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Environmentally driven forecasts of northern rock sole (*Lepidopsetta polyxystra*) recruitment in the eastern Bering Sea

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Abstract

Northern rock sole recruitment in the eastern Bering Sea has been hypothesized to (a) depend on wind-driven surface currents linking spawning and nursery areas, (b) be density-dependent, and (c) be negatively impacted by cold bottom temperatures over a large nursery area during the first summer of life. A suite of models was developed to test these hypotheses. Data included 32 years of recruitment and spawning biomass estimates derived from a stock assessment model and wind and temperature indices customized to the environmental exposure of age-0 northern rock sole in the eastern Bering Sea. The predictive ability of the models was evaluated, and the models were used to forecast recruitment to age-4 for recent year classes which are poorly retained by the standard multi-species bottom trawl survey gear. Models which included wind and temperature indices performed better than a naïve forecast based on the running mean. The best-performing model was a categorical model with wind and temperature thresholds, which explained 49% of the variation in recruitment. Ricker models performed more poorly than models without a spawning biomass term, providing no evidence that recruitment is related to stock size. The models forecast higher recruitment for the most recent year classes (2015–2018) than for prior year classes with observed poor recruitment (2006–2013). These environment-based recruitment forecasts may improve recruitment estimates for the most recent year classes and facilitate study of the effects of future climate change on northern rock sole population dynamics.

KEYWORDS

biological dynamics, cold-pool, forecast, model, northern rock sole, oceanography, recruitment, temperature, winds

1 | INTRODUCTION

Recruitment variability drives large fluctuations in fish populations, which has led to a long history of attempts to understand the environmental causes of recruitment variability (Cushing, 1982; Hjort, 1914; Rice & Browman, 2014). Understanding how the environment impacts recruitment for a stock could lead to early predictions of year-class strength (De Oliveira & Butterworth, 2005) and predictions of the effects of long-term climate change (Hollowed et al., 2009). The success of environment-recruitment studies, however, has been extremely limited. Environmental effects on recruitment are complicated (Essington et al., 2016), and reported environment–recruitment relationships usually fail when retested with additional data (Myers, 1998). Hypothesized reasons for model predictive failure include spurious environment–recruitment correlations caused by testing large numbers of potential environmental variables (De

Oliveira & Butterworth, 2005; Lehodey et al., 2006; Myers, 1998) and overfitting the data with too many model parameters (De Oliveira & Butterworth, 2005). Mechanistic understanding of environment–recruitment relationships should decrease the probability of spurious relationships, and a proposed approach to improve environment–recruitment models is to limit potential environmental factors to effects hypothesized a priori (Burnham & Anderson, 2002; De Oliveira & Butterworth, 2005). Furthermore, poor model performance may occur when ocean-basin-wide environmental parameters are used, which are mismatched temporally and/or spatially to the environmental exposure of early life stages of the studied fish population (Stachura et al., 2014).

Environmental effects on recruitment of northern rock sole in the Eastern Bering Sea (EBS) have been studied periodically over the past few decades. Northern rock sole (*Lepidopsetta polyxystra*) is a commercially fished species in the Gulf of Alaska and EBS, with an EBS mean annual catch of over 50,000 metric tons over the past 10 years, including a high value roe fishery (Wilderbuer, Ianelli, & Nichol, 2018). The large northern rock sole biomass in the EBS (20-year average biomass estimated at about 2 million metric tons; Wilderbuer et al., 2018) also makes the species an important trophic component of the EBS (Aydin & Mueter, 2007). Northern rock sole recruitment in the EBS varies inter-annually, and also over multi-year periods (Wilderbuer et al., 2002; Wilderbuer, Stockhausen, & Bond, 2013). The stock assessment provides recruitment estimates for year classes; however, the estimates are delayed until the relatively slow-growing fish are well-sampled (at least age-4) in the fish aging protocols during the annual bottom trawl survey (Wilderbuer et al., 2018). Therefore, there is little information to inform the stock assessment model estimates of year-class strength for the last (most recent) 4 or 5 years. Recruitment for the 2006–2013 year classes was poor, including some of the lowest estimates in the time series, and causing an ongoing decline in stock biomass; however, the 2014 year class is estimated to be higher than average (Wilderbuer et al., 2018).

Northern rock sole spawn in the EBS from December through March (Wilderbuer et al., 2018) over the outer continental shelf (Figure 1; Cooper, Duffy-Anderson, Stockhausen, & Cheng, 2013) and settle during the summer at bottom depths between about 30 and 50 m on the shelf (Figure 1; Cooper, Duffy-Anderson, Norcross, Holladay, & Stabeno, 2014). Predominant currents near the spawning areas (Figure 1; Stabeno & Reed, 1994) would transport larvae along the Alaska Peninsula or toward the Pribilof Islands (Cooper et al., 2013; Lanksbury, Duffy-Anderson, Mier, Busby, & Stabeno, 2007). Age-0 settled fish have been observed at a large nursery area off of mainland Alaska between Nunivak Island and Cape Newenham (hereafter referred to as the northern nursery area), and also along a similar depth range along the Alaska Peninsula (Cooper et al., 2014; Hurst, 2016). While the relative contributions of the nursery areas to the production of recruits are unknown, the nursery area near the Alaska Peninsula is on a narrower strip of benthos due to a steeper depth gradient (Figure 1; Cooper et al., 2014; Hurst, 2016), and the northern nursery area is large enough to produce enough juveniles to impact year-class strength for the entire EBS (Cooper et al., 2014).

Environmental effects on recruitment have been reported for northern rock sole in the EBS. Recruitment is positively correlated with onshore (from the west) winds during the larval drift period (Wilderbuer et al., 2002, 2013), and recruitment is also thought to be density-dependent, with reduced recruitment when spawning biomass is high (Wilderbuer et al., 2002, 2013). Temperature may also affect recruitment. A prominent physical feature of the EBS is an area of cold temperature (often defined as <2°C bottom temperature) below the surface mixed layer that is formed each year under winter and spring sea ice, and called the cold pool (Stabeno, Bond, Kachel, Salo, & Schumacher, 2001). The annual cold pool extent varies greatly because of variability in sea ice extent (Stabeno, Kachel, et al., 2012). In cold years, such as 1999, the cold pool can extend to near the Alaska Peninsula, while in warm years, such as 2005, the cold pool does not extend into the southeastern EBS (Figure 1). The northern nursery area produced large numbers of age-0 settled fish in a warm year, but no fish in a cold year (Cooper et al., 2014), and long-term distribution and abundance patterns of small juveniles are consistent with reduced age-0 survival at the northern nursery area during cold years (Cooper & Nichol, 2016). One proposed mechanism for poor recruitment in the northern nursery area in cold years is reduced growth and condition of larvae that pass through the cold pool, because larval growth at 2°C is reduced to the point that they would not reach settlement size during their first summer (Laurel, Danley, & Haines, 2014). Juvenile growth is also reduced at 2°C (Hurst & Abookire, 2006), and settling in the cold pool could cause mortality related to low growth rates (Cooper & Nichol, 2016).

In this study, we model northern rock sole recruitment in the EBS with a suite of models using environmental factors during the age-0 year for the 1982–2014 year classes. Models include a standard Ricker stock–recruit model, Ricker models with environmental factors, and models with environmental factors alone. Specific hypotheses we test include (a) onshore winds during the larval drift period enhance recruitment, (b) the presence of the cold pool over the northern nursery area reduces recruitment, and (c) recruitment is related to stock biomass. We evaluate model performance and use two methods to test the predictive ability of the models to evaluate their use for predicting recruitment. We then use the best-performing models to predict recruitment for the four most recent year classes (2015–2018).

2 | MATERIAL AND METHODS

For each northern rock sole year class from 1982 to 2014, estimates of recruitment to age-4 and the population spawning biomass which created each year class were taken from the Aleutian Islands and eastern Bering Sea northern rock sole stock assessment (Wilderbuer et al., 2018). The assessment uses an age-structured model which combines length and age composition data from both fishery observations and annual fishery-independent trawl surveys conducted

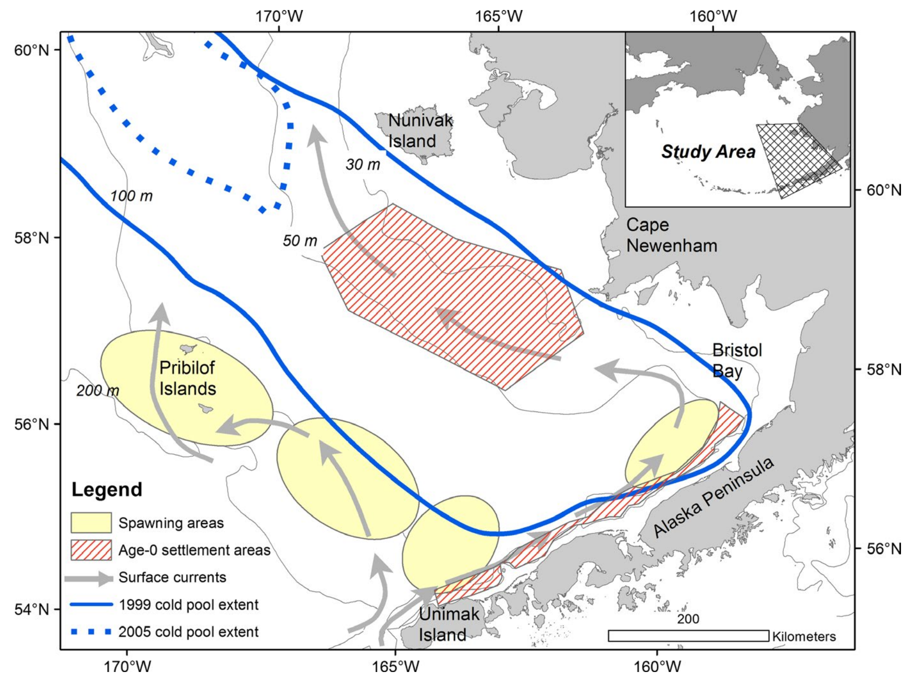

FIGURE 1 Map of northern rock sole spawning areas (yellow ellipses) and known age-0 habitat areas (red hatched areas) in the southeastern Bering Sea. Gray arrows depict predominant surface currents (from Stabeno & Reed, 1994). Dotted blue line and solid blue line are the maximum extents of the cold pool (bottom temperature < 2°C) in 2005 and 1999, respectively

by the National Marine Fisheries Service (NMFS) and biomass estimates from the trawl surveys.

Environmental indices were developed to quantify the cold pool coverage on the northern nursery area and winds during the larval drift period each year. The first step to develop an index of the cold pool effect on the northern nursery area was to delineate the northern nursery area. To do this, the area containing age-0 northern rock sole in 2003 (Cooper et al., 2014) was delineated as a polygon using ARCMAP 10.4 (ESRI, 2016; Figure 1). Areas with presence of age-0 fish near the Pribilof Islands that were not contiguous with the main nursery area were not included. Next, summer bottom temperatures from 1982 to 2018 were obtained from the annual NMFS EBS shelf trawl survey (Dan Nichol, NOAA, personal communication). Bottom temperatures were interpolated using the inverse distance weighted method (Philip & Watson, 1982) tool in ARCMAP to create a raster (2.5 km × 2.5 km grid squares) of bottom temperature values for each year. The interpolated temperature grid within the bounds of the delineated northern nursery area was used to calculate the portion of the northern nursery area covered by various low temperatures values (0, 0.5, 1.0, 1.5, and 2°C). The best fit between percent of nursery area covered by the cold pool and resulting recruitment was for a 1.5°C definition of the cold pool (See the "Results" section), and 1.5°C was used as the definition of the cold pool for this study.

The Ocean Surface Current Simulations (OSCURS) model (Ingraham & Miyahara, 1988) was used to create an index of winds during the larval period for northern rock sole from 1982 to 2018. Simulated larvae were released in the model each year at the estimated center of the spawning concentrations (56°N, 165°W) based on commercial fishery locations when fleets were in pursuit of northern rock sole roe (Wilderbuer et al., 2013). Simulations ran for a 90-day period from April 1 to June 30. The OSCURS model calculates 24-hr water movement in the North Pacific Ocean and EBS by converting the daily sea-level pressure grid to wind direction and surface mixed layer current velocity and then adding the long-term geostrophic currents (Ingraham & Miyahara, 1988). End points of the simulated drift were used as an estimator for the location where settlement occurred. The wind index was a categorical variable, similar to the usage by Wilderbuer et al. (2002, 2013). Winds were characterized according to the longitude of the endpoint for each larval drift simulation where all end points east of 168°W longitude were classified as on-shelf and those west of 168°W longitude as off-shelf.

A suite of recruitment models was evaluated, ranging from a simple Ricker stock–recruit model, to Ricker models with environmental covariates, to models with only environmental covariates. We considered the Ricker stock–recruit model, rather than other formulations such as Beverton-Holt, based on previous studies (Wilderbuer et al., 2002, 2013) and its current use in the stock assessment for northern rock sole (Wilderbuer et al., 2018). Models that included an interaction between the cold pool effect and winds were also considered, as nursery habitat conditions may only matter if winds are favorable for onshore transport. The response variable in all models was natural log-transformed recruitment of fish to age-4 (*lnR*) as estimated in the stock assessment for northern rock sole (Wilderbuer et al., 2018).

The first model included a Ricker spawner–recruit relationship in its linearized (log-transformed) form:

$$\ln R = \beta_0 + \ln S - \beta_1 S + \varepsilon,$$

where ln*S* is the log-transformed spawning stock biomass (SSB), included as an offset in the model, *S* is SSB, betas are model parameters, and epsilon is a normally distributed process error term. The next set of models included a Ricker spawner–recruit relationship together with environmental covariates and their interaction:

$$\ln R = \beta_0 + \ln S - \beta_1 S + \beta_2 C + \beta_3 W + \beta_4 CW + \varepsilon,$$

where C is the cold pool index (1.5°C) as a continuous variable, and W is the wind index. Models with single environmental covariates, both covariates, and both covariates together with their interaction were considered. The third set of models included only environmental covariates without a Ricker relationship (i.e., no ln$S$ offset or SSB term). For parsimony, we also considered simple naive forecasting models, whereby recruitment was forecast as either the value observed the previous year ("Previous Year model") or as the mean of the observed historical recruitment ("Running Mean model"). Finally, as a simpler alternative to the environment–recruitment models described above, we considered two models: one model with a categorical cold pool index (two levels: cold > 16% cold pool coverage, not cold < 16% coverage, see "Results" section for the rationale for the levels) together with the (categorical) wind index (ColdpoolCat + Wind model), and one model with the Ricker relationship combined with the categorical cold pool and wind terms (Ricker + ColdpoolCat + Wind model) To test the robustness of our 16% cold pool category threshold level, we also considered ColdpoolCat + Wind models with cold pool categorical threshold levels from 13% to 21%. Spawning stock biomass and environmental covariates were available from 1982 to 2018, whereas age-4 recruitment estimates were only available through the 2014 year class. Models were thus fit to 32 years of historical data.

We compared model performance using the Akaike information criterion adjusted for low sample sizes (AICc; Burnham & Anderson, 2002), as well as by using two out-of-sample prediction methods. First, we used a leave-one-year-out (LOYO) analysis: We left out one year of data, fit the model to the remaining 31 years of data, and then compared the prediction for the left-out year to the observed (i.e., stock assessment lnR) value. Second, we did a one-step-ahead forecast: Beginning with year 11 (1992), we used the data collected up to that year to fit the model and then compared the prediction for that year with the observation. We repeated for all remaining years. For model comparison, we calculated the mean squared error (*MSE*) between predicted and observed lnR. Assessing model performance using one-step-ahead predictions is most appropriate when the purpose of the model is to generate forward-looking forecasts, whereas AICc is best for assessing which model parsimoniously explains the most variance in the data.

Finally, we used the best-supported models to generate recruitment predictions for the most recent years (2015–2018) for which environmental data were available but recruitment at age-4 had yet to be estimated. All statistical analyses were conducted using R (R Core Team, 2017).

We compared the cold pool index created in this study with two available temperature indices, the Pribilofs winter sea surface temperature index (see Wilderbuer et al., 2002) and the EBS mean summer bottom temperature index (Zador, Holsman, Aydin, & Gaichas, 2017).

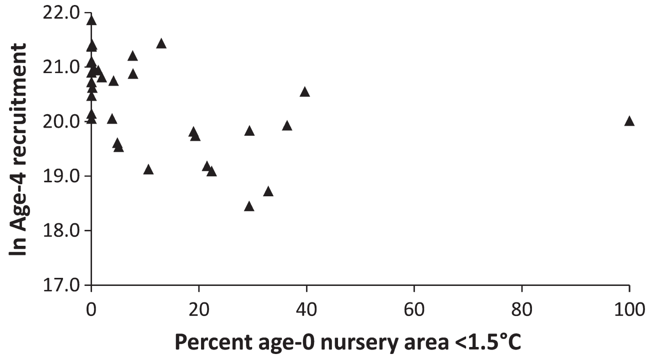

FIGURE 2 Natural log-transformed age-4 northern rock sole recruitment estimates for the 1982–2014 year classes (Wilderbuer et al., 2018) by the 1.5°C cold pool index

3 | RESULTS

Recruitment was negatively related to the cold pool index for all temperature definitions of "cold" (0, 0.5, 1, 1.5, and 2°C). The temperature value with the best fit (r^2 = .16, Figure 2) between recruitment and the cold pool index was 1.5°C, which was selected as the temperature to define the cold pool for the cold pool index used in the recruitment models. The cold pool hypothesis was made following observation of an absence of age-0 fish in the northern nursery area in 2010, when 21% of the northern nursery area was covered by water <1.5°C. In 1999, the entire northern nursery area was covered by the cold pool (cold pool index = 100%); however, recruitment in 1999 was not lower than in several other cold years (Figure 2). Because the exact form of the relationship between the cold pool index and recruitment is unknown, we also treated the cold pool index as a categorical variable in two models, (ColdpoolCat + Wind and Ricker + ColdpoolCat + Wind). Values of the cold pool index >16% were grouped as "cold" years, and <16% were grouped as "not cold" years. We also tested categorical index threshold values from 21% (level in 2010 when the northern nursery area did not contain age-0 fish) down to 13% to determine if the ColdpoolCat + Wind model results were robust to specification of this value.

The Previous Year model was one of the models with the lowest recruitment prediction error over the time series. It had the lowest *MSE* of all models using both the one-step-ahead method and LOYO prediction methods (Table 1, Figure 3). This suggests strong autocorrelation in the recruitment process; however, by definition, the model cannot predict further than one year into the future past a known recruitment estimate, and therefore was not used to create recruitment predictions for the most recent year classes.

The recruitment models based on environmental factors that performed the best included both the wind and cold pool indices. Of these models, the ColdpoolCat + Wind model had the lowest AICc and the lowest prediction error using both the one-step-ahead and LOYO prediction methods, and explained 49% of the variance in log-recruitment (Table 1, Figure 3). For the "not cold" category years, recruitment was greater in years with on-shelf winds rather than off-shelf winds; however in cold years, recruitment was low

TABLE 1 Comparison of recruitment models for northern rock sole. Performance is indicated by model AICc and the mean squared error (*MSE*) based on leaving 1 year out at a time (LOYO) and predicting 1 year ahead. In all cases, lower values indicate better model performance. N par indicates the number of parameters estimated

Model	*N* par	AICc	*MSE* (LOYO)	*MSE* (one-step-ahead)	R^2
Ricker	2	90.9	0.76	0.91	.09
Ricker + Coldpool	3	88.1	0.80	0.91	.23
Ricker + Wind	3	92.5	0.77	0.91	.11
Ricker + Coldpool +Wind	4	88.1	0.78	0.85	.28
Ricker + Coldpool*Wind	5	89.0	0.78	0.93	.32
Ricker + ColdpoolCat +Wind	4	75.0	0.59	0.67	.50
Coldpool	2	83.1	0.74	0.82	.18
Wind	2	88.6	0.77	0.86	.04
Coldpool + Wind	3	82.3	0.70	0.77	.26
Coldpool*Wind	4	82.9	0.70	0.84	.31
ColdpoolCat + Wind	3	70.1	0.51	0.60	.49
Previous Year	NA	NA	0.50	0.52	.49
Running Mean	NA	NA	0.75	0.89	.12

for years with both off- and on-shelf winds (Figure 4). After the ColdpoolCat + Wind model, the environmental factors based on models with the lowest prediction errors were the Coldpool*Wind and Coldpool + Wind using the LOYO method, and the Coldpool + Wind using the one-step-ahead method (Table 1, Figure 3).

All of the Ricker models with environmental covariates performed worse than their corresponding models without Ricker terms. Ricker models had the highest AICc scores and the highest *MSE* of all models, except for the Wind model evaluated using the one-step-ahead prediction method (Table 1, Figure 3). Notably, all but one Ricker + environment model performed worse than predictions based on only the historical mean recruitment (Running Mean model). At the observed biomass levels in this study, the models do not provide evidence that recruitment is strongly related to spawning stock size. The Ricker + ColdpoolCat + Wind model did perform better than many models, but performed worse than the simpler ColdpoolCat + Wind model.

The models with a categorical cold pool index far outperformed those with the continuous cold pool index (ΔAICc > 12). In particular, the ColdpoolCat + Wind model improved model performance in cold years compared to the models with continuous cold pool covariates. The models which included the continuous cold pool index (e.g., Coldpool*Wind and Cold Pool + Wind) predicted very low recruitment for the 1999 year class (Figure 3), because 100% of the northern nursery area was covered by the cold pool in 1999 (Figure 3). In contrast, the Categorical ColdpoolCat + Wind model did not underestimate recruitment in 1999 as drastically as the continuous models, or overestimate recruitment as much as the continuous models in cold years such as 2007 and 2008 (Figure 3). The ColdpoolCat + Wind model was robust to changes in the "cold"/"not cold" threshold for cold pool index values between 13% and 21%, as the model remained the best-performing model throughout this range of cold pool index threshold values.

All of the non-Ricker models which included environmental effects better predicted recruitment with lower *MSE* (both LOYO and step-ahead method, except for the Wind model *MSE* using the LOYO method) than the Running Mean model, (Table 1, Figure 3) which simulates the default recruitment estimate a stock assessment scientist would use without informative data. These models can predict recruitment for the year classes that have available wind and cold pool indices, but which have not yet been observed in sufficient numbers in the bottom trawl surveys to estimate abundance (2015–2018). All of the models predict recruitment from 2015 to 2018 to be higher than the low recruitment levels of the 2006–2013 year classes (Figure 3) due to the absence of "cold" category years after 2012 (Figure 3).

The cold pool index developed in this study was correlated with other readily available temperature indices to differing degrees (Figure 5). The cold pool index was not strongly correlated (r^2 = .03) with the Pribilof Islands winter sea surface temperature index. Correlation was stronger with the more broad scale EBS mean summer bottom temperature index (r^2 = .56); however, the two indices have some key differences at the scale of the northern nursery area. For instance, years within a small range of 2.0–2.5°C in the EBS mean summer bottom temperature index have corresponding cold pool index values ranging from 0 to over 40% coverage of the northern nursery area (Figure 5).

4 | DISCUSSION

We found evidence for increased young-of-the-year recruitment in years with onshore winds during the larval period and when the cold pool did not extend over the northern nursery area. Increased recruitment during years with onshore winds is consistent with the conclusions of Wilderbuer et al. (2002) and Wilderbuer et al. (2013). The extended time series and different methodology of this study provides additional evidence that this relationship continues to hold true. This study also provides the first quantitative evidence that the presence of the cold pool on the northern nursery area during the

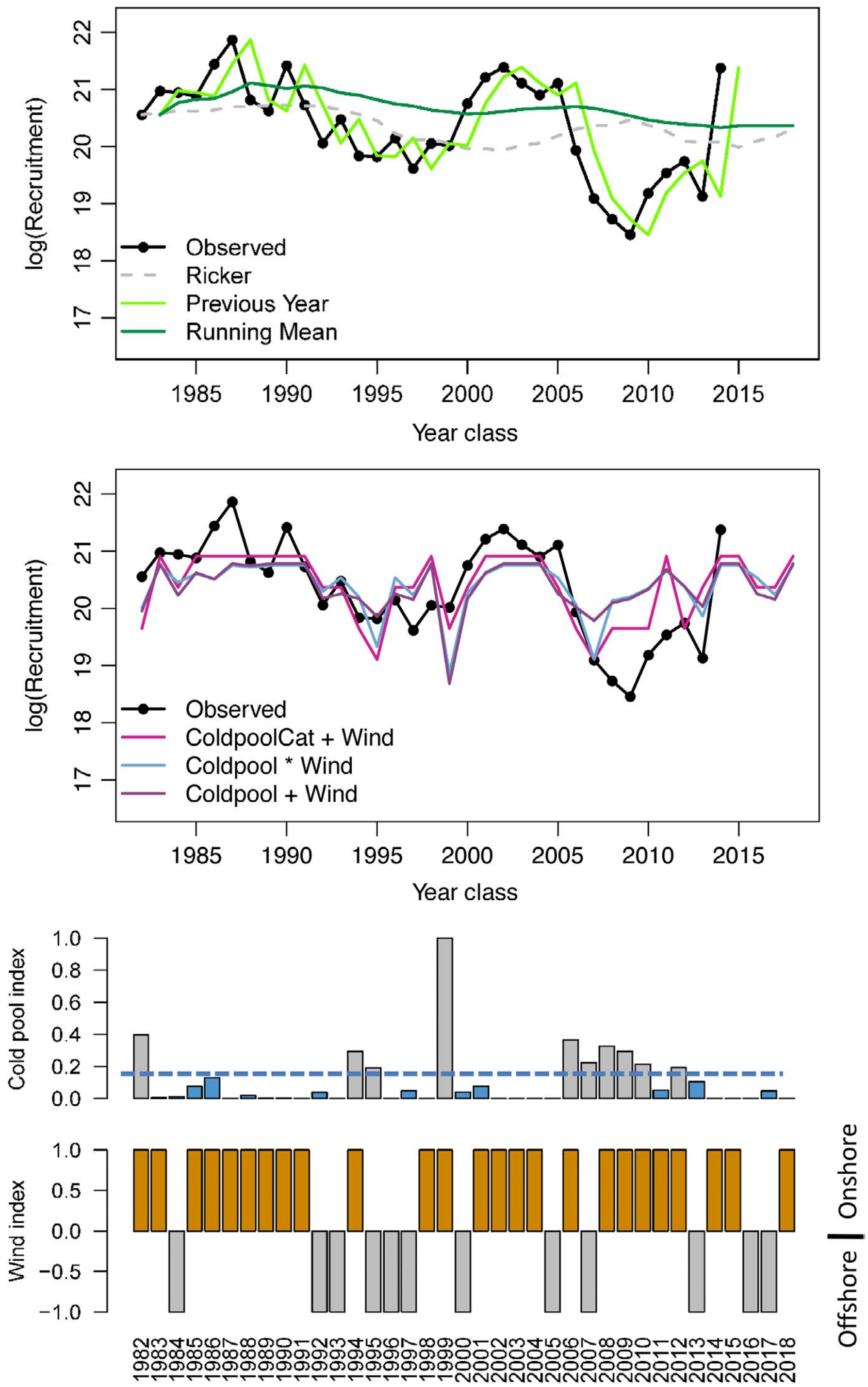

FIGURE 3 Observed northern rock sole recruitment over time and model predicted recruitment for recent year classes (top two panels). The bottom panel depicts the cold pool index over the time series (gray and blue bars represent "cold" and "not cold" category years in the ColdpoolCat + Wind model, respectively), and the wind index over the time series

first summer reduces recruitment, a finding that has long-term significance as the cold pool is projected to move north and decrease in size as sea ice is reduced under climate change (Stabeno, Farley, et al., 2012). Finally, by including these covariates in a recruitment model, we were able to explain 49% of the variance in log-transformed recruitment, significantly outperforming models that did not include environmental information.

Ricker stock–recruit models performed poorly relative to non-Ricker models. This contradicts conclusions of previous studies (Wilderbuer et al., 2002, 2013) which found evidence for density dependence in the recruitment dynamics of northern rock sole. The difference is likely due to the different time series used in the studies. The previous studies included recruitment data from 1978 to 1981 which is not included in the current study because temperature data to create the cold pool index do not exist. From 1978 to 1981, stock sizes were low, and recruitment levels were above average (Wilderbuer et al., 2013), which makes this time range supportive of density dependence. Additionally, during recent years (2005–2014) which are not included in the previous studies, stock levels declined while recruitment levels fell (Wilderbuer et al., 2018),

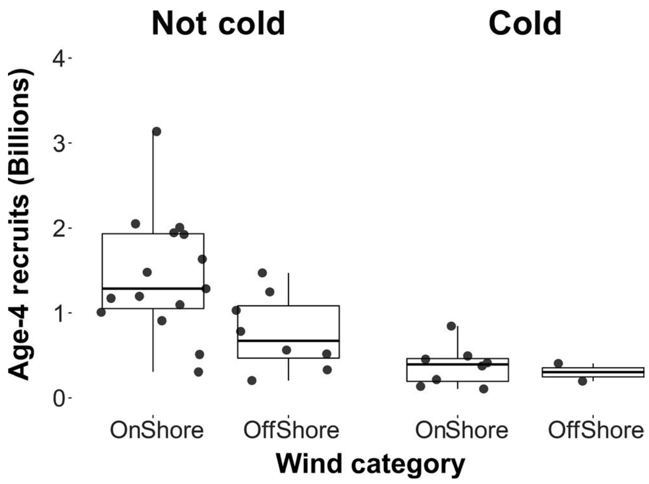

FIGURE 4 Estimated age-4 northern rock sole recruitment (Wilderbuer et al., 2018) categorized by cold pool index and wind categories. Boxplots represent the median, 25th, and 75th recruitment percentiles. Dots represent recruitment values for all years in each category

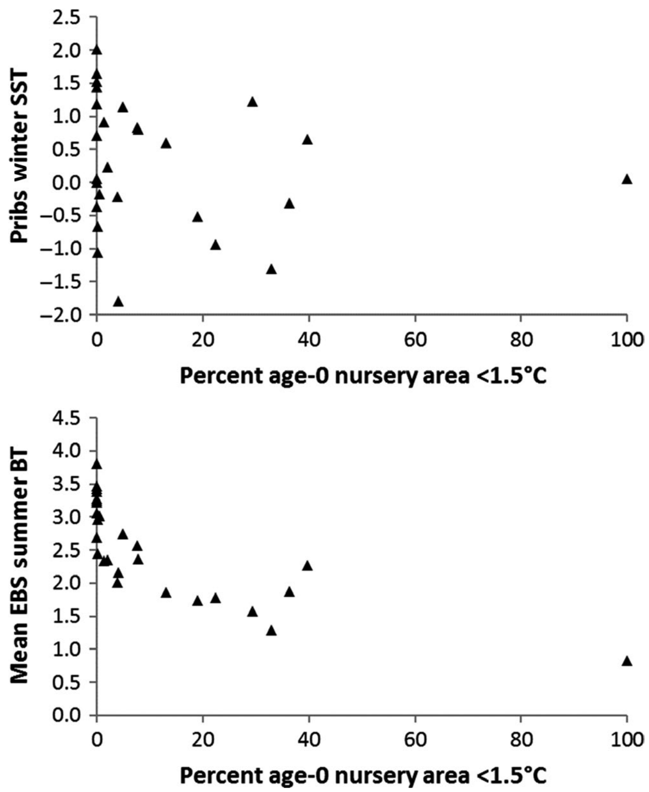

FIGURE 5 Cold pool index versus Pribilofs winter sea surface temperature (top panel), and eastern Bering Sea mean bottom temperature (bottom panel) indices

which also does not support density dependence. As suggested by Wilderbuer et al. (2002) and Wilderbuer et al. (2013), previous evidence for density dependence in northern rock sole may be indicative of recruitment regimes, with high and low periods of recruitment followed by increases or decreases in SSB in following years. This pattern has been documented in many fish stocks (Szuwalski, Vert-Pre, Punt, Branch, & Hilborn, 2015; Vert-Pre, Amoroso, Jensen, & Hilborn, 2013) and can create apparent density dependence even in the absence of such an effect. Our models suggest that the environment is a better predictor of year-class strength than spawning stock biomass, and indeed, models with only environmental covariates outcompeted those with additional Ricker biomass terms.

Reported environment–recruitment relationships usually fail when later retested with additional data (Myers, 1998); however, attempts have been made in this study to reduce known and suspected reasons for failure. We limited the number of potential environment factors to two, which decreased the probability of spurious environment–recruitment relationships caused by using many potential environment factors (De Oliveira & Butterworth, 2005; Myers, 1998). Also, the two potential environmental factors used in this study were both hypothesized, a priori, to affect northern rock sole recruitment in the EBS based on a mechanistic understanding of processes affecting early life stages (Cooper & Nichol, 2016; Wilderbuer et al., 2002, 2013). Using environmental variables with hypothesized recruitment effects and mechanisms has been suggested by several authors as a method to reduce spurious environmental–recruitment correlations (De Oliveira & Butterworth, 2005; Lehodey et al., 2006; Myers, 1998). Furthermore, one type of environment–recruitment relationship that has remained statistically significant upon retesting with additional data is correlation between recruitment and temperature for stocks near their northern or southern range limit (Myers, 1998), and the reduced northern rock sole recruitment in the EBS during cold years in this study fits this pattern. Myers (1998) cites positive temperature–recruitment correlations for fish at the polar limit of their ranges, negative temperature–recruitment correlations for fish stocks at their equatorial range limits, and more recent studies continue to discover these relationships (Able, Grothues, Morson, & Coleman, 2014; Arnott & Ruxton, 2002; Ottersen et al., 2013).

This study used environmental indices relevant to recruitment of the studied fish population. A challenge to identifying environment–recruitment relationships is measuring environmental factors at relevant spatial and temporal scales (Essington et al., 2016; Stachura et al., 2014). Early life stages of fish stocks are exposed to and respond to environmental factors based on their ontogenetic stage-specific location and timing (Doyle & Mier, 2012), and the environmental factors which affect recruitment may not be adequately described by easily obtainable ocean-basin-wide indices (Stachura et al., 2014). The wind index in this study is a customized measure of winds during the time of year when northern rock sole larvae are in the water column, and is also spatially relevant; that is, the starting point for larvae is a known northern rock sole spawning area (Cooper et al., 2013; Wilderbuer et al., 2002). The cold pool index was also customized for the stock based on empirical data of the location of the northern nursery area (Cooper et al., 2014) and the hypothesized reduction in recruitment when the northern nursery area is covered by the cold pool (Cooper et al., 2014; Cooper & Nichol, 2016). An available index of winter sea surface temperatures near the Pribilof Islands was tested as a potential recruitment predictor, but was unrelated to northern rock sole recruitment (Wilderbuer et al., 2002). The Pribilof Islands sea surface temperature index is mismatched both temporally and spatially with the cold pool index developed for this study, so it is unsurprising that the two indices area poorly correlated. The cold pool index developed in this study was more strongly correlated with the readily available EBS mean summer bottom temperature index; however, the observed differences between the indices could be important in ecological investigations at the scale of the northern nursery area.

The best model in the study (cold pool and winds as categorical variables) assumes a temperature threshold response, where recruitment is greatly reduced when more than ~16% of the northern nursery habitat is covered by the cold pool, but what is the underlying mechanism for a threshold effect? One possibility is that the deep, offshore portion of the northern nursery area is critical to recruitment success. Inspection of annual cold pool maps shows that the cold pool covers the deep edge of the northern nursery area during years such as 2010 and 1986, when the cold pool index is near the "cold" year threshold values (13%–21% northern nursery area covered by the cold pool) considered in this study (Figure 6). Due to larval transport patterns, northern rock sole likely settle at this deep edge, with subsequent shoreward movement (Cooper et al., 2014). Both northern rock sole larvae (Laurel et al., 2014) and juveniles (Hurst & Abookire, 2006) grow very slowly at temperatures <2°, and thus, reduced temperatures at the deepest edge of the nursery may prevent juveniles from inhabiting the entire northern nursery area. A cold pool threshold is consistent with the idea that environment–recruitment effects can be non-linear (Ciannelli, Chan, Baily, & Stenseth, 2004). A similar, but reversed temperature–recruitment threshold pattern is hypothesized for American flounder at the equatorial edge of their range, where poor recruitment always occurs during warm years (Able et al., 2014). The form of the cold pool index and recruitment relationship is important because model form mis-specification decreases the predictive capabilities of recruitment models (De Oliveira & Butterworth, 2005), and this relationship should be re-examined in the future when more data are available to evaluate the hypothesized threshold effect and possibly refine the threshold value. This will be especially important to improve model predictability for years with cold pool index values near our current understanding of the temperature threshold.

Juvenile recruitment in the northern nursery area affects overall EBS juvenile recruitment because of the potentially high, and highly variable amount of juvenile production there (Cooper et al., 2014). However, other northern rock sole nursery areas are present in the

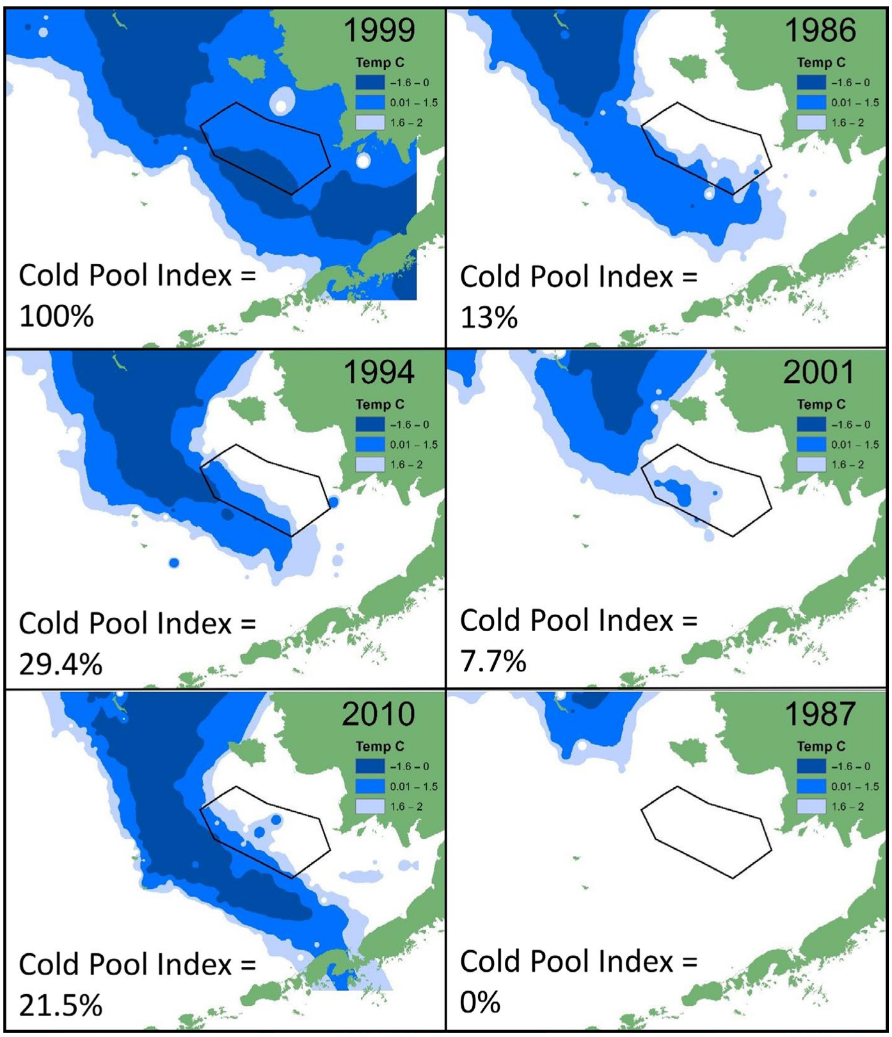

FIGURE 6 Eastern Bering Sea cold pools are shown for several years in order of decreasing (top to bottom and left to right) cold pool index values. The polygon represents the area defined as the northern nursery area in this study and used to create the cold pool index

EBS along the northern side of the Alaska Peninsula, in Bristol Bay, and near the Pribilof Islands (Cooper et al., 2014; Hurst, 2016), and the EBS population likely consists of a portfolio of subpopulations (Schindler et al., 2010) from all of these nursery areas. Nursery areas along the Alaska Peninsula and in Bristol Bay would not be affected by the cold pool, but do contribute fish to the EBS population each year. This mismatch between our response variable (overall recruitment) and our hypothesized effect (cold pool coverage on only one of many nursery areas) is a limitation of our model and reduces our ability to understand environmental effects on recruitment. If the cold pool on the northern nursery area does affect recruitment, we have only discovered it because the nursery area is so large and the effect of the cold pool is severe. The ability to assign fish in the adult population to their juvenile nursery areas would allow the study of environmental effects at each nursery area and possibly increase our ability to understand environment–recruitment effects. This is likely true for many species in the EBS with multiple spawning and nursery areas.

Models which link environmental conditions to recruitment outcomes can provide useful qualitative and quantitative information to fisheries managers. Qualitatively, information about ecosystem conditions relevant to a particular species can influence catch limits under an ecosystem approach to fisheries management (Zador et al., 2017). Such information is routinely considered in the management process by the North Pacific Fishery Management Council, which sets fishing limits for this stock. Furthermore, the Council requires stock assessment authors to explore whether any set of fisheries or environmental observations would support the inference of an impending severe decline (at least 20%) in stock biomass. If an issue of concern is identified, then an integrated analysis of all relevant environmental factors linked to a population decline is required. For NRS, environmental information can provide an early warning to managers of impending changes in stock biomass, prior to when biological monitoring data are available. Currently, a prolonged period of poor recruitment (2006–2013) associated with cold conditions has led to an ongoing decline in stock biomass (Wilderbuer et al., 2018); however, model predictions for the most recent and poorly surveyed year classes (2015–2018) are above average, suggesting that stock biomass will increase in the near future.

On a longer time scale, environmentally driven recruitment models may provide useful projections of recruitment and stock dynamics under climate change. Previously, EBS northern rock sole stock dynamics have been projected into the future using Intergovernmental Panel on Climate Change (IPCC) climate models to predict future springtime winds (Hollowed et al., 2009; Wilderbuer et al., 2013). These studies predicted northern rock sole recruitment to increase slightly or stay stable through 2050; however, these projections did not have a temperature component. The cold pool index could be downscaled from IPCC-class climate models (Hollowed et al., 2009) to incorporate the effects of possible future warming into long-term projections of northern rock sole stock dynamics. Projections of future conditions are important for developing management strategies that are robust to climate change (Busch et al., 2016). Future projections can also be used to inform climate adaptation strategies for the fishing industry and communities as fishing opportunities change (Rogers et al., 2019).

Finally, development of ecosystem-linked stock assessment models is a priority for fisheries management in the United States (Lynch, Methot, & Link, 2018). Quantitatively, environmentally driven predictions of recruitment for recent year classes could be incorporated directly into the stock assessment for northern rock sole. Simulation studies have found mixed outcomes for fish stocks and management objectives when effects of climate on recruitment are incorporated into stock assessments (A'mar, Punt, & Dorn, 2009; Castillo-Jordan et al., 2019; Ianelli, Hollowed, Haynie, Mueter, & Bond, 2011; Punt et al., 2014; Schirripa, Goodyear, & Methot, 2009), but incorporating environmental effects into stock assessment seems to do better when the environmental effects on recruitment are well known (Punt et al., 2014). Environmental effects on recruitment may also be more likely to improve management of a species when climate conditions are expected to trend in one direction (Schirripa et al., 2009), such as if future warming in the EBS causes fewer cold years. However, a full management strategy evaluation is needed to assess whether using wind and cold pool indices to predict recruitment for the most recent year classes would improve the performance of the assessment of northern rock sole and subsequent harvest advice. Our study provides a set of recruitment models, based on species-specific ecological understanding and supported by historical data, which can be used to forecast recruitment of northern rock sole, and if incorporated into the assessment process (either qualitatively or quantitatively), serve to advance Ecosystem-Based Fisheries Management in the Bering Sea.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

DC, LR, and TW all made substantial contributions to the conception of this study. LR designed and analyzed the recruitment models. TW provided the wind index, spawning biomass estimates, and year-class recruitment estimates, and DC provided the cold pool index. DC led the writing with contributions from LR and TW. All authors interpreted results, edited and revised the manuscript.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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