Timing of ice retreat alters seabird abundances and distributions in the southeast Bering Sea

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Abstract

Timing of spring sea-ice retreat shapes the southeast Bering Sea food web. We compared summer seabird densities and average bathymetry depth-distributions between years with early (typically warm) and late (typically cold) ice-retreat. Averaged over all seabird species, densities in early-ice-retreat-years was 10.1% [95%CI: 1.1%–47.9%] of that in late-ice-retreat-years. In early-ice-retreat-years, surface-foraging species had increased numbers over the middle shelf (50–150 m) and reduced numbers over the shelf slope (200–500 m). Pursuit-diving seabirds showed a less clear trend. Euphausiids and the copepod *Calanus marshallae/glacialis* were 2.4 and 18.1 times less abundant in early-ice-retreat-years, respectively, whereas age-0 walleye pollock *Gadus chalcogrammus* near-surface densities were $51\times$ higher in early-ice-retreat-years. Our results suggest a mechanistic understanding of how present and future changes in sea-ice-retreat-timing may affect top predators like seabirds in the southeastern Bering Sea.

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Introduction

The southeastern Bering Sea is characterised by great inter-annual variation sea ice extent and retreat timing [1, 2]. In turn, ice-retreat timing affects the availability of sea-ice algae needed for zooplankton egg-production and growth [3, 4, 5]. In early-ice-retreat-years, zooplankton recruitment and biomass are low over the middle shelf, (50–100 m) [3, 5, 6, 7]. Consequently, age-0 walleye pollock *Gadus chalcogrammus*, a zooplanktivorous fish species of major commercial importance, is thought to experience low survival because age-0 fish are unable to accumulate sufficient lipid to survive their first winter and therefore cannot recruit into the fishery [6, 8, 9].

Seabird abundance and community composition in the southeastern Bering Sea change seasonally and spatially along the cross-shelf bathymetry gradient [10, 11]. Here, we quantify the summer abundance of crustacean zooplankton and age-0 pollock, which are key prey items for seabirds [12, 13], in years of early- and late-spring-ice-retreat. We then compare the summer distribution and abundance of seabirds as they relate to variability in the timing of spring sea-ice-retreat and abundance of their prey.

We hypothesise that summer densities of seabirds will respond to variability in the timing of spring ice-retreat, mediated through the food web. From this we predict that in early ice-retreat-years: 1. summer densities of surface-foraging seabirds are reduced, 2. surface-foraging seabirds die or move to better foraging grounds away from the middle shelf, and 3. pursuit-diving species, which can access most of the water column, are more resilient than surface feeders and show smaller effects.

Methods

We defined early-ice-retreat-years (data from the National Ice Center) as those below the 40 percentile, and late years as those above the 60 percentile of mean April ice-coverage (table 1). We estimated relative densities of copepods from oblique bongo net tows and age-0 pollock with surface trawls at pre-defined, regularly-spaced stations [6]. Euphausiids were surveyed hydro-acoustically [14].

We obtained records of seabirds in the North Pacific Pelagic Seabird Database [15] that were collected in the southeastern Bering Sea study area (see supplementary figure 1), from 1975 to 2014 between 1 June, by which time ice has almost completely disappeared, and 15 September. We categorised each species as a surface-forager or pursuit-diver (table 2). Seabirds were sampled opportunistically, therefore we standardised for effort and pro-rated unidentified birds as described previously [10]. Samples from all years within each ice-retreat-catogory were merged to maximise sample sizes. Mean bathymetry-depth is the density-weighted mean depth of waters where species were recorded, the center-of-gravity of a species' distribution within the study

area. Shearwaters *Ardenna spp.* forage both as pursuit-divers and surface-feeders. We analysed them separately because their high numbers would have overwhelmed any pattern from the remaining species.

Results

From 1975 to 2014, 16 years were designated as years with early-ice-retreat and 16 years with late-ice-retreat (table 1). Annual mean April sea-ice coverage ranged from 0% to 45.8%, averaging 14.4% in late-ice-retreat-years and 0.004% in early-ice-retreat-years.

Densities of large zooplankton species were reduced in early-ice-retreat-years, having densities $0.41\times$, $0.055\times$, and $0.36\times$ relative to late-ice-retreat-years for Euphausiids, *Calanus marshallae/glacialis*, and *Neocalanus spp.*, respectively (figure 1). Near-surface densities of age-0 walleye pollock displayed an opposing trend, and were $51\times$ more abundant in early- than in late-ice-retreat-years (figure 1).

Most seabird species were found in lower densities in early- than late-ice-retreat-years (figure 2*a*). Averaging the results of all individual seabird species, we find that early-ice-retreat-year-densities were 10.1% (95% CI: 1.1%–47.9%) of the density in late years. Five species virtually disappeared, with densities in early-ice-retreat-years over six orders of magnitude lower. One species displayed an early-ice-retreat-year density over $10\times$ higher than seen in late years. The total number of birds was largely driven by shearwaters and was $2.0\times$ higher in early- than in late-ice-retreat-years. Surface-foraging and pursuit-diving species showed decreased densities in early-ice-retreat-years, with broadly overlapping confidence intervals between the two groups. Surface-foragers tended to be in shallower, and pursuit-divers in deeper waters in early-ice-retreat-years than in late-ice-retreat-years; however, 95% confidence intervals overlapped (figure 2*b*).

In early-ice-retreat-years, shearwaters were less abundant by a factor ≈ 50 over deep waters and more common by a factor of ≈ 5 over the shelf than in late years (figure 2*d*). We found the densities of all pursuit-divers, combined, decreased in the shallow and deep extremes of the study area and between 80 and 150 m, but increased over the middle shelf and around 200 m at the shelf-edge (figure 2*c*). Densities of the remaining surface-foraging species over shelf-slope waters were depressed in early-ice-retreat-years by a factor of 2, elevated over much of the middle shelf, and depressed in the shallow waters of the inner shelf (figure 2*e*).

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Discussion

We found that summer densities and distributions of seabird species in the southeastern Bering showed substantial differences associated with the timing of sea-ice-retreat in the preceding spring. It is currently unclear if these changes represent changes in population size or short-term shifts in and out of the study area, both of which we consider possible. In either case, our results can be interpreted as changes in the suitability of the environment of the study area for a species. This is the first time that such a data-set has been used to examine the responses of an entire seabird community to the timing of sea-ice-retreat.

Paradoxically, while the euphausiids and copepods that we sampled showed a strong negative response to an early-ice-retreat, age-0 pollock in near-surface waters were found in much greater densities in these years. Since we sampled age-0 pollock only in the upper water layers, we do not know whether these fish had a larger population size in early-ice-retreat-years or if their vertical distribution in the water column changed. Low densities of large, lipid-rich crustacean zooplankton may be responsible for age-0 pollock foraging longer near the surface to accumulate lipids needed for winter survival [9], thereby delaying their ontogenetic vertical migration during early-ice-retreat-years [16].

Our results mostly matched the prediction that in early-ice-retreat years, seabirds would be found in lower densities. We also saw large-scale redistributions of seabirds along the bathymetry gradient, with surface-foragers moving into shallower waters, and pursuit-divers into deeper waters. Even though divers showed a small level of decline over the outer shelf, but, contrary to our prediction, shearwaters and surface feeders were more abundant over the middle shelf (50–100 m depth) in early- than in late-ice-retreat-years. Many surface-foraging seabirds prey on juvenile pollock [13], and would find these fish more available in years with early ice retreat. The decrease of shearwaters and surface-feeders over deep waters in early-ice-retreat-years may result from improved conditions over the shelf, or possibly from increased stratification and decreased near-surface-prey availability over deep waters.

Our results are based on the association of inter-annual variability in the timing of sea-ice-retreat, and therefore may provide insight into the eventual effects of climate warming. A warmer southeastern Bering Sea will have reduced winter and spring ice cover, even though major variability will persist [2]. With little sea-ice cover in early spring, there will be a gap in time between the availability of ice-algae and the open-water spring bloom. This gap in the availability of primary production will deprive the current key prey species, *Thysanoessa raschii* and *C. marshallae/glacialis*, of the food they need for reproduction [1, 3, 5, 9]. Without these lipid-rich prey, and if no other suitable prey species emerge, populations of age-1 and older walleye pollock [17], most seabirds and other top predators will likely decline. Such changes will result in a very different eastern Bering Sea ecosystem and fishery than we know today.

Ethics

Seabird data were obtained from a publicaly available database. NOAA National Marine Fisheries Service, Alaska Fisheries Science Center does not require IACUC protocols for standard, long-term monitoring surveys.

Data accessibility

The seabird data used in this paper are publically available at the North Pacific Pelagic Seabird Database (NPPSD), located at `http://alaska.usgs.gov/science/biology/nppsd/index.php`. The raw acoustic data for assessing the abundance of euphausiids in the eastern Bering Sea can be obtained at `http://www.ngdc.noaa.gov/maps/water_column_sonar/index.html`. Data on the abundance of age-0 pollock can be obtained at `http://tinyurl.com/hc3o5vf` Data on *Neocalanus* and *Calanus* copepods can be obtained from Lisa Eisner while the data and metadata are being prepared for submission to `http://www.afsc.noaa.gov/ABL/datasets.htm`. Sea-ice data is available at `http://nsidc.org/data/docs/daac/nsidc0079_bootstrap_seaice.gd.html`.

Author's contributions

All authors participated in the framing of the questions examined; MR, JFP and GSD developed the database and curated the data, MR and GLH collaborated on data analysis; MR, GLH, LBE, KJK, and SS were the principal writers of the manuscript, and all authors participated in its editing. All authors have read the final version of the manuscript, have approved it for submission, and agree to be held accountable for its content.

Competing interests

None of the authors has a competing interest in the research results presented in this paper.

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Table 1: Ice cover, designated ice-retreat-year categories, and sample sizes.

Year	April ice %	category	seabirds [km^2]	zoopl. & pollock	euphausiid [0.5 nmi]
1975	11	late	152	0	0
1976	46	late	159	0	0
1977	8.6	late	35	0	0
1978	0.055	neutral	218	0	0
1979	0	early	111	0	0
1980	0	early	145	0	0
1981	0	early	758	0	0
1982	8.6	late	170	0	0
1983	0	early	25	0	0
1984	0.48	neutral	22	0	0
1985	12	late	41	0	0
1986	2.3	neutral	0	0	0
1987	0	early	0	0	0
1988	7.2	late	0	0	0
1989	0.22	neutral	19	0	0
1990	0	early	0	0	0
1991	0.02	early	0	0	0
1992	15	late	0	0	0
1993	0	early	0	0	0
1994	1.8	neutral	24	0	0
1995	15	late	0	0	0
1996	0	early	0	0	0
1997	3.8	late	314	0	0
1998	0	early	530	0	0
1999	4.7	late	575	0	0
2000	0.05	early	10	0	0
2001	0	early	0	0	0
2002	0	early	0	0	0
2003	0	early	0	124	0
2004	1	neutral	288	145	10069
2005	0	early	0	120	0
2006	0.55	neutral	295	144	8494
2007	2	neutral	807	200	10118
2008	11	late	1073	33	9997
2009	29	late	1726	106	9597

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Table 1 – continued from previous page

Year	April ice %	category	seabirds [km^2]	zoopl. & pollock	euphausiid [0.5 nmi]
2010	15	late	871	176	9746
2011	7.2	late	317	0	0
2012	27	late	56	0	10463
2013	8	late	128	0	0
2014	0	early	265	0	9823

Table 2: Abbreviations for seabird species used in figure 2, average densities and assigned foraging modes.

Abbr.	common	latin	density [km^2]	forage mode
ALTE	Aleutian Tern	*Onychoprion aleuticus*	0.00303	surface
ANMU	Ancient Murrelet	*Synthliboramphus antiquus*	0.358	diver
ARTE	Arctic Tern	*Sterna paradisaea*	0.0582	surface
BFAL	Black-footed Albatross	*Phoebastria nigripes*	0.00817	surface
BLKI	Black-legged Kittiwake	*Rissa tridactyla*	0.999	surface
CAAU	Cassin's Auklet	*Ptychoramphus aleuticus*	0.0255	diver
COMU	Common Murre	*Uria aalge*	0.893	diver
CRAU	Crested Auklet	*Aethia cristatella*	0.0143	diver
DCCO	Double-crested Cormorant	*Phalacrocorax auritus*	0.00000532	diver
FTSP	Fork-tailed Storm-Petrel	*Oceanodroma furcata*	1.68	surface
GLGU	Glaucous Gull	*Larus hyperboreus*	0.00239	surface
GWGU	Glaucous-winged Gull	*Larus glaucescens*	0.0667	surface
HEGU	Herring Gull	*Larus argentatus*	0.00111	surface
HOPU	Horned Puffin	*Fratercula corniculata*	0.022	diver
KIMU	Kittlitz's Murrelet	*Brachyramphus brevirostris*	0.0284	diver
LAAL	Laysan Albatross	*Phoebastria immutabilis*	0.0268	surface
LEAU	Least Auklet	*Aethia pusilla*	0.0563	diver
LESP	Leach's Storm-Petrel	*Oceanodroma leucorhoa*	0.000356	surface
LTJA	Long-tailed Jaeger	*Stercorarius longicaudus*	0.00309	surface
MAMU	Marbled Murrelet	*Brachyramphus marmoratus*	0.18	diver
MOPE	Mottled Petrel	*Pterodroma inexpectata*	0.00286	surface
NOFU	Northern Fulmar	*Fulmarus glacialis*	5.21	surface
PAAU	Parakeet Auklet	*Aethia psittacula*	0.0631	diver
PAJA	Parasitic Jaeger	*Stercorarius parasiticus*	0.0101	surface

Table 2 – continued from previous page

| Abbr.	common	latin	density [km^{-2}]	forage mode
PECO	Pelagic Cormorant	*Phalacrocorax pelagicus*	0.00188	diver
PIGU	Pigeon Guillemot	*Cepphus columba*	0.000518	diver
POJA	Pomarine Jaeger	*Stercorarius pomarinus*	0.0202	surface
REPH	Red Phalarope	*Phalaropus fulicarius*	0.243	surface
RFCO	Red-faced Cormorant	*Phalacrocorax urile*	0.00017	diver
RHAU	Rhinoceros Auklet	*Cerorhinca monocerata*	0.000081	diver
RLKI	Red-legged Kittiwake	*Rissa brevirostris*	0.115	surface
RNPH	Red-necked Phalarope	*Phalaropus lobatus*	0.0199	surface
SAGU	Sabine's Gull	*Xema sabini*	0.00423	surface
STAL	Short-tailed Albatross	*Phoebastria albatrus*	0.00279	surface
TBMU	Thick-billed Murre	*Uria lomvia*	0.401	diver
THGU	Thayer's Gull	*Larus thayeri*	0.000129	surface
TUPU	Tufted Puffin	*Fratercula cirrhata*	0.326	diver
UNSH	Unidentified Shearwater	*Ardenna spp.*	27.6	diver *
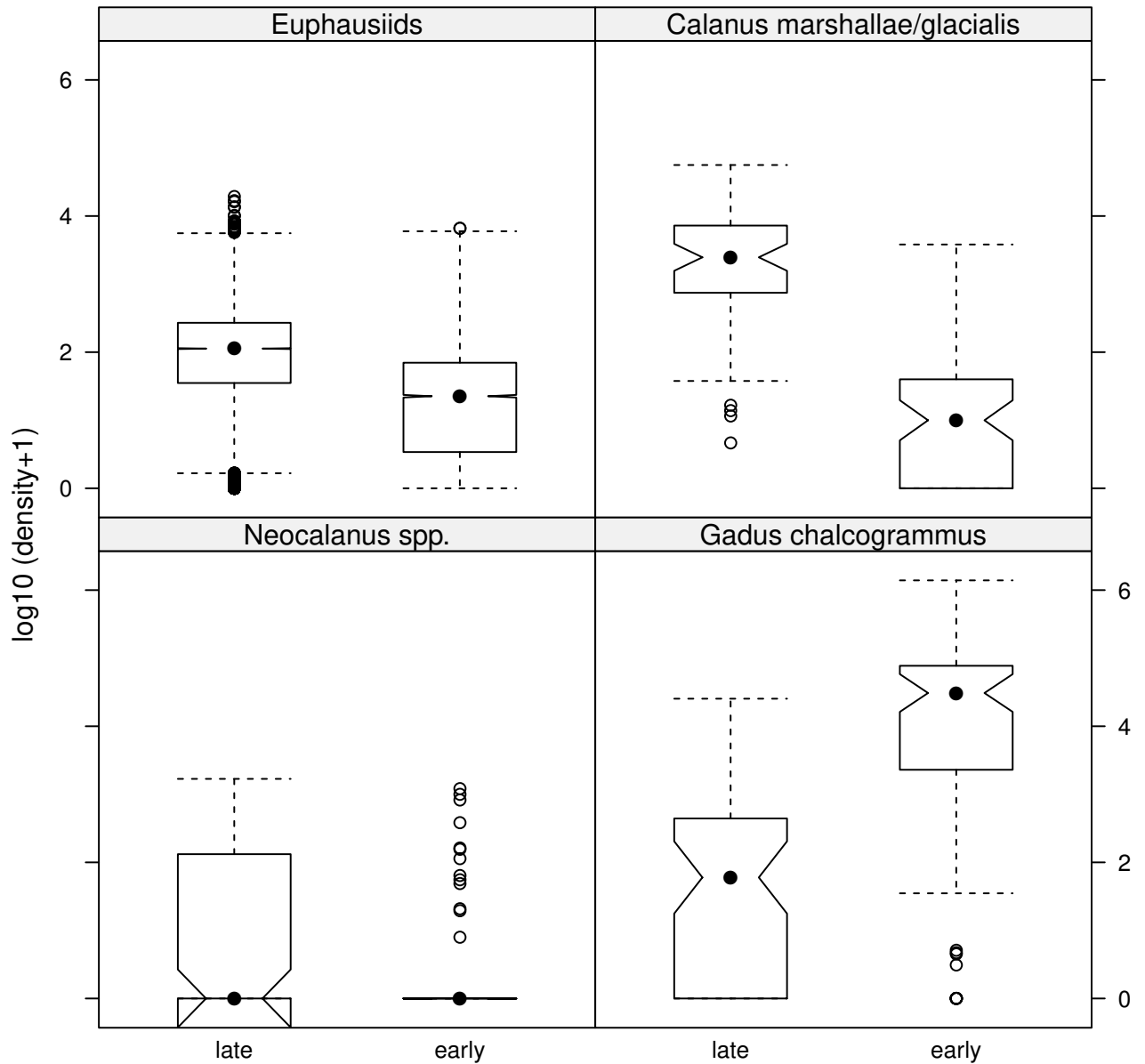
Figure 1: Densities of key crustacean zooplankton species (whole water column) and near-surface age-0 walleye pollock *Gadus chalcogrammus* in years of late- and early-ice-retreat. The notches indicate 95% confidence intervals.
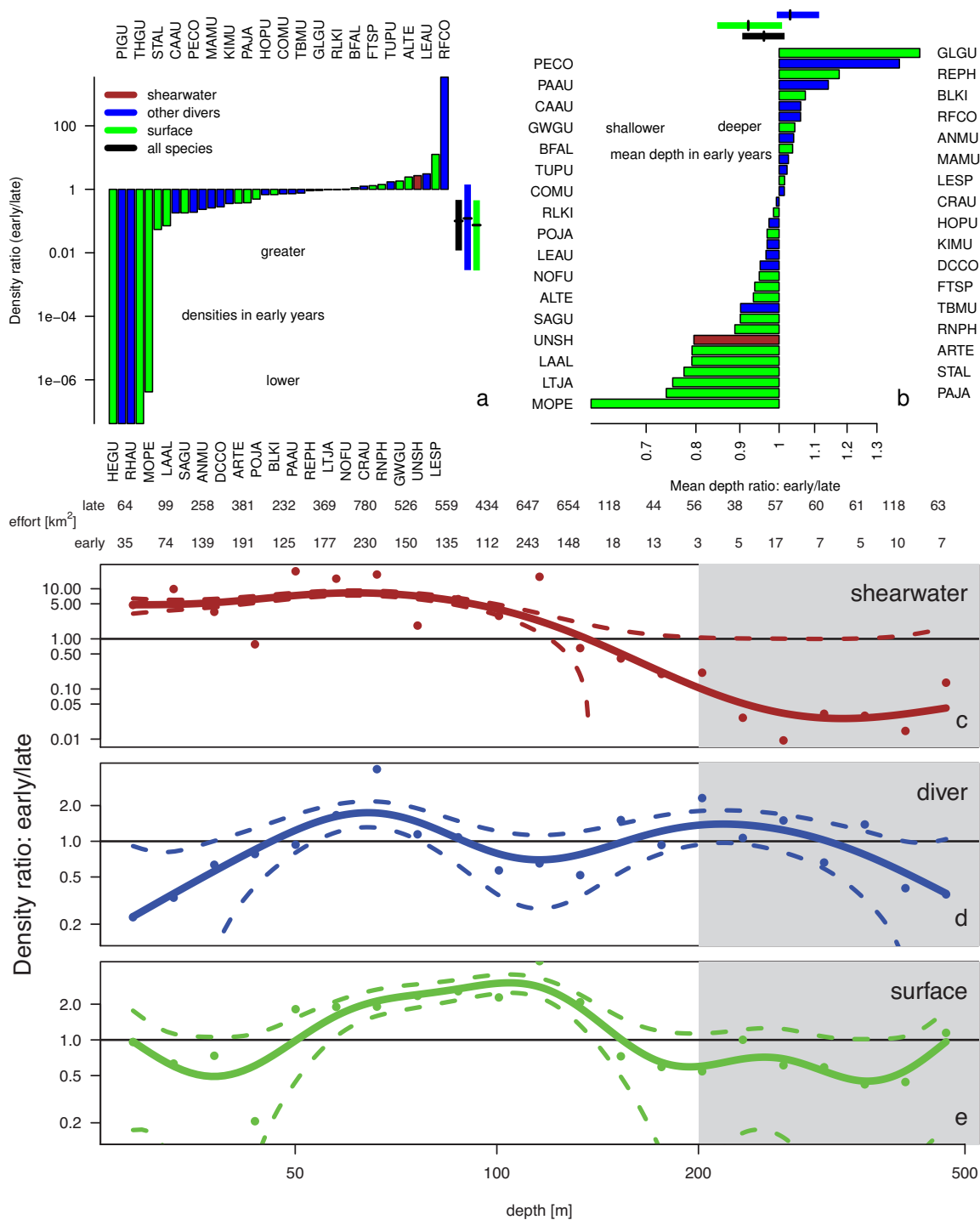
Figure 2: Differences in seabird densities and distributions between years of early and late-ice-retreat. *a*: Density ratios of individual seabird species and, to the right the 95% CI for the respective groups. *b*: Changes in the mean bathymetry depth-distribution of each species are shown with 95% CI for each group. Change in density was not uniform across the bathymetry gradient. Panels *c–e* show densities in early-ice-retreat-years, relative to late-ice-retreat-years across the gradient for the two foraging groups and shearwaters. Dashed lines represent 95% CI. Grey shading denotes deep water; no shading the continental shelf. All axes are log-scales with linear-scaled labels. Effort denotes the area surveyed within each bathymetry-slice in early- and late-ice-retreat-years, respectively.

Supplemental Material
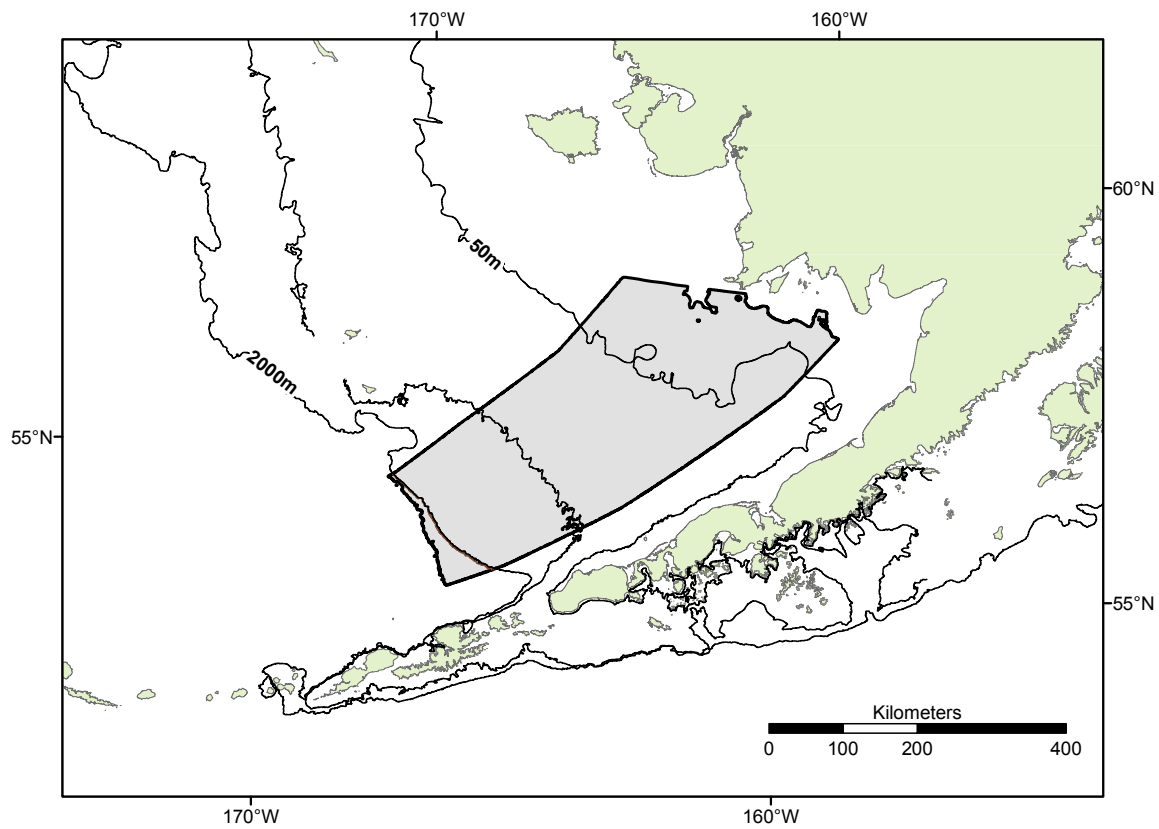
Map of study area in the southeastern Bering Sea and locations of relevant isobaths.

Details on Methods

Study area

The study area ranged from the shallow waters of Bristol Bay over the edge of the continental shelf ($\approx$200 m) to the Bering Sea Basin, in the southeastern Bering Sea, which is similar to the area selected in a previous study of seabird communities over the shelf [10].The continental shelf here is unusually wide, stretching over almost 500 km, gradually increasing in depth from east to west. In contrast to our previous study, we constricted the present study area to range from the 30 m to the 500 m isobath to avoid low sample sizes from the shallowest and deepest waters. We further restricted our study of the seabird, forage fish, and zooplankton community to the summer months between 1 June and 15 September, when the water column is generally stratified where the bottom depths are 50 m and greater [1,10].

Bathymetry

We used the AlaskaRegionBathymetricDEMv1.04, provided by the Alaska Ocean Observing System (AOOS).

Sea ice

We needed a measure to quantify the timing of sea-ice-retreat in the southeastern Bering Sea. Because the southern extent of sea ice in this area is wind driven, and can easily return after disappearing for the first time, there is not necessarily a clearly defined date of ice break-up. Instead, we used the proportion of ice cover within the study area, between the 50 m isobath and the 500 m isobath, during the usual time of breakup (the month of April) as a measure of the timing of ice-retreat. A low proportion of ice-cover in April would equate to an early, warm year.

We used two sources of ice data to determine ice extent. From 1972–1994, we used weekly sea-ice concentration, on a 0.25 degree grid, which we obtained from the Joint US Russian Sea Ice Atlas (Environmental Working Group Joint U.S. Russian Sea Ice Atlas (distributed by the National Snow and Ice Data Center September 2001). Overlapping that dataset, from 1978 to the present we used data from the National Snow and Ice Data Center; their Bootstrap algorithm, on a 25 km grid (http://nsidc.org/data/docs/daac/nsidc0079_bootstrap_seaice.gd.html). These data are semi-daily before 1987, and daily after that time. We calculated the daily mean sea-ice concentration in six regions over the southeastern Bering Sea shelf from the ice concentrations of the

data-points within each region. For data before 1987, we linearly extrapolated daily ice extents from semi-daily or weekly data.

In contrast to most previous studies comparing warm and cold years in the region [1], we used three categories, late, neutral, and early sea-ice-retreat-years. We defined early-sea-ice-retreat-years as those between the 0 and 40 percentile of ice-coverage, and late years as those between the 60 and 100 percentile. Neutral years were ignored for this study. It would have been more desirable to treat the continuous variable "percentage of April sea-ice" continuously, rather than as an artificial categorical variable. Unfortunately, our sample sizes were not sufficient to calculate the mean bathymetry depth distribution of seabirds reliably on an annual basis. We therefore aggregated years over the early/late categories.

There is autocorrelation in the timing of sea-ice-retreat between years up to a time lag of 1-2 years. We do not consider this an issue for our study of summer distribution and abundance, because migration, dispersion, and displacement by sea ice will effectively reset the distribution of seabirds, fish, and zooplankton every winter.

Zooplankton and forage fish abundance

We estimated relative densities of zooplankton species from oblique bongo net tows sampled over the water column at predefined, regularly spaced stations during the years 2003–2010 [6]. The copepod species *Calanus marshallae* and *C. glacialis* cannot be distin-guished using standard identification techniques and were therefore lumped in our analy-sis. Euphausiid species, which tend to be fast swimmers and escape a small zooplankton net deployed in daytime, were surveyed hydro-acoustically in eight years between 2004 and 2014 [14]. Forage fish densities were estimated from near-surface trawls that sampled the upper 15–20 m of the water column [19].

Seabirds

Data from seabird surveys, conducted between 1975 and 2014, were extracted from the North Pacific Pelagic Seabird Database [15]. Note that we therefore had data from several early and late ice-retreat episodes for seabirds, but much more restricted data for zooplankton and forage fish. We adjusted for differences in survey methods as described previously [10, 20]. Unidentified birds of species pairs like common and thick-billed murre, *Uria aalge* and *U. lomvia*, were pro-rated, following the scheme described in previously [10]. It is difficult to identify shearwaters *Ardenna spp.* reliably in the field. While we know the vast majority of shearwaters in the area to be short-tailed shearwaters *A. tenuirostris*, we feel that the identification challenges preclude a reliable analysis of the

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distribution of the rarer sooty shearwater *A. griseus* and therefore combined both species as "unidentified shearwater".

To gain further insights into the interactions between seabirds and forage species, we categorised seabird species into surface-foragers and pursuit-divers (table 2). While it would be desirable to have clear categories of planktivorous and piscivorous species, most of the seabird species at hand consume both fish and plankton at times. With the exception of shearwaters, all seabirds occurring within our region are easily classified into surface-foragers or pursuit-divers. Because shearwaters are of such dominant abundance and forage both on the surface and by diving, we retained them in their own category.

In contrast to the surveys on forage species, which were conducted on a regular grid, seabird data were obtained from numerous sources, resulting in heterogeneous sampling effort across the study area. To standardise for these differences in effort, we averaged seabird densities over 21 slices between logarithmically spaced isobaths. Mean seabird densities for the entire study area were then calculated by averaging all samples within each bathymetry slice and then averaging those densities over the entire study area.

The mean depth-distribution of each species was calculated as a weighted mean (mean depth of bathymetry slices, weighted by average density within the respective slice), being equivalent to the center of gravity of the respective species' distribution.

Supplemental Literature

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