analysis, spatial independence of seabird densities and acoustically-determined biomass of fish and zooplankton must be confirmed. In clumped distributions, such as seabird flocks, adjacent observations are often more similar than would be expected in randomly distributed data, indicating positive autocorrelation (Schneider, 1990). 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). Lag size was defined as an interval of 1 km. Moran's *I* statistics ranges from -1 (negative autocorrelation) to +1 (positive autocorrelation), with null values being indicative of a lack of spatial structure (Sokal and Oden, 1978). In preliminary analyses all seabird foraging guilds, except shearwaters, and acoustically-determined biomass of fish and zooplankton showed weak positive spatial autocorrelation (0.01 < Moran's *I* < 0.31) at 1–4 km scales and reduced spatial autocorrelation at larger scales between 5 and 30 km scales (Appendix B). Shearwaters showed no evidence of spatial autocorrelation at any spatial scale both in 2017 and 2018 (Appendix B). Therefore, we divided transects into 5-km intervals and used them as a sampling unit for statistical analysis.

We compared the seabird density and acoustically-determined biomass of fish and zooplankton among three water masses using the Steel-Dwass pairwise non-parametric test. We used Mann-Whitney *U* tests for two-year comparisons (2017 vs. 2018) of seabird density and acoustically-determined biomass of fish and zooplankton. Spatial relationships between the density of foraging seabirds and acoustically-determined biomass of fish and zooplankton were evaluated using Pearson's correlation coefficient at four spatial scales (5, 10, 20, and 30 km bin sizes) because seabird-prey relationships are typically scale-dependent (e.g. Hunt and Schneider, 1987; Hunt et al., 1992; Fauchald et al., 2002).

Table 2

Summary of species identified during seabird surveys around St. Lawrence Island in the northern Bering Sea in 2017 and 2018.

Foraging guild/species	Scientific name	Seabird density (birds km ⁻²)			
		2017		2018	
		Foraging	Non-foraging	Foraging	Non-foraging
Piscivorous divers		14.676	3.822	4.656	4.880
Horned Puffin	<i>Fratercula corniculata</i>	0.029	0.088	0.363	0.396
Tufted Puffin	<i>Fratercula cirrhata</i>	0.173	0.254	0.539	0.415
Common/Thick-billed Murre	<i>Uria</i> spp.	14.393	3.355	3.579	3.783
Ancient Murrelet	<i>Synthliboramphus antiquus</i>	0.066	0.110	0.149	0.247
Pigeon Guillemot	<i>Cephus columba</i>	0	0	0.013	0.019
Pacific Loon	<i>Gravia pacifica</i>	0.015	0	0.006	0
Yellow-billed Loon	<i>Gravia adamsii</i>	0	0.007	0.006	0
Unidentified Loon	<i>Gravia</i> spp.	0	0.007	0	0
Pelagic Cormorant	<i>Phalacrocorax pelagicus</i>	0	0	0	0.019
Planktivorous divers		10.252	5.810	5.136	17.014
Crested Auklet	<i>Aethia cristatella</i>	2.800	1.367	1.596	6.145
Least Auklet	<i>Aethia pusilla</i>	6.563	3.880	3.043	10.243
Parakeet Auklet	<i>Aethia psittacula</i>	0.816	0.529	0.496	0.620
Unidentified Auklet	<i>Aethia</i> spp.	0.073	0.033	0	0.006
Shearwaters		11.931	7.805	0.733	4.643
Short-tailed shearwater	<i>Ardenna tenuirostris</i>	11.931	7.805	0.733	4.643
Surface feeders		11.854	22.827	6.612	5.441
Northern Fulmar	<i>Fulmarus glacialis</i>	5.751	18.171	4.510	1.648
Fork-tailed Storm-Petrel	<i>Oceanodroma furcata</i>	1.051	2.106	0.045	0.714
Red Phalarope	<i>Phalaropus fulicarius</i>	0.838	0.096	1.739	2.229
Pomarine Jaeger	<i>Stercorarius pomarinus</i>	0	0	0.019	0.019
Parasitic Jaeger	<i>Stercorarius parasiticus</i>	0	0	0	0.013
Long-tailed Jaeger	<i>Stercorarius longicaudus</i>	0	0.015	0	0
Black-legged kittiwake	<i>Rissa tridactyla</i>	4.215	2.366	0.292	0.740
Sabine's Gull	<i>Xema sabini</i>	0	0.007	0	0.019
Glaucous Gull	<i>Larus hyperboreus</i>	0	0.007	0.006	0.032
Glaucous-winged Gull	<i>Larus glaucescens</i>	0	0.007	0	0.006
Herring Gull	<i>Larus argentatus</i>	0	0.051	0	0.013
Slaty-backed Gull	<i>Larus schistisagus</i>	0	0	0	0.006
Total seabirds		48.714	40.476	17.137	31.977

3. Results

3.1. Seabirds

We observed 25 seabird species (19 species in 2017, 22 species in 2018) during our surveys (Table 2). The density of total seabirds was nearly half in 2018 (49.1 birds km⁻²) compared to 2017 (89.2 birds km⁻²); all foraging guilds but planktivorous divers declined in 2018 (Table 2).

Dominant species among foraging guilds were similar between 2017 and 2018. Among foraging piscivorous divers, murre were the most

abundant in both years (98% in 2017, 77% in 2018). Within the planktivorous divers, least auklet was the most abundant (64% in 2017, 59% in 2018). Among foraging surface feeders, northern fulmar was most abundant (49% in 2017, 68% in 2018) (Table 2).

Water mass preference by foraging seabirds was different among foraging guilds and between years. Piscivorous divers occurred in each of the water masses, with higher densities in BSW in 2017 and in AW in 2018 (Table 3). Planktivorous divers showed a strong preference for AW in both years and were absent from ACW (Table 3). Shearwaters favored BSW in 2017 and ACW in 2018 (Table 3). Surface feeders preferred AW in both years (Table 3).

Table 3

Mean (\pm SE) density of foraging seabird (birds km⁻²) and mean (\pm SE) acoustically-determined biomass of fish and zooplankton (m²nmi⁻²) between water masses (ACW: Alaska Coastal Water, BSW: Bering Sea Water, AW: Anadyr Water) for 2017 and 2018. The results of the Steel-Dwass test (*t*-statistics and *p*-value) are also shown.

Variables	Year	ACW	BSW	AW	Steel-Dwass test (t-statistics, p-value)		
					ACW vs. BSW	ACW vs. AW	BSW vs. AW
Piscivorous divers	2017	1.51 \pm 0.53	16.90 \pm 14.86	6.65 \pm 1.11	0.45, p = 0.89	4.04, p < 0.05	4.61, p < 0.05
	2018	4.63 \pm 1.34	2.76 \pm 0.53	9.16 \pm 2.77	2.10, p = 0.09	1.02, p = 0.57	3.47, p < 0.05
Planktivorous divers	2017	0	1.48 \pm 0.36	40.84 \pm 12.22	2.65, p < 0.05	5.40, p < 0.05	5.91, p < 0.05
	2018	0.04 \pm 0.04	0.92 \pm 0.40	19.51 \pm 5.45	1.91, p = 1.35	4.75, p < 0.05	5.81, p < 0.05
Shearwaters	2017	0.81 \pm 0.68	12.93 \pm 10.53	9.39 \pm 5.02	0.95, p = 0.61	2.73, p < 0.05	2.37, p < 0.05
	2018	2.50 \pm 1.13	0.19 \pm 0.08	0.12 \pm 0.07	4.43, p < 0.05	3.38, p < 0.05	0.01, p = 1.00
Surface feeders	2017	1.26 \pm 0.34	11.34 \pm 7.24	11.60 \pm 2.00	1.65, p = 0.22	5.00, p < 0.05	4.71, p < 0.05
	2018	1.38 \pm 0.57	0.79 \pm 0.14	26.23 \pm 8.63	0.15, p = 0.99	3.07, p < 0.05	4.44, p < 0.05
Fish in upper layer (9–24 m)	2017	115.27 \pm 30.42	161.44 \pm 25.40	131.81 \pm 21.02	0.22, p = 0.97	0.98, p = 0.59	0.59, p = 0.83
	2018	11.45 \pm 2.36	20.20 \pm 4.04	115.37 \pm 23.25	0.84, p = 0.68	4.88, p < 0.05	5.60, p < 0.05
Fish in lower layer (24–59 m)	2017	10.85 \pm 3.56	133.34 \pm 21.19	232.97 \pm 64.31	5.42, p < 0.05	3.13, p < 0.05	0.12, p = 0.99
	2018	14.37 \pm 8.16	69.96 \pm 9.16	33.63 \pm 8.89	4.35, p < 0.05	3.63, p < 0.05	2.32, p = 0.05
Zooplankton in upper layer (9–24 m)	2017	41.92 \pm 13.19	47.18 \pm 6.44	49.46 \pm 5.81	0.04, p = 1.00	2.06, p = 0.10	1.61, p = 0.24
	2018	6.67 \pm 2.92	5.51 \pm 0.89	33.64 \pm 8.62	0.51, p = 0.87	4.23, p < 0.05	6.03, p < 0.05
Zooplankton in lower layer (24–59 m)	2017	5.40 \pm 0.97	37.97 \pm 6.00	53.12 \pm 12.81	5.31, p < 0.05	3.37, p < 0.05	0.11, p = 0.99
	2018	1.59 \pm 0.52	28.87 \pm 12.10	16.46 \pm 7.14	4.88, p < 0.05	4.29, p < 0.05	0.99, p = 0.58

Except for planktivorous divers, seabird foraging guilds showed lower densities of foraging birds in 2018 compared to 2017 (Fig. 2). The lower density of foraging planktivorous divers in 2018 was not statistically significant (Fig. 2). Except for surface feeders (34% foragers in 2017, 55% in 2018), the proportion of foraging seabirds (i.e. density of foraging birds/density of total birds) was significantly lower in 2018 (piscivorous divers: 49% foragers, planktivorous divers: 23%, shearwaters: 14%) than in 2017 (piscivorous divers: 79% foragers, planktivorous divers: 64%, shearwaters: 60%) (Fisher's exact tests, $p < 0.05$).

3.2. Fish and zooplankton biomass

Acoustically-determined biomasses of fish and zooplankton differed among water masses and between years. In 2017, the biomass of fish in the upper layer (9–24 m depth) showed similar values among the three water masses, while that in the lower layer (24–59 m depth) was greatest in AW or BSW (Table 3). In 2018, the biomass of fish in the upper layer was greatest in AW, and that in the lower layer was greatest in AW or BSW (Table 3). For zooplankton, relationships between acoustically-determined biomass and water masses were similar to those of fish (Table 3). In 2018, acoustically-determined biomasses of both fish and zooplankton were smaller than those in 2017 (Fig. 3). In summary, both fish and zooplankton were highest in AW, particularly in the upper layer water, and both had higher biomass in 2017 than in 2018.

3.3. Bongo net sample

Biomass of total zooplankton collected using the bongo net in 2018 was significantly smaller than in 2017 (Table 4). Biomass of all large-sized zooplankton (amphipods, euphausiids, *Calanus marshallae*, and *Neocalanus* copepods) appeared to be smaller in 2018, but the differences were not statistically significant except for *Neocalanus flemingeri* (Table 4).

3.4. Spatial relationships between seabirds and prey

In 2017, positive relationships (0.4–0.9 of Pearson's correlation coefficient) were found between the densities of foraging seabirds and acoustically-determined biomass at scales between 5 and 30 km for piscivorous divers, shearwaters, and surface feeders (Fig. 4a). No

correlations were found between planktivorous divers and prey in 2017 (Fig. 4a). In contrast, in 2018, the correlations (–0.2–0.3 of Pearson's correlation coefficient) were weak and non-significant, except for planktivorous divers, which had a positive relationship (0.5 of Pearson's correlation coefficient) with zooplankton that year, at 20 km scale (Fig. 4b).

4. Discussion

4.1. Seabirds and water masses

Our findings on seabird habitat preference with respect to water masses are mostly consistent with previous works conducted in the Chirikov Basin during summer (July–August); planktivorous species such as auklets and short-tailed shearwaters use Anadyr Water and Bering Shelf Water more frequently and piscivorous species, including murre, either exhibited no preference for any water mass or occurred more often in Alaska Coastal Water (Elphick and Hunt, 1993; Haney and Schauer, 1994). The preference of predominantly planktivorous species for Anadyr Water and Bering Shelf Water is likely due to the presence of larger zooplankton species such as copepods (*Neocalanus* spp., *Eucalanus bungii*) and euphausiids (*Thysanoessa* spp.) (Hunt et al., 1990; Piatt and Springer, 2003). In Alaska Coastal Water, these larger prey are not abundant and small zooplankton predominate (Hunt and Harrison, 1990; Piatt and Springer, 2003; Eisner et al., 2013).

4.2. Seabird density and prey biomass

In general, we found reduced numbers of birds in our study area in 2018. Largest declines in total density were for shearwater, fulmar, kittiwakes, and murre. The decline in murre, while greatest in 2018, appears to have occurred in the northern Bering Sea over several years (Kuletz et al., 2020 (this issue)). In contrast, planktivorous auklet densities were up slightly in 2018. The increase in auklets also fits the pattern observed by Kuletz et al., 2020 (this issue), showing higher auklet densities in the Chirikov Basin during 2017–2019.

We found that densities of foraging seabirds, including both piscivores and planktivores, were lower in 2018 than in 2017. Similarly, the acoustic surveys and zooplankton net samples showed lower biomasses of fish and zooplankton in 2018. Thus, the low density of foraging

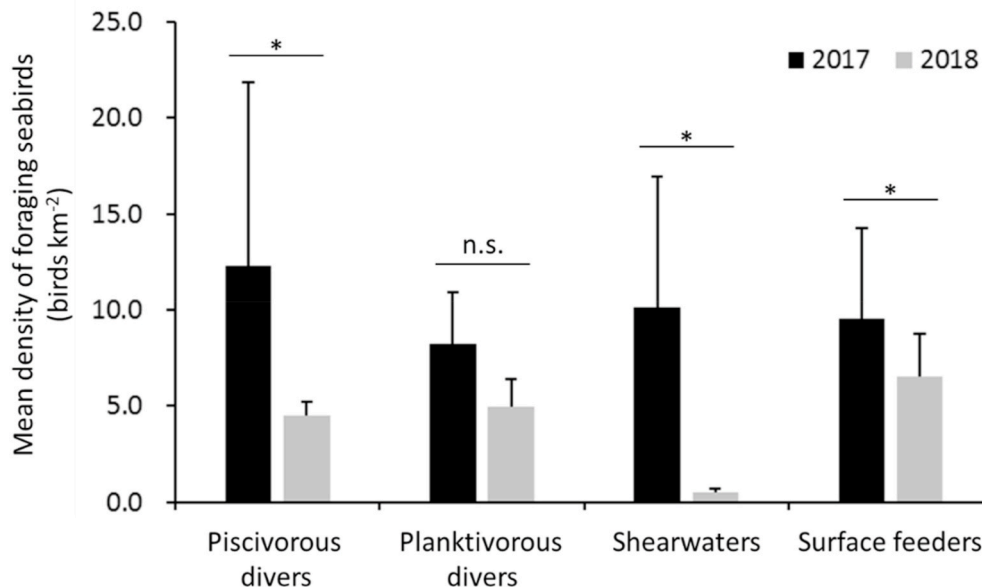


Fig. 2. Mean (+SE) densities (birds km⁻²) of foraging piscivorous divers, planktivorous divers, shearwaters, and surface feeders for 2017 and 2018. Asterisks represent significance of difference ($p < 0.05$) for two-year comparisons using Mann–Whitney U tests.

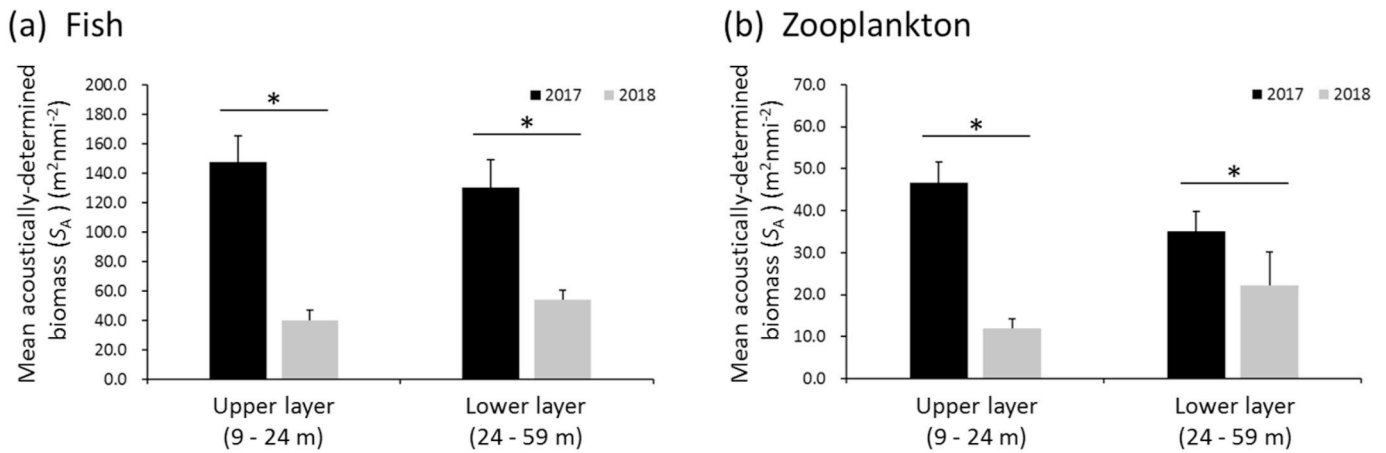


Fig. 3. Mean (+SE) acoustically-determined biomass (S_A) ($m^2 nmi^{-2}$) of fish (a) and zooplankton (b) in the upper layer (9–24 m) and lower layer (24–59 m) for 2017 and 2018. Asterisks represent significance of difference ($p < 0.05$) for two-year comparisons using Mann–Whitney U tests.

Table 4

Zooplankton biomass (mg Wet Weight m^{-3}) collected using bongo net. Values are mean \pm SD with range in parentheses. Sample size and the results of Mann–Whitney U tests are also shown.

	2017	2018	U test
Samples (n)	11	11	–
Amphipods	8.0 \pm 20.8 (0–72.8)	2.4 \pm 7.7 (0–26.8)	$U = 71.0, p = 0.33$
Euphausiids	91.0 \pm 87.9 (0–248.7)	68.1 \pm 74.5 (0–231.6)	$U = 64.0, p = 0.84$
<i>Neocalanus cristatus</i>	20.6 \pm 45.2 (0–141.2)	0	$U = 71.5, p = 0.17$
<i>Neocalanus flemingeri</i>	83.3 \pm 89.2 (0–245.3)	8.6 \pm 17.3 (0–57.9)	$U = 89.0, p < 0.05$
<i>Calanus marshallae</i>	268.2 \pm 234.8 (70.7–802.6)	133.0 \pm 116.9 (6.4–441.0)	$U = 83.0, p = 0.15$
Others	195.0 \pm 178.7 (27.1–562.3)	118.5 \pm 119.2 (2.6–349.2)	$U = 79.0, p = 0.24$
Total zooplankton	666.2 \pm 378.9 (126.4–1275.7)	330.5 \pm 233.9 (19.1–703.1)	$U = 92.0, p < 0.05$

seabirds in 2018 reflected the lower prey biomass.

We were not able to identify the prey species responsible for the acoustic backscatter. However, acoustic surveys using the dual frequencies (38 and 120 kHz) can provide relative biomass of fish and zooplankton (Mitson et al., 1996; Kokubun et al., 2008; De Robertis et al., 2010; Sigler et al., 2012). Our acoustically-determined fish biomass could reflect the presence of midwater fish such as juvenile walleye pollock (*Gadus chalcogrammus*), capelin (*Mallotus villosus*), and juvenile salmon (*Oncorhynchus* spp.), all of which are important prey items for murre. Murres were the most abundant piscivorous divers in our study, and they are an important component of the offshore avifauna in the region (Kuletz et al., 2020). The estimates of zooplankton biomass that we obtained could include euphausiids and other zooplankton such as copepods, which are the main prey species for planktivorous auklets (least, crested, and parakeet) and short-tailed shearwaters during summer in the Bering Sea (Bédard, 1969; Ogi et al., 1980; Hunt et al., 2002; Gall et al., 2006).

The lower biomasses of fish and zooplankton in 2018 could be related to the lack of sea ice. In 2017, sea-ice coverage extended south of St. Lawrence Island even in mid-April, while in April 2018 the sea ice had completely retreated to the north of St. Lawrence Island (Fukai

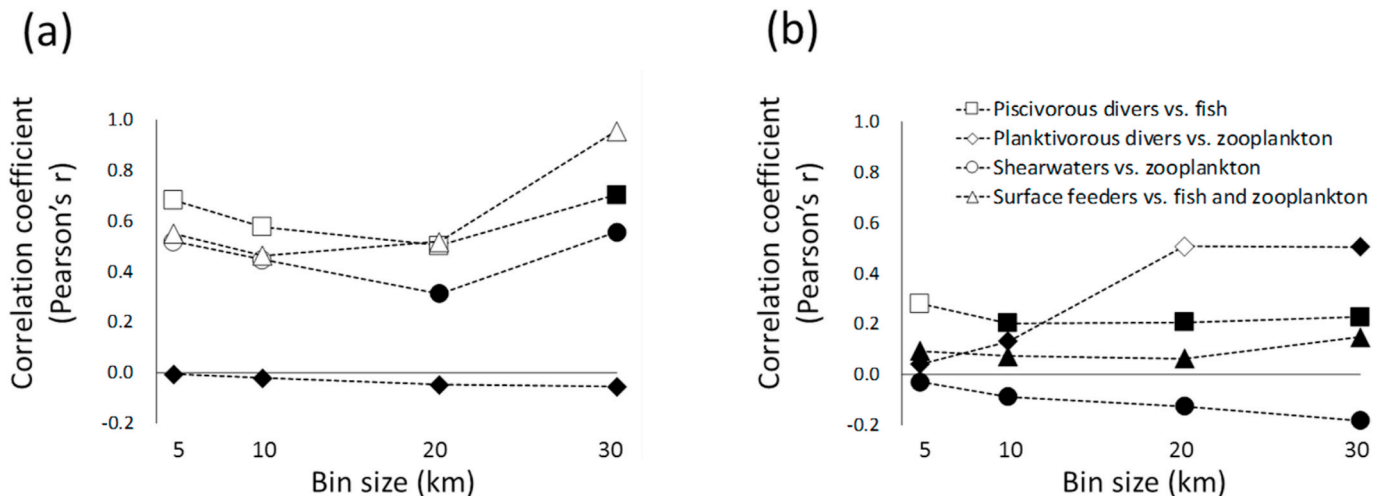


Fig. 4. Pearson's correlation coefficient between the densities of foraging seabirds and acoustically-determined biomass at four different spatial scales (5, 10, 20, and 30 km bin sizes) for 2017 (a) and 2018 (b). Squares = piscivorous divers vs. fish in the upper (9–24 m) and lower layers (24–59 m) combined; diamonds = planktivorous divers vs. zooplankton in the upper (9–24 m) and lower layers (24–59 m) combined; circles = shearwaters vs. zooplankton both in the upper (9–24 m) and lower layers (24–59 m) combined; triangles = surface feeders vs. both fish and zooplankton in the upper (9–24 m) layers. Filled symbols represent statistically non-significant ($p > 0.05$).

et al., 2019; Appendix A). Due to these sea-ice conditions, there was no ice-edge phytoplankton bloom and only small-magnitude open water blooms in the northern Bering Sea in 2018 (Duffy-Anderson et al., 2019). Lack of ice algae and ice-edge blooms in warm water might lead to depressed production of large-sized zooplankton (*Calanus* spp., *Thysanoessa* spp., *Themisto* spp.) in the Bering Sea (Hunt et al., 2011; Sigler et al., 2016; Duffy-Anderson et al., 2019).

Large-sized zooplankton (*Calanus* spp., *Thysanoessa* spp., *Themisto* spp.) are important food for midwater forage fish such as juvenile walleye pollock, juvenile salmon, capelin and Pacific herring (*Clupea pallasii*) in the Bering Sea (Aydin et al., 2007; Coyle et al., 2011; Andrews et al., 2016). Therefore, the acoustically-determined lower biomass of fish might reflect lower biomass of large-sized zooplankton in 2018. The trawl surveys in the summer of 2018 in the northern Bering Sea showed that Pacific herring abundance was lower than in 2017, although the abundance of capelin and age-0 pollock were similar between these two years (Duffy-Anderson et al., 2019).

4.3. Spatial relationships for foraging seabirds

We found that, at the scales of 5–30 km, correlations between the density of foraging seabirds and acoustically-determined prey biomass were weaker in 2018, when prey biomass was small, than in 2017; this pattern occurred for all seabird foraging guilds except planktivorous divers. The results contradicted the general conclusion of Vlietstra et al. (2005), wherein stronger correlations between seabirds and prey occurred when prey availability was low. These stronger correlations between seabirds and prey can be interpreted as seabird responses to high and intermediate absolute prey abundance when prey-tracking could be an energetically efficient foraging strategy (Vlietstra et al., 2005). In contrast, studies reporting weaker correlations between seabirds and prey when prey availability declined (Fauchald and Erikstad, 2002; Becker and Beissinger, 2003; this study) may have characterized responses to intermediate and low levels of absolute prey abundance. In this case, seabirds may be limited in their ability to locate prey patches and would benefit by searching elsewhere for more abundant food (Gray and Kennedy, 1994; Spencer et al., 1996; Fauchald, 1999). Indeed, the proportion of non-foraging individuals was larger in 2018 than in 2017, indicating that seabirds may have spent more time searching for prey within our study area, or moving to areas with better foraging conditions.

5. Conclusions

Compared to 2017, we found lower overall density of seabirds at sea, low prey biomass, low density of foraging seabirds, a high proportion of non-foraging seabirds, and weak seabird-prey relationships in 2018, when sea ice and ice-edge blooms were absent in the northern Bering Sea. In 2018, seabirds appeared to have difficulty locating prey patches, which could have contributed to poor body conditions and ability to deliver food to their chicks (Chastel et al., 1995; Thayer and Sydeman, 2007). The evidence for lower prey abundance and weak predator-prey relationships may have led to increased nutritional stress of seabirds (murres, black-legged kittiwake, least and crested auklets) breeding on St. Lawrence between 2017 and 2018 (Will et al., 2020b (this issue)). Further evidence of poor foraging conditions was the mass mortality of murres and poor reproductive success of seabirds, including murres, black-legged kittiwakes, and least and crested auklets observed in 2018 (Siddon and Zador, 2018; Dragoo et al., 2019; Romano et al., 2020 (this issue)). In the northern Bering Sea, such a strong ecosystem response to the lack of sea ice has not been well studied (but see Siddon and Zador, 2018; Duffy-Anderson et al., 2019). Our findings highlight the importance of tracking upper trophic levels such as seabirds to understand the ecosystem level response to the unprecedented loss of sea ice.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the captain, officers, and crews of the T/S *Oshoro-Maru*, as well as Dr. Atushi Ooki and Dr. Toru Hirawake (chief scientists of the T/S *Oshoro-Maru* cruise in 2017 and 2018) for their help with the field operations. Support for the U.S. Fish and Wildlife (USFWS) observer was from a grant from the Bureau of Ocean Energy Management (Inter-agency Agreement M17PG00039). Elizabeth Labunski (USFWS) assisted with data compilation. This study was supported by MEXT (Japanese Ministry of Education, Culture, Sports, Science and Technology) through the Arctic Challenge for Sustainability Project.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr2.2020.104898>.

Author contributions

Bungo Nishizawa: Conceptualization, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Nodoka Yamada: Formal analysis, Investigation, Writing - review & editing, Haruka Hayashi: Investigation, Writing - review & editing, Charlie Wright: Investigation, Writing - review & editing, Kathy J. Kuletz: Conceptualization, Writing - review & editing, Hiromichi Ueno: Investigation, Writing - review & editing, Tohru Mukai: Formal analysis, Writing - review & editing, Atsushi Yamaguchi: Formal analysis, Investigation, Writing - review & editing, Yutaka Watanuki: Conceptualization, Writing - original draft, Writing - review & editing

References

- Alabia, I.D., García Molinos, J., Saitoh, S.I., Hirawake, T., Hirata, T., Mueter, F.J., 2018. Distribution shifts of marine taxa in the Pacific Arctic under contemporary climate changes. *Divers. Distrib.* 24, 1583–1597.
- Andrews III, A.G., Strasburger, W.W., Farley Jr., E.V., Murphy, J.M., Coyle, K.O., 2016. Effects of warm and cold climate conditions on capelin (*Mallotus villosus*) and Pacific herring (*Clupea pallasii*) in the eastern Bering Sea. *Deep Sea Res. Part II* 134, 235–246.
- Aydin, K., Gaichas, S., Ortiz, I., Kinzey, D., Friday, N., 2007. A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. U.S. Department of Commerce, NOAA Technical Memorandum. NMFS-AFSC-178. 298 pp.
- Becker, B.H., Beissinger, S.R., 2003. Scale-dependent habitat selection by a nearshore seabird, the marbled murrelet, in a highly dynamic upwelling system. *Mar. Ecol. Prog. Ser.* 256, 243–255.
- Bédard, J., 1969. Feeding of the least, crested, and parakeet auklets around St. Lawrence Island, Alaska. *Can. J. Zool.* 47, 1025–1050.
- Chastel, O., Weimerskirch, H., Jouventin, P., 1995. Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* 76, 2240–2246.
- Coachman, L.K., Coachman, L.K., Aagaard, K., Tripp, R., 1975. Bering Strait: the Regional Physical Oceanography. University of Washington Press.
- Cornwall, W., 2019. Vanishing Bering Sea ice poses climate puzzle. *Science* 364, 616–617.
- Coyle, K.O., Eisner, L.B., Mueter, F.J., Pinchuk, A.I., Janout, M.A., Cieciel, K.D., Farley, E.V., Andrews, A.G., 2011. Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the oscillating control hypothesis. *Fish. Oceanogr.* 20, 139–156.
- De Robertis, A., McKelvey, D.R., Ressler, P.H., 2010. Development and application of an empirical multifrequency method for backscatter classification. *Can. J. Fish. Aquat. Sci.* 67, 1459–1474.
- Dragoo, D.E., Renner, H.M., Kaler, R.S.A., 2019. Breeding Status and Population Trends of Seabirds in Alaska, 2018. U.S. Fish and Wildlife Service Report AMNWR 2019/03. Homer, Alaska.
- Duffy-Anderson, J.T., Stabeno, P., Andrews, A.G., Cieciel, K., Deary, A., Farley, E., Fugate, C., Harpold, C., Heintz, R., Kimmel, D., 2019. Responses of the northern Bering Sea and southeastern Bering Sea pelagic ecosystems following record-breaking low winter sea ice. *Geophys. Res. Lett.* 46, 9833–9842.

- Eisner, L., Hillgruber, N., Martinson, E., Maselko, J., 2013. Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi seas. *Polar Biol.* 36, 87–113.
- Elphick, C.S., Hunt Jr., G.L., 1993. Variations in the distributions of marine birds with water mass in the northern Bering Sea. *Condor* 95, 33–44.
- Fauchald, P., 1999. Foraging within a hierarchical patch system. *Am. Nat.* 153, 603–613.
- Fauchald, P., Erikstad, K.E., 2002. Scale-dependent predator-prey interactions: the aggregative response of seabirds to prey under variable prey abundance and patchiness. *Mar. Ecol. Prog. Ser.* 231, 279–291.
- USFWS (U.S. Fish and Wildlife Service), 2014. North Pacific Seabird Colony Database. <http://axiom.seabirds.net/maps/north-pacific-seabirds>.
- Foote, K.G., Knudsen, H.P., Vestnes, G., MacLennan, D.N., Simmonds, E.J., 1987. Calibration of acoustic instruments for fish density estimation: practical guide. ICES Coop. Res. Rep. 144, 57.
- Fukai, Y., Matsuno, K., Fujiwara, A., Yamaguchi, A., 2019. The community composition of diatom resting stages in sediments of the northern Bering Sea in 2017 and 2018: the relationship to the interannual changes in the extent of the sea ice. *Polar Biol.* 42, 1915–1922.
- Gall, A.E., Roby, D.D., Irons, D.B., Rose, I.C., 2006. Inter-annual variation in diet and nest survival of plankton feeding auklets on St. Lawrence Island, Alaska. *Mar. Ecol. Prog. Ser.* 308, 279–291.
- Gray, R.D., Kennedy, M., 1994. Perceptual constraints on optimal foraging: a reason for departures from the ideal free distribution? *Anim. Behav.* 47, 469–471.
- Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006. Ecosystem dynamics of the pacific-influenced northern bering and chukchi seas in the amerasian arctic. *Prog. Oceanogr.* 71, 331–361.
- Haney, J.C., Schauer, A.E.S., 1994. Environmental variability facilitates coexistence within an alcid community at sea. *Mar. Ecol. Prog. Ser.* 103, 221–237.
- Hunt Jr., G.L., Harrison, N.M., 1990. Foraging habitat and prey taken by least auklets at King Island, Alaska. *Mar. Ecol. Prog. Ser.* 65, 141–150.
- Hunt Jr., G.L., Schneider, D., 1987. Scale-dependent processes in the physical and biological environment of marine birds. pp 7–41. In: Croxall, J.P. (Ed.), *Seabirds: Feeding Ecology and Role in Marine Ecosystems*. Cambridge University Press, Cambridge.
- Hunt Jr., G.L., Harrison, N.M., Cooney, R.T., 1990. The influence of hydrographic structure and prey abundance on foraging of least auklets. *Stud. Avian Biol.* 14, 7–22.
- Hunt Jr., G.L., Heinemann, D., Everson, I., 1992. Distributions and predator-prey interactions of macaroni penguins, Antarctic Fur seals, and Antarctic krill near Bird Island, South Georgia. *Mar. Ecol. Prog. Ser.* 86, 15–30.
- Hunt Jr., G.L., Coyle, K.O., Hoffman, S., Decker, M.B., Flint, E.N., 1996. Foraging ecology of short-tailed shearwaters near the pribilof islands, Bering Sea. *Mar. Ecol. Prog. Ser.* 141, 1–11.
- Hunt Jr., G.L., Russell, R.W., Coyle, K.O., Weingartner, T., 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Mar. Ecol. Prog. Ser.* 167, 241–259.
- Hunt Jr., G.L., Baduini, C., Jahncke, J., 2002. Diets of short-tailed shearwaters in the southeastern Bering Sea. *Deep-Sea Res. Part II* 49, 6147–6156.
- Hunt Jr., G.L., Coyle, K.O., Eisner, L.B., Farley, E.V., Heintz, R.A., Mueter, F., Napp, J.M., Overland, J.E., Ressler, P.H., Salo, S., 2011. Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. *ICES J. Mar. Sci.* 68, 1230–1243.
- Hunt Jr., G.L., Blanchard, A.L., Boveng, P., Dalpadado, P., Drinkwater, K.F., Eisner, L., Hopcroft, R.R., Kovacs, K.M., Norcross, B.L., Renaud, P., 2013. The Barents and Chukchi Seas: comparison of two Arctic shelf ecosystems. *J. Mar. Syst.* 109, 43–68.
- Jones, T., Divine, L.M., Renner, H., Knowles, S., Lefebvre, K.A., Burgess, H.K., Wright, C., Parrish, J.K., 2019. Unusual mortality of tufted puffins (*Fratercula cirrhata*) in the eastern Bering Sea. *PLoS One* 14, e0216532.
- Kokubun, N., Iida, K., Mukai, T., 2008. Distribution of murre (*Uria* spp.) and their prey south of St. George Island in the southeastern Bering Sea during the summers of 2003–2005. *Deep-Sea Res. Part II* 55, 1827–1836.
- Acoustic target classification. In: Korneliussen, Rolf J. (Ed.), *ICES Coop. Res. Rep. No. 344*, 104. <https://doi.org/10.17895/ices.pub.4567>.
- Kuletz, K., Cushing, D.A., Labunski, E.A., 2020. Distributional shifts among seabird communities of the Northern Bering and Chukchi seas in response to ocean warming during 2017–2019. *Deep-Sea Res. Part II* (this issue).
- Li, W.K., McLaughlin, F.A., Lovejoy, C., Carmack, E.C., 2009. Smallest algae thrive as the Arctic Ocean freshens. *Science* 326, 539, 539.
- Mitson, R., Simard, Y., Goss, C., 1996. Use of a two-frequency algorithm to determine size and abundance of plankton in three widely spaced locations. *ICES J. Mar. Sci.* 53, 209–215.
- Nishizawa, B., Onishi, H., Watanuki, Y., 2019. Seabird densities and species and hydrographic features across amchitka pass, aleutian islands. *Fish. Sci.* 85, 53–60.
- Ogi, H., Kubodera, T., Nakamura, K., 1980. The pelagic feeding ecology of the short-tailed shearwater *Puffinus tenuirostris* in the subarctic Pacific region. *J. Yamashina Inst. Ornithol.* 12, 157–182.
- Perovich, D.K., Richter-Menge, J.A., 2009. Loss of sea ice in the Arctic. *Ann. Rev. Mar. Sci.* 1, 417–441.
- Piatt, J., Springer, A., 2003. Advection, pelagic food webs and the biogeography of seabirds in Beringia. *Mar. Ornithol.* 31, 141–154.
- Reiss, C.S., Cossio, A.M., Loeb, V., Demer, D.A., 2008. Variations in the biomass of antarctic krill (*Euphausia superba*) around the south shetland islands, 1996–2006. *ICES J. Mar. Sci.* 65, 497–508.
- Renner, M., Salo, S., Eisner, L.B., Ressler, P.H., Ladd, C., Kuletz, K.J., Santora, J.A., Piatt, J.F., Drew, G.S., Hunt Jr., G.L., 2016. Timing of ice retreat alters seabird abundances and distributions in the southeast Bering Sea. *Biol. Lett.* 12, 20160276.
- Romano, M.D., Renner, H.M., Kuletz, K.J., Parrish, J.K., Jones, T., Burgess, H.K., Cushing, D.A., Causey, D., 2020. Die-offs, reproductive failure, and changing at-sea abundance of murre in the Bering and Chukchi Seas in 2018. *Deep-Sea Res. Part II* (this issue).
- Santora, J.A., Ralston, S., Sydeman, W.J., 2011. Spatial organization of krill and seabirds in the central California Current. *ICES J. Mar. Sci.* 68, 1391–1402.
- Schneider, D.C., 1990. Spatial autocorrelation in marine birds. *Polar Res.* 8, 89–97.
- Sheffield Guy, L.M., Roby, D.D., Gall, A.E., Irons, D.B., Rose, I.C., 2009. The influence of diet and ocean conditions on productivity of auklets on St. Lawrence Island, Alaska. *Mar. Ornithol.* 37, 227–236.
- Siddon, E.C., Zador, S. (Eds.) *Ecosystem Status Report 2018: Eastern Bering Sea*. 230 pp. North Pacific Fishery Management Council, 605 W. 4th Avenue, Suite 306, Anchorage, AK 99301.
- Sigler, M.F., Kuletz, K.J., Ressler, P.H., Friday, N.A., Wilson, C.D., Zerbini, A.N., 2012. Marine predators and persistent prey in the southeast Bering Sea. *Deep-Sea Res. Part II* 65, 292–303.
- Sigler, M.F., Napp, J.M., Stabeno, P.J., Heintz, R.A., Lomas, M.W., Hunt Jr., G.L., 2016. Variation in annual production of copepods, euphausiids, and juvenile walleye pollock in the southeastern Bering Sea. *Deep-Sea Res. Part II* 134, 223–234.
- Sokal, R.R., Oden, N.L., 1978. Spatial autocorrelation in biology I. Methodology. *Biol. J. Linn. Soc.* 10, 199–228.
- Spencer, H.G., Kennedy, M., Gray, R.D., 1996. Perceptual constraints on optimal foraging: the effects of variation among foragers. *Evol. Ecol.* 10, 331–339.
- Stabeno, P.J., Bell, S.W., 2019. Extreme conditions in the Bering Sea (2017–2018): record-breaking low sea-ice extent. *Geophys. Res. Lett.* 46, 8952–8959.
- Stabeno, P.J., Kachel, N.B., Moore, S.E., Napp, J.M., Sigler, M., Yamaguchi, A., Zerbini, A.N., 2012. Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. *Deep-Sea Res. Part II* 65, 31–45.
- Tasker, M.L., Jones, P.H., Dixon, T., Blake, B.F., 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk* 101, 567–577.
- Thayer, J.A., Sydeman, W.J., 2007. Spatio-temporal variability in prey harvest and reproductive ecology of a piscivorous seabird, *Cerorhinca monocerata*, in an upwelling system. *Mar. Ecol. Prog. Ser.* 329, 253–265.
- Ueno, H., Komatsu, M., Ji, Z., Dobashi, R., Muramatsu, M., Abe, H., Imai, K., Ooki, A., Hirawake, T., 2020. Stratification in the northern Bering Sea in early summer of 2017 and 2018. *Deep-Sea Res. Part II* (this issue).
- Vlietstra, L.S., 2005. Spatial associations between seabirds and prey: effects of large-scale prey abundance on small-scale seabird distribution. *Mar. Ecol. Prog. Ser.* 291, 275–287.
- Walsh, J.J., McRoy, C., Coachman, L., Goering, J., Nihoul, J., Whitedge, T., Blackburn, T., Parker, P., Wirick, C., Shuert, P., 1989. Carbon and nitrogen cycling within the Bering/Chukchi Seas: source regions for organic matter effecting AOU demands of the Arctic Ocean. *Prog. Oceanogr.* 22, 277–359.
- Will, A., Thiebot, J.B., Ip, H.S., Shoogukwruk, P., Annogyuk, M., Takahashi, A., Shearn-Boschler, V., Killian, M.L., Torchetti, M., Kitaysky, A., 2020a. Investigation of the 2018 thick-billed murre (*Uria lomvia*) die-off on St. Lawrence Island rules out food shortage as the cause. *Deep-Sea Res. Part II* (this issue).
- Will, A., Takahashi, A., Thiebot, J.B., Martinez, A., Kitaiskaia, E., Britt, L., Nichol, D., Murphy, J., Dimond, A., Tsukamoto, S., Nishizawa, B., Niizuma, Y., Kitaysky, A., 2020b. The breeding seabird community reveals that recent sea ice loss in the Pacific Arctic does not benefit piscivores and is detrimental to planktivores. *Deep-Sea Res. Part II* (this issue).