Effect of Temperature on Flathead Sole (*Hippoglossoides elassodon*) Spawning in the Southeastern Bering Sea During Warm and Cold Years

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Abstract

Between 2001 and 2013 the southeastern Bering Sea alternated between multi-year periods of relatively warm (2001-2005) and relatively cold (2007-2013) years. Adult Flathead Sole *Hippoglossoides elassodon* in the southeastern Bering Sea shift their spatial distribution pattern in relation to bottom water temperature indicating the importance of the thermal environment in determining fish habitat. The objective of this study was to infer Flathead Sole spawning area in the southeastern Bering Sea in May from ichthyoplankton surveys of their eggs using generalized additive models to assess how warm (2002, 2003, and 2005) and cold (2008, 2009, 2010, and 2012) years affected the location of their spawning site. Three mechanisms through which temperature could affect egg distribution were investigated: 1) additively, assuming a similar effect of temperature across the spatial domain, 2) as a spatially variable term, assuming that the effect of temperature changes across locations, and 3) as a threshold effect on the spatial distribution of eggs, assuming the distribution of eggs changes abruptly in relation to the annual average temperature. The model including temperature as a spatially variable effect had the smallest AIC score and therefore was chosen as the best fit. This model showed that the effect of temperature on egg density varied across the study area and indicated a northeastward expansion of the spawning site as temperature increased. The area of expansion may correspond with the outer reach of a cold-water mass (called the cold pool) that extends in the Bering Sea middle domain during late spring and summer, and forms as a result of the previous winter ice coverage. Flathead Sole are known to avoid temperatures colder than 2°C that is also used as the boundary for the cold pool, thus spawning fish may have moved relative to the spatial extent of the cold pool.

Keywords
Flathead Sole
Hippoglossoides elassodon
Bering Sea
Spawning
Temperature

1. Introduction

Temperature affects many aspects of fish biology including spatial distribution of species, indicating the importance of the thermal environment in determining fish habitat (Mueter and Litzow, 2008; Spencer, 2008; Kotwicki and Lauth, 2013; González-Irusta and Wright, 2016a). Northward movements of bottom fish species in relation to warmer bottom water temperatures and southward movement due to colder temperatures have been shown for multiple species in the eastern Bering Sea (Mueter and Litzow, 2008, e.g., Flathead Sole, *Hippoglossoides elassodon).* Temperature can also alter location of spawning (Petrik et al., 2015; Ottosen et al. 2018). A biological-physical modeling study of the transport of eggs and larvae of Walleye Pollock (*Gadus chalcogrammus*) in the southeastern Bering Sea showed that differences in the spatial distribution of eggs and larvae between warm and cold years could be attributed to water temperature influencing spawning location (Petrik, 2015). There was a northeastward shift in the spawning location of Cod (*Gadus morhua*) in the northern spawning area of the Faroe Plateau in relation to increasing temperature (Ottosen et al. 2018). Additionally, Cod prefer areas where the temperature is between 5° to 7°C for spawning and may avoid temperatures ≥ 8°C (González-Irusta and Wright, 2016b).

The southeastern Bering Sea continental shelf is used by many flatfish species as spawning habitat during the spring (e.g., Northern Rock Sole *Lepidopsetta polyxystra*, Yellowfin Sole *Limanda aspera*, Flathead Sole; Fig. 1). Flathead Sole are a commercially exploited species that inhabit the southeastern Bering Sea shelf at depths between approximately 50 to 200 m (Lauth and Nichol, 2013), and the continental slope to 500 m depth (Hoff, 2013). They over-winter on the upper continental slope (Rose, 1982) and move to the shallower waters of the shelf during the spring (20-180 m; Witherell, 2000). There is little seasonal variation in temperature off shelf

(Ortiz et al., 2016), so it is likely that during the winter Flathead Sole on the slope experience similar temperatures from year to year. Flathead Sole spawning in the Gulf of Alaska begins during April and peaks in May based on the occurrence of postovulatory follicles in June (Stark 2004), and they have a similar spawning season in the eastern Bering Sea as well (Stark 2004). The depth range for spawning near Kodiak Island in the Gulf of Alaska was 42 to 196 m (Stark, 2004), and that corresponds to the approximate depths where spawning occurs in the Bering Sea. Studies based on ovary maturity indicate that Flathead Sole spawning occurs centrally over the southeastern Bering Sea shelf between 50 and 200 m depth, and near Unimak Island and the Alaska Peninsula (Stark, 2004; TenBrink and Wilderbuer, 2015). Ichthyoplankton surveys conducted during the spring had largest catches of Flathead Sole eggs in the vicinity of Unimak Island and the Alaska Peninsula (Grigorev and Fadeev, 1995) suggesting that spawning was occurring in that area. Eggs are pelagic and in the Gulf of Alaska they are found throughout the water column (near surface to greater than 200 m depth) depending on their developmental stage (Porter, 2005), and may be as deep as 261 m but low density (S. Porter unpublished data). Larvae hatch about 15 days after fertilization at 5.5°C (Alderdice and Forrester, 1974).

The broad continental shelf region of the southeastern Bering Sea is divided into three hydrographic domains bounded by fronts and defined by bathymetry: coastal (< 50 m depth), middle (50 to 100 m depth), and outer domains (100 to 200 m depth; Fig. 1; Coachman, 1986). Annual mean near surface current flow at a mooring located near the center of the shelf was westward and weak (1.5 cm/s), and flow near Unimak Island and the peninsula was also weak (3.5 cm/s) and to the northeast, parallel to the coast (Stabeno et al., 2016). Depth-averaged temperature measured at the mooring is used to classify water temperature conditions for the spring, summer, and fall (warmer than average, colder than average, or average, here after referred to as warm, cold or average; Stabeno et al., 2012). A positive depth-averaged temperature anomaly indicates warm years and a negative anomaly is associated with cold years relative to the mean annual temperature from 1995 to 2009 (Stabeno et al. 2012). Between 2001 and 2013 the southeastern Bering Sea shelf alternated between multi-year periods of warm (2001-2005) and cold (2007-2013) conditions during the spring, summer and fall, and 2006 was an average year between the two periods (Stabeno et al., in review).

Flathead Sole are at the northern most extent of their range in the Bering Sea (Mecklenberg et al., 2002) and so are most likely to be strongly affected by changes in marine climate (temperature) in that area (Myers, 1998), more so than in centrally located parts of their range. Adults avoid temperatures colder than 2°C (Rooper et al., 2005) and those temperatures are likely to be present during the spring in cold years in the southeastern Bering Sea, thus spawning site may change due to fish avoiding areas with unfavorable temperatures. The objective of this study was to infer Flathead Sole spawning area in the southeastern Bering Sea from ichthyoplankton surveys of their eggs and use generalized additive models to assess how warm and cold years affected spawning location, a method similar to that used in other studies to explain the spawning distribution of fishes (e.g., Fox et al., 2000; Bacheler et al., 2009). Location and timing of spawning are thought to be connected to environmental conditions beneficial for early life survival such as dispersal of larvae into favorable habitats, and overlap of larvae and their prey (Leggett, 1985, Ciannelli et al., 2015), so any changes in timing or location can potentially have consequences on early-life survival and recruitment.

2. Material and methods

2.1 Egg collections

Flathead Sole egg density (number/10m^2) was determined from ichthyoplankton surveys conducted yearly during the spring in the southeastern Bering Sea by the NOAA, Alaska Fisheries Science Center (Seattle, WA). Eggs were sampled from a systematic grid design of fixed stations and areal coverage was not consistent among years. Eggs were collected using a 60-cm bongo frame fitted with 333 or 505-µm mesh nets towed obliquely to a maximum depth of 300 m or 10 m off bottom, whichever was shallower. The depth range for Flathead Sole eggs in the Bering Sea is unknown, but mature females have been caught in Bering Canyon (depth > 200m; TenBrink and Wilderbuer, 2015). If eggs have a vertical distribution similar as to those in the Gulf of Alaska, then an oblique tow to depth of 300 m should have collected most of the eggs in the water column. Water temperature was measured at maximum gear depth using a Sea-Bird SBE 19 SeaCat or SBE 39 FastCat CTD profiler attached to the towing wire. Ichthyoplankton samples were preserved in 5% formalin, and then eggs were sorted and identified to species at the Plankton Sorting and Identification Center in Szczecin, Poland. The number of eggs caught was standardized to number/10 m^2 based on net mouth area, tow depth, and duration (here after referred to as egg density; Matarese et al., 2003). We classified years used in our study as warm or cold from warm and cold years designated in Stabeno et al. (2012). Data were limited spatially to an area of the southeastern Bering Sea along the Alaska Peninsula and the vicinity of Unimak Island because this is where the greatest number of net tows occurred among years, and past studies have indicated that Flathead Sole may spawn in that area (Grigorev and Fadeev, 1995; TenBrink and Wilderbuer, 2015; Fig. 2). Temporal coverage varied by year so we limited the analysis to May observations because this was the only month in common to all years that eggs were present. May is also thought to be when peak Flathead Sole spawning occurs in the Bering Sea (Stark, 2004). There were no net tows conducted within the study area during May 2001 or

2004. 2006 was classified as an average year (Stabeno et al., 2012) so it was not included in our study. Years 2007, 2011, and 2013 were also excluded due to poor spatial coverage within our study area (less than 16 stations sampled each year). Eggs from another possible spawning area located north of our study area were not included because only 4 warm-period tows occurred there in May (Fig. 2).Three warm years (2002, 2003, and 2005; total number of tows = 180) and four cold years (2008, 2009, 2010, and 2012; total number of tows = 291) were used for comparing egg density and distribution among years (Table 1). The number of days sampled during May varied among years, ranging from eight (2003) to 24 (2012; Table 1).

2.2 Generalized additive models

We used generalized additive models (GAM) to analyze Flathead Sole spawning in relation to local (i.e., changing across space and time) and global (i.e., changing only over time) covariates. GAMs are non-parametric regression techniques, in which the effect of a covariate is estimated with a smooth function, typically a natural cubic spline, and therefore may not necessarily be linear (Wood, 2006). Given the zero inflated and overdispersed nature of the egg data set (42% of the tows did not catch Flathead Sole eggs; see Table 1 for variability in egg density by year) a two-step approach to investigate and predict the spawning distribution of fish based on egg density was used (Fox et al., 2000). Both a binomial presence-absence model with a logit link function and a positive abundance model with lognormal distribution family (i.e., a model using only tows with egg density > 0 as the response variable) were formulated. The predicted egg density for each tow was the product of the predictions from the two models. An advantage of the two-step approach is that it takes into account the possibility that there are different processes affecting the presence and density of eggs (Potts and Elith, 2006); that is, there can be different covariate effects in each model.

Global covariates included were day of year (d) to account for differences in egg density due to survey date, and estimated female spawning stock biomass (SSB) in the Bering Sea and Aleutian Islands regions to account for different spawning output (98% of the female Flathead Sole spawning stock biomass is located on the eastern Bering Sea shelf; Stockhausen et al., 2012). In the presence/absence GAM model SSB is included as a factor, therefore affecting the model intercept. As SSB varies annually, this equates to estimating a different intercept for each year. In the positive abundance models SSB is included either as a factor or continuous variable. Local covariates included location of a net tow (latitude (ϕ) and longitude (λ)), and near bottom water temperature (t). Location (latitude and longitude) and depth on the southeastern Bering Sea shelf are highly correlated because shelf bathymetry is relatively flat with maximum depth at the shelf break (Stabeno et al. 2016), so any depth effect on egg density was accounted for in our models by latitude and longitude. For the binomial presence-absence model all covariates were included additively, as follows:

$$\mathrm{E}\ (p_i) = \mu_i$$

$$p_i \sim \mathrm{B}(1, \mu_i) \quad var(p_i) = \mu_i\ (1-\mu_i)$$

$$logit(\mu_i) = a_{\mathrm{y}} + g_1(d) + g_2(t_{\phi,\lambda,\mathrm{y}}) + g_3(\phi,\lambda)$$

Where p_i is the probability of Flathead Sole eggs being present in the i^{th} sample, conditional on the covariate ϕ, λ, d, and t, a is the model intercept, which varies annually (subscript y) according to the female spawning stock biomass, the gs are nonparametric smoothing functions.

For the positive abundance model, the covariates were the same as those of the binomial presence-absence model, but the effect of water temperature was modeled in three ways, reflecting three mechanisms through which temperature could affect egg distribution. Namely, i) additively, assuming a similar effect of temperature across the spatial domain, ii) as a spatially variable term, assuming that the effect of temperature changes across locations, and iii) as a threshold effect on the spatial distribution of eggs. Female SSB was included either as a factor, which allows for an unconstrained change of egg density in relation to biomass by estimating a different intercept for each year, or as a smooth term (standardized values used), which only allows smooth changes of egg density in relation to biomass. Standardized natural log anomalies were used as values for SSB when this covariate was included as a smooth term (Bacheler et al., 2009). Thus, we formulated six abundance models from pairwise combinations of three temperature and two female spawning biomass terms. The exact formulation of these positive abundance models is shown in equations 2-7.

The additive abundance model is similar to the presence-absence model, namely:

$$\ln(x_{y,\mathrm{d},\mathrm{t},\phi,\lambda}) = a_y + g_1(d) + g_2(t_{\phi,\lambda,y}) + g_3(\phi, \lambda) + \mathcal{E}_{y,\mathrm{d},\mathrm{t},\phi,\lambda} \quad (2)$$

or

$$\ln(x_{y,\mathrm{d},\mathrm{t},\phi,\lambda}) = s(SSB_y) + g_1(d) + g_2(t_{\phi,\lambda,y}) + g_3(\phi, \lambda) + \mathcal{E}_{y,\mathrm{d},\mathrm{t},\phi,\lambda} \quad (3)$$

Where x is the local Flathead Sole egg density (number/10m^2), and SSB is modeled either as an annually variable intercept (a_y, Eq. 2) or a smooth ($s(SSB_y$, Eq. 3)) effect.

The model that assumes a spatially variable effect of temperature was formulated as a variable-coefficient generalized additive model (VCGAM) (Bacheler et al., 2009). Namely,

$$\ln(x_{y,\mathrm{d},\mathrm{t},\phi,\lambda}) = a_y + g_1(d) + \alpha_{\phi,\lambda}(t_{\phi,\lambda,y}) + g_3(\phi, \lambda) + \mathcal{E}_{y,\mathrm{d},\mathrm{t},\phi,\lambda} \quad (4)$$

or

$$\ln(x_{y,\mathrm{d},\mathrm{t},\phi,\lambda}) = s(SSB_y) + g_1(d) + \alpha_{\phi,\lambda}(t_{\phi,\lambda,y}) + g_3(\phi, \lambda) + \mathcal{E}_{y,\mathrm{d},\mathrm{t},\phi,\lambda} \quad (5)$$

Where x is the eggs density, and α is a slope parameter for the effect of temperature, which changes smoothly over space ($\alpha_{\phi,\lambda}(t_{\phi,\lambda,y})$). Thus, in the variable coefficient model formulation, the effect of water temperature on egg abundance is linear, but spatially variable (Bacheler et al., 2009, Ciannelli et al., 2012).

Lastly, the framework of the threshold formulation was used to test whether there were changes in egg spatial distributions associated with warm versus cold years (Ciannelli et al., 2004). Namely,

$$\ln(x_{y,\mathrm{d},\mathrm{t},\phi,\lambda}) = a_y + g_1(d) + g_2(t_{\phi,\lambda,y}) + I_{w,y} g_3(\phi, \lambda) + I_{c,y}\, g_3(\phi, \lambda) + \mathcal{E}_{y,\mathrm{d},\mathrm{t},\phi,\lambda} \quad (6)$$

or

$$\ln(x_{y,\mathrm{d},\mathrm{t},\phi,\lambda}) = s(SSB_y) + g_1(d) + g_2(t_{\phi,\lambda,y}) + I_{w,y} g_3(\phi, \lambda) + I_{c,y}\, g_3(\phi, \lambda) + \mathcal{E}_{y,\mathrm{d},\mathrm{t},\phi,\lambda} \quad (7)$$

Where *Iw* and *Ic* are indicator variables for warm or cold years, which are a-priori determined based on the thermal regime of each examined year (Stabeno et al. 2012). In our application, years 2002, 2003 and 2005 are designated as warm and years 2008-2010 and 2012 are designated as cold. This designation is consistent with the average observed temperature in each year (Table 1).

All six model formulations (Eqs. 2-7), are consistent with a change in distribution in relation to temperature, albeit for different reasons. In 2-3, the change of distribution between cold and warm years can only occur if temperature changes at different rates over different locations. This contrasts with the scenario represented by the 4-5 formulations, where the change of distribution is driven by the spatially variable and linear effect of temperature on local abundance. This scenario could result in a change of egg distribution, even when temperature increases/decreases by a similar amount throughout the study region. Lastly, the scenario represented by formulations 6-7 assumes that the distribution of eggs changes abruptly as a result of a global change in temperature (i.e., annual average temperature), resulting in two different egg distribution patterns – one in the warm years of the 2002-2005 period, and another in the cold years of 2008-2012 period.

These three ways in which we have modeled the effect of temperature on egg distribution (i.e., additive, spatially variable effects, and threshold effect) are not comprehensive of all the possible ways in which temperature can affect egg distribution. For example, it is possible that egg distribution abruptly changes depending on annual average water temperature (case 3), and that within each of these regimes, the local temperature effect could also change with space (case 2). However, this case would require an extensive data set, larger than the one available for analyses, and therefore was not pursued. There is also the possibility that temperature has a non-linear effect on egg density and that such effect changes over space. However, when a spatially variable quadratic term was in model 4 the Akaike Information Criterion (AIC) score increased, so we did not pursue this option. It is also important to note that the range of water temperature at any given location sampled is smaller than that observed globally, and therefore its effect is sufficiently captured by a linear model.

Variable selection for each model was based on AIC using a backward stepwise process. The AIC is a measure of the model goodness of fit (negative log-likelihood) penalized by the model number of parameters. A covariate with a p-value > 0.05 was removed from the model and the model was rerun. The covariate was not included in the final model formulation if the AIC decreased, and if AIC increased the covariate was included. AIC score was also used to select which of the final formulations of the six abundance models was most supported by the data. Residuals for each model were visually assessed to check for normality and independence. All models were run in R version 3.3.1 (R Core Team, 2016) using the mgcv package (version 1.8-12; Wood, 2006). Contour plots of predicted egg density and observed temperature were made using the kriging option in ArcMap 10.4 (ESRI Inc., 2015). The spatial resolution of the GAM predictions used as data for kriging are at the original sampled stations.

3. Results

3.1 Temperature

Near bottom water temperature was warmest in 2003 and 2012 was the coldest year (Table 1). Temperature across the study area during the warm period varied the most in 2002, and the northern most area sampled this year was colder than 2°C (Fig. 3). Temperatures in 2003 and 2005 were more homogenous and > 3° C (Fig. 3). During the cold period years (2008, 2009, 2010, and 2012) temperatures varied greatly from east to west. Sub-zero temperatures were located on the eastern side of the study area and temperature increased westward to near 4° C on the outer domain and continental slope (Fig. 4).

3.2 Egg density and distribution

Covariates included in the presence/absence model were female spawning stock biomass, day of year, temperature, and location, and $R^2 = 0.46$ (Table 2, equation 1). The probability of eggs being present generally decreased as spawning stock biomass became smaller (Fig. 5a). Day of year appeared to have a weak effect on the presence of eggs because zero was included within the 95% confidence interval for all days of this covariate (Fig. 5b). The probability of eggs being present declined with temperatures colder than 2°C (Fig. 5c). The effect of location showed that the highest predicted probability of egg occurrence in May was near the center of the study area and decreased toward the peninsula and to the northeast and southwest (Fig. 5d).

The positive abundance model including female spawning stock biomass as a factor, day of year, spatially variable temperature effect, and a location effect (Table 2, equation 4) had the smallest AIC score and therefore was chosen as the best fit model of the six models tested (Table 2). This model explained 59% of the variance and indicated that the effect of temperature on predicted positive egg abundance varied across the study area and changes in abundance due to temperature were gradual among years. The model with temperature as an additive effect (Table 2, equation 2) had the second lowest AIC score, while the models with changes in egg abundance and distribution over thermally contrasting years were the least supported by the data (Table 2, equations 6 and 7). The effect of spawning stock biomass on positive egg abundance was similar to the presence/absence model, in that egg abundance generally decreased as biomass became smaller (Fig. 6a). Error associated with day of year was large and included zero in the 95% confidence interval so the effect of this covariate on egg abundance was most likely weak, and the trend of the relationship was for abundance to decrease after midmonth (Fig. 6b). The partial effect of location showed that predicted positive egg abundance in May was greatest near the center of the study area and decreased toward the peninsula and toward the shelf break (Fig. 6c). The inshore areas of the peninsula, and the shelf break are areas where Flathead Sole spawning would not be expected to occur based on water depth there. Predicted egg density taken as the product of the predicted probability of occurrence and predicted positive egg abundance from equation 4 showed a distribution pattern similar to the observed data indicating that the model chosen was appropriate (Figs. 7, 8). Egg density was over estimated at locations where the observed data were zero, but most predictions at those locations indicated very low density and were smaller than the lowest observed positive density so they could be considered as being zero (Figs. 7, 8). The variable coefficient term of temperature showed that predicted egg density in

May increased over the middle and outer domains as temperature increased as indicated by significantly increasing slope coefficients for temperature in that area (Fig. 9). Near the Alaska Peninsula egg density decreased with increasing temperature, this may be inconsequential because for most years egg densities in that area were zero or low, except for 2002 (Figs. 7, 8, 9).

Spawning stock biomass was included additively as a factor in both the presence/absence model and the best fit positive abundance model (Table 2, equations 1, 4). As such, spawning stock biomass will only have an effect on the average egg density for each year, but will not change the predicted spatial distribution of eggs. To reduce the confounding factor of differences in spawning stock biomass among years affecting egg density, predicted egg density in May was calculated (the product of the predicted probability of occurrence and predicted positive abundance from equation 4) with spawning stock biomass held constant (value = 3) for all years (Table 1, Fig 9). The highest predicted egg densities occurred near the center of the study area over the western portion of the middle domain and the eastern side of the outer domain, an area were spawning Flathead Sole have been found (Fig. 9; TenBrink and Wilderbuer, 2015). The spatial distribution pattern of eggs was similar to the partial effect of location for the positive abundance model (Fig. 6c). The slope coefficients of the temperature covariate in that area indicated that egg density increased as temperature increased, suggesting a greater occupancy in the core of the spawning distribution and a limited northeastward expansion of the spawning site as temperature increases (Fig. 9).

4. Discussion

Predicted egg density was greatest over the middle and outer domains in an area where spawning Flathead Sole have been found (TenBrink and Wilderbuer, 2015) and was within the depth range expected for spawning Flathead Sole (42 to 196 m; Stark, 2004), so the highest predicted egg densities most likely indicated an area where Flathead Sole spawning occurred in May. The variable coefficient GAM showed that egg density over the middle and outer domains was positively affected by temperature, and suggests spawning location in May slightly expanded northeasterly due to warmer temperatures. Additionally, the presence/absence model showed that cold temperatures can negatively affect the presence of eggs. The expansion and contraction of spawning area due to changes in temperature between years has also been shown for Walleye Pollock in the Bering Sea (Petrik et al., 2015). The full extent of the increase in size of the spawning area of Flathead Sole is unknown and could have continued outside of our study area. The expansion of the spawning area within our study area may be related to changes in the spatial extent of a cold-water mass called the cold pool. Water from melting sea ice on the southeastern Bering Sea shelf mixes in the water column to create a bottom layer of cold water (< 2°C) 40 to 50 m thick that persists in the late spring and summer (Stabeno et al., 2001). The spatial extent of the cold pool varies interannually depending on the coverage of sea ice. In warm years the extent of the cold pool is limited further north than in cold years, when it can extend southward down the middle domain as far as the Alaska Peninsula (Kotwicki and Lauth, 2013). Shifts in the spatial distribution of many groundfish species are related to the location of the cold pool (Ciannelli and Bailey, 2005, Pacific Cod, *Gadus macrocephalus*; Ciannelli et al. 2012, Arrowtooth Flounder, *Atheresthes stomias*; Kotwicki and Lauth, 2013, e.g. Rock Sole, *Lepidopsetta* spp.; Bering Flounder *Hippoglossoides robustus*; Pacific Halibut, *Hippoglossus stenolepis*), including Flathead Sole that showed a significant positive relationship between their movement and location of the cold pool (Mueter and Litzow, 2008; Spencer, 2008). The 2°C isotherm is used as the boundary for the cold pool (Stabeno et al., 2001) and water colder than

2°C was present in the northeastern areas sampled during all the cold years of our study (Fig. 4). Adult Flathead Sole avoid temperatures colder than 2°C (Rooper et al., 2005) so cold temperatures may have prevented fish from moving northeastward during cold years. Flathead Sole spawning in the southeastern Bering Sea has been reported in water ranging from 1.7° to 6.1°C (Stark, 2011). For the most part, water temperatures were greater than 2°C at the locations sampled during the warm years (Fig. 3). Flathead Sole spawning site during that time was probably not limited by temperature, so that allowed the spawning area to expand. We acknowledge that higher spawning stock biomass during the warm years could also be a factor contributing to the expansion of the spawning area. However, in our analyses spawning stock biomass is included additively and as such can only affect the magnitude of egg density and not the distribution. We could not include a spatially variant effect of spawning stock biomass because that would have conflicted with the effect of water temperature. As we gather more observations and contrasts between spawning stock biomass and water temperature, it will be of interest to disentangle the effect of these two covariates.

Both satellite-tracked drifters with drogue centered at ~40 m depth and water current measurements from moorings located on the southeastern Bering Sea shelf have shown that mean current flow over much of the shelf is relatively weak (< 5 cm/s, Stabeno et al., 2016), thus advection probably had a minimal effect on the overall density and distribution pattern of Flathead Sole eggs during the approximate two week time interval examined in our study. Delayed spawning could have affected egg density during cold years, and a small number of samples taken in June during 2008, 2009, and 2010 (19 samples taken; no samples taken in 2012) indicated that for those years mean egg density in June was less than in May suggesting that spawning was not delayed (S. Porter unpublished data). There were no surveys conducted in

June during warm years for comparison. Another factor that could affect egg density among years is egg transport through Unimak Pass from the Gulf of Alaska. We observed Flathead Sole eggs in the proximity of Unimak Pass during both warm and cold years indicating that the pass could be a conduit for Gulf of Alaska eggs into the Bering Sea. Fish larvae from the Gulf of Alaska are transported through Unimak Pass (Lanksbury et al., 2007; Siddon et al., 2011) but there have been no studies of Flathead Sole egg transport through the pass so we did not include a measure of transport in our analyses. Alternatively or in addition to transport, eggs observed in the pass may have been spawned there due to a relatively warm water temperature during all years (≥ 2°C) that our analyses predicted should not negatively affect spawning.

Ocean temperature, circulation and wind patterns, and biotic factors in the southeastern Bering Sea vary between warm and cold years (Stabeno et al., 2001; Stabeno et al., 2012), and those differences can potentially affect Flathead Sole early-life survival and recruitment. Flathead Sole are at the northern most limit of their range in the Bering Sea so they may be more susceptible to the effects of temperature and other abiotic factors there than near the center of their geographical range (Meyers, 1998). For marine fish species near the northern geographical limit of their range there is a positive correlation between temperature and recruitment (e.g., Pacific Herring *Clupea harengus*, Cod *Gadus morhua*, Meyers, 1998; Sprat, *Sprattus sprattus*, MacKenzie and Köster, 2004). Thermal conditions altering Flathead Sole spawning location may subsequently affect their recruitment by changing the advection of larvae or causing a mismatch of larvae with their prey. Stronger Flathead Sole recruitment years are associated with eastward on-shelf springtime winds that may advect larvae toward nursery areas (Wilderbuer et al., 2013). Those winds are present during the late spring, summer and fall in warm years (Stabeno et al., 2012). Additionally, age-3 recruitment estimates for larvae that hatched during the years of our study indicate that Flathead Sole recruitment was in most cases higher during warm years than during cold years (McGilliard et al., 2016). The largest recruitment year class during the years of our study was from larvae that hatched in 2003 and lowest recruitment was 2012, corresponding with the warmest and coldest years respectively. Warm conditions may be beneficial for the recruitment of Flathead Sole but it remains to be determined conclusively which mechanisms are most favorable for their recruitment in the Bering Sea.

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Figure Captions

Fig. 1. The southeastern Bering Sea shelf region. The shelf is divided into three domains, coastal (< 50 m depth), middle (50 to 100 m depth), and outer (100 to 200 m depth). The location of a mooring where water temperature and current measurements are taken is also shown.

Fig. 2. Observed Flathead Sole (*Hippoglossoides elassodon*) egg densities in the southeastern Bering Sea. Egg densities (number/10 m^2) collected throughout the year for 2001 to 2005 (warm period), and 2007 to 2013 (cold period). Study area is enclosed in the box.

Fig. 3. Ocean temperatures in the southeastern Bering Sea study area in May for warm period years. Near bottom water temperatures (°C) for 2002, 2003, and 2005. Plots were made using the kriging option in ArcMap 10.4 (ESRI Inc., 2015).

Fig. 4. Ocean temperatures in the southeastern Bering Sea study area in May for cold period years. Near bottom water temperatures (°C) for 2008, 2009, 2010, and 2012. Plots were made using the kriging option in ArcMap 10.4 (ESRI Inc., 2015).

Fig. 5. Presence/absence model for Flathead Sole eggs in the southeastern Bering Sea study area in May. Partial effects of female spawning stock biomass used as a factor (a). Largest spawning stock biomass is 1 and smallest biomass is 7. Also shown are partial effects of day of year (b), near bottom water temperatures (c), and location (d). 95% confidence interval is shown by dashed lines (a, b, c). Tick marks on the x-axis show sampling intensity (b,c). Predicted occurrence of eggs increases from purple to orange (d).

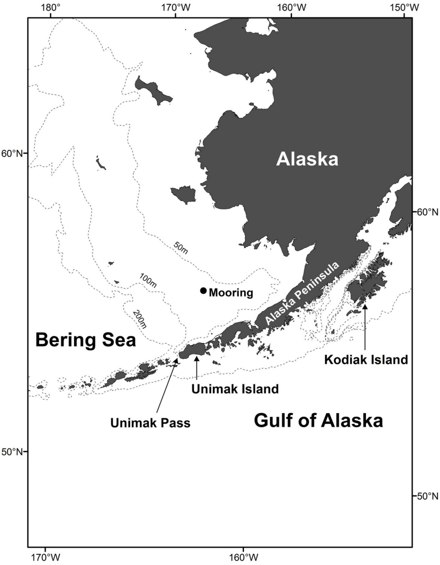
Fig. 6. Positive abundance model for Flathead Sole egg density (ln(number 10/m^2)) in the southeastern Bering Sea study area in May that includes temperature as a spatially variable covariate. Partial effects of female spawning stock biomass used as a factor (a). Largest spawning stock biomass is 1 and smallest biomass is 7. Also shown are the partial effects of day of year (b), and location (c). 95% confidence interval is shown by dashed lines (a, b). Tick marks on the x-axis show sampling intensity (b). Predicted positive egg abundance increases from purple to orange (c).

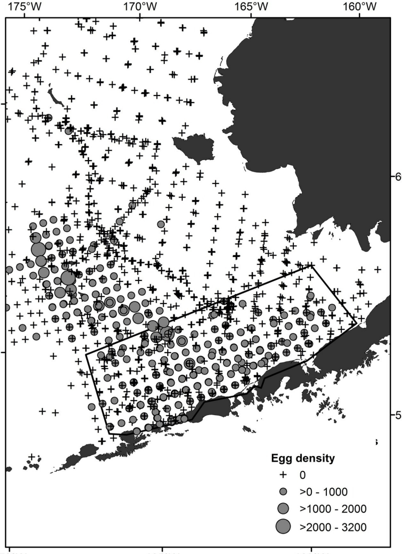
Fig. 7. Observed and predicted Flathead Sole egg densities in the southeastern Bering Sea study area in May for warm period years. Natural log transformed egg densities (ln(number/10 m^2)) for 2002, 2003, and 2005. Size of bubbles is of the same scale for both observed and predicted egg densities. Predicted egg densities are the product of the predicted probabilities of occurrence and predicted positive egg abundance from equation 4 (see text).

Fig. 8. Observed and predicted Flathead Sole egg densities in the southeastern Bering Sea study area in May for cold period years. Natural log transformed egg densities (ln(number/10 m^2)) for 2008, 2009, 2010, and 2012. Size of bubbles is of the same scale for both observed and predicted egg densities. Predicted egg densities are the product of the predicted probabilities of occurrence and predicted egg positive abundance from equation 4 (see text).

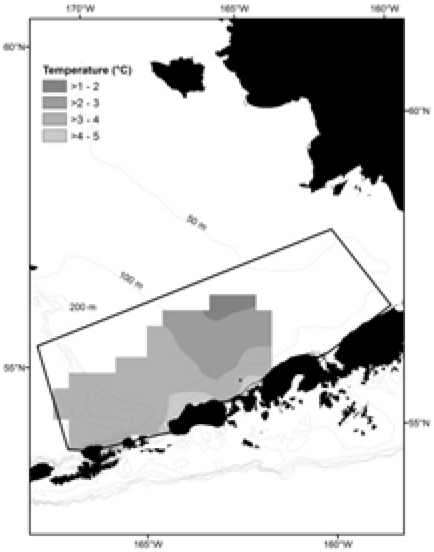
Fig. 9. Predicted Flathead Sole egg density (ln(number of eggs/10m^2) in the southeastern Bering Sea study area in May with female spawning stock biomass kept constant for all years (grey

scale). Predicted egg densities are the product of the predicted probabilities of occurrence and predicted positive egg abundance from equation 4 (see text). Red bubbles indicate an increase in egg density with a 1-unit increase in temperature (slope coefficient for temperature). Blue bubbles indicate a decrease in egg density with temperature. Slope coefficients significantly different from 0 are shown. Plot of predicted egg density was made using the kriging option in ArcMap 10.4 (ESRI Inc., 2015) that smoothed the predicted densities.

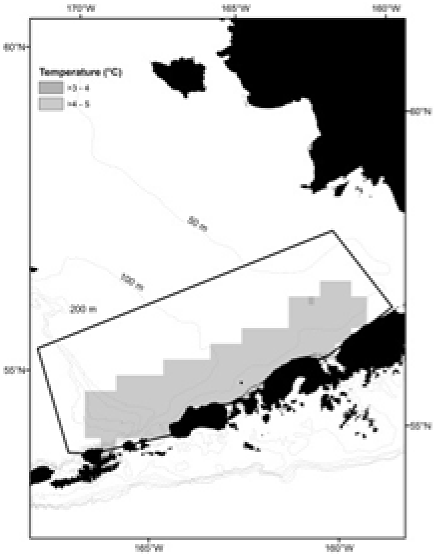

180°
170°W
160°W
150°W
60°N
60°N
50°N
50°N
170°W
160°W
Alaska
50m
100m
200m
Mooring
Alaska Peninsula
Bering Sea
Unimak Island
Unimak Pass
Kodiak Island
Gulf of Alaska


175°W
170°W
165°W
160°W
60°N
55°N
60°N
55°N
170°W
165°W
160°W
Egg density
+ 0
● >0 - 1000
● >1000 - 2000
● >2000 - 3200

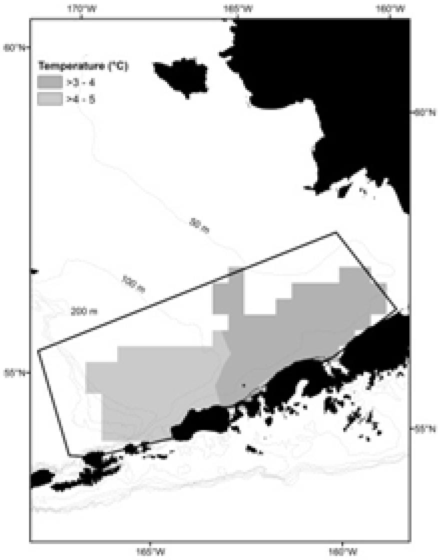
2002



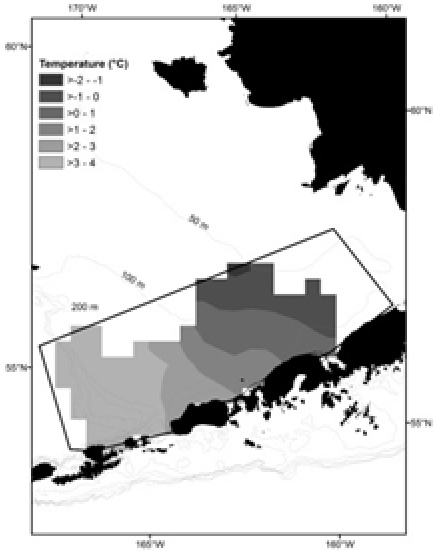
2003



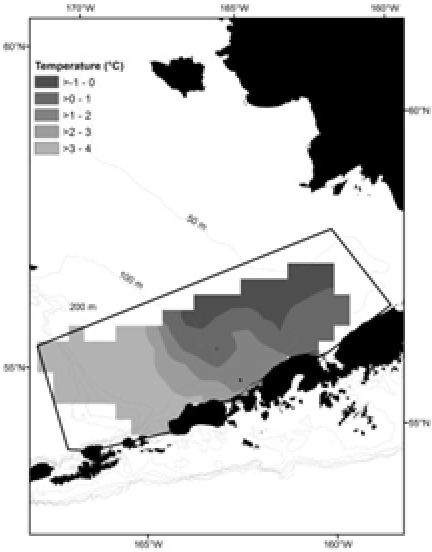
2005



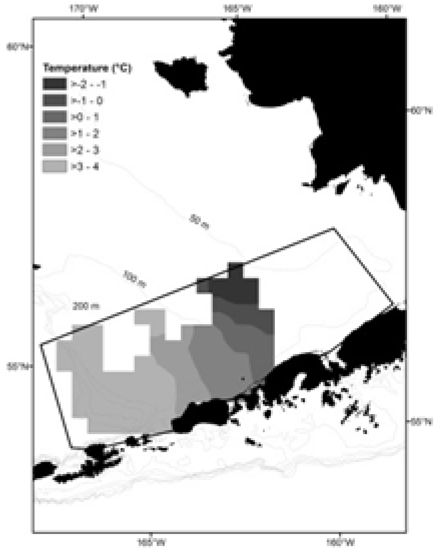
2008



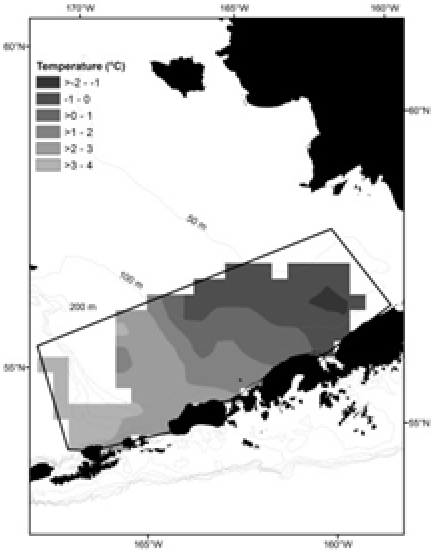
2009

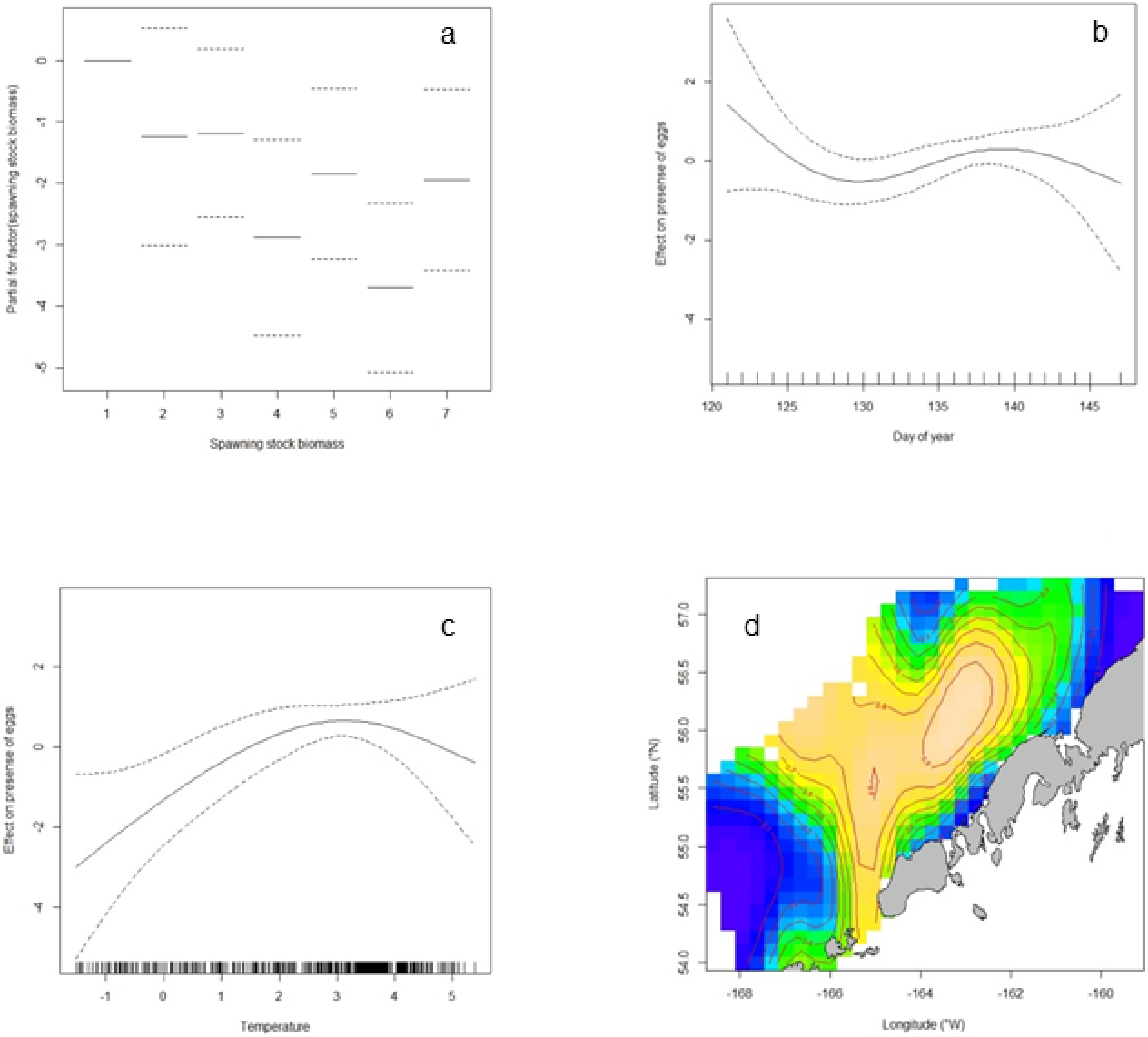


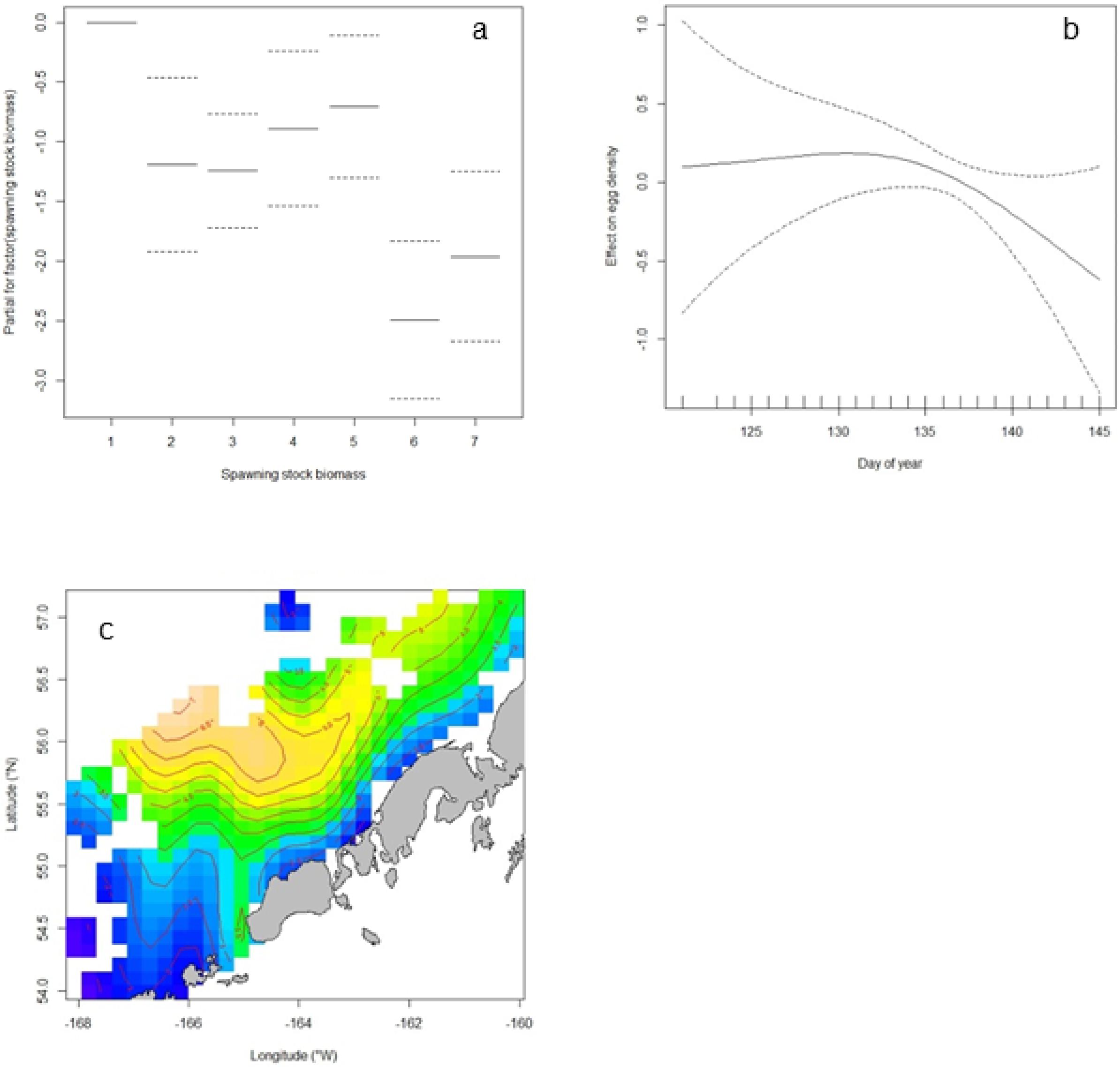
2010



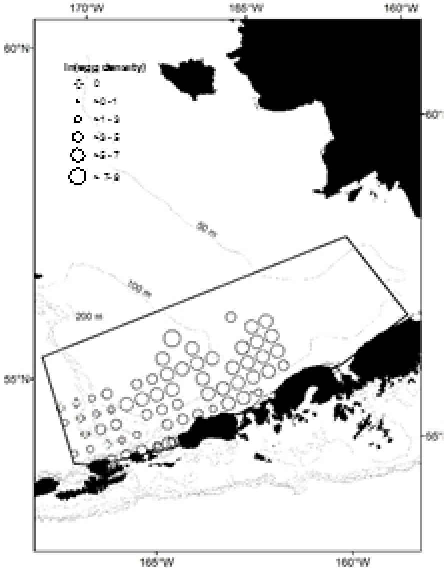
2012



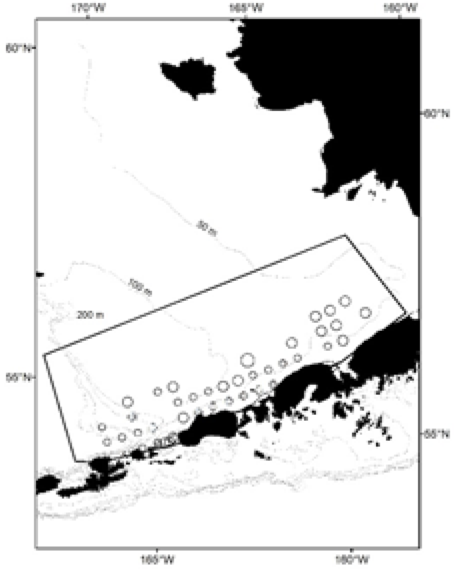

a
Partial for factor(spawning stock biomass)
0
-1
-2
-3
-4
-5
1
2
3
4
5
6
7
Spawning stock biomass
b
Effect on presense of eggs
2
0
-2
-4
120
125
130
135
140
145
Day of year
c
Effect on presense of eggs
2
0
-2
-4
-1
0
1
2
3
4
5
Temperature
d
Latitude (°N)
57.0
56.5
56.0
55.5
55.0
54.5
54.0
-168
-166
-164
-162
-160
Longitude (°W)


a
Partial for factor(spawning stock biomass)
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
-3.0
1
2
3
4
5
6
7
Spawning stock biomass
b
Effect on egg density
1.0
0.5
0.0
-0.5
-1.0
125
130
135
140
145
Day of year
c
Latitude (°N)
57.0
56.5
56.0
55.5
55.0
54.5
54.0
-168
-166
-164
-162
-160
Longitude (°W)

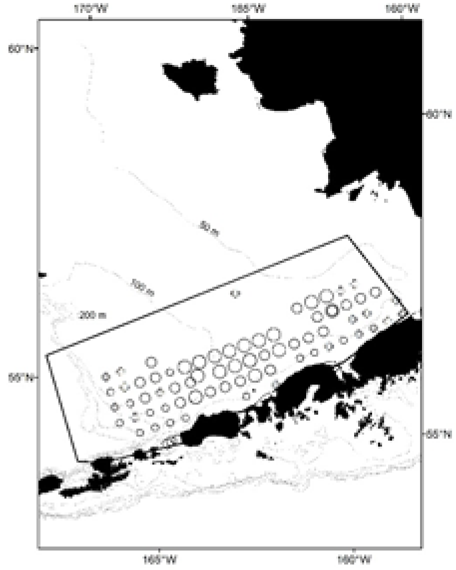
2002 observed



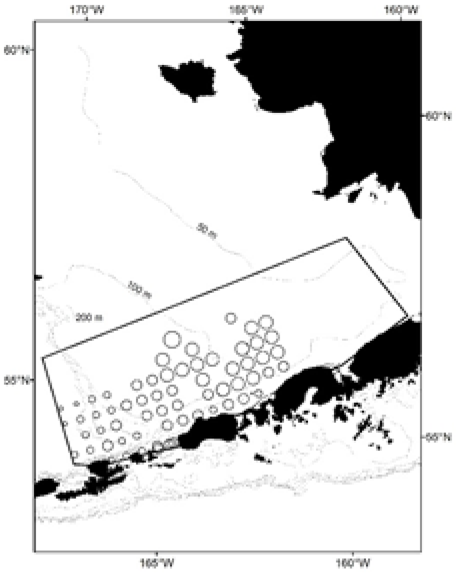
2003 observed



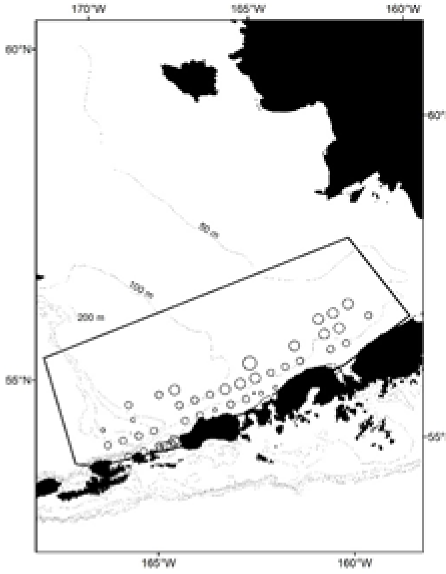
2005 observed



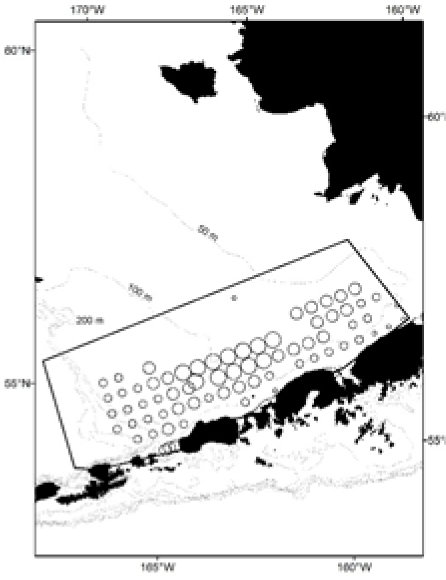
2002 predicted

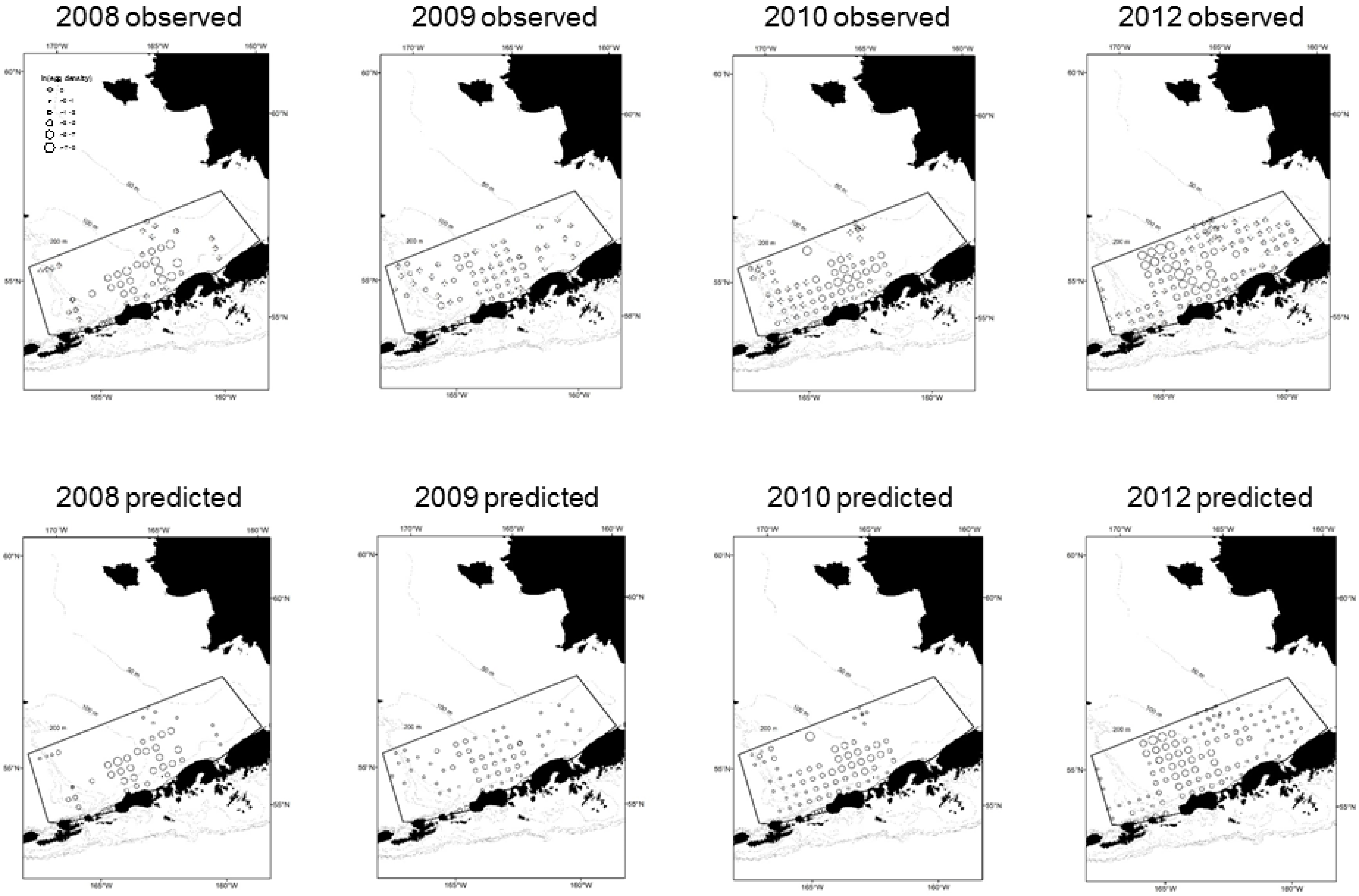


2003 predicted



2005 predicted





2008 observed

2009 observed

2010 observed

2012 observed

2008 predicted

2009 predicted

2010 predicted

2012 predicted

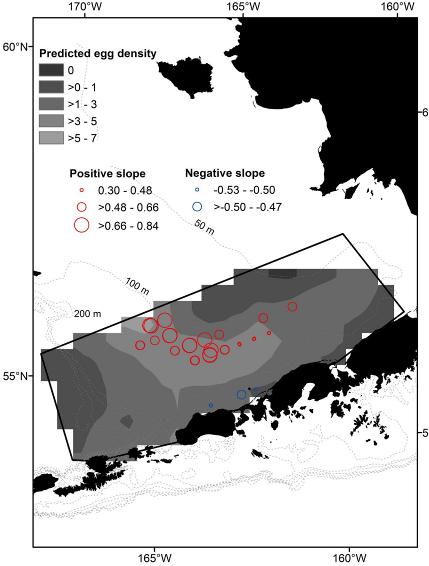

170°W
165°W
160°W
60°N
60°N
Predicted egg density
0
>0 - 1
>1 - 3
>3 - 5
>5 - 7
Positive slope
0.30 - 0.48
>0.48 - 0.66
>0.66 - 0.84
Negative slope
-0.53 - -0.50
>-0.50 - -0.47
50 m
100 m
200 m
55°N
55°N
165°W
160°W

Table 1

Survey years of Flathead Sole eggs in the southeastern Bering Sea used to model the effect of water temperature on spawning location.

Year	Sampling Dates	No. Tows[a]	SSB[b]	SSB Anomaly[c]	Mean Near Bottom Temp.[d]	Mean Egg Density[e]
Warm						
2002	12 – 21 May	64	299.5	1.925	3.41	231.62 ± 269.45
2003	17 – 24 May	43	288.7	1.388	4.50	32.66 ± 44.56
2005	10 – 27 May	73	268.1	0.313	3.86	105.88 ± 170.40
Cold						
2008	7 – 20 May	50	251.6	-0.612	1.89	86.94 ± 183.47
2009	8 – 17 May	63	246.6	-0.901	1.89	6.80 ± 18.93
2010	1 – 17 May	70	244.9	-1.005	2.29	48.99 ± 137.49
2012	1 – 24 May	108	252.1	-0.581	1.15	119.58 ± 390.03

[a] Number of bongo net tows conducted within the study area.

[b] Estimated female spawning biomass (1000 tons) in the Bering Sea and Aleutian Islands regions (McGilliard et al., 2016).

[c] Standardized anomalies of natural log transformed spawning stock biomass.

[d] Mean water temperature (°C) at maximum gear depth (for most net tows this was 10 m above bottom) across all stations sampled within the study area.

[e] Mean egg density (number/10m^2) ± standard deviation within the study area.

Table 2

Generalized additive models tested to examine the effect of warm and cold years on presence/absence and density of Flathead Sole eggs in the southeastern Bering Sea study area in May. The terms *additive*, *local* and *threshold* refer to the three model formulations used to assess the effect of water temperature on egg density. In the *additive* model, the temperature effect is assumed to be equally applying to all locations sampled and can be non-linear. In the *local* model, the effect of temperature is locally linear, but smoothly changing over space. In the *threshold* model the distribution of eggs changes abruptly in relation to the annual average temperature, resulting in two different egg distribution patterns – one in the warm years of 2002-2005, and another in the cold years of 2008-2012.

Model	Equation	SSB[a]	d[b]	t[c]	Location[d]	edf[e]	AIC[f]	R^2
Presence/Absence	1	factor	additive	additive	additive	33.15	433.7	0.46
Abundance	2	factor	additive	additive	additive	32.00	814.4	0.57
Abundance	3	smooth	-[g]	additive	additive	27.22	821.5	0.55
Abundance	4	factor	additive	local	additive	40.12	807.3	0.59
Abundance	5	smooth	-[g]	local	additive	34.96	814.6	0.58
Abundance	6	factor	additive	threshold	nonadditive	46.26	836.0	0.56
Abundance	7	smooth	additive	threshold	nonadditive	42.44	841.2	0.54

[a] female spawning stock biomass. Standardized natural log anomalies were used as values when SSB was included as a smooth term.

[b] day of year

[c] water temperature (°C) at maximum gear depth (for most net tows this was 10 m above bottom)

[d] latitude and longitude

[e] estimated total degrees of freedom

[f] Akaike's information criterion value

[g] - covariate not included in final model