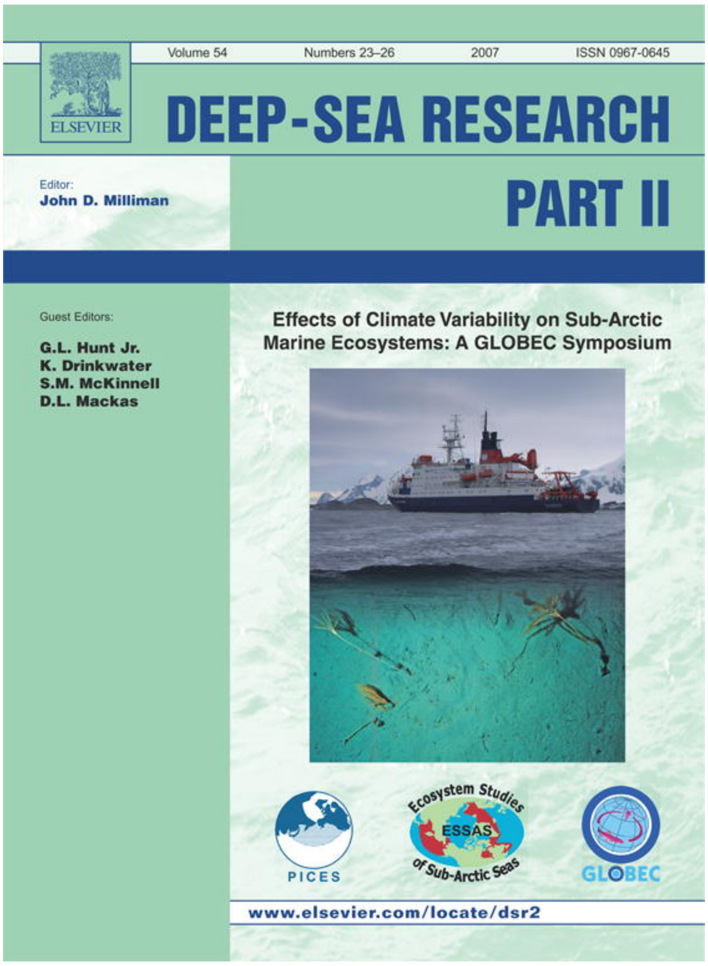
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Migration dynamics of Pacific herring (*Clupea pallasii*) and response to spring environmental variability in the southeastern Bering Sea

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Abstract

In the southeastern Bering Sea, Pacific herring (*Clupea pallasii*) migrate from the Pribilof Islands region where they overwinter, to the Alaska coast where they spawn in spring. The migration sustains a nearshore commercial fishery that targets roe-bearing females just prior to spawning. Herring also are taken as bycatch in groundfish trawl fisheries, where time and area closures in these fisheries are triggered by herring bycatch caps. Using herring bycatch data collected since the 1970s by National Marine Fisheries Service (NMFS) observers aboard groundfish fishing vessels, a retrospective analysis was conducted to describe the seasonal migration pattern of Pacific herring in the southeastern Bering Sea and to study its spatial and temporal variability. Observed changes in herring catch per unit of effort were compared with variability in climate and oceanographic conditions. The seasonal migration is complex, but annual shifts in migration routes and a possible northward shift of the overwintering grounds was identified. Pre-spawning herring aggregated in different areas depending on whether spawning occurred early or late in spring. The thermal structure of the ocean around the ice edge appears to influence herring migration timing and route as well as spawning date. Thus, on the basis of recent changes in sea-ice extent and duration, we suggest that the herring bycatch savings area that was developed from data collected in the 1980s should be revised to reflect prevailing conditions.

Keywords: Pacific herring; Bering Sea; Spawning migration; Sea ice; Thermal structure

1. Introduction

Pacific herring (*Clupea pallasii*) are widely distributed in the temperate waters of the North Pacific from the California coast to the Aleutian Islands and from the Bering Sea across the Pacific Ocean to the Yellow Sea (Hay, 1985). They are closely associated with the continental shelf and coastal environment, although they migrate through a variety of habitats depending on population and life stage (Hay and McCarter, 1997). In general, Pacific herring spawn earliest at southern latitudes and later at higher latitudes, in association with the northward progression of the spring bloom. Herring spawn in shallow subtidal or intertidal areas along coastlines each spring and then move offshore to

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feed (Mecklenburg et al., 2002). In fall, they move to deeper overwintering grounds where the diel vertical migration patterns associated with feeding become less distinct (Hay, 1985). Northern Bristol Bay herring, the largest herring spawning population in the eastern Bering Sea (EBS), migrate from an area northwest of the Pribilof Islands to Bristol Bay to an area north of Unimak Pass and back, a total distance of approximately 2100 km (Fig. 1).

The first studies of EBS herring migration were based upon data collected from foreign fisheries operating off the Alaskan coast. The demand for Alaskan herring increased following the collapse of the Japanese herring fisheries in the 1950s. Intensive trawl and gillnet fisheries, conducted mainly by Japanese and Russian fishermen, followed the seasonal migration of EBS herring. These foreign fisheries were phased out of the US Exclusive Economic Zone (EEZ) following passage of the Magnuson Fisheries Conservation and Management Act in 1976.

A clockwise migration pattern of Bristol Bay herring (Fig. 1) was indicated by many studies of fishery data collected before 1976 (Dudnik and Usol'tsev, 1964; Prokhorov, 1970; Rumyantsev and Darda, 1970; Wespestad, 1978; Barton and

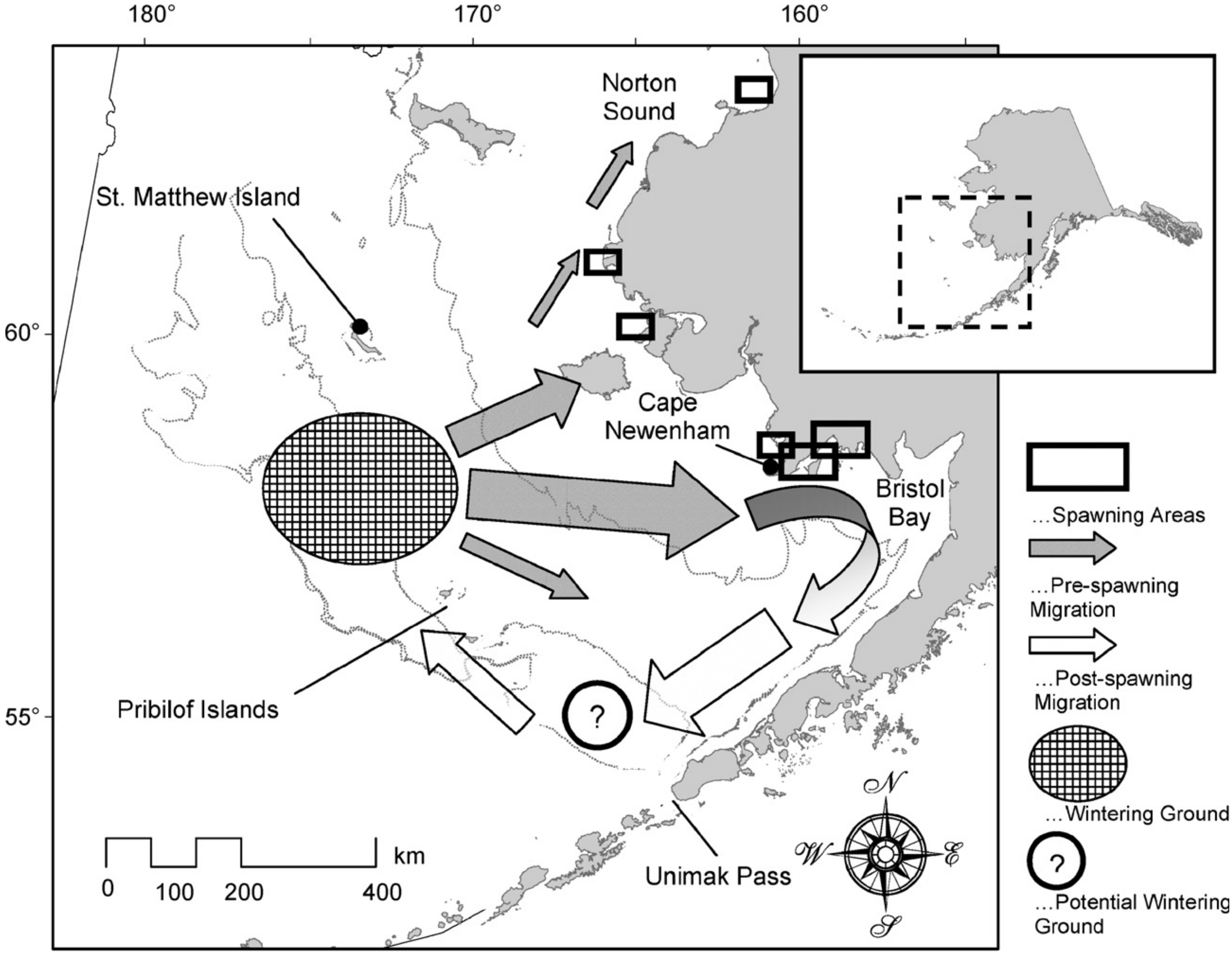


Fig. 1. Locations of spawning stocks of Pacific herring in the eastern Bering Sea and historically postulated migration pattern with wintering ground (modified from Barton and Wespestad, 1980). The gray lines are the 50-, 100-, and 200-m isobaths. Thick rectangles show historical spawning locations. The two largest rectangles represent the (largest) northern Bristol Bay spawning stock. The gridded circle at 58°N represents the major wintering ground in the southeastern Bering Sea (Dudnik and Usol'tsev, 1964; Prokhorov, 1970, Rumyantsev and Darda, 1970; Funk, 1990; Wespestad, 1978; Wespestad and Gunderson, 1991; Wespestad and Barton, 1981). The gray boxed arrows show pre-spawning movements, and the white boxed arrows show post-spawning movements. The blank circle with question mark is the speculated minor wintering ground (Barton and Wespestad, 1980).

Wespestad, 1980; Funk, 1990). Herring were found to overwinter mainly off-bottom to the northwest of St. Paul Island and to disperse over the shelf beginning in early spring. From April to May, they migrated to the coast where they spawned from May to June, although in recent years spawning has begun occasionally in late April. After spawning, herring remained in the spawning area or migrated southward along the Alaska Peninsula, where most of the herring accumulated near Unimak Pass to feed before moving north across broad feeding areas along the continental shelf and slope in summer (Rumyantsev and Darda, 1970). In fall, herring concentrations gradually moved to locations northwest of the Pribilof Islands to overwinter.

The objective of this study was to re-examine the seasonal migration of Pacific herring, including its spatial and temporal variability, using more extensive information than was available from the foreign fisheries. Specific objectives were to: (1) determine herring migration pathways using herring bycatch data collected from the foreign and domestic groundfish fisheries, (2) analyze the general pre-spawning migration relative to oceanographic conditions in spring, and (3) explain variability of herring migration patterns relative to variability in EBS oceanography. This study was motivated, in part, by the possibility that herring migration patterns may have changed in association with climate regime shifts in 1976–1977 and 1989. The latter shift started a period of rapid warming in the southeastern Bering Sea, accompanied by declines in both the extent and concentration of sea ice cover (Overland et al., 2004). A shift in herring migration route might be anticipated because a congener, the Atlantic herring (*Clupea harengus*), has changed its wintering and feeding grounds in the North Sea several times since 1950 (Corten, 2002). Episodic environmental shifts have been implicated as the cause of changes in northern Norway herring migrations (Slotte, 1999a, b).

2. Methods

2.1. Data collection and processing

2.1.1. Herring data

Records of herring bycatch in groundfish trawl fisheries from 1977 to 2003 were obtained from the Alaska Fisheries Science Center, National Marine Fisheries Service (NMFS) observer database. Herring bycatch in these fisheries was recorded as metric tons. Fishing effort associated with this bycatch was measured as tow duration (minutes), unique tow number, and number of records. A "record" is the number of fishing trips each day in same area, and each record can include multiple tows. Fishing locations were identified by the location where the gear was retrieved, recorded to the nearest minute of latitude and longitude. ArcGIS 9.0 (ESRI) was used to stratify retrieval locations by $50 \times 50\,\mathrm{km}^2$ cells. To comply with confidentiality requirements, cells with fewer than three tows were excluded from the analyses.

Catch per unit of effort (CPUE) was calculated by dividing the biomass of herring taken as bycatch in a haul by the duration of the tow. As hauls lacking tow duration accounted for 65% of the records and many of these hauls were made nearshore, exclusion of these records would have introduced spatial bias in geographic coverage. For cases when tow duration was missing, it was estimated from a linear model that predicted tow duration from frequency of tows by month in each $50 \times 50\,\mathrm{km}^2$ cell. There was a statistically significant relationship between total tow duration and total numbers of tows for each available fishery type for both joint-venture and non-joint venture fisheries before 1990 ($P<0.001$, $r^2>0.65$). If the number of tows was not available, then duration was estimated from a linear model based on the number of fishing records; tow duration and numbers of fishing records were statistically significantly correlated ($P<0.001$, $r^2>0.42$). In the case of mothership fisheries, fishing records may represent deliveries from multiple tows. Data were excluded if neither proxy was available. During preliminary analysis, it was found that tow duration in the 1990s had large variance, so hauls with missing durations from the 1990s were omitted from the analysis.

To describe monthly spatial distributions of herring, an index of their relative abundance was developed using CPUE of herring bycatch in each fishing operation. Because herring CPUE varies as a function of several factors, in addition to their abundance in a grid cell, the CPUE data were stratified and standardized to accommodate the influence of three factors: (1) type of fishery (e.g., mothership, small trawler, or large trawler operations for joint venture fisheries and foreign fisheries during 1977–1990 and non-pelagic, pelagic, mixed, pair, and shrimp trawls for domestic fisheries during 1990–2003), (2) general level of herring biomass in the EBS (three annual levels created using 33rd and

67th percentiles of annual spawning biomass estimates from the ADF&G Togiak herring management area over 1977–2003 so that years of high herring abundance did not dominate the interpretation of herring distributional patterns), and (3) month (to adjust for seasonal differences). To do this, hauls with no herring bycatch were omitted and herring CPUE values in the remaining hauls were natural-log transformed (lnCPUE). Next, for each grid cell in a given year and month, each lnCPUE observation was standardized by subtracting the mean within each fishery type, biomass level, and month, dividing by the corresponding standard deviation, and adding 3.0 ($\mu \pm 3\sigma$ encompasses all measurements) to convert all standard normal deviates to positive values

$$Z_{g,b,f,y,m,i} = \frac{\ln \text{CPUE}_{g,b,f,y,m,i} - \bar{X}_{b,f,m}}{\text{SD}_{b,f,m}} + 3, \quad (1)$$

where $Z_{g,b,f,y,m,i}$ is the standardized log-transformed deviate for each CPUE i observed in grid cell g in month m of year y for herring biomass level b in fishery f. A CPUE observation is typically an individual haul or trawl tow except for foreign motherships where fishing records (deliveries) sometimes represent multiple tows. Eq. (1) simply scales the CPUE deviates in each grid cell to have a common mean and variance to allow comparison across different herring population levels and fishery types. For a given fishery type, a simple average of these standardized CPUE deviates for each grid cell, biomass level, year and month is $\bar{Z}_{g,b,f,y,m}$. To combine these fishery-specific values into an overall mean value (representing all fisheries combined) for each cell in each month and each year, we calculated weighted averages as

$$\bar{Z}_{g,y,m} = \frac{\sum_{\text{all}\_f} \sum_{\text{all}\_b} n_{g,b,f,y,m} \bar{Z}_{g,b,f,y,m}}{N}, \quad (2)$$

where $n_{g,b,f,y,m}$ is the number of observations in each grid cell for each biomass level and fishery type by year and month, and N is the overall total number of observations, including hauls with no bycatch. Weighted averages at this level Eq. (2) allowed analysis of herring relative abundance for each month and year, whereas a simple average of these weighted averages ($\bar{Z}_{g,m}$) across all years (1977–2003) allowed analysis of average monthly herring distributions independent of year.

To summarize herring distributions from the CPUE data, kernel density contours were estimated in ArcGIS Spatial Analyst. The kernel ($f_{(x)}$) is estimated by

$$\hat{f}_{(x)} = \frac{1}{nh} \sum_{i=1}^{n} K\left(\frac{x - X_i}{h}\right), \quad (3)$$

where h is the smoothing parameter or bandwidth, X_i is the ith observation, x is the exact location over the study area, n is sample size, and K is the kernel function giving the weights to the values for estimation (Silverman, 1986). K determines the basic shape of the smoothed lines and h determines the degree of horizontal generalization and is set as the "searching radius" (Silverman, 1986). We set the kernel function to the default value used by ArcGIS 9.0 (ESRI), which approximates the Gaussian kernel. The searching radius was defined as 142,000 m (the diagonal of two 50-km cell widths), which allowed us to generalize the CPUE values using at least two neighborhood points even in the isolated corners of the grid.

To visualize both the general movement and the variability of herring distribution and migration, two types of plots were generated from the kernel density surface: one from the abundance index in each calendar month combined over years (biomass concentration plot), and another from the abundance index in individual months from individual years (peak plots). In the biomass concentration plots, monthly density surfaces revealed the general seasonal movement regardless of the interannual variability of herring population parameters. The peak plots showed the detailed monthly distributions of CPUE in each year.

For the biomass concentration plots, contours of constant density were fitted to the kernel density surfaces. Using these contours, the spatial arrangements of the monthly upper quartiles were assumed to represent the general movement of herring and its seasonal variability. For the peak plots, any individual month with <30 grid cells with CPUE data was discarded. Then, a kernel density surface was fit to the remaining months, by year. From the fitted density contours, we calculated the upper quartiles to display areas of peak herring abundance in each month in each year. The locations of the centroids of these peaks was determined for every year and month. The percentiles of the kernel density surfaces were classified with ArcMap based upon the estimated density index ($f_{(x)}$). A Visual Basic in Application (VBA) function in ArcGIS was used to calculate the centroids. An analysis of the dispersion of these centroids in each month and year was used to reveal interannual variability of the geographic location of herring and identified the months of greatest variability in herring location.

2.1.2. Environmental data

Two environmental variables were hypothesized to affect herring pre-spawning (April–May) migration dynamics: sea-surface temperature (SST) and sea-ice total concentration (SITC). The SST data were collected by vessels of opportunity and reported by latitude and longitude in the Comprehensive Ocean-Atmosphere Dataset (COADS) from the National Climate Data Center (NCDC). The SITC data were taken from the Environmental Working Group Joint US-Russian Sea Ice Atlas (Arctic Climatology Project) from the National Snow and Ice Data Center (NSIDC) and archived sea ice charts by National Ice Center (NIC).

The spatial overlap between the COADS SST data and the herring distribution data was not great, so the SST data were smoothed by kriging with a geostatistical analyst (ESRI), one of the ArcGIS extensions. Distance and directional autocorrelations were used in deriving the estimated SST field, and extrapolations were cross-validated to obtain the most representative estimates (Tojo, 2006). For this analysis, grid cells were defined as 1 km^2.

The SITC dataset with 12.5 km^2 grid cells was produced in raster format until 1994. After 1994 the data were recorded in vector format with smooth lines to partition the polygons. Vector format data were converted to raster format for consistency. Missing or corrupted GIS ice charts in the NIC data archive were repaired or replaced by digitizing the original NIC ice charts. Because the conversion algorithm produces misleading wiggly lines connecting the centers of the individual cells, an inverse distance weighting (IDW) of the extrapolated surface was used. The IDW method simply weights the values as an inverse linear function of the distances.

2.2. Analyses

2.2.1. General migration pattern

To visualize the general migration pattern of EBS herring, the centers of statistical quartiles of herring distributions from CPUE density surfaces were plotted by month for years with sufficient data for analysis. For this purpose, the same equal-area projection was applied as was used for the data processing. By plotting the upper quartile of the density surfaces, we aimed to clarify the areas where herring were concentrated.

2.2.2. Variability of migration patterns

The dispersion of annual peaks of herring distribution was calculated by the average nearest-neighbor distance among the centroids of those peaks. The larger the average nearest-neighbor distance indicates more dispersion among these centroids. The month with the greatest dispersion was identified as the month with the most inter-annual variability of migration.

The pre-spawning migration season (April and May) was known from previous studies (Barton and Wespestad, 1980; Hay, 1985) and from our observations of spawning sites in 2003 and 2004. Therefore, herring distributions were compared with environmental conditions by overlaying the GIS layers for herring (centroids of CPUE peaks) with the corresponding SST and SITC interpolated surfaces. Monthly SITC and SST surfaces were compared with the timing of herring arrival at the northern shore of Bristol Bay, determined from historical aerial surveys conducted by the Alaska Department Fish and Game (ADF&G). We binned years as early (1982, 1985, 1986, 1988, 1990, 1992, 1994) or late (1981, 1983, 1987, 1993, 1998, 2000, 2001, 2003) based on the upper and lower quartiles of arrival date on the spawning grounds (Table 1).

3. Results

3.1. General migration pattern during 1977–2003

The spatial distribution of fishing effort was sufficiently broad (Fig. 2) to allow the use of fishery bycatch CPUE data to examine the seasonal migrations of herring. Overall, from 1977 to 2003, fishing effort was distributed throughout the EBS, extending into the Aleutian Basin. Fishing effort was most heavily concentrated in the middle domain (50–100 m), especially in spring and summer, and in the outer domain (depth >100 m) of the southeastern Bering Sea. Fishing in deep areas such as the Pribilof Canyon, southwest of the Pribilof Islands, was associated with the walleye pollock (*Theragra chalcogramma*) fishery.

Monthly distributions of herring biomass often had peaks in two regions, one located west of St. Matthew Island and the other between St. George Island (the southernmost Pribilof Island) and Unimak Pass throughout most of the year

Table 1
Arrival timings of herring to northern Bristol Bay spawning area, sorted by statistical percentile

Julian day	Year	Percentile	Bin	
111	2003	0	Early	
112	1981	4	Early	
114	1987	8	Early	
114	1993	8	Early	
115	2000	16	Early	
116	1983	20	Early	
116	1998	20	Early	
116	2001	20	Early	…early 25th percentile
117	1997	32	Normal	
119	1980	36	Normal	
119	1996	36	Normal	
120	1979	44	Normal	
121	1978	48	Normal	
122	1995	52	Normal	
122	2002	52	Normal	
123	1984	60	Normal	
124	1990	64	Normal	
125	1989	68	Normal	
126	1991	72	Normal	…late 25th percentile
127	1986	76	Late	
128	1994	80	Late	
129	1988	84	Late	
132	1982	88	Late	
135	1999	92	Late	
137	1992	96	Late	
139	1985	100	Late	

Upper and lower 25th percentiles (thick underlines) were used for the borders to define both early and late bin years in analyses.

(Fig. 3). This bimodal distribution was least apparent in June, when herring were concentrated north of Unimak Pass. The spatial extent of area in the upper quartiles was minimum in December (125,042.5 km^2) and maximum in September (266,366.8 km^2). The average size of the area encompassing the upper quartile was 190,190.7 km^2 (95% c.i.−159,208.8 to 221,172.6 km^2). From November to March, the areas covered by the upper quartiles were smaller than the lower confidence interval of the monthly mean, indicating tighter concentration of herring from winter to early spring.

Among the pre-spawning months in spring, the greatest variability in the location of annual peaks was in April when the centroid peaks began to expand shoreward over the southeastern shelf (Fig. 3). Among months with adequate observations ($n>30$), the high ratio of the observed average monthly nearest-neighbor distances to the expected average nearest-neighbor distances based on a random distribution indicates greater dispersion in April compared to other months (Fig. 4). The z-score of the observed average nearest-neighbor distance in April was −1.71, which is not significantly different from the expected average nearest-neighbor distance in random distribution ($z^* \pm 1.96$, $\alpha = 0.05$). In general, the largest concentrations of herring biomass occurred approximately 250 km east of the Pribilof Islands. In years of maximum eastern extent, the distribution in April reached the vicinity of major coastal spawning areas. In May, herring were concentrated along the shoreline in areas such as northern Bristol Bay (58.5°N, 160.5°W), and between the Pribilof Islands and western Yukon-Kuskokwim area (59°N, 163°W). In June, the major concentrations of herring extended along the coast of the Alaska Peninsula to Unimak Pass (Fig. 3). The concentration was broadly spread over Bristol Bay. The centroids of annual peaks developed as small clusters in various locations. The western "tail" of the herring concentrations shifted eastward by about 125 km compared to May. In July, herring concentrations showed a broad O-shaped pattern on the southeastern Bering Sea shelf (Fig. 3), and monthly peaks became more prominent at Unimak Pass. A minor concentration appeared south and offshore of St. Matthew Island along the slope. This bimodal feature intensified through fall and early winter. The northern mode was located west of St. Matthew Island (59°N, 177°W) and the southern mode extended northwest of Unimak Pass.

In November and December, the herring distribution was mostly limited to an area of the northern EBS centered near 59.5°N, 179°W although annual peaks occurred in the southeast in some years. Herring appeared to be sparse along the 65 m isobath but monthly fishing effort data were insufficient to provide any certainty for these detailed features. The overwintering concentration west of St. Mathew Island in November and December (59.5°N 179°W) was located more to the northwest after 1976 than in earlier years (Wespestad, 1978; Appendices in Tojo, 2006).

3.2. Interannual variability in herring migration: comparisons to variability in ocean conditions

As the greatest interannual variability in the location of herring distribution peaks occurred in April, it may be a key month for determining

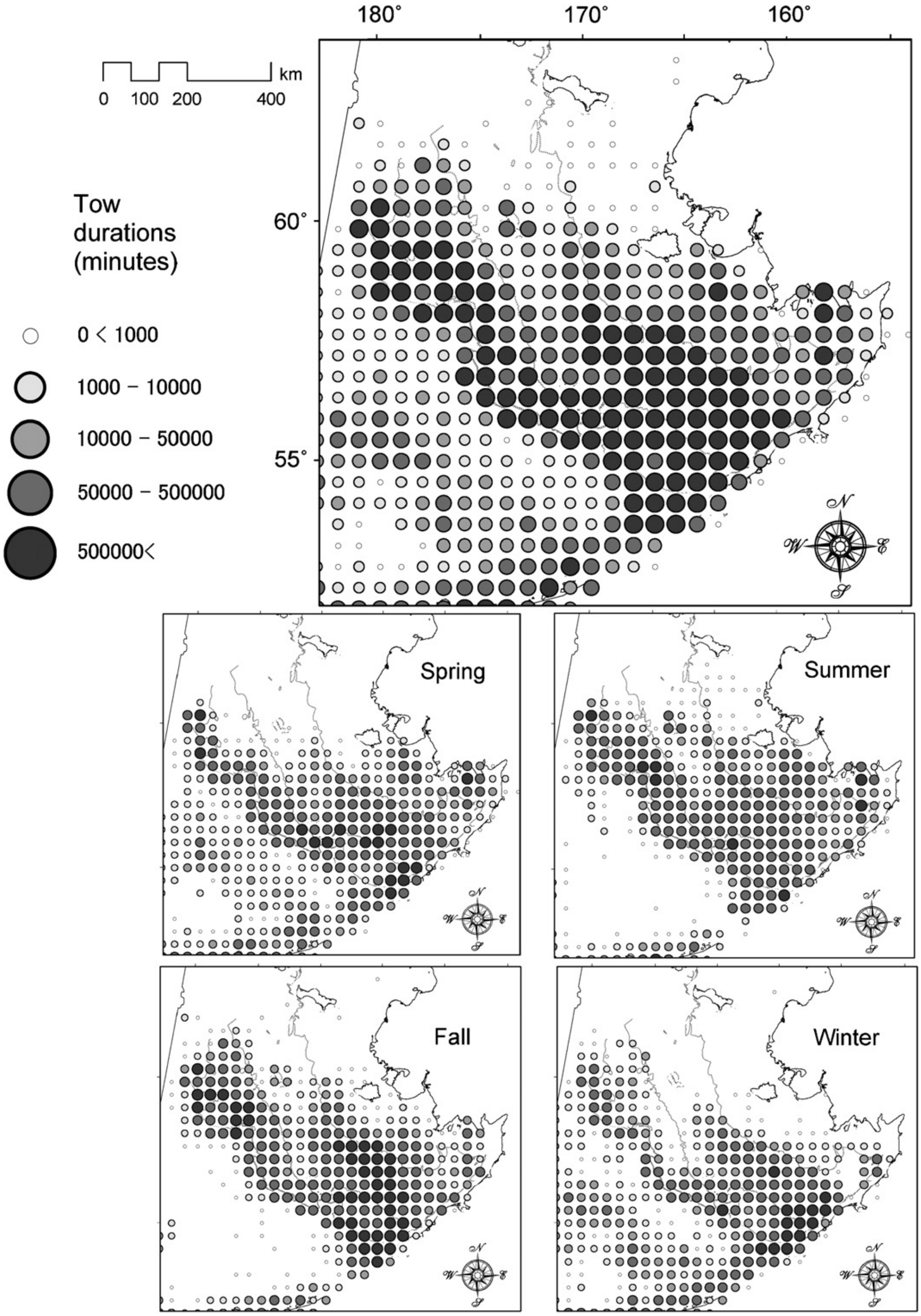


Fig. 2. Historical and seasonal distributions of fishing effort from 1977 to 2003. Total duration of all tows is used as an index of fishing effort for all years combined. Gray lines show the 50-, 100-, and 200-m isobaths.

whether herring migrate early or late in the season, perhaps owing to environmental conditions that affect gonadal maturation. The ice edge in April was ~150 km farther north in early versus late arrival years, especially in the coastal areas of northern Bristol Bay (Fig. 5A). For both arrival years, centroids of peaks occurred in areas of less ice from sea-ice edge to the open sea; 17 of 18 centroids in early years and 11 of 13 in late years in April were present in the area where SITC was less than 25% (Fig. 5A).

In April the ratio of observed to expected average nearest-neighbor distances among peak centroids was 0.83 in early arrival years and 0.65 in late arrival years. The average nearest-neighbor distance among peak centroids in late arrival years (z-score $= -2.14$, $\alpha = 0.05$) indicated statistically significant clustering of centroids, indicating a clumped distribution of centroids and less detectable variability in migration patterns in late arrival years. On the other hand, the z-score (-1.45) in early arrival years fell within the 95% confidence interval, indicating that the among-centroid distances in early arrival years could not be distinguished from random dispersions in these years. Coastal waters, extending northward from the northeast corner of Bristol Bay, were enclosed by the $>55\%$ isoclines of SITC in late arrival years. The SST observations generally revealed a larger expanse of cold water on the southeastern continental shelf in the late arrival years than in the early arrival years. On the other hand, there was no obvious difference in ice distribution/concentration or SST along the continental shelf edge, Aleutian Basin area, or northern portion of the EBS among early and late arrival years.

Where they occurred, differences in sea-ice distribution among early and late arrival years persisted into May (Fig. 5B). In early arrival years, sea ice receded more to the north and the coastal area was mostly ice-free in the spawning areas except in Norton Sound. In May in late arrival years, the coastal zone remained covered with sparse sea ice, and a distinctive feature was the

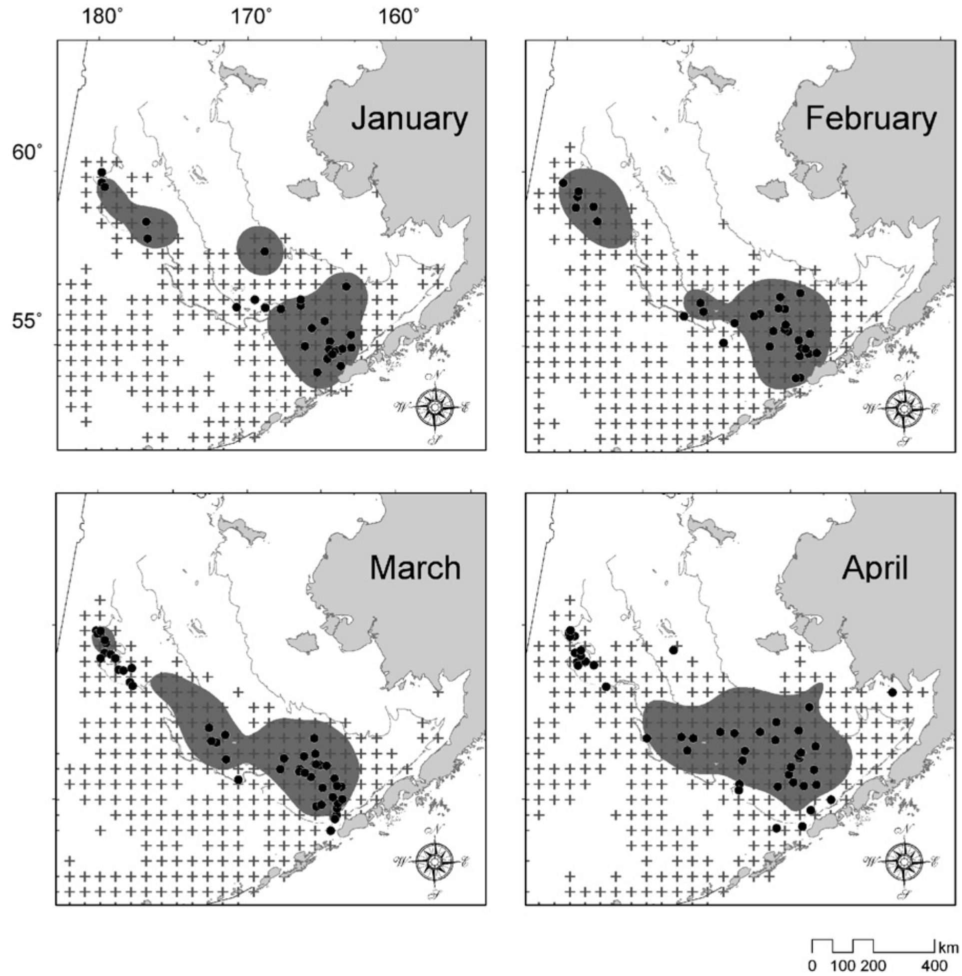


Fig. 3. General migration pattern of herring in the eastern Bering Sea from 1977 to 2003. Gray shaded areas represent the upper 25th-percentile monthly contours of catch-per-unit-effort (biomass concentration plot: gray shaded) averaged across all years and black dots represent the annual peak locations within yearly centroids of herring concentrations by month. Cross marks indicate fishing efforts yielding no reported herring catches.

southward tongue-like extension of >10% sea ice isoclines (and cold SST) between Cape Newenham and the Pribilof Islands. In early arrival years, herring tended to occur in open water, whereas herring seemed to be more associated with the ice edge in late arrival years (Fig. 5B).

4. Discussion

4.1. General migration pattern of EBS herring

We confirmed the general inshore–offshore seasonal migration pattern of Bristol Bay herring found in earlier studies, but there were some important exceptions. Previous studies (e.g., Prokhorov, 1970; Rumyantsev and Darda, 1970; Barton and Wespestad, 1980; Funk, 1990) concluded that herring migrated in clockwise pattern in the EBS (Fig. 1), overwintering mainly off-bottom to the northwest of St. Paul Island. In contrast, we identified two concentrations in fall/winter. One was located farther to the northwest of the Pribilof Islands than had been reported previously, and the other was a new location north of Unimak Pass, extending to the northwest in the direction of the Pribilofs (Fig. 6). There was some speculation about the existence of a southern overwintering ground (Barton and Wespestad, 1980), but it was not clearly indicated in the pre-1976 analyses (Wespestad, 1978). Our concept of seasonal migration places herring in both southern and northern overwintering areas, spreading eastward over the middle shelf in spring and heading toward the coast (Fig. 6). Spawning generally occurred from May to June, as indicated in previous studies, but it has begun to occur in late April in recent years. As previously reported, herring were sparse around the spawning area after spawning as at that time they were migrating southward along the Alaska Peninsula. The majority of the herring spawners, mainly from northern Bristol Bay, accumulated near Unimak Pass to feed. Some of the other northern stocks

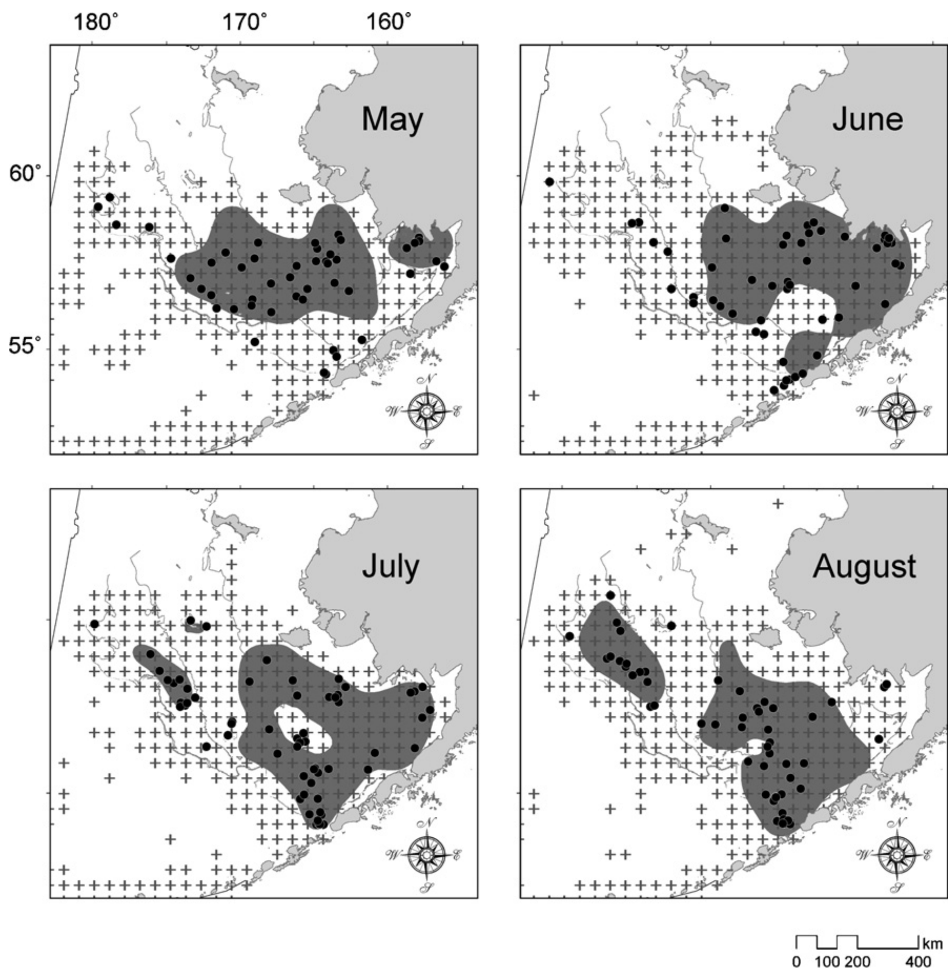
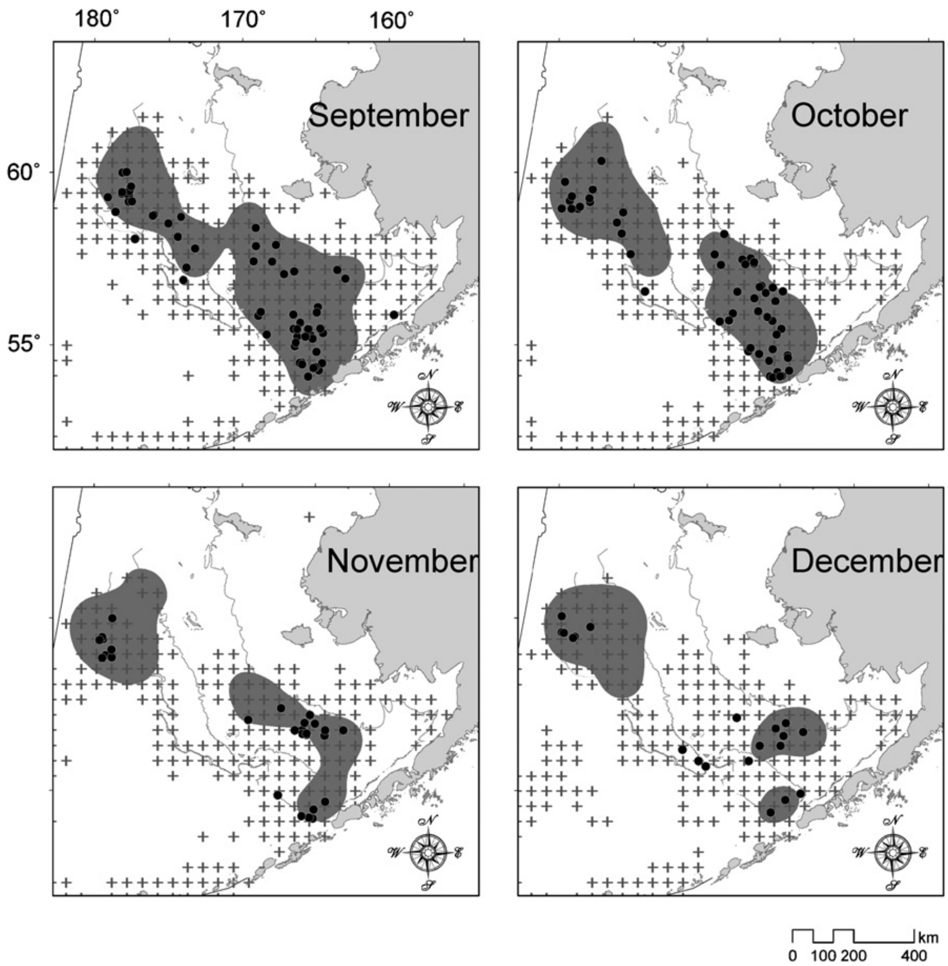


Fig. 3. (*Continued*)



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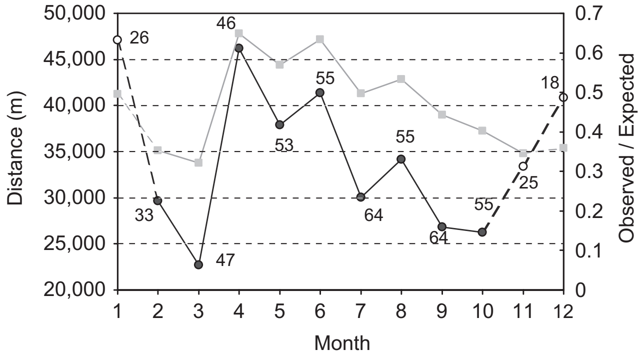

Fig. 4. Monthly change of average nearest neighborhood distances (average NND: black dots) and observed average NND to expected average NND ratio (solid rectangles). The average NDD is computed between centroids for consecutive months. The expected average NND were calucurated with the ArcGIS argorithm by assuming random distribution within same area extent of observed datasets. The numbers next to the dots or rectangular are the numbers of observations each month. NND in the months without adequate observations ($n \leqslant 30$: January, November, and December) were noted with open symbols. The spike in NND for April indicates movement between March and April. Low NND values in March and fall indicate that herring were most clustered in those months.

migrated across the shelf, as well. Whereas previous studies have indicated that herring move northward along the continental shelf and slope in summer and fall (Rumyantsev and Darda, 1970), we found that some herring followed this pattern, whereas others remained behind to overwinter north of Unimak Pass. Thus, the migration of Bristol Bay herring cannot be simply characterized as "clockwise" pattern as was previously proposed. Instead, we suggest a modified conceptual model of EBS herring migration with both northern and southern over-wintering and feeding grounds (Fig. 6).

In Atlantic herring, large-scale migrations have been related to schooling behavior (Huse et al., 2002) and spawning timing is related to body length of pre-spawning individuals (Slotte and Fiksen, 2000; Slotte, 1999a) as well as responses to oceanographic factors (Messieh, 1987). The persistence of general migration patterns, perhaps learned by younger age classes from older age classes, was proposed for Atlantic herring (Corten, 2002). In British Columbia, spawning waves occur in association with gonad maturation level and migration speed depends upon the differences of body size or age (Ware and Tanasichuk, 1989). Our data do not allow us to conclude whether migration patterns of young herring are learned from old herring, but from 1978 to 2004, larger herring do tend to spawn first in northern Bristol Bay (Tojo and Kruse, unpublished data).

A conceptual model of fish migration was developed by Harden Jones (1968, 1980), and

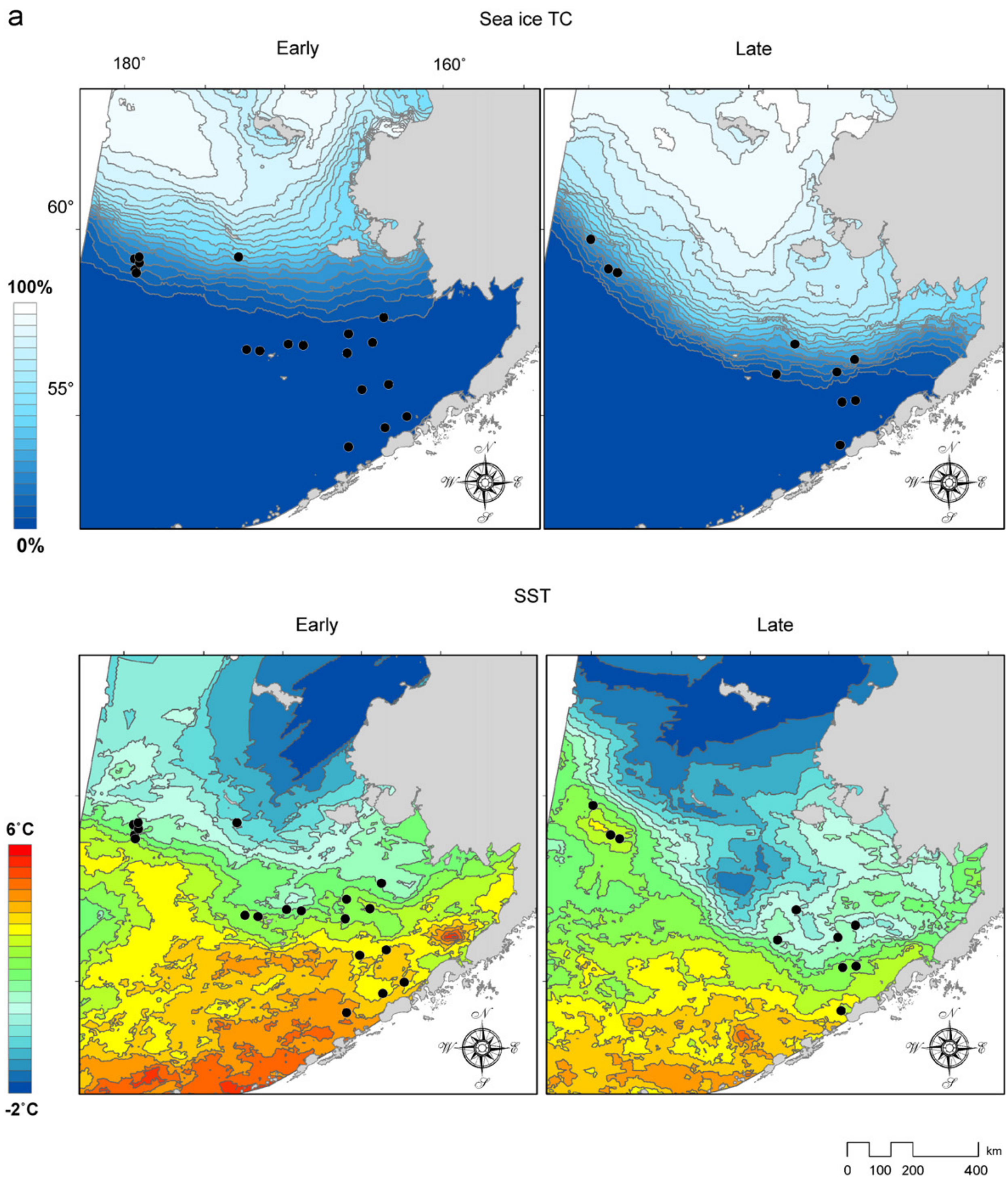

Fig. 5. Comparisons of monthly herring distributions for early and late spawning years in (A) April and (B) May. Herring distributions are shown for early (left panels: 1981, 1983, 1987, 1993, 1998, 2000, 2001, 2003) and late spawning years (right panels: 1982, 1985, 1986, 1988, 1992, 1994, 1999). For each comparison, the top panel is a comparison between the monthly peaks of herring (dots) and average total concentration of sea ice (%) and the bottom panel is a comparison of catch-per-unit-effort with average SST (°C) for the same years.

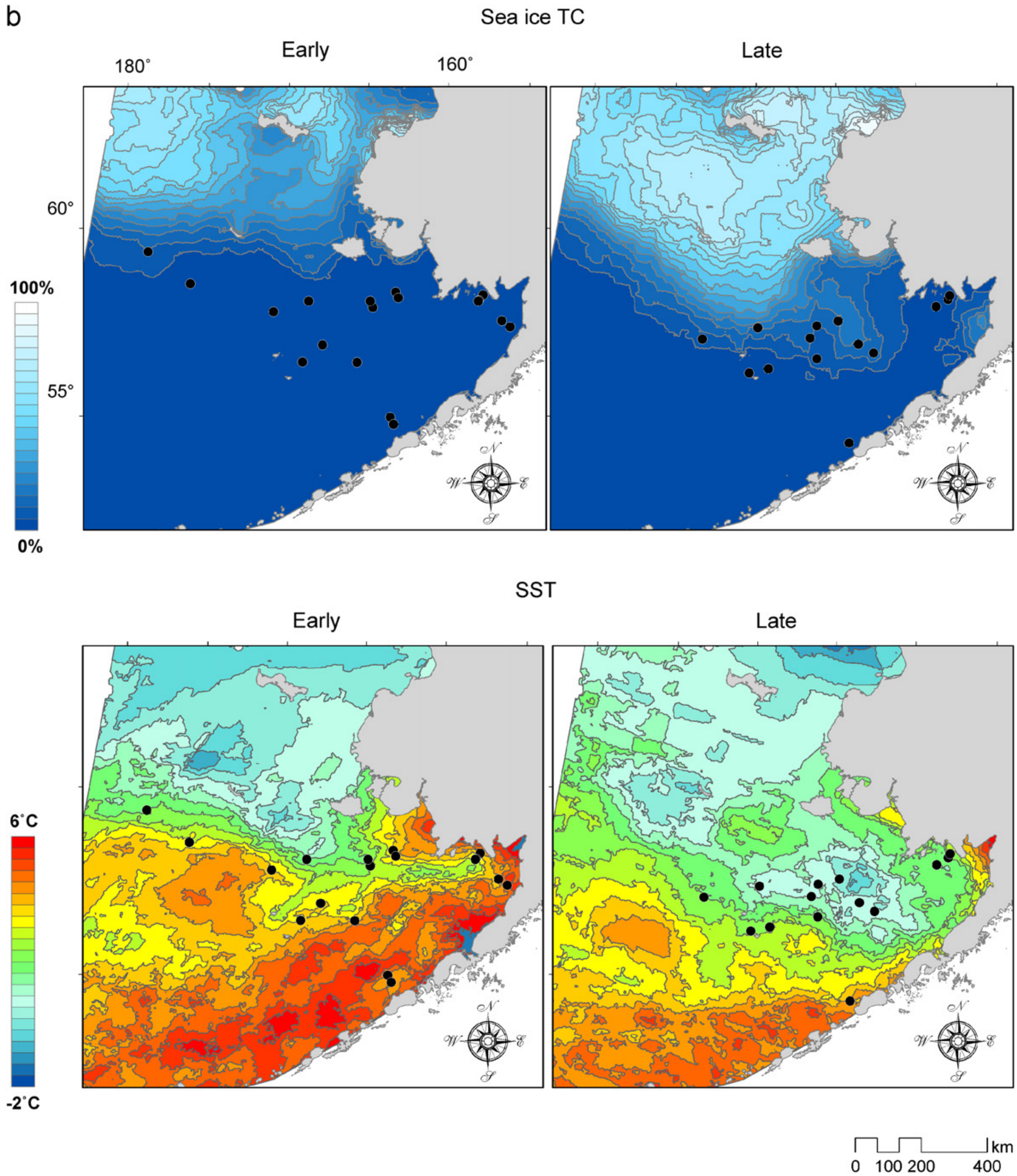

Fig. 5. (*Continued*)

improved by Cushing (1981) and others (e.g., Secor, 2002) to incorporate an ontogenetic component of migration. In overview, this conceptual model involves a triangle of fish movement throughout their life history. It includes advection of larvae from a spawning area (one point of the triangle) to a nursery area (a second point of the triangle). Once herring attain sexual maturity, they join the adult population, with repeated seasonal migrations between feeding (the third point of the triangle) and the spawning areas. Based on our analysis, it seems that this migration model does not fit the EBS herring very well. Although after spawning some herring probably return to the major overwintering grounds northwest of the Pribilof Islands for feeding, another major herring concentration can

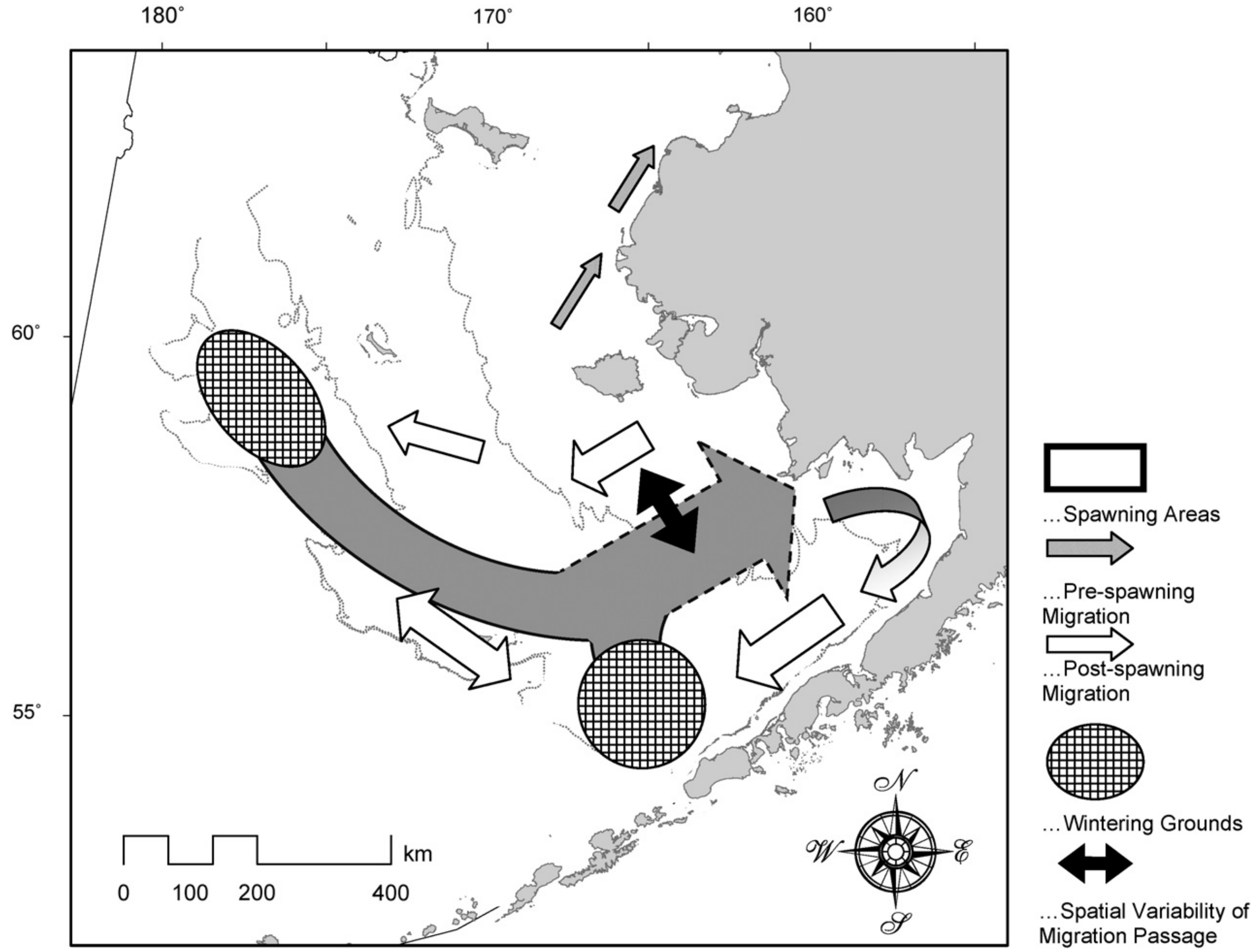

Fig. 6. Revised eastern Bering Sea (EBS) herring migration pattern and spatial variability in pre-spawning migration. The gray lines are the 50-, 100-, and 200-m isobaths. Thick rectangles show historical spawning locations. The two gridded circles represent the major wintering grounds. The gray boxed arrows show pre-spawning movements, and the open boxed arrows show post-spawning movements. The thick black arrow indicates postulated spatial variability of major pre-spawning migration passage of herring (dotted gray box arrow) due to sea ice edge thermal dynamics.

be found north of Unimak Pass in summer. Presumably, these post-spawning herring are actively feeding so the major feeding and overwintering grounds do not always coincide. Likewise, although there is a clear northward movement of herring in the fall, some herring remain in the southern habitat around the southeastern EBS shelf area in the winter (Fig. 6), counter to the simple Harden Jones migration triangle.

A northwestward shift of the northern overwintering concentration has occurred in recent years that could be related to regional warming that began in 1989 with a shift in the Arctic Oscillation (Overland et al., 2004). However, such ideas require cautious interpretation because of the potential influence of other factors. The distribution of herring that spawn in the Gulf of Anadyr can overlap the distribution of EBS herring in their overwintering area northwest of the Pribilof Islands (Wespestad and Gunderson, 1991). Therefore, all herring bycatch in groundfish fisheries in the US EEZ is not necessarily of US origin.

Because of their long-distance migration and their abundance, Pacific herring play important roles in energy transfer throughout the Bering Sea ecosystem. Firstly, their seasonal migration facilitates cross-shelf transport of energy among offshore and inshore environments. Secondly, as forage fishes they are important conveyors of energy from lower trophic levels (planktonic organisms) to various upper trophic levels, including various bird species (Bishop and Green, 2001; Suryan et al., 2002; Rodway et al., 2003) and large megafauna (Sharpe and Dill, 1997; Sharpe, 2002; Gende et al., 2001; Thomas and Thorne, 2001).

Environmental conditions associated with the northern and southern feeding/wintering grounds likely affect predator and prey interactions and bioenergetics. The northward shift of overwintering aggregations may have both costs and benefits to herring. Costs may include some energetic expenditures necessary to swim greater distances between feeding and spawning areas. Potential benefits include the avoidance of predation by groundfish species that are abundant in the south (Adlerstein and Trumble, 1998), better local feeding conditions, and/or lower basal metabolic rates associated with colder temperatures to the north. Norwegian Atlantic herring show size- and age-specific differences in migration distances due to costs and benefits during the feeding migration (Kvamme et al., 2003). Perhaps EBS herring schools make a choice of migration route based on similar trade-offs.

Shifts in location of herring overwintering areas have practical management implications. In 1991, the North Pacific Fishery Management Council created a herring savings area (58–60°N, 172–175°W) to protect overwintering herring from incidental bycatch in other fisheries, particularly the winter walleye pollock fishery. The herring savings area is closed to fishing if observed herring bycatch reaches the Prohibited Species Catch (PSC) limit, which is set annually at 1% of the estimated EBS herring biomass. However, closure of the herring savings area has rarely been triggered. With apparent shifts in the overwintering grounds of herring, it may be necessary to realign the winter herring savings area to protect herring in the future. Also, relationships of other overwintering herring populations in this region may need additional considerations, particularly for determinations of the "unit stock" and accounting of total fishing mortality experienced during the herring's life history.

In conducting this analysis of patterns, herring bycatch data were used as an index of relative abundance. By doing so, it was assumed that trawl fishing gears sampled herring in proportion to their local densities and that representative samples of the catches were taken by onboard observers. Data were not collected in a way that would allow us to examine potential day/night differences in the vertical distributions of herring and associated differences in catch rates nor to examine differences among juvenile and adult herring. Although there is no way to test these assumptions with the available data, the general similarity between monthly herring distributions inferred from herring bycatch estimates (Fig. 3) and those inferred from the historical foreign fisheries that targeted herring (e.g., Wespestad, 1978, also see Appendix 1.A in Tojo, 2006), suggest that inferences about adult herring biomass distributions from these observations are reasonable. Because multiple observations were smoothed over time and space, the results are not very sensitive to deviations from these assumptions for individual tows.

4.2. Relationship between interannual herring migration dynamics and EBS ice edge variability

We posit that interannual variability of pre-spawning EBS herring migration timing and migration route in spring, particularly in April, is an adaptive response by herring to ice edge thermal dynamics (Fig. 5). In the western Atlantic Ocean, the size of the sub-zero water mass in spring determines whether shoreward movements of herring are inhibited during their spawning migration in the southern Gulf of St. Lawrence (Messieh, 1987). In the southeastern Bering Sea, cold melt-water extending from the ice edge (Alexander and Niebauer, 1981) and a stable thermocline (Muench and Schumacher, 1985) may guide herring schools along optimal isotherms as they migrate to the spawning grounds.

Responses of herring to sea ice are probably complex due to schooling behaviors and variable availability of optimal habitats. Temperature gradients appear to affect the distribution of Atlantic herring off Norway (Misund et al., 1998; Nøttestad et al., 1999), and temperature may influence Pacific herring distribution in the EBS (Barton and Wespestad, 1980). Energy expenditures during herring pre-spawning migrations are higher than during overwintering in northern Norwegian herring (Slotte, 1999b). It appears that Pacific herring follow specific isotherms along their migration route from offshore overwintering areas to coastal spawning grounds, but it is unclear whether there is a bioenergetic basis for this phenomenon.

There are records of pre-spawning herring occurring in sub-zero temperatures in the EBS (Rumyantsev and Darda, 1970), including observations of herring spawning under the ice in cold years in northern Bristol Bay (Jim Browning, 2003, personal communication). Similar instances were observed in other coastal regions of the southeastern Bering Sea (Christie Hendrich, 2003, personal communication). Likewise, information provided by local residents identified some small wintering aggregations under the ice in Norton Sound (Barton and Wespestad, 1980). These contradictory observations might be explained by herring schooling behavior (Fernö et al., 1998; Huse et al., 2002). For instance, a simulation study of Atlantic herring revealed changes in direction of an entire school when more than 7% of herring moved in a certain direction (Huse et al., 2002). The coarse sampling scheme of our data does not allow us to examine such school dynamics for EBS herring. Physiological status and ecological experiences of segments of herring schools need to be taken into account to realistically predict migration dynamics or distribution. Such sampling can only be attained through a directed at-sea sampling program. Based on the aggregate samples available for this analysis, we propose that pre-spawning herring tend to avoid cold temperatures associated with high ice concentrations, unless a proportion of a school reaches the physiological requirements for spawning. When a proportion of herring in a school reaches a spawning-ready threshold, the whole school may move into cold water that they otherwise would have avoided.

An ongoing decline of sea ice in the EBS (Overland and Stabeno, 2004) presents an important research opportunity to investigate changes in the distribution and role of herring in the marine ecosystem. How will herring respond to a future lack of sea ice? Shifts in overwintering grounds to the northwest of the Pribilofs, and the apparent bifurcation of herring distribution in winter including a concentration north of Unimak Pass, are precursors, perhaps, of further responses. Should the system proceed toward ice-free conditions, herring will experience a new thermal regime beyond the range of historical observations. Additional future research should include detailed field investigations, including herring genetic identification studies to examine the habitat overlap of Gulf of Anadyr and EBS spawning populations in winter, and effects of climate-driven oceanographic changes on herring distributions and abundance, as well as the impacts of such changes in this ecologically important species on upper trophic levels.

5. Conclusions

EBS herring have a basic migration pattern that is characterized by southern and northern overwintering areas, an inshore movement in spring, and migration along the Alaska Peninsula after spawning in summer and early fall. Significant interannual variability exists in the pre-spawning herring migration pathways, largely in response to sea ice variability. The exact response of herring to sea ice is probably related to water conditions in the migration route between the offshore northern and southern wintering areas and coastal spawning sites. The recent and continuing decline of sea ice in the EBS will undoubtedly affect herring in the future. The potential impacts of a warmer EBS with no sea ice on herring migration are not predictable, because they are outside the range of historical observations. However, continuing environmental changes provide opportunities to conduct new research on the interactions between sea ice and herring and their environment. Given the ecological importance of herring to upper trophic levels, as well as the economic and social importance of herring fisheries to coastal residents of this region, such studies will be important, both to understand the effects of global warming on the Bering Sea ecosystem, as well as to fishery management. Possible changes in the northern overwintering grounds and details of the southern overwintering concentrations pose scientific and management challenges and research opportunities. The understanding of herring migration dynamics that we have tried to advance with our research should be validated and expanded by *in-situ* field studies, as well as laboratory investigations of reproductive physiology and behavior.

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