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One contribution to the special feature

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

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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 were 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× 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.

## 1. Introduction

The southeastern Bering Sea is characterized by great inter-annual variation in sea-ice extent and retreat timing [1,2]. Ice-retreat timing affects the availability of sea-ice algae needed for zooplankton egg production and growth [3–5]. In early-ice-retreat-years, zooplankton recruitment and biomass are low over the middle shelf (50–100 m) [3,5–7]. 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 hypothesize that summer densities of seabirds will respond to variability in the timing of spring ice-retreat, mediated through the food web. From

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

year	April ice %	category	seabirds (km <sup>2</sup> )	zoopl. and 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	10 069
2005	0	early	0	120	0
2006	0.55	neutral	295	144	8494
2007	2	neutral	807	200	10 118
2008	11	late	1073	33	9997
2009	29	late	1726	106	9597
2010	15	late	871	176	9746
2011	7.2	late	317	0	0
2012	27	late	56	0	10 463
2013	8	late	128	0	0
2014	0	early	265	0	9823

this, we predict that in early-ice-retreat-years: (i) summer densities of surface-foraging seabirds are reduced, (ii) surface-foraging seabirds die or move to better foraging grounds away from the middle shelf, and (iii) pursuit-diving species, which can access most of the water column, are more resilient than surface feeders and show smaller effects.

## 2. Material and 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,

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

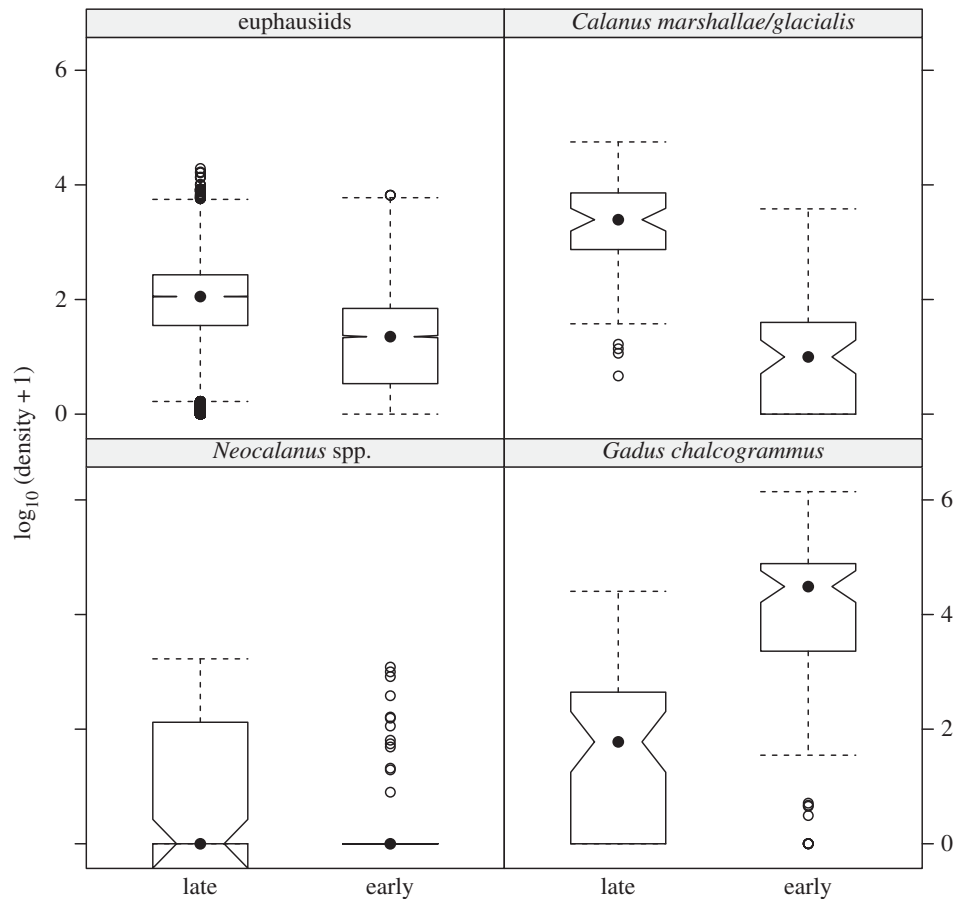
abbr.	common	Latin	density (km <sup>2</sup> )	forage mode
ALTE	Aleutian tern	<i>Onychoprion aleuticus</i>	0.00303	surface
ANMU	ancient murrelet	<i>Synthliboramphus antiquus</i>	0.358	diver
ARTE	Arctic tern	<i>Sterna paradisaea</i>	0.0582	surface
BFAL	black-footed albatross	<i>Phoebastria nigripes</i>	0.00817	surface
BLKI	black-legged kittiwake	<i>Rissa tridactyla</i>	0.999	surface
CAAU	Cassin's auklet	<i>Ptychoramphus aleuticus</i>	0.0255	diver
COMU	common murre	<i>Uria aalge</i>	0.893	diver
CRAU	crested auklet	<i>Aethia cristatella</i>	0.0143	diver
DCCO	double-crested cormorant	<i>Phalacrocorax auritus</i>	0.00000532	diver
FTSP	fork-tailed storm petrel	<i>Oceanodroma furcata</i>	1.68	surface
GLGU	glaucous gull	<i>Larus hyperboreus</i>	0.00239	surface
GWGU	glaucous-winged gull	<i>Larus glaucescens</i>	0.0667	surface
HEGU	herring gull	<i>Larus argentatus</i>	0.00111	surface
HOPU	horned puffin	<i>Fratercula corniculata</i>	0.022	diver
KIMU	Kittlitz's murrelet	<i>Brachyramphus brevirostris</i>	0.0284	diver
LAAL	Laysan albatross	<i>Phoebastria immutabilis</i>	0.0268	surface
LEAU	least auklet	<i>Aethia pusilla</i>	0.0563	diver
LESP	Leach's storm petrel	<i>Oceanodroma leucorhoa</i>	0.000356	surface
LTJA	long-tailed jaeger	<i>Stercorarius longicaudus</i>	0.00309	surface
MAMU	marbled murrelet	<i>Brachyramphus marmoratus</i>	0.18	diver
MOPE	mottled petrel	<i>Pterodroma inexpectata</i>	0.00286	surface
NOFU	northern fulmar	<i>Fulmarus glacialis</i>	5.21	surface
PAAU	parakeet auklet	<i>Aethia psittacula</i>	0.0631	diver
PAJA	parasitic jaeger	<i>Stercorarius parasiticus</i>	0.0101	surface
PECO	pelagic cormorant	<i>Phalacrocorax pelagicus</i>	0.00188	diver
PIGU	pigeon guillemot	<i>Cepphus Columba</i>	0.000518	diver
POJA	pomarine jaeger	<i>Stercorarius pomarinus</i>	0.0202	surface
REPH	red phalarope	<i>Phalaropus fulicarius</i>	0.243	surface
RFCO	red-faced cormorant	<i>Phalacrocorax urile</i>	0.00017	diver
RHAU	rhinoceros auklet	<i>Cerorhinca monocerata</i>	0.000081	diver
RLKI	red-legged kittiwake	<i>Rissa brevirostris</i>	0.115	surface
RNPH	red-necked phalarope	<i>Phalaropus lobatus</i>	0.0199	surface
SAGU	Sabine's gull	<i>Xema sabini</i>	0.00423	surface
STAL	short-tailed albatross	<i>Phoebastria albatrus</i>	0.00279	surface
TBMU	thick-billed murre	<i>Uria lomvia</i>	0.401	diver
THGU	Thayer's gull	<i>Larus thayeri</i>	0.000129	surface
TUPU	tufted puffin	<i>Fratercula cirrhata</i>	0.326	diver
UNSH	unidentified shearwater	<i>Ardenna</i> spp.	27.6	diver <sup>a</sup>

<sup>a</sup>Shearwaters forage on and below the surface.

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 electronic supplementary material, figure S1), from 1975 to 2014 between 1 June, by which time ice has almost completely disappeared, and 15 September. We categorized each species as a surface forager or pursuit diver (table 2). Seabirds were sampled opportunistically, therefore we

standardized for effort and pro-rated unidentified birds as described previously [10]. Samples from all years within each ice-retreat category were merged to maximize sample sizes. Mean bathymetry depth is the density-weighted mean depth of waters where species were recorded, the centre 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.



**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% CIs.

### 3. 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).

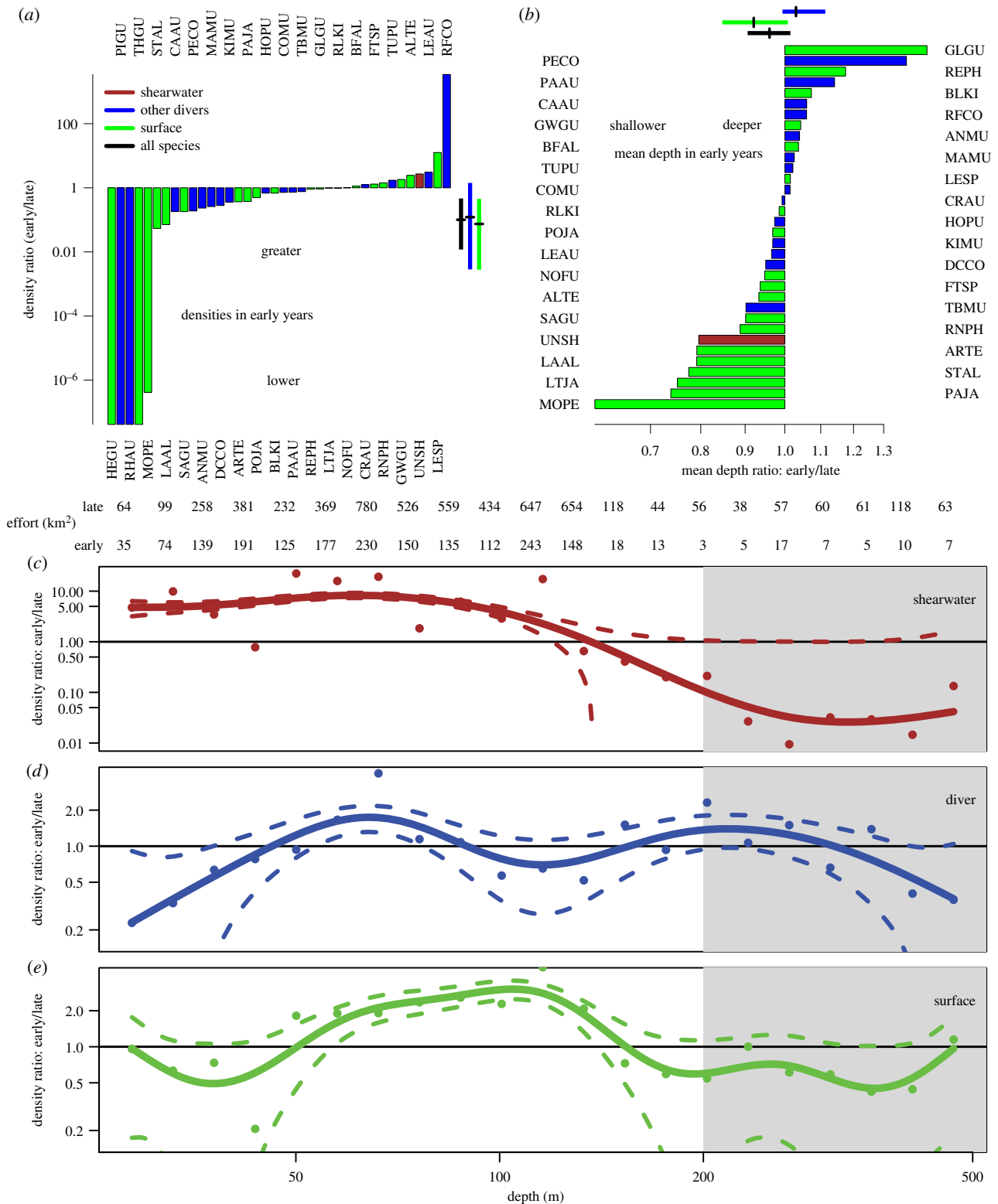
Most seabird species were found in lower densities in early- than late-ice-retreat-years (figure 2a). Averaging the results of all individual seabird species, we find that early-ice-retreat-year densities were 10.1% (95% CI: 1.1–47.9%) of the density in late years. Five species virtually disappeared, 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% CIs overlapped (figure 2b).

In early-ice-retreat-years, shearwaters were less abundant by a factor  $\approx 50$  over deep waters and more common by a factor of  $\approx 5$  over the shelf than in late years (figure 2d). 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 2c). 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 2e).

### 4. 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 whether 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 dataset 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. Because we sampled



**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.

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 probably 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 publicly 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](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 are available at [http://nsidc.org/data/docs/daac/nsidc0079\\_bootstrap\\_seaice.gd.html](http://nsidc.org/data/docs/daac/nsidc0079_bootstrap_seaice.gd.html).

**Authors' contributions.** All authors participated in the framing of the questions examined; M.R., J.F.P. and G.S.D. developed the database and curated the data, M.R. and G.L.H. collaborated on data analysis; M.R., G.L.H., L.B.E., K.J.K. and S.S. 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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