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Contribution to the Theme Section 'How do marine heatwaves impact seabirds?'

Seabird responses to ecosystem changes driven by marine heatwaves in a warming Arctic

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ABSTRACT: In the Pacific Arctic, the Chukchi Sea has been warming for decades, and exhibited an exceptionally warm period from 2015 to 2021. We examined changes in seabird distribution and abundance in the Chukchi Sea, and their relationships to environmental and prey conditions between 2 contrasting periods. We sampled systematically placed stations in late summer during 2 years before (2012, 2013) and 2 years during the warm period (2017, 2019; characterized by multiple marine heatwaves). Ship-based bird counts were used to model at-sea density of 5 seabird foraging guilds relative to oceanographic (water temperature, salinity, chlorophyll) and prey (large copepods, euphausiids, 3 forage fish taxa) variables. Relative to cool years, heatwave years were characterized by warmer, saltier waters, low abundance of large copepods and euphausiids, and elevated fish abundance, including an unprecedented abundance of age-0 walleye pollock *Gadus chalcogrammus*. Seabird species richness was higher during heatwave years but diversity was lower, driven by an influx of shearwaters. The best models for surface feeding and diving piscivores and diving planktivores included oceanographic and prey variables, plus a heatwave interaction term, indicating that responses to variables differed between cool and heatwave periods, with greatest disparity exhibited by diving planktivores. Models for surface planktivores were inconclusive, whereas shearwater distribution was associated with geographic variables (latitude, distance offshore), with relationships differing during cool and heatwave periods. We propose a conceptual model of how a prolonged period of marine heatwaves may affect the offshore seabird community via changes in prey species composition and distribution.

KEY WORDS: Marine heatwave · Seabird foraging · Seabird response · Arctic marine ecology · Chukchi Sea · *Aethia* auklets · Short-tailed shearwater

1. INTRODUCTION

Global warming from anthropogenic carbon emissions has led to (and has been exacerbated by) the loss of Arctic sea ice (Kumar et al. 2020, Carvalho et al. 2021), exemplified by an estimated 84% decline in annual sea-ice extent minima across the western Arctic between 1979 and 2018 (Stroeve & Notz 2018). As subarctic and Arctic atmospheric temperatures have increased (Clark & Lee 2019), there has also been an increase in the occurrence of marine heatwaves (MHWs) (Timmermans & Labe 2020, Barkhordarian et al. 2022). In the Chukchi Sea, sea surface temperatures (SSTs) have increased since the 1990s (~0.43°C decade^{-1}), and mean monthly spring SST anomalies during 2014–2018 peaked at 3.4°C above average

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(Danielson et al. 2020). An unprecedented warm period from 2017 to 2019 further reduced winter sea ice extent and duration, with subsequent impacts to water mass properties during the boreal summer (Baker et al. 2020a, Danielson et al. 2020). South of the Chukchi Sea, the Bering Sea 'cold pool', a pool of cold bottom water (<2°C), typically formed each winter during sea ice growth, but did not form in the winter of 2017/2018 (Stabeno & Bell 2019). The lack of a cold pool removed a thermal barrier and ultimately led to a shift in biological communities in the Bering and Chukchi Seas in 2018 and 2019 (Baker et al. 2020a, Siddon et al. 2020). These changes and alterations of lower trophic levels appeared to have direct and indirect consequences for upper trophic level consumers (Duffy-Anderson et al. 2019, Huntington et al. 2020, Mueter et al. 2021).

Large numbers of seabirds occupy the Chukchi Sea in summer, including resident breeding species and others that migrate to forage on abundant prey (Piatt & Springer 2003, Kuletz et al. 2015, Gall et al. 2017). During the 2017–2019 warm period, both breeding and migratory birds contended with ecosystem-wide alterations of environmental conditions. In the adjacent northern Bering Sea, birds at some colonies did not attempt nesting, while other colonies experienced complete breeding failures (Romano et al. 2020, Will et al. 2020a,b). In addition, shifts in at-sea distribution (Kuletz et al. 2020) and unusual mortality events were also observed (Romano et al. 2020, Will et al. 2020b, Kaler & Kuletz 2022, Jones et al. 2023 in this Theme Section).

Globally, the frequency of MHWs has increased in recent decades (Amaya et al. 2020) and, given current anthropogenic carbon emissions, may be a prelude to future conditions (Frölicher et al. 2018, Hobday et al. 2018, Laufkötter et al. 2020, Ballinger & Overland 2022). To facilitate planning and management actions, it is critical to better understand where and how MHWs impact seabirds. MHWs have been associated with low breeding success of seabirds (Eizenberg et al. 2021, Montevecchi et al. 2021), changes in distribution and diet (Osborne et al. 2020, Fromant et al. 2021), and mass mortality events (Jones et al. 2018, 2023, Romano et al. 2020). High ocean temperatures impact seabird populations indirectly by altering prey availability (Sydeman et al. 2015). However, different seabird species have shown opposing responses to the same warming event (Whelan et al. 2022), and even closely related seabird species vary in their apparent ability to adapt to heatwave properties (Eizenberg et al. 2021), reflecting differences in physiology and behavior (Cairns 1987, Piatt et al. 2007).

Seabirds depend on the marine environment for food, but the energetic requirements and foraging flexibility of individuals will vary during the breeding season. Nonbreeding seabirds must meet their own energetic requirements to support daily activity, migration, and wing molt. Seabirds that are actively breeding face elevated nutritional and physical demands as they incubate eggs and raise chicks and are thus restricted by central place foraging (Cook et al. 2020, Eizenberg et al. 2021, Glencross et al. 2021). Seabird prey are affected by changing physical conditions like ocean temperature and salinity (Yasumiishi et al. 2020, Kimmel et al. 2023); thus, we need to understand how different types of seabirds respond to changes in ocean conditions and subsequent changes in prey distribution.

As with most of the subarctic and Arctic (Huang et al. 2021a), the northern Bering and Chukchi Seas have been undergoing systemic changes as sea ice declines and ocean temperatures warm (Arrigo et al. 2008, Mueter & Litzow 2008, Danielson et al. 2020). Stanzas of relatively cooler periods, such as 2006–2013, have alternated with warmer periods such as 2014–2017 (Stabeno et al. 2012, 2017, Stevenson & Lauth 2012). In a historical context, 2012 and 2013 were part of a long-term warming trend in the region (Stabeno & Bell 2019, Baker et al. 2020a); however, those years were followed by a much warmer period (Baker et al. 2020a, Carvalho et al. 2021), characterized by a series of MHWs in the Bering Sea (Jones et al. 2023). The excess heat exemplified by MHW conditions observed in the Bering Sea extended into the Chukchi Sea (Carvalho et al. 2021; see Text A1 in the Appendix). Our goal was to determine how heat-induced changes in environmental and prey conditions during this period of MHWs affected Chukchi seabird community composition and distribution.

Seabirds in the Chukchi Sea feed on resident and advected zooplankton and fish species (Hunt et al. 1998, 2000), which have been impacted by higher water temperatures and new species entering the ecosystem from the Bering Sea (Mueter et al. 2021, Levine et al. 2023). A separate 2 yr study in the Chukchi Sea indicated that spatial associations between seabirds and other taxa (bacteria to fish), were correlated in summer of 2015 (a relatively cool year), but absent in 2017 (Mueter et al. 2021), amidst the period of MHW events. We hypothesized that avian feeding guilds may have responded differently to the environmental changes that occurred during the period characterized by MHWs, indicative of varied responses to an altered prey base. We predicted that planktivorous seabirds, which do not nest in the Chukchi region, should maintain a closer relationship with the distribution of their prey even during heatwave years, because individual birds are not tied to colonies and can follow prey. Furthermore, large zooplankton aggregate near well-defined physical features and water masses (Hopcroft et al. 2010, Pinchuk & Eisner 2017, Kim et al. 2020), and planktivorous birds should be concentrated in these same areas (Hunt et al. 1998). In contrast, at least some portion of breeding piscivorous seabirds, which nest on the Chukchi coastline, may still be tied to their colonies during late summer, and could thus exhibit less overlap with prey located beyond the foraging range from the colony.

Foraging behavior (i.e. surface feeding vs. diving) and inherent physiological limitations can also affect access to prey. Surface feeders can range farther, whereas diving birds can access more of the water column but are less efficient at flying (Pennycuick 1987, Ballance et al. 1997, Elliott et al. 2013). Thus, a combination of diet and foraging behavior could interact to influence seabird response to heat-induced changes in prey, and their ability to adapt to changing conditions.

We examined how seabird foraging guilds (defined by primary diet and foraging mode) at sea responded to 2 contrasting periods of ocean temperatures: a relatively cool period vs. a period with multiple MHWs, wherein the latter had documented ecosystem-wide impacts (Danielson et al. 2020, Mueter et al. 2021). We compared seabird response to environmental and prey conditions during these 2 periods by using data from vessel-based studies focused on the Chukchi Sea during 2 years of the cooler period (2012, 2013) and 2 years of the heatwave period (2017, 2019), with the latter defined by SSTs above the threshold defining an MHW (Hobday et al. 2016). We present a conceptual model that proposes how physical drivers and biological conditions in the Chukchi Sea affect seabird prey and seabird responses under heatwave conditions, as a guide for future efforts to better understand seabird community responses to a warming Arctic.

2. MATERIALS AND METHODS

2.1. Study area

The study area includes the continental shelf of the US sector of the eastern Chukchi Sea (Fig. 1), bounded by the Bering Strait (65° 30′ N) to the south and extending northward to the shelf break at ~72° N. The eastern boundary is defined by the coastline of Alaska and to the west by the US—Russia maritime boundary (168° 58′ 37″ W). The Chukchi Sea is shallow (average depth 57 m) on the shelf (Danielson et al. 2020), except for Barrow Canyon in the northeastern portion, which opens to the deep Arctic Basin.

2.1.1. Physical environment

The Chukchi Sea is a marginal sea of the Arctic Ocean that historically was covered with sea ice most of the year, but now has little sea ice on the shelf from June to November (Baker et al. 2020a, Danielson et al. 2020). The seasonally melting winter sea ice results in 'melt water' that influences salinity, water temperatures, and prevailing currents (Lin et al. 2019, Danielson et al. 2020). The Chukchi Sea is also physically and biologically linked to the Bering Sea (Sigler et al. 2011, 2017), primarily via water masses flowing north through the Bering Strait (Fig. 1): Anadyr Water (cold, saline, nutrient-rich), Bering Shelf Water (similar, but less nutrient rich, and contributes to the Chukchi Shelf Current), and Alaskan Coastal Water (warmer, fresher, nutrient-poor) (Coachman et al. 1975, Weingartner et al. 1999). These water masses advect nutrients, heat, and plankton northward, supporting high productivity (Springer & McRoy 1993, Grebmeier et al. 2006 and references therein). The Anadyr and Bering Shelf waters encircle Hanna Shoal, a shallow area (40 m depth) on the northeastern Chukchi Shelf, making it a nutrient-rich area (Dunton et al. 2017). Along the northern shelf slope, the area is also influenced by eastward-flowing deep Atlantic water and the westward-flowing Beaufort Gyre (Fig. 1). The properties, extent, and mixing of these water masses vary seasonally and interannually due to changes in atmospheric circulation, regional wind patterns, and sea ice extent (Weingartner et al. 1999, 2005, Woodgate et al. 2005).

2.1.2. Seabirds

The Bering Strait and eastern Chukchi Sea harbor 4 large colonies within our study area (Fig. 1) that support tens of thousands to several million seabirds each, extending from the Diomede Islands located in the Strait to Cape Thompson and Cape Lisburne on the southeast coast of the Chukchi (Stephensen & Irons 2003, Kuletz et al. 2015, their Table A1). Birds nesting at the Chukchi colonies are primarily piscivorous, and include alcids (10 species), larids (4 species), and cormorants (2 species). North of Cape Lisburne, cliff- and cavity-nesting habitat is lacking, with

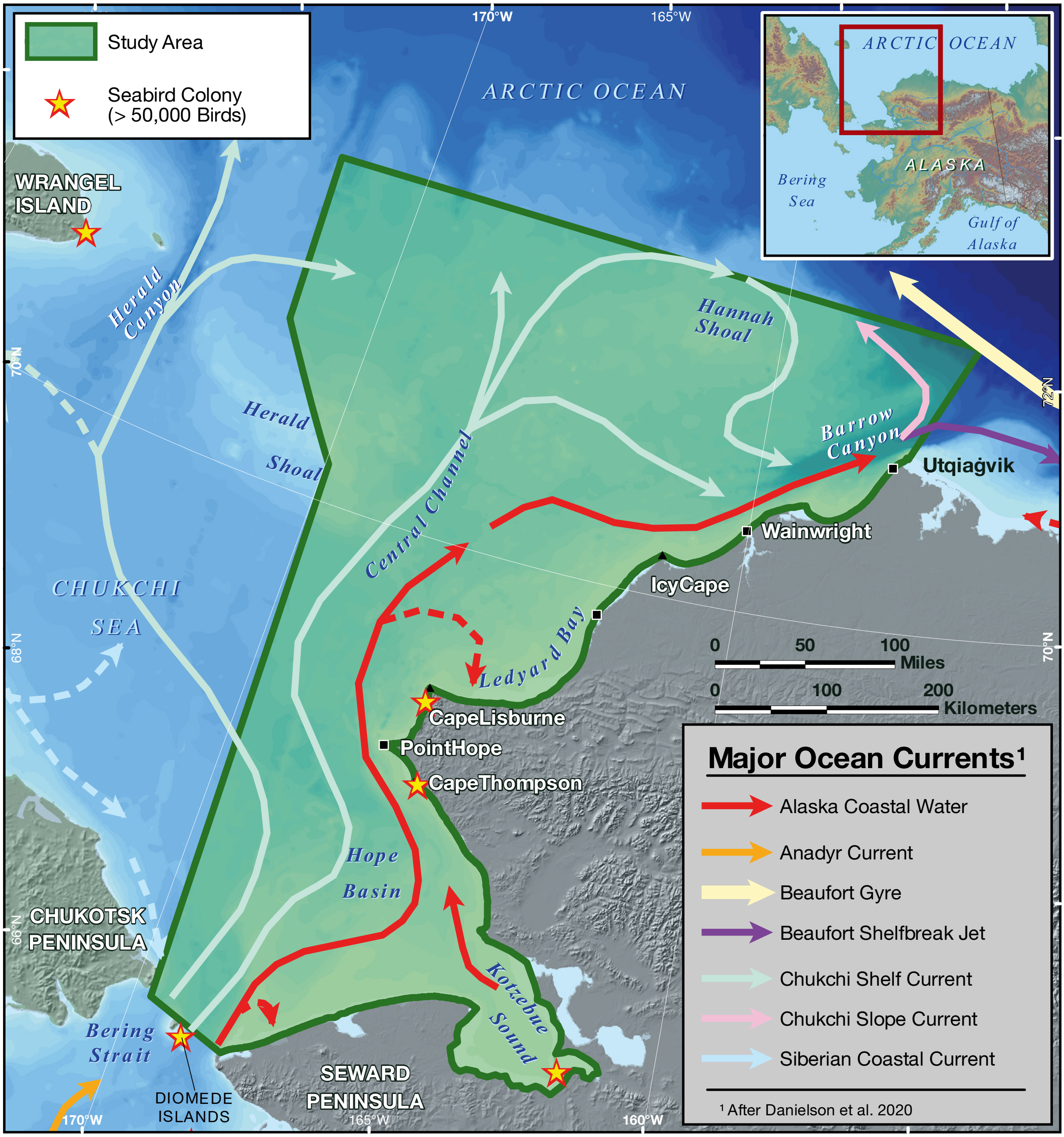

Fig. 1. Chukchi Sea study area (green shading), major water masses (colored arrows), and seabird colonies (stars)

only a few small colonies. In addition, birds migrate to the Chukchi Sea during summer and fall, particularly *Aethia* auklets and short-tailed shearwaters, which numerically dominate the offshore avifauna, and other migrants including alcids, larids, and procellariids (Gall et al. 2013, Kuletz et al. 2015). At-sea observations indicative of migration into the Chukchi are consistent with documented movements of crested auklets *A. cristatella* (Maftei & Russ 2014), thick-billed murres *Uria lumvia* (Takahashi et al. 2021), and short-tailed shearwaters *Ardenna tenuirostris* (Yamamoto et al. 2015).

2.1.3. Seabird prey

Studies in the Chukchi show that seabirds consume a wide variety of invertebrates and fish (Springer et al.

1984, Drummond 2016). Key prey for planktivorous seabirds include large copepods originating in the Arctic, such as *Calanus hyperboreus*, and species advected from the Bering Sea, primarily *C. glacialis*, *C. marshallae*, and *Neocalanus* spp. (Spear et al. 2020, Ashjian et al. 2021). Euphausiids (*Thysanoessa* spp.) are consumed primarily by planktivorous seabirds, but also contribute to the diets of primarily piscivorous seabirds (Hunt et al. 2000, Jones et al. 2014, Drummond 2016). The most common forage fishes in the Chukchi Sea include Arctic cod *Boreogadus saida*, saffron cod *Eleginus gracilis*, Pacific herring *Clupea pallasii*, Arctic sand lance *Ammodytes hexapterus*, capelin *Mallotus villosus*, and recently, juvenile subarctic gadids (primarily walleye pollock *Gadus chalcogrammus* and Pacific cod *G. macrocephalus*) (Levine et al. 2023).

2.2. Data collection

In situ data were collected during the Arctic Ecosystem Integrated Survey (2012, 2013; Mueter et al. 2017) and the Arctic Integrated Ecosystem Research Program (2017, 2019; Baker et al. 2020b), hereafter referred to as 'Chukchi surveys'. Detailed methods of sampling for oceanographic characteristics, zooplankton, and fishes, and results from these studies are available elsewhere (Pinchuk & Eisner 2017, Kimmel et al. 2023, Levine et al. 2023). Because we used a subset of the sampled stations, we present new data summaries (Text S1–S3, Figs. S1–S3 & Table S1 in the Supplement at www.int-res.com/articles/suppl/m14493_supp.pdf) relevant to interpretation of our seabird-focused and station-based models.

2.2.1. Sea surface temperature (SST) and MHW analyses

Remotely sensed oceanographic data were used to characterize broad-scale ocean conditions between the 2 time periods. Base data for the northern Bering, southern Bering, and Chukchi Sea large marine ecosystems (LMEs) were acquired from the NOAA OI SST V2 High Resolution Dataset provided by the NOAA PSL (Huang et al. 2021b). Data consisted of daily maps (lat/long resolution: 0.25°) of SST and % ice cover, which were converted into 2 separate products described below.

LME scale measures were created by first averaging base data across each LME resulting in daily measures of SST and % ice cover from 1981 to 2022. These data were then used to calculate the 30 yr climatology (1982–2011), providing the threshold for MHW classification for each day of the year (details in Text A1) following Hobday et al. (2016). Results from these preliminary analyses of SST and ice anomalies place our study years in context of longer-term conditions (Text A1).

Anomaly and MHW maps were then constructed for the Chukchi LME using SST only by calculating the climatology (Text A1) for each spatial grid cell (resolution: 0.25°) within the Chukchi LME. Cell-specific climatologies were then used to calculate spatially explicit measures of SST anomaly for each day in 2012, 2013, 2017, and 2019, which were then averaged across all days in each year to provide a year-averaged map of SST anomalies. MHW maps were constructed by calculating the number of days where SST exceeded the climatological threshold for MHW conditions on a cell-by-cell basis within each year. These were then mapped as the proportion of MHW days within each year to show the spatial occurrence of MHW conditions. We also examined the Chukchi region average SST through time for each study year to show the progression of temperature changes relative to climatology.

2.2.2. Survey-based data

The Chukchi surveys sampled 240 fixed stations (Fig. 2). During daytime transits between oceanographic stations, 5160 km of seabird surveys and 7107 km of acoustic-trawl fish surveys were conducted (Table 1). Over 90% of the acoustic tracklines occurred in water <60 m deep (Levine et al. 2023). At each station, water temperature and salinity were profiled using a conductivity-temperature-depth (CTD) data logger. To measure chlorophyll *a* (hereafter, chlorophyll), water was sampled from 0 to 50 m or 5 m above bottom, whichever was shallower, and averaged over the water column (mg m^{-3}; see Text S1). Chlorophyll was sampled at fewer stations than the other variables in 2012 and 2013; therefore, we used natural neighbor interpolation to map the chlorophyll values throughout the study area. We then applied the values from the interpolated surface for stations that were missing *in situ* measurements of chlorophyll. Zooplankton samples were collected at each trawl station from surface to near bottom using an oblique bongo tow of a single size or 2 different mesh size nets (Kimmel & Duffy-Anderson 2020) (Text S2 & Fig. S2). Zooplankton were identified to the lowest taxonomic level possible.

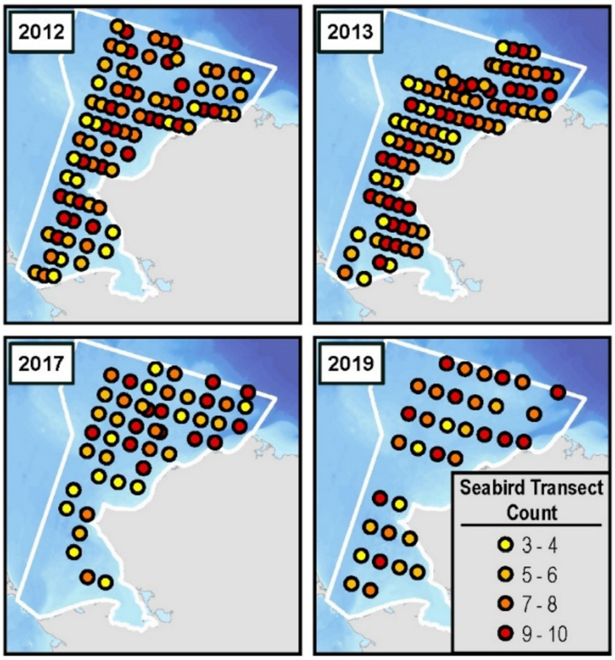

Fig. 2. Seabird survey effort (number of 3 km segments per cell) by year. Circles represent the station locations where water samples, zooplankton, and fish trawls were conducted

The abundance and distribution of pelagic fish along the survey transects were quantified by means of acoustic-trawl surveys (De Robertis et al. 2017, Levine et al. 2023) (Text S3 & Fig. S3). Acoustic data were collected using a calibrated echosounder, and midwater trawl hauls were used to characterize the size and species composition of fish aggregations along the survey trackline.

We conducted seabird surveys when the ship was moving along a straight-line course (speed ≥9 km h^{-1}) using standard protocols (Kuletz et al. 2008). A single observer scanned the water ahead of the ship using binoculars as necessary for identification. Distances of birds from the vessel were estimated using a rangefinder or geometrically marked dowel. We recorded all birds within 300 m of one side of the vessel and in a 90° arc from the centerline of travel. Transect width was occasionally reduced to 200 m or 100 m due to visibility conditions; surveys were discontinued if visibility was <100 m due to fog or seas of Beaufort Scale >6.

We recorded the species, number of birds, and their behavior. Birds on the water or actively foraging were counted continuously, whereas flying birds were recorded during quick 'scans' of the transect window. Scan intervals were based on ship speed and timed for every 300 m to avoid double-counting birds. Based on the transect window surveyed, we calculated density (birds km^{-2}), which we refer to as a measure of abundance. Because we compared observed abundance of birds among years using the same protocol, we assumed no bias in detectability of birds. Observations were recorded along with the ship's position using the program DLog3 (Ford Ecological Consultants, Inc. Portland, OR).

2.3. Data analysis

2.3.1. Oceanographic variables

We initially considered 7 explanatory variables to characterize the oceanographic environment: temperature and salinity in the upper layer (upper 10 m of the water column), temperature and salinity in the bottom layer (bottom 10 m of the water column), temperature and salinity gradients from the upper layer to the bottom layer, and averaged water column chlorophyll concentration (Table 2). Annual means for each variable were calculated by averaging station values within a year. We used variance inflation factor (VIF) values to examine for multicollinearity among predictor variables, and removed correlated predictors from the full set until VIF values across all remaining predictors were <4 (O'Brien 2007). The retained oceanographic predictor variables were temperature and salinity in the upper layer of the water-column, temperature gradient, and integrated water column chlorophyll. We also considered a categorical interaction term (hot or cold) with oceanographic predictors to examine whether covariate effects differed between cool (2012, 2013) and heatwave (2017, 2019) years.

2.3.2. Prey variables

We considered 5 prey variables: large copepods, euphausiids, Arctic cod, walleye pollock (hereafter,

Table 1. Survey effort, dates, and sample sizes for Chukchi Sea surveys

	Year			
	2012	2013	2017	2019
Survey dates	9 Aug – 11 Sep	10 Aug – 8 Sep	1 Aug – 28 Sep	1 Aug – 30 Sep
Number of stations	80	81	45	34
Area surveyed (km^2)	456	446	228	182
Number of 3 km segments	570	621	352	265

Table 2. Variables used to construct the 11 models used to describe distribution of each of 5 seabird foraging guilds. All variables within a category were included together in a model

Category (Code)	Variable	Description
Oceanographic (O)	Upper temperature	Mean water temperature (°C) in upper 10 m of water column, based on CTD cast
	Bottom temperature	Mean water temperature (°C) in bottom 10 m of water column, based on CTD cast
	Temperature gradient	Difference in °C between upper and bottom temperature
	Upper salinity	Mean salinity in upper 10 m of water column, based on CTD cast
	Bottom salinity	Mean salinity in bottom 10 m of water column, based on CTD cast
	Salinity gradient	Difference between upper and bottom salinity
	Chlorophyll *a*	Chlorophyll *a* concentration (natural log transformation; mg m^{-3}), averaged for water column from collected water samples
Prey distribution (P)	Large copepods	Number m^{-3} (natural log transformation)
	Euphausiids	Number m^{-3} (natural log transformation)
	Arctic cod	Number km^{-2} (natural log transformation)
	Walleye pollock	Number km^{-2} (natural log transformation)
	Other fish	Number km^{-2} (natural log transformation)
Geographic (G)	Latitude	Latitude at station center
	Distance to shore	Distance (km) from station center to nearest mainland
Heatwave indicator (HC)	Hot-Cold	Grouped 2012 and 2013 as cold years and 2017 and 2019 as heatwave years.
Interannual variability	Year	2012, 2013, 2017, 2019

pollock), and other forage fishes. Large copepods ($\geqslant$2 mm) were primarily *Calanus* spp. and lower numbers of *Neocalanus* spp.; both groups are common prey items for planktivores (Gall et al. 2006, Guy et al. 2009). Euphausiids are common prey items for crested auklets (Gall et al. 2006, Guy et al. 2009), short-tailed shearwaters (Hunt et al. 2002, Baduini et al. 2006, Nishizawa et al. 2017), and sometimes thick-billed murres (Renner et al. 2012, Jones et al. 2014). Estimating abundance of euphausiids is challenging; they are difficult to detect via acoustics when large fractions of the water column are occupied by fish (De Robertis et al. 2017) and they are capable of net avoidance (Hunt et al. 2016, Spear et al. 2020). Nonetheless, the combined counts of 3 life stages (furcilia, juveniles, and adults) serve as an index of relative euphausiid abundance (Kimmel & Duffy-Anderson 2020, Spear et al. 2020).

Six species of fish were sufficiently abundant to estimate via acoustic-trawl methods (De Robertis et al. 2017, Levine et al. 2023): Pacific herring, Pacific capelin, saffron cod, Arctic cod, juvenile Pacific cod, and juvenile pollock. To ensure prey variables were representative of fish that could be consumed by seabirds, we included fish $\leqslant$15.5 cm in length, which Springer et al. (1984) identified as the upper limit for nearly all samples obtained for kittiwakes and murres breeding at 2 Chukchi colonies. This size range also comprised ~99% of all fish found during our study (DeRobertis et al. 2017, Levine et al. 2023) (Table S1). Because of their numerical dominance, Arctic cod and pollock were considered as independent prey items, while the remaining less abundant forage fish species (herring, capelin, saffron cod, Pacific cod), were combined into a single category of 'other fish'. Although Arctic sand lance are consumed by seabirds, the lack of a swim bladder makes them difficult to survey using acoustics when fish with swim bladders are also present (De Robertis et al. 2017), so they were not included.

2.3.3. Seabird community analyses

We used seabird survey transects of ca. 3 km sampling units (segments) for analysis. The total area surveyed for a segment was adjusted by transect width assigned at the time of survey (in 100 m increments to 300 m). Densities (birds km^{-2}) were calculated for each species in each 3 km segment based on the adjusted area. We limited seabird community analysis to species that forage in the marine environment: *Phalaropus* (phalaropes), Stercorariidae (jaegers), Alcidae (auks), Laridae (gulls, terns), Gaviidae (loons), and Procellariidae (fulmars, shearwaters), and marine species of Anatidae (eiders, scoters, other sea ducks). We retained all marine bird species in estimates of species richness and diversity. In other analyses, we omitted Anatidae spp. because they had very low encounter rates offshore and because we did not have corresponding prey data for benthic-feeding Anatidae.

While most seabirds can switch prey taxa to some degree within or among seasons, we grouped species into foraging guilds that represented a combination of their primary prey and foraging behavior: surface-feeding planktivores (phalaropes), surface-feeding piscivores (jaegers, larids, and fulmars), diving planktivores (auklets, family Alcidae), diving piscivores (other Alcidae and loons), and short-tailed shearwaters (hereafter, shearwaters). Shearwaters feed primarily on large zooplankton, but consume a variety of other invertebrates and fish, and forage by surface-seizing and diving (Hunt et al. 2002, Baduini et al. 2006, Berlincourt et al. 2015). We made shearwaters a singular foraging guild because of their flexible diet and foraging behavior and because their large numbers numerically eclipse other species (Kuletz et al. 2015, Gall et al. 2017).

We used segments as the basic sampling unit and computed species richness (total number of species) and Shannon diversity indices to compare among years (Chao et al. 2014). To account for the differences in sampling effort among years, we created rarefaction curves by plotting species richness and diversity indices for a randomized selection of 3 km segments in each year. We made 200 random draws at each interval and then used quantiles to calculate 95% confidence intervals. When calculating the number of species present, we only included higher-order taxa not identified to species when no lower-order taxa were identified in any segments within a year. When calculating diversity indices, birds identified to genus were apportioned to species based on the proportion of birds identified to species in the field. We used the package 'vegan' v.2.5−7 (Oksanen et al. 2020) in R (R Core Team 2020) for community analyses and the packages 'vegan' and 'ggplot2' (Wickham 2016) for visualizations.

2.3.4. Models: factors influencing seabird distribution and abundance

We used oceanographic sampling stations (Fig. 2, Table 1) and associated waters defined by a 15 km buffer radius around each station center as the basic unit for analysis of distribution and abundance of seabird foraging guilds (N = 240). We selected only stations where data on water temperature, salinity, and zooplankton were collected within 3 km and 48 h of one another, and that had a minimum of 9 km of transect sampling for fish and birds conducted within 15 km and 48 h of the oceanographic sampling. Although most seabird surveys were done on the same transit routes as the fish sampling, the timing and extent of sampling varied due to seabird surveys requiring acceptable daylight and sea conditions.

We used generalized additive models (GAMs) to examine the distribution of seabirds near sampling stations using the 'mgcv' package in R (Wood 2017). The count of birds for each foraging guild that were observed at a station was the response variable and the natural logarithm of total area searched at each station was included as an offset term for sampling effort. We modeled the seabird numbers using a negative binomial distribution to account for overdispersion in the numbers of birds observed at different stations.

We used a natural logarithm transformation for chlorophyll and fish density to account for skewed distributions with a few high values. Two guilds had 1 large outlier (2−5 times greater than the second highest value) in seabird density; these anomalously high seabird numbers were set to equal the density of the second highest density value, so that they were not overly influential in the GAM results.

We used a model-selection process to examine a suite of factors representing the physical and biological environment. We compared 4 categories of models (geographic, oceanographic, prey, and oceanographic plus prey) for each foraging guild.

The geographic models included the variables latitude and distance to shore. The oceanographic models included the variables upper layer temperature, upper layer salinity, temperature gradient, and integrated chlorophyll concentration. The prey distribution models included the variables large copepods, euphausiids, pollock, Arctic cod, and other forage fish. However, because large copepods and pollock densities were highly correlated (correlation coefficients >0.60), we did not include both variables in the same model. To use the most likely potential prey for each guild, we included the large copepods variable for the 2 planktivore guilds and shearwaters, and the pollock variable for the 2 piscivore guilds.

All models were run with and without the heatwave indicator (a variable termed 'hot-cold'), which grouped 2012 and 2013 as cold years and 2017 and 2019 as heatwave years. When the hot-cold variable was included, each variable was allowed to have different relationships with seabird densities for hot and cold years. For the oceanographic plus prey models, we considered 6 models by including the hot-cold variable for just oceanographic, just prey, and for both.

This resulted in a total of 11 models for each foraging guild (2 geographic models, 2 oceanographic models, 2 prey distribution models, 4 oceanographic plus prey models, and a null model with only year).

All models included year as a factor to account for interannual differences in seabird densities in some foraging guilds. Therefore, our model selection process tested whether seabird distribution over a 4 yr period could best be explained by geographic location, oceanographic variables, the distribution of different prey species, or a combination of oceanographic and prey distribution.

For each of the 11 models in the candidate model set, we ran the model using the option that adds an extra penalty so that individual terms can be penalized to zero (Marra & Wood 2011). With this option, the smoothing parameter estimation conducted during the model fitting process removed variables from the model if there was not adequate support for that variable. We then used Akaike's information criterion (AIC) to select the best model from the candidate model set (Burnham & Anderson 2002). The difference in AIC relative to the model with the lowest AIC (ΔAIC) and the probability that a model was the best model in the candidate set (Akaike weights; ω_i) were used to infer support for candidate models (Burnham & Anderson 2002). Models with $\Delta AIC < 2$ were considered well-supported by the data. We assessed model fit using the proportion of deviance explained (Pedersen et al. 2019). We evaluated the parameter estimates from the best-supported model, to identify which factors influenced seabird distribution and abundance and visualized the factors by plotting the fitted partial effects of covariates along with their 95% confidence intervals.

All data processing, analysis, and statistical tests were performed in R version 4.0.3 (R Core Team 2020), with values considered significant at $p < 0.05$. Means are presented ± standard error (SE), unless otherwise noted. Maps were created using ArcGIS v. 10.8, and other figures were produced using package 'ggplot2' (Wickham 2016) in R.

3. RESULTS

3.1. Oceanographic and prey conditions

3.1.1. Ocean climate during the two study periods

The occurrence of MHWs in the Chukchi Sea exhibited similar patterns as the southern and northern Bering Sea between 2000 and 2022, albeit of shorter duration within years (Text A1 & Fig. A1 in the appendix). MHW conditions (>6 d with SSTs >1.5°C above climatology) were prevalent from 2015 through 2020, with 34% of days exceeding MHW thresholds during this period (Fig. A1). The most prolonged and intense MHW episode during this time occurred in 2019, peaking at 3.4°C above climatology, and lasting 6 mo, from mid-June to December (Fig. 3A). No large-scale MHWs were evident in 2012 or 2013. Low ice cover anomalies in the Chukchi Sea were not exhibited in 2012 or 2013, but were evident for all years from 2014 to 2020 (Fig. A1).

SSTs displayed marked differences between the periods 2012–2013 and 2017–2019 (Fig. 3). Averaged across the Chukchi Sea, SST was near the climatological average (1982–2011) in 2012 and 2013, at no time exceeding the threshold for MHW identification (90th percentile of SST observed over the 30 yr baseline period; Fig. 3A). In contrast, SST in 2017 and 2019 was elevated year-round, exceeding MHW thresholds for 109 d in 2017 and 165 d in 2019 (Fig. 3A). MHW intensity reached maximums of 2.4 and 3.4°C above the climatological mean in 2017 and 2019, respectively, with both maximums occurring in early to late August (Fig. 3A). During the years sampled, the seasonal pattern of SST also varied between cool years and heatwave years; cool years exhibited a plateau of high SSTs (still lower than heatwave years) from late July to early September, whereas during heatwave years, SST increased towards a single peak in mid-August, and then declined steadily from late August through September (Fig. 3A). Thus, our on-site measurements were taken during peak temperatures of each cool year, but a portion of SST measurements during heatwave years occurred after peak SSTs in the Chukchi region.

When viewed across the Chukchi Sea, cooler than average SST was prevalent in 2012, with moderately elevated SST in 2013 north of the Bering Strait (Fig. 3B). In 2017 and 2019, elevated SST was prevalent throughout the Chukchi Sea, with year-averaged SST anomalies exceeding +1°C across 32% (n = 2002 grid cells) and 66% of the Chukchi in 2017 and 2019, respectively (Fig. 3B). Highest SST anomalies and prevalence of MHW conditions were concentrated in the northern and eastern portion of the study area, with cooler less anomalous conditions to the west (Fig. 3C).

3.1.2. In situ oceanographic conditions

During the Chukchi surveys, average ocean temperatures in the upper layer (upper 10 m) were similar

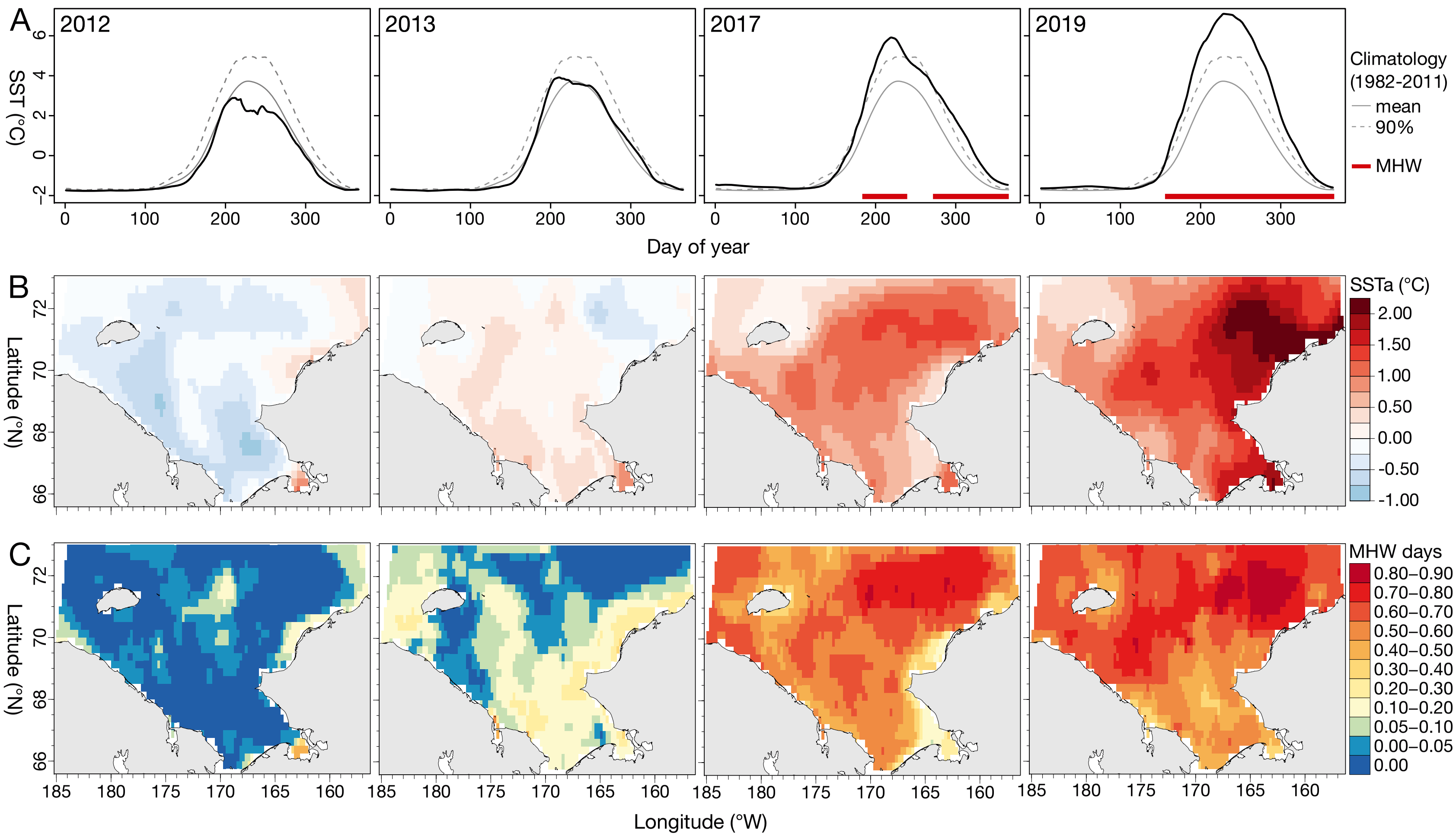

Fig. 3. Sea surface temperature (SST) conditions and marine heatwave (MHW) occurrence in the Chukchi Sea across the 4 study years. (A) Mean daily SST for each study year (solid black line) with the 30 yr (1982–2011) long-term climatological mean (grey line) and 90th percentile of SST (dashed grey line). Periods where SST exceeded the MHW threshold (90th percentile) are indicated by horizontal red bars along the *x*-axis. Heatmaps show (B) year-averaged SST anomaly (SSTa, i.e. SST minus the long-term climatological mean) and (C) the proportion of MHW days (proportion of days where SST exceeded MHW thresholds) per grid cell, as an illustration of the spatial extent and organization of anomalous SST conditions

during the 2 cool years and in 2017 (5.5–6.0°C) but averaged 7.9°C in 2019 (Table 3). Bottom layer temperatures were ~3–4°C in all years except 2013 when they were >1°C cooler (Table 3). The temperature gradient between the upper and lower layers ranged from 2.4 to 4.2°C and was greatest in 2019 (Table 3). Upper layer temperatures were much cooler in the northern than the southern Chukchi region during cool years, but were uniformly high throughout the Chukchi Sea during heatwave years (Fig. S1A). Annual mean salinity in the upper layer ranged from 29.8 in 2013 to 31.2 in 2017 (Table 3). Mean bottom layer salinity was similar across years (Fig. S1B). Upper layer salinity values show fresher waters concentrated in the northern Chukchi during cool years, whereas higher salinities occurred throughout the northern Chukchi during heatwave years (Fig. S1C). Bottom layer salinity was more uniform throughout the study area except in 2012, when fresher water predominated in nearshore waters (Fig. S1D).

Mean integrated water column chlorophyll was lowest during cool years (Table 3), particularly in the northern Chukchi and offshore, with the exception of stations off Cape Thompson in 2013 (Fig. S1E). During heatwave years, moderate to high chlorophyll levels (0.5–3.0 mg m^{-3}) were detected throughout the region, with a few higher values (>5 mg m^{-3}) observed in the northern Chukchi (Fig. S1E).

3.1.3. Prey conditions

Large copepods were more abundant during cool years, averaging >4 times the abundance recorded during heatwave years (Table 3). Large copepods were dispersed throughout the Chukchi Sea during cool years, and were nearly absent during the heatwave years, except at a few stations in the northern Chukchi (Fig. S2A). Euphausiids were also more abundant during cool years, with 2017 having the lowest abundance (Table 3). During cool years, euphausiids were abundant in the southern Chukchi and extended offshore as far as 70° N. During heatwave years, euphausiid abundances were low and they were found at fewer stations, mainly in the southern Chukchi (Fig. S2B).

There were clear shifts in forage fish species composition, distribution, and abundance during the study. Arctic cod was the most abundant forage fish in all years, with highest abundance in 2017 and lowest abundance in 2012 (Table 3). During all years, Arctic cod were primarily observed in the northern Chukchi, although they extended into the southern Chukchi during cool years (Fig. S3A). Pollock were extremely rare during cool years, but during heatwave years, they were widespread and were the second most abundant fish (Fig. S3B). Pollock exhibited the highest densities in 2017 and comprised a high proportion (30%) of forage fish in 2019 (Table 3). The group des-

Table 3. Mean (SE) of variables measured at oceanographic stations during Chukchi Sea surveys

Model variable	2012	2013	2017	2019
Oceanographic				
Upper temperature (°C)	5.96 (2.65)	5.74 (3.10)	5.59 (1.10)	7.95 (1.82)
Bottom temperature (°C)	3.05 (3.65)	1.93 (3.33)	3.22 (2.05)	3.75 (3.53)
Temperature gradient	2.91 (1.88)	3.81 (1.44)	2.36 (1.57)	4.20 (2.41)
Upper salinity	30.15 (1.53)	29.75 (1.73)	31.22 (1.04)	30.00 (1.25)
Bottom salinity	31.97 (1.32)	32.07 (0.74)	32.29 (0.48)	32.19 (0.88)
Salinity gradient	−1.82 (1.67)	−2.32 (1.92)	−1.07 (1.25)	−2.19 (1.29)
Chlorophyll *a* (mg m^{-3})	0.81 (0.45)	0.93 (1.11)	1.37 (0.58)	1.52 (1.77)
Prey				
Large copepods (no. m^{-3})	2.79 (0.97)	2.42 (0.93)	0.53 (0.72)	0.61 (0.46)
Euphausiids (no. m^{-3})	0.64 (0.73)	0.36 (0.48)	0.12 (0.18)	0.26 (0.38)
Arctic cod (no. km^{-2})	348 700 (934 504)	1 698 387 (3 321 326)	4 150 035 (2 779 278)	494 900 (769 175)
Walleye pollock (no. km^{-2})	2837 (14 498)	2.2 (19.9)	1 227 928 (782 534)	228 057 (363 483)
Other fish (no. km^{-2})	17 550 (41 817)	71 771 (178 587)	132 672 (393 714)	40 759 (78 508)
Total fish (no. km^{-2})	369 086 (930 120)	1 770 161 (3 299 928)	5 510 635 (3 210 645)	763 717 (924 203)
Foraging guild (birds km^{-2})				
Surface-feeding planktivore	0.15 (0.55)	0.56 (1.55)	1.35 (4.51)	1.02 (3.33)
Surface-feeding piscivore	0.37 (0.66)	0.40 (0.73)	1.11 (3.04)	0.95 (0.99)
Diving planktivore	1.51 (3.27)	1.07 (2.07)	3.11 (7.43)	0.32 (0.80)
Diving piscivore	0.80 (1.58)	0.44 (1.05)	0.35 (0.57)	0.23 (0.45)
Shearwater	0.10 (0.46)	2.42 (11.62)	19.50 (49.89)	7.21 (18.39)

ignated 'other fish' was also most abundant in 2017 (Table 3); they were widespread offshore in 2012, but more nearshore in 2013 (Fig. S3C). This group was evenly distributed across the shelf in 2017 and patchily distributed in 2019.

3.2. Seabird community

3.2.1. Species richness and diversity

Species richness of seabirds was higher during heatwave years, compared to cool years, with 2019 exhibiting the highest richness (Fig. 4A). In contrast, species diversity was lower during heatwave years (Fig. 4B), when 77% of the seabird community was composed of shearwaters (for 2017 and 2019 combined). During heatwave years, species richness curves did not reach their asymptotes, indicating that the ca. 24 estimated species was conservative. Four seabird species were observed exclusively during cool years: red-necked phalarope *Phalaropus lobatus* (surface-feeding planktivore), Sabine's gull *Xema sabini* (surface-feeding omnivore), Arctic tern *Sterna paradisaea* (surface-feeding piscivore), and pigeon guillemot *Cepphus columba* (diving piscivore). Six species were observed exclusively during heatwave years: 3 benthivores — spectacled eider *Somateria fischeri*, king eider *S. spectabilis*, and long-tailed duck *Clangula hyemalis*; 3 diving piscivores — Pacific loon *Gavia pacifica*, common loon *G. immer*, and ancient murrelet *Synthliboramphus antiquus* (Table 4).

3.2.2. Species composition and abundance

Both species composition and abundance changed dramatically among years, primarily due to high densities of shearwaters in 2017, and to a lesser extent in 2019 (Fig. 5). Total seabird abundance was low during cool years (average <5 birds km^{-2}) and was numerically dominated by diving planktivores in 2012, with a moderate influx of shearwaters in 2013, which comprised nearly half of total birds that year (Table 3, Fig. 5). Shearwaters were abundant in 2017, averaging >18 birds km^{-2} across the study area (Fig. 5). The density (Table 3) and proportion (Fig. 5) of diving planktivores also greatly increased in 2017, driven primarily by high densities of crested auklets (>5 birds km^{-2}; Table 4).

Both surface planktivores and surface piscivores increased during heatwave years, but their respective overall densities each remained ~1 bird km^{-2}. Diving planktivores, which peaked in 2017, were nearly absent from the Chukchi in 2019 (Fig. 5), although the parakeet auklet *A. psittacula* increased in abundance that year (Table 4). Diving piscivores, already low at a mean of 0.6 birds km^{-2} during cool years, decreased by half during heatwave years (Table 3).

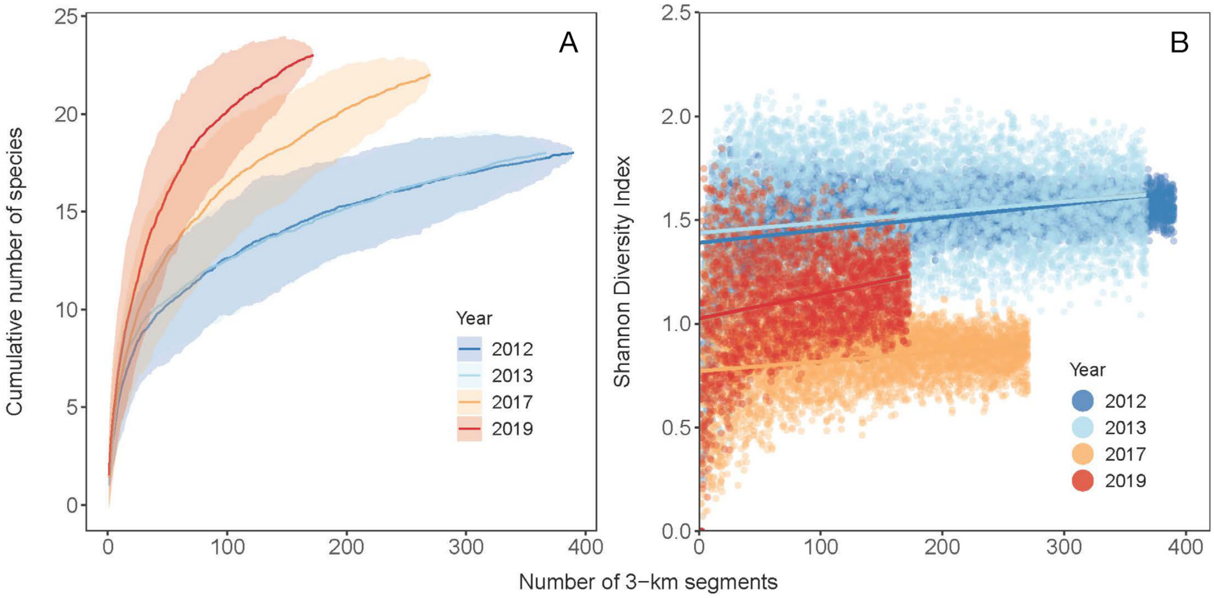

Fig. 4. Species (A) richness and (B) diversity (Shannon) rarefaction curves, using random draws from all 3 km transect segments during Chukchi seabird surveys. Annual values were from 2012 and 2013 (cool years) and 2017 and 2019 (heatwave years). Values for 2012 and 2013 species richness are closely aligned

Table 4. Mean (SE) densities (birds km^{-2}) of species encountered during Chukchi Sea surveys, organized by foraging guild. Symbols after English names indicate whether the species is a potential local breeder (*), breeds in northern Bering Sea, but a non- or post-breeder in the Chukchi Sea (**), breeds in Alaska outside of the Chukchi coast and is non- or post-breeding (+), or a non-breeding long-distant migrant (++)

Foraging guild	English name	Scientific name	2012	2013	2017	2019
Benthic feeders	Spectacled eider +	*Somateria fischeri*	0	0	0.033 (0.03)	0
	King eider +	*Somateria spectabilis*	0	0	0	0.013 (0.013)
	Unidentified eider +	*Polysticta* or *Somateria* sp.	0	0	0.035 (0.035)	0.004 (0.004)
	Long-tailed duck +	*Clangula hyemalis*	0	0	0.005 (0.005)	0
Surface-feeding planktivores	Red-necked phalarope +	*Phalaropus lobatus*	0	0.005 (0.005)	0	0
	Red phalarope +	*Phalaropus fulicarius*	0.022 (0.018)	0.066 (0.026)	0	0.922 (0.399)
	Unidentified phalarope +	*Phalaropus* sp.	0.128 (0.065)	0.471 (0.131)	0.936 (0.376)	0.069 (0.041)
Surface-feeding piscivores	Pomarine jaeger *	*Stercorarius pomarinus*	0.004 (0.003)	0.002 (0.002)	0.019 (0.014)	0.025 (0.015)
	Parasitic jaeger *	*Stercorarius parasiticus*	0.010 (0.004)	0	0.003 (0.003)	0.017 (0.009)
	Unidentified jaeger *	*Stercorarius* sp.	0	0.002 (0.002)	0.011 (0.007)	0.009 (0.006)
	Black-leggedlKittiwake *	*Rissa tridactyla*	0.285 (0.059)	0.282 (0.062)	0.775 (0.171)	0.454 (0.063)
	Sabine's gull +	*Xema sabini*	0.002 (0.002)	0.002 (0.002)	0	0
	Glaucous gull *	*Larus hyperboreus*	0.006 (0.003)	0.005 (0.003)	0.033 (0.012)	0.149 (0.049)
	Unidentified Laridae *		0.004 (0.003)	0	0.014 (0.009)	0
	Arctic tern *	*Sterna paradisaea*	0	0.007 (0.006)	0	0
	Northern fulmar **	*Fulmarus glacialis*	0.047 (0.012)	0.094 (0.019)	0.182 (0.044)	0.142 (0.052)
Diving planktivores	Parakeet auklet *	*Aethia psittacula*	0	0.011 (0.007)	0.007 (0.007)	0.125 (0.054)
	Least auklet **	*Aethia pusilla*	0.204 (0.040)	0.151 (0.044)	0.230 (0.067)	0.070 (0.054)
	Crested auklet **	*Aethia cristatella*	1.392 (0.233)	0.770 (0.138)	5.744 (2.165)	0.090 (0.028)
	Unidentified auklet **	*Aethia* sp.	0.022 (0.011)	0.012 (0.005)	0.051 (0.024)	0.025 (0.019)
Diving piscivores	Common murre *	*Uria aalge*	0.158 (0.029)	0.040 (0.014)	0.061 (0.026)	0.009 (0.006)
	Thick-billed murre *	*Uria lomvia*	0.036 (0.011)	0.179 (0.034)	0.057 (0.020)	0.043 (0.017)
	Unidentified murre *	*Uria* sp.	0.663 (0.141)	0.220 (0.083)	0.094 (0.027)	0.043 (0.021)
	Pigeon guillemot *	*Cepphus columba*	0.002 (0.002)	0	0	0
	Kittlitz's murrelet +	*Brachyramphus brevirostris*	0.003 (0.003)	0	0.003 (0.003)	0
	Ancient murrelet +	*Synthliboramphus antiquus*	0	0	0.074 (0.034)	0.066 (0.043)
	Unidentified murrelet +	*Brachyramphus* sp.	0.006 (0.003)	0.005 (0.004)	0	0.004 (0.004)
	Horned puffin *	*Fratercula corniculata*	0.011 (0.009)	0.004 (0.004)	0.007 (0.005)	0.004 (0.004)
	Tufted puffin *	*Fratercula cirrhata*	0.002 (0.002)	0	0	0.009 (0.006)
	Pacific loon +	*Gavia pacifica*	0	0	0.006 (0.006)	0.039 (0.021)
	Common loon +	*Gavia immer*	0	0	0.006 (0.005)	0.009 (0.006)
	Unidentified loon +	*Gavia* sp.	0	0	0.019 (0.009)	0.009 (0.006)
Shearwaters	Short-tailed shearwater ++	*Ardenna tenuirostris*	0.078 (0.031)	1.995 (0.741)	18.186 (4.354)	5.370 (1.282)
	Unidentified *Ardenna* spp.++		0	0	0.010 (0.010)	0

3.2.3. Distribution of seabird foraging guilds

Surface planktivores were most abundant in the central Chukchi Sea in 2013 and farther north over Hanna Shoal in 2017, but were concentrated in the southern Chukchi (south of Point Hope) in 2019 (Fig. 6A). Surface piscivores were the most widely dispersed of the seabird guilds, with generally higher densities in the southern Chukchi in all years (Fig. 6B). During heatwave years, there were aggregations of surface piscivores off Cape Lisburne, with more northerly distributions in 2019. Diving planktivores were offshore in the region of the Central Channel (between ~70 and 71° N) during cool years, and were highly aggregated farther north (between ~71 and 72.5° N) in 2017; they were sparse and mainly confined to the northern Chukchi in 2019 (Fig. 6C). During cool years, diving piscivores aggregated offshore between Cape Thompson and Cape Lisburne (seabird colony sites) as far as 71° N, but during heatwave years, densities were lower and farther north, with few aggregations near the colonies (Fig. 6D). Shearwater densities were low and scattered in 2012, and in 2013 were mainly aggregated on the northern Chukchi Shelf (Fig. 6E). During heatwave years, shearwaters extended broadly across the northern shelf in 2017 but were more evenly dispersed and southerly in 2019, with highest densities throughout the western edge of the study area.

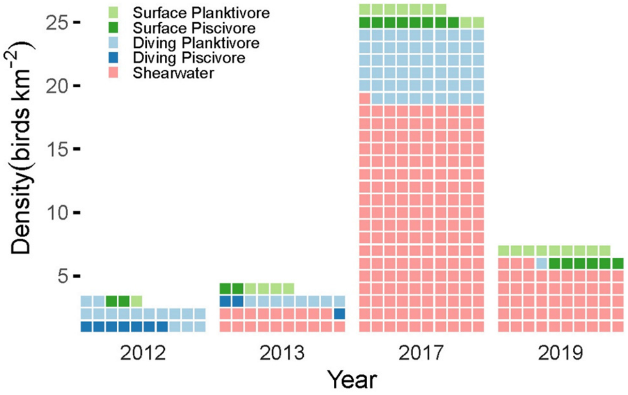

Fig. 5. Seabird community composition for 2 cool years (2012, 2013) and 2 heatwave years (2017, 2019) in the Chukchi Sea during seabird surveys. Seabirds were grouped by foraging guild (Table 4, excluding benthivores). Each square represents a density of 0.1 bird km^{-2}

3.3. Seabird response to environmental and prey variables

3.3.1. GAMs

The best models for seabird foraging guild distribution performed well for diving piscivores and shearwaters, with 62 and 60% of deviation explained for those guilds, respectively; in both cases, only a single candidate model was selected (Table 5). The models also performed moderately well for diving planktivores (42% deviance explained) and surface piscivores (34% deviance explained).

Models for surface planktivores had low explanatory power (17% deviance explained), with no single model being unequivocally supported based on AIC (5 models with ΔAIC < 2; Table 5). However, all 5 models with ΔAIC < 2 contained prey predictors, indicating that prey abundance was likely the primary factor influencing surface planktivore density of those considered. These results also suggest that despite being included in the highest ranked model, oceanographic factors were only weakly associated with surface planktivore density (Table 5). This conclusion was further supported by a non-significant ($\alpha = 0.05$) likelihood ratio test result between the highest-ranked prey (P), oceanographic (O) (hot-cold, HC) model and the second-best P, O model (df = 1.03, deviance = 1.84, p = 0.1812), suggesting that there is insufficient evidence in favor of the more complex model over the simpler P model. While we present fitted relationships for the highest-ranked (based on AIC) P, O (HC) model, we acknowledge that prey factors were primary and that model uncertainty is high for this group, such that the model results should be interpreted with caution.

For the other foraging guilds, the candidate models with lowest AIC included the heatwave indicator (HC variable) for at least 1 of the variable suites, underscoring that seabird relationships to covariates often differed during cool vs. heatwave years. With the exception of shearwaters, the highest-ranked models for these foraging guilds included prey and oceanographic variables in addition to the heatwave indicator as an interaction term with one or both main effects. For shearwaters, the model containing geographic variables (latitude and distance from shore) as an interaction term with the heatwave indicator performed best.

3.3.2. Seabird guild response to variables

Surface planktivores showed no relationship with copepods or euphausiids (Fig. 7B,D), but they were associated with low Arctic cod abundance during both cool and heatwave years (Fig. 7F). They favored

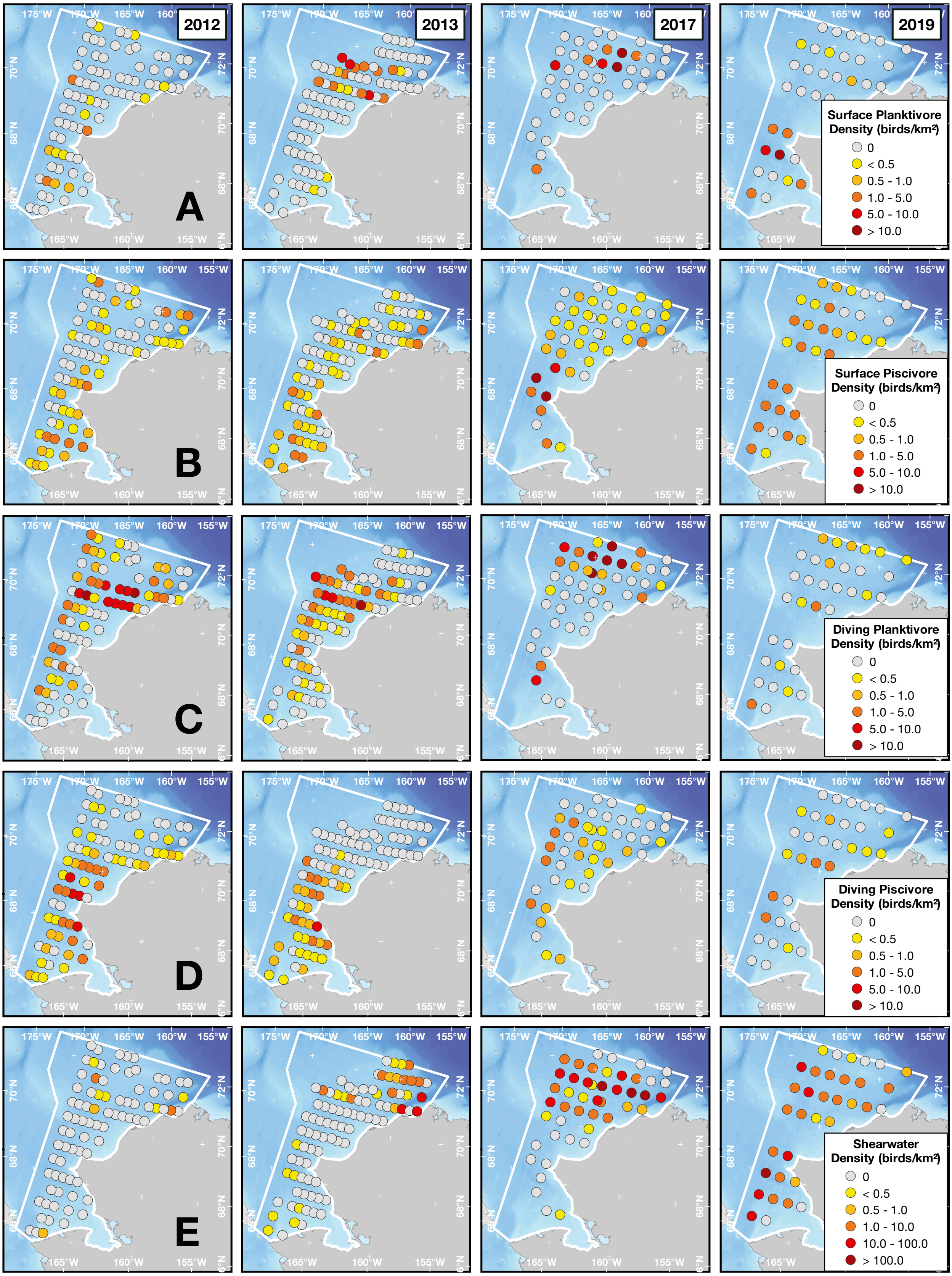

Fig. 6. Distribution of seabird foraging guilds during Chukchi surveys, by year. Circles indicate sampling stations; seabird densities (birds km^{-2}) were calculated from all 3 km segments within a 15 km radius of each station center. Columns are years. Rows are by foraging guild: (A) surface planktivores, (B) surface piscivores, (C) diving planktivores, (D) diving piscivores, (E) shearwaters

Table 5. Models with ΔAIC < 2.0 for each foraging guild for generalized additive models of seabird distribution in the Chukchi Sea 2012, 2013, 2017, and 2019. P: prey variables; O: oceanographic variables; G: geographic variables; HC: hot and cold years (a categorical heatwave indicator)

Foraging guild	Model	AIC	ΔAIC	Akaike weights (ωi)	Deviance explained
Surface-feeding planktivores	P, O (HC)	582.211	0	0.253	0.17
	P, O	582.387	0.176	0.232	0.16
	P	582.877	0.666	0.181	0.14
	P (HC), O	583.639	1.427	0.124	0.18
	P (HC)	583.924	1.7130	0.108	0.15
Surface-feeding piscivores	P, O (HC)	951.0632	0	0.4198	0.34
	G (HC)	951.487	0.424	0.339	0.33
	P (HC), O (HC)	952.267	1.204	0.230	0.34
Diving planktivores	P, O (HC)	1095.385	0	0.659	0.42
	P (HC), O (HC)	1096.718	1.333	0.339	0.42
Diving piscivores	P (HC), O (HC)	777.136	0	0.980	0.62
Shearwaters	G (HC)	982.237	0	0.988	0.60

low upper temperatures during cool years (Fig. 7A), whereas during heatwave years, they were associated with areas of high salinity (Fig. 7C). However, models for this foraging guild explained little deviance, and results for these relationships may be spurious. Surface piscivores had positive associations with pollock and other fish during both cool and heatwave years (Fig. 8F,H) but a negative response to Arctic cod abundance (Fig. 8D). During heatwave years, surface piscivores were associated with low temperature gradients (Fig. 8E) and upper salinity near 31 (Fig. 8C).

Diving planktivores were associated with higher abundances of Arctic cod (Fig. 9F), but with lower abundance of other fish (Fig. 9H). During heatwave years, they were found within narrow ranges of upper layer temperature (Fig. 9A; ~3°C) and high salinity (Fig. 9C; >31) and sites with little or no temperature gradient (Fig. 9E). They were associated with low chlorophyll only during heatwave years (Fig. 9G). Diving piscivores were associated with high abundances of other fish during cool years, but this relationship was not evident during heatwave years (Fig. 10H), when they were only weakly associated with low abundance of Arctic cod (Fig. 10D). Compared to other guilds, diving piscivores had the most consistent and positive association with oceanographic variables (Table 6) and were found where upper layer temperatures and salinity were higher (Fig. 10A,C), and to lesser extent, with higher chlorophyll (Fig. 10G).

Shearwaters, described best by geographic variables, were most abundant at the southern and northernmost latitudes of the study area (Fig. 11A), and during cool years tended to be >200 km offshore, but were widespread during heatwave years (Fig. 11B). Models including oceanographic or prey variables were not supported by the data.

In summary, seabird response was often not intuitive with respect to primary prey type. For example, the planktivorous guild did not show a positive response to copepods or euphausiids, nor did either of the piscivorous guilds have a positive response to Arctic cod abundance. Overall, fitted relationships (Table 6, Figs. 7–11) indicated that seabirds for which oceanographic and prey variables were important more often showed a functional response to upper layer temperature or salinity (and less so to chlorophyll), Arctic cod, and other fish. In most cases, seabird response was weak or non-existent for temperature gradient (except for diving planktivores), copepods, euphausiids, or pollock (except for surface piscivores).

4. DISCUSSION

We examined the seabird community response to a period with multiple MHW events in the eastern Chukchi Sea, utilizing concurrent data on oceanographic conditions, primary production, and prey distribution. We provide a conceptual framework (Fig. 12) by which to examine how a prolonged series of MHW events in the Pacific Arctic could affect seabird populations in the Chukchi Sea. The Chukchi region has been warming for decades (Stabeno & Bell 2019, Danielson et al. 2020) and recently has shown evidence of 'borealization' in both lower and upper

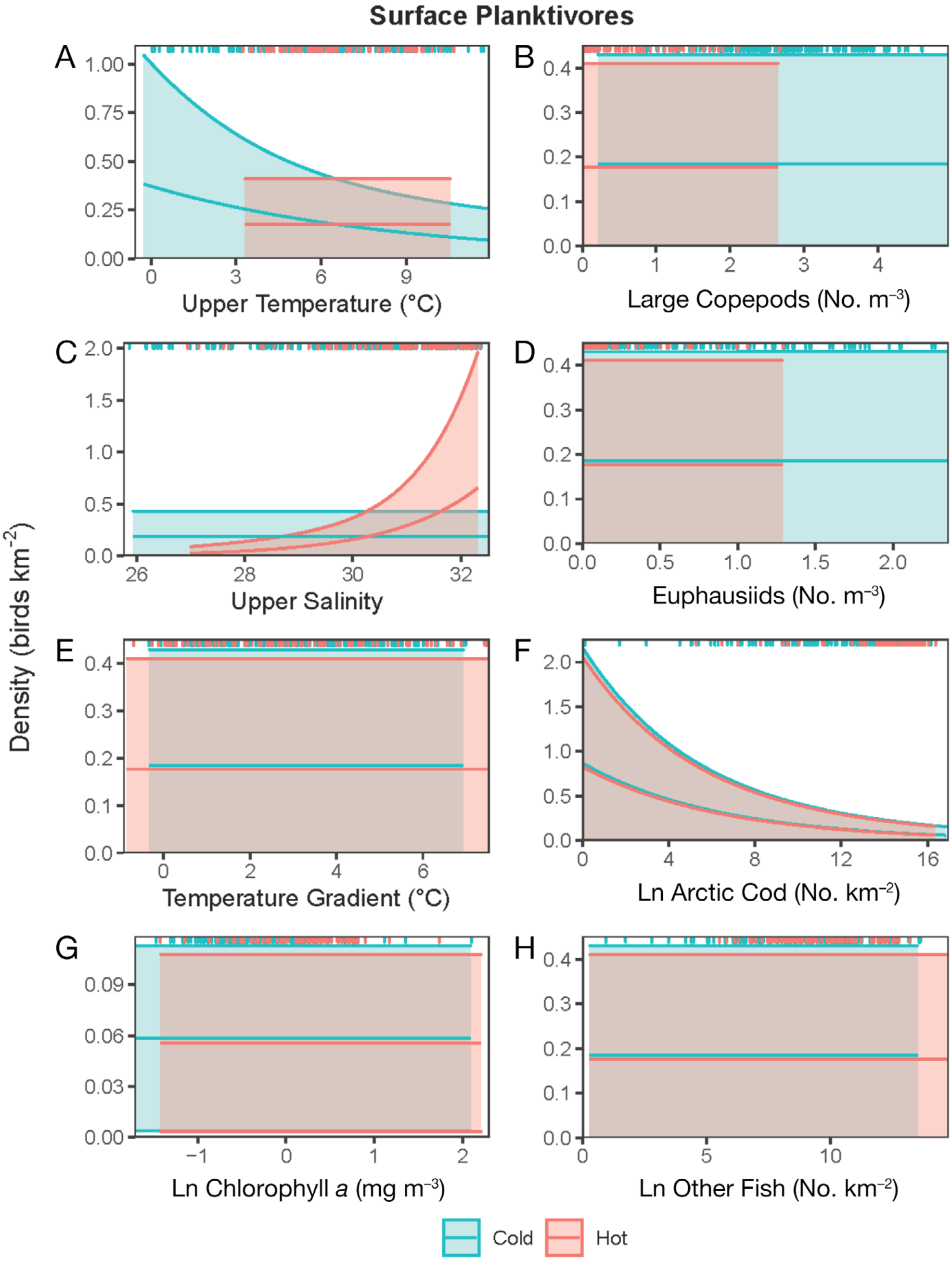

Fig. 7. Fitted partial effects of covariates for abundance of surface-feeding planktivorous seabirds during cool years (2012, 2013; blues) and heatwave years (2017, 2019; reds). The middle solid line indicates estimated value and shading indicates 95% CI. See Table 6 for model results

trophic levels (Mueter et al. 2021), as sub-Arctic species have moved northward (Stafford et al. 2022). To describe these broad-scale ecosystem changes, we examined functional seabird foraging guilds rather than individual species. This approach was complicated by the variations in phenology and behavior therein, and by the predominance of 1 or 2 species within a guild. Late summer is also a time of flux for seabirds in the Arctic, and timing of breeding and migration can vary within and among species. However, seabird phenology in the Arctic is limited by the short summer season, and our 4 surveys occurred during comparable time frames. The longer survey period in 2017 and 2019 started earlier in August (potentially more birds near colonies) and extended later into September (potentially more post-breeding birds dispersed), both of which could have influenced counts. If birds did not attempt to breed or failed early

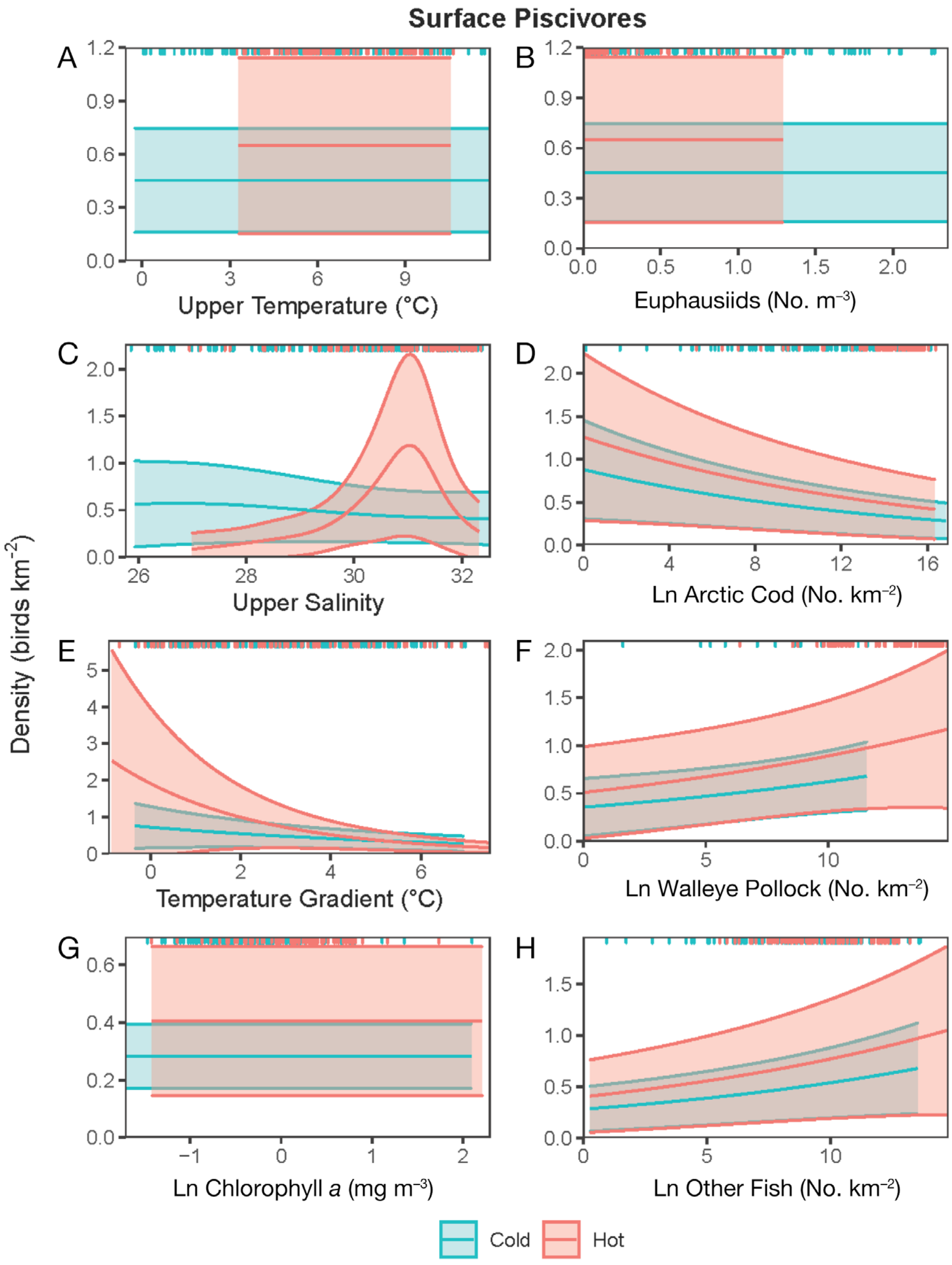

Fig. 8. Fitted partial effects of covariates for abundance of surface-feeding piscivorous seabirds during cool years (2012, 2013; blues) and heatwave years (2017, 2019; reds). The middle solid line indicates estimated value and shading indicates 95% CI. See Table 6 for model results

in the season, more birds dispersed offshore could have increased counts during surveys; we propose that is what occurred in 2017, when crested auklet numbers increased dramatically. Finally, changes in seabird population sizes could affect counts at sea, although the brief span of 5 yr between cool and heatwave years should have minimized the influence of long-term changes. Where there was evidence of population declines (i.e. common murres; Piatt et al. 2020), we consider this a component of the MHW impacts.

4.1. Oceanographic conditions and the prey field

Our study period occurred during a remarkable transformation in the Chukchi Sea that was influenced by Arctic atmospheric patterns and con-

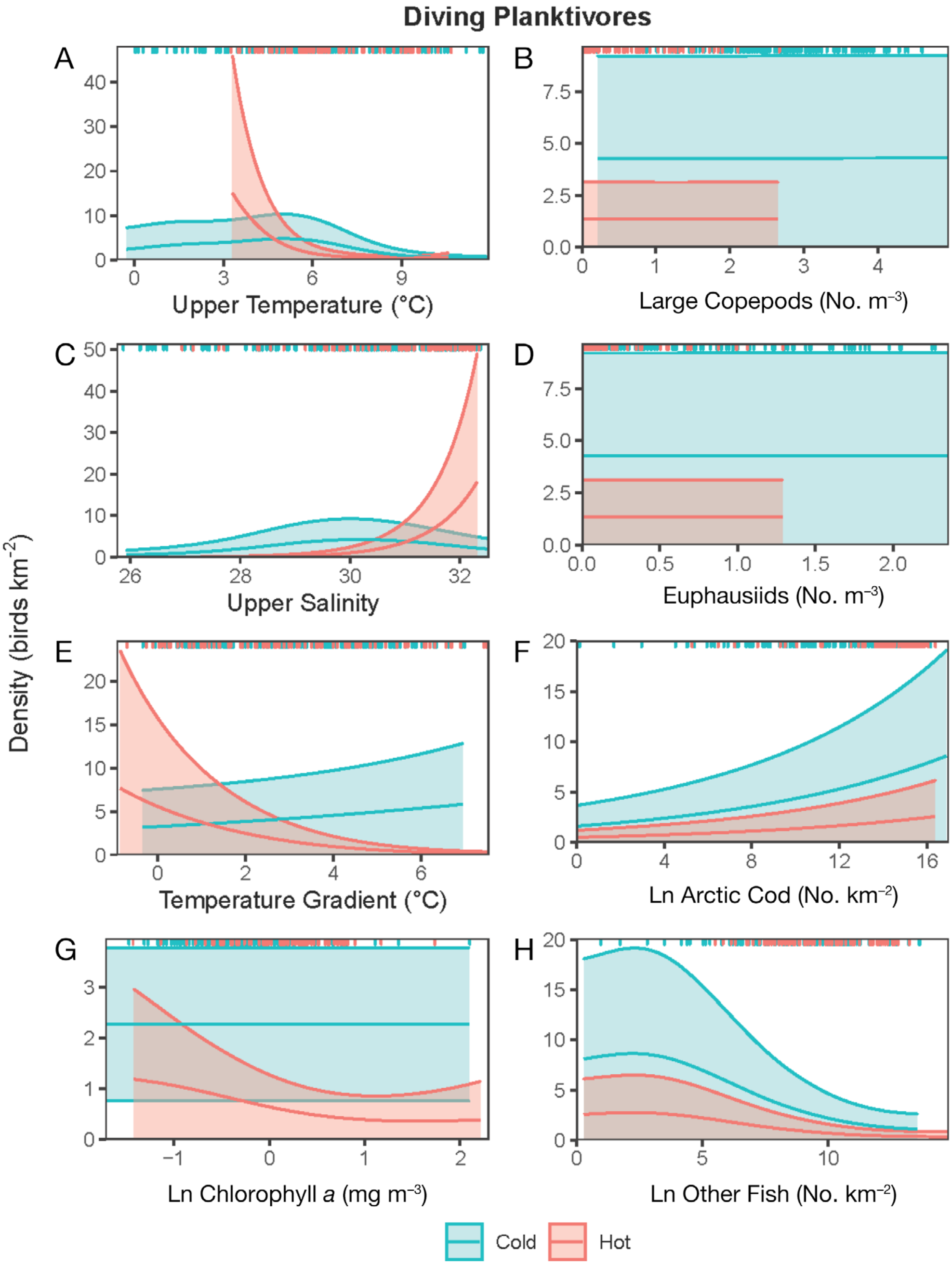

Fig. 9. Fitted partial effects of covariates for abundance of diving planktivorous seabirds during cool years (2012, 2013; blues) and heatwave years (2017, 2019; reds). The middle solid line indicates estimated value and shading indicates 95% CI. See Table 6 for model results

ditions in the Bering Sea (Ballinger et al. 2019, Danielson et al. 2020). Greatly reduced winter sea ice on the Bering Sea Shelf resulted in reduced formation of the Bering Sea cold pool in 2018 and 2019 (Duffy-Anderson et al. 2019, Eisner et al. 2020). Concurrently, warmer seas coupled with a collapse of the climatological Beaufort High (Ballinger & Overland 2022) promoted southerly winds, and increased transport of warmer, saltier water (i.e. greater heat) into and across the Chukchi Shelf during heatwave years (Danielson et al. 2020). These conditions removed the thermal barrier blocking northward movement of southern Bering Sea gadids, primarily adult pollock (Stevenson & Lauth 2019). Increased spawning of pollock near the Bering Strait, combined with increased advection through the Strait, likely drove the enormous influx of age-0 pollock into the Chukchi Sea (Fig. 12) observed in 2017 and 2019 (Levine et al. 2023) (Fig. S3).

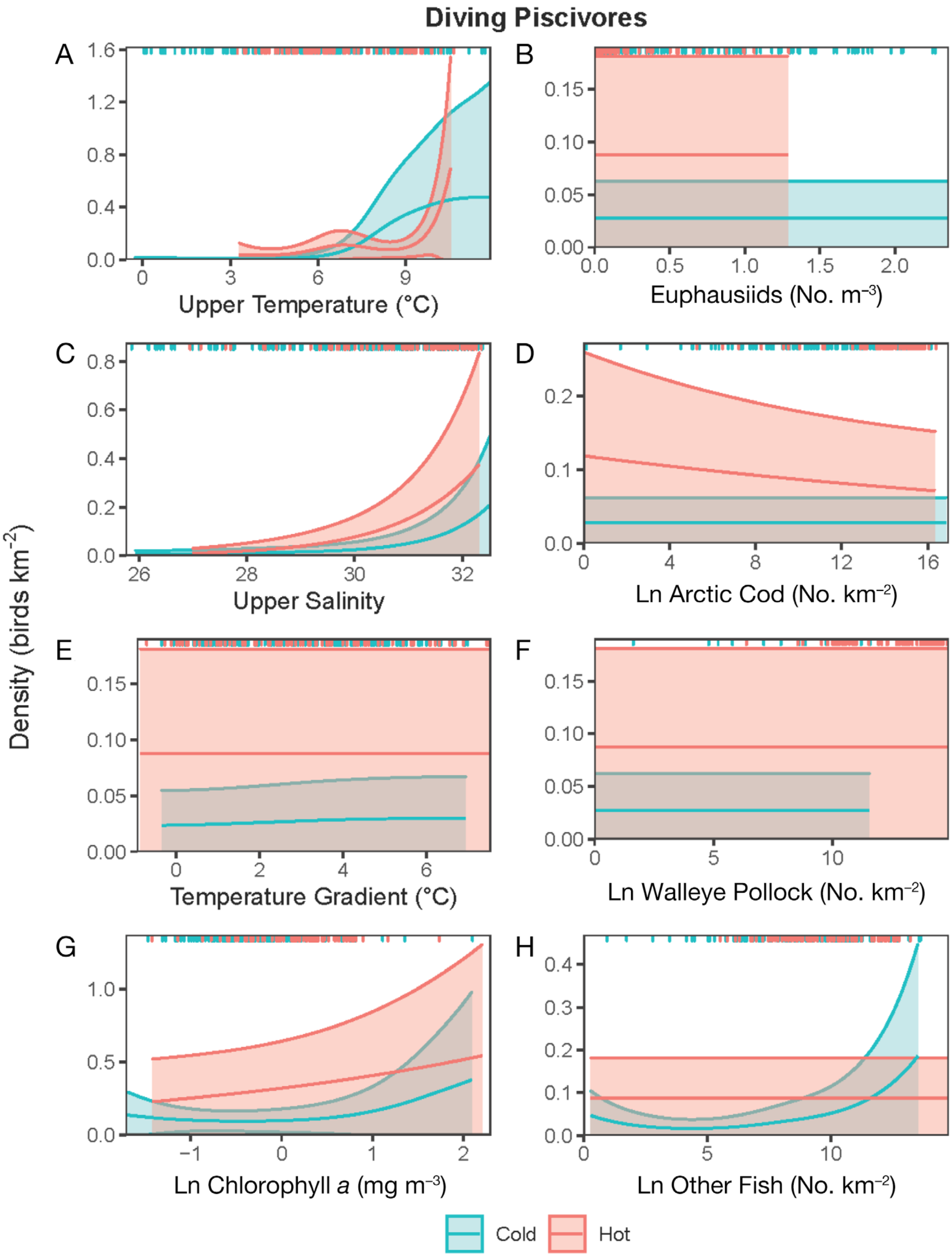

Fig. 10. Fitted partial effects of covariates for abundance of diving piscivorous seabirds during cool years (2012, 2013; blues) and heatwave years (2017, 2019; reds). The middle solid line indicates estimated value and shading indicates 95% CI. See Table 6 for model results

In the Chukchi Sea, spring sea ice conditions set the physical stage for the summer prey field. During cool years (2012, 2013), sea ice persisted in the northern Chukchi until mid-August (Text S4 & Table S2 in the Supplement), and cold water remained in the northern Chukchi Shelf into late summer, with relatively fresh water in the upper layer (Fig. S1A). These conditions facilitated the late summer abundance of large-bodied *Calanus* copepods and euphausiids (Spear et al. 2019, 2020) (Fig. S2). *Calanus* species are larger and more energy-rich than many other copepod genera (Eisner et al. 2018) and they are important prey for many seabirds, including least and crested auklets (Gall et al. 2006, Guy et al. 2009).

During heatwave years (2017, 2019), the northern Chukchi Sea was mostly ice-free by mid-July (Text S4 & Table S2); warm, saline water occurred throughout the shelf, phytoplankton biomass was slightly higher

Table 6. Summary of generalized additive model (GAM) results from the best predictive model of seabird response to environmental conditions and prey, based on Chukchi surveys during 2012 and 2013 (cool years) and 2017 and 2019 (heatwave years). Blank indicates no significant response. Shearwaters had no significant response to these variables and are not included in this table. Surface planktivore relationships are shown for the model with lowest AIC, although model uncertainty was high for this guild. +: positive response; –: negative response; ∩: unimodal; (): weak response

Species	Cool or warm years	Upper temperature	Upper salinity	Temp gradient	Chl *a*	Large copepods	Euphausiids	Arctic cod	Walleye pollock	Other fish
Surface planktivores	Cool	–						–		
	Heatwave		+					–		
Surface piscivores	Cool							–	+	+
	Heatwave		∩					–	+	+
Diving planktivores	Cool			(+)				+		–
	Heatwave	–	+	–	–			(+)		(–)
Diving piscivores	Cool	+	+		+					+
	Heatwave	(+)	+		+			–		

and widespread, and large zooplankton were nearly absent except over the northern shelf (large copepods; Fig. S2A) or near Hope Basin (euphausiids; Fig. S2B). This absence of large zooplankton in most of the Chukchi altered the prey field directly for planktivores, and perhaps indirectly for piscivores (Fig. 12). Forage fish were abundant, but Arctic cod were restricted to the northern shelf (Fig. S3A), whereas age-0 pollock occupied much of the eastern shelf and dominated the fish assemblage in the southern Chukchi Sea (Levine et al. 2023; Fig. S3B). Seabirds breeding on the eastern Chukchi coast had to travel farther north for Arctic cod or disperse farther offshore for pollock; such changes would have been energetically prohibitive for birds still raising chicks, and may be why (in conjunction with late season sampling) diving piscivores were not as aggregated near the Chukchi colonies during heatwave years (Fig. 6D). A comparable situation occurred at a smaller scale in the adjacent Beaufort Sea, where Arctic cod followed a northward shift of the ice edge, and loss of access to this prey was detrimental to the breeding success of black guillemots *Cepphus grylle* nesting on a barrier island (Divoky et al. 2021).

Given that both zooplankton (Kim et al. 2020) and fish communities (Levine et al. 2023) showed changes in abundance and distribution between cool and heatwave years, it is not surprising that the seabird community also showed altered distribution and species composition. In general, the influence of temperature and salinity on seabird distribution (Table 6) was indicative of the importance of different water masses and the formation of fronts between them. In particular, Anadyr or Bering water supports elevated productiv-

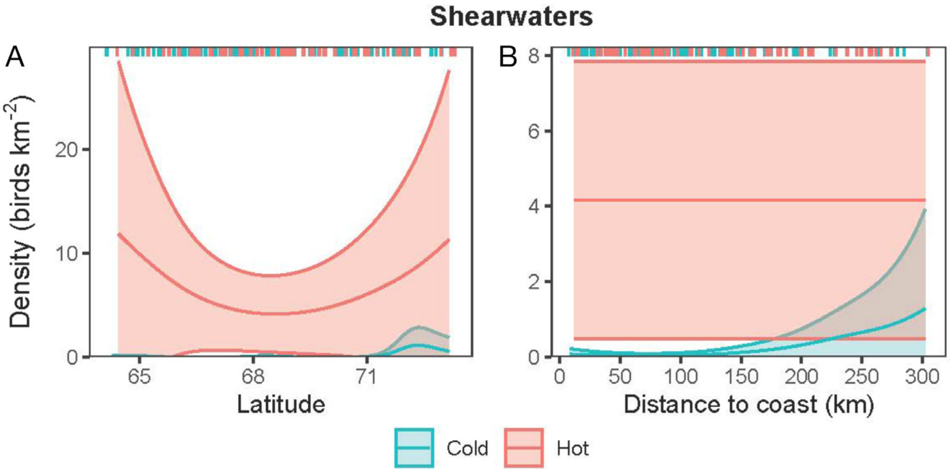

Fig. 11. Fitted partial effects of covariates for abundance of shearwaters during cool years (2012, 2013; blues) and heatwave years (2017, 2019; reds). The middle solid line indicates estimated value and shading indicates 95% CI. See Table 6 for model results

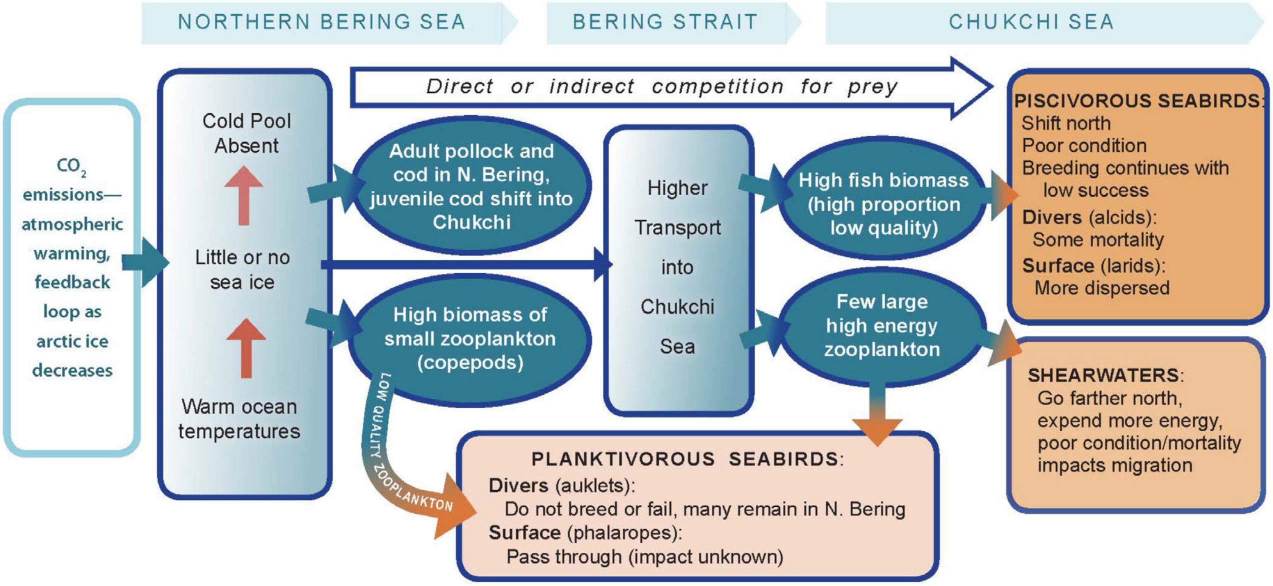

Fig. 12. Conceptual model illustrating the physical drivers and biological components of the Chukchi Sea ecosystem that can affect seabirds during marine heatwave years. During 2017–2019, conditions in the Bering Sea (left) led to lack of a thermal barrier for pelagic fish (primarily pollock) and increased transport of heat, nutrients, zooplankton, and fish into the Chukchi Sea (center). Planktivorous seabirds (bottom; some breeding in the northern Bering Sea and in the Bering Strait) could be directly affected by lack of large zooplankton, and late summer migration to the Chukchi curtailed. Piscivorous birds (top right) could be directly and indirectly affected via competition with pelagic fish, but the surface foragers can disperse to search for prey. Shearwaters (bottom right) could be impacted by lack of sufficient, high-lipid prey and higher cost of traveling further

ity, high zooplankton abundance (Springer et al. 1989), and high seabird densities (Gall et al. 2022). The flooding of Bering Shelf Water across the Chukchi Shelf may have also diminished well-defined fronts between water masses (Lu et al. 2015), which would affect the distribution of seabirds such as shearwaters that use these features to access prey (Russell et al. 1999, Jahncke et al. 2005).

4.2. Seabird species richness and diversity

During heatwave years, we observed higher seabird species richness coupled with lower seabird diversity (Fig. 4), as shearwaters moved into the region in large numbers. Our results suggest that surface-feeding birds, particularly those that are predominately piscivorous, could increase over time as a proportion of total seabird numbers. During heatwave years, we observed 6 additional species that are typically more coastal in distribution (sea ducks and loons) or migrants from the south (ancient murrelet). Surveys later in the season might have increased our encounter rate of these migrants, but alternatively, sea ducks (benthic feeding) and loons (piscivorous) expanded into more pelagic habitat concurrent with the spread of warmer water across the Chukchi Shelf. The ancient murrelet (piscivorous, but also eats zooplankton) is a relatively recent, albeit intermittent, post-breeding migrant to the Chukchi Sea (Day et al. 2013).

4.3. Seabird foraging guild responses

4.3.1. Planktivores

Surface feeding planktivores were comprised primarily of red phalarope *Phalaropus fulicarius*, with occasional sightings of red-necked phalarope *P. lobatus* (the latter during cool years only). Red phalaropes nest on the Arctic tundra and then migrate south, and they are predominately marine most of the year (Tracy et al. 2020). While phalaropes were more abundant during heatwave years, their mean densities were highly variable among years (Table 5). Our results were consistent with observations of satellite-tagged red phalaropes (Saalfeld et al. 2024), which showed variability among individuals in migration timing and routes, and between 2 heatwave years (2017 and 2018). Individual birds pass through the region in <3 wk, and they also forage nearshore and in estuaries. Their flexible foraging habitats and brief tenure in the region (Saalfeld et al. 2024) could have provided a buffer against low abundance of large zooplankton during heatwave years, contributing to the poor performance of our models for this guild.

The patterns observed in diving planktivores were largely driven by crested auklets, which increased dramatically in 2017 but were nearly absent in 2019. Least auklets apparently did not migrate to the northern Chukchi in 2017 but remained in high numbers near northern Bering Sea colonies during 2017–2019 (Kuletz et al. 2020). Crested auklets occurred in large numbers in the northern Chukchi in late summer 2017, but after 2 yr of poor breeding success in the northern Bering (Will et al. 2020b), few returned to the Chukchi in 2019 (Table 3). This pattern suggests a lag effect in auklet post-breeding migration following successive years of poor foraging conditions near Bering Sea colonies (Romano et al. 2020, Will et al. 2020b). The ~600 km journey to Hanna Shoal in the Chukchi, typically a hotspot for large copepods (Ashjian et al. 2017, Dunton et al. 2017) and foraging auklets (Kuletz et al. 2015, Gall et al. 2022), was either not necessary for birds that did not nest in 2019 or was not energetically advantageous due to low prey availability. Furthermore, large copepods were of much lower abundance in the central and northern Chukchi in 2017, and were farther north over the shelf edge in 2019 (Fig. S2A).

4.3.2. Piscivores

The 2 piscivorous guilds did not show the dramatic changes in abundance and distribution evidenced by the 2 planktivorous guilds and shearwaters. Surface piscivores were widespread and were associated with 2 fish groups, contradicting the prediction that local breeders would be too restricted by colony location to follow prey. The most abundant piscivores in our study, murres and kittiwakes, typically forage <100 km and sometimes up to 200 km from their colony (Osborne et al. 2020, Patterson et al. 2022, their Table S2). The typical foraging range would have precluded trips between the Cape Thompson or Cape Lisburne colonies and the northern Chukchi, and even the maximum range would not have reached the main regions occupied by Arctic cod in 2019 (Fig. S3A). The association between piscivorous birds and fish even during heatwave years may have been indicative of a high proportion of non-breeders (not tied to colonies) in the study area during late summer, although notably, black-legged kittiwakes can increase their foraging range during MHWs (Osborne et al. 2020). Later surveys in 2017 and 2019 could have encountered more post-breeding birds; nonetheless, associations between surface piscivores and their prey were similar between cool and heatwave years (Fig. 8D,F,H), perhaps because environmental changes facilitated increased forage fish abundance and new prey species. Diversity of forage fish species can buffer temporary lack of any one species, although the advantage can be lost following a prolonged heatwave that affects all fish species, as occurred during the 2014–2016 Gulf of Alaska MHW (Arimitsu et al. 2021).

The high overall abundance and widespread distribution of forage fish, especially during heatwave years, may have contributed to the disconnect between piscivorous seabirds and Arctic cod. Arctic cod were abundant in 2017, but they exhibited less lipid content than in previous years, and newly available pollock were less lipid-rich compared to Arctic cod (Copeman et al. 2022). In addition, Arctic cod were distributed farther north in 2019 (Fig. S3A). Given these changes, piscivorous seabirds would have had to forage farther for lower energetic return. Furthermore, available fish appeared to be comprised of smaller, younger age classes than recorded from the 1950s to 1980s (Springer et al. 1984), as was documented for breeding seabirds in the Bering Sea (Sinclair et al. 2008, Renner et al. 2012). During the late 1970s, Springer et al. (1984) found that reproductive success of kittiwakes and murres at Cape Thompson and Cape Lisburne increased as fish sizes increased, concurrent with ocean warming and reduced sea ice. Following further ocean warming, however, recent studies (including this one) found that over 95% of pelagic fish sampled were <10 cm in length (Levine et al. 2023) (Table S1), and were primarily age-0 fish (De Robertis et al. 2017, Levine et al. 2023). Thus, piscivorous birds, regardless of breeding status, required greater energy expenditure to access high-lipid Arctic cod farther north, or to consume greater numbers of low-lipid fish.

Diving piscivores were never a high proportion of total seabirds and were even less abundant at sea during heatwave years. Unlike the diving planktivores, diving piscivores (primarily murres) may not have been merely displaced for 1 or 2 yr; their low numbers in 2017 and 2019 may have reflected a real population decline, despite increases in murres (both *Uria* spp. combined) at the Cape Lisburne colony from 1986 to 2014 (Dragoo et al. 2020). Murres were affected by poor prey availability during breeding and die-offs in the northern Bering Sea (Romano et al. 2020, Will et al. 2020a), and murres that starved in the Gulf of Alaska during the 2014/2015 winter could have included birds overwintering from other regions (Piatt et al. 2020). Indeed, region-specific stable isotopic signatures of common murre feathers indicated that a large number of birds found dead that winter in the Gulf of Alaska were from the northern Bering/Chukchi regions (A. Kitaysky et al. unpubl.). Thus, murre populations, particularly common murres, faced adverse impacts in both breeding and wintering grounds that could have reduced their numbers in the Chukchi Sea. Information on seabirds breeding in the Chukchi is sparse; however, colony attendance of murres (*Uria* spp.) at study plots on Cape Lisburne (Dragoo et al. 2020) had been increasing since 1986, but declined in 2019 (no data were available for 2017 or 2018). Infrequent counts at Cape Thompson since 1960 indicate long-term declines in murres. In contrast, black-legged kittiwake counts continued their positive trend throughout that period at Cape Lisburne, and showed no discernable trend at Cape Thompson (Dragoo et al. 2020). The positive or stable trend for kittiwakes at these 2 colonies is consistent with our conceptual model (Fig. 12), which proposes continued presence and dispersal of surface piscivores as the region continues to warm.

4.3.3. Shearwaters

The most striking change in avifauna during heatwave years was the influx of shearwaters, particularly in 2017 (Fig. 5). Short-tailed shearwaters primarily consume euphausiids in Alaska waters, and track adult euphausiids as they move northward across the Bering Sea during summer (Toge et al. 2011, Nishizawa et al. 2017). Alternatively, they can consume a variety of invertebrates, larval fish, and small fish (Hunt et al. 2000, 2002, Toge et al. 2011), particularly in late summer (Baduini et al. 2006). The lack of association between shearwaters and prey could reflect their omnivorous diet. During cool years, we found shearwaters associated with offshore areas near Anadyr/Bering Shelf waters, but during heatwave years, they were distributed throughout the eastern Chukchi Shelf, concurrent with warm, saline Bering Shelf Water and the dispersal of forage fish. Notably, there were shearwater die-offs in Alaska from 2017 to 2019, with the largest occurring in the southern Bering in 2019 (Jones et al. 2023). The 2019 shearwater die-off occurred primarily in July (Siddon & Zador 2019, Kaler & Kuletz 2022), prior to shearwater occupation of the Chukchi (Yamamoto et al. 2015, K. J. Kuletz unpubl. data). Over 10 000 shearwaters were found emaciated and dead or in poor condition, indicative of lack of food (Jones et al. 2023).

The high numbers of shearwaters occupying the Chukchi Sea during heatwave years could have been precipitated by lack of food in the Bering Sea (Baduini et al. 2001, Yamamoto et al. 2015). The extended surveys during heatwave years could have increased counts; however, other surveys have found that when shearwaters occupy the Chukchi, high numbers remain there throughout August and September (Kuletz et al. 2015, Yamamoto et al. 2015, Gall et al. 2017). Furthermore, there is evidence that between 2007 and 2019, a progressive northward shift in shearwater distribution began in 2014 (Kuletz et al. 2020). Thus, the 2017 irruption of shearwaters was preceded by a pattern of increasing numbers that tracked the regional trend towards longer open water seasons (Danielson et al. 2020) and increases in zooplankton (Gall et al. 2017), albeit comprised of more small, low-lipid species (Spear et al. 2019).

4.4. Seabird community response to changes in the prey field

There were 2 glaring contradictions between observed seabird abundance and abundance of key prey. The decline (by half) of diving piscivores during heatwave years coincided with substantial increases in abundance of prey fish groups, and shearwaters increased and moved farther north despite declines in euphausiid abundance. The dietary flexibility of many seabirds, as well as imperfect indices of prey abundances (Hunt et al. 2016), likely confounded our ability to find clear relationships. Nonetheless, there were signals of changes in trophic-level interactions between cool and heatwave years, as reflected in the prevalence of the heatwave indicator term in models for most guilds (Table 5).

The abrupt, widespread occurrence of age-0 pollock, and to a lesser degree age-0 Pacific cod, into the Chukchi ecosystem set the conditions for direct and indirect competition with seabirds (Fig. 12), despite the use of these fish as prey. Juvenile gadids primarily consume copepods, but also feed on various life stages of euphausiids and other invertebrates (Strasburger et al. 2014) and, as indicated by the close association between copepods and pollock in our study (correlation coefficients >0.60), juvenile pollock closely track their prey (Schabetsberger et al. 2000). Thus, juvenile pollock and Pacific cod could compete directly for prey of planktivorous feeding seabirds, and indirectly with piscivorous seabirds by competing with other forage fish that consume zooplankton. For example, direct competition for prey was indicated by a significant negative relationship between pink salmon *Oncorhynchus gorbuscha* biomass and short-tailed shearwater body condition indices, where both taxa were feeding on euphausiids in the central Bering Sea (Toge et al. 2011). Indirect competition between predatory fish and seabirds was found in the North Pacific 2 yr cycle of pink salmon, wherein years of high salmon abundance corresponded to low reproductive success of short-tailed shearwater in Australia (Springer et al. 2018) and late nesting of tufted puffins *Fratercula cirrhata* (a piscivorous bird) in the Aleutian Islands (Springer & VanVliet 2014).

While changes in the abundance and distribution of some seabird species were concurrent with heatwave years (e.g. shearwaters), others exhibited a lag effect (e.g. diving planktivores). As outlined in the conceptual model (Fig. 12), heatwave years were characterized by increased transport of warm saline water into the Chukchi Sea, which initially resulted in an increase in primary production and zooplankton biomass (advected from the Bering Sea or from recent overwintering in the Chukchi Sea; Spear et al. 2019, Kim et al. 2020, Ashjian et al. 2021). Planktivorous birds faced shifts in the zooplankton community, encountering prey with lower lipid concentrations (Eisner et al. 2018), as well as competition with juvenile gadids for those prey. Piscivorous birds were likely less directly impacted, and their typical (Arctic cod) diet could have been augmented or replaced by other more abundant forage fish species, including juvenile pollock, albeit of smaller size and lower nutritional value.

In general, diving birds predominated during cool years and then declined, while surface-feeding birds (including shearwaters) maintained or increased their presence during heatwave years (Table 3). Surface-feeding birds, with their lower wing-loading, are generally more capable of long-distance flight and can more efficiently search over wider areas for dispersed prey (Pennycuick 1987, Ballance et al. 1997, Elliott et al. 2013). Notably, the 2 strictly planktivorous *Aethia* auklets (least and crested auklets) were less abundant in 2019, yet parakeet auklets were more abundant during both heatwave years. The parakeet auklet is the least abundant of the *Aethia* auklets but consumes fish in addition to zooplankton (Hunt et al. 1998, 2000), which may have given it an advantage when fish were abundant. The presence of 'new' species of piscivorous birds during heatwave years (Table 5) suggests that increases in fish-eating birds in the Pacific Arctic is possible.

Our results were consistent with the expected divergent responses of seabirds with different dietary requirements and behavioral limitations (sensu Cairns 1987, Piatt et al. 2007), and MHWs are expected to differentially impact seabird species due to risks associated with seabird life-history traits (Woehler & Hobday 2023 in this Theme Section). Our observations during heatwave years suggest that as the Arctic warms the number of seabird species could increase, and wide-ranging surface piscivores and short-tailed shearwaters may eventually predominate in offshore waters. However, total numbers of birds frequenting the Chukchi may not increase, given the apparent lack of high-nutrient prey available during heatwave years for both planktivorous and piscivorous seabirds.

We focused on the Chukchi Sea ecosystem, but clearly it is important to consider the connectivity of large marine ecosystems. Some Chukchi seabirds were likely impacted by MHW events in the Gulf of Alaska (e.g. overwintering murres) or in the Bering Sea (e.g. migrating shearwaters). The conceptual model (Fig. 12) derived from these results and in combination with other studies is an effort to synthesize the links between oceanographic conditions, prey communities, and seabird communities during a period of elevated ocean temperatures in the Chukchi Sea. Managers can consider the links highlighted in this study when developing monitoring and response plans. We recommend that the potential for competition between seabirds and non-avian predators using similar prey be incorporated into fisheries ecosystem management plans. Our model serves as a template to guide future studies of the evolving ecosystem of the Pacific Arctic.

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Appendix.

Text A1. Remotely-sensed oceanographic data were used to characterize broad-scale ocean conditions in the Chukchi Sea, using data from the NOAA OI SST V2 High Resolution Dataset provided by the NOAA PSL (Huang et al. 2021b). Large marine ecosystem scale measures were created by averaging base data across the region resulting in daily measures of sea surface temperature (SST) and % ice cover from 1981 to 2022. These data were used to calculate the 30 yr climatology (1982—2011) providing the threshold for marine heatwave (MHW) classification for each day of the year (SST: 90th percentile; % ice cover: 10th percentile, each based on a 10 d window about the focal day of the year, following Hobday et al. 2016). Climatological means were used to calculate SST and % ice cover anomalies for the entire period (1981—2022), and the 90%/10% thresholds were used to identify MHWs as any contiguous period of 6 or more days where values were above (SST) or below (% ice cover) climatological thresholds. For each MHW, we calculated the average anomaly as a measure of intensity. A period of relatively average SST and ice cover is evident from 2008 to 2014 (with brief exceptions in 2010—2011), in contrast to an extended period of marine heatwave events and low ice cover from 2015—2021 (Fig. A1)

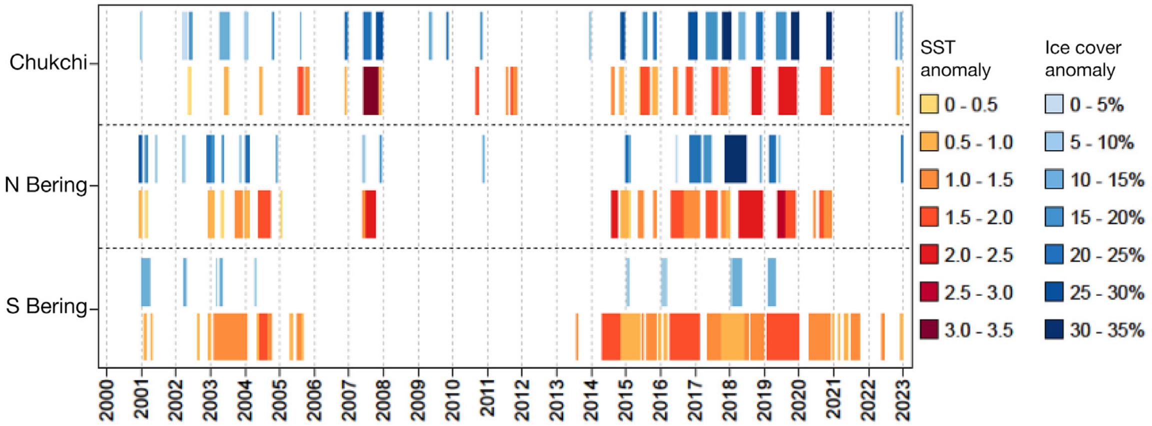

Fig. A1. Timeline of marine heatwaves/extended periods of anomalously low sea-ice extent for the South Bering Sea, North Bering Sea, and Chukchi Sea, from 2000 to 2023. Duration of anomalous conditions are indicated by box size, with color indicating average intensity (mean sea-surface temperature (SST) anomaly; mean % ice cover anomaly relative to 1982—2011 climatology) throughout the duration of the corresponding event

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