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Key Points:

- Response of the southeastern Bering Sea to lack of sea ice has been documented, but lack of sea ice in the north (2017–2018) is unprecedented
- Selected bottom-up cascading pelagic ecosystem responses to record-low sea ice are similar in the NBS and SEBS, though other components of the ecosystem may respond differently
- The SEBS may be used as a model to inform understanding of effects in the pelagic NBS, especially with continued warm ecosystem conditions persisting through 2019

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Responses of the Northern Bering Sea and Southeastern Bering Sea Pelagic Ecosystems Following Record-Breaking Low Winter Sea Ice

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Abstract Bering Sea sea ice during winter 2017–2018 was the lowest ever recorded. Ecosystem effects of low ice have been observed in the southeastern Bering Sea, but never in the northern Bering Sea. Observations in both systems included weakened water column stratification, delayed spring bloom, and low abundances of large crustacean zooplankton. Summer Cold Pool presence was extremely limited. Young walleye pollock production and condition were similar to prior warm years, though catches of other pelagic forage fishes were low. Summer seabird die-offs were observed in the northern Bering Sea, and to lesser extent in the southeastern Bering Sea, and reproductive success was poor at monitored colonies. Selected bottom-up responses to lack of sea ice in the north were similar to those in the south, potentially providing environmental indicators to project ecosystem effects in a lesser studied system. Results offer a potential glimpse of the broader Bering Sea pelagic ecosystem under future low-ice projections.

Plain Language Summary During the winter of 2017–2018, there was a lack of winter sea ice in the northern and southeastern Bering Sea. This was unprecedented, and its implications were unknown, especially for the northern Bering Sea. Ecosystem surveys showed that oceanic plants and animals at the base of the food web were delayed in their spring production and food quality was generally low. Abundances of young walleye pollock, a commercial species important to the global fish market, were average in 2018, but catches of other forage fishes were lower. Seabird die-offs in the northern Bering Sea were extensive. If heat-related ecosystem changes previously observed in the southeastern Bering Sea ecosystem are now happening in the northern Bering Sea, disruptions to food webs and increased die-offs could occur if oceans continue to warm in the future.

1. Introduction

Sea ice extent, ice thickness, duration over the shelf, and timing of retreat are key variables associated with production (Lomas et al., 2012). Mechanisms by which spring sea ice initiates Bering Sea production are varied, but one model posits that lipid-rich, under-ice algae are advected southward with advancing winter ice. Spring melting causes algae to drop out of the ice layer as sea ice retreats (Brown & Arrigo, 2013), seeding the shelf with large-celled, lipid-rich phytoplankton and providing a base of primary production in spring. Large-celled, chain-forming diatoms are grazed by lipid-rich *Calanus* spp. copepods near the ice edge, fueling spring copepod egg production (Campbell et al., 2016). Younger *Calanus* spp. stages and other zooplankton serve as prey for forage fish that ultimately support commercially important fish stocks (Pacific halibut, Pacific cod, walleye pollock, and Pacific salmon), seabirds, and marine mammals. This suite of interacting, cascading trophic connections, and how they change during ice and ice-free years, is brought together as the Oscillating Control Hypothesis (OCH; Hunt et al., 2002, 2011).

The OCH was developed to describe processes regulating pelagic production in the Southeastern Bering Sea (SEBS; 54°N to 60°N latitude) ecosystem, which has experienced variable winter ice exposure (warm and cold multiyear stanzas). The northern Bering Sea (NBS; 60°N to 66°N) pelagic ecosystem was never envisioned as being governed by this cascade, being comparatively insulated due to the consistent presence of

Table 1*Ecosystem Surveys Conducted by the National Oceanic and Atmospheric Administration and the Alaska Department of Fish and Game Over the Northern Bering Sea and Southeastern Bering Sea Continental Shelves*

Date (2018)	Trophic levels monitored
29 April to 10 May	Ocean physics, phytoplankton, zooplankton
13 May to 1 June	Ocean physics, phytoplankton, zooplankton, fish
1 April to 30 September	Seabirds
15 May to 15 September	Colonial nesting seabirds
3 June to 17 November	Seabirds
27 August to 20 September	Ocean physics, phytoplankton, zooplankton, fish, seabirds
13 August to 26 August	Zooplankton, seabirds
19 September to 6 October	Ocean physics, phytoplankton, zooplankton, fish, seabirds
30 September to 13 October	Ocean physics, phytoplankton, zooplankton, seabirds

sea ice in winter, a residual Cold Pool (bottom water temperatures <2 °C) in summer, and a fixed light regime that is different from that in the SEBS. The prevailing hypothesis has been that the two ecosystems were fundamentally linked but functionally separate. However, winter of 2017–2018 was exceedingly warm and beset with late storms affecting sea ice duration and extent (Stabeno & Bell, 2019). Both systems experienced record-shattering low sea ice over winter, an unprecedented event in the NBS, which caused concern about the potential implications for the ecosystem and the people that depend on its productive waters.

We lacked a working hypothesis for the response of the NBS ecosystem to loss of winter sea ice, but we have over a decade of study from the SEBS. If components of the NBS ecosystem respond to low sea ice similarly to the SEBS, the OCH could provide a first model of understanding and a suite of predictive tools to inform remediation and preparedness efforts. The goals of this paper are to compare trophic conditions in the SEBS and NBS pelagic ecosystems after a year of record-low winter sea ice by combining physical, biological oceanographic, fish, and seabird data and to evaluate the utility of the SEBS OCH as a model for the NBS.

2. Data and Methods

2.1. Study Areas and Sampling

Multidisciplinary ecosystem surveys were seasonally conducted in the NBS and SEBS. Observations were made from oceanographic moorings, and ship-based, beach, and aerial surveys. Physical measurements were collected from moorings sites and gridded surveys (temperature, salinity, oxygen, and fluorescence), and biological samples were collected from gridded surveys (chlorophyll *a* [Chl*a*], mesozooplankton, larval, juvenile fish, forage fishes, and seabirds; Table 1).

2.2. Sea Ice and Ocean Temperature

Sea ice concentration data were retrieved from daily Version 3 Bootstrap Sea Ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS (<http://nsidc.org/data/nsidc-0079>). Physical ocean data (temperature, conductivity [salinity], depth, oxygen, photosynthetically active radiation, and chlorophyll fluorescence) were collected from mooring arrays.

2.3. Phytoplankton

Prawler (Profiling Crawler) devices attached to Mooring 2 (M2, SEBS) and Mooring 5 (M5, NBS; Figure 1) provided fluorescence information over the moored water column depth. Prawlers were not deployed at other moorings, though physical data collected from M8 is summarized in Stabeno and Bell (2019). Water samples, including Chl*a*, were collected from standard CTD rosette systems at discrete depths and integrated over the water column to estimate total integrated Chl*a* (mg/m²).

2.4. Zooplankton

Zooplankton collected using oblique tows of paired bongo nets and an at-sea assessment of zooplankton community structure (Rapid Zooplankton Analysis) provided a preliminary, real-time index of zooplankton composition and relative abundances (Duffy-Anderson et al., 2017). Results from 2018 were compared to historical estimates of plankton abundances in the SEBS and NBS (middle shelf). Lipid content of

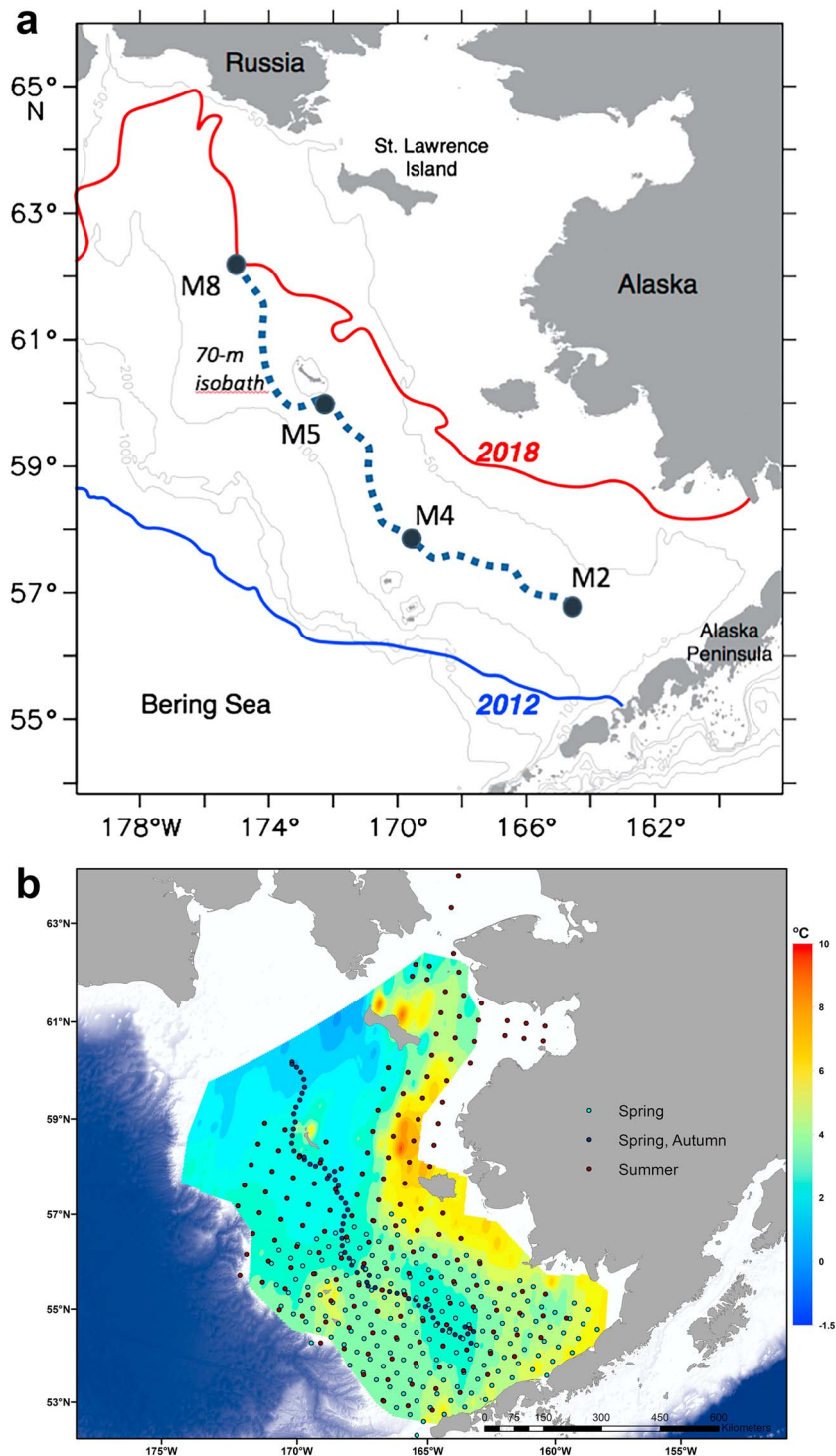


Figure 1. (a) Maximum (2012) and minimum (2018) annual sea ice extent over the northern Bering Sea (NBS) and south-eastern Bering Sea (SEBS) shelves. Moorings (filled circles) along the 70-m isobath (dashed line) are M2, M4, M5, and M8. (b) Summer bottom temperatures in the NBS and SEBS in 2018 (color ramp); spring–autumn sampling stations during 2018 (dots). Cold Pool is defined as temperatures $<2^{\circ}\text{C}$. Results show the lack of a Cold Pool.

zooplankton (euphausiids and copepods) was determined using a modified colorimetric method (Van Handel, 1985). All lipid values reported are in terms of percent wet weight. Lipid content data acts as a proxy for energy content.

2.5. Fishes

Larval fish were collected using paired bongo nets. Abundance of selected groundfish larvae (walleye pollock, Pacific cod, northern rock sole, rock sole, and rockfishes) were estimated at sea. Larval walleye pollock, a species that supports one of the world's largest fisheries (hereafter, pollock), were photographed to provide an estimate of condition. The condition index was the ratio of $D:L$ (D , body depth at anus; L , body length; <0.067 = unhealthy larvae; S. Porter, National Oceanic and Atmospheric Administration Alaska Fisheries Science Center, unpublished data, 2016). Condition data for other larval species collected from SEBS surveys were not available.

Midwater fishes (age-0 pollock, Pacific herring, and capelin) were collected from surface trawls in the NBS and SEBS (Farley et al., 2005). Geostatistical modeling was used to estimate biomass of each fish species using the Vector Autoregressive Spatio-Temporal (VAST, version 4.2.0) package in R (R Core Team, 2019; Thorson et al., 2015). Time series were available from Yasumiishi et al. (2018). The VAST model is a delta geostatistical model that includes two linear predictors, one for the probability of encounter and the other for positive catch rate. We specified a Poisson delta link model with gamma distribution on observations. Age-0 pollock condition data from autumn were not available.

2.6. Seabirds

Relative seabird densities (birds/km²) were obtained annually from 2006 to 2018 by vessel-based visual surveys (Kuletz & Labunski, 2017), typically in conjunction with other collections (Table 1). In 2018, ~3,000 km of transects in the SEBS and 5,355 km in the NBS were surveyed, with similar effort in previous years. Seabird colony data were collected by the Alaska Maritime National Wildlife Refuge at selected monitoring sites (Dragoo et al., 2019). We focus on two murre species (common murre, *Uria aalge*; and thick-billed murre, *U. lomvia*), because they are primarily piscivorous, widespread, and resilient to minor environmental perturbations (Gaston & Hipfner, 2000), and two auklet species (crested auklet, *Aethia cristatella*; and least auklet, *A. pusilla*), because they are planktivorous and abundant in the region.

3. Results and Discussion

3.1. Sea Ice and Ocean Temperatures

Prior to 2018, Bering Sea sea ice arrived in December and was advected southward with maximum ice extent in March (Stabeno et al., 2012). In extensive ice cover years, sea ice covered the entire eastern Bering Sea shelf (Figure 1a). Ice persisted in the vicinity of M8 for at least 5 months each year. In 2018, however, there were only 2 days of ice at areal concentrations of $>10\%$, and extent was the lowest ever recorded (160 years; Frey et al., 2018). Lack of ice was driven by the presence of strong, southerly winds in fall 2017, which delayed formation, advected heat, and contributed to mixing (Stabeno & Bell, 2019).

Sea ice extent controls ocean temperature, and years with extensive ice in spring yield cold bottom temperatures in summer. In May 2018, bottom temperatures at M8 were $>0^{\circ}\text{C}$ and by July had warmed to almost 2°C (Figure 1b). The Cold Pool was virtually absent ($<1\%$ occurrence over the shelf) over either the southern or northern shelf, marking the first time this phenomenon has ever been observed (typically $>70\%$ coverage of the continental shelf; Figure 1b).

3.2. Phytoplankton

Springtime 2018 estimates of integrated Chl_a remained low ($<100\text{ mg/m}^2$; Figure 2a). This is in contrast to previous years that had higher levels of Chl_a ($1,000\text{--}1,800\text{ mg/m}^2$) composed of long, centric diatom chains near the ice edge in the NBS (Duffy-Anderson et al., 2017) despite a warmer, ice-free SEBS. At M2 (SEBS) a phytoplankton bloom began approximately 1 week after stratification (25 May), delayed timing but not unprecedented (Figure 2b). The bloom began late at M5 (NBS and SEBS border), approximately 12 June (Figure 2c), due to the lack of fresh water input from melting sea ice. This resulted in weak stratification and nutrient mixing into the surface layer.

The late bloom and low chlorophyll concentrations in the NBS (M5) are in contrast with the extensive and early ice-associated bloom reported for regions north of St. Lawrence Island. (Osborne et al., 2018). This suggests that with future warming, the Chukchi Sea may bloom prior to an ice-free Bering Sea. In addition, the absence of sea ice and the associated flux of ice algae to the bottom likely had a profound impact on the

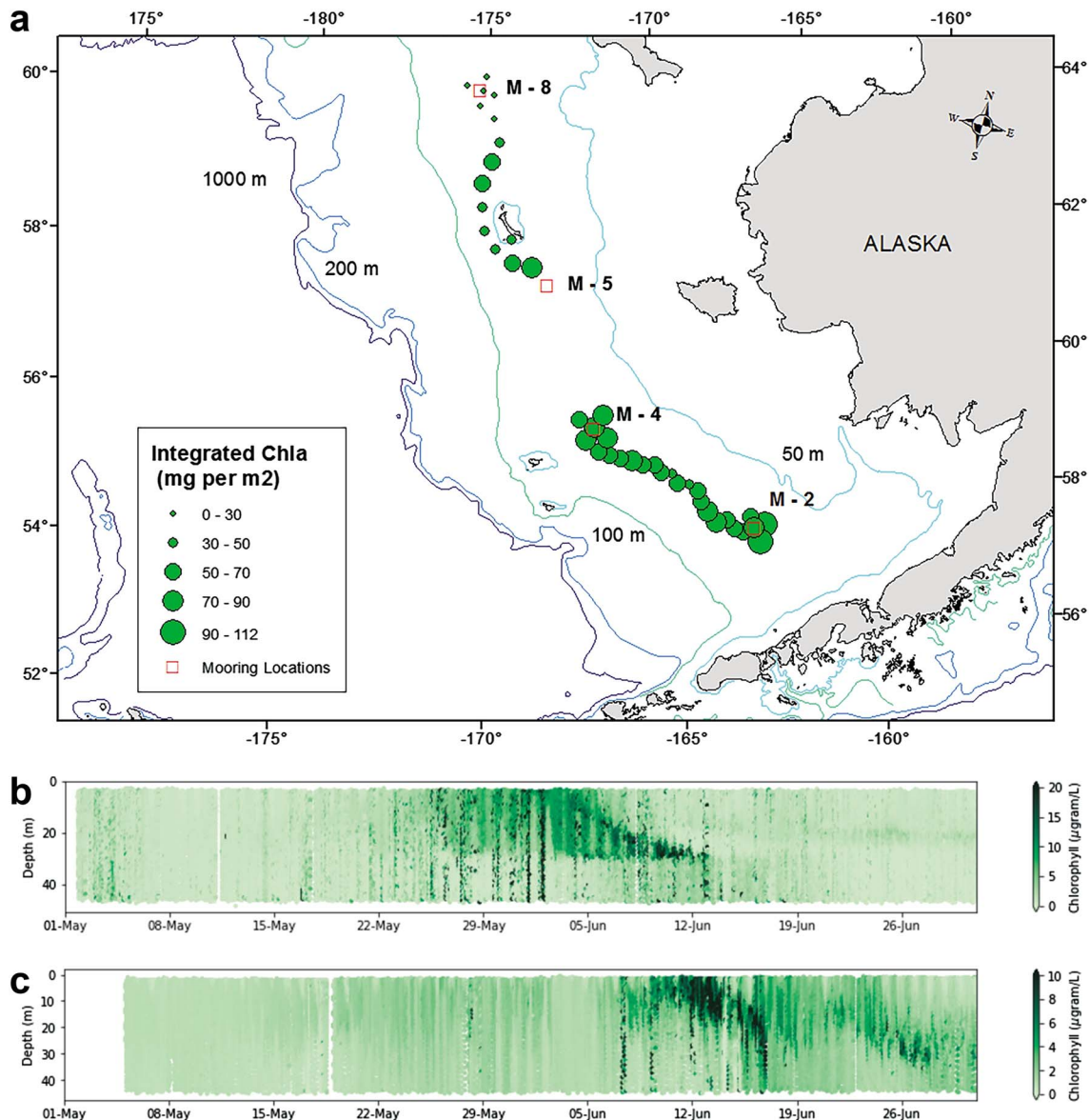


Figure 2. (a) Estimates of integrated chlorophyll depicting low abundances in May 2018 (sampling along the 70-m isobath). (b and c) Fluorescence derived from Prawler arrays deployed at (top) M2 and (bottom) M5 in 2018. Prawler arrays not deployed at other mooring stations.

relatively high, but varying, benthic community biomass found over the northern shelf (Grebmeier et al., 2006; Grebmeier et al., 2018).

3.3. Zooplankton

High abundances of small (low-lipid) and low abundances of large (high-lipid) copepods were observed during summer (Figures 3a–3d), as has been noted on the SEBS shelf during warm years (Eisner et al., 2014; Kimmel et al., 2018). Copepod abundances in the NBS followed a similar trend, though comparisons with the historical record indicate large copepod levels have been as low in prior years (Stabeno et al., 2018). Reduced ice cover, elevated temperatures, and delayed spring bloom served to depress large copepod production but permitted rapid proliferation of small copepods through spring and summer. Increased zooplankton growth rates may have led to lower carbon export to the benthos, negatively impacting the food supply to benthic organisms. Numbers of small euphausiids were low over the SEBS shelf (Figure 3f), though numbers in the NBS were higher (Figure 3e). Reduced ice cover, elevated temperatures, and delayed spring

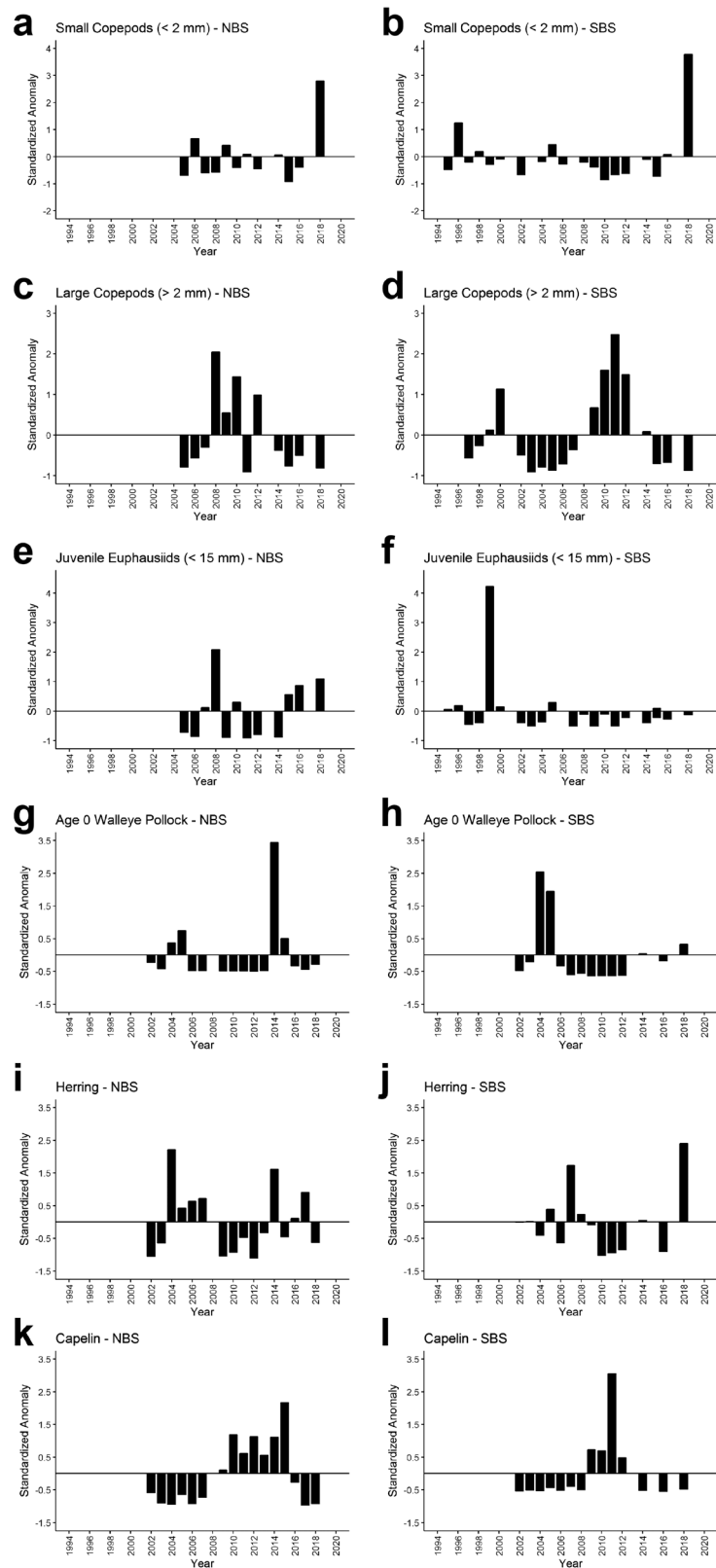


Figure 3. Time series of biological data (zooplankton and fish) from the (a, c, e, g, i, k) northern Bering Sea (NBS) and (b, d, f, h, j, l) southeastern Bering (SEBS), expressed as anomalies. Thermal stanzas of note are 2001–2005 (warm), 2008–2012 (cold), and 2015–2018 (warm).

Table 2
Condition Metrics (± 1 standard deviation) of Zooplankton (% Lipid Wet Weight) in the NBS and SEBS in 2018, Showing Comparable Levels Between the Two Systems, and Young Pollock (% Unhealthy) in the SEBS

	NBS	SEBS
Zooplankton (copepods; summer)	8.1 ($\pm 5\%$)	12.9 ($\pm 6\%$)
Zooplankton (euphausiids, summer)	1.6 ($\pm 2\%$)	3.4 ($\pm 3\%$)
Walleye pollock (larvae; spring)	N/A	<12

Note. NBS = northern Bering Sea; SEBS = southeastern Bering Sea; N/A = not applicable.

bloom likely were responsible for these patterns. A mismatch between sea ice grazing, *Calanus* spp., and the presence of algae can result in reduced reproduction and lipid storage (Søreide et al., 2010). The very high numbers of small copepods suggest that warm conditions led to enhanced growth rates and egg production, resulting in population increases (Kimmel et al., 2018). Results from 2018 are in contrast to previous work that reported increased large copepod and euphausiid abundances near ice edges in the NBS during a prior warm stanza (2014–2016; Duffy-Anderson et al., 2017).

Condition indices indicated similar lipid content for plankton in both the NBS and the SEBS (Table 2), suggesting that conditions for zooplankton provisioning in the NBS were least comparable to those in the SEBS. Levels in both systems were lower than measurements taken during high ice extent years ($\sim 14\%$ for copepods).

3.4. Fish

Larval fish catch varied by species; however, abundances of pollock, Pacific cod, northern rock sole, rock sole, and rockfishes were similar to 2016 (Porter et al., 2018), which was a single year of average thermal ocean conditions during a protracted warm stanza (2013–2017). As such, fish production in spring 2018 over the SEBS shelf appeared to be similar to prior warm-year observations and little affected by the record-low sea ice presence in the NBS. Warm-year spatial distributions may be driven by temperature-mediated distributional shifts in spawning adults (Cooper & Nichol, 2016; Petrik et al., 2014). Thermally mediated shifts in spawning phenology of pollock has been documented (Rogers & Dougherty, 2018; Smart et al., 2012), and mismatches in timing of fish production with prey production are possible. However, body condition of pollock larvae was fairly robust (Table 2), suggesting sufficient food resources at this stage. We conclude that while the spring bloom was delayed and the copepod prey base was altered by warm conditions, effects on springtime production of larval fish were modest and consistent with observations from prior warm stanzas. All observations derived primarily from outer and middle domain sampling.

Adequate provisioning and low mortality of young fishes through their first summer and autumn (age-0 individuals) are critical to overwinter survival and recruitment to the harvested fishery. Poor food quality has been postulated as the cause of population declines of pollock during prior warm year stanzas (2001–2005, Heintz et al., 2013). Age-0 pollock spawned over the SEBS shelf in 2015 may have been able to mitigate the effects of the recent warm stanza (2014–2017) by refuging in the productive waters of a residual northerly Cold Pool (Duffy-Anderson et al., 2017) in the NBS despite warm conditions over the southern shelf. However, the lack of a Cold Pool in the SEBS and NBS in 2018 suggests that there was little refuge potential, and low catches of age-0 pollock in the NBS (Figures 3g and 3h) indicate limited utility of northerly waters. Collections of other pelagic foragers, Pacific herring and capelin, were below average in both systems with the exception of herring in the SEBS; Figures 3h–3l). Notably, a concurrent aerial survey of herring in 2018 (Togiak Bay, the largest herring spawning stock in Alaska waters) found depressed biomass (Buck & Dressel, 2018), indicating spatiotemporal differences in NBS herring. It has been previously documented that forage fish biomass generally declines during warm year stanzas (Andrews et al., 2016).

3.5. Seabirds

Seabird surveys and monitoring results were consistent with other Bering Sea observations. The delayed plankton bloom and reduced biomass of large copepods, as well as low forage fish abundances, were mirrored in low seabird abundance at sea, low reproductive success, and an increase in die-off events (most prevalent in the NBS). Densities of seabirds at sea were lower overall in 2018, although mean density was above the long-term average in the NBS (Figure 4a) due to an unusually high abundance of planktivorous auklets offshore (Figures 4b and 4c). The abundance of auklets in the NBS in 2018 may have been a response to the large biomass of small copepods or reflect lack of attendance and breeding failure at colonies in the NBS (A. Will, University of Alaska, Fairbanks, personal communication, 2018). Only low numbers of crested and least auklets from the NBS used the Chukchi Sea in late summer (K. Kuletz, unpublished data, 2018), where they had been abundant in offshore waters previously (Kuletz et al., 2019).

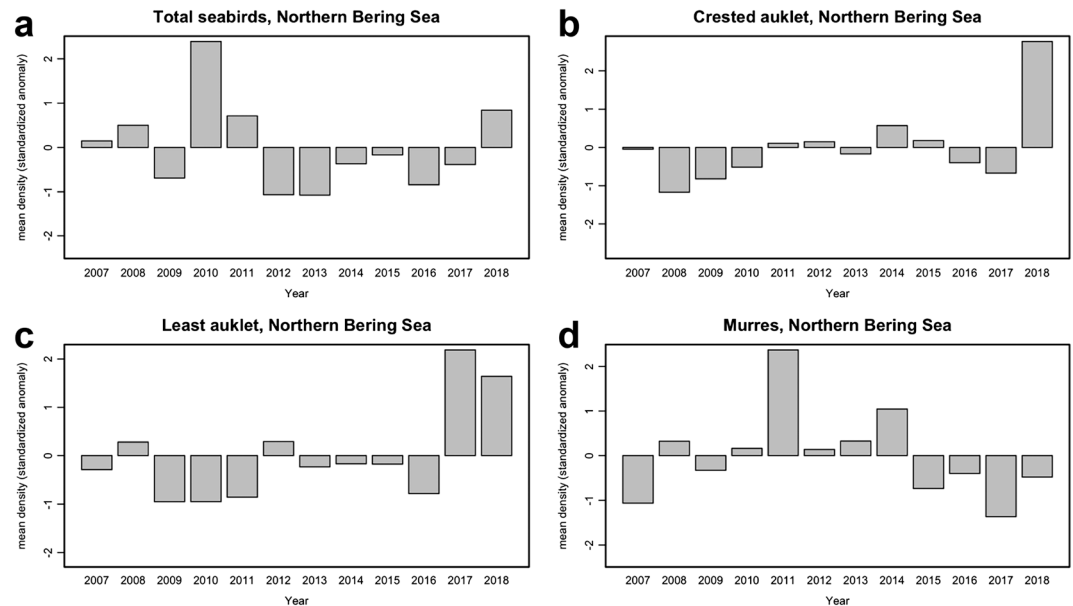


Figure 4. Time series of annual mean density of seabirds in the northern Bering Sea (2007–2018) expressed as anomalies: (a) total seabirds, (b) crested auklet, (c) least auklet, and (d) murres.

Common and thick-billed murres combined had low densities in 2018, and abundances were well below the long-term average (NBS, Figure 4d). Thick-billed murres include substantial zooplankton, primarily euphausiids, in their diet (Gaston & Hipfner, 2000) and may have been impacted to a greater degree than did common murres; on St. Lawrence Island they failed to show up entirely or did not attempt nesting until late in the season (A. Will, University of Alaska, Fairbanks, unpublished data, 2018). At St. Paul and St. George islands thick-billed murres, along with five of six other monitored species, had diminished reproductive success, as did murres in the Aleutian Archipelago (Dragoo et al., 2019). Seabird reproductive success (breeding attendance and fledgling success) is a good indicator of prey availability (Sydeman et al., 2017), and observations in 2018 suggest a lack of high quality prey or a timing mismatch.

Murres comprised the majority of dead or sick birds that washed up on shores around Norton Sound and on St. Lawrence Island. Seabird die-offs occurred throughout the SEBS but were most prevalent in the NBS in 2017 and 2018, affecting primarily shearwaters and fulmars in summer and fall of 2017 and common and thick-billed murres in spring and early summer of 2018 (Jones & Parrish, 2019). Mass seabird mortality events have generally coincided with anomalously warm oceans (Jones et al., 2019) with nearly all birds showing severe emaciation. While such events have been sporadically recorded in the SEBS prior to 2017, NBS events are the first on record.

The combination of low seabird abundance at sea, low reproductive success, and die-offs suggest impacts from conditions associated with low sea ice. Effects were most pronounced in the NBS. Both piscivorous and planktivorous species were affected, suggesting warm ocean effects were propagated through the food web.

4. Conclusions

Winter of 2017–2018 was an unprecedented period of low Bering Sea sea ice. The response of the ecosystem to lack of ice in the south were previously described, but the response in the north was unknown. Many of the short-term, bottom-up, cascading ecosystem responses in the NBS are similar to those over the SEBS shelf as predicted by the OCH. Weak stratification, delays in the timing of the spring bloom, and a paucity of large copepods were observed. Abundance and distribution of young pollock in the SEBS were commensurate with prior warm year estimates, though a reduced zooplankton prey base and the lack of refuging potential in a northerly Cold Pool portends reduced survivorship. Abundances of other forage fishes were depressed, suggesting reduced energy transfer to upper trophic levels. The seabird response to these

conditions reflected that impact. Despite response similarities, we caution that (1) long-term effects remain unknown and (2) other trophic responses of the NBS are unique, such as northward shifting adult fish populations (Stevenson & Lauth, 2019). While the SEBS can be an example for the NBS, it is not conclusive that all responses will be similar. This is particularly true considering the differing light regimes between the two systems and the need for biological organisms originating from the south to adapt to a NBS light schedule that has no precedence in the south. Nevertheless, winter 2018–2019 was also warm, with sea ice extent as low as in 2017–2018. Sustained ocean heating will continue cascading ecosystem effects documented here, providing a glimpse of the pelagic ecosystem under future projections of sea ice loss.

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