



Detecting temporal trends and environmentally-driven changes in the spatial distribution of bottom fishes and crabs on the eastern Bering Sea shelf



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ARTICLE INFO

Available online 14 March 2013

Keywords:

Spatial distribution
Population shift
Cold pool
Bottom fish
Crab
Bering Sea shelf

ABSTRACT

This study uses a 30-year time series of standardized bottom trawl survey data (1982–2011) from the eastern Bering Sea shelf to model patterns of summer spatial distribution for various bottom fishes and crabs in response to changes in the areal extent of the cold pool, time lag between surveys, and fluctuations in population abundance. This investigation is the first to include data for the 2006–2010 cold period and to use between-year comparisons of local and shelf-wide spatial indices to test specific responses to three different isothermal boundaries within the cold pool. Distributional shifts in population varied considerably among species and directional vectors for some species were greater in magnitude to the east or west than to the north or south; however, in general, eastern Bering Sea shelf populations shifted southward in response to the increasing cold pool size, and after accounting for differences in temperature and population abundance, there was still a temporal northward shift in populations over the last three decades despite the recent cooling trend. Model results for local and shelf-wide indices showed that survey time lag and cold pool extent had a greater effect on spatial distribution than population abundance, suggesting that density-independent mechanisms play a major role in shaping distribution patterns on the eastern Bering Sea shelf. The area enclosed by the 1 °C isotherm most commonly affects both local and shelf-wide spatial indices suggesting that 1 °C is a more important boundary for describing temperature preferences of eastern Bering Sea bottom fishes and crabs than is the 2 °C isotherm used for designating the physical boundary for the cold pool.

Published by Elsevier Ltd.

1. Introduction

The distributions of bottom fishes and crabs on the eastern Bering Sea continental shelf are affected by many different biotic and abiotic factors. A subsurface layer of cold water (< 2 °C) known as the “cold pool” (Stabeno et al., 2001) is a major abiotic factor affecting the distribution of fish populations on the eastern Bering Sea shelf (Spencer, 2008; Stabeno et al., 2012a; Wyllie-Echeverria and Wooster, 1998). Retreating seasonal ice and the diminishing areal extent of the summer cold pool during a warm period lasting from 2000 through 2005 was related to a community-wide northward shift in bottom fishes and invertebrates (Mueter and Litzow, 2008). Studies have focused primarily on climate change and a general warming trend as the mechanism for shelf-wide temporal shifts in the eastern Bering Sea. From 2006 to 2010, the eastern Bering Sea shelf environment entered into a relatively cold period when the spatial extent of winter sea ice and the summer cold pool both increased

(Sigler et al., 2011; Stabeno et al., 2012a,b). This is the first investigation to include an analysis of data for the 2006–2010 cold period to determine if increases in the size of the summer cold pool reversed the northward temporal shift in populations on the eastern Bering Sea shelf, and to investigate more specifically how distributions may be affected by three different isothermal boundaries within the cold pool.

A fundamental problem to studying ecological processes is that they are variable over a range of different spatial, temporal, and organizational scales (Ciannelli et al., 2008; Levin, 1992). Spatial analyses of bottom fishes and crabs on the eastern Bering Sea shelf are complex because the physical and biological processes are dynamic, and the organisms, as well as the cold pool, are not homogeneously distributed in space and time along latitudinal or longitudinal axes or gradients. This makes direct comparisons between years or over the scale of the entire eastern Bering Sea shelf difficult. Moreover, studies focusing on population shifts have lacked spatially-explicit information about how a species is likely to respond to different temperature levels within the cold pool. Interannually, the spatial extent of the cold pool varies substantially during the late spring and summer period. During warm

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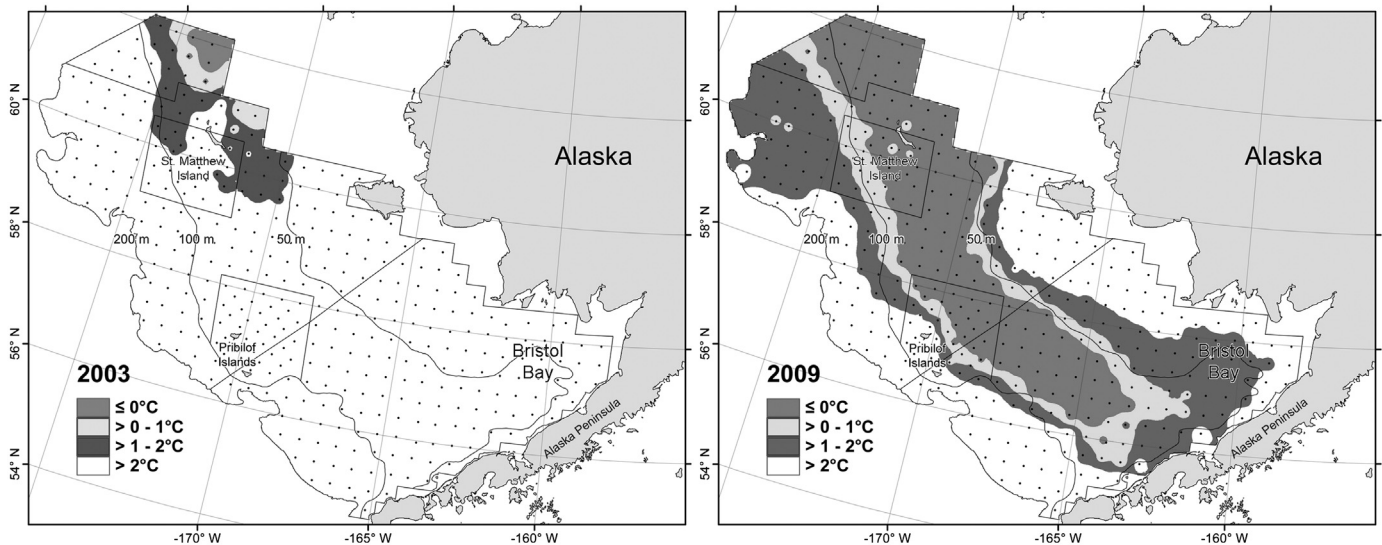


Fig. 1. Variation in the extent of the summer cold pool during a warm year (2003) and a cold year (2009) on the eastern Bering Sea shelf as measured during bottom trawl surveys. Also shown are the 50-m, 100-m, and 200-m isobaths, survey stratum boundaries, and sampling stations (dots).

years, the extent of the cold pool can be restricted to the northern shelf, which contrasts sharply to cold years when the extent of the cold pool can extend down the middle shelf as far as the Alaska Peninsula and eastward into Bristol Bay (Fig. 1). Between warm and cold periods, there is also spatial heterogeneity in the size and shape of the two-dimensional areas bounded within the 0, 1, and 2 °C isotherms. Given the large variability in the hydrographic structure and extent of the cold pool, one might expect corresponding changes in local spatial patterns within a population, as well as distribution shifts in the combined population, especially for migratory temperate species having a low tolerance for water temperatures typically observed within the cold pool (−1.7 to +2 °C).

This study uses a 30-year time series of standardized bottom trawl survey data (1982–2011) from the eastern Bering Sea shelf to model between-year responses of spatial distribution indices for selected bottom fishes and crabs against between-year differences in the areal extent of the cold pool using three different isothermal boundaries. There are other factors besides changes in temperature that can affect distribution, including natural fluctuations in population abundance (Spencer, 2008) and the temporal autocorrelation of spatial patterns (Pyper and Peterman, 1998) also known as the time lag effect; i.e., snapshots of a spatial distribution for a particular species that are closer in time may be more similar than those separated by longer periods of time. Hence, in addition to temperature, we investigate variability in spatial distribution patterns due to between-year changes in population abundance as well as the time lag between survey years.

The temporal scale we used was limited to the available survey data, but to determine if processes shape local patterns of distribution differently than shelf-wide patterns of distribution, we chose two indices as dependent variables in the model: (1) a shelf-wide index comparing between-year responses of population centers across the eastern Bering Sea shelf, and (2) a spatially-explicit local index comparing between-year responses of abundance location-by-location. A generalized additive model (GAM) framework was used to model responses using the two spatial indices for all possible survey year combinations. The basic thesis is that these models will explain the observed variability in spatial distribution of populations at shelf-wide and local levels, and determine the relative contribution of a changing cold pool, fluctuating population abundance, and time lag between surveys to the distributional changes observed in various bottom fishes and crabs on the eastern Bering Sea shelf.

2. Methods

2.1. Surveys

Since 1982, the National Marine Fisheries Service (NMFS) (NMFS, 2012) eastern Bering Sea shelf standardized bottom trawl survey has been conducted annually using chartered commercial fishing vessels to sample stations within a systematic grid design consisting of ten strata and 356 fixed stations (Fig. 1). In 1987, an additional two strata with 20 fixed stations were added to the northwestern most part of the shelf. The inner, middle, and outer shelf strata have different hydrographic structure and circulation and are nominally delineated by the 50, 100, and 200-m isobaths (Coachman, 1986) and a diagonal line across the middle of the shelf delineates regions of the survey area that were originally established to separate different southern and northern populations of principal bottom fishes and crabs (Pereyra et al., 1976). Strata in the vicinity of St. Matthew Island and the Pribilof Islands are sampled at a higher density than the other strata. All bottom trawl surveys were conducted within the same 3-month time period (May–August) using standardized gear and methods (Stauffer, 2004). Survey catch data were standardized to catch per unit of effort (CPUE) for each station by dividing total catch weight (kg) by the area-swept for each survey trawl haul in hectares (ha). The mean CPUE for each taxa in each stratum was weighted by the proportion of the total stratum area and then summed for all strata to obtain population abundance (*ABUND*) for each year. Bottom water temperatures were recorded at each station by deploying an expendable bathythermograph from the survey vessel (1982–1991) or by attaching a digital thermometer to the trawl headrope (1992–2011). Station bottom temperatures were weighted by stratum area before calculating an average survey bottom temperature. Linear regression analyses were used to test for significance of trends in total cold pool area (< 2 °C) and average survey bottom temperature over time. ArcMap² v9.3 was used to plot trawl station bottom temperatures by year and to generate isotherms in one degree intervals within the standard survey area using the inverse distance-weighted squared interpolation method.

² Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

An Albers Equal Area Conic projection was used to calculate the area within the polygons generated from the 0, 1, and 2 °C isotherms.

The primary criterion for selecting the taxa used in the analysis (Table 1) was that bottom trawl abundance for a taxon had to be a credible index of abundance over time. Excluded taxa failed to meet this criterion for a variety of reasons: (1) bottom trawl not designed for quantitative sampling of pelagic species, (2) historical changes in the specificity and consistency of field identifications (Stevenson and Hoff, 2009), (3) historical changes in the consistency of subsampling rare or singular species from large catches, and (4) rare or patchily distributed species with insufficient data for analyses. Accordingly, Alaska skate (*Bathyraja parmifera*) and northern rock sole (*Lepidopsetta polyxystra*) were combined into the broader taxonomic groups *Bathyraja* spp. and *Lepidopsetta* spp., respectively. In both cases, the other species combined into these taxonomic groups had overlapping spatial distributions, but composed only a small percentage of the total abundance within

Table 1

List of taxa considered for the analysis. An “*” next to the common name indicates that the taxa was included in the analysis and a number in the last column indicates the rationale (see below) for those taxa excluded from the analysis.

Common name	Scientific name	Exclusion
Skates*	<i>Bathyraja</i> spp.	
Arrowtooth flounder*	<i>Atheresthes stomias</i>	
Kamchatka flounder	<i>Atheresthes evermanni</i>	2,4
Greenland turbot*	<i>Reinhardtius hippoglossoides</i>	
Pacific halibut*	<i>Hippoglossus stenolepis</i>	
Flathead sole*	<i>Hippoglossoides elassodon</i>	
Bering flounder*	<i>Hippoglossoides robustus</i>	
Rex sole*	<i>Glyptocephalus zachirus</i>	
Yellowfin sole*	<i>Limanda aspera</i>	
Longhead dab*	<i>Limanda proboscidea</i>	
Sakhalin sole	<i>Limanda sakhalinensis</i>	4
Starry flounder*	<i>Platichthys stellatus</i>	
Rock sole*	<i>Lepidopsetta</i> spp.	
Alaska plaice*	<i>Pleuronectes quadrituberculatus</i>	
Sawback poacher	<i>Leptagonus frenatus</i>	2,3
Sturgeon poacher*	<i>Podothecus accipenserinus</i>	
Bering poacher	<i>Ocella dodecahedron</i>	4
Pacific sand lance	<i>Ammodytes</i> spp.	1
Searcher	<i>Bathymaster signatus</i>	3,4
Pacific herring	<i>Clupea pallasii</i>	1
Yellow Irish lord	<i>Hemilepidotus jordani</i>	4
Butterfly sculpin*	<i>Hemilepidotus papilio</i>	
Warty sculpin	<i>Myoxocephalus verrucosus</i>	2
Great sculpin	<i>Myoxocephalus polyacanthocephalus</i>	2
Plain sculpin	<i>Myoxocephalus jaok</i>	2
Spinyhead sculpin	<i>Dasycottus setiger</i>	3,4
Bigmouth sculpin	<i>Hemitripterus bolini</i>	3
Pacific sandfish	<i>Trichodon trichodon</i>	4
Pacific cod*	<i>Gadus macrocephalus</i>	
Arctic cod	<i>Boreogadus saida</i>	1,2
Saffron cod	<i>Eleginus gracilis</i>	4
Walleye pollock*	<i>Theragra chalcogramma</i>	
Whitespotted greenling	<i>Hexagrammos stelleri</i>	3,4
Eulachon	<i>Thaleichthys pacificus</i>	1
Capelin	<i>Mallotus villosus</i>	1
Rainbow smelt	<i>Osmerus mordax</i>	1
Marbled eelpout	<i>Lycodes varidens</i>	2,4
Wattled eelpout*	<i>Lycodes palearis</i>	
Shortfin eelpout*	<i>Lycodes brevipes</i>	
Decorator crab	<i>Oregonia gracilis</i>	2
Tanner crab*	<i>Chionoecetes bairdi</i>	
Snow crab*	<i>Chionoecetes opilio</i>	
Helmet crab	<i>Telmessus cheiragonus</i>	4
Red king crab*	<i>Paralithodes camtschaticus</i>	
Blue king crab*	<i>Paralithodes platypus</i>	
Horsehair crab	<i>Erimacrus isenbeckii</i>	4

1. Bottom trawl not designed for quantitative sampling of pelagic species.
2. Historical changes in the specificity and consistency of field identifications.
3. Historical changes in the consistency of subsampling rare or singular species.
4. Rare or patchily distributed species with insufficient data for spatial analyses.

that group in any given year ($< 5\%$). Flathead sole (*Hippoglossoides elassodon*) and Bering flounder (*H. robustus*) are difficult to differentiate; however, their zoogeography differs (Mecklenburg et al., 2002) and there was a concerted effort to separate the two species since 1982, so the two species were analyzed separately. Two other similar species, arrowtooth flounder (*Atheresthes stomias*) and Kamchatka flounder (*A. evermanni*) were not identified separately in the survey until 1992, so the analysis for arrowtooth flounder was confined to the 1992–2011 time period. A separate analysis for Kamchatka flounder was not conducted due to insufficient data.

2.2. Spatial indices

Two spatial indices were used for analyzing pairwise comparisons among all bottom trawl survey years: the global index of collocation (*GIC*) and the local index of collocation (*LIC*; Bez, 2007). The *GIC* and *LIC* provide different ways of quantifying the degree of similarity in a population's spatial distribution between years. The *GIC* indicates whether a population center of abundance has shifted between years using a pairwise comparison of center of gravity (*CG*) within a large geographical area taking into account the respective dispersion of that population in each of those years. In contrast, the *LIC* measures variability in local spatial distribution patterns between years using a location-by-location pairwise comparison of standardized catch.

Indices for both the *GIC* and *LIC* range from 0 to 1 with higher values indicating greater between-year similarity in the spatial distribution of an organism. Fig. 2 is a set of hypothetical grids to

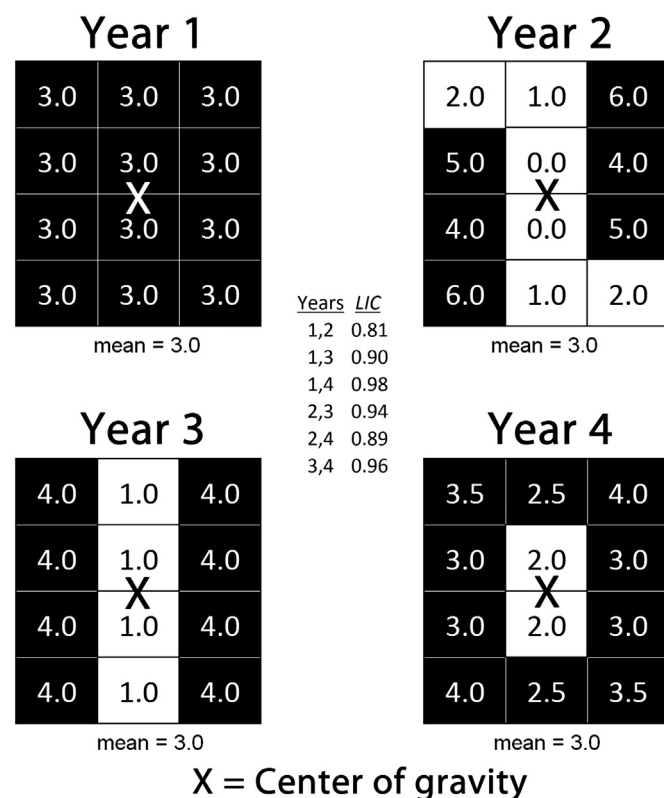


Fig. 2. Set of hypothetical grids illustrating different kinds of spatial variability. Numbers inside each grid cell represent an organism's abundance. White grid cells illustrate how an environmental feature such as temperature (e.g., cold pool ≤ 2.0 °C) might also vary at the same time. Regardless of the obvious heterogeneity within the grid cells, all 4 years have an identical center of gravity (*CG*) indicating no changes to the spatial distribution. In contrast, a grid cell-by-grid cell comparison using the local index of collocation (*LIC*) between years indicates changes in spatial distribution.

illustrate the difference between the *LIC* and the *GIC* and to underscore the importance of different kinds of spatial variability when choosing a metric for investigating distributional change. Suppose each grid cell represents an organism's abundance sampled annually during the same season in 4 consecutive years. White grid cells illustrate how an environmental feature such as temperature (e.g., cold pool $\leq 2.0^\circ\text{C}$) might also vary at the same time. All 4 years have the same CG; hence, $\Delta\text{CG}=0$ and the calculated values of *GIC* for all six between-year comparisons are equal to 1 indicating no changes to the spatial distribution. In contrast, the between-year comparisons for *LIC* are grid cell-by-grid cell; hence, the calculated values of *LIC* are all different and are less than 1 indicating that the spatial distribution pattern between years has changed.

The *GIC* and the *LIC* were calculated using data from the 30-year NMFS eastern Bering Sea shelf standardized bottom trawl survey, which resulted in up to 435 pairwise comparisons of all the different year \times year combinations for each taxon. The *GIC* (1) compares the similarity in the CG for each pairwise year combination. The value of dispersion *I* (2) accounts for the variance for all weighted positions around the CG. The *GICs* were calculated using the fixed set of stations common to all survey years ($n=356$).

$$GIC = 1 - \frac{\Delta\text{CG}^2}{\Delta\text{CG}^2 + I_1 + I_2}, \quad (1)$$

where ΔCG is the distance in kilometers (km) between the CGs for a given pair of years (see details below) and I_1 is the dispersion for year one and I_2 for year two.

$$I = \frac{\sum_{i=1}^n (\Delta\text{CG})^2 z_i}{\sum_{i=1}^n z_i} \quad (2)$$

The CG_{lat} (latitude) and CG_{long} (longitude) for each survey year and taxon 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 (3). The (CG_{lat} , CG_{long}) was plotted by year for selected taxa.

$$\text{CG}_{\text{lat}} = \frac{\sum_{i=1}^n \text{lat}_i z_i}{\sum_{i=1}^n z_i} \quad \text{CG}_{\text{long}} = \frac{\sum_{i=1}^n \text{long}_i z_i}{\sum_{i=1}^n z_i} \quad (3)$$

The ΔCG was calculated for each pairwise comparison of years using radians in the formula for the great-circle distance where R is the mean radius of the earth (6,371 km).

$$\Delta\text{CG} = \arccos(\sin(\text{CG}_{\text{lat}_1}) \sin(\text{CG}_{\text{lat}_2}) + \cos(\text{CG}_{\text{lat}_1}) \cos(\text{CG}_{\text{lat}_2}) \\ * \cos(\text{CG}_{\text{long}_1} - \text{CG}_{\text{long}_2})) * R \quad (4)$$

Variability in local spatial patterns of distribution were measured using the *LIC* (5), which makes pairwise comparisons at each survey station between years, where

$$LIC = \frac{\sum_{i=1}^n z_{i1} z_{i2}}{\sqrt{\sum_{i=1}^n z_{i1}^2} \sqrt{\sum_{i=1}^n z_{i2}^2}}, \quad (5)$$

where z_{i1} and z_{i2} are the organism densities by taxon at station i for each set of paired years. Survey catch data from all 376 stations were included for calculating the *LIC* if they were available. The *GICs* and *LICs* were pooled for all years by taxa to calculate a range, mean, and standard deviation for each.

2.3. Model

A GAM was used to investigate how the *GIC* and the *LIC* responded to the between-year absolute differences in the areal extent (km^2) of the cold pool (ΔCPA_T) at a threshold temperature T ($^\circ\text{C}$), the absolute difference in population abundance (ΔABUND), and the time lag (ΔYEARS) by taxon. For simplicity, absolute differences in predictor variables will be referred to as “differences” in the remainder of the paper. The GAMs were run using the “mgcv” package in R (Wood, 2006) with the smoothing spline protocol (Wood, 2003). The basic form of the GAM used in the analysis was:

$$LIC \text{ or } GIC \sim s(\Delta\text{CPA}_T) + s(\Delta\text{ABUND}) + s(\Delta\text{YEARS}) + \text{factor}(\text{VESSEL}) \\ + \text{factor}(\text{YEAR1}),$$

where s indicates variables fitted with a cubic spline and *factor* indicates categorical variables.

To investigate more specific responses to a range of cold pool bottom temperatures, backward variable selection was performed for three different temperature thresholds: CPA_0 , CPA_1 , and CPA_2 $^\circ\text{C}$, where a temperature threshold defines the two-dimensional boundary within the cold pool. Factors representing survey *VESSEL* and the first year of the comparison pair (*YEAR1*) were included in the model to account for the random or systematic errors that were considered to be artifacts of sampling methodology such as vessel or skipper effects (Munro, 1998; von Szalay and Brown, 2001), survey timing, and technology creep (Zimmermann et al., 2003).

Because the data used in the modeling were not completely independent (e.g., the *LIC* derived from a comparison between 1982 and 1983 was not independent of the *LIC* derived from a comparison between 1982 and 1984), we could not use the P -values provided by the mgcv package. Instead we derived P -values from the delete- d jackknife variance estimates around predictions, which is preferable to the delete-one jackknife because it produces a consistent variance estimate (Shao, 1989). A backward variable elimination was performed using jackknife-derived p -values by eliminating one variable at a time. The variable with the largest P -value was eliminated first and the jackknife was then repeated to estimate new p -values for the reduced model. This process was continued until remaining P -values for all variables were $P < 0.01$. A more stringent $P < 0.01$ was chosen instead of $P < 0.05$ to minimize the possibility of a Type I error. Confidence bounds around predictions were also estimated using model predictions from the jackknife. Among the different temperature models the final one was chosen based on the lowest generalized cross-validation (GVC) score (Wood, 2006). The time lag variable was used to account for any temporal trends that may be present in the survey time series and residuals from the final models were inspected visually using a linear modeling and smoothing spline to ensure the absence of temporal autocorrelation and linear or non-linear trends in the residuals.

Our null hypothesis was that there was no relationship between the interannual differences in local or shelf-wide patterns of spatial distribution by taxon and the interannual differences observed in the predictor variables. Rejection of the null hypothesis implies that a predictor variable has an effect on the spatial index, and thus affects the spatial distribution of a taxon. For example, if the magnitude of the difference in ΔABUND is negatively correlated with a spatial index (i.e., greater ΔABUND corresponds to decreasing similarity of the spatial index) then the population abundance influences the spatial distribution.

To illustrate effects on the *GIC*, plots of spatial distribution by taxon were made for ΔCPA_T , ΔABUND and ΔYEARS if they were significant. As a proxy for each significant effect, median values among all years for each of the predictor variables by taxon were

used as cut-off values to subdivide all 30 years of the catch data into “cold” and “warm” years (ΔCPA_T), “high” and “low” abundance years ($\Delta ABUND$), and “early” and “recent” years ($\Delta YEARS$). A mean CG was taken for each pooled set of data and a great-circle distance (4) and bearing (6) between mean CGs (ΔCG) were calculated for each of the significant predictor variables. Radian values from the bearing calculation (θ) were converted to degrees and modular arithmetic was used to transform negative degree values to make them positive

$$\theta_{\Delta CG} = a \tan 2(\sin(CG_{long_2} - CG_{long_1}) * \cos(CG_{lat_2}), \cos(CG_{lat_1}) * \sin(CG_{lat_2}) - \sin(CG_{lat_1}) * \cos(CG_{lat_2}) * \cos(CG_{long_2} - CG_{long_1})) \quad (6)$$

The ΔCG s were plotted by taxa for each significant predictor variable to compare their relative effects on the shelf-wide spatial distribution, where distance represents magnitude and bearing represents direction of the ΔCG in response to the predictor variable. A more detailed examination of spatial analyses was done for three taxa of particular interest to the Bering Sea Integrated Ecosystem Research Program (BSIERP) because of their important role in the eastern Bering Sea ecosystem: arrowtooth flounder, Pacific cod (*Gadus macrocephalus*), and walleye pollock (*Theragra chalcogramma*). To illustrate effects on the *LIC* for these taxa, plots of spatial distribution were made for ΔCPA_T , $\Delta ABUND$ and $\Delta YEARS$ if they were significant. Again, as a proxy for each significant effect, median values among all years for each of the predictor variables by taxon were used as cut-off values to categorize the catch data (see above). ArcMap was used to produce inverse distance-weighted squared interpolation plots of mean CPUE by category and by taxon.

3. Results

3.1. Survey bottom temperatures and extent of cold pool

Mean survey bottom temperatures and areal extent of the cold pool showed considerable interannual variability from 1982 to 2011 (Fig. 3). The coldest survey year in 1999 resulted in the largest deviation from the mean and the largest areal extent of

cold pool in the time series (393,595 km²). This extremely cold year was followed by a 5-year period (2001–2005) with above average survey bottom temperatures. The areal extent of cold pool was at its minimum size (48,000 km²) during the warmest survey year (2003). The $CPA_0^\circ C$ was absent (1996) or generally small during years when the mean survey bottom temperature was above the long-term mean (Fig. 3). From 2005 to 2006, the warm trend reversed and there was a sharp decline in the mean bottom temperature, coinciding with colder than average survey bottom temperatures for a 5-year period (2006–2010). In 2011, the cold pool decreased in size, especially the $CPA_0^\circ C$, resulting in a mean survey bottom temperature that was slightly above the 30-year mean. For the 30-year period, regression analyses showed an increasing trend in total cold pool area ($P=0.37$) and a decreasing trend in mean survey bottom temperature ($P=0.26$), but neither were significant.

3.2. Model results

The *LIC*s generally had lower similarities and greater variability than *GIC*s for all taxa (Table 2). The mean *LIC* ranged from 0.32 to 0.78 compared to the mean *GIC* which ranged from 0.83 to 0.98, and standard deviations were on average 2.5 times greater for *LIC* than *GIC*. Also, the highest *GIC* for every taxon was 1.0, compared to the highest *LIC* values which varied from 0.67 to 1.0.

The $\Delta YEARS$ was a significant effect for most *LIC*s (86%) and *GIC*s (82%) with the dominant trend being decreasing similarity in spatial indices with increasing $\Delta YEARS$ (Table 2). The *LIC* was significantly affected by the areal extent of the cold pool for a majority of taxa (77%), compared to about half (55%) for the *GIC* (Table 2). The $\Delta CPA_1^\circ C$ most frequently affected both *LIC* and *GIC* (61%), followed by $\Delta CPA_0^\circ C$ (23%) and $\Delta CPA_2^\circ C$ (16%). The $\Delta ABUND$ was a significant effect for a greater percentage of the *LIC* models (59%) than for the *GIC* models (41%), with most taxa showing decreasing similarity with the *LIC* and variable trends in similarity with the *GIC* (Table 2).

The *GIC* for all taxa except longhead dab showed a significant response to at least one of the predictor variables (Table 2),

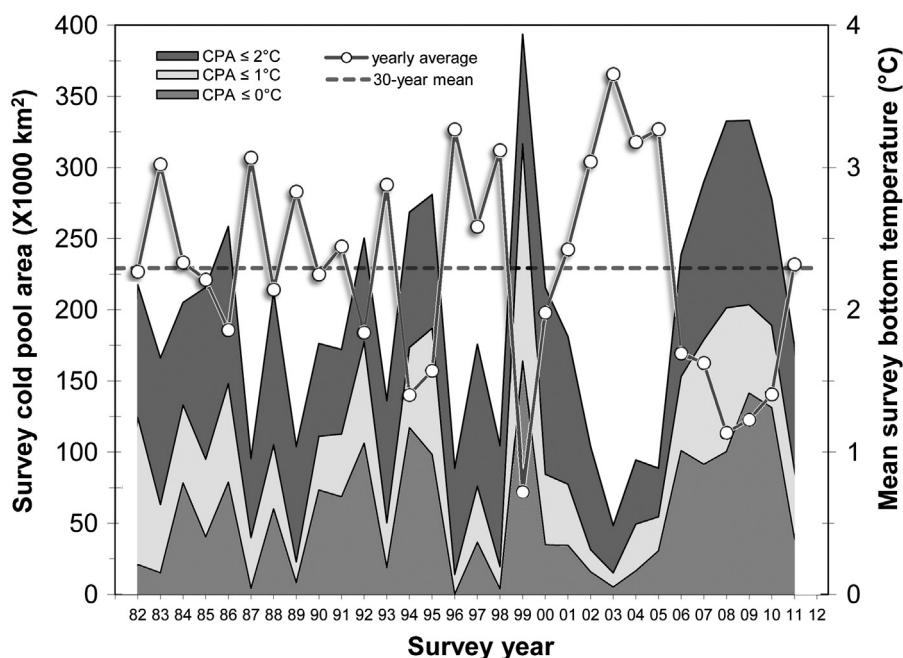


Fig. 3. Annual variation in the average survey bottom temperature, the 30-year mean survey bottom temperature, and the area (km²) of the cold pool (CPA_T) for three different isothermal boundaries, 0, 1, and 2 °C.

Table 2

Range, average, and standard deviation of local (*LIC*) and global (*GIC*) collocation indices and general additive model results of and indices of collocation for selected taxa from the eastern Bering Sea shelf. Predictor variables include pairwise interannual comparisons of survey cold pool area (ΔCPA_T) within isothermal boundaries of $=0$, 1 , and 2 °C, abundance ($\Delta ABUND$), and survey time lag ($\Delta YEARS$). The level of significance for listed predictor variables is < 0.01 . Dashes indicate that the variable dropped out from the model during the selection process, and “d”, “n”, and “i” indicate whether trend in the response variable was decreasing, neutral or increasing, respectively.

LIC									GIC							
Common name	Min.	Max.	Avg.	SD	Trend ΔCPA_T	Trend $\Delta ABUND$	Trend $\Delta YEARS$	Deviance explained (%)	Min.	Max.	Avg.	SD	Trend ΔCPA_T	Trend $\Delta ABUND$	Trend $\Delta YEARS$	Deviance explained (%)
Skates	0.19	0.72	0.49	0.11	d 1°	d	d	69.6	0.79	1.00	0.97	0.03	n 1°	–	d	76.6
Arrowtooth flounder	0.27	0.84	0.64	0.13	d 1°	d	–	56.6	0.88	1.00	0.98	0.02	d 1°	–	–	39.7
Greenland turbot	0.26	0.83	0.54	0.11	d 1°	–	d	48.1	0.60	1.00	0.93	0.08	–	n	d	67.2
Pacific halibut	0.23	0.71	0.46	0.09	d 2°	d	d	41.9	0.80	1.00	0.97	0.03	n 1°	–	i	66.9
Flathead sole	0.08	0.85	0.44	0.16	–	d	d	67.3	0.85	1.00	0.97	0.04	–	d	d	30.6
Bering flounder	0.04	0.84	0.46	0.15	d 0°	–	d	48.0	0.71	1.00	0.92	0.06	d 2°	d	n	48.5
Rex sole	0.38	0.99	0.78	0.13	d 0°	–	d	60.4	0.84	1.00	0.97	0.03	i 0°	i	i	52.6
Yellowfin sole	0.35	0.87	0.59	0.09	d 2°	i	d	58.3	0.88	1.00	0.98	0.02	–	–	d	51.6
Longhead dab	0.09	0.92	0.57	0.16	–	d	d	41.7	0.58	1.00	0.93	0.08	–	–	–	64.4
Starry flounder	0.03	0.84	0.37	0.18	d 0°	–	n	55.9	0.44	1.00	0.90	0.12	d 1°	–	n	76.9
Rock sole	0.28	0.91	0.57	0.12	d 1°	d	d	62.7	0.69	1.00	0.96	0.05	n 1°	–	n	87.4
Alaska plaice	0.21	0.82	0.53	0.13	d 2°	–	d	43.7	0.83	1.00	0.97	0.03	–	–	d	23.1
Sturgeon poacher	0.07	0.89	0.46	0.17	–	–	d	61.9	0.51	1.00	0.91	0.09	d 1°	–	d	65.2
Butterfly sculpin	0.01	1.00	0.46	0.25	n 1°	–	–	43.8	0.47	1.00	0.84	0.13	–	i	–	49.4
Pacific cod	0.12	0.80	0.37	0.12	d 1°	d	n	54.8	0.81	1.00	0.97	0.03	–	i	d	58.3
Walleye pollock	0.08	0.67	0.32	0.10	–	d	–	37.0	0.74	1.00	0.95	0.05	d 0°	–	d	36.8
Wattled eelpout	0.08	0.71	0.38	0.13	d 0°	–	d	53.4	0.56	1.00	0.90	0.10	n 1°	i	n	39.0
Shortfin eelpout	0.00	0.85	0.48	0.19	d 1°	d	d	62.1	0.09	1.00	0.85	0.21	n 1°	–	–	66.3
Tanner crab	0.09	0.89	0.36	0.17	d 1°	i	d	55.3	0.55	1.00	0.92	0.08	–	i	n	81.1
Snow crab	0.08	0.73	0.43	0.11	i 1°	d	d	47.5	0.66	1.00	0.95	0.06	–	–	n	48.5
Red king crab	0.03	0.95	0.38	0.19	d 2°	d	d	53.4	0.45	1.00	0.91	0.10	d 0°	–	n	61.6
Blue king crab	0.03	0.97	0.44	0.22	–	–	d	54.9	0.31	1.00	0.83	0.18	–	n	d	51.2

indicating a community shift in the shelf-wide distribution of demersal fauna on the eastern Bering Sea shelf. The $\Delta YEARS$ was significant for a majority of taxa (82%), and compared to the temperature and abundance effects, the ΔCG for early relative to recent years showed the largest magnitude of displacement (mean=45 km) and the broadest range of directional shifts with 18 of the 22 taxa undergoing a northward shift (Table 3; Fig. 4a). The effect of increasing ΔCPA_T on ΔCG fell along a southeast to northwest axis and had a mean displacement of 34 km southward (Table 3; Fig. 4b). Changes in abundance had the smallest effect on ΔCG , with a mean displacement of 23 km along a relatively narrow southeast–northwest axis (Fig. 4c).

3.3. Selected species

Walleye pollock: The shelf-wide distribution of pollock decreased in similarity with both an increase in ΔCPA_0 °C and $\Delta YEARS$ (Table 2). The cold year CGs were generally west of warm year CGs along a southeast–northwest axis (Fig. 5) resulting in a mean CG for cold years that shifted 42 km toward the shelf edge (262°; Table 3). Among the 8 years with the most northerly distribution (latitude $> 58^{\circ}05'N$), four of those years, 1999 and 2008–2010, were the coldest in the survey time series (Fig. 5). The pollock population had a mostly southeastern distribution during early years, but switched to a more northwestern distribution during recent years, shifting 50 km to the northwest (309°; Table 3; Fig. 5). For pollock, similarities in local distribution patterns were not significantly affected by ΔCPA_T at any temperature, but there was decreasing similarity with increasing $\Delta ABUND$ (Table 2; Fig. 6). During high abundance years, pollock are spread further across the middle and inner shelf, and there were higher densities along the northwest outer shelf east of Zhemchug Canyon, in the vicinity of the Pribilof Islands, and north of Unimak Island and the Alaska Peninsula (Fig. 6).

Pacific cod: The shelf-wide distribution of Pacific cod was significantly affected by $\Delta ABUND$ and $\Delta YEARS$, but not ΔCPA_T (Table 2). There was a decreasing similarity in the *GIC* with increasing $\Delta YEARS$, and the years 2000–2008 generally had a lower abundance and more northwestern CGs than other years (Fig. 7). With the increasing abundance of Pacific cod starting in 2009, the CGs shifted southeast (Fig. 7). The direction of the ΔCG was similar between high and low abundance years and between early and recent years (Table 3; Fig. 7).

The similarity in local distribution patterns were significantly affected by all three predictors: ΔCPA_1 °C, $\Delta ABUND$, and $\Delta YEARS$ (Table 2). For the *LIC*, the similarity between spatial distributions decreased with increased differences in both ΔCPA_1 °C and $\Delta ABUND$ (Fig. 8). There was also a decrease in similarity with $\Delta YEARS$ up to 10 years after which similarity generally increased, but not consistently. In the cold, high abundance, and early years, numerous concentrated pockets of Pacific cod were spread across the shelf including the north side of Bristol Bay. In general, the highest densities of Pacific cod were observed outside the 1 °C isotherm, and except during the cold years, a dense pocket of Pacific cod (> 80 kg/ha) was present at the northern end of St. Matthew Island (Fig. 8; top).

Arrowtooth flounder: Both the *GIC* and *LIC* indices decreased significantly with an increase in ΔCPA_1 °C, and similarity in local distribution patterns also decreased with an increase in $\Delta ABUND$ (Table 2). The ΔCG from warm to cold years shifted 36 km to the southeast (Table 3; Fig. 9). Arrowtooth flounder were absent or densities were generally below 1 kg/ha inside the 1 °C isotherm boundary (Fig. 10). During the cold and high abundance years, densities were higher on the outer shelf near Pribilof Canyon and north of Unimak Island. During the warm and high abundance years, the distribution of arrowtooth flounder expanded to occupy most of the northern middle shelf and a greater proportion of the inner shelf (Fig. 10).

Table 3

The distance and bearing associated with a change in the center of gravity (ΔCG) by species for warm relative to cold years, high relative to low abundance years, and early relative to recent years are shown to illustrate the magnitude and direction of the predictor variables ΔCPA_T (cold pool area at isotherm temperature T), $\Delta ABUND$ (change in abundance), and $\Delta YEARS$ which had a significant effect on the global index of collocation (GIC).

Species	Approximated predictor variable	ΔCG distance (km)	ΔCG bearing (deg)
Skates	ΔCPA_{1°	30	196
	$\Delta YEARS$	61	28
Arrowtooth flounder	ΔCPA_{1°	36	136
Greenland turbot	$\Delta ABUND$	16	147
	$\Delta YEARS$	24	336
Pacific halibut	ΔCPA_{1°	35	119
	$\Delta YEARS$	54	306
Flathead sole	$\Delta ABUND$	33	131
	$\Delta YEARS$	90	301
Bering flounder	ΔCPA_{2°	37	205
	$\Delta ABUND$	20	135
	$\Delta YEARS$	21	45
Rex sole	ΔCPA_{0°	6	264
	$\Delta ABUND$	17	294
	$\Delta YEARS$	22	132
Yellowfin sole	$\Delta YEARS$	19	85
Starry flounder	ΔCPA_{1°	21	116
	$\Delta YEARS$	35	20
Rock sole	ΔCPA_{1°	31	161
	$\Delta YEARS$	42	316
Alaska plaice	$\Delta YEARS$	21	52
Sturgeon poacher	ΔCPA_{1°	5	244
	$\Delta YEARS$	36	230
Butterfly sculpin	$\Delta ABUND$	13	334
Pacific cod	$\Delta ABUND$	32	292
	$\Delta YEARS$	40	303
Walleye pollock	ΔCPA_{0°	42	262
	$\Delta YEARS$	50	309
Wattled eelpout	ΔCPA_{1°	79	296
	$\Delta ABUND$	16	296
	$\Delta YEARS$	113	112
Shortfin eelpout	ΔCPA_{1°	54	128
Tanner crab	$\Delta YEARS$	42	211
Snow crab	$\Delta ABUND$	35	152
	$\Delta YEARS$	57	303
Red king crab	ΔCPA_{0°	31	240
	$\Delta YEARS$	11	90
Blue king crab	$\Delta YEARS$	68	337

4. Discussion

4.1. Community level effects

Studies have shown that both density-independent and density-dependent factors can affect bottom fish distribution (Ciannelli et al., 2008; Spencer, 2008). The prevalence of the time lag variable in our study suggests that some unknown combination of density-independent and density-dependent factors, other than temperature or population abundance specifically, have the most influence on the spatial distribution of species. Density-independent environmental factors are frequently attributed to the effects of climate change as approximated by water temperature (e.g., Mountain and Murawski, 1992; Swain, 1999; Spencer, 2008); however, distribution shifts can also result from changes in other density-independent biological factors such as migrations involving ontogeny, spawning, and feeding (Nichol, 1998; Ernst et al., 2005; Kotwicki et al., 2005; Sohn et al., 2010), in situ light conditions (Kotwicki et al., 2009), primary production patterns, or fishing pressure (Garrison and Link, 2000). Additionally, density-dependent factors such as food availability (e.g., Dorn, 1995; Nøttestad et al., 1999) and competition between species or predation (Ciannelli et al., 2008), are also mechanisms that can affect spatial distribution patterns.

The change in area occupied by the cold pool was the second most common significant effect, suggesting that it is an important mechanism affecting spatial patterns of distribution on the eastern Bering Sea shelf. The cold pool affected local distribution patterns for a higher percentage of taxa (77%) than shelf-wide patterns (55%) indicating that distributional changes due to temperature are more frequently contained within certain areas of the eastern Bering Sea shelf rather than involving distributional shifts for the entire population. Our analyses show that increasing cold pool size is partly responsible for driving the short-term interannual variability in both local and shelf-wide spatial distribution patterns. The cold pool area enclosed by the 1°C isotherm was the temperature threshold most commonly affecting both spatial indices, suggesting that 1°C is a more important boundary for describing temperature preferences of eastern Bering Sea bottom fishes and crabs than is the 2°C isotherm commonly used for designating the cold pool boundary (e.g., Stabenot et al., 2001).

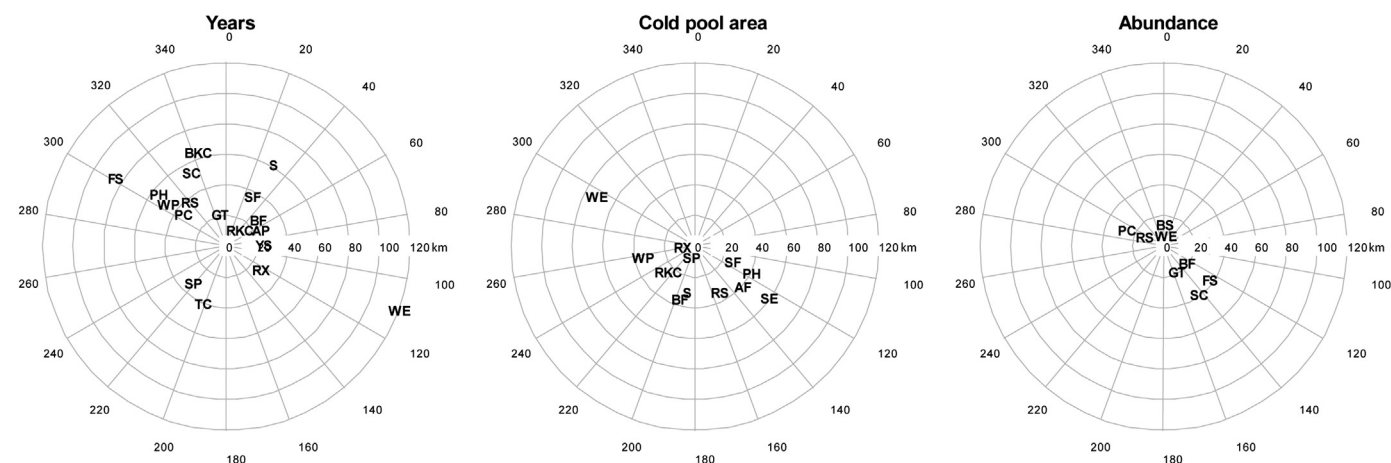


Fig. 4. Relative shifts in the centers of gravity for species that had statistically significant effects in the GAM models for: (a) time lag (early vs. recent years; early years are set to be in the center of the graph), (b) cold pool area (warm vs. cold years; warm years are set to be in the center of the graph), and (c) abundance (low vs. high relative abundance years; low abundance years are set to be in the center of the graph). Alaska plaice (AP), arrowtooth flounder (AF), Bering flounder (BF), blue king crab (BKC), butterfly sculpin (BS), flathead sole (FS), Greenland turbot (GT), Pacific cod (PC), Pacific halibut (PH), red king crab (RKC), rex sole (RX), rock sole (RS), shortfin eelpout (SE), skates (S), snow crab (SC), starry flounder (SF), sturgeon poacher (SP), Tanner crab (TC), walleye pollock (WP), wattled eelpout (WE), yellowfin sole (YS).

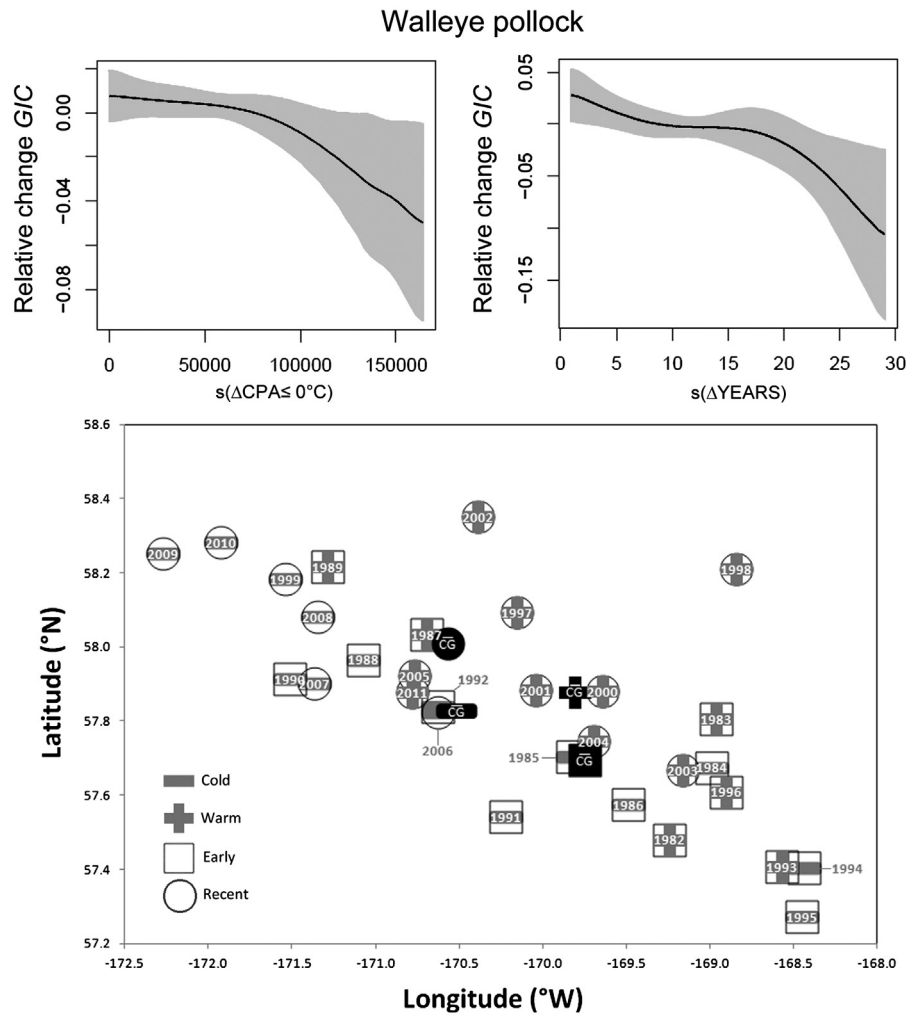


Fig. 5. GAM results for walleye pollock with 99% confidence intervals (gray) showing a. decreasing trend in the global index of collocation (GIC) with increasing ΔCPA_0 and $\Delta YEARS$ (top). The center of gravity for the walleye pollock population by year during cold (minus) and warm (plus) years, early (square) and recent (circle) years, and their respective means (CG; below).

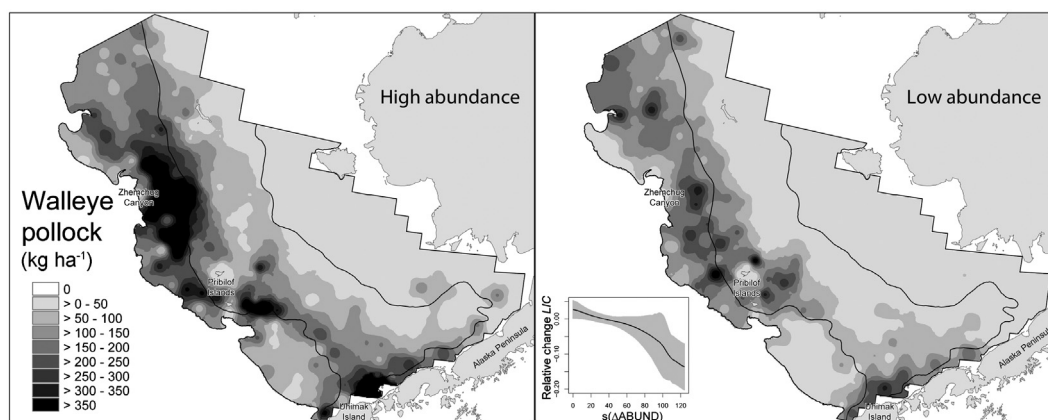


Fig. 6. Variability in the spatial distribution of walleye pollock during the high and low abundance years illustrating the decreasing similarity in the local index of collocation (LIC) associated with an increased change in abundance ($\Delta ABUND$). The gray shaded area represents the 99% confidence intervals.

Changes in spatial distribution of many fish populations are attributed to warmer temperatures associated with climate change (Perry et al., 2005; Mueter and Litzow, 2008; Nye et al., 2009). Twelve of the 14 taxa that were found to have a northward displacement in the Mueter and Litzow (2008) study were also found to have a northward displacement in our study, and four taxa that were found to have a southward displacement in that

study were also found to have a southward displacement in our study; however, the temporal northward shift detected in this study was attributed to a time lag effect that is not directly related to cold pool temperatures or population abundance. There was no long-term trend in the declining size of the cold pool detected on the EBS shelf over the last 30 years, and despite inclusion of recent data from the extended cold period from 2006 to 2010, we still

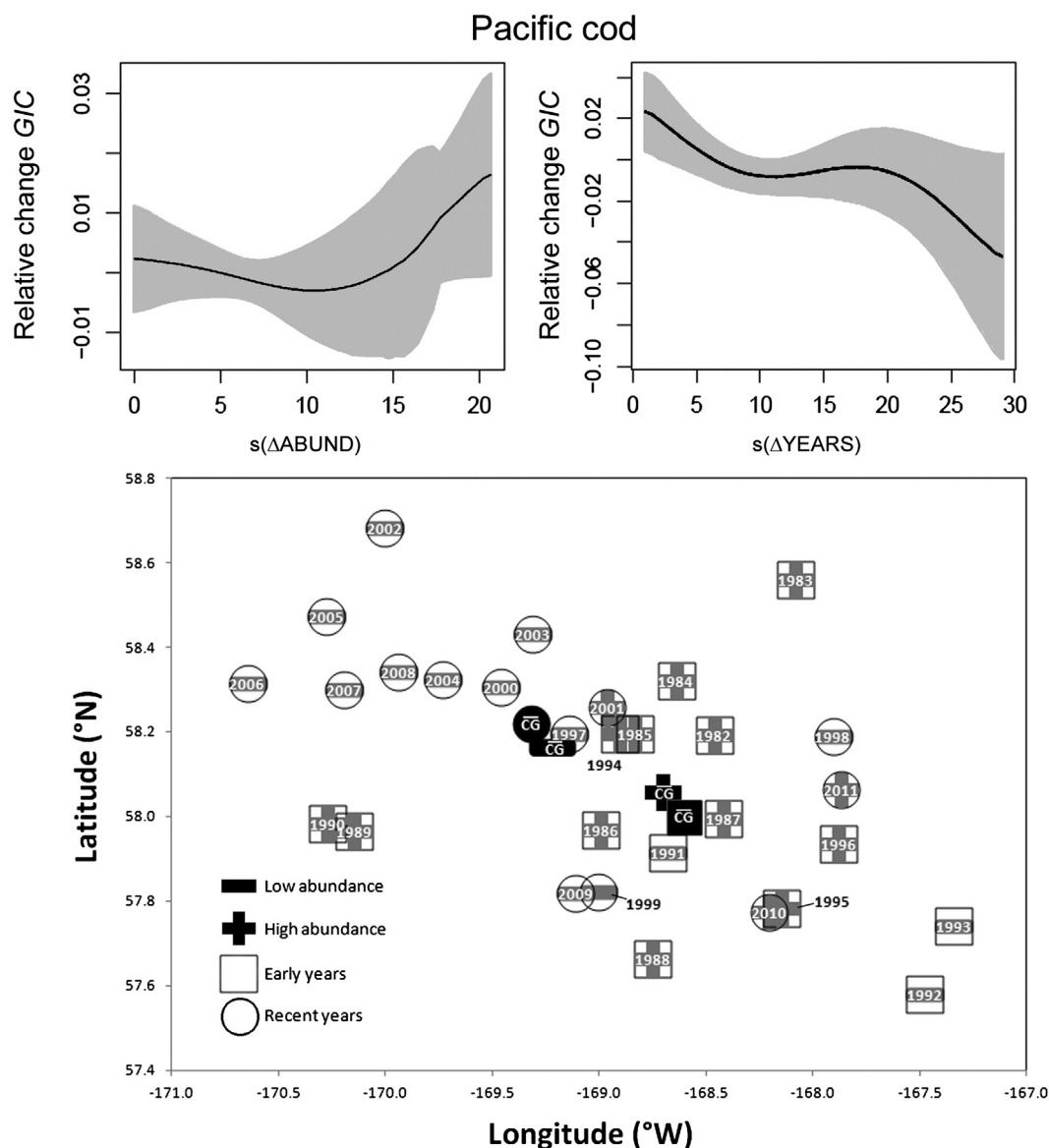


Fig. 7. GAM and center of gravity results for Pacific cod. See Fig. 5 for details with the exception that the plus signs represent high abundance years and the minus signs represent low abundance years.

observed a temporal northward shift. The patterns observed in this study do not support the thesis that a general warming trend on the eastern Bering Sea shelf was the primary mechanism for the temporal northward distributional shift that was proposed in a previous study by Mueter and Litzow (2008). Nevertheless, the short-term interannual variability in spatial patterns do appear to respond to fluctuations in the area occupied by the cold pool, suggesting that populations will indeed respond similarly to decreasing cold pool extent over the long-term by shifting northward. Predictions for the next half-century are that winter ice cover and a summer cold pool will persist on the northern Bering Sea shelf and continue to act as a barrier to northward migration of subarctic species (Sigler et al., 2011; Stabeno et al., 2012a).

We also looked at the spatio-temporal displacement of populations in all directions rather than just along a north-south axis. Directional vectors representing temporal shifts in populations varied considerably by response variable and among taxa suggesting a variety of species-specific biological or environmental mechanisms or perhaps different responses to the same mechanism. In response to changing cold pool size, vectors for some taxa were greater in magnitude to the east-west than to the north-south

suggesting that cross-shelf expansion or contraction of populations on the eastern Bering Sea shelf are affected by interannual variation of the hydrographic boundaries imposed by the cold pool.

Another possible mechanism for the northward temporal displacement is disproportional commercial fishing effort on the southeastern Bering Sea shelf. Commercial fishing can impact fish distribution and can change community structure (Garrison and Link, 2000; Ciannelli et al., in press). There is a major fishing port in close proximity to the Bering Sea shelf located in Dutch Harbor, Alaska. Among all U.S. fishing ports, Dutch Harbor was ranked number one in total commercial fishery landings for most of the past 20 years with annual totals ranging from 230 to 413 thousand metric tons (National Marine Fisheries Service, 2012). Practical considerations such as winter ice cover and regional management closures (e.g., Abbott and Haynie, 2012), or financial incentives such as travel time and fuel costs, may favor fishable waters closer to Dutch Harbor and result in disproportionate fishing pressure on the southeast portion of the shelf. Ten of the 22 taxa investigated here have been, or continue to be, targeted by a commercial fishery on the Bering Sea shelf, and 8 of the 10 commercially exploited taxa show a northward temporal displacement. The

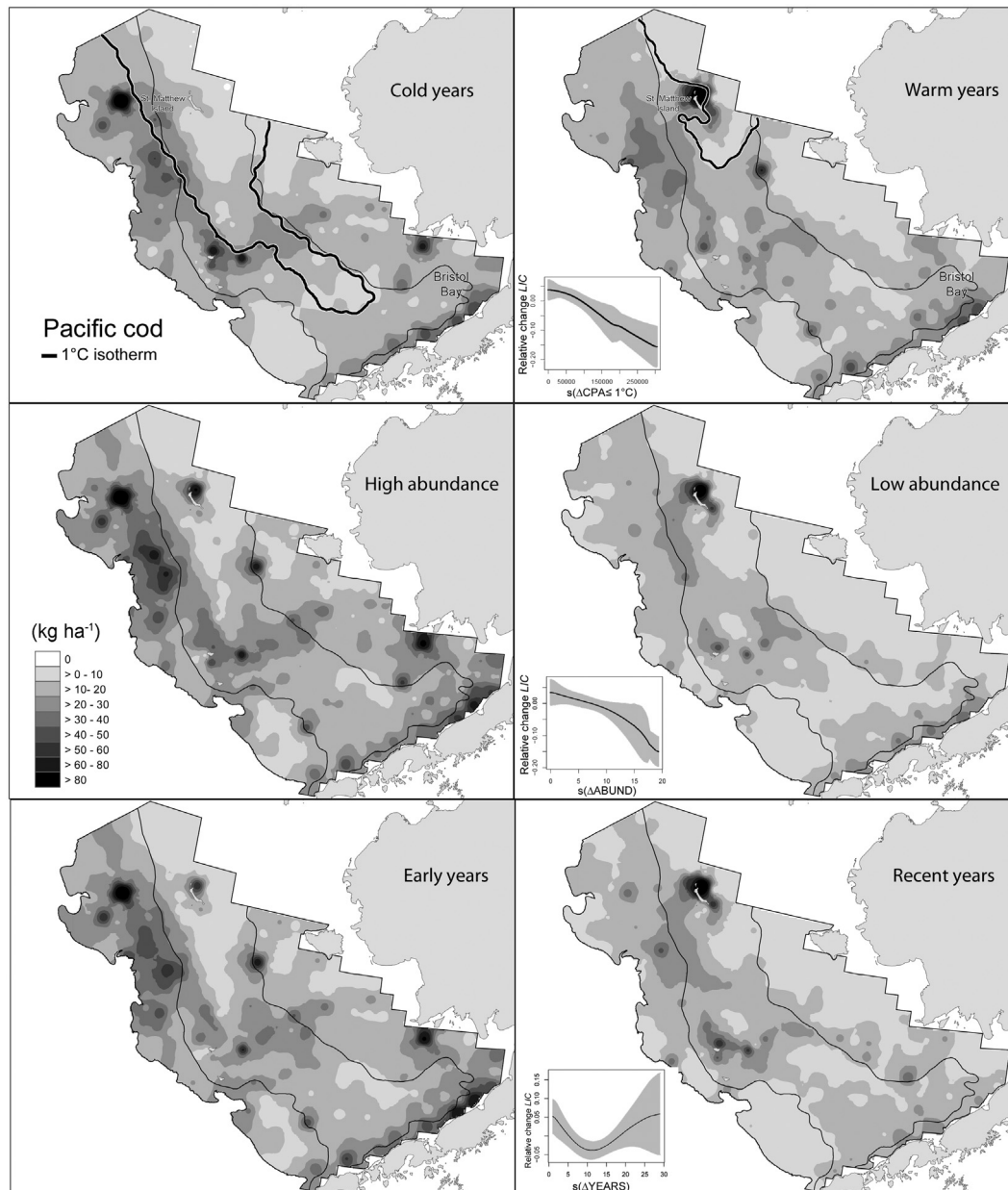


Fig. 8. Variability in the spatial distribution of Pacific cod during cold and warm years (upper panels), high and low abundance years (middle panels) and early and late years (bottom panels) to illustrate the decreasing similarity of the local index of collocation (*LIC*) to the effects of increasing $\Delta CPA_{1^\circ C}$ and $\Delta ABUND$ and the neutral response to $\Delta YEARS$. The gray shaded area represents the 99% confidence interval.

largest trawl fishery on the Bering Sea shelf by weight is walleye pollock, and the relative commercial fishing effort between the southeast and northwest shelf varies by season and by year (Bailey, 2011; Pfeiffer and Haynie, 2012). Another major trawl fishery for yellowfin sole and rock sole catches a majority of their annual quota on the southeastern shelf (Wildebuer and Nichol, 2011; Wildebuer et al., 2011). Commercial harvest of king crabs (*Paralithodes* spp.) occurred around the Pribilof Islands and St. Matthew Island until the late 1990s; however, population declines in both areas resulted in closures that are still in effect (Gish, 2010; Gaeuman, 2012). The only remaining major commercial harvest of king crab on the southeastern Bering Sea shelf is for red king crab (*Paralithodes* spp.) in Bristol Bay where populations have also declined dramatically (Dew and McConnaughey, 2005). Historical area- and species-specific commercial fishery data are available and can be used to investigate how disproportional fishing effort on the southeastern Bering Sea shelf during the last 30 years is a

contributing factor to the apparent northward temporal shift in bottom fish and crab populations.

Fluctuations in population abundance affected local distribution patterns (59%) more often than shelf-wide patterns (41%). Population growth creates greater competition for resources, forcing animals within a population to spread more into outlying areas (Swain and Wade, 1993; Atkinson et al., 1997). In the 1980s, there was rapid growth in the populations of several eastern Bering Sea flatfish species, which corresponded to significant increases in the dispersion of those species (McConnaughey, 1995). Increases in the population abundance of “arrowtooth flounder” (combined *Atheresthes stomias* and *A. evermanni*) and rock sole (*Lepidopsetta* spp.) on the eastern Bering Sea shelf were shown to be strongly related to increased spatial coverage of their populations, while increases in the area occupied by the cold pool have been associated with decreased spatial coverage of these species (Spencer, 2008).

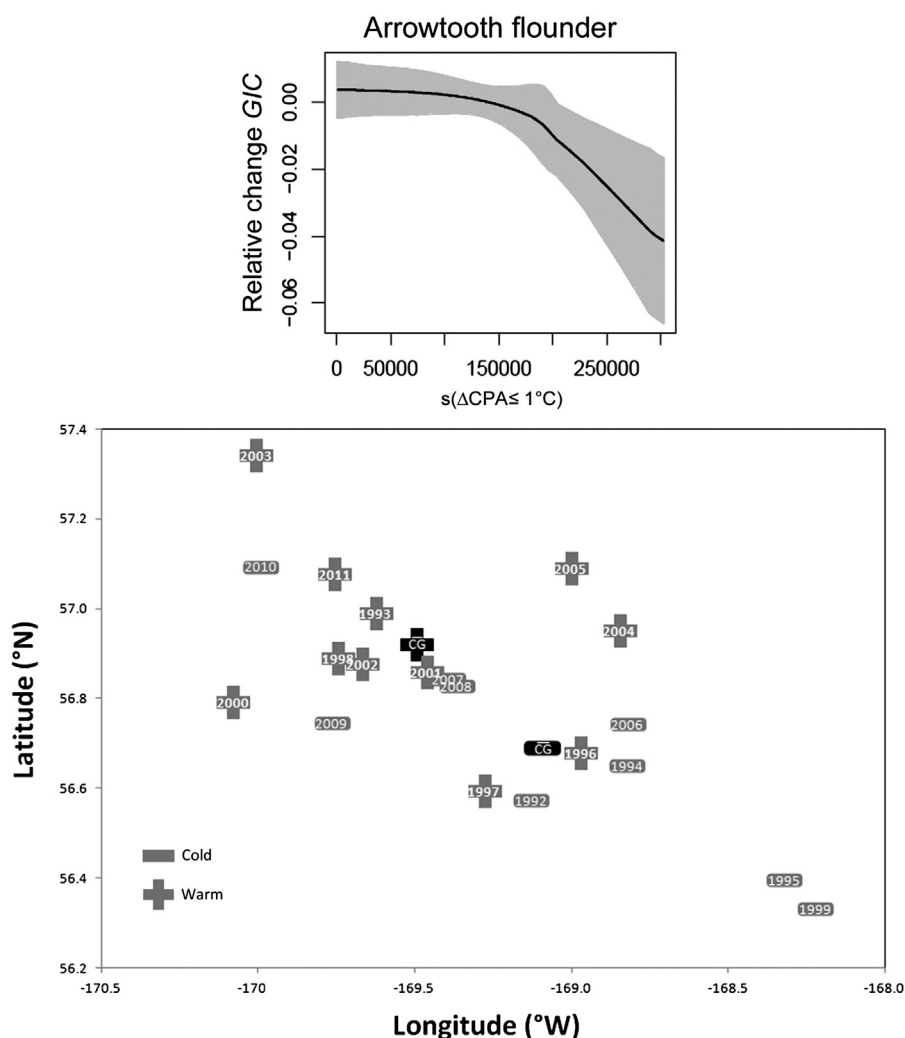


Fig. 9. GAM and center of gravity results for arrowtooth flounder. See Fig. 5 for details.

An easily overlooked factor that could have affected spatial distribution patterns for many of the species we investigated from the eastern Bering Sea shelf is immigration to and emigration from other areas outside the survey area. The geographical distributions of a number of the species we investigated are contiguous with other areas of the Bering Sea for which there is insufficient data to include in this analysis. The shelf extends hundreds of kilometers to the north where there is a significant biomass of Alaska plaice (*Pleuronectes quadrituberculatus*), yellowfin sole (*Limanda aspera*), and snow crab (*Chionoecetes opilio*), and along the outer shelf, deeper living species such as arrowtooth flounder and Greenland turbot (*Reinhardtius hippoglossoides*) can inhabit both the shelf and slope regions (Lauth, 2011).

4.2. Implication for studies of spatial dynamics in the eastern Bering Sea ecosystem

Spatial relationships in relation to environmental factors are key components in constructing models of marine ecosystems (Rose et al., 2010). Accounting for environmental factors in spatial dynamics studies can be challenging, especially in cases like the eastern Bering Sea, where spatial data for many stocks is limited to summer months when feeding migrations predominate. Spatial data from winter or early spring, when many bottom fishes are spawning (e.g., Nichol, 1998) might show entirely different trends in relation to environmental factors. Although this study lacks data

on intra-annual or seasonal variability, we attempted to capture more interannual variability by quantifying similarities in summer fish distribution between all possible survey year combinations. The modeling framework used in this study could be extended to address more specific questions regarding the spatial dynamics of the Bering Sea ecosystem. Data from the survey time series could be categorized into functional groups based on life history stage, feeding guilds, or some other criterion to investigate environmental responses to cannibalism, predator–prey relationships, or interspecies competition. Catch data categorized by age or size could be used for analyzing processes that may shape spatial recruitment patterns (Petitgas et al., 2009) or segregation of different age groups (Woillez et al., 2007). The analysis could also be expanded to include other environmental variables such as bottom type (McConnaughey and Smith, 2000; McConnaughey and Syrjala, 2009), cold pool volume or thermocline depth (Swartzman et al., 1994).

4.3. Choice of predictors

We believe the approach and model are robust for detecting temporal trends and environmentally-driven changes in the spatial distributions of bottom fish and crab populations on the eastern Bering Sea shelf. The model incorporates more variability than previous studies by comparing similarities between the predictor and response variables for all possible survey year

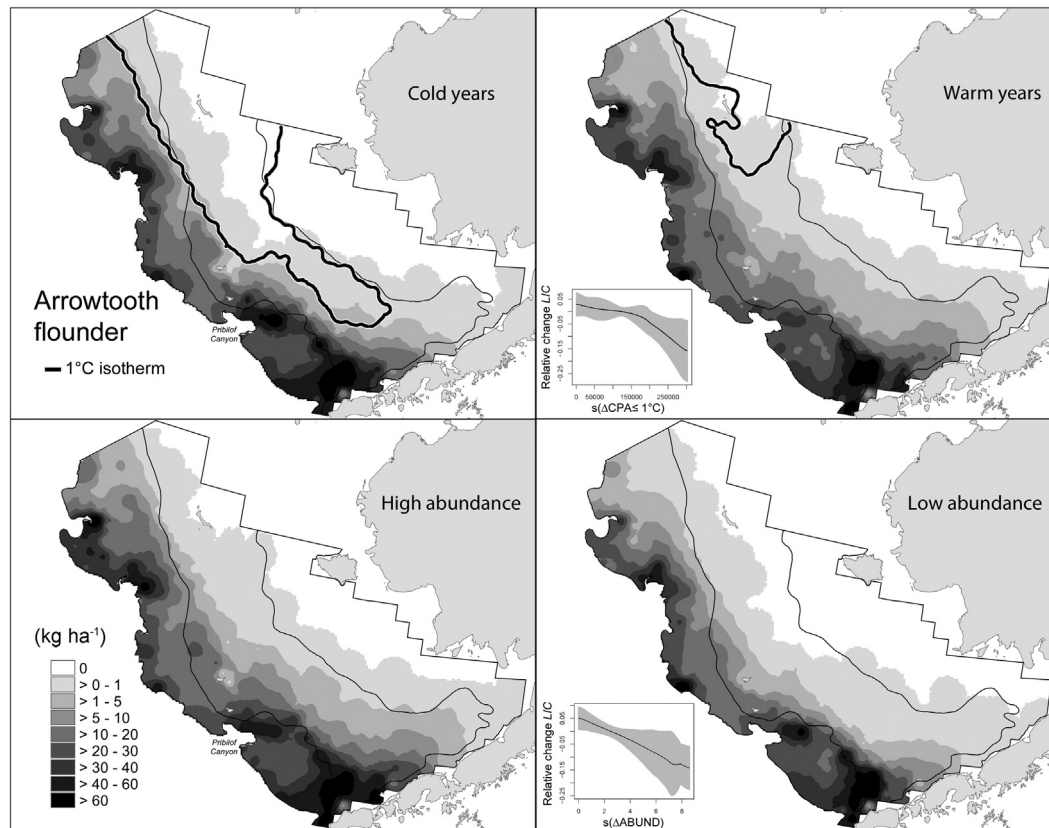


Fig. 10. Variability in the spatial distribution of arrowtooth flounder during cold and warm years and the high and low abundance years to illustrate the decreasing similarity of the local index of collocation (*LC*) to the effects of increasing $\Delta CPA_{1^\circ C}$ and $\Delta ABUND$. The gray shaded area represents the 99% confidence interval.

combinations rather than comparing similarities for only two populations (e.g., [Syrjala, 1996](#)) or a linear trend in the time series. For modeling spatial variability, we chose only taxa that we felt provided a consistent index of abundance over the 30-year time series. We also chose response variables for detecting differences in both local and shelf-wide spatial patterns of distribution. Moreover, we also considered magnitude and distance in the spatio-temporal displacement of populations for each of the predictors. Three predictors were chosen for investigating local and shelf-wide spatial patterns: (1) the areal extent of the cold pool at three different temperature levels, (2) population abundance, and (3) time lag in survey years. These variables were chosen because other studies have suggested that they affect spatial distribution ([Kotwicki et al., 2005](#); [Mueter and Litzow, 2008](#); [Spencer, 2008](#)), and because data for all three were available from the eastern Bering Sea time series. Temperature and population abundance are often cited by other researchers as important in determining the distribution of a species (e.g., [Ciannelli et al. 2008](#); [Spencer, 2008](#)). The third, time lag in survey years, is also very important because through covariation it incorporates temporal trends about other factors in the eastern Bering Sea marine ecosystem that are dynamic and unrelated to temperature or population abundance. We also used spatial indices that measured general similarity in the distribution, but did not require assumptions about the direction of the temporal displacement (e.g., [Mueter and Litzow, 2008](#)).

In contrast to the previous studies, we evaluated three different temperature levels to model temperature effects on bottom fish and crab distributions. Past studies have used mean temperature over the eastern Bering Sea shelf area ([Mueter and Litzow, 2008](#)), or the proportion of the area that was covered by the cold pool defined as the area where bottom temperature was below a single threshold (e.g., $< 2^\circ C$; [Spencer, 2008](#)). Although both of these

metrics are adequate indicators of the general bottom temperature conditions over the eastern Bering Sea shelf, neither provides a direct measure of the extent of the cold pool. Moreover, different fish taxa have different temperature preferences ([Scott, 1982](#)) and an arbitrary choice of one temperature level may not be adequate to assess the effect of the cold pool on specific bottom fish or crab distributions. Thus, we chose a more explicit model that was allowed to choose a best fit to the data using three different temperature levels.

Acknowledgments

We thank the legions of people for their extraordinary efforts to create and maintain the eastern Bering Sea shelf bottom trawl survey time series. This includes survey gear specialists, data managers, survey support and administrative staff, captains and crews of chartered fishing vessels, and most important, survey participants from within our own ranks at the AFSC, as well as scores of others representing too many organizations to list. We also thank Matt Baker, Dan Nichol, Dave Somerton, Paul Spencer, Paul von Szalay, Duane Stevenson, and four anonymous reviewers whose valuable comments greatly improved the quality of this manuscript. The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of National Marine Fisheries Service, NOAA. This is BEST-BSIERP Bering Sea project publication number 80 and NPRB publication number 395.

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