# Climate-related changes in the biomass and distribution of small pelagic fishes in the eastern Bering Sea during late summer, 2002-2018

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## ABSTRACT

Climate change is altering the distribution and biomass of marine species in Arctic and sub-Arctic waters. In this study, we investigate the influence of sea temperature on the annual distribution and biomass of pelagic fishes in the eastern Bering Sea during late summer, 2002-2018. The distribution (easting, northing, and area occupied) and biomass of capelin, Pacific herring, juvenile chum salmon, juvenile pink salmon, juvenile sockeye salmon, and age-0 walleye pollock collected by surface trawl were estimated using a standardized geostatistical delta-generalized linear mixed modeling approach. Species showed varied responses to warming on a temporal scale. Warming corresponded with more northerly distributions for capelin and juvenile sockeye salmon, a more westerly distribution of juvenile sockeye salmon, and range expansions for juvenile chum and sockeye salmon. Warming corresponded to a decrease in the annual biomass of capelin and an increase in the biomass of herring, age-0 pollock, and juvenile sockeye salmon. The spatio-temporal covariation in sea temperature and the distribution was nonlinear for juvenile pink salmon and age-0 pollock, positive for juvenile chum salmon and juvenile pink salmon, and negative for capelin indicating different responses of the distribution of pelagic fishes to warming in the eastern Bering Sea during late summer. In warmer areas, we found that the catch rates were higher for juvenile pink salmon, lower for capelin, and not significantly different for juvenile chum salmon, herring, age-0 pollock, and juvenile sockeye salmon. Juvenile sockeye salmon, a southerly distributed species in the survey area, appeared most responsive to warming. In this study, sockeye salmon and pollock are the most commercially important species while chum salmon are important for subsistence fishing. These temperature related changes during early life history stages for survival may have impacts on the numbers of these fishes recruiting to the fisheries.

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## 1. Introduction

Climate-related changes in ecosystems have altered the distribution and biomass of plants, zooplankton, jellyfish, insects, birds, fishes, and mammals within the last century (Rose et al., 2000; Perry et al., 2005; Cieciel et al., 2009; VanDerWal et al., 2013; Andrews et al., 2016; Ash et al., 2017; Hunt et al., 2018). Physical and biological influences on the growth, survival, and reproduction of ecological communities can change the distribution and biomass of species that in turn alters species richness and ecosystem dynamics (Carscadden et al., 2001; Hiddink and Ter Hofstede, 2008). Understanding temperature related changes in distribution and biomass will aid in understanding and predicting climate-related changes in the recruitment of fishes to fisheries.

At high latitudes, sea temperature and ice dynamics influence poleward shifts in fish species distribution (Hollowed et al., 2012; 2013). For example, a 1.5-3°C warming in the North Atlantic and North Pacific oceans led to a more northerly distribution of bottom fishes since the 1980s (Perry et al., 2005; Mueter and Litzow, 2008; Stevenson and Lauth, 2019). A benthic "cold pool" (<2°C) can form in the eastern Bering Sea (EBS) as a result of water cooling from melting sea ice during spring and strong vertical stratification during summer (Stabeno and Bell, 2019). In 2018, the cold pool extent was reduced to a near historic minimum. When present, this benthic cold pool persists through the summer and limits the northward movement of some benthic fish and crab species (Mueter and Litzow, 2008). Limited movement can depend on fish size and location (Wylie-Echeverria and Wooster, 1998; Cianelli and Bailey, 2005; Kotwicki et al., 2005; Mueter and Litzow, 2008; Barbeaux and Hollowed, 2018; Li et al., 2019). This physical/biophysical barrier does not exist for small pelagic fishes because they are above the pycnocline and thus avoid the cold pool in the EBS, and they are able to move northward more freely.

Small pelagic fishes in the EBS are important prey for fishes (Bailey, 1989; Aydin and Mueter, 2007), seabirds (Decker and Hunt, 1996), and marine mammals (Sinclair, 1994). This group of fishes commonly includes capelin (*Mallotus villosus*), Pacific herring (*Clupea pallasii*, hereafter referred to as herring), juvenile chum salmon (*Oncorhynchus keta*), juvenile pink salmon (*O. gorbuscha*), juvenile sockeye salmon (*O. nerka*), and age-0 walleye pollock (*Gadus chalcogrammus*, hereafter referred to as age-0 pollock) during their first year of life. The National Oceanic Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center conducted surface trawl surveys in the EBS, 2002-2018. Published results showed a shift northward for age-0 pollock, juvenile salmon, herring, and capelin during the 2002-2005 warm stanza relative to the 2006-2011 cool stanza in the EBS (Moss et al., 2009a; Hollowed et al., 2012; Andrews et al., 2016). However, little is known about temperature related changes in the distribution and biomass of pelagic fishes in the EBS over multiple climate stanzas.

Several mechanisms have been proposed for the regulation of the distribution and biomass of pelagic fish species in the EBS via temperature. First, the Oscillating Control Hypothesis describes that during cold years, sea ice extends farther south and persists later in the year. The delayed departure of sea ice facilitates an ice-associated algal bloom (Hunt et al., 2002, 2011). The ice-associated algal bloom is food for zooplankton during late winter and spring which in turn, these zooplankton are lipid-rich prey for small pelagic fishes resulting in higher body lipid content and higher survival (Hunt et al., 2002; Andrews et al., 2009; Coyle et al., 2011; Hunt et al., 2011). Hence cooler temperatures would favor increased biomass for small pelagic fish in the eastern Bering Sea. Second, the distribution and biomass of small pelagic fishes may be influenced by the use of the benthic cold pool as a barrier or refuge from predators or as a thermal refuge (Ciannelli and Bailey, 2005; Duffy-Anderson et al., 2017), hence they may migrate north to use the benthic cold pool as a refuge from predators or as a thermal refuge to conserve energy (Duffy-Anderson et al., 2017). Studying a period of sequential warm-cool-warm stanzas could provide insight into factors influencing the distribution and biomass when temperature variation is high over a short period of time.

There is limited information on the influence of temperature on pelagic fishes over multiple climate stanzas in the EBS. The goal of our study was to examine the impact of changing annual summer sea surface temperatures (SST) on the distribution and biomass of six fish species in the pelagic waters of the EBS continental shelf during late summer from 2002-2018. This time period includes several alternating stanzas of warm (2002-2005, 2014-2018) and cold (2006-2013) years. With warming, we expected pelagic fishes in the EBS to: H1) decrease in biomass, H2) extend movement northward, and H3) expand their overall distribution. Regression models between indices and SST were used to examine changes in the distribution and biomass.

## 2. Material and methods

### *2.1. Study area*

In the northeastern Pacific Ocean, the EBS is bound by the Aleutian Chain in the south and Bering Strait in the north. Movement pathways include the Bering Strait to the Chukchi Sea in the north and multiple passes through the Aleutian Chain in the south to the Gulf of Alaska (Fig. 1). The broad shallow continental shelf has few geographic barriers and allows for fish movement north to south and east to west. Shelf bathymetry is typically separated into three oceanographic domains, which are defined by their physical characteristics (Coachman, 1986). The nearshore area is weakly stratified and consists of nutrient-poor coastal waters (Kachel et al., 2002). The middle shelf is a nutrient-rich environment; the benthos supplies; benthic nutrients are carried to the euphotic zone via storm induced mixing (Sambrotto et al., 1986). The offshore area is nutrient-poor relative to the other areas (Springer et al., 1996). The survey area included from nearshore (~50 m) to the shelf break (<150 m depth), latitudes 54.7 °N to 65.5 °N, and longitude -173 °W to -159 °W.

### *2.2 Dataset*

#### *2.2.1. Fish collection*

Juvenile and small fishes were collected in pelagic waters of the EBS during late summer as part of the Alaska Fisheries Science Centers' Bering Arctic Sub-Arctic Integrated Survey (BASIS), 2002-2018 (Farley et al., 2007; Moss et al., 2009a). A total of 1521 stations was sampled for fish (Fig. 2). The number of stations per year ranged from 62 to 157, and averaged 117. Surface trawl surveys were not conducted in the south (<60 °N) during 2013, 2015, and 2017 and north (≥60 °N) during 2008. These years were excluded from our analysis. The remainder of the surveys covered the majority of the EBS, but sampling designs evolved over time because of logistical constraints but were all systematic in nature. In theory, the VAST model's spatially and temporally random effects can effectively estimate the underlying distribution across these different spatial designs.

Six commonly captured small fishes in pelagic waters of the EBS including capelin, herring, juvenile chum salmon, juvenile pink salmon, juvenile sockeye salmon and age-0 pollock were used in our analysis. Stations were approximately 30 nm apart from 2002 to 2015, and 60 nm apart in the southern grid starting in 2016 and 2018. A CanTrawl net was towed from a vessel in the upper 20 m. The trawl was towed at 3.5-5 knots (6.5-9.3 km/h) for approximately 30 minutes. Area swept by the net at each station was estimated as the product of horizontal net opening and distance towed. On average the horizontal spread of the net was 55 m (Farley et al., 2007). Distance towed was calculated as the great circle distance (km) from the time of equilibrium to haul back of the net (i.e. the initial retrieval of the net). Trawl catch was sorted and weighed (kg) by species at each station.

#### *2.2.2. Sea surface temperature*

In our analysis, we used measurements of sea surface temperature (SST) collected at stations sampled during the same survey as we collected fish, i.e. the Alaska Fisheries Science Center pelagic surface trawl survey in the eastern Bering Sea, 2002-2018 (Fig. 2). We calculated annual means from stations most frequently investigated in the survey across time including from a region -169° to -167° and 60°N to 63.5°N in the north and the region -166° to -162° and 54°N to 59°N in the south. The mean annual SST had a range of 4.1°C varying from 8.0°C to 12.1°C among years (Fig. 3). Late summer SSTs were relatively warm from 2002 to 2005 and in 2007, cool in 2006 and from 2008 to 2012, and warm again from 2014 to 2018. We used annual mean SST to examine temporal variation in SST in relation to annual mean distribution (northing easting, area occupied) and total annual biomass. We also used the predicted values of the normalized SST across the survey area to examine the relationship between spatio-temporal variation in sea temperature and spatio-temporal variation in distribution (probability of encounter) and abundance (positive catch rates) (Fig. 4).

### 2.3. Statistical methods

To estimate the biomass and distribution (northing, easting, area occupied) by species and year in the EBS survey area we used the geostatistical vector autoregressive spatio-temporal (VAST) model for single species (Thorson et al., 2015; Thorson et al., 2016a; b; c; Thorson and Barnett, 2017; Thorson, 2019). The model integrates spatial variation in average density across years ("spatial variation") as well as spatial variation for each individual year ("spatio-temporal variation") when estimating fish biomass over the BASIS survey area. Spatial and spatio-temporal variation in the estimates of biomass were included to improve density predictions in areas with few or missing data (Shelton et al., 2014).

We specified conventional settings in VAST for index standardization. This included a stochastic partial differential equation approximation to spatial and spatio-temporal variables, which involved specifying a triangulated mesh. We used 60 "knots" for the mesh survey design, where the location of these knots was identified using a k-means algorithm based on the location of data. We used the epsilon bias-correction estimator for the index to reduce bias from calculating derived quantities of biomass as a nonlinear function of random effects or high variance in random effects (Thorson and Kristensen, 2016). We then extrapolated densities over a spatial domain that was identified by overlaying a mesh grid with 42 kilometer spacings.

We applied the VAST package (version 8_2_0) with Microsoft open R (version 3.5.3) (R Core Team, 2016). The VAST model is a delta geostatistical model that includes two linear predictors, one for the probability of encounter and the other for positive catch rate (Thorson et al., 2015, Thorson, 2019). Each linear predictor includes a spatial, spatio-temporal, and covariate effects. The first linear predictor, encounter probability for sample *i* is given as:

$$p_1(i) = \sum_{f=1}^{1} \omega_1(\quad) + \sum_{f=1}^{\varepsilon 1} \varepsilon_1(\quad, t\ ) + \sum_{p=1}^{p} \gamma_1(\ t\ , p) X(x\ , t\ , p)$$

Where $\sum_{f=1}^{1} \omega_1(\quad)$ is the spatial effect, $\sum_{f=1}^{\varepsilon 1} \varepsilon_1(\quad, t\ )$ is the spatio-temporal effect, and $\sum_{p=1}^{p} \gamma_1(\ t\ , p) X(x\ , t\ , p)$ is the density covariate. Symbols include   for knot location, $t$ for year, *i* is sample or station, X is the covariate (SST). Parameters include omega $(\omega)$, epsilon $(\varepsilon)$, and gamma $(\gamma)$. Positive catch rates $p_2(i)$ the second component given as

$$p_2(i) = \sum_{f=1}^{2} \omega_2(\quad) + \sum_{f=1}^{\varepsilon 2} \varepsilon_2(\quad, t\ ) + \sum_{p=1}^{p} \gamma_2(\ t\ , p) X(x\ , t\ , p)$$

Linear predictors are used to predict population density and abundance, see Thorson (2019) for additional model details. Including spatio-temporal variation in the estimates of density improves density predictions in areas with little data (Shelton et al., 2014), ideal for our survey with limited coverage in some years (Fig. 1).

Total biomass $I(t)$ (units: kilograms) was predicted from density for the entire survey area by year *t* for a given species from Thorson et al. (2015):

$$I(t) = \sum_{s=1}^{s} (a(\ ) \times d(\ ,t))$$

where $a(\ )$ is the area associated with extrapolation-cell  (Shelton et al., 2014; Thorson et al., 2015).

The center of the distribution (kilometers relative to reference locations), called the “center of gravity”, was calculated for each species as (Thorson et al., 2016b; 2017):

$$X(t) = \sum_{s=1}^{s} x(\ ) \frac{(a(\ ) \times d(\ ,t))}{I(t)}$$

where $x(\ )$ is a matrix of distances (center of gravity). Northing, or the center of the latitudinal distribution, is the distance from the Equator to the pole representing the north-south movement of fish. Easting, or center of the longitudinal distribution, is the distance in kilometres from the 180 degree line representing East-West movement of fish. Standard error for $I$ and $X$ are calculated with Template Model Builder, an auto differentiation software library (Kristensen et al., 2016).

Effective-area occupied $A(t)$ was calculated as the area required to contain the population at the average density, and indicates range expansions and contractions (Thorson et al., 2016c):

$$A(t) = \frac{I(t)}{\bar{d}(t)}$$

Where the biomass-weighted average density was:

$$\bar{d}(t) = \sum_{s=1}^{s} \frac{a(\ ) \times d(\ ,t)}{I(t)} d(\ ,t)$$

Model performance was examined with expected probability and observed frequency of encounter for encounter probability, quantile plots for residuals of the positive catch rates, and spatial trends in the Pearson residuals for encounter probability and positive catch rate components by knot.

Comparison of the base model without the covariate and model with the covariate SST (covariate model) for encounter probability and positive catch rate were compared by significance of the gamma parameter. The Akaike Information Criterion (AIC) was also used to compare performance of the base mode with the covariate model (Akaike, 1974). Parameters were considered significance at t-value ≥ 1.34. To examine relationships between SST and fish we used a nonlinear formula for the covariate effect of SST on encounter probability and positive catch rates of fish in the model.

Temporal synchrony among species for each index of distribution and abundance was examined by relating time series of annual indices of distribution and biomass between species using Pearson product moment correlation analysis. A Bonferroni correction factor was applied to account for the 15 among species correlations within each correlation matrices by index. Statistically significant p-values for n years were 0.05/15=0.00333, which results in statistical significance when the Pearson correlation coefficients are greater than or equal to 0.7.

Linear regression models were used to describe relationships between the annual summer SST index and the annual distribution and biomass indices by species. We explored the possibility that range expansions occurred to compensate for density effects. Linear regression models were used to related annual values of effective area occupied to annual values of biomass as in (Thorson et al., 2016c). Coefficient of determination was used to describe the proportion of variation in the dependent variable explained by the predictor variable. Analyses were conducted using the lm package in R.

## 3. Results

### *3.1. Trends and coherence in distribution and biomass among pelagic fish species*

The general distribution and biomass of the six pelagic fish species in our study varied temporally and spatially over the EBS shelf from 2002-2018 with three regional groupings (Figs. 5-10: Appendix 1). In general, juvenile sockeye salmon tended to be distributed in the south EBS; herring were found in the north EBS; and juvenile pink salmon, juvenile chum salmon, age-0 pollock, and capelin were in the north and south EBS. Capelin were typically in the middle shelf region spanning the north and south EBS during cold years, and found in the north EBS during warm years (Fig. 5). Capelin hot spots include around St. Lawrence Island and south of Nunivak Island. Herring were distributed more nearshore in Norton Sound and around Nunivak Island but were also found broadly across the north EBS (Fig. 6). Juvenile chum salmon were in nearshore and middle shelf regions (Fig. 7). Juvenile pink salmon were distributed throughout the EBS among years (Fig. 8). Juvenile sockeye salmon were distributed in the middle and nearshore regions of the south EBS (Fig. 9). Age-0 pollock were found primarily in middle and nearshore regions of the south EBS and in the middle shelf area of the north EBS (Fig. 10).

Mean biomass (mt) estimates were dominated by age-0 pollock (94,419) and herring (75,450) followed by capelin (10,974), juvenile sockeye salmon (9335), juvenile pink salmon (4627) and juvenile chum salmon (4476). Age-0 pollock and herring dominated pelagic fish biomass during warm years and by herring and capelin during cold years (Appendix 1). Interannual range in biomass was highest for age-0 pollock (314,231) and herring (131,316). Highest biomass levels occurred in 2004 for herring and age-0 pollock, 2011 for capelin, 2014 for juvenile sockeye, and 2018 for juvenile pink and chum salmon.

Northings (km from the Equator), or the center of the latitudinal distribution distance from the Equator (km), indicate two latitudinal groupings of fishes, juvenile sockeye salmon and age-0 pollock in the south EBS, and capelin, herring, juvenile chum salmon, and juvenile pink salmon in the north EBS. The northernmost distribution occurred for herring (6903 km) and capelin (6848), and southernmost distributed fishes included age-0 pollock (6407), and juvenile sockeye salmon (6382). Inter-annual range in northings was highest for juvenile pink salmon (475), and least variable for juvenile sockeye salmon (158). Distributions were farthest north in 2002 for capelin, in 2011 for herring and juvenile chum salmon, and in 2014 for juvenile pink salmon, juvenile sockeye salmon, and age-0 pollock.

Eastings (km from 180° longitude), or center of the longitudinal distribution, were farthest east for juvenile sockeye salmon (522), intermediate for herring (424), age-0 pollock (381), and juvenile chum salmon (366), and farthest west (closest to the 180° longitude) for capelin (280) and juvenile pink salmon (267) (Appendix 1). The east-west distribution of the fishes varied more interannually for juvenile sockeye salmon (246) and age-0 pollock (300), the southern species possibly due to wider habitat. Fishes were farthest east, more nearshore, during 2003 for age-0 pollock, 2007 for juvenile sockeye, in 2011 for capelin and herring, 2016 for juvenile pink salmon, and in 2018 for juvenile chum salmon. Fishes were farthest offshore in 2002 for age-0 pollock, in 2009 for capelin, juvenile chum salmon, and juvenile pink salmon, and in 2014 for herring and juvenile sockeye.

The effective area occupied (km$^2$) was on average greatest for juvenile pink salmon (258,227) and juvenile chum salmon (230,198) followed by age-0 pollock (148,362) (Appendix 1). The amount of area occupied overlapped highly among the six species. Inter-annual range in the mean effective area occupied was the highest for juvenile chum salmon (338,496). Fishes occupied the largest area in 2002 for capelin, 2005 for juvenile pink salmon, 2009 for herring, 2016 for juvenile sockeye salmon, and in 2018 for juvenile chum salmon and age-0 pollock.

Temporal synchrony in the biomass and distribution of pelagic fishes varied among species (Fig. 10). Time series of biomass was positively correlated among juvenile chum, pink, and sockeye salmon and between age-0 pollock and juvenile sockeye salmon. Synchrony in northings, easting, and area occupied occurred only between juvenile pink and chum salmon.

### *3.2. Pelagic fish biomass and annual SST*

Biomass of three of six species was significantly related to annual mean summer SST in the EBS (Tables 1 and 2). Capelin biomass significantly decreased with sea surface warming with SST explaining 38% of the variation in biomass. Capelin biomass was higher in years with SST below 5.1°C. The biomass of herring, juvenile sockeye salmon, and age-0 pollock increased with a rise in SST. SST explained 24% of the variation in herring biomass, 47% of the variation in the biomass of juvenile sockeye salmon, and 35% of the variation in age-0 pollock biomass as indicated by the coefficient of determination of the linear regression models.

### *3.3. Pelagic fish distribution and annual SST*

Northings increased with warming for capelin and juvenile sockeye salmon (Tables 1 and 2). SST accounted for 65% of the annual variation in the latitudinal center of gravity for juvenile sockeye salmon and 35% of the annual variation in the northing of capelin.

Eastings decreased with increasing sea temperatures for one of the six species (Table 1, 2). SST accounted for 73% of the variation in the easting of juvenile sockeye salmon. Results indicate that juvenile sockeye salmon were distributed farther west or offshore during warm years.

The effective area occupied increased with warming sea temperatures for juvenile chum and sockeye salmon, but not for capelin, herring, juvenile pink salmon, or age-0 pollock (Table 1, 2). SST accounted for 57% of the variation in the effective area occupied by juvenile sockeye salmon, and 31% of the variation in the range expansion of juvenile chum salmon.

### *3.4. Spatio-temporal covariation between SST and fish encounter and catch rate*

Table 3 shows the estimates and standard errors of the gamma parameter for the effect of SST on encounter probability and positive catch rate and AIC values for the base and covariate models. Probability of encounter was significantly related to SST for all species except herring. The effect of SST on the probability of encounter was negative for capelin, nonlinear for juvenile pink salmon and age-0 pollock, and positive for juvenile chum salmon and juvenile sockeye salmon. The effect of SST on positive catch rates given an encounter were negative for capelin, positive for pink salmon, and not significantly related to the catch rates of juvenile chum salmon, herring, age-0 pollock and juvenile sockeye salmon. The AIC was lowered when adding SST to the capelin, chum salmon, and pollock models, but not for the herring, juvenile pink salmon, and juvenile sockeye salmon models.

### *3.5. Range expansions and biomass*

Table 4 indicates possible range expansions due to density-dependent increases in biomass. Chum salmon area occupied was positively related to the biomass of juvenile chum salmon, juvenile pink salmon, and juvenile sockeye salmon. Annual variation in mean effective are occupied by juvenile chum salmon were explained by juvenile chum salmon biomass ($r^2$=0.45, p-value=0.005), juvenile pink salmon ($r^2$=0.38, p-value=0.01), and juvenile sockeye salmon ($r^2$=0.36, p-value=0.01). No other species had significant positive relationships between area occupied and biomass.

## 4. Discussion

Our analysis expanded upon prior analyses of the distribution and biomass of pelagic fishes in the EBS during late summer (Farley et al., 2007; Cieciel et al., 2009; Hollowed et al., 2012; Andrews et al., 2016) by including multiple climate stanzas: warm (2002-2005, 2007), cold (2006, 2008-2013), and warm (2014-2018). Our results are based on correlation and linear regression models that should be viewed as correlative, not causative. Biomass of herring, juvenile sockeye salmon, and age-0 pollock showed an increase with warming, while capelin showed a decrease with warming. Two of the six pelagic fishes in our study changed their distribution with warming SST. Juvenile sockeye salmon were found farther offshore to the west with warming. Two juvenile salmon species had range expansions with warming. A differential responses to the effect of SST on encounter probability and catch rates occurred among the fishes in our study. This indicates that some pelagic fish species are coming up against their maximum temperature threshold in the EBS.

### *4.1. Trends and coherence in distribution and biomass among pelagic fish species*

Synchronous changes in juvenile pink and chum salmon biomass, northing, easting, and effective area occupied over time unrelated to SST suggests a different mechanism than temperature in driving distribution and biomass of these two species. Juvenile chum and pink salmon in our survey have similar body sizes and primarily originate from rivers entering Norton Sound (Kondzela et al., 2009). Their migration path is south and west, where they spend time growing and feeding in the central Bering Sea and North Pacific Ocean. Juvenile pink and chum salmon feed on similar prey items (Davis et al., 2009). Synchronous changes in the biomass of juvenile sockeye and age-0 pollock indicate a potential for competition or movement in relation to prey within a habitat and year. This hypothesis could be examined more closely by including age-0 pollock and zooplankton as covariates of the distribution of juvenile sockeye salmon.

### *4.2. Pelagic fish biomass and annual SST*

The response of changes in the biomass of pelagic fish in relation to SST varied among species in the southern EBS. Capelin was the only species to increase in biomass with cooler SSTs, similar to results of previous studies from the same survey but with fewer years of data (Eisner et al., 2015; Andrews et al., 2016). Capelin in the northern portion of the study area consumed more lipid-rich prey (e.g. *Calanus* spp.) than in the south and were more abundant during cold years than warm years in the northern EBS, 2003-2011 (Eisner et al., 2015; Andrews et al., 2016). These zooplanktivorous fishes may have a higher population biomass and higher survival when more lipid-rich copepods are available as prey, according to the Oscillating Control Hypothesis (Hunt et al., 2002; Hunt et al., 2011; Heintz et al., 2013).

In contrast, warming favored the biomass of herring, age-0 pollock, and juvenile sockeye salmon in the pelagic waters of the EBS shelf, 2002-2018. Our results confirm findings based on earlier years of BASIS survey data showing that age-0 pollock were more abundant in surface waters during warm years than cold years, 2003-2010 (Hollowed et al., 2012; Eisner et al., 2015). Age-0 pollock are distributed throughout the water column, whereas the BASIS trawl gear catches only reflect the biomass in the upper 20 m of the water column. With acoustics, Parker-Stetter et al. (2013) found that age-0 pollock distributed in higher densities in the cooler waters below the pycnocline during a cold year period 2006-2010. Therefore, we cannot determine how well our biomass index represents the population biomass for age-0 pollock. Several mechanisms exist to explain the warming associated increases in age-0 pollock abundance on the EBS shelf, such as increased egg production, and wind and current driven transport of eggs and larvae onto the shelf during warm years (Hollowed et al., 2012).

Although age-0 pollock are abundant in the surface waters during warm years, the recruitment success of age-0 pollock to older ages is correlated with increased sea ice during spring, cooler summers, and higher large copepod densities (Hunt et al., 2011; *In Press*; Eisner et al., 2020). This climate-recruitment relationship has changed over time (Hunt et al., in press). Hunt et al. (in press) found that pollock survival was tightly coupled with sea ice and zooplankton densities for the year period 2000-2015, but found no significant correlation between sea ice and pollock recruitment during the 1979-1999 year period. Hunt et al. (in press) attribute this change in relationship due to an alternating pattern of warm and cold years prior to 2000 followed by a shift to multi-year periods, or stanzas, of warm and cold periods after 1999. Prior to 2000, Quinn and Niebauer (1995) found a positive relationship between the survival of pollock to age-2 and air and bottom temperatures, but not sea surface temperatures, during the age-1 life stage, 1964-1990. In contrast, Mueter et al. (2011) recruitment modeling studies showed a higher survival of pollock with lower summer temperatures in the EBS for the period 1963-2009 (Mueter et al., 2011). Yasumiishi et al. (2015) found that a cold summer during the age-0 life stage followed by a warm age-1 during the spring was strongly correlated with pollock year class strength. A winter survey of age-0 pollock and spring survey of age-1 pollock would aid in understanding mechanisms driving survival variability in pollock.

For sockeye salmon, the increase in biomass associated with warming indicates improved environmental conditions for early marine growth and survival. Farley et al. (2007) and Yasumiishi et al. (2016) noted faster growth rates and higher body condition of juvenile sockeye salmon following warmer spring and summer sea temperatures. Recently, adult sockeye salmon to Bristol Bay returns are stable over time with historical high catches of >35 million of fish over the last four years (Salomone et al., 2019). Juvenile sockeye salmon distribute in the upper 20 m of the water column, therefore the surface trawl catches may represent the numbers of juvenile sockeye leaving Bristol Bay and may have value in predicting returns of sockeye salmon to Bristol Bay.

Pacific herring biomass increased with warming in our study. Similar patterns were seen in the Gulf of Alaska with higher productivity during positive phases of the Pacific Decadal Oscillation (warmer nearshore conditions) from 1902 to 1995 (Brown, 2002). However, some stocks show declines in production during El Niño events and the years of regime shifts depending on location (Mantua, 1997; Schweigert et al., 2002; Ito et al., 2015). Togiak herring, a stock from Bristol Bay in the eastern Bering Sea, showed increases in growth rates with warming, while southern stocks showed decreases in growth rates with warming (Ito et al., 2015). Body size at age of herring was also positive correlated with peak zooplankton densities in Prince William Sound, 1973 to 1999 (Brown, 2002). Changes in growth and survival of herring are likely due to varied threshold effects of density-dependence, prey quality and quantity, and other environmental drivers depending upon location and time.

### *4.3. Pelagic fish distribution and annual SST*

Northward movement of fishes with warming was observed for capelin and juvenile sockeye salmon. These zooplanktivorous fishes may move north to take advantage of large lipid rich zooplankton, such as krill and large copepods, that thrive in cold waters. In a correlative study, densities of large copepod in the south EBS were positively related to a later timing of ice melt and a larger area of ice coverage during spring (Hunt et al., in press). In the EBS, juvenile sockeye consumed more krill and large copepods during cold years and more age-0 pollock during warm years (Coyle et al., 2011; Heintz et al., 2013). In addition, these fishes may migrate north to use the benthic cold pool as a refuge from predators or as a thermal refuge to conserve energy (Duffy-Anderson et al., 2017). In contrast, juvenile pink and chum feed on a wider variety of prey items than juvenile sockeye salmon and capelin and likely have a wider range of essential feeding habitats (Davis et al., 2009).

The northward movement and reduced biomass of capelin with warming in the EBS have implications on the survival of their predators such as Chinook salmon from western Alaska. For example in other large marine ecosystems, the northward shift in adult Atlantic cod (*Gadus morhua*) was thought, in part, due to changes in the distribution and abundance of capelin, a preferred prey item (Rose et al., 2000). Atlantic cod that consumed capelin had both larger livers and gonads indicating that capelin are a nutrient-rich prey source (Rose and O'Driscoll 2002). Capelin are an important forage fish for juvenile Chinook salmon in the northern EBS that originate from western Alaska (Davis et al., 2009; Murphy et al., 2009). Yasumiishi et al. (2019) found increased summer growth of juvenile Chinook salmon in the EBS was linked to higher densities of large copepods and a higher proportion of capelin in their diets. In 2007, a warm year, both juvenile Chinook salmon and capelin were found in the Chukchi Sea (Logerwell et al., 2015). Therefore, changes in the distribution and biomass of capelin have potential to influence the migratory pathway or pattern of juvenile Chinook salmon emerging from western Alaska, such as the Yukon and Kuskokwim rivers.

The lack of statistically significant movement northward with warming was observed for three of the four fish species in the northern EBS, specifically herring, juvenile chum salmon, and juvenile pink salmon. To the north of the EBS lies the Chukchi Sea. In 2007, juvenile salmon captured in the Chukchi Sea originated from western Alaska rivers that drain into the EBS indicating that Bering Sea salmon have begun to forage north of the Bering Strait and into the Chukchi Sea (Farley et al., 2007; Kondzela et al., 2009; Moss et al., 2009b). Our finding possibly suggests either a differential response of small pelagic fishes to warming in the north than in the south or that movement north was not detected due to movement of the three fish species north or west out of the survey area.

A westward movement with warming was observed for juvenile sockeye salmon, but none of the other species in our study. Pacific salmon spawn and rear in freshwater, enter saltwater during spring and early summer, rear nearshore during the first summer at sea, and then move offshore during late summer (Farley et al., 2007). Farley et al. (2007) observed juvenile sockeye salmon farther offshore from Bristol Bay in the EBS during warm years (2002-2003) relative to a cooler year (2001). Observed westward location with warming indicates an earlier timing of migration from freshwater to nearshore and/or from nearshore to offshore with warming (Taylor, 2008; Kovach et al., 2013). Changes in capture location also indicate a migration pathway farther to the north and west, possibly in search of preferred prey, such as krill or age-0 pollock as indicate from diet analyses (Coyle et al., 2011). This hypothesis would require further spatio-temporal analysis of the distribution of these fishes with respect to the distribution and abundance of their prey.

Warming associated range expansions occurred for juvenile chum salmon and more significantly for juvenile sockeye salmon but not for capelin, herring, pink salmon, and age-0 pollock. Range expansions may have occurred for other species and were possibly not detected in our analysis due to shifts outside of the survey area. Factors other than temperature that influence the distribution of pelagic fishes include movement, migration, fishing, disease, parasites, physiology, predation, competition, prey abundance, and habitat (Link et al., 2020).

### *4.4. Spatio-temporal covariation between SST and fish encounter probability and catch rates*

The positive and negative impacts of spatio-temporal covariation between SST and the distribution and abundance of fish in our survey indicate a differential response of pelagic fishes to rising sea temperatures in the EBS. The nonlinear response of probability of encounter to SST by juvenile pink salmon and age-0 pollock indicates that temperatures may have reached and/or exceeded optimal temperatures, prey availability, or predation pressure in specific areas of the Bering Sea for these species. In response, these fishes may seek cooler SSTs for thermal regulation, seek prey associated with cooler SSTs, and/or seek thermal refuge from predators (Duffy-Anderson et al., 2017). The positive linear response of the spatio-temporal variation in the distribution of juvenile chum salmon and juvenile sockeye salmon to SST indicate that these fishes are moving through warm waters and conditions are more optimal for the distribution of these two species, than the other species in our study. Catch rates increased in warmer waters for juvenile pink salmon in our study. Finally, the negative impact of SST on the spatio-temporal distribution and catch rates of capelin indicate less favorable conditions for capelin in the pelagic waters of the EBS with warming.

### *4.4. Range expansions and biomass*

We examined the possibility of density-dependent effects of increases in fish biomass on range expansions. Juvenile chum salmon were the only species that showed a response of increased area occupied with increased densities of juvenile salmon. Juvenile chum salmon are the least selective feeder of all juvenile salmon species (Davis et al., 2009). We hypothesize that juvenile chum salmon, as found with adult chum salmon, move to other locations to feed on lower quality prey when abundances of other species increase (Kaeriyama et al., 2004). We also noted an intra-specific response of range expansion with warming by juvenile chum salmon. The range expansion of juvenile sockeye salmon was more strongly correlated with sea temperature than fish biomass.

## 5. Conclusions

Impacts of temporal and spatial changes in summer sea temperature were positive, neutral, and negative on the distribution and biomass of pelagic fish in the EBS. Due to the importance of early life history on the survival of fish species and their importance as prey items for many marine fishes, birds, and mammals, further monitoring is needed to track changes in the distribution and biomass of pelagic fishes during warming. Future studies should examine the relationship between early life history distribution and biomass of pelagic fishes in relation to estimates of year class strength later determined by stock assessments or fishery catches.

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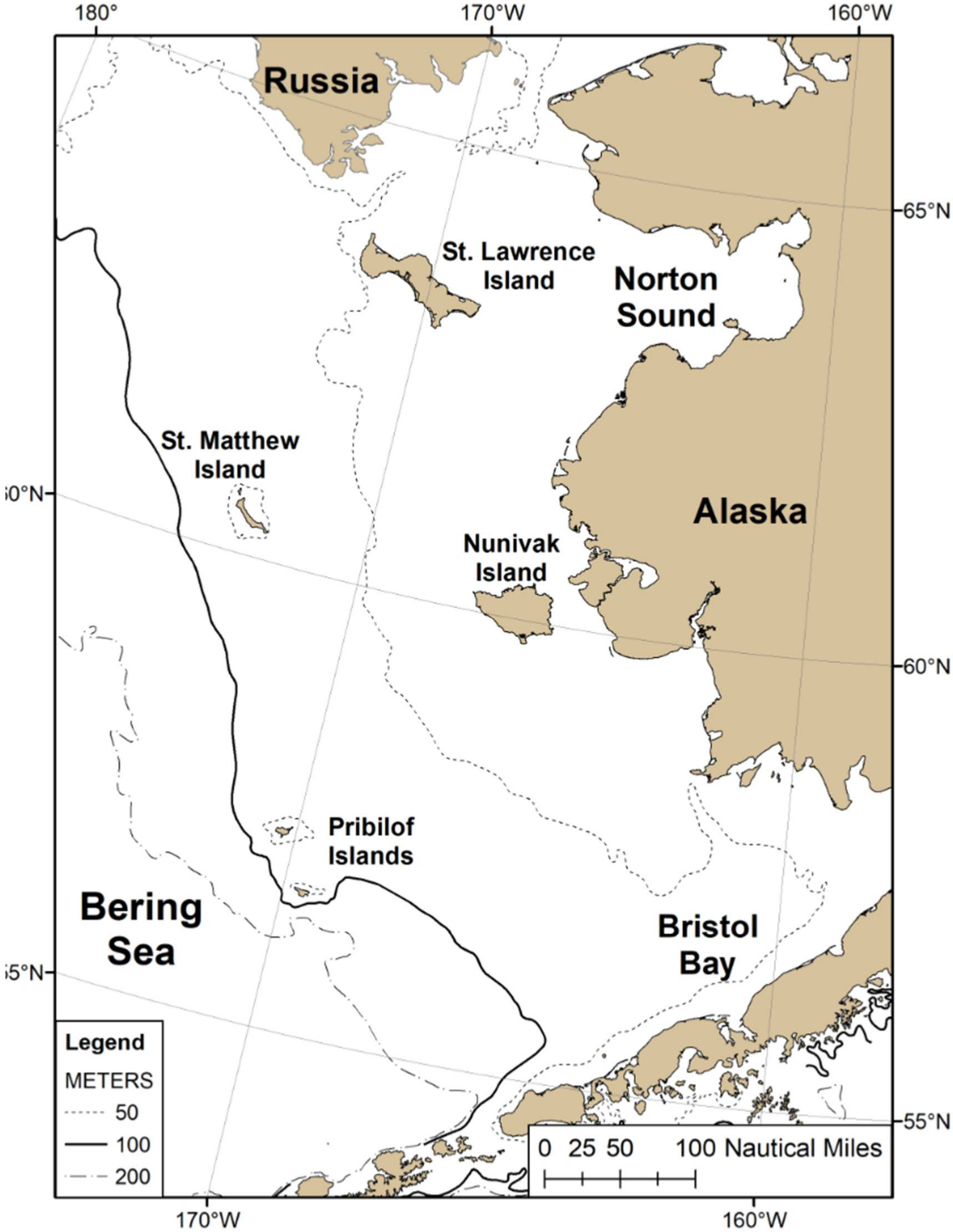
180°
170°W
160°W
Russia
St. Lawrence Island
Norton Sound
65°N
St. Matthew Island
Alaska
Nunivak Island
60°N
Pribilof Islands
Bering Sea
Bristol Bay
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50
100
200
0 25 50 100 Nautical Miles
170°W
160°W

Figure 1. Map of the eastern Bering Sea.

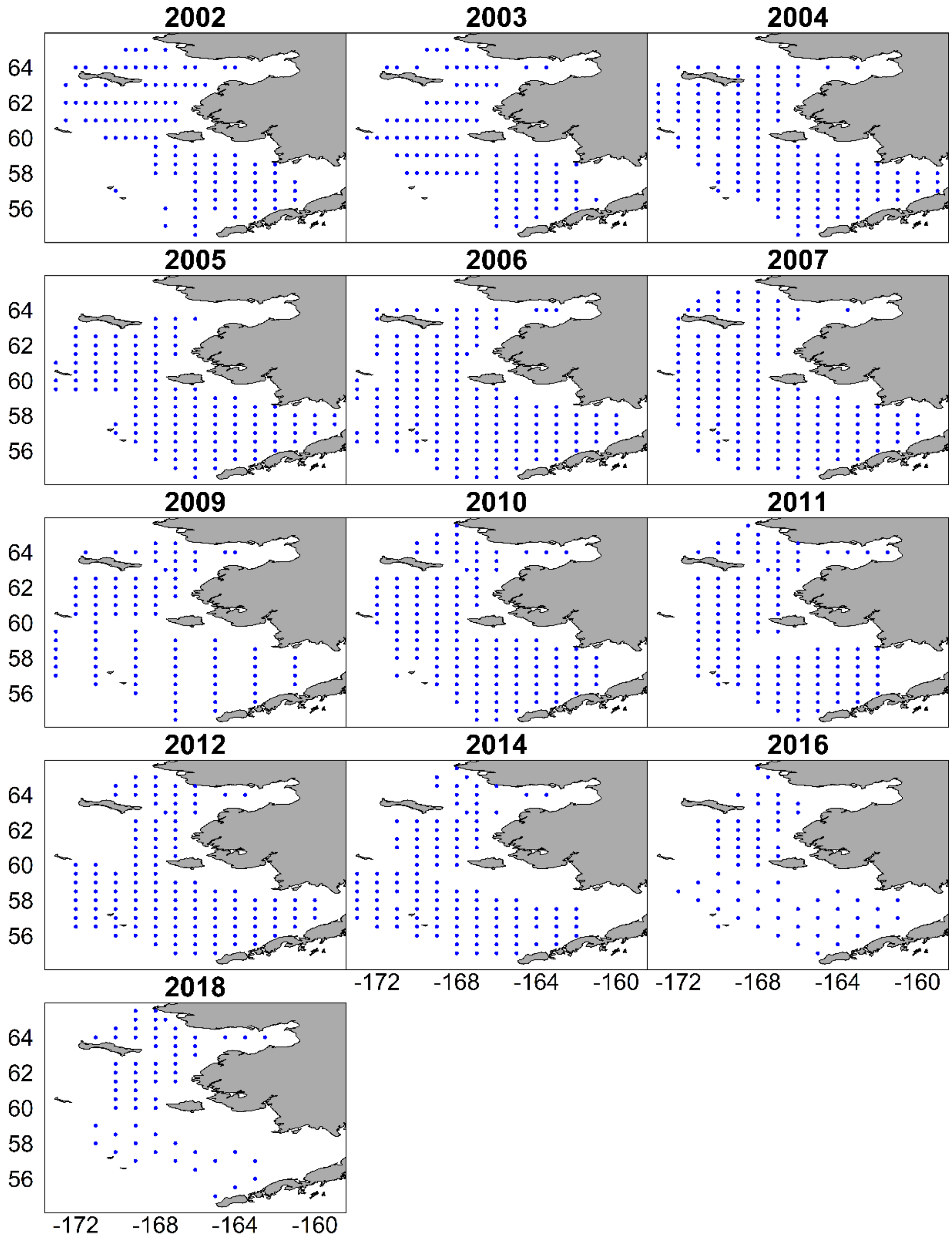


Figure 2. Surface trawl survey locations in the eastern Bering Sea during late summer, 2002-2007, 2009-2012, 2014, 2016, and 2018. The number of stations per year were 109 in 2002, 101

in 2003, 142 in 2004, 126 in 2005, 157 in 2006, 156 in 2007, 97 in 2009, 134 in 2010, 123 in 2011, 130 in 2012, 118 in 2014, 66 in 2016 and 62 in 2018.

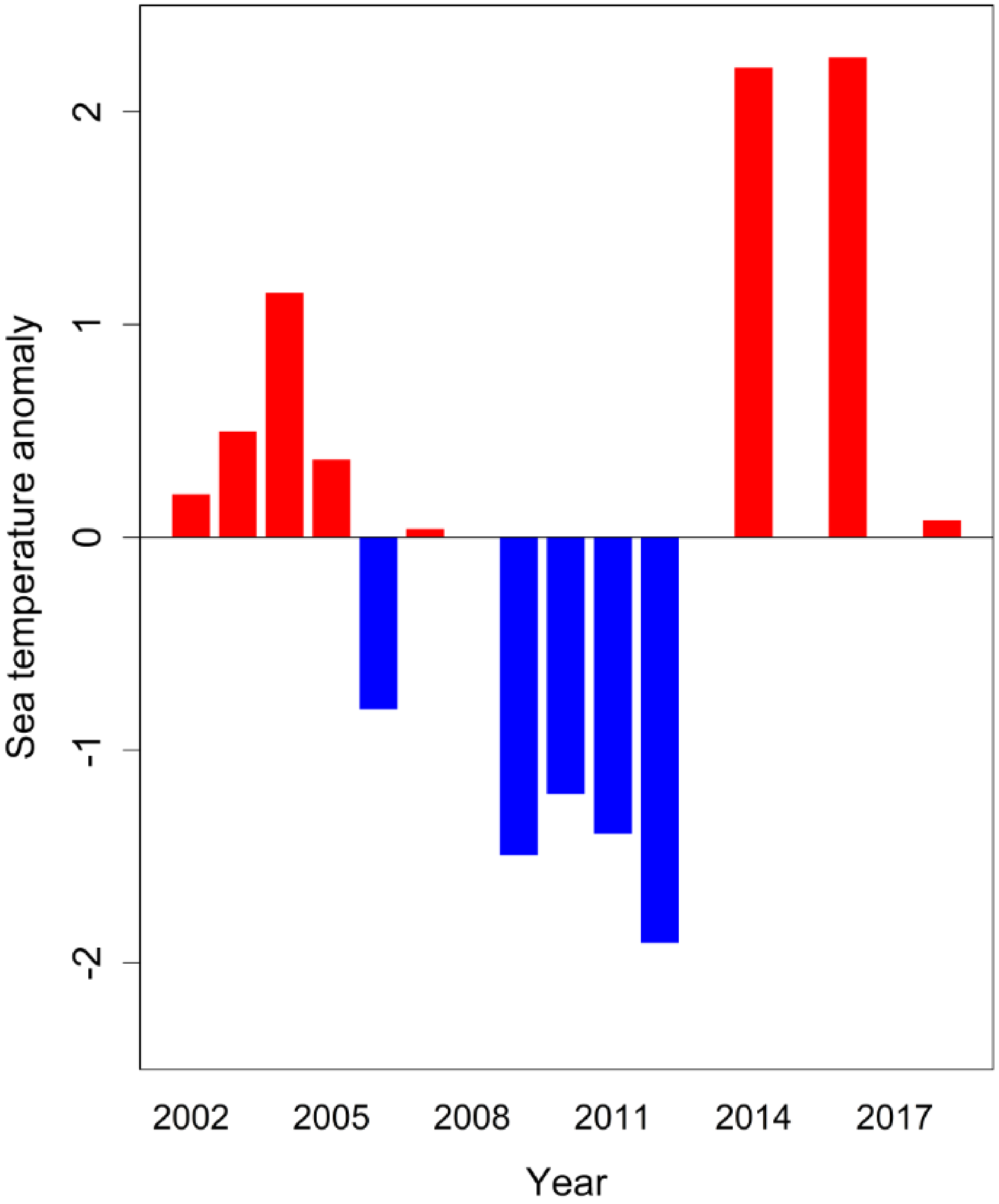


Figure 3. Anomalies of average top 10 m sea temperatures from the Alaska Fisheries Science Center pelagic trawl survey in the eastern Bering Sea during late summer, 2002-2018. Missing years include 2008, 2013, 2015, and 2017.

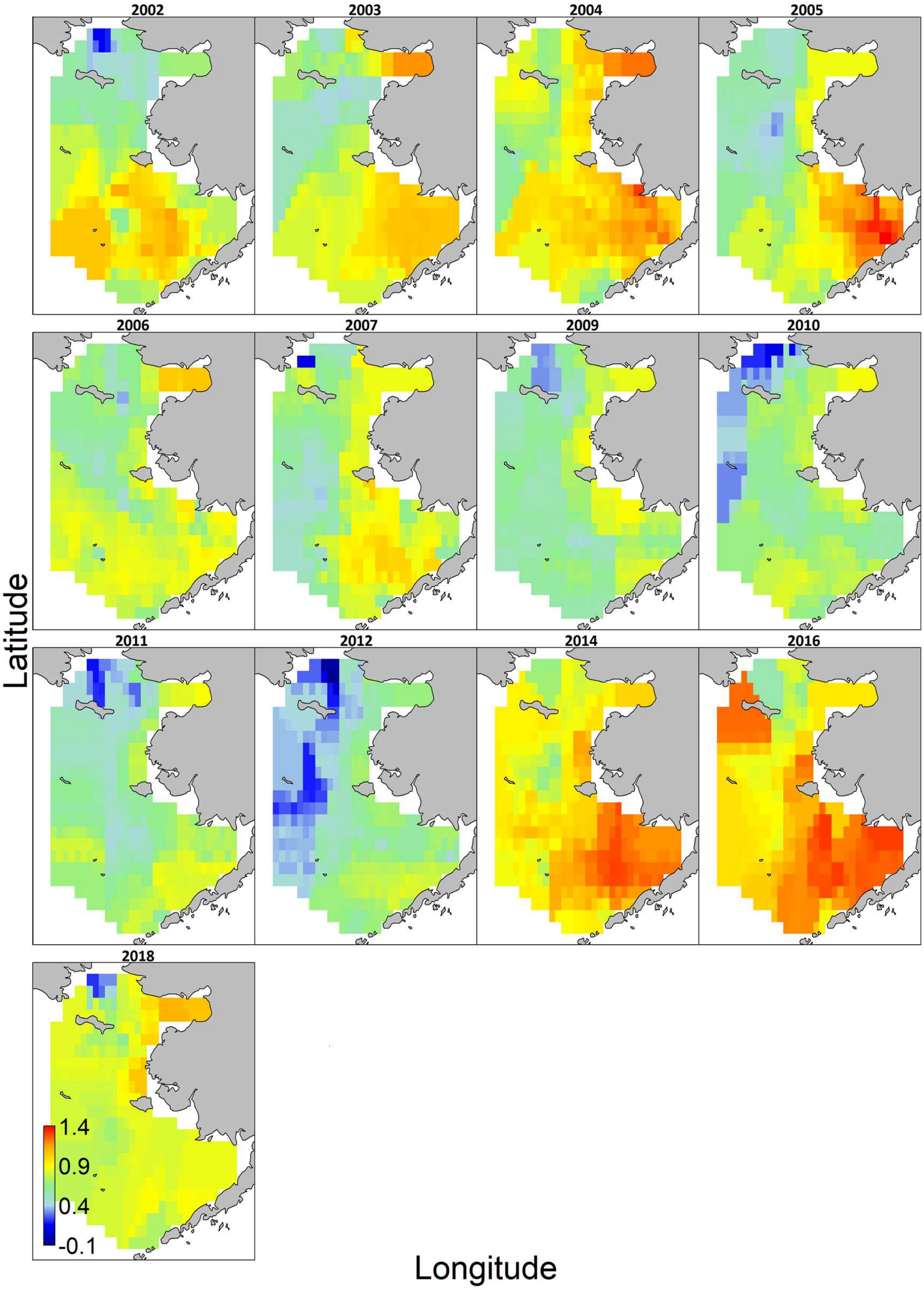


Figure 4. Predicted values of the normalized top 10 m sea temperatures from the Alaska Fisheries Science Center pelagic trawl survey in the eastern Bering Sea during late summer, 2002-2018. Missing years include 2008, 2013, 2015, and 2017.

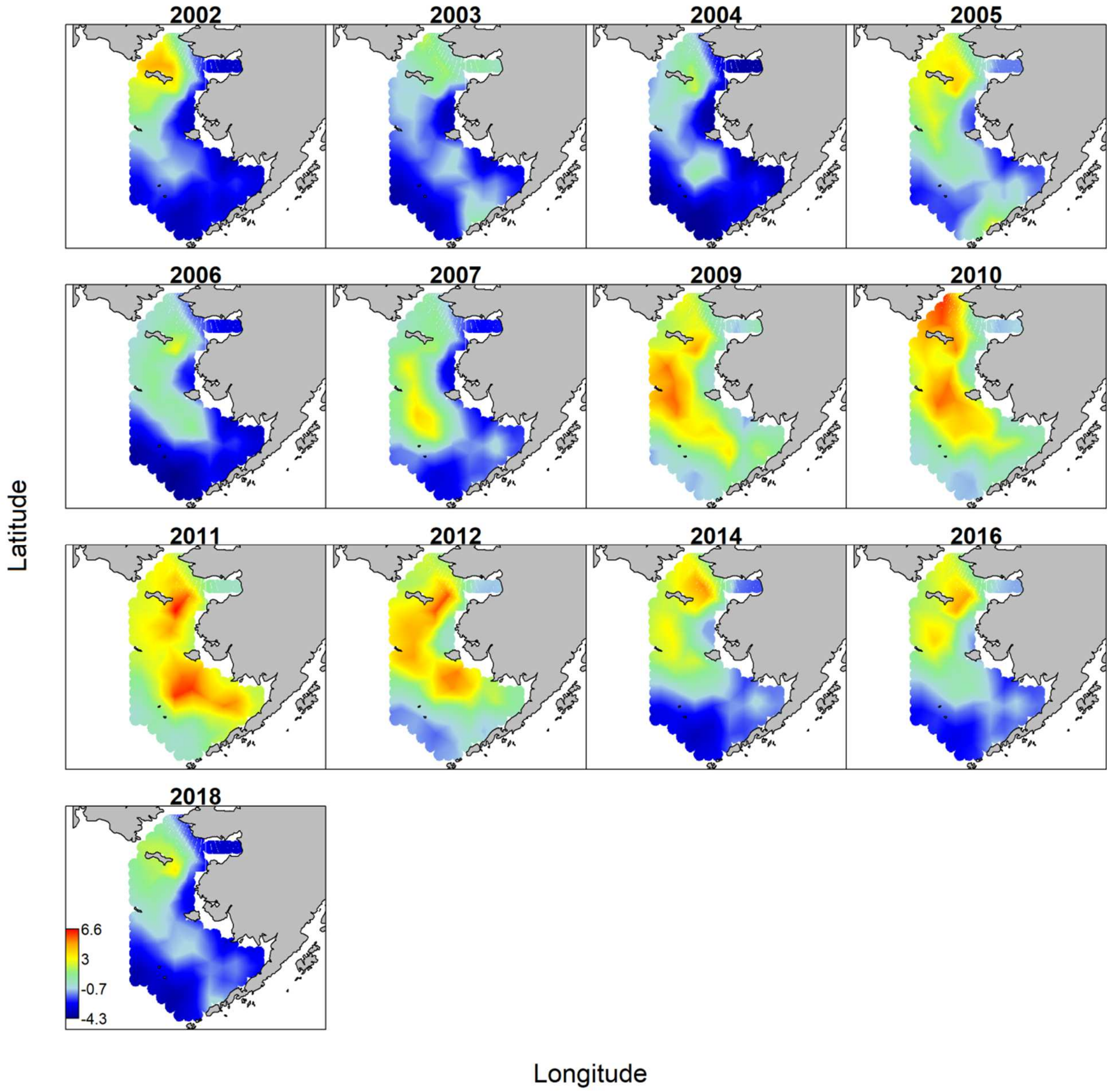


Figure 5. Distribution and density (ln(kg/km$^2$)) of capelin in the eastern Bering Sea during late summer, 2002-2018.

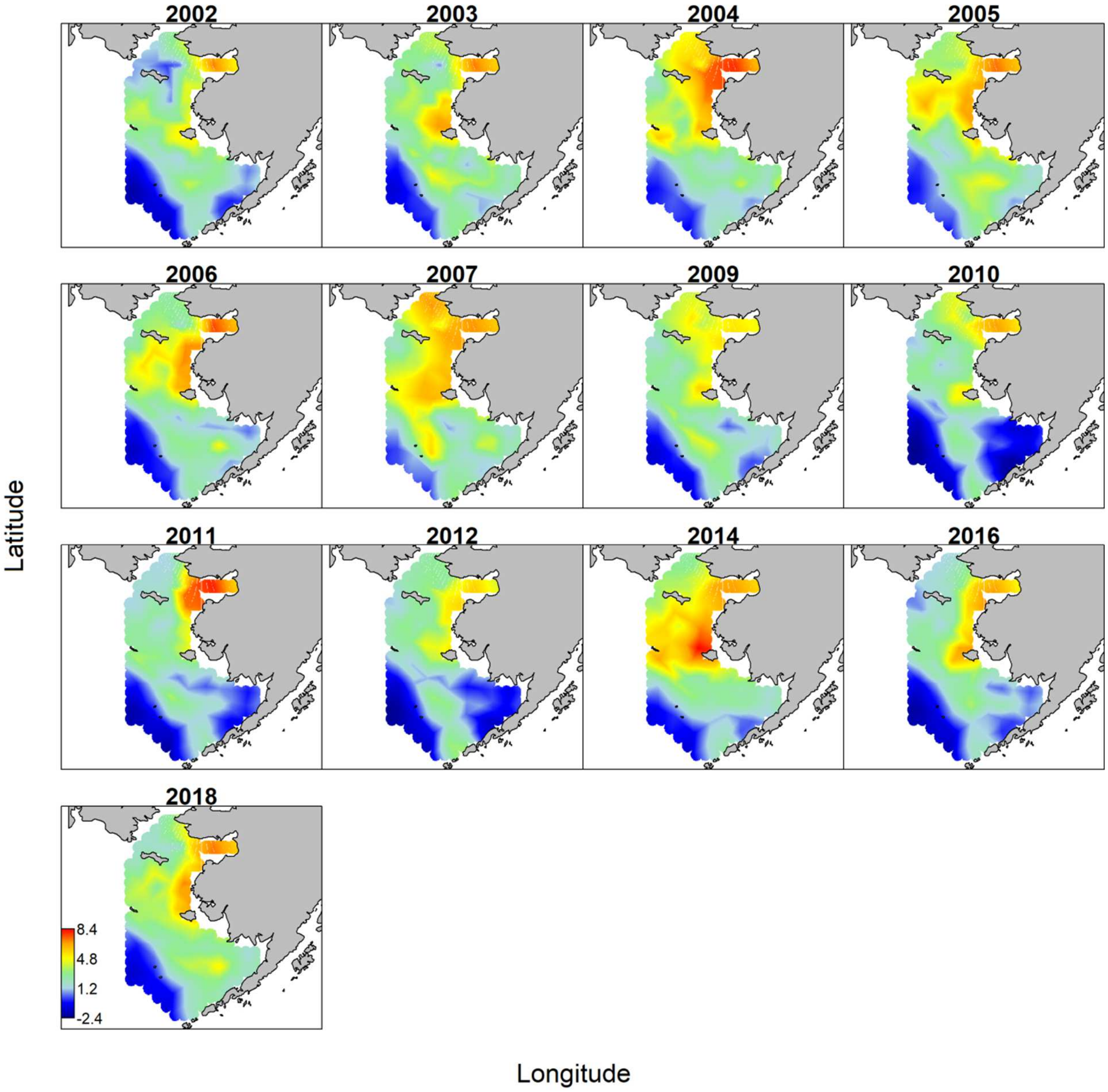


Figure 6. Distribution and density (ln(kg/km$^2$)) of Pacific herring in the eastern Bering Sea during late summer, 2002-2018.

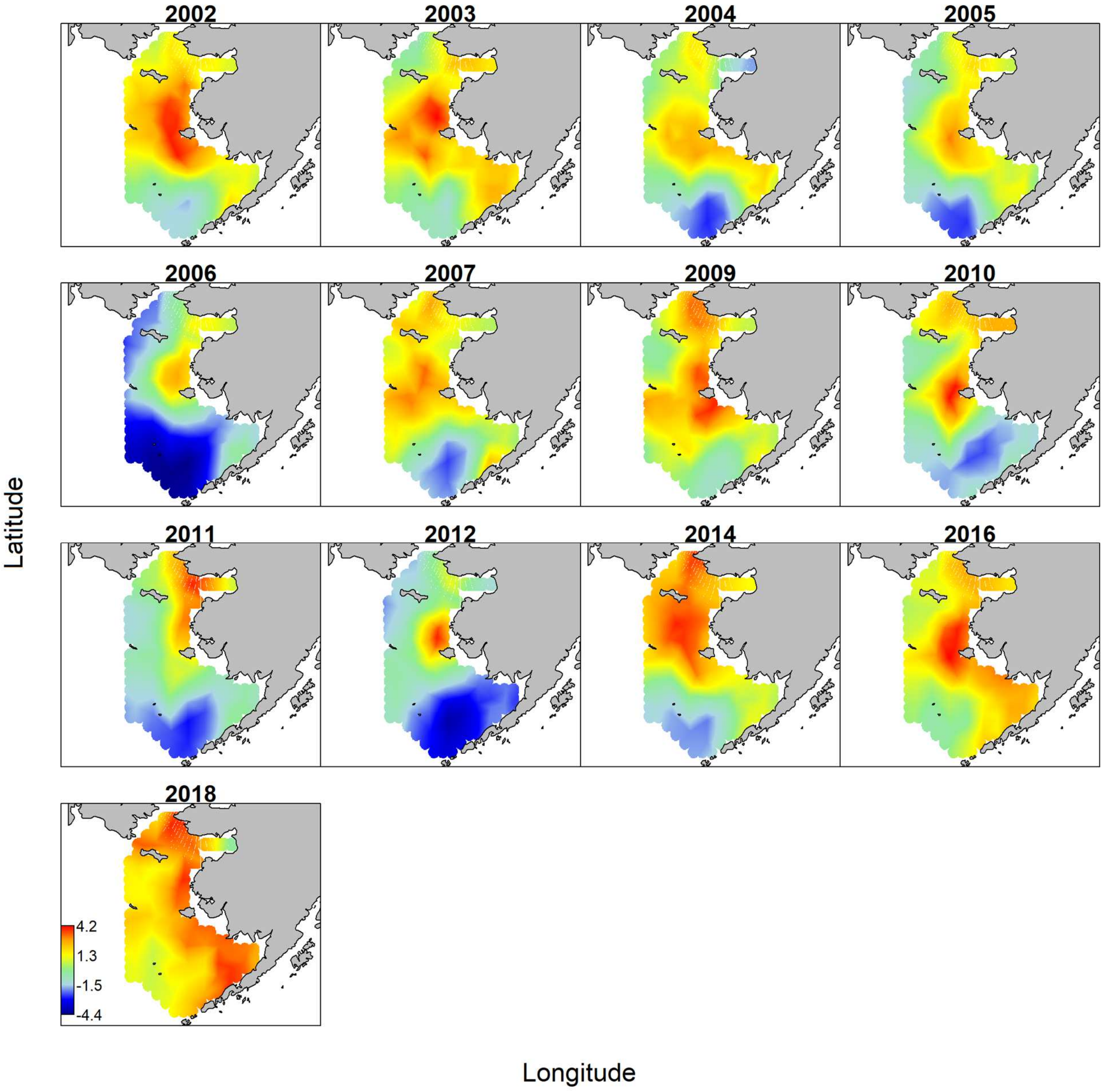


Figure 7. Distribution and density (ln(kg/km$^2$)) of juvenile chum salmon in the eastern Bering Sea during late summer, 2002-2018.

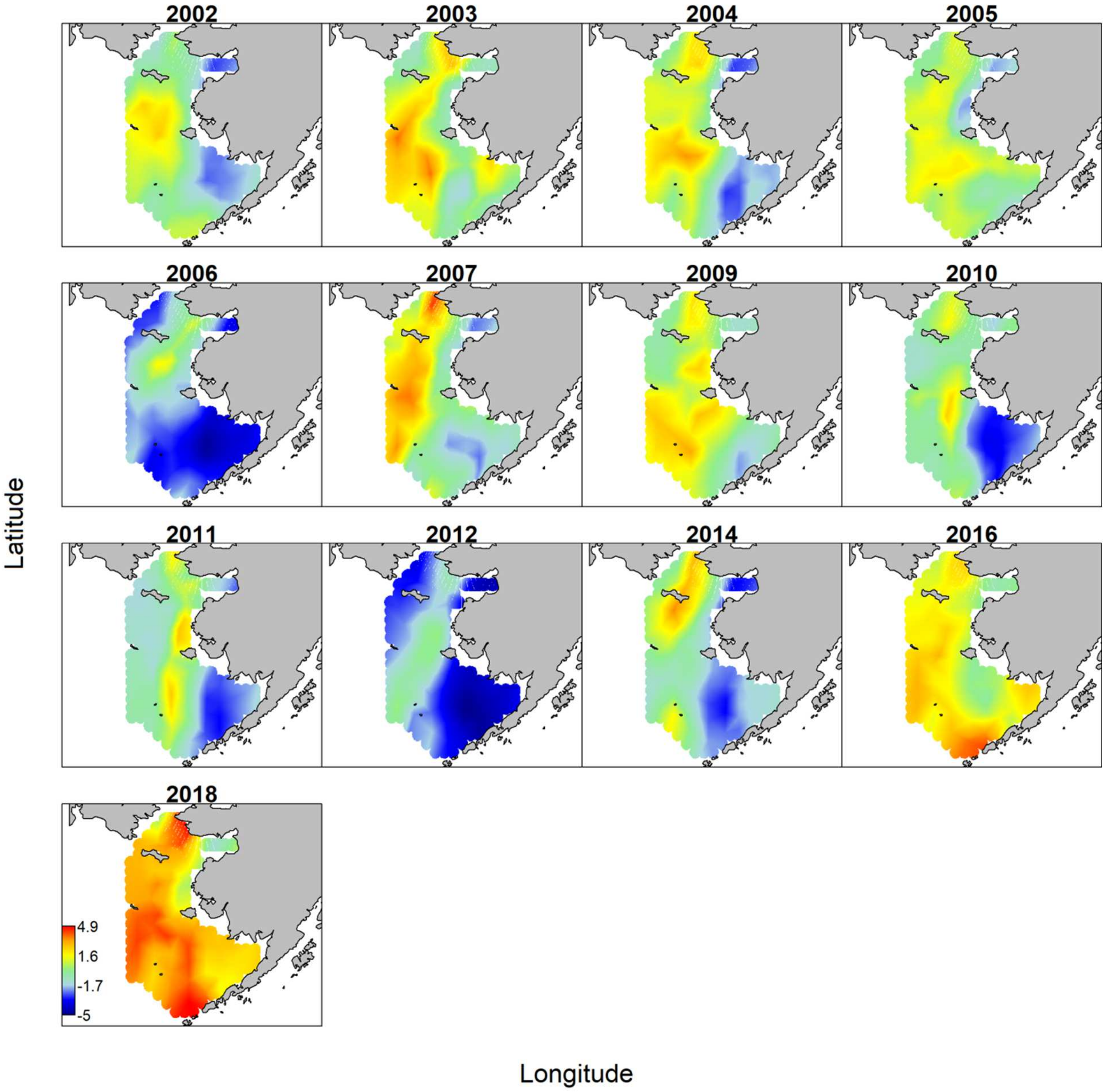


Figure 8. Distribution and density (ln(kg/km$^2$)) of juvenile pink salmon in the eastern Bering Sea during late summer, 2002-2018.

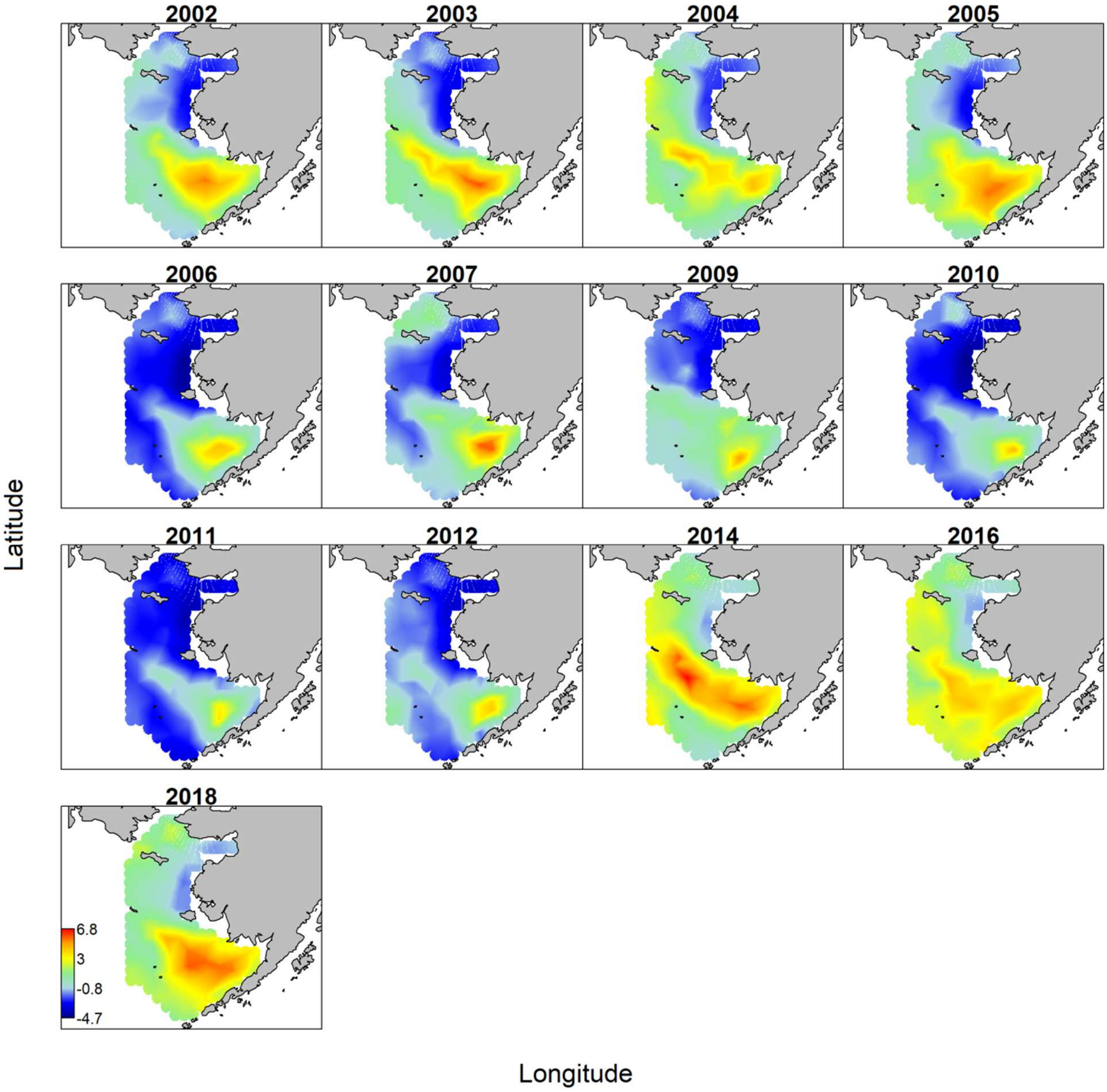


Figure 9. Distribution and density (ln(kg/km$^2$)) of juvenile sockeye salmon in the eastern Bering Sea during late summer, 2002-2018.

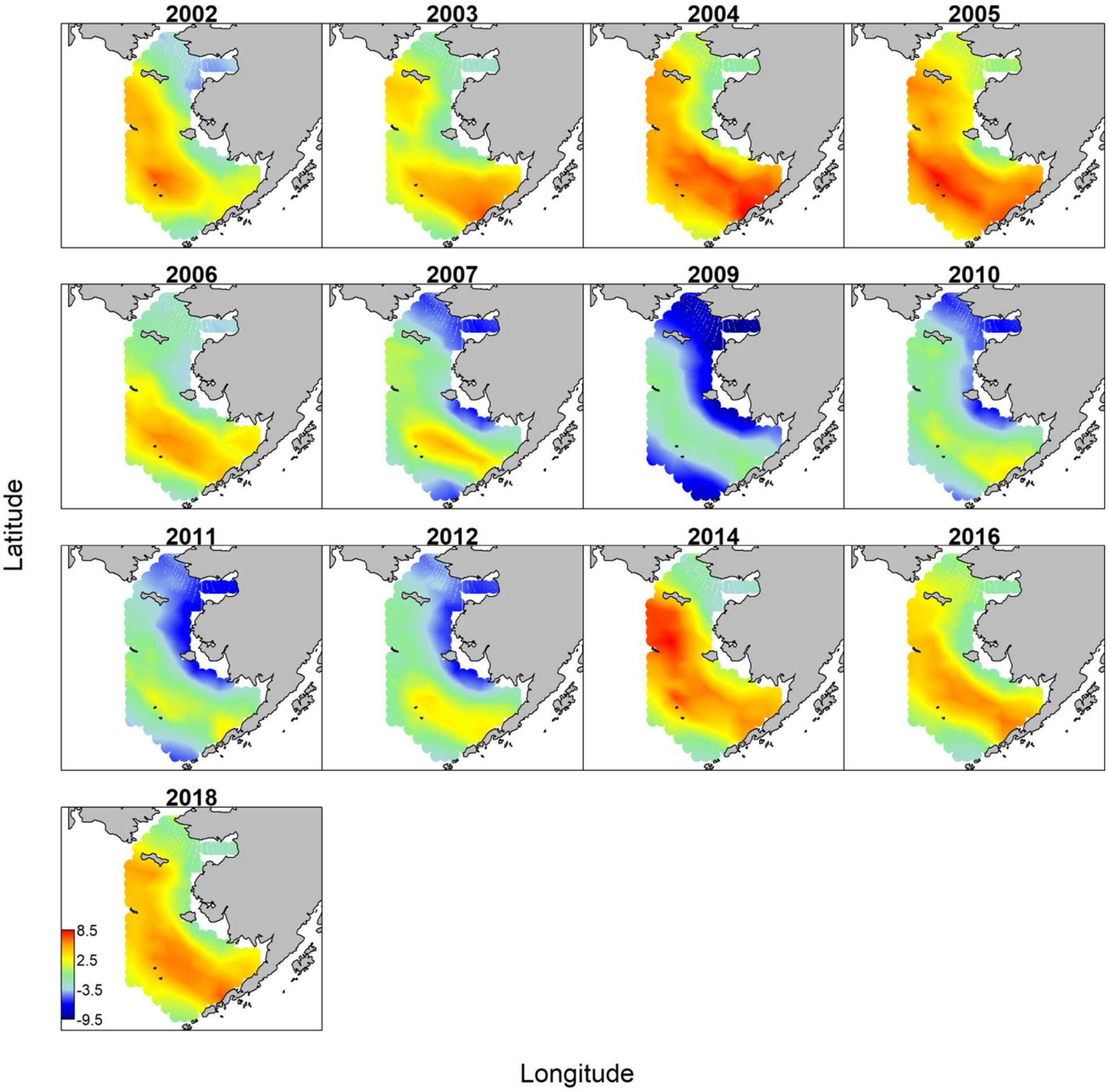
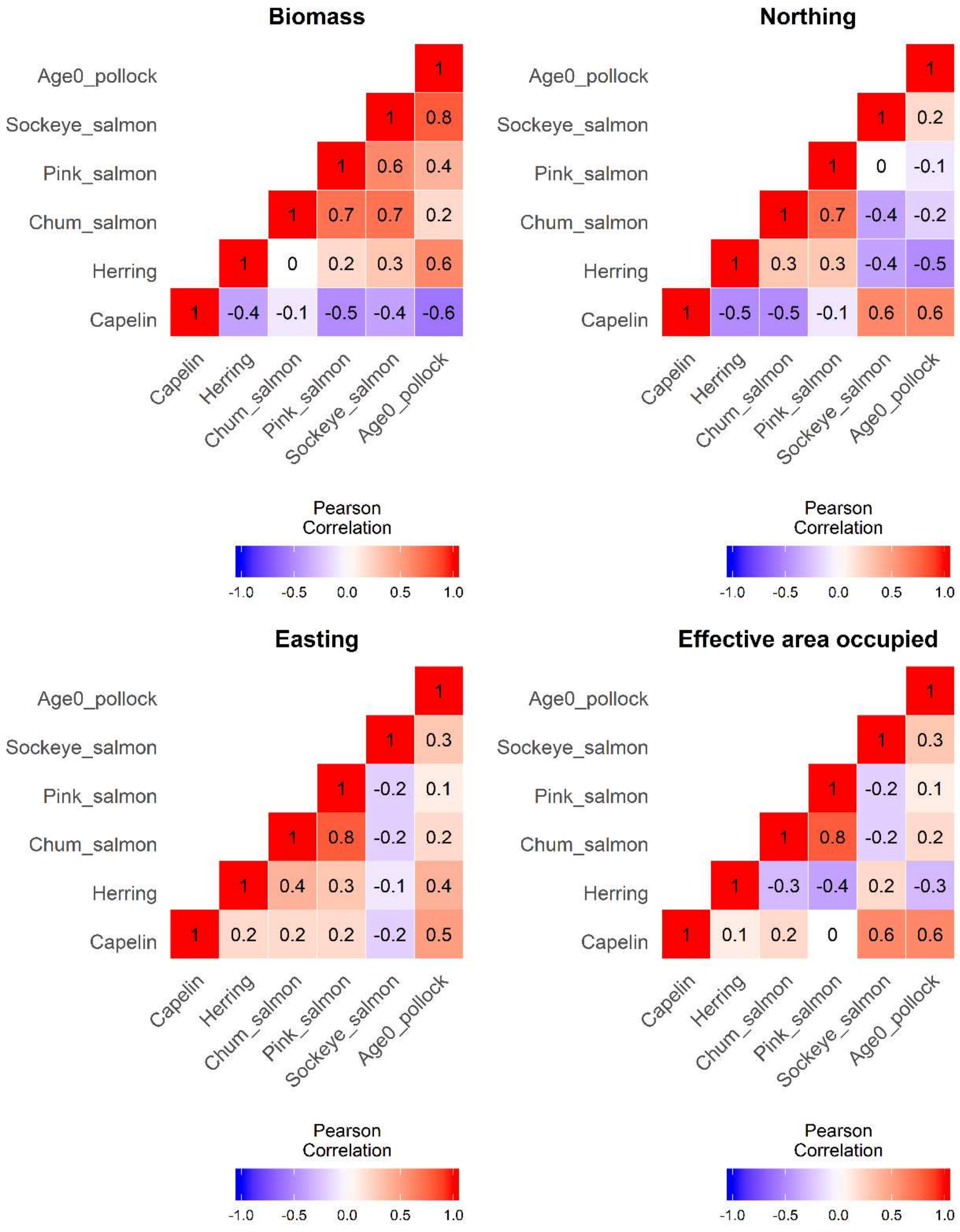


Figure 10. Distribution and density (ln(kg/km$^2$)) of age-0 pollock in the eastern Bering Sea during late summer, 2002-2018.



Biomass

Northing

Easting

Effective area occupied

Figure 11. Among species correlations for biomass, northing, easting, and effective area occupied of six small fish in pelagic waters of the eastern Bering Sea, 2002-2007, 2009-2012, 2014, 2016, and 2018. Statistically significant correlation coefficients were ≥ 0.7 and ≤ -0.7.

Table 1. Trends in the significant slope coefficients for the linear regression relationships between sea surface temperature and indices of abundance and habitat range of pelagic fish species in the eastern Bering Sea, 2002-2018, excluding 2008, 2013, 2015, and 2017.

| Species | Biomass | Northing | Easting | Area occupied |
|---|---|---|---|---|
| Capelin | decrease | northward | -- | -- |
| Herring | increase | -- | -- | -- |
| Chum salmon | -- | -- | -- | increased |
| Pink salmon | -- | -- | -- | -- |
| Sockeye salmon | increase | northward | westward | increased |
| Age-0 pollock | increase | -- | -- | -- |

Table 2. Linear regression model results relating indices of annual abundance and distribution of pelagic fish species in the eastern Bering Sea to annual summer sea temperature, 2002-2018, excluding 2008, 2013, 2015, and 2017. Model statistics include standard error of the estimate (S.E.), test statistics (t-value), probability of the test statistic (Pr(>|t|)), adjusted coefficient of determination (adjusted $r^2$), and probability of the test statistic of the adjusted $r^2$.

| Species | Slope coefficients Estimate (S. E.) | t-value | Pr(>\|t\|) | adjusted $r^2$ | p-value |
|---|---|---|---|---|---|
| **Biomass** | | | | | |
| Capelin | -0.653 (0.219) | -2.987 | 0.011 | 0.38 | 0.011 |
| Herring | 0.543 (0.238) | 2.238 | 0.045 | 0.24 | 0.045 |
| Chum salmon | 0.448 (0.258) | 1.735 | 0.108 | 0.13 | 0.108 |
| Pink salmon | 0.189 (0.284) | 0.667 | 0.517 | <0.01 | 0.517 |
| Sockeye salmon | 0.713 (0.203) | 3.52 | 0.004 | 0.47 | 0.004 |
| Age-0 pollock | 0.634 (0.223) | 2.843 | 0.015 | 0.35 | 0.015 |
| **Northing** | | | | | |
| Capelin | 0.632 (0.224) | 2.822 | 0.015 | 0.35 | 0.015 |
| Herring | -0.412 (0.263) | -1.567 | 0.143 | 0.10 | 0.143 |
| Chum salmon | -0.369 (0.268) | -1.374 | 0.063 | 0.06 | 0.064 |
| Pink salmon | -0.002 (0.289) | -0.006 | 0.995 | <0.01 | 0.995 |
| Sockeye salmon | 0.809 (0.170) | 4.760 | 0.0005 | 0.65 | 0.0005 |
| Age-0 pollock | 0.525 (0.246) | 2.137 | 0.053 | 0.22 | 0.053 |
| **Easting** | | | | | |
| Capelin | -0.033 (0.289) | -0.114 | 0.911 | <0.01 | 0.911 |
| Herring | -0.327 (0.273) | -1.197 | 0.254 | 0.03 | 0.254 |
| Chum salmon | 0.001 (0.289) | 0.002 | 0.999 | <0.01 | 0.999 |
| Pink salmon | 0.062 (0.288) | 0.215 | 0.833 | <0.01 | 0.833 |
| Sockeye salmon | -0.837 (0.158) | -5.288 | 0.0002 | 0.67 | 0.0002 |
| Age-0 pollock | -0.207 (0.283) | -0.733 | 0.477 | <0.01 | 0.477 |
| **Effective Area Occupied** | | | | | |
| Capelin | -0.498 (0.250) | -1.991 | 0.070 | 0.19 | 0.069 |
| Herring | -0.145 (0.286) | -0.508 | 0.620 | <0.01 | 0.620 |
| Chum salmon | 0.599 (0.231) | 2.590 | 0.024 | 0.31 | 0.024 |
| Pink salmon | -0.007 (0.289) | -0.023 | 0.982 | <0.01 | 0.982 |
| Sockeye salmon | 0.777 (0.182) | 4.284 | 0.001 | 0.57 | 0.001 |
| Age-0 pollock | 0.200 (0.283) | 0.709 | 0.492 | <0.01 | 0.491 |

Table 3. Coefficient estimate (standard deviation) of the gamma parameter for the effect of sea temperature at sampling stations on the probability of encounter and positive catch rates of pelagic fish species in the eastern Bering Sea, 2002-2018. Akaikie Information Criterion (AIC) and difference (Δ) in the AIC are given for the base model and covariate model with sea temperature (SST). Bold text indicates statistically significant parameters.

| | Probability of encounter | | Positive catch rate | | AIC for models | | |
|---|---|---|---|---|---|---|---|
| Species | SST | SST$^2$ | SST | SST$^2$ | Base | Covariate | Δ |
| Capelin | **-2.30 (0.60)** | -- | **-5.41 (0.84)** | -- | 2417 | 2369 | -48 |
| Chum salmon | **2.03 (0.52)** | -- | -0.67 (0.52) | -- | 3506 | 3493 | -13 |
| Herring | 0.74 (0.49) | -- | -0.67 (0.57) | -- | 6826 | 6828 | 2 |
| Pink salmon | **3.00 (1.70)** | **-2.04 (1.13)** | **3.55 (1.87)** | -1.98 (1.22) | 2883 | 2882 | -1 |
| Pollock | **7.48 (1.88)** | **-4.49 (1.21)** | 3.81 (2.89) | -2.79 (1.77) | 4980 | 4961 | -19 |
| Sockeye | **4.17 (2.08)** | -- | 3.24 (2.37) | **--** | 3523 | 3522 | -1 |

Table 4. Trends in the significant slope coefficients and p-values for the linear regression relationships between estimates of area occupied and biomass of pelagic fish species in the eastern Bering Sea, 2002-2018, excluding 2008, 2013, 2015, and 2017. Bold text indicate statistically significant slope coefficients.

| Area Occupied | Biomass Capelin | Chum | Herring | Pink | Pollock | Sockeye |
|---|---|---|---|---|---|---|
| Capelin | 0.29 (0.32) | **-0.55 (0.04)** | -0.10 (0.74) | -0.26 (0.37) | -0.19 (0.52) | -0.49 (0.07) |
| Chum | **-0.66 (0.01)** | **0.70 (0.005)** | 0.38 (0.18) | **0.65 (0.01)** | 0.20 (0.10) | **0.40 (0.01)** |
| Herring | 0.16 (0.60) | -0.02 (0.95) | 0.05 (0.87) | <0.01 (0.99) | -0.06 (0.84) | -0.08 (0.77) |
| Pink | -0.16 (0.60) | 0.09 (0.31) | 0.08 (0.32) | 0.43 (0.12) | 0.25 (0.38) | 0.18 (0.54) |
| Pollock | -0.29 (0.31) | 0.38 (0.18) | -0.03 (0.91) | 0.48 (0.08) | 0.47 (0.09) | 0.42 (0.13) |
| Sockeye | -0.40 (0.16) | 0.41 (0.14) | 0.18 (0.53) | 0.30 (0.30) | 0.42 (0.13) | 0.22 (0.09) |

Appendix 1. Estimated annual (mean and one standard error of the mean) biomass (tons), northing (km from Equator), easting (km from 180 longitude), and area occupied (kg/km$^2$) for capelin, herring, juvenile chum salmon, juvenile pink salmon, juvenile sockeye salmon, and age-0 pollock captured in pelagic waters of the eastern Bering Sea during late summer, 2002-2018, excluding 2008, 2013, 2015, and 2017.

| | **Capelin** | | **Herring** | | **Chum salmon** | | **Pink salmon** | | **Sockeye salmon** | | **Pollock** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S. E. | Mean | S. E. | Mean | S. E. | Mean | S. E. | Mean | S. E. | Mean | S. E. |
| **Biomass** | | | | | | | | | | | | |
| 2002 | 3,751 | 1,525 | 28,266 | 8,919 | 6,017 | 1,035 | 1,572 | 392 | 8,591 | 1,833 | 55,572 | 22,858 |
| 2003 | 660 | 280 | 56,708 | 14,463 | 5,550 | 949 | 4,854 | 1,090 | 10,712 | 2,263 | 62,723 | 16,613 |
| 2004 | 447 | 206 | 157,847 | 40,180 | 2,372 | 372 | 2,658 | 515 | 6,202 | 981 | 314,326 | 67,851 |
| 2005 | 4,546 | 2,074 | 98,113 | 27,471 | 2,082 | 382 | 1,898 | 369 | 13,078 | 2,360 | 308,865 | 73,520 |
| 2006 | 787 | 360 | 81,655 | 19,568 | 785 | 183 | 232 | 61 | 1,808 | 554 | 31,212 | 7,439 |
| 2007 | 2,638 | 903 | 119,113 | 23,094 | 3,409 | 565 | 4,517 | 870 | 5,311 | 1,678 | 5,668 | 1,593 |
| 2009 | 20,939 | 6,295 | 30,838 | 6,365 | 5,351 | 1,262 | 3,194 | 636 | 1,877 | 544 | 95 | 28 |
| 2010 | 31,317 | 9,216 | 26,531 | 7,053 | 2,872 | 585 | 803 | 158 | 911 | 360 | 1,073 | 288 |
| 2011 | 39,802 | 11,760 | 89,403 | 29,082 | 2,154 | 553 | 954 | 208 | 599 | 227 | 844 | 248 |
| 2012 | 24,378 | 7,249 | 20,386 | 4,893 | 1,044 | 323 | 166 | 49 | 1,177 | 376 | 2,312 | 506 |
| 2014 | 6,211 | 2,438 | 154,948 | 34,729 | 7,048 | 1,520 | 1,539 | 430 | 29,376 | 5,654 | 277,235 | 85,353 |
| 2016 | 6,002 | 3,051 | 50,502 | 15,362 | 7,154 | 1,310 | 8,344 | 2,057 | 14,552 | 2,503 | 61,698 | 15,169 |
| 2018 | 1,182 | 689 | 66,545 | 15,868 | 12,344 | 3,058 | 29,415 | 7,038 | 27,163 | 7,733 | 105,824 | 28,456 |
| Average | 10,974 | 3,542 | 75,450 | 19,004 | 4,476 | 931 | 4,627 | 1,067 | 9,335 | 2,082 | 94,419 | 24,609 |
| **Northing** | | | | | | | | | | | | |
| 2002 | 7,066 | 43 | 6,883 | 116 | 6,713 | 29 | 6,644 | 53 | 6,377 | 13 | 6,495 | 67 |
| 2003 | 6,895 | 136 | 6,833 | 97 | 6,662 | 40 | 6,589 | 58 | 6,388 | 13 | 6,309 | 52 |
| 2004 | 6,870 | 114 | 6,988 | 42 | 6,653 | 43 | 6,654 | 68 | 6,467 | 25 | 6,372 | 41 |
| 2005 | 6,919 | 128 | 6,894 | 93 | 6,673 | 62 | 6,568 | 70 | 6,337 | 14 | 6,390 | 36 |
| 2006 | 6,831 | 99 | 6,911 | 59 | 6,815 | 37 | 6,840 | 55 | 6,328 | 16 | 6,373 | 22 |
| 2007 | 6,650 | 71 | 6,903 | 62 | 6,743 | 40 | 6,752 | 75 | 6,364 | 16 | 6,357 | 18 |
| 2009 | 6,709 | 50 | 6,863 | 75 | 6,715 | 67 | 6,539 | 58 | 6,338 | 31 | 6,492 | 85 |
| 2010 | 6,860 | 118 | 6,983 | 56 | 6,799 | 50 | 6,682 | 68 | 6,357 | 29 | 6,304 | 44 |
| 2011 | 6,628 | 84 | 7,040 | 26 | 6,966 | 53 | 6,632 | 65 | 6,347 | 28 | 6,341 | 52 |
| 2012 | 6,745 | 70 | 6,885 | 67 | 6,771 | 28 | 6,619 | 69 | 6,364 | 22 | 6,311 | 25 |
| 2014 | 6,984 | 77 | 6,809 | 45 | 6,860 | 47 | 6,891 | 70 | 6,486 | 25 | 6,692 | 74 |
| 2016 | 6,940 | 77 | 6,869 | 101 | 6,653 | 50 | 6,416 | 105 | 6,436 | 42 | 6,429 | 55 |
| 2018 | 6,928 | 88 | 6,876 | 69 | 6,636 | 94 | 6,493 | 107 | 6,376 | 22 | 6,427 | 82 |
| Average | 6,848 | 89 | 6,903 | 70 | 6,743 | 49 | 6,640 | 71 | 6,382 | 23 | 6,407 | 50 |

## Appendix 1. Continued

| | Capelin | | Herring | | Chum salmon | | Pink salmon | | Sockeye salmon | | Pollock | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S. E. | Mean | S. E. | Mean | S. E. | Mean | S. E. | Mean | S. E. | Mean | S. E. |
| **Easting** | | | | | | | | | | | | |
| 2002 | 233 | 26 | 459 | 77 | 335 | 23 | 228 | 34 | 499 | 27 | 219 | 35 |
| 2003 | 364 | 64 | 431 | 66 | 367 | 45 | 237 | 45 | 512 | 33 | 519 | 58 |
| 2004 | 284 | 31 | 434 | 42 | 371 | 27 | 239 | 32 | 418 | 39 | 485 | 53 |
| 2005 | 273 | 42 | 404 | 82 | 392 | 24 | 286 | 39 | 514 | 22 | 332 | 59 |
| 2006 | 282 | 39 | 428 | 57 | 378 | 22 | 291 | 30 | 585 | 26 | 333 | 37 |
| 2007 | 215 | 25 | 372 | 43 | 283 | 29 | 199 | 31 | 636 | 21 | 397 | 34 |
| 2009 | 209 | 36 | 386 | 43 | 350 | 26 | 258 | 28 | 537 | 34 | 325 | 88 |
| 2010 | 266 | 22 | 457 | 57 | 349 | 26 | 286 | 24 | 615 | 44 | 501 | 56 |
| 2011 | 383 | 37 | 490 | 26 | 416 | 20 | 322 | 22 | 576 | 38 | 430 | 93 |
| 2012 | 305 | 54 | 419 | 51 | 344 | 17 | 231 | 42 | 596 | 47 | 420 | 47 |
| 2014 | 286 | 43 | 347 | 36 | 305 | 29 | 261 | 25 | 390 | 49 | 221 | 50 |
| 2016 | 280 | 50 | 433 | 59 | 417 | 43 | 328 | 61 | 412 | 52 | 409 | 72 |
| 2018 | 260 | 50 | 448 | 43 | 452 | 79 | 304 | 53 | 501 | 51 | 368 | 73 |
| Average | 280 | 40 | 424 | 52 | 366 | 32 | 267 | 36 | 522 | 37 | 381 | 58 |
| **Area Occupied** | | | | | | | | | | | | |
| 2002 | 60,022 | 26,629 | 63,760 | 65,660 | 227,445 | 52,019 | 264,977 | 70,004 | 96,144 | 33,537 | 127,297 | 85,382 |
| 2003 | 193,580 | 127,354 | 91,089 | 47,802 | 267,994 | 79,851 | 262,313 | 66,269 | 83,164 | 34,099 | 123,141 | 71,510 |
| 2004 | 135,523 | 101,992 | 90,472 | 39,110 | 319,520 | 53,746 | 258,343 | 71,176 | 188,903 | 52,838 | 171,835 | 91,167 |
| 2005 | 155,681 | 91,765 | 134,154 | 109,290 | 262,554 | 72,006 | 449,702 | 71,797 | 115,867 | 34,092 | 214,953 | 85,776 |
| 2006 | 161,252 | 148,741 | 83,627 | 35,636 | 115,384 | 36,509 | 138,575 | 60,189 | 54,810 | 19,814 | 140,008 | 38,608 |
| 2007 | 132,240 | 81,529 | 202,353 | 54,664 | 307,521 | 54,434 | 192,213 | 60,551 | 33,128 | 13,801 | 70,410 | 25,640 |
| 2009 | 146,046 | 60,198 | 214,015 | 68,629 | 266,624 | 86,823 | 336,266 | 65,025 | 59,754 | 48,855 | 192,017 | 65,031 |
| 2010 | 150,213 | 97,484 | 67,123 | 44,877 | 140,108 | 50,962 | 233,531 | 88,665 | 37,898 | 29,650 | 99,434 | 57,080 |
| 2011 | 155,799 | 78,752 | 40,166 | 13,507 | 105,974 | 37,392 | 181,359 | 64,009 | 49,980 | 28,557 | 105,680 | 76,190 |
| 2012 | 171,195 | 68,976 | 119,730 | 59,305 | 58,439 | 26,786 | 249,970 | 76,166 | 47,905 | 23,905 | 148,193 | 25,430 |
| 2014 | 97,274 | 71,459 | 100,572 | 62,945 | 260,484 | 47,714 | 128,110 | 54,070 | 128,762 | 56,460 | 138,910 | 67,048 |
| 2016 | 104,582 | 83,660 | 81,060 | 29,548 | 263,586 | 78,953 | 286,565 | 184,114 | 325,664 | 76,711 | 178,822 | 49,681 |
| 2018 | 109,772 | 95,687 | 95,407 | 39,723 | 396,935 | 91,348 | 374,977 | 173,581 | 132,601 | 40,863 | 218,006 | 78,132 |
| Average | 136,398 | 87,248 | 106,425 | 51,592 | 230,198 | 59,119 | 258,223 | 85,047 | 104,198 | 37,937 | 148,362 | 62,821 |