Ecological responses to climate perturbations and minimal sea ice in the Northern Bering Sea

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For Deep-Sea Research II Special Issue: Impacts of Unusually Light Sea Ice Cover on the Northern Bering Sea Marine Ecosystem

Abstract

The winter of 2017/2018 saw a composite of weather events that delayed sea ice formation in the northern Bering Sea (NBS) into early 2018. Residual warmth in the water column and strong southerly (i.e., warm) winds in February resulted in the lowest ice extent on record. Salinity has historically driven vertical stratification of the water column in the NBS, but with little sea ice formation and rejection of salty brine, there was a greatly diminished contribution of salinity to the stratification of the water column. The reduction of sea ice extent and duration likely resulted in a reduction in the amount of ice algae, which is an important subsidy for both the pelagic and benthic food webs. In 2018, the NBS had low abundances of large, lipid-rich copepods, while there were above average numbers of small, lipid-poor copepods. Shifts in the distribution of crab and fish populations over the eastern Bering Sea shelf occurred in response to the unusually warm sea temperatures in winter and spring 2018. More than 50% of Pacific cod biomass in the eastern Bering Sea was found over the northern shelf in 2018 concurrent with unexpectedly high abundance of snow crab in the NBS. A seabird die-off event in summer 2018 was unprecedented in terms of spatial and temporal scale and widespread reproductive failures also occurred. High numbers of dead marine mammals were found along the shorelines of the NBS and an Unusual Mortality Event, an official designation for marine mammals, was declared for bearded, ringed, and spotted seals in September 2019. The 2018 events indicate that when climate warming results in extended periods of reduced sea ice cover in the NBS, there may be long-term changes in energy flow and ecosystem structure. Following the low sea ice conditions of 2018, winter 2018/2019 brought a second year of low sea ice. Although it is clear that the climate perturbations experienced in 2018 and 2019 had acute impacts on many components of the NBS marine ecosystem, it is less clear what the long term impacts of this event will be if there is a return to “normal” sea ice cover in future years.

Key words: sub-Arctic, climate warming, ecosystem response, species distributions, diatoms, zooplankton, commercially important fish, snow crab, seabird ecology, marine mammal die-offs, ice seals

1.0 Introduction

The northern Bering Sea (NBS; north of 60°N), an unusually complex region oceanographically, is the Pacific gateway to the Arctic (Fig. 1). In the Chirikov Basin of the NBS, three distinct water masses, the Alaska Coastal Water (ACW), Bering Shelf Water (BSW), and Anadyr Water (AW) converge on Bering Strait. Capping these water masses is seasonal sea-ice that (i) supports ice-associated algae, (ii) determines the amount of light reaching the water column, and (iii) contributes to water-column stratification. Sea ice is a defining ecological feature in the NBS and plays a key role in determining when and where primary production will occur. Because ice algae usually sinks rapidly to the benthos, whereas phytoplankton may remain suspended in the upper water column for a time, the presence or absence of sea ice has been thought to influence the fate of primary production. When ice is present, ice algae supports the benthic food web; in contrast, while phytoplankton remains suspended, it benefits the pelagic system (Grebmeier, 2012). However, O'Daly et al. (2020) demonstrate that phytoplankton in the water column sink rapidly to the seafloor with little or no remineralization on the way. Their observations call into the question the notion that a lack of sea ice may fundamentally alter the routing of primary production in the NBS. Thus, it remains to be seen whether changes in sea-ice cover have an outsized role in determining the structure and function of NBS marine ecosystem processes. Recent papers provide an overview of the physical and biological oceanography of the region (Duffy-Anderson et al., 2019; Stabeno and Bell, 2019; Stabeno et al., 2019; Baker et al., 2020; Danielson et al., 2020).

In the NBS, seasonal sea-ice cover has shown relatively little interannual variability in timing and extent when compared to the southeastern Bering Sea (SEBS). The NBS has been consistently ice covered each winter, whereas ice timing and extent vary interannually in the SEBS (e.g., Stabeno et al., 2012a). However, the winter of 2017/2018 saw a composite of environmental conditions that resulted in an unprecedented reduction in the extent and duration of sea ice in the NBS (Stabeno and Bell, 2019; Thoman et al., 2020; Baysuk and Zuenko, this issue). These conditions included: (i) residual heat from 2017 maintained above-average water temperatures that caused delayed freeze-up (e.g., the Chukchi Sea remained ice-free into January 2018, ice in the NBS arrived late [March] and departed early [April]), (ii) a large and persistent high-pressure system from February through April over the Aleutian Islands and southern Bering Sea shifted the position of the Aleutian Low Pressure System (ALPS) northwest over Siberia, and (iii) as a result, anomalous (at the time) winds from the southwest brought warm air over the Bering Sea and prevented sea ice from forming until March. The composite of events in winter 2017/2018 resulted in 2018 marking the lowest ice-year on record for the eastern Bering Sea (EBS; Thoman et al., 2020). Bottom temperatures in the NBS were 1°C to 2°C rather than <-1°C, and no cold pool formed (Siddon and Zador, 2018; Baysuk and Zuenko, this issue). The annually variable, but typical, cold pool of bottom water on the Bering Sea shelf structures the productivity and distribution of the summer food web (e.g., Mueter and Litzow, 2008; Thorson, 2019; Uchiyama et al., 2020). In the NBS, 2018 was extraordinarily different from the experience of scientists visiting the region or from community members living in the region (see community observations contributed to Siddon and Zador, 2018).

In this paper, we synthesize the ecosystem responses documented in this Special Issue and provide context across trophic levels for the unprecedented conditions experienced in the NBS during 2018. Additionally, we look ahead to conditions experienced through 2019. Changes in sea ice dynamics have already had direct impacts on human activity within and beyond the NBS, from local subsistence activities to large scale commercial fisheries (Ianelli et al., 2018; Thompson, 2018; Eisner et al., this issue; Fedewa et al., this issue). Northward shifts in species' distributions in response to an intermittently ice-free NBS, such as that seen for Pacific cod (*Gadus macrocephalus*), have changed the U.S. federal fisheries management landscape. Both scientists and managers considered the potential impacts of shifts in the food web dynamics in the NBS in their analysis and decision-making. As further disruptions to ice dynamics are projected across the Arctic (Alabia et al., 2020; Guarino et al., 2020; Landrum and Holland, 2020), better understanding of ecological impacts are necessary for anticipating short- and long-term responses of ecosystem components, including commercially important species.

2.0 Physical Oceanography

2.1 *Currents, and water masses*

The NBS is a highly advective system (Danielson et al., 2014; Stabeno et al., 2012, 2016; Basyuk and Zuenko, this issue) with several distinct water masses that differ in origin, mode of stratification, nutrient availability, and both the species composition and the abundance of biota (Fig. 1; Sigler et al., 2017). All eventually flow through the Bering Strait from the Bering Sea to the Chukchi Sea (e.g. Woodgate, 2018). The nomenclature for these water masses has changed over time. Early studies identified three distinct water masses: from east to west, Alaska Coastal Water (ACW), Bering Shelf Water (BSW), and Anadyr Water (AW) (Coachman et al., 1976; Coachman, 1993), whereas Danielson et al. (2017) describe the BSW as being made up of Anadyr Water as well as Bering Shelf Winter Water (BSWW) and Bering Shelf Summer Water (BSSW). In the west, the Navarin Current flows from the Bering Sea slope northward into the Gulf of Anadyr before turning northeastward and exiting the Gulf of Anadyr as Anadyr Water (Kinney et al., 2009; Ladd, 2014; Basyuk and Zuenko, this issue).

In the present issue, most authors have used ACW, BSW and AW, whereas others have identified BSSW as a separate water mass (e.g., Fukai et al, this issue; Ueno et al., this issue). In Basyuk and Zuenko (this issue) what is likely BSWW is identified as the St. Lawrence Cold Water Pool (LCWP). It is important to understand how these water masses are related, as they differ in stratification (Basyuk and Zuenko, this issue; Uneo et al, this issue), phytoplankton species and abundance (Fukai et al., this issue; Kikuchi et al., this issue), zooplankton species and abundance (Kimura et al., this issue; Maekakuchi et al., this issue), fish (Eisner et al., this issue; Nishio et al., this issue; Yasumiishi et al., this issue), and seabirds (Nishizawa et al., this issue).

In 2018, changes in the circulation were observed with stronger northward currents over the NBS shelf (Eisner et al., this issue). Unusually, the northward currents around St. Lawrence Island were stronger on the east side of the island in spring of 2018 and 2019 than on the west side (Baysuk and Zuenko, this issue). Based on the OSCURS oceanographic model, Baysuk and Zuenko (this issue) suggest that a proportion of the Anadyr Water flowed eastward, south of St. Lawrence Island, before turning to the north. There were also observations of ACW to the southwest of St. Lawrence Island in 2018, a result that was not expected (Kimura et al., this issue; Ueno et al., this issue).

2.2 *Water temperatures*

A series of warm years in the EBS commenced in 2014 and continued through at least 2020 (Danielson et al., 2020; Watson, 2020). This warm stanza has been greater in duration and intensity for both the SEBS and NBS than the warm stanza in the early 2000s (Stabeno et al., 2012b). Within the NBS, 1 September 2017 to 31 August 2018 had the highest total cumulative sea surface temperature of any ice-year on record (sum of daily temperatures, Watson, 2020). In the Gulf of Anadyr to the west, Basyuk and Zuenko (this issue) found air temperatures in February in 2014-2019 to be above the long-term mean (1948-2019), with air temperatures in 2018 being the highest in the time series. Upper mixed layer temperatures in the northwestern Bering Sea in summer 2017 were +1 - +4 °C (Basyuk and Zuenko, this issue).

In 2017, water column temperatures below 50 m in the western NBS showed > +3.0 °C anomalies and may have been augmented by heat transported north in the Bering Slope Current (Baysuk and Zuenko, this issue). They hypothesize that warm Pacific Water was advected through the Aleutian Passes and was carried northwestward in the Bering Slope Current. In both 2017 and 2018, there was apparently northward advection of this relatively warm and saline water from the deep basin onto the shelf and into the Gulf of Anadyr. In winters 2017/2018 and 2018/2019, cooling of the water column was weak, and resulted in warm anomalies at depth in the summers of 2018 and 2019. The cold pool over the eastern Bering Sea shelf was missing in 2018 and greatly reduced in 2019 (Eisner et al., this issue).

2.3 *Sea Ice and Stratification*

Sea ice is formed primarily in polynyas in the north of the Bering Sea, and is driven southward by cold northerly winds (Pease, 1980). For the Bering Sea as a whole, the mean sea ice extent in January-April of 2017 was 8% below the climatological mean (1948-2019), while in 2018 it was 25% below the climatological mean (Basyuk and Zuenko, this issue). In 2018, the eastern Bering Sea middle shelf had almost no sea ice present below 60 °N (Stabeno and Bell, 2019). Where there was sea ice in the eastern portions of the NBS, it was thin and patchy (Boveng et al., this issue), and in the western Bering Sea, in the Gulf of Anadyr, in 2018 there were extensive areas of open water (Basyuk and Zuenko, this issue). The distribution of open water in the western Bering Sea reflected the prevailing southerly winds (Basyuk and Zuenko, this issue).

Historically, salinity was the primary driver of vertical stratification of the water column in the NBS (Stabeno et al., 2012). In 2018, with reduced sea ice formation in polynyas and in leads of ice covered waters (Danielson et al., 2006), and the consequent decrease in brine rejection, there was little high salinity water at depth. With little ice to melt in spring, there was also a reduced contribution of low salinity water at the surface to water column stratification (Duffy-Anderson et al., 2019; Stabeno and Bell, 2019). Water column stratification varied spatially over the eastern Bering Sea shelf in 2018 (Ueno et al., this issue). Areas north and south/southwest of St. Lawrence Island were weakly stratified, consistent with less freshwater in the surface layer above warmer, less saline bottom water. The weak salinity structure resulted in greater vertical mixing (Stabeno and Bell, 2019). The coastal domain, including the Bering Strait area, remained strongly stratified in early summer 2018, reflecting surface warming of the low-salinity Alaska Coastal Water (Ueno et al., this issue).

Stratification impacts vertical habitat availability and, combined with horizontal shifts in currents and circulation patterns, can have profound impacts on species distributions. Taken together, these physical oceanographic responses to the reduction in sea-ice cover had broad ecosystem-level implications summarized below.

3.0 Lower Trophic-level Dynamics

3.1 *Phytoplankton and primary production*

The unusually low area of sea-ice cover and its early melt-back in the spring of 2018 likely resulted in a reduced availability of ice algae and a delayed phytoplankton bloom (Duffy-Anderson et al., 2019; Kikuchi et al., this issue). Ice algae are important, as they are a critical fuel for zooplankton egg production (e.g., Søreide et al., 2010; Durban and Casas, 2013; Pleuthner et al., 2016). Additionally, without the presence of stratification from ice-melt, the spring bloom was delayed (~1 month later than typical) until thermal stratification was established (Duffy-Anderson et al., 2019; Kikuchi et al., this issue), similar to what has been described for the southeastern Bering Sea shelf (e.g. Sigler 2014). The spring bloom fuels secondary production of the zooplankton prey community that forms the base of the marine food web of fish, seabirds, and marine mammals. In 2018, a low proportion of large phytoplankton cells was observed, consistent with indications of low productivity (Fujiwara et al., 2016; Fukai, et al., this issue). As noted by Fukai et al. (this issue), in 2017, the diatom community was dominated by cold water species, whereas, in 2018, smaller, cosmopolitan species with a preference for warmer waters dominated.

3.2 Harmful Algal Blooms (HABs)

As a result of warming sea surface temperatures, blooms of toxic algae, commonly referred to as harmful algal blooms (HABs), are becoming more widespread and prevalent in the Arctic (Anderson et al., 2018; Huntington et al., 2020). Although this issue lacks a paper on HABs, this is an important area of research and public health that requires attention. In 2018, a large-scale, coordinated series of HAB surveys and studies was initiated in the Pacific Arctic Sector, centered around the Bering Strait and Chukchi Sea/Bering Sea regions that continues to this day. Data analysis and publications are in progress (D. M. Anderson, R. Pickart, K. Lefebvre, K. Hubbard, E. Fachon, unpub. data), adding greatly to our baseline understanding of HAB species abundance, distribution, and toxin presence in the region. These studies are corroborating and expanding upon recent observations by Natsuike et al. (2013, 2017) who documented large concentrations of sedimented resting cysts and motile, vegetative cells in surface waters of a HAB-causing dynoflagellate, *Alexandrium catenella*. These cysts and motile cells were at concentrations that are worrisome in terms of recurrent threats to human and ecosystem health. The ongoing studies are also documenting the presence of a second HAB group – diatoms in the genus *Pseudo-nitzschia* that cause human and wildlife illness and mortalities via food web transfer of toxin. The next few years should tell us much more about the current extent of HABs in the NBS and Arctic, and the nature of the threat to human and ecosystem health, particularly to indigenous communities that depend on subsistence harvest of fish, shellfish, seabirds, seals, walruses, and whales.

3.3 *Zooplankton*

Crustacean zooplankton have species-specific seasonal cycles of abundance that are related to overwintering ecology and reproductive cycles. Sampling of crustacean zooplankton in the NBS, and in the Chirikov Basin in particular, has occurred sporadically since at least the 1960s, with some investigators obtaining samples from foraging seabirds and in other cases from deployment of plankton nets (Sigler et al., 2017). Since 2002, there have been annual zooplankton surveys in the NBS conducted by NOAA’s Alaska Fisheries Science Center (Kimmel et al., 2020). Only two studies have obtained monthly or more frequent samples from early spring to late fall. Bédard (1969) sampled auklet stomachs bi-weekly from early spring until fall in the 1960s, and Kimura et al., (this issue) sampled zooplankton in 2017 at approximately monthly intervals from May to September. Both papers show that there is as seasonal progression in the types and age classes of zooplankton present in the NBS, and thus when comparing results from different years, it is important to account for seasonality (see also Kimmel et al., 2020).

Bédard (1969) sampled the gut contents of auklets (*Athia* spp.) at their colonies in northwestern St. Lawrence Island during the 1960s and found that they seasonally switched from eating a wide variety of zooplankton (May to July) to a specialized diet during chick rearing (early August to early September). During chick rearing, least auklet (*Athia pusilla*) chick diets were 89% *Calanus finmarchicus.* [Since 1969, a considerable amount of work has been done on the taxonomy of *Calanus* spp. in the Bering Sea, and the most recent evidence supports the conclusion that these were most likely *C. glacialis* (Nelson et al., 2009; Hunt et al., in press).] In contrast, crested auklets (*A. cristatella*) fed their chicks a varied diet. Auklet chick diets from 2017- 2018 were strikingly different (Will and Kitaysky, 2020; Will et al., this issue, a). Will and Kitaysky (2020) found that, starting in 2017, both least auklet and crested auklet diets during the chick stage were almost completely dominated by euphausiids. While this was not highly unusual for crested auklets, it was for least auklets, and could be interpreted as an indication that the large, lipid-rich copepods, which least auklets usually prefer, were scarce in these years.

In 2018, plankton net sampling of zooplankton abundances found low numbers of large copepods, and above average numbers of small copepods that have a low lipid content (Kimmel et al., 2018, 2020; Duffy-Anderson et al., 2019). Anecdotally, the large copepods that were present were predominantly *Eucalanus bungii*, not a lipid-rich species (Kimmel et al., 2018). The abundance of juvenile euphausiids (furcillia) in spring was above average (Duffy-Anderson et al., 2019; Kimmel et al., 2020). The lack of larger, lipid-rich copepods and euphausiids impacts zooplanktivores like thick-billed murres (*Uria lomvia*), and crested and least auklets, as well as forage fish (Bédard, 1969; Hunt and Harrison, 1990; Duffy-Anderson et al., 2019; Will et al., this issue a).

Ctenophores (comb jellies) and jellyfish are pelagic consumers of zooplankton and small fishes. Abundances of both ctenophores and jellyfish were low in 2018 compared to 2017, and it is hypothesized that food limitations were the cause (Maekakuchi et al., this issue). They argue that with the faster sea ice retreat in 2018 relative to 2017, there were poor foraging conditions in 2018 that limited the growth and survival of ctenophores and jellyfish, like *Chrysaora melanaster*, in the NBS.

4.0 Crab

4.1 *Snow crab*

Snow crab (*Chionoecetes opilio*) prefer cold bottom waters associated with the cold pool (waters <2°C) (Ernst et al., 2004), and it was therefore hypothesized that, in the mid latitudes of the eastern Bering Sea shelf, their thermal envelope was exceeded in recent years with low ice cover (Fedewa et al., this issue). Recent increases in the abundance of snow crab in the NBS followed the northward retraction of the cold pool, and spatial patterns across the shelf showed large males were more dispersed. Female and small male snow crabs aggregated in northern regions. In contrast, over the southeastern shelf, environmental drivers did not explain a significant portion of the variation in snow crab distribution for any size-sex group. That said, temperatures occupied by snow crab tracked bottom temperatures, and 2018 marked a dramatic increase in temperatures that may have exceeded snow crab thermal thresholds in the southeastern Bering Sea (Fedewa et al., this issue).

5.0 Fish

5.1 Demersal assemblages

Nishio et al. (this issue) examined the inter-annual variability in the distributions of demersal fish in the NBS and Chukchi Sea over 12 summers between 1990 and 2013. They caught 31 species of fish, with walleye pollock (*Gadus chalcogrammus*) the numerically dominant species, followed by Bering flounder (*Hippoglossoides robustus*) and Arctic cod (*Boreogadus saida*). Nishio et al. (this issue) categorized their 134 trawl samples into four faunal assemblages: a boreal assemblage southeast of St. Lawrence Island, two arctic assemblages in the Chukchi Sea, and a group of stations with a mix of artic and boreal species southwest of St. Lawrence Island. Timing of sea ice retreat was the most important environmental variable and explained 19.4% of the overall variance in fish species' density and 57.7% of the variance explained by environmental factors. For arctic species' abundance, timing of ice retreat was the most important variable, whereas for boreal species, bottom temperature was the most important predictor of abundance (Nishio et al., this issue).

5.2 Gadids

Distributions of fish populations shifted over the EBS shelf in response to the unusually low sea-ice cover in winter 2017/2018 (Spies et al., 2019; Stevenson and Lauth, 2019; Eisner et al., this issue). NOAA Fisheries summer surveys documented the presence of walleye pollock and Pacific cod in the NBS in 2017 and 2018 in greater numbers than had been seen previously (Ianelli et al., 2019; Stevenson and Lauth, 2019) and it is hypothesized that those populations persisted overwinter from 2017 to 2018 in the NBS due to the lack of sea ice. Community members from coastal villages provided invaluable observations of ecosystem response to the lack of sea ice, including that large Pacific cod were caught in crab pots in Nome, Alaska during winter 2017/2018, further supporting that these adult fish may have remained over the northern shelf that winter (see community observations contributed to Siddon and Zador, 2018). Scientists, fisheries managers, and community members alike wondered: would fish overwinter in the northern Bering Sea, and if so, would they become ‘trapped’ by advancing sea ice and experience high overwinter mortality rates? If they overwintered, would they spawn in the north and would subsequent year classes be strong?

Pollock biomass (total weight of all fish in the population) in the northern Bering Sea declined slightly from 2017 to 2018, while more than 50% of Pacific cod biomass in the eastern Bering Sea was found over the northern portion of the shelf in 2018 (Stevenson and Lauth, 2019; Eisner et al., this issue). With half of the Pacific cod biomass in the northern survey area, the Pacific cod assessments for 2018 and 2019 considered NBS data for the first time (e.g., Thompson, 2018; Thompson and Thorson, 2019).

Changes in sea ice and bottom temperature combined with changes in circulation (stronger northward currents over the northeastern shelf in 2018) led to changes in the distribution of age-1 and adult pollock in both US and Russian sectors of the northern Bering Sea shelf, with adult pollock concentrated north of St. Lawrence Island (Eisner et al., this issue). Size structure comparisons between sectors of the shelf suggested that movement of fish between US and Russian waters may have been highest in 2019, one of the two warmest years, and lowest in 2010, the coldest year. Continued warming presents the possibility of US–Russia stock mixing; international research collaborations will be key to understanding responses to climatic variability in these fisheries stocks.

Age-1 pollock have a broader thermal tolerance than adult pollock (e.g., Wyllie-Echeverria and Wooster, 1998; Eisner et al., this issue), but are likely more sensitive to changes in prey availability (Siddon et al., 2013). Northward flow around St. Lawrence Island (particularly in the spring) was stronger on the west side in 2010 and 2017 and stronger on the east side in 2018 and 2019. Such variations in flow may have impacted prey availability and movement of age-1 and adult pollock to the Chukchi Sea. In 2018, adult pollock to the east of St. Lawrence Island were in poorer condition, while adult pollock sampled north of St. Lawrence Island were `plump and healthy' (R. Lauth, pers. obs.).

5.3 Forage Fish

Juvenile forage fish (e.g., capelin, herring), important prey resources for birds and mammals, showed downward trends in abundance over the northern portion of the shelf in 2018 as documented in NOAA Fisheries surface trawl surveys (Yasumiishi et al., 2018; this issue). Capelin responded negatively to warming conditions over the Bering Sea shelf as a whole, while herring responded positively to temperature and appear to prefer the warmer conditions over the NBS shelf in recent years. Because capelin are important forage for juvenile salmon, the spatial distribution of capelin may influence the migratory pathway of juvenile Chinook salmon emerging from western Alaska, such as the Yukon and Kuskokwim rivers (Yasumiishi et al., 2019, this issue). In recent years (2018, 2019), a leading indicator of Chinook salmon abundance was below average; abundance of Chinook salmon has impacts on the bycatch caps in the pollock fishery three to four years in the future (Murphy et al., 2019).

5.4 Salmonids

The biomass of juvenile sockeye salmon in the NBS has increased with temperature (Yasumiishi et al., this issue). However, synchronous changes in juvenile pink and chum salmon biomass appear unrelated to temperature and suggest a different mechanism, or suite of mechanisms, may be driving their dynamics. Juvenile pink and chum salmon feed on similar prey items and both species experienced a 2-fold increase in biomass in 2018 (Farley et al., 2020; Yasumiishi et al., this issue). Differential responses to temperature by various juvenile salmonid species indicate that temperatures may have reached and/or exceeded the optimal temperature envelopes for these species

(Yasumiishi et al., this issue). In response, these fishes may seek cooler temperatures for thermal regulation and thus prey associated with those cooler waters.

6.0 Seabirds

The NBS supports a vast array of seabirds; at least 17 species nest there in colonies with an aggregate of nearly 11.3 million individuals, about 75% of the 15.1 million seabirds nesting in the Bering Sea from Unimak Pass to the top of Bering Strait (Marc Romano, pers. comm.). Particularly prominent in the NBS are the planktivorous auklets. Early studies of the breeding biology and prey selection of seabirds in the NBS include the work of Bédard (1969) (discussed earlier) and Drury et al. (1981) on the breeding biology and food habits of seabirds in the Chirikov Basin and northward into the Chukchi Sea.

Drury et al. (1981) were some of the first investigators to recognize that the timing of sea ice retreat affected the types and abundance of forage fish available to nesting seabirds in the NBS. Murphy et al. (2016) followed up on this work with a 33-year study of seabird breeding success at several Bering Sea and Chukchi Sea seabird colonies. Most relevant to the present issue, they found that piscivorous kittiwakes breeding on the cliffs at Bluff in Norton Sound had their greatest reproductive success when the spring was warm and sea ice retreated early. Working in the Sea of Okhotsk, Kitaysky and Golubova (2000) also found that piscivorous puffins had higher reproductive success in warm years with light sea ice cover whereas planktivorous least and crested auklets had better success in colder years when sea ice lingered. Similarly, at the Pribilof Islands, Benowtiz-Fredericks et al. (2008) found that, over two years, planktivorous auklets and piscivorous kittiwakes alternated years with high and low reproductive success, likely due to climate-related interannual shifts in the availability of forage fish and zooplankton prey (see also Byrd et al., 2008; Dorresteijn et al., 2012; Hovinen et al., 2014). Thus, based on studies of seabird reproduction in cold oceans, there is strong evidence that the prey of planktivorous seabirds is more available in years with substantial sea ice in spring, whereas seabirds dependent on forage fish may have greater reproductive success when ice retreat is early and water temperatures are higher.

6.1 Seabird die-offs and Reproductive failures

A seabird die-off event in summer 2018 in the NBS was unprecedented in terms of spatial and temporal scale (Siddon and Zador, 2018; Romano et al., this issue; Will et al., this issue a). High numbers of seabirds (mainly thick-billed murres *Uria lomvia* and shearwaters *Puffinus* sp.) washed ashore from Bering Strait southward through Norton Sound, and along the shores of St. Lawrence Island. Thick-billed murres comprised more of the beach cast murre carcasses than the proportions of the two murre species in local breeding colonies (Will et al., this issue b). Based on body condition of beach-cast birds, starvation was identified as the most likely cause of death for many of the birds (Romano et al, this issue). Additionally, analyses of corticosterone concentrations in the plasma of Black-legged kittiwakes, common murres, least auklets and crested auklets at St. Lawrence Is. indicated that these seabirds were severely food stressed in the summer of 2018 (Will et al., this issue a).

There was also widespread reproductive failure of seabirds in the NBS during summer 2018. Reproductive failures and poor reproductive success of murres, crested and least auklets, and black-legged kittiwakes were observed by community members, subsistence eggers, and scientists (Siddon and Zador, 2018; Will et al., this issue a). Those birds that did nest, nested very late (Romano et al., this issue). All murre reproductive effort failed north of St. Matthew Island, including at St. Lawrence Island (Romano et al., this issue; pers. comm.). Murres in the NBS that attempted nesting did not produce chicks, which is exceptional; prior to an extensive heatwave in 2016, widespread murre reproductive failures had not been observed. Will et al. (this issue, b) also documented colony-wide reproductive failures of planktivorous crested and least auklets during 2018 and 2019 at St. Lawrence Island. Subsistence hunters at St. Lawrence Island usually capture 30-40/day crested and least auklet fledglings, but in 2018, a hunter stopped trying after he pulled 13 dead fledglings and no live ones from their nests (Siddon and Zador, 2018). At Sledge Island in Norton Sound, 50-70% of murres were missing from cliffs and those that were there were not laying eggs; there was a complete lack of subsistence harvest (Siddon and Zador, 2018).

6.2 Seabird diets and prey availability

Crested and least auklets prey on large crustacean zooplankton; thick-billed murres and shearwaters prey on euphausiids, amphipods, and forage fish; common murres largely prey on forage fish. The historical diet composition of seabirds affected in the 2018 die-off event suggests that large, lipid-rich zooplankton were in short supply in 2018 (Will et al., b, this issue). Likewise, Maekakuchi et al. (this issue) suggested that the low numbers of gelatinous zooplankton found in 2018 probably reflected a lack of large crustacean zooplankton. The importance of sea-ice algae for the production of these large lipid-rich zooplankton species is well established (e.g., Søreide et al., 2010; Durban and Casas, 2013; Pleuthner et al., 2016), and it seems very likely that the near absence of sea ice in winter 2018 precipitated a lack of this prey source. As an elder from St. Lawrence Island commented “when there is no dirty ice, there is less food for the krill, and consequently, no food for the birds" (Siddon and Zador, 2018). Will et al. (this issue b) also discussed how top down competition from adult gadids and gelatinous zooplankton (see Maekakuchi et al., this issue) may have limited the availability of euphausiids to foraging crested auklets, and suggested that top-down impacts may have contributed to the increased nutritional stress levels of 4 planktivorous seabird species in 2018 and 2019.

In contrast, at St. Lawrence Island in summer 2018, thick-billed murres did not show signs of food stress based on analyses of corticosterone concentrations in their plasma (Will et al., this issue b). However, there was some evidence that thick-billed murre mortality there may have been caused by a novel reassortment of the H10 strain of avian influenza with Eurasian components (Will et al., this issue b). The finding of the virus in one of two dying murres raises the possibility for synergistic effects of reduced prey abundance and viral infection on the survival of seabirds nesting in large colonies, especially colonies with the possibility of localized prey depletion (Furness and Birkhead, 1984; Hunt et al., 1986).

Based on at-sea surveys in 2018, Nishizawa (this issue) documents lower densities of seabirds, forage fish, and zooplankton in 2018 compared to 2017, providing supporting evidence for bird-die offs to be related to food. Kuletz et al. (this issue) discuss longer-term changes in at-sea seabird distribution that might reflect spatial shifts in productivity. Total seabird density declined 27% in the NBS between 2007-2016 and 2017-2019 although over the same period, it increased in the Chirikov Basin by 73%. During 2017-2019, the abundance of piscivorous murres (*Uria* spp.) decreased everywhere. Planktivorous auklet densities increased by 70% in the Chirikov Basin, possibly because of deserting their colonies after reproductive failure, and migrant wintering short-tailed shearwaters (*Ardenna tenuirostris*) expanded farther into the northern Chukchi Sea, with nearly twice the density of the previous decade (Kuletz et al., this issue). Similar to findings in other regions, warming in the NBS has had adverse impacts on seabirds that primarily consume zooplankton and to a lesser extent those that forage on pelagic forage fish (Kitaysky and Golubova, 2000; Dorresteijn et al., 2012).

7.0 Marine Mammals

7.1 Ice seals

In 2018, observations of marine mammals by Bering Strait community members (provided via Gay Sheffield, University of Alaska, Fairbanks – Sea Grant, Nome, Alaska, to Siddon and Zador, 2018) that indicated significant changes in the marine ecosystem. For example, beginning in February, residents in shoreside communities reported benthic-feeding walruses (*Odobenus rosmarus*) were harvested off St. Lawrence Island, an earlier time of year than when they typically have been accessible. The walruses were `fat and in good condition'. In contrast, ice-dependent seals were not faring as well. By early June, there were reports of exceptionally high numbers (i.e., 50) of dead seals on beaches (primarily young bearded seals) along the north side of St. Lawrence Island, and 48 beach-cast ice seals (bearded, ringed, and sub-adult spotted seals) near Wales. The beach-cast seals appeared to have poor body condition and empty stomachs. There were also reports of sick and dead seals outside of their normal range; seals were absent or unusually scarce in the Port Clarence area.

Several species of pinnipeds are collectively known as “ice seals” because they haul out on sea ice to rest between foraging bouts, mate, give birth to and nurse their young (Boveng et al., this issue). Their distributions were dramatically impacted by the lack of sea ice over the NBS shelf (Siddon and Zador, 2019; Boveng et al., this issue). In 2018, the nearest ice edge over the shelf was about 375 km to the northeast of where it has been historically found. Observations made during a NBS expedition to study ice seals revealed that ice seals (particularly ribbon seals) were unusually scarce with no evidence that they moved northeast or into Norton Sound following the ice edge (Boveng et al., this issue). It was unclear whether or where ribbon seals were successful at producing and rearing pups in 2018. Spotted seal pups weighed less than in recent years, continuing a declining trend in body condition and blubber thickness since 2014 (Boveng et al., this issue).

Ribbon seals are more adapted for deep diving and foraging off the shelf than spotted seals. This difference led Boveng et al. (2013) to predict that ribbon seal reproductive success in the Bering Sea would be sensitive to future declines in ice extent. A northward retraction of the ice edge, away from deeper water over the shelf slope, would displace ribbon seal mother-pup pairs from their preferred foraging habitat. Spotted seals, on the other hand, were anticipated to be more resilient to the loss of sea ice due to foraging habits more suited to shallow inshore waters where they fed on epibenthic communities (Boveng et al., 2009). The observations in 2018 seem to bear out these predictions.

7.2 Marine Mammal mortality events:

Dead marine mammals are occasionally beach cast. In 2018, high numbers of dead marine mammals were found along the shorelines from north of Bering Strait, throughout Norton Sound, and on St. Lawrence Island beginning in June 2018 (Sheffield, 2018; Boveng et al., this issue). A UME, an official designation for a marine mammal Unusual Mortality Event, was declared for bearded, ringed, and spotted seals, in September 2019 (NOAA Fisheries, 2020a). In 2018, seals were emaciated. Symptoms during a previous UME in 2011 – 2016 were different (hair loss, delayed molting, skin ulcers, lethargy, and labored breathing) and no specific cause of the these symptoms was identified (NOAA Fisheries, 2020b).

The co-occurrence of the 2019 UME with record low sea ice extent and an absence of ice from vast portions of the birthing and nursing areas for all four species of ice-associated seals in the Bering Sea supports the hypothesis that climate warming will have a major impact on ice seal populations. Boveng et al. (this issue) suggest that the ecological variability experienced in the past two decades may be beginning to exceed the long-term bounds to which these species are adapted, and that the impacts of loss of sea ice on the condition and vital rates of phocid seals are likely to become more clear if conditions seen in 2018 and 2019 become more frequent.

8.0 What happened in 2019?

In winter 2018/2019, the EBS experienced a second year with little winter sea ice and a reduced cold pool extent (summer 2019) due to: (i) residual heat in the Chukchi Sea in fall of 2018, and (ii) the second year of highly unusual winds from the south in February 2019 causing early ice retreat (Stabeno and Bell, 2019; Siddon and Zador, 2019). The 2018-2019 mean sea ice extent was the second lowest of record (only 2017-2018 was lower; Stabeno and Bell, 2019; Thoman et al., 2020). A small cold pool was located over a portion of the northern Bering Sea shelf during summer 2019 (Overland et al., 2019).

Sea-ice accumulation in winter 2018/2019 differed from winter 2017/2018. Residual heat delayed freeze up until mid-December (similar to 2017/2018) (Overland et al., 2019). Nevertheless, accumulation approached the long-term mean sea-ice extent through January 2019 (whereas 2018 sea ice never approached normal levels) (Overland et al., 2019). But then persistent southerly winds during February 2019 reduced sea ice (similar between years).

During the second year of low ice conditions in the NBS (2019), the timing of the peak spring bloom was earlier than the long-term average and earlier than in 2018 (Nielsen et al., 2019). The zooplankton community was dominated by small copepods, typical of warm-year conditions over the shelf, while large copepod and euphausiid abundances remained low (Kimmel et al., 2019). It was hypothesized that warm temperatures increased copepod secondary production rates.

In 2019, NOAA bottom trawl surveys in the NBS documented a substantial increase in the abundance of larger (≥61 mm carapace width) male snow crab from 2018 to 2019 (Fedewa et al., this issue). The origin of these large male crab in the NBS remains unknown, but snow crabs may have shifted their distributions northward seeking the cooler waters in the retracted cold pool (Fedewa et al., this issue). This may have management implications as the commercial crab fisheries track stocks into more northern latitudes (Fedewa et al., this issue).

The formation of sea ice in early winter 2018/2019 may have impacted the distribution of groundfish over the eastern shelf. It is hypothesized that the retracted cold pool over the northwest portion of the shelf provided a thermal barrier that contributed to an increased biomass of adult pollock over the southern shelf in 2019. The 2019 NOAA bottom trawl survey showed a 75% increase in pollock biomass over the SEBS from 2018 to 2019 (Stevenson and Lauth, 2019). This suggests that adult fish moved into the region (recruitment of small fish could not account for such a large increase in biomass). However, adult pollock (>250 mm TL) that remained in the NBS in 2019 had increased condition (based on length/weight residuals) relative to 2018, while juvenile pollock (100-250 mm TL) were in average condition (Rohan and Laman, 2020).

The declaration of an Unusual Mortality Event (UME) for ice seals in 2019 reflects cumulative impacts of ecosystem conditions experienced in 2018 and 2019. The increased mortality of seals and the apparent decline in pup condition demonstrate immediate and delayed impacts of the loss of sea ice habitat for pupping and nursing in both years. They could also demonstrate broader ecosystem effects, such as competition for prey from northward shifts of fish populations (see Section 5.2, above).

Lagged (delayed) impacts of poor feeding conditions experienced during 2018 also may partially explain a gray whale UME (Savage, 2019). Gray whales (*Eschrichtius robustus*) feed in the northern Bering and Chukchi seas and are typically benthic feeders (e.g., amphipods, crab larvae). The 2019 mortality events may reflect 2018 feeding conditions in the Bering Sea, conditions experienced during migrations to the south, or a lack of available prey to complete the return migration to the Bering Sea in 2019 (Siddon and Zador, 2019). The 2019 grey whale UME may also be related to the population approaching carrying capacity. In 2001, Moore et al. first suggested that grey whales might be reaching the carrying capacity of their NBS and Chukchi Sea foraging grounds. At that time, there were an estimated 26,635 grey whales (Moore et al., 2001). The estimated population as of 2019 was 27,000 (Calambokidis, in: Paris, 2019).

9.0 Discussion

The NBS in 2018 was strikingly different from what was expected based on the recent past. The dramatic decrease in sea-ice cover seen in 2018 was unprecedented. Modeling efforts have predicted that such changes, forced by climate change, were most likely to be first-seen in the 2040s to 2050s, not prior to 2020 (Wang et al., 2012; Wang and Overland, 2015; Thoman et al., 2020). Sea ice was scarce not only in the eastern portions of the NBS, but also in the west, with little sea ice present in the Gulf of Anadyr (Basyuk and Zuenko, this issue). The flow of Anadyr Water differed in summer 2018 in that much of it went around the south side of St. Lawrence Island and then turned northward on the eastern side of the Chirikov Basin (Basyuk and Zuenko, this issue).

The impacts of the lack of sea ice cascaded through the ecosystem from phytoplankton to marine birds and mammals, but apparently not to the benthic community. Ice algae is an important contributor of energy to the benthic ecosystem (Grebmeier et al., 1988; Tamelander et al., 2006; Leu et al., 2011; Lovvorn et al., 2016; Koch et al., 2020). With a lack of sea ice in 2018, it was hypothesized that seabirds might switch from a benthic supported food web to a pelagic food web, but such a switch was not evident (Will et al., this issue a). It seems likely that the benthic system is resilient to rapid change, as much of the energy stored in organic matter is contained in the sediments and the organisms that recycle this material, remaining available to the benthic food web through at least one year of lost sea ice (e.g., North et al., 2014).

The lack of sea ice contributed to a delayed phytoplankton bloom (Duffy-Anderson et al., 2019; Kikuchi et al., this issue). Likely due to the combination of little sea ice in the Gulf of Anadyr, the delayed phytoplankton bloom, and the eastward flow of Anadyr Water around the south side of St. Lawrence Island, large copepods were scarce in the western Chirikov Basin. Not only were the large, ice-dependent Arctic *C. glacialis* largely absent from the diets of planktivorous auklets nesting on the northwest coast of St. Lawrence Island, but so were the *Neocalanus* spp. which overwinter in the Bering Sea basin (Springer et al., 1987; Will and Kitaysky, 2020; Will et al, this issue a), possibly due to the re-routing of the Anadyr Water. Seabirds that depend on these large, lipid-rich zooplankton for fueling their reproduction largely failed to fledge young. This was particularly true along the northwest coast of St. Lawrence Island (Will et al., this issue a), a region where many seabirds seek zooplankton prey normally abundant in the Anadyr Water to the west (Springer et al., 1987; Hunt et al., 1990; Elphick and Hunt, 1993). North of St. Matthew Island, seabird reproduction was poor, and most, if not all, murre colonies experienced reproductive failure (Romano et al., this issue).

The impact of the lack of sea ice in 2018 on ice-dependent seals was immediate and severe. Ribbon seals were scarce in the eastern portion of the NBS as there was no ice near the shelf edge on which they could rest, give birth, or nurse their pups (Boveng et al., this issue). Other species of ice seals, including ringed, spotted, and bearded seals were encountered on beaches, sick or dead, in unusually high numbers; and many of the carcasses showed evidence of emaciation (Boveng, 2019). Reduced sea-ice cover limited this critical platform, and the limited ice that was present may have been in areas with poor prey availability for ice-dependent seals.

The movements of pollock, Pacific cod, and snow crab into the NBS will provide challenges to both the fishing industry and to fisheries managers if commercial fishing/processing activities increase in the NBS. The fishing industry will have to evaluate the trade-offs between longer travel times between productive fishing grounds and off-loading ports. Presently, there are no equivalent processing facilities in the NBS to Dutch Harbor in the Aleutians. For fisheries managers, major shifts in distribution of commercial crab and groundfish stocks will require adjustments in survey effort and evaluations of new ways to manage these fisheries. For the local and indigenous communities that populate the shorelines of the NBS, there will be new opportunities for fishing species previously out of range of their communities and for port services supporting commercial fishing/processing activities and other industrial vessel traffic.

We have now observed changes in the NBS ecosystem in response to two consecutive years of an oceanographic perturbation. However, we caution that ecosystem responses to future years of low to no sea ice may not have the same ecosystem responses because the balance of the food web may be changed. The ecological responses in 2018 and 2019 may have shifted the balance of the food web or altered top-down versus bottom-up controls. Thus, a reorganized northern Bering Sea ecosystem may respond differently to future years of minimal sea ice coverage. Likewise, it is not clear what the long-term impacts of this event will be if there is a return to “normal” sea ice cover in future years.

The two consecutive winters of low sea ice in the northern Bering Sea presented a ‘stress test’ to the physical environment. We have since seen that these warm, nearly ice-free years had extensive ecosystem impacts as described in papers in this issue. There are lessons to be learned from a similar major environmental perturbation in an adjacent marine ecosystem, the Gulf of Alaska, a few years prior to the change in the NBS.

In the Gulf of Alaska (GOA), a prolonged heatwave from 2014-2016 caused extensive ecosystem responses, including an apparent temporary reorganization of the food web. A large decline in an apex groundfish predator, Pacific cod, was linked to increased metabolic requirements due to the increase in ambient water temperature (Barbeaux et al., 2020). Apparently, the increased food demand could not be met by increased consumption. This led to increases in the natural mortality of cod, and subsequent closure of directed fisheries, but also to the largest die off of common murres, whose diet overlaps with that of Pacific cod, that had been seen in the northern GOA (Barbeaux et al., 2020, Piatt et al., 2020). A second heatwave occurred in in the GOA in 2019, but did not appear to have the same ecosystem impacts, likely due in part to the decreased abundances of Pacific cod and common murres, and additional changes, that persisted from the previous heatwave and the resulting rebalancing of the food web (Zador et al., 2019).

Climate change is creating major perturbations in the marine ecosystems of Alaska. The GOA experienced marked declines in several commercially important species, including salmon and Pacific cod. There were also high mortality rates or reproductive failures in other top predators such as seabirds. In the NBS elevated water temperatures and subsequent declines in sea ice cover resulted in die offs and reproductive failures of seabirds and marine mammals. However, in the NBS unlike the GOA, the warmer sea temperatures apparently facilitated the northward migration of commercially important fish populations (e.g., Pacific cod and pollock). As has been predicted for other high latitude regions, fish communities have shifted northward. Whether these are short term adjustments or the start of a long-term trend in the redistribution and biomass of Alaska’s fish stocks remains to be seen.

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Figure Caption:

Fig. 1. The northern Bering Sea, showing water masses and currents, as well as place names mentioned in the text. Figure courtesy of Seth Danielson, University of Alaska Fairbanks.

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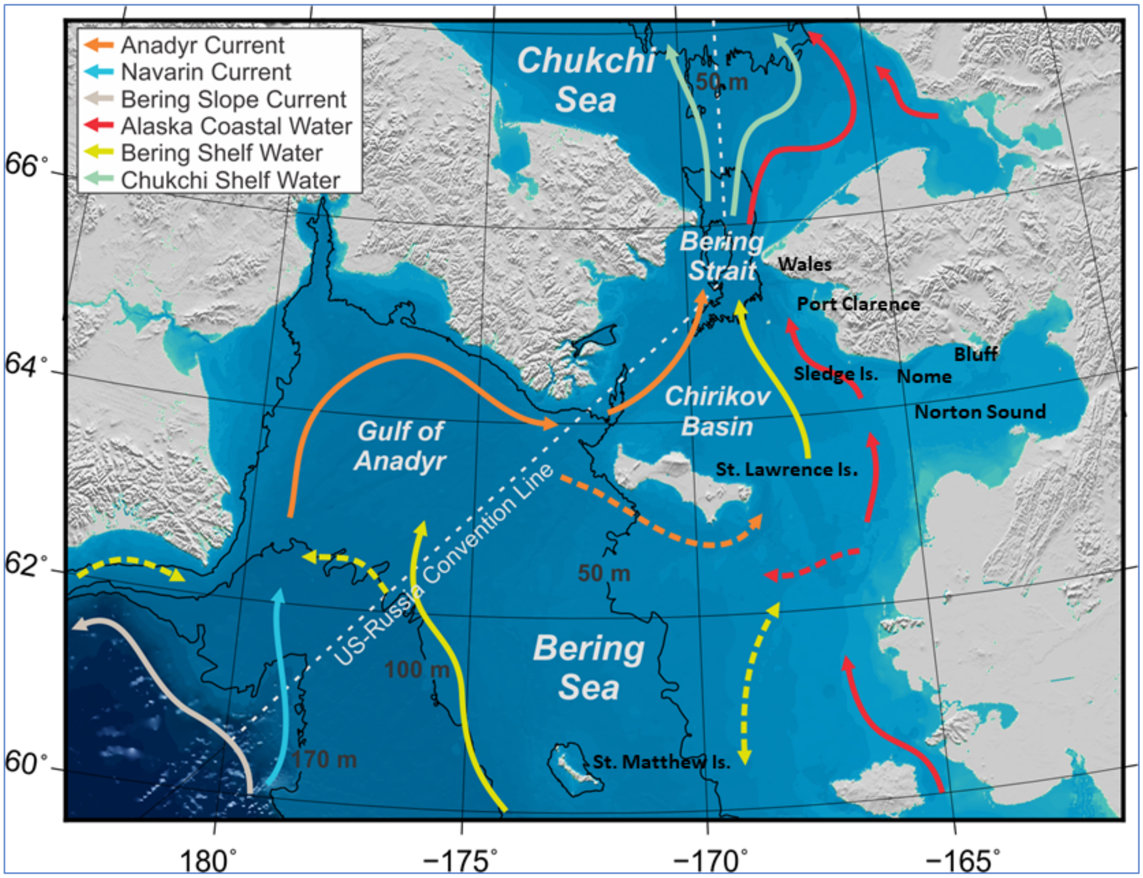

Figure 1. The northern Bering Sea, showing water masses and currents, as well as place names mentioned in the text. Figure courtesy of Seth Danielson, University of Alaska Fairbanks.