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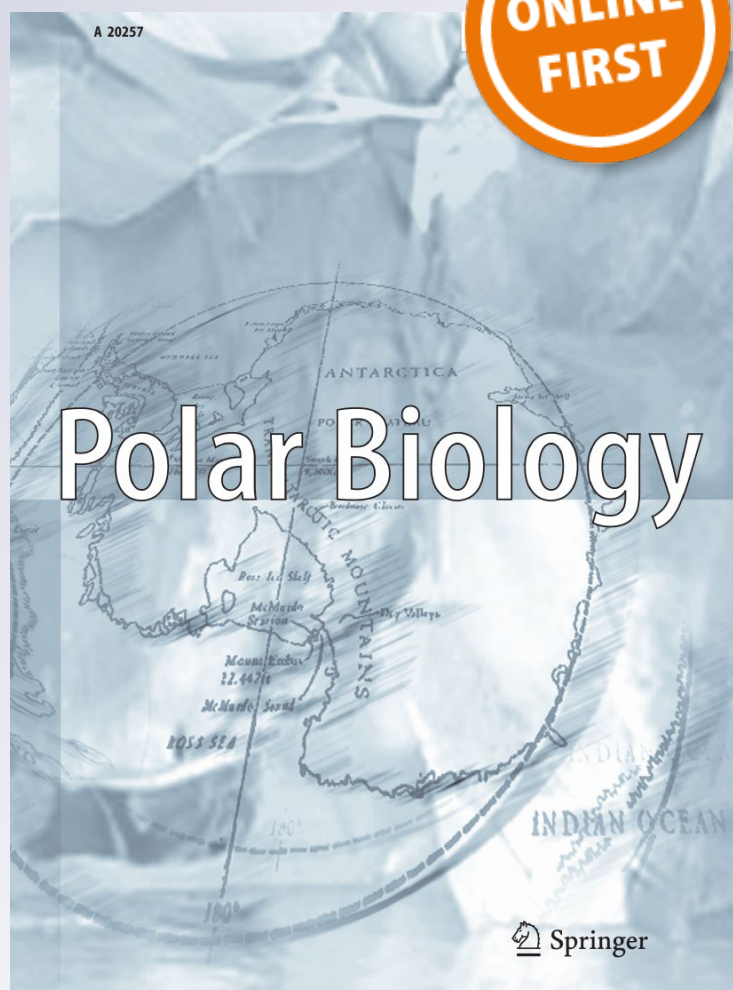
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Bottom trawl surveys in the northern Bering Sea indicate recent shifts in the distribution of marine species

Duane E. Stevenson¹ · Robert R. Lauth¹

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Abstract

The climate regime in the eastern Bering Sea has recently been dominated by a pattern of multi-year stanzas, in which several successive years of minimal sea-ice formation and warm summer temperatures (e.g., 2002–2005, 2014–2017) alternate with several years of relatively extensive sea-ice formation and cold summer temperatures (e.g., 2006–2013). This emerging climate pattern may be forcing long-term changes in the spatial distributions of the Bering Sea's marine fauna. The National Marine Fisheries Service's Alaska Fisheries Science Center recently conducted two bottom trawl surveys covering the entire Bering Sea shelf from the Alaska Peninsula to the Bering Strait. The first, in the summer of 2010, was conducted during a cold year when the majority of the continental shelf was covered by a pool of cold ($< 2^{\circ}\text{C}$) water. The second, in the summer of 2017, was during a warmer year with water temperatures above the long-term survey mean. These two surveys recorded significantly different spatial distributions for populations of several commercially important fish species, including walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), and several flatfish species, as well as jellyfishes. Population shifts included latitudinal displacement as well as variable recruitment success. The large-scale distributional shifts reported here for high-biomass species raise questions about long-term ecosystem impacts, and highlight the need for continued monitoring. They also raise questions about our management strategies for these and other species in Alaska's large marine ecosystems.

Keywords Cold pool · Climate shift · Arctic · Biogeography

Introduction

The Bering Sea is a highly productive, dynamic marine ecosystem that accounts for 30–40% of the total annual commercial fish catch of the United States (Van Vorhees and Lowther 2010; Lowther and Liddell 2015). Its broad southeastern shelf supports large fisheries for walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), yellowfin sole (*Limanda aspera*), northern rock sole (*Lepidopsetta polyxystra*), and a variety of other flatfish species, while its upper continental slope supports valuable sablefish (*Anoplopoma fimbria*) and Greenland turbot (*Reinhardtius hippoglossoides*) fisheries. The populations

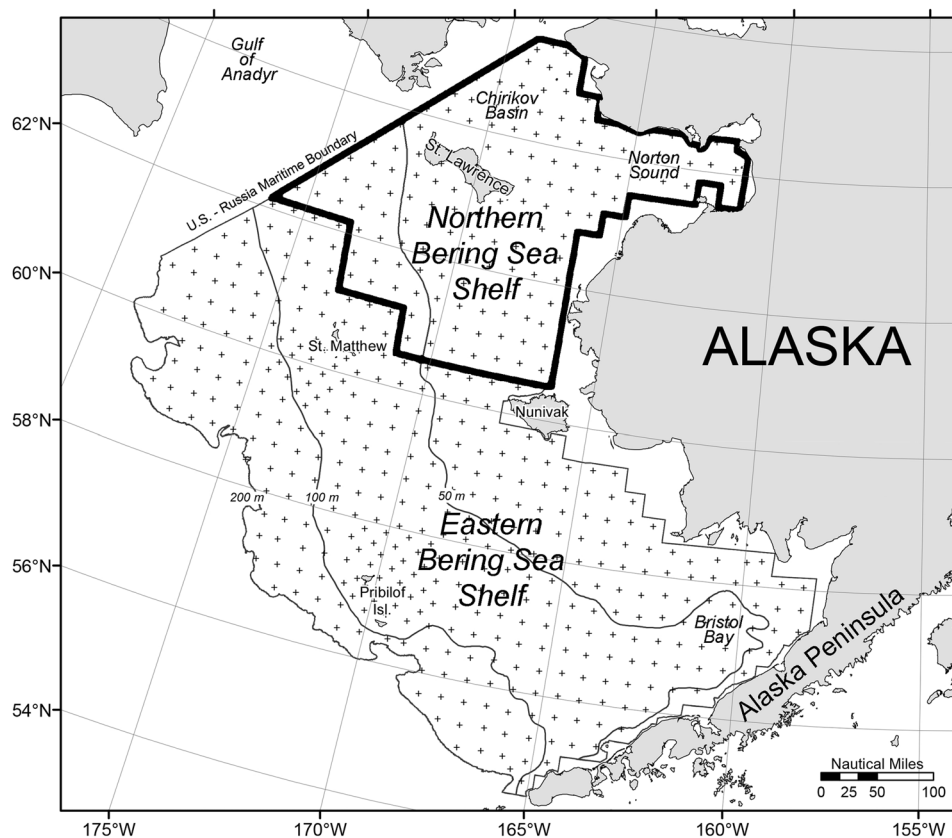
that support these fisheries prey upon a broad variety of both benthic and pelagic invertebrates and forage fishes, many of which are subject to large-scale interannual variations in distribution and abundance (Napp et al. 2002; Grebmeier et al. 2006; Aydin and Mueter 2007; Hunt et al. 2011; Ressler et al. 2012).

As a transition zone between the cold-temperate waters of the North Pacific Ocean and the Arctic waters of the Chukchi Sea, the Bering Sea is an important area for monitoring long-term climate trends and their influences on oceanographic processes. The variable extent of annual sea-ice formation is the major factor influencing the physical and biological environments on the eastern Bering Sea (EBS) shelf (Stabeno et al. 2001, 2012a, b). The extent of the annual sea-ice maximum, and the timing of its retreat, affects the biomass and species composition of the zooplankton community in the EBS, which in turn has profound effects on the recruitment of fish species, particularly walleye pollock, as well as other widespread ecosystem effects (Coyle et al. 2011; Hunt et al. 2011; Stevenson and Lauth 2012;

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Fig. 1 Map of the survey area for bottom trawl surveys of the eastern Bering Sea (EBS) and northern Bering Sea (NBS); “+” marks indicate survey stations



Stabeno et al. 2012b). In general, as latitude increases in the EBS, the benthic community shifts from a high-biomass assemblage dominated by large gadids and flatfishes to a low-biomass assemblage composed of smaller gadids, flatfishes, and sculpins, but predominated by invertebrates such as sea stars, crabs, snails, and tunicates (Grebmeier et al. 2006; Stevenson and Lauth 2012).

Over the last 36 years, the climate regime in the Bering Sea has shifted from one of high interannual variability, with warm and cold years alternating, to a multi-year pattern consisting of two prolonged warm periods (2002–2005, 2014–2017) with a cold period (2006–2013) in between (Stabeno et al. 2012b, 2017; Stevenson and Lauth 2012). One persistent oceanographic feature of the EBS shelf is a pool of cold ($< 2^{\circ}\text{C}$) water that extends southward along the middle domain (50–100 m depth) from the Bering Strait (Wyllie-Echeverria and Wooster 1998) after the annual retreat of the sea ice. In warm years, the cold pool is restricted to the northern portion of the EBS shelf, generally extending south to approximately St. Matthew Island (Fig. 1), while in cold years, it may extend nearly to the Alaska Peninsula (Stevenson and Lauth 2012; Stabeno et al. 2012a; Kotwicki and Lauth 2013). This cold pool is an important factor shaping fish distributions, as there is evidence that at least some life history stages of the primary commercial species inhabiting the EBS (e.g., walleye pollock, Pacific cod, and most flatfish

species) avoid these cold temperatures, particularly $< 1^{\circ}\text{C}$ (Kotwicki and Lauth 2013).

Since 1982, the Alaska Fisheries Science Center (AFSC) of the U.S. National Marine Fisheries Service (NMFS) has conducted annual bottom trawl surveys on the EBS shelf, from the Alaska Peninsula north approximately to St. Matthew Island (Fig. 1). These surveys provide annual indices of abundance that are critical to stock assessments for several commercially important species in the U.S. waters of the Bering Sea. Two recent survey years, 2010 and 2017, have included a “northern Bering Sea” (NBS) extension to study the effect that diminishing seasonal sea ice is having on the Bering Sea ecosystem. This NBS extension consisted of 144 additional bottom trawl stations north of the typical survey area in the Bering Sea. These stations extended the survey area north to the Bering Strait, including all of Norton Sound, and the Chirikov Basin (Fig. 1). The 2010 survey was conducted during a cold year, which was preceded by a season of extensive sea-ice formation, and featured a cold pool that covered nearly the entire middle domain of the shelf and encroached significantly on the inner domain (< 50 m depth), particularly north of 60°N (Lauth 2011). In contrast, the 2017 survey was conducted during a relatively warm year, in which the cold pool was more restricted, and the inner domain of the NBS shelf was dominated by a region of warm water ($> 4^{\circ}\text{C}$). Thus, these two surveys

provide a basis for contrasting the distributions and abundances of fishes and invertebrates in the sub-Arctic Bering Sea in a year during the cold period of 2006–2010 with those in a year of the current warm period. Here we contrast the results of these two surveys, in terms of the distributions and abundances of four broadly distributed marine species and in the context of the most recent time series of EBS bottom trawl surveys, and relate these patterns to prevailing oceanographic conditions.

Materials and methods

This study includes standardized catch data from the annual NMFS bottom trawl surveys of the EBS and NBS conducted during the summer months of 2002 through 2017. For the surveys conducted in 2010 and 2017, the survey area extended from the Alaska Peninsula to the Bering Strait, including Bristol Bay and Norton Sound, and was bounded on the northwest by the U.S.-Russia Maritime Boundary (Fig. 1). For all other survey years, the area extended from the Alaska Peninsula to approximately 61°N. Depths at trawl stations ranged from 11 to 192 m. Multiple surveys were conducted on each of the following chartered commercial fishing vessels: FV *Aldebaran*, FV *Arcturus*, FV *Alaska Knight*, FV *Northwest Explorer*, and FV *Vesterdaalen*. The 2010 survey was conducted from 3 June through 15 August 2010, and the 2017 survey was conducted from 4 June through 2 September 2017. The 2010 and 2017 surveys each included approximately 520 stations: 376 stations in the EBS, and 144 stations in the NBS. All other surveys included only the 376 stations in the EBS.

Survey trawl gear and research trawling operations were standardized among surveys, and adhered to the specifications and protocols found in Stauffer (2004). All surveys used an 83–112 Eastern otter trawl constructed with a 102-mm stretched mesh body, 89-mm stretched mesh intermediate, 32-mm mesh codend liner, 25.3-m headrope, and a 34.1-m footrope. The research trawl was spread by a pair of 1.8 × 2.7-m 816-kg steel V-doors connected to the trawl by a pair of 54.9-m dandyines, and the vessel towing speed was 3 knots. Net opening width for trawls included in this study averaged approximately 16.7 m, and the distance towed averaged 2.80 km.

Bottom water temperatures were recorded using a Sea-Bird SBE-39 datalogger (Sea-Bird Electronics, Inc., Bellevue, WA)¹ attached to the headrope of the trawl. Mean annual bottom temperatures were calculated for each survey year (for EBS stations only) as the mean of bottom

temperatures recorded at each survey station, weighted by stratum area. The grand mean bottom temperature for the study period in the EBS was calculated by taking simple average of all mean annual temperatures.

Catch data at each station were standardized to catch per unit effort (CPUE), with catch expressed as species weight (kg) and effort, expressed as area swept, calculated by multiplying the mean net width by the distance towed (Alverson and Pereyra 1969), expressed in hectares. Survey biomass estimates (hereafter referred to as “biomass”) were calculated using the methods of Wakabayashi et al. (1985) and can be found in the data reports from each year’s survey (e.g., Lauth 2011; Lauth and Conner in Review). Detailed catch data for these surveys can be accessed online at https://www.afsc.noaa.gov/RACE/groundfish/survey_data/default.htm. Temperature and CPUE plots were created in Arc-Map 10.5.1 (Esri, Inc., Redlands, CA) using the inverse distance-weighted squared interpolation method.

Geographic centers of biomass (CG) were calculated for each of the four species for each survey year (2002–2017), using only the data from the EBS portion of the survey. The CG_{lat} (latitude) and CG_{long} (longitude) for each survey year and species were calculated by weighting the latitude (lat_i) or longitude ($long_i$) by the taxon density at each station (z_i) and dividing their respective sums by the sum of all z_i s by year:

$$CG_{lat} = \frac{\sum_{i=1}^n lat_i z_i}{\sum_{i=1}^n z_i} \quad CG_{long} = \frac{\sum_{i=1}^n long_i z_i}{\sum_{i=1}^n z_i}$$

General latitudinal trends in CPUE were investigated by plotting logtransformed CPUE versus start latitude for all trawls conducted during the two survey years, and by plotting the proportion of fishes (fish catch weight/total catch weight) versus latitude for each trawl. Trend lines of locally weighted means with 95% confidence intervals were generated in R version 3.4.1 (R Core Team 2017) using the “geom_smooth” function of the ggplot2 package (Wickham 2009).

Results

Temperature regimes

Water temperatures in the EBS have varied considerably since 2002, with survey mean bottom temperatures ranging from 1.0 to 4.4 °C (Fig. 2). Bottom temperatures were above average in the surveys conducted from 2002 through 2005, then below average in 2006 through 2013 (although the 2011 mean was almost exactly the same as the long-term average), and again above average in surveys conducted from 2014 through 2017. The EBS was colder than average in 2010 (1.5 °C vs. 2.5 °C), and warmer than average

¹ Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Fig. 2 Mean annual bottom temperatures recorded on the bottom trawl survey of the eastern Bering Sea shelf from 2002 through 2017. The dashed line represents the grand mean of bottom temperatures recorded during the time series (2.5 °C)

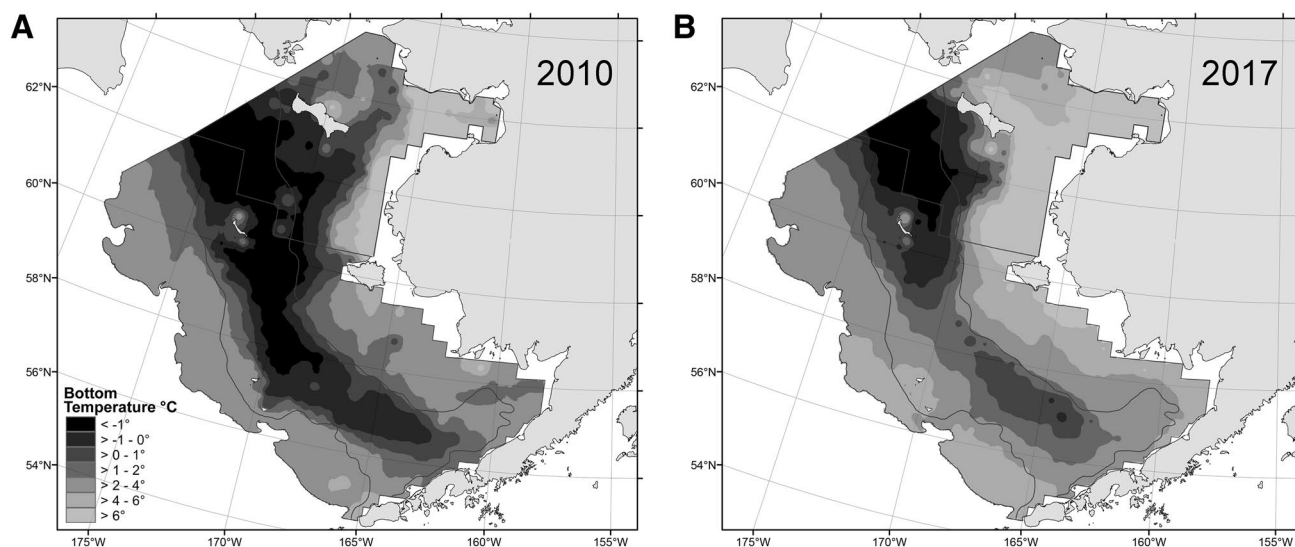
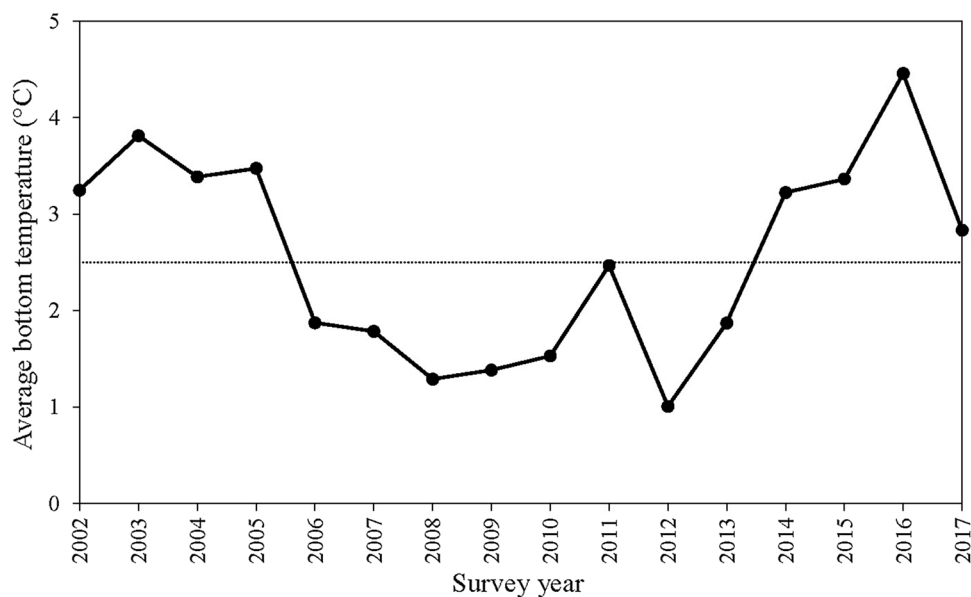


Fig. 3 Map of mean bottom temperatures from **a** the 2010 bottom trawl survey, and **b** the 2017 bottom trawl survey of the eastern and northern Bering Sea

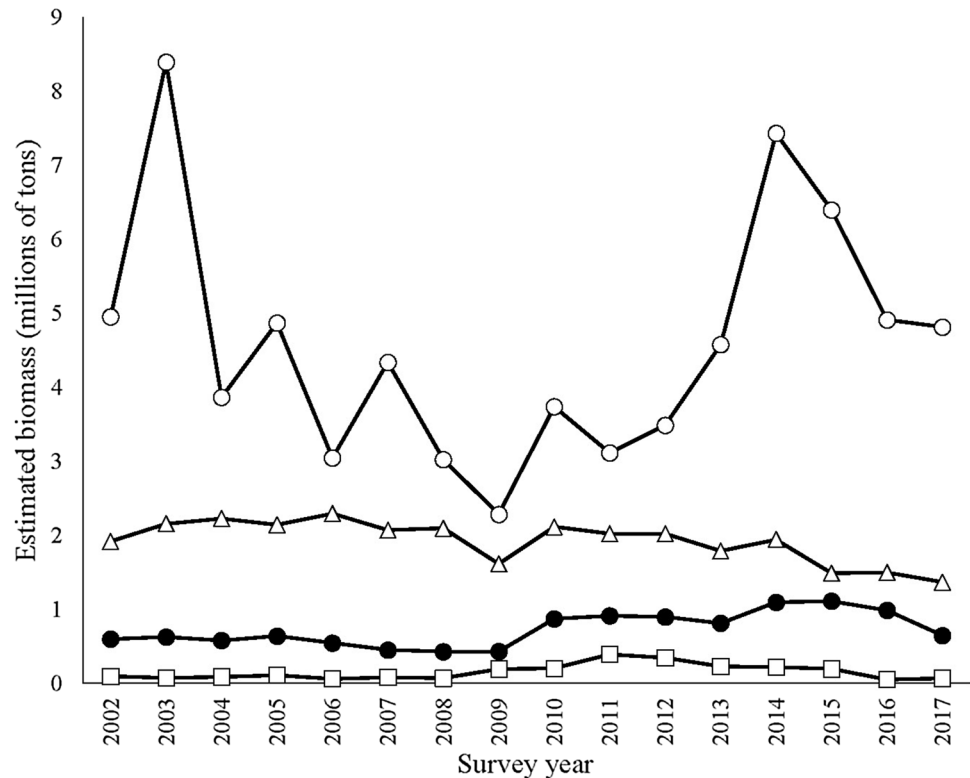
in 2017 (2.8 °C). In 2010, the cold pool of < 2 °C bottom water covered nearly the entire middle domain, from the Alaska Peninsula to the U.S.-Russia Maritime Boundary, as well as most of the inner domain (depth < 50 m) in the northern survey area (Fig. 3a). Coastal waters from Bristol Bay to Norton Sound were warmer, but the only areas > 6 °C were the shallow waters from Nome to Nunivak Island. The majority of Chirikov Basin was < 2 °C with only a small area of warmer water just north of St. Lawrence Island. In 2017, the cold pool again covered almost the entire middle domain, but very little of the inner domain (Fig. 3b). The warmest waters (> 6 °C) covered most of the inner domain in the

northern portion of the survey area, including the southern portion of Chirikov Basin, and extended south well beyond Nunivak Island.

Species distribution patterns

The total biomass estimate derived from the EBS shelf survey for walleye pollock has varied dramatically since 2002 (Fig. 4), ranging from a high of over 8 million t in 2003 to a low of 2.3 million t in 2009. Total biomass estimates for 2010 and 2017 from the EBS were both near the middle of the range (3.7 and 4.8 million t, respectively).

Fig. 4 Biomass estimates calculated for walleye pollock (white circles), Pacific cod (black circles), northern rock sole (white triangles), and jellyfish (white squares) from bottom trawl surveys of the eastern Bering Sea conducted from 2002 through 2017



The geographic center of biomass for pollock in the EBS was generally farther east during warm years than during cold years (Fig. 5a), and the centers of biomass for 2010 and 2017 were near the far western and eastern ends, respectively, of the distribution. In 2010, pollock biomass in the EBS was concentrated on the outer shelf, with a dense cluster in the southernmost portion of the survey area and high density at depths of 70–200 m north of 56°N (Fig. 6a). Pollock biomass was consistently low on the inner and middle shelves, and pollock were almost completely absent from the NBS. Total pollock biomass from the EBS was 3.7 million t, while pollock biomass from the NBS was only 0.02 million t. All pollock encountered in the NBS were either very large (> 70 cm FL) or very small (< 20 cm FL), while in the EBS most of the pollock measured were between 35 and 55 cm FL (Fig. 7a). In 2017, pollock biomass in the EBS was concentrated on the middle shelf, from the Alaska Peninsula to St. Matthew Island, with additional clusters on the outer shelf to the south and west of the Pribilof Islands (Fig. 6b). In the NBS, there was a high concentration of pollock biomass in Chirikov Basin to the north of St. Lawrence Island, as well as a small cluster to the southeast of St. Matthew Island. Total pollock biomass from EBS was 4.8 million t, while pollock biomass from the NBS was 1.3 million t. The length–frequency distribution of pollock in 2017 in the NBS was more similar to that found in the EBS, with

clear modes at approximately 15 cm FL and 50 cm FL (Fig. 7b).

Survey-derived biomass estimates for Pacific cod in the EBS have ranged from 0.4 to 1.1 million t (Fig. 4) since 2002. The biomass for 2010 was near the upper end of the range (0.9 million t), while the estimate for 2017 (0.6 million t) was just below the overall mean for the time period. The geographic center of biomass for cod in the EBS was generally farther north during warm years than during cold years (Fig. 5b), and the centers of biomass for 2010 and 2017 were near the far southern and northern ends, respectively, of the distribution. In 2010, Pacific cod biomass in the EBS was concentrated in Bristol Bay and on the middle and outer shelves from the Pribilof Islands north to St. Matthew (Fig. 6c). Cod biomass was low in the vicinity of Nunivak Island and throughout the NBS. Total cod biomass from the EBS was 870,639 t, while biomass from the NBS was only 29,091 t. As with walleye pollock, in 2010, the size distribution for Pacific cod in the NBS mostly consisted of very large and small fish, with a notable lack of intermediate size classes (Fig. 8a). In 2017, Pacific cod biomass was distributed differently (Fig. 6d). Although cod were highly concentrated in a few areas of the EBS, such as upper Bristol Bay and around St. Matthew Island, cod biomass on the shelf was generally low, particularly on the middle and outer shelves in the southern parts of the survey area. In contrast, cod biomass in the NBS was high, particularly in the Chirikov basin

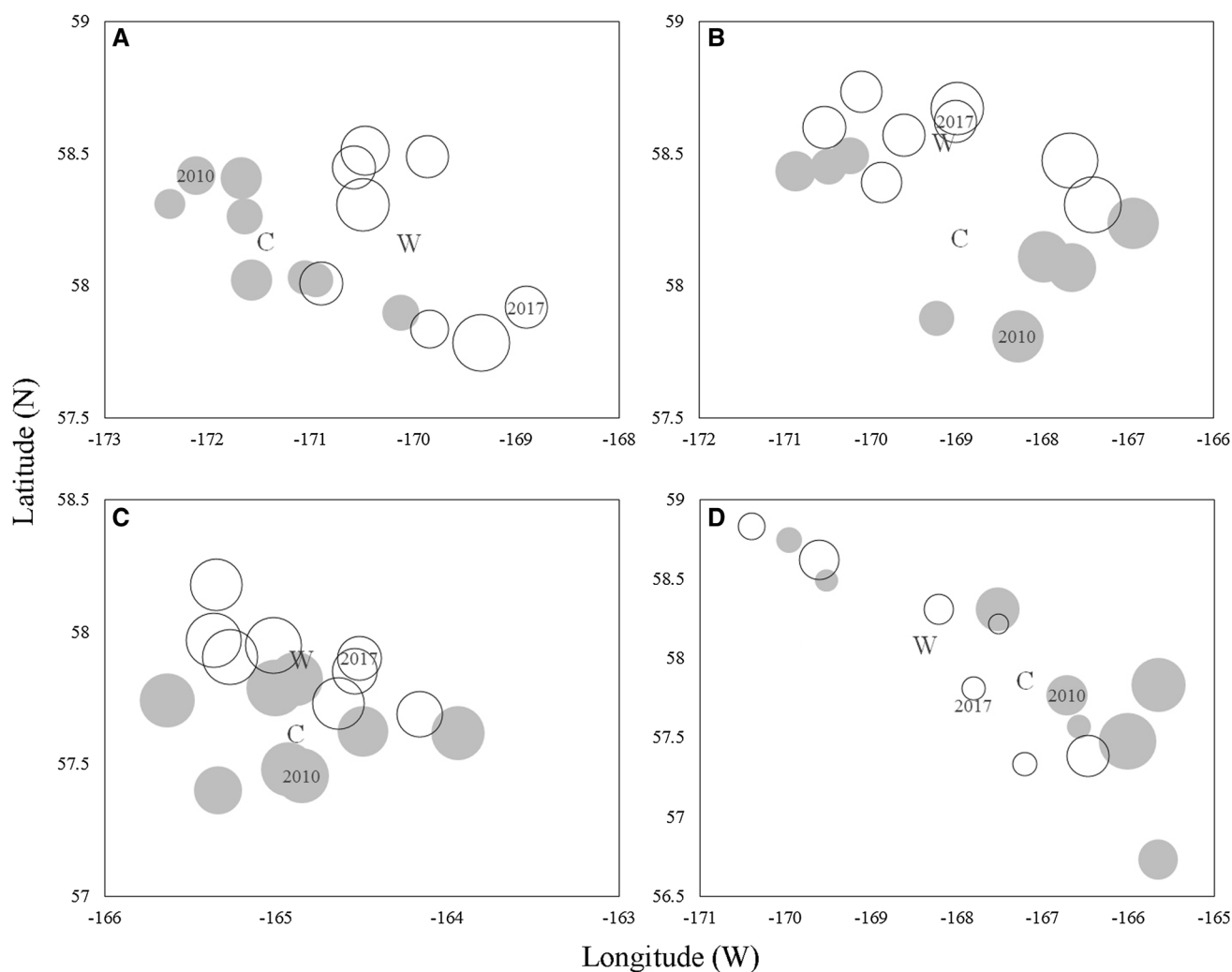


Fig. 5 Geographic centers of biomass for **a** walleye pollock, **b** Pacific cod, **c** northern rock sole, and **d** jellyfish recorded on bottom trawl surveys of the eastern Bering Sea from 2002 through 2017. White circles represent years in which the mean bottom temperature was warmer than the 35-year mean, and gray circles represent years in

which the mean bottom temperature was colder; circle size is proportional to the biomass estimate. Years in which additional surveys of the northern Bering Sea were conducted (2010 and 2017) are labeled: “W” represents the mean geographic center for warm years; “C” represents the mean geographic center for cold years

and to the south of St. Lawrence Island. Total estimated cod biomass from the EBS was 643,953 t, while that of biomass from the NBS was 283,479 t. In 2017; the size distribution for cod in the NBS was more similar to that in the EBS, with the most abundant size class at 50–65 cm, and a smaller mode at 30–35 cm (Fig. 8b). In both survey years, Pacific cod were notably absent from the cold pool.

Biomass estimates for northern rock sole in the EBS were relatively consistent, at approximately 2 million t (Fig. 4), from 2002 through 2014, including the 2010 survey year (2.1 million t). However, estimates for the latest three survey years (including 2017) have been consistently lower, at about 1.5 million t (1.4 million t in 2017). The geographic center of biomass for northern rock sole in the EBS was generally farther north during warm years than during cold

years (Fig. 5c). Northern rock sole were concentrated in the southeastern portion of the EBS survey area for both survey years (Fig. 9a, b). In 2010, northern rock sole were almost completely absent from the cold pool and from the NBS, while in 2017 significant numbers were encountered to the south and east of St. Matthew Island and in the southern NBS. Northern rock sole biomass decreased significantly in the EBS, from 2.1 million t in 2010 to 1.3 million t in 2017, while it doubled in the NBS, from 21,245 t in 2010 to 53,949 t in 2017. The majority of northern rock sole recorded in the NBS in 2017 were small juveniles (< 20 cm), while very few small rock soles were reported in the NBS in 2010 (Fig. 10).

Jellyfish biomass in the EBS (which consists almost exclusively of *Chrysaora melanaster*) was consistently estimated at approximately 0.1 million t from 2002 through

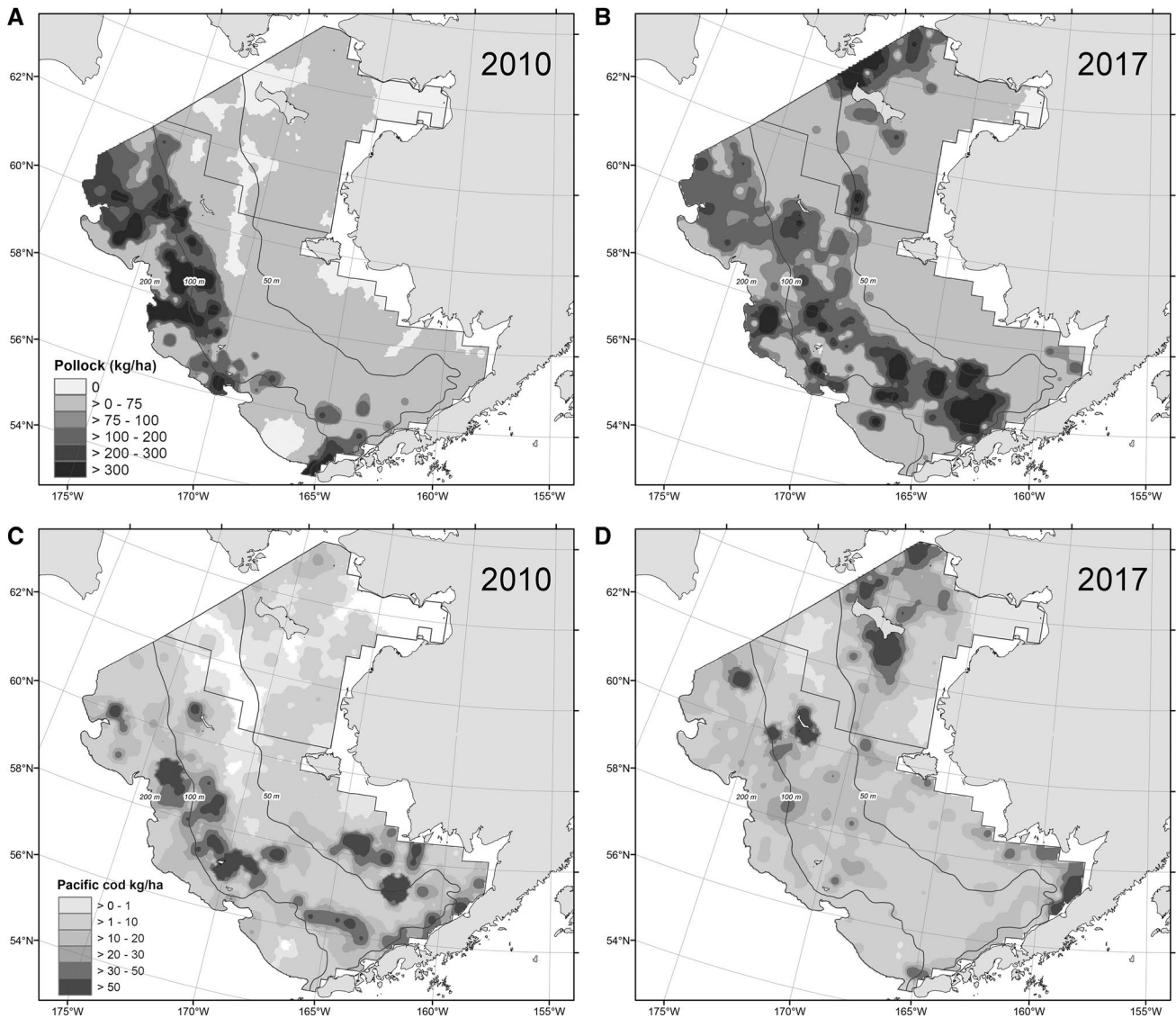


Fig. 6 Spatial distribution of large gadids, in terms of mean CPUE (kg/ha), observed during the 2010 and 2017 bottom trawl surveys of the eastern and northern Bering Sea: **a** walleye pollock (*Gadus chalcogrammus*) in 2010, and **b** walleye pollock in 2017; **c** Pacific cod (*Gadus macrocephalus*) in 2010, and **d** Pacific cod in 2017

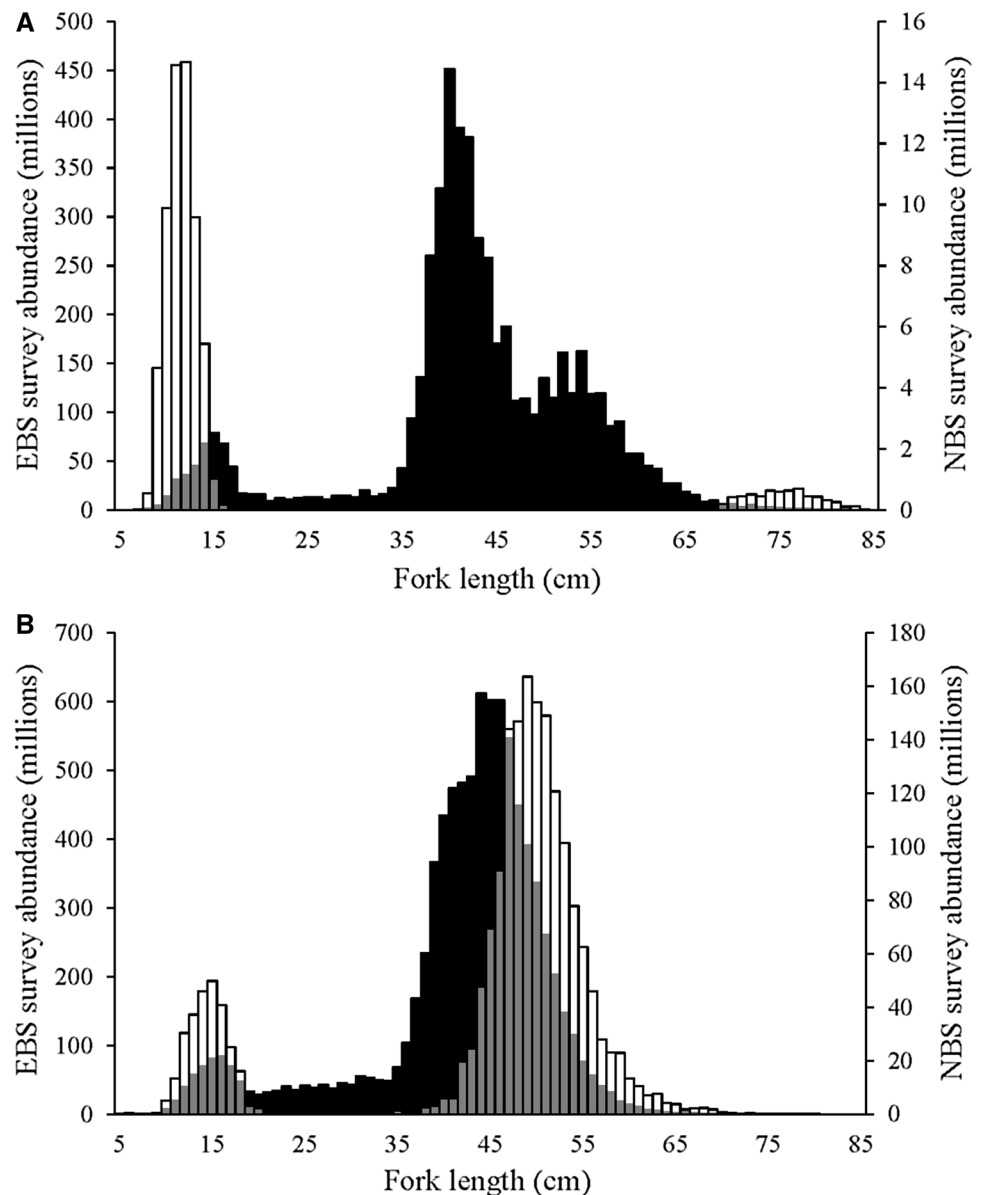
Although there was again a dense population of jellyfish in the southeastern EBS, near the Alaska Peninsula, the majority of jellyfish biomass (63% of the combined total) was encountered in the NBS, particularly in the outer portion of Norton Sound and to the east and southeast of St. Lawrence Island (Fig. 9d). The combined jellyfish biomass for the EBS and NBS declined from 193,000 t in 2010 to 105,000 t in 2017.

2008. Biomass increased markedly in 2009 and remained high through 2015, then returned to previous levels in 2016 and 2017 (Fig. 4). The geographic center of biomass for jellyfish tended to be farther north and west in warm years than in cold years (Fig. 5d), but for both 2010 and 2017 the centers of biomass were near the middle of the distribution. However, although the centers of biomass for jellyfish were similar in 2010 and 2017, details of their distribution on the Bering Sea shelf were very different. In 2010, jellyfish were concentrated on the middle shelf in the southwestern part of the EBS survey area (Fig. 9c). There were additional small pockets of jellyfish farther west, particularly just west of St. Matthew Island, but only 7% of the overall biomass was located in the NBS. In 2017, the pattern was very different.

Latitudinal trends

Total CPUE for the bottom trawl surveys conducted in the Bering Sea in 2010 and 2017 (Fig. 11a) was generally highest in the middle latitudes of the eastern Bering

Fig. 7 Size composition of walleye pollock (*Gadus chalcogrammus*) in the eastern Bering Sea (EBS: black bars, left vertical axis) and northern Bering Sea (NBS: white bars, right vertical axis) for **a** 2010 and **b** 2017. Gray-shaded areas represent overlap between the two distributions

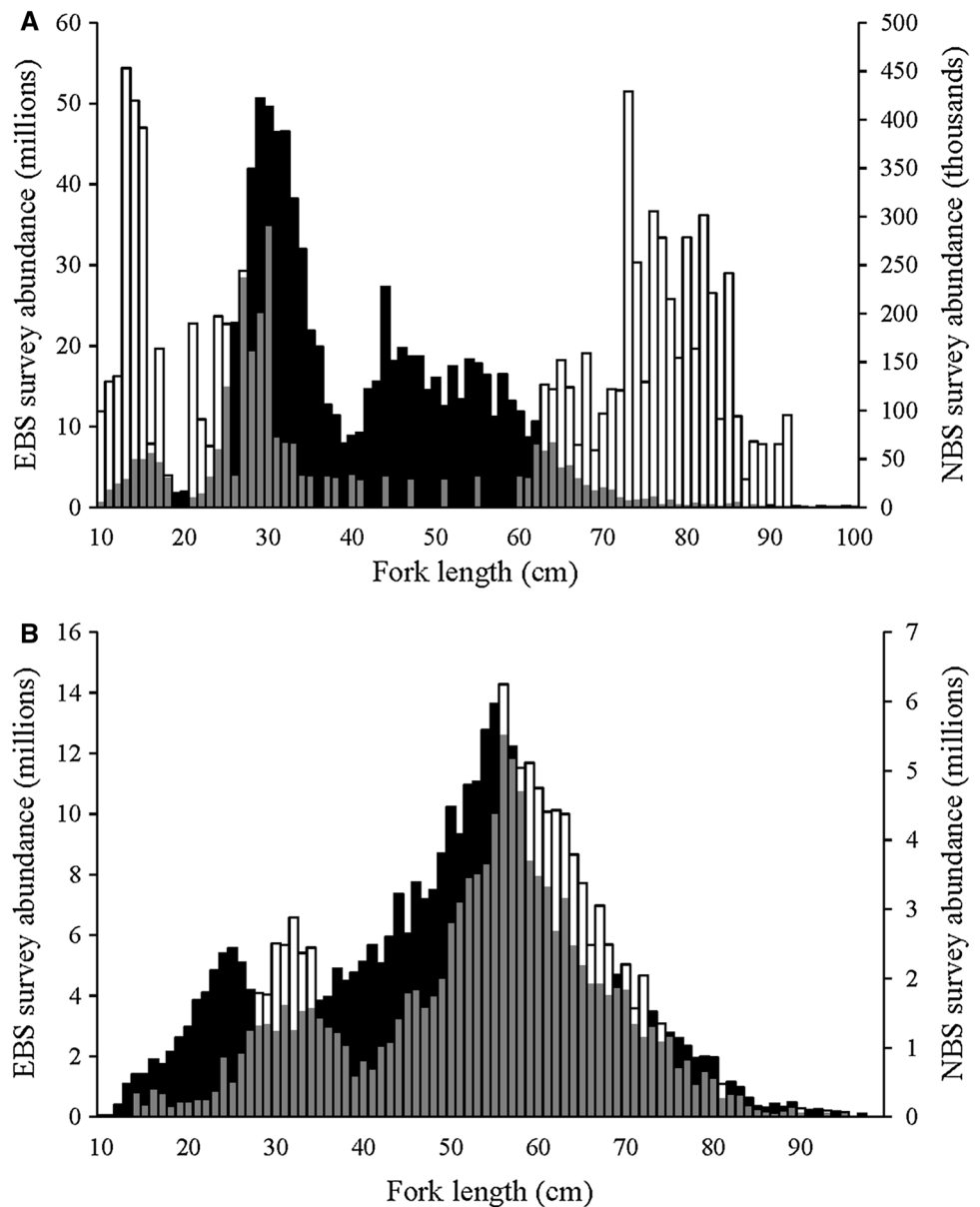


Sea (57–59°N). Total catches were lower in the southernmost stations of the survey area, as well as in the latitudes between St. Matthew and St. Lawrence Island (61–63°N). Over most of the survey area, particularly in the southern part of the Bering Sea, the overall trend of CPUE versus latitude in 2017 was very similar to that of 2010, and the locally weighted regression curves fitted to the two survey years are essentially indistinguishable from 55°N through about 62°N. However, north of 62°N the curves begin to diverge, as the CPUE values calculated for the 2017 survey increased dramatically through to the northernmost stations of the survey area, while those calculated for the 2010 survey increased only slightly in the northern survey area. Thus, for the 2010 survey, the total CPUE values for the northernmost stations were among the lowest in the

entire Bering Sea survey area, while in 2017 they were among the highest.

In general, the ratio of fish biomass to invertebrate biomass declined with increasing latitude in the Bering Sea (Fig. 11b) for both 2010 and 2017 surveys. In the southernmost stations, fishes made up 75–100% of the trawl-caught biomass, while in the northernmost stations fishes made up only 25–50% of the total biomass. For both survey years, the proportion of fish biomass declined from the southern stations to about 57°N, then increased again slightly from 57°N to about 59°N, and then declined steadily to its minimum at the northernmost stations. Although the overall trends in fish:invertebrate biomass were the same for both survey years, the decline in fish biomass in the NBS was much steeper in 2010 than in 2017, while invertebrate biomass

Fig. 8 Size composition of Pacific cod (*Gadus macrocephalus*) in the eastern Bering Sea (EBS: black bars, left vertical axis), and northern Bering Sea (NBS: white bars, right vertical axis) for **a** 2010 and **b** 2017. Gray-shaded areas represent overlap between the two distributions



remained essentially unchanged. Thus, the relatively high fish:invertebrate ratios recorded for trawls at the northern stations in 2017 were driven by an increase in fish biomass against a background of relatively static invertebrate biomass.

Discussion

The spatial distribution of fish and invertebrate populations in the Bering Sea can vary dramatically between cold and warm years. During the summer of 2010, mobile temperate species, notably walleye pollock and Pacific cod, effectively avoided the massive Bering Sea cold pool. Pollock were restricted to the outer shelf on the EBS, and almost

completely excluded from the NBS. Pacific cod were widely distributed over the southern portion of the EBS, but were restricted to deeper waters at northern latitudes and were almost completely absent from the NBS. In contrast, the 2017 cold pool was more restricted, particularly in the NBS, where a broad swath of warm water extended from Nunivak Island north to the Bering Strait, including all of Chirikov Basin. In 2017, unlike in 2010, dense aggregations of walleye pollock and Pacific cod were encountered in the NBS, particularly in Chirikov Basin. Thus, the centers of distribution for both cod and pollock in the Bering Sea were displaced northward. The aggregations of both walleye pollock and Pacific cod that were found in the NBS in 2017 were well separated from their EBS populations, and the origin of the northern populations is uncertain. If the northern

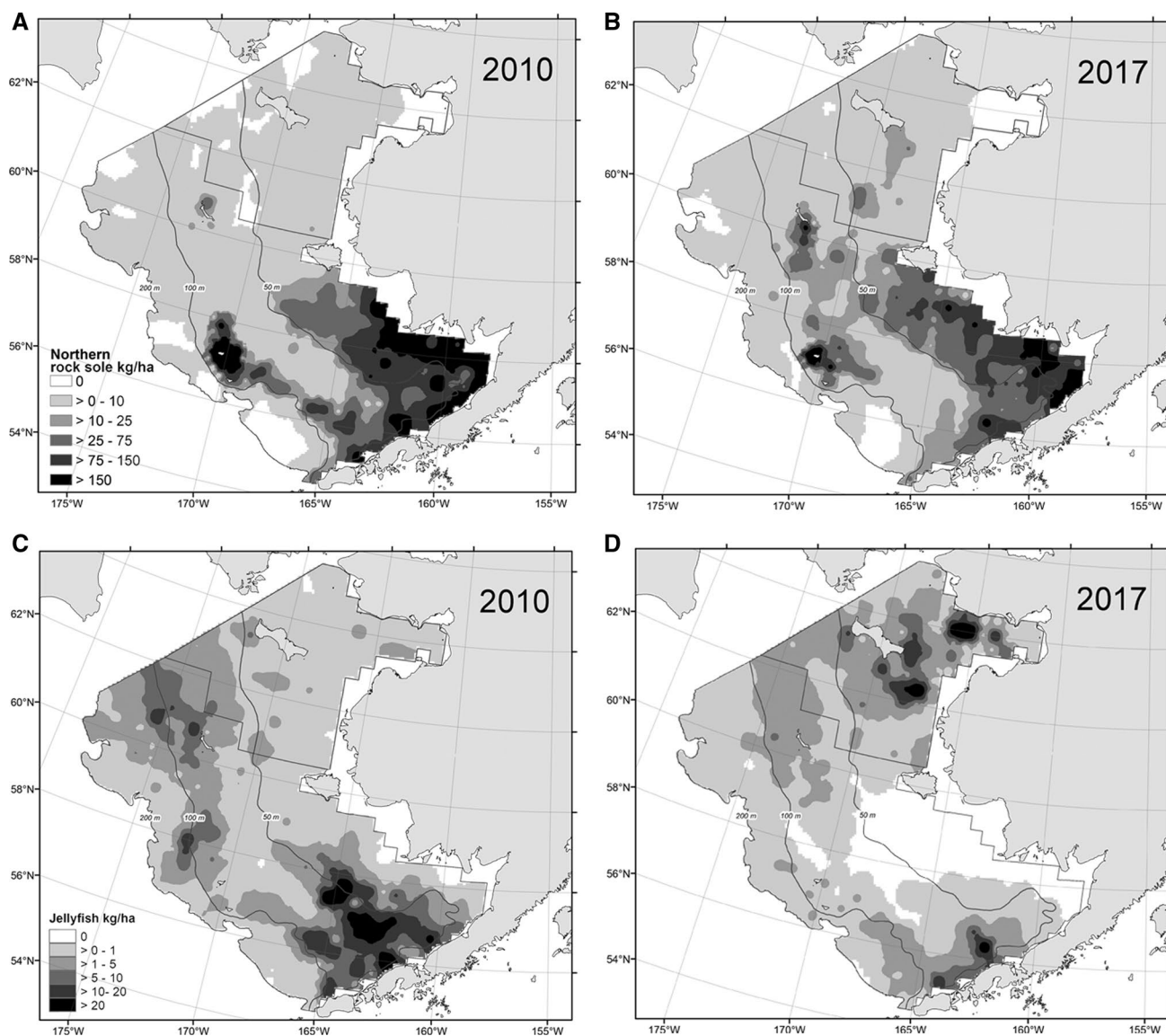


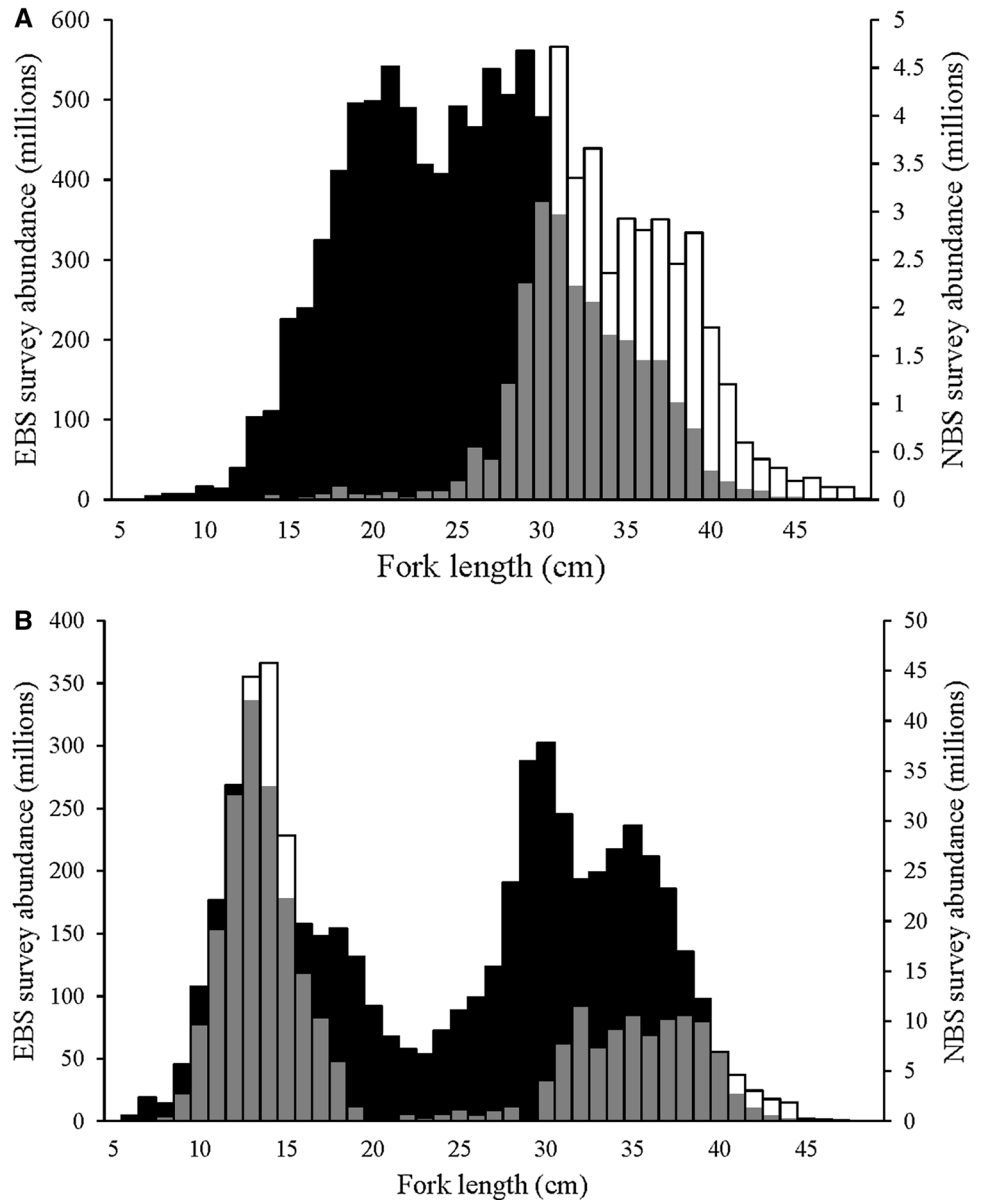
Fig. 9 Spatial distribution, in terms of mean CPUE (kg/ha), observed during the 2010 and 2017 bottom trawl surveys of the eastern and northern Bering Sea: **a** northern rock sole (*Lepidopsetta polyxystra*) in 2010, **b** northern rock sole in 2017, **c** jellyfish in 2010, and **d** jellyfish in 2017

aggregations were composed primarily of small individuals (1–2 year-olds), then their origin could be explained by a recent recruitment pulse, either within the NBS or in the northern portion of the EBS, but length frequency distributions for both species (Figs. 7, 8) indicate that these NBS aggregations were made up primarily of mature adults at least several years old (mostly the 2012 year class), and with size structures similar to their EBS counterparts. There was no indication that the biomass of pollock or cod was particularly high in the EBS in 2017, and there is no clear long-term trend of increasing biomass for either species in the region, so it is unlikely that the northern aggregations are the result of density-dependent displacement by a growing population. Thus, these changes in distribution patterns are more likely

the result of adult migration rather than a recruitment event (see “Discussion” below for northern rock sole) or general population expansion.

It appears that in the summer of 2017 masses of fish from the EBS migrated northward along the inner domain until they reached colder water near the Bering Strait, and found enough resources there to remain at the northern latitudes, at least for the summer. Pollock in the EBS typically migrate northward and shoreward following food resources in the spring and summer (Kotwicki et al. 2005), and the results presented here indicate that pollock are distributed more shoreward (farther east) in warmer summers when the cold pool on the middle shelf is not as extensive. The fact that large aggregations of pollock were found in the NBS

Fig. 10 Size composition of northern rock sole (*Lepidopsetta polyxystra*) in the eastern Bering Sea (EBS: black bars, left vertical axis) and northern Bering Sea (NBS: white bars, right vertical axis) for **a** 2010 and **b** 2017. Gray-shaded areas represent overlap between the two distributions



in 2017 may simply indicate that a portion of the population migrated shoreward and farther north during that warm year. Likewise, our results show that Pacific cod are generally distributed farther north on the EBS shelf during warm years, and their overall distribution patterns clearly suggest that the cold pool acts as a barrier to their movement, so it is not surprising that they may migrate north into the NBS during warm summers, particularly when there is no cold pool barrier.

Whether or not significant numbers of pollock and cod remain in the NBS later in the year when water temperature begins to drop again is unknown. Both species generally avoid the cold pool, and the capacity for long-term survival of both species at subzero temperatures is largely unknown. Avoidance of subzero temperatures by pollock has been

previously noted (Swartzman et al. 1994), and there is at least anecdotal historical evidence of Pacific cod becoming moribund or frozen in the Bering Sea (Cobb 1916; Veniaminov 1984) under extremely cold conditions. However, both species have been encountered in bottom trawl surveys at subzero temperatures in the EBS, and Atlantic cod (*Gadus morhua*) can produce antifreeze glycoproteins in response to cold temperatures (Hew et al. 1981; Fletcher et al. 1987). Thus, it is possible that these northern fish may remain in northern waters as winter ice formation commences, subsisting on the resources available below the sea-ice layer, or simply starving. Alternatively, they may migrate southward onto the EBS shelf again when the water cools in the fall.

While the distributional shifts noted here for pollock and cod are most likely due to latitudinal movement of adults,

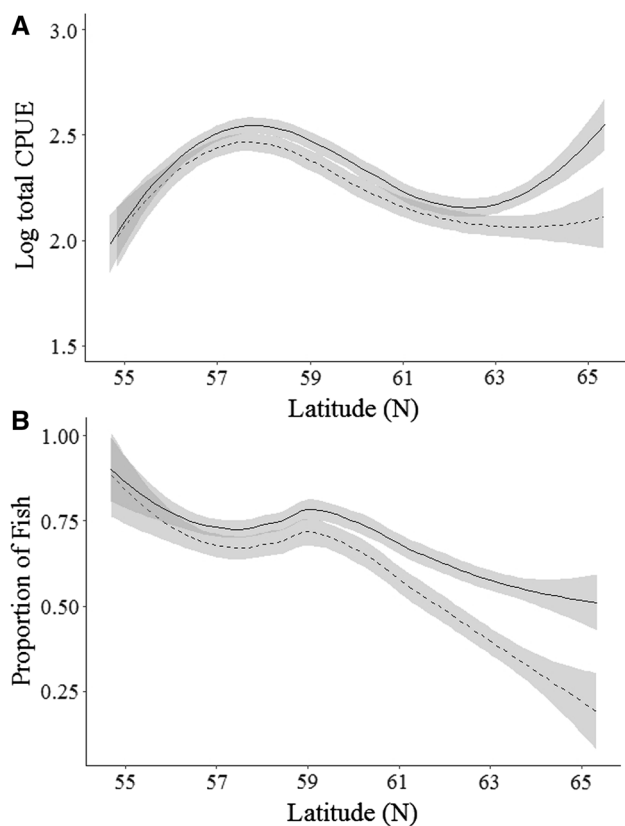


Fig. 11 Locally weighted means (with 95% confidence intervals) for **a** logtransformed total catch per unit effort (CPUE) versus latitude, and **b** proportion of total catch weight represented by fishes versus latitude for bottom trawls conducted during the 2010 (dashed line) and 2017 (solid line) surveys of the eastern and northern Bering Sea

distributional shifts can also result from changes in recruitment patterns. In 2010, the distribution of northern rock sole was heavily concentrated in the southeastern portion of the EBS survey area, outlining the southern terminus of the cold pool, and very few northern rock soles were encountered in the NBS. In 2017, northern rock soles were still concentrated in the southeastern EBS, but additional pockets of rock sole biomass were documented farther north, near St. Matthew Island and in the southern part of the NBS region. This pattern corresponds with the findings of Spencer (2008), who noted significant correlations between the area of the cold pool and the distribution of rock soles in the southeastern portion of the Bering Sea. The length frequency distribution of rock soles in the NBS in 2017 suggests that the northern group results at least partially from recent successful recruitment. The primary mode of this distribution is 12–14 cm (Fig. 10), which corresponds with 2–3 year old rock sole (Walters and Wilderbuer 2000). The recent warm period in the Bering Sea began in 2014, and bottom temperatures were well above the long-term mean from 2014 through 2016 (Conner and Lauth 2017). Cooper and Nichol (2016) found

that the distribution of juvenile rock soles is correlated with bottom temperature at settlement time (age-0), which would have been 2014 or 2015 for the specimens encountered in the NBS in 2017. Thus, the large number of juvenile rock soles encountered in the NBS in 2017 likely indicates successful recruitment in the region during the most recent warm period. Whether these juveniles will survive and remain in the NBS, particularly when another cold period begins, is uncertain.

Jellyfish populations have undergone dramatic biomass fluctuations in the eastern Bering Sea over the past few decades (Brodeur et al. 2008). Warm water temperatures and low sea-ice cover have been interpreted as unfavorable conditions for jellyfish populations in the EBS (Brodeur et al. 2008), while moderate and cold temperatures have been considered favorable. Our results confirm this previously described pattern and offer at least a partial explanation. During cold years, when primary productivity and zooplankton bloom activity is low in the northern waters, jellyfish populations are concentrated in the southeastern portion of the Bering Sea and, from an EBS perspective, their biomass is relatively high. During more moderate and warmer years, such as 2017, jellyfish populations shift northward into the NBS, perhaps in response to the abundant zooplankton and ichthyoplankton resources available in that region. In fact, jellyfish are dependent on essentially the same food resources as planktivorous pelagic fishes, such as walleye pollock, so it is not surprising that jellyfish populations shift in parallel with those species. This is an important pattern to recognize, as high densities of jellyfish may influence fish populations both through direct competition for zooplankton resources and through predation on the pelagic early life history stages of many fish species (Purcell and Arai 2001).

There is a latitudinal gradient in the Bering Sea marine ecosystem, from the sub-Arctic pattern in the south, which is characterized by long food chains and dominated by pelagic consumers, to the Arctic conditions of the north, where there is little pelagic consumption of the primary productivity and the majority of the carbon resources settle to the benthos (Grebmeier et al. 1988, 2006). Previous studies of latitudinal gradients in the fish and invertebrate community composition of the Bering Sea (e.g., Mueter and Litzow 2008; Stevenson and Lauth 2012) have shown that groundfish biomass declines with increasing latitude, and that fish populations tend to move farther north in the Bering Sea during warmer periods. This study further demonstrates that under favorable climatic conditions significant portions of the Bering Sea's total groundfish biomass can be found at its highest latitudes. A large influx of pelagic consumers such as pollock and jellyfish into the northern Bering Sea could potentially have profound effects on such a benthic-dominated ecosystem. The presence of these pelagic consumers indicates the availability of a significant zooplankton food resource, which in

turn must be supported by primary production in the water column. As more of the primary production is consumed by grazing zooplankton, which are then consumed by pelagic predators, less productivity reaches the benthic community and the tight pelagic–benthic coupling of the system may be disrupted (Grebmeier et al. 2006). This, in turn, may have a significant negative impact on the benthic invertebrate communities that support benthic-feeding birds and mammals, including sea ducks (Lovvorn et al. 2003), Pacific walrus (Jay et al. 2014), and gray whales (Highsmith and Coyle 1992; Moore et al. 2003).

Although the two surveys presented here provide contrasting snapshots of the northern Bering Sea ecosystem under different climatic conditions, we still do not know to what extent either condition represents an anomaly, or perhaps the early stages of a transition. The results of Stevenson and Lauth (2012), which were a composite of several surveys of the northern Bering Sea region from 1982 through 2010, suggest that the pattern presented here for the 2010 survey, in which fish biomass is very low in the NBS and trawl catches are dominated by invertebrates, is much more historically typical than the 2017 survey. Partial surveys of the NBS were conducted triennially from 1976 through 1991 (Wolotira et al. 1977; Bakkala and Wakabayashi 1985; Bakkala et al. 1985, 1992; Sample and Wolotira 1985; Walters et al. 1988), and a U.S.-Russian cooperative survey sampled much of the NBS, including the Gulf of Anadyr, in 1990 (Sample and Nichol 1994; Zimmermann et al. 1994). Some of those surveys reported relatively large CPUE numbers for both pollock and Pacific cod south of St. Lawrence Island, but the only two surveys that covered Chirikov Basin (in 1976 and 1979) found walleye pollock and Pacific cod “only in trace amounts” (Wolotira et al. 1977, p. 77; Sample and Wolotira 1985, p. 22), and those that they did encounter were relatively small (< 20 cm). The first of these two surveys was conducted during a cold period that persisted for several years during the early 1970s, while the second was conducted during a warm period that lasted from the late 1970s into the 1980s (Overland et al. 2012), but neither survey encountered significant biomass of large gadids. The U.S.-Russian cooperative survey of 1990—a year that was characterized by moderate temperatures near the long-term mean—found low concentrations of both species throughout the NBS and in the Gulf of Anadyr (Sample and Nichol 1994). Thus, although the presence of significant populations of both species north of the standard EBS survey area is not unprecedented, the finding of high concentrations of pollock and cod biomass north of St. Lawrence Island in the Chirikov Basin has not previously been documented.

Like the Bering Sea, other sub-Arctic and Arctic seas have recently been experiencing reduced ice cover and warming temperatures (Mackenzie and Schiedek 2007; Smedsrud et al. 2013). These climatic trends have been

accompanied by documented changes in the marine communities throughout the sub-Arctic and Arctic regions of the Northern Hemisphere, including the northward expansion of Atlantic cod and other fishes in the Barents Sea (Johansen et al. 2013; Fossheim et al. 2015) and changes in latitudinal and depth distributions of fishes in the North Sea (Perry et al. 2005; Dulvy et al. 2008). This process, which has become known as “borealization” (Fossheim et al. 2015), has been well documented in the North Atlantic, and the data presented here give a strong indication that it is happening in the northern Bering Sea as well.

The distribution shifts presented here have important implications for fisheries management in the Bering Sea. We now have good evidence that significant portions of commercially important groundfish species may be in areas outside the EBS shelf survey area during the summer sampling period. This is a management concern because the principal products of trawl surveys are fishery-independent indices of stock abundance used in stock assessment models that assume constant proportionality between true population abundance and survey-derived indices of abundance (Walsh 1997). For this assumption to be true, an entire population or stock, or at least a constant proportion, must be available within the standard survey area throughout the time series (Francis et al. 2003). Hence, the current survey-derived estimates of abundance for some commercial groundfishes from the EBS may be biased because they do not account for interannual variability in survey availability due to these distributional population shifts. Moreover, the coefficients of variation surrounding current survey abundance estimates do not incorporate nor propagate additional uncertainty associated with areal shifts in availability within the EBS survey area (Kotwicki and Ono In review). To address potential bias and account for added uncertainty, it will be necessary to work toward developing alternatives to the design-based abundance indices and variance estimates currently used to inform stock assessment models. One option is developing customized spatiotemporal model-based estimates of survey abundance for each species to account for other sources of uncertainty associated with biological and physical process errors in the Bering Sea (e.g., Thorson et al. 2015).

At present, we have only two recent survey years for the NBS, and therefore only two data points, so it will be crucial to extend this time series by continuing the NBS bottom trawl survey in future years. We must also pursue other directed research efforts to learn more about migration patterns, population stock structure, and to determine how fish populations and the community structure of the ecosystem are responding to the dynamic and changing environment in the Bering Sea. This research will help to reduce the bias of EBS survey abundance indices and provide more realistic estimates of survey variance for weighting abundance indices in stock assessment models. If the current trend

in the climate pattern of the Bering Sea continues into the future, additional research efforts in the NBS will become an increasingly important component of our strategy for the effective management and conservation of the Bering Sea marine ecosystem.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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