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Skate egg nursery habitat in the eastern Bering Sea: a predictive model

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ABSTRACT: Alaska skate species utilize localized egg nursery sites along the interface of the continental slope and shelf in the eastern Bering Sea to lay eggs in high densities. These egg nursery sites persist across years and are thought to be related to environmental conditions. The objective of this analysis was to predict the potential habitat of skate egg nursery sites using species distribution models. Skate egg nursery locations (n = 26) for 6 species were identified from bottom trawl survey catches and underwater camera surveys. Maximum entropy models were developed using 10 environmental variables to predict the probability of suitable skate egg nursery habitat; 7 variables were included in the best model. Potential habitat peaked at seafloor slopes <2%, in areas of low temperature variability and in areas of high oxygen concentrations. These were the 3 most important variables in the model. Most of the predicted high probability egg nursery suitable habitat for skates was in canyons (e.g. Bering Canyon and the southern arm of Pribilof Canyon) in a relatively narrow band on the upper slope. The most important finding of this modeling study was that there is a limited area of the upper continental slope where conditions would support potential skate egg nursery areas; however, much of the area is unexplored and likely to remain so in the near future. Management actions for important conservation questions can look to modeling studies such as these for guidance in the absence of comprehensive surveys.

KEY WORDS: Nursery habitat · Maximum entropy · Suitable habitat · Elasmobranch · Alaska

1. INTRODUCTION

Elasmobranchs are vulnerable to mortality from habitat degradation and both directed and incidental fisheries (Holden 1974, Dulvy et al. 2000, Dulvy & Reynolds 2002). In general, elasmobranchs have low productivity and are large, slow growing, late to mature and produce few, large juveniles. Thus, they are susceptible to population declines, as they choose offspring quality over quantity to achieve higher survivorship to adulthood (MacArthur & Wilson 1967, Pianka 1970, Adams 1980). High survivorship for elasmobranchs is achieved by lowered mortality through the egg and juvenile stages in stable nursery habitats. Embryo development time is highly correlated with water temperature (Berestovskii 1994, Hoff 2007). Sediment type, current patterns and O_2 concentrations related to the metabolic requirements of elasmobranch eggs have also been linked to the presence of egg nurseries (Leonard et al. 1999, Hoff 2007, 2008, Love et al. 2008), indicating that optimal environmental conditions for embryo development could potentially be used to predict the occurrence of elasmobranch egg nursery sites.

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One of the most abundant and diverse taxonomic groups of elasmobranchs in Alaska are the skates (Rajidae). The group is comprised of a putative 16 species found in the larger marine ecosystems of Alaska, with 13 found in the eastern Bering Sea. In the eastern Bering Sea, skate biomass is dominated (>95% of skate biomass) by 2 species: the Alaska skate *Bathyraja parmifera* and the Aleutian skate *B. aleutica*. The Alaska skate is the dominant skate species in the shelf environment (20–200 m) and the Aleutian skate is most abundant at all depths of the upper continental slope (200–1200 m). Both are relatively large species, reaching maturity at total lengths of 90 cm or greater (Matta & Gunderson 2007, Haas 2011, Haas et al. 2016). Both species are retained as bycatch in the eastern Bering Sea commercial fisheries, but to date do not support directed fisheries. As with most oviparous elasmobranch species, Aleutian and Alaska skates place egg cases in distinct egg nursery sites (Hoff 2008, 2009, 2016). These egg nursery sites are relatively small (~2 km^2; Hoff 2008), persistent through time and are primarily distributed on the upper continental slope of the eastern Bering Sea (Hoff 2008). Incubation time in the egg nursery habitat is 3–4 yr, with multiple year classes often represented in a single egg nursery (Hoff 2008).

In the eastern Bering Sea, fisheries management has recognized the importance of the limited number of skate egg nursery sites discovered to date (National Oceanic and Atmospheric Administration 2015). In 2015, the North Pacific Fishery Management Council designated 6 sites (including 8 skate egg nursery sites) as habitat areas of particular concern (HAPC), recognizing their uniqueness and importance as essential fish habitat. However, there has been no systematic effort to define the extent of egg nursery habitat in the eastern Bering Sea, and since 2015, the number of known sites has increased from 8 to 26 locations (G. R. Hoff unpubl. data). Thus, the objective of this modeling study was to better define the potential area of skate egg nursery habitat by modeling the potential presence of suitable egg nursery habitat based on environmental conditions. To accomplish this, we developed a maximum entropy model (Phillips et al. 2006) that utilized observations from both bottom trawl surveys and underwater camera surveys. We tested widely available environmental variables to determine those that were related to the presence of skate nurseries and then used relationships between known skate egg nursery sites and environmental conditions in those areas to predict the probability of suitable habitat for additional skate egg nursery sites.

2. MATERIALS AND METHODS

2.1. Study area

The eastern Bering Sea is dominated by a broad, shallow continental shelf that stretches east to west from the Alaska mainland to the continental slope roughly 700 km away (Fig. 1). The eastern Bering Sea shelf is commonly divided into 3 domains based on bathymetry and oceanographic fronts: the inner shelf (0–50 m), the middle shelf (50–100 m) and the outer shelf (100–180 m) (Coachman 1986). The shoreward boundary of the outer shelf is based on

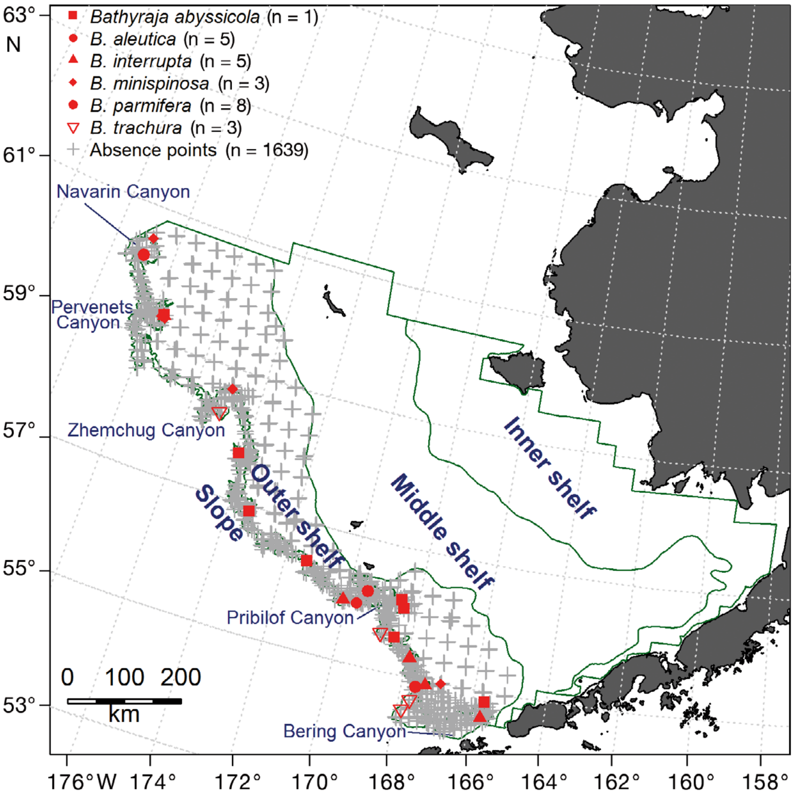

Fig. 1. Eastern Bering Sea continental shelf and slope. Symbols indicate observed skate egg nursery areas according to species, and crosses are absence points (both from bottom trawl surveys and underwater camera surveys) on the outer shelf and slope

the usual location of an oceanic front during summer (100 m) (Coachman 1986). The geological boundary between the continental shelf and slope (the shelf break) is defined as a prominent change in seafloor gradient at a slope of 1% (Sigler et al. 2015). The shelf break is typically at 180 to 200 m depth, except at the northern edge of Bering Canyon, where the shelf break is at 500 m (Sigler et al. 2015). The eastern Bering Sea slope is indented by 5 major canyons (Bering, Pribilof, Zhemchug, Pervenets and Navarin canyons) and numerous smaller canyons (Fig. 1). This study focused on the eastern Bering Sea slope and the outer domain (defined by the 100 m isobath) of the eastern Bering Sea shelf.

2.2. Presence and absence data

Since 2002, a total of 26 skate egg nursery sites have been discovered and confirmed on the eastern Bering Sea shelf and slope (Table 1, Fig. 1). Two were discovered during underwater camera surveys (Rooper et al. 2016), one during a manned submersible survey (Miller et al. 2012) and the remainder from bottom trawl surveys (Hoff 2010). The 26 skate egg nursery sites represent data from 6 distinct species with known differences in depth distribution (Hoff 2010). Because of this, it is likely that combining data across species provides a different and more generic answer than if presence or absence data were modeled for individual species. However, modeling individual species was not possible due to the small number of presence observations for skate egg nursery sites. In addition to the 26 presence locations, there were 248 confirmed absence locations from the underwater camera survey conducted by Rooper et al. (2016). Bottom trawl survey data with zero catches (n = 1391) were also used as absence data in the models (Hoff 2013, Conner & Lauth 2017). On the eastern Bering Sea shelf, depths from 30–200 m have been sampled annually since 1982 using an 83-112 eastern otter trawl with 34.1 m footrope (Conner & Lauth 2017). On the eastern Bering Sea slope, depths from 200–1200 m have been sampled biennially since 2002 (with gaps in 2006 and 2014) using a poly Nor'Eastern high-opening bottom trawl with 24.2 m roller gear constructed with 36 cm rubber bobbins separated by 10 cm rubber disks (Hoff 2013). It should be noted that the data used in this analysis resulted from 3 different survey designs; the eastern Bering Sea shelf bottom trawl survey samples the same stations within strata annually on a stationary grid, the eastern Bering Sea slope bottom trawl survey samples according to a depth and area stratified-random survey design and the underwater camera survey chose stations based on an area stratified-random survey design where stations were allocated into strata based on the probability of coral presence. The submersible survey did not have a statistically based sample design. The locations of bottom trawl and camera data and all other spatial data used in these analyses were projected into an Alaska Albers Equal Area Conic projection (center latitude: 50° N, center longitude: 154° W), and degrees of longitude and latitude were transformed into eastings and northings.

Table 1. Known skate egg nursery areas (n = 26) in the eastern Bering Sea listed by species. Year indicates the year of discovery and source indicates the source of discovery: bottom trawl survey (BTS), underwater camera survey (UCS) or submersible study (SS)

Species/ year	Latitude (°N)	Longitude (°W)	Depth (m)	Source
Bathyraja abyssicola				
2016	55.969	169.716	768	BTS
Bathyraja aleutica				
2004	55.305	167.930	311	BTS
2005	54.588	165.721	380	BTS (Hoff 2010)
2007	59.412	177.653	320	BTS (Hoff 2010)
2012	54.931	167.359	325	BTS
2014	55.972	170.117	311	UCS (Rooper et al. 2016)
Bathyraja interrupta				
2004	59.385	177.605	256	BTS
2006	55.005	166.938	155	BTS (Hoff 2010)
2008	60.498	178.844	292	BTS
2008	59.402	177.735	419	BTS (Hoff 2010)
2010	58.689	174.920	192	BTS
Bathyraja minispinosa				
2010	54.876	167.613	639	BTS
2012	60.200	178.940	528	BTS
2016	56.190	169.487	487	BTS
Bathyraja parmifera				
2005	54.843	165.674	145	BTS (Hoff 2008, 2010)
2006	56.927	173.373	217	BTS (Hoff 2010)
2006	59.437	177.668	316	BTS (Hoff 2010)
2010	56.184	168.485	214	BTS
2012	55.571	168.471	209	BTS (Hoff 2010)
2012	56.054	168.377	227	BTS
2012	57.750	174.160	250	SS (Miller et al. 2012)
2014	56.424	171.385	207	UCS (Rooper et al. 2016)
Bathyraja trachura				
2004	54.482	167.870	1016	BTS
2008	55.590	168.882	1069	BTS
2016	58.274	175.098	652	BTS
2016	54.657	167.700	821	BTS

2.3. Habitat variables

Fourteen independent variables representing environmental and habitat conditions were initially considered for this analysis (Table 2). Independent variables available for analyses included 5 geological variables: bathymetry, slope, distance from the shelf break, sediment grain size and sediment sorting. Digitized depth soundings from National Ocean Service smooth sheets collected during hydrographic surveys (S. Lewis, Alaska Regional Office, NMFS, pers. comm.) were transformed to a fine-scale (1 ha) bathymetric grid from 35–1200 m using inverse distance weighting implemented in R software (R Core Development Team 2016) (Table 2). Maximum seafloor gradient (slope expressed as percent gradient) at each grid cell (the maximum depth difference between each cell and the adjacent 8 cells) was computed using the raster package in R software (Horn 1981, Hijmans & van Etten 2012, R Core Development Team 2016) (Table 2). The distance to the shelf break (defined as in Sigler et al. 2015) was measured using the 'raster' and 'rgeos' packages in R (Hijmans & van Etten 2012, R Core Development Team 2016, Bivand & Rundel 2017) (Table 2). All information, including the seafloor gradient and bathymetry, was aggregated using the mean value into a standard 1 km^2 grid for further analysis.

Two measurements of sediment type were used in these analyses: sediment grain size and sediment sorting (Eastern Bering Sea Sediment Database, EBSSED; Richwine et al. 2018) (Table 2). Mean grain size (mm) is expressed as 'phi', which is a negative $\log_2$ transform of grain size (e.g. a large 'phi' indicates fine grains). Sediment sorting is defined as the standard deviation of phi in each sediment sample. The sampling tools for this sediment information are bottom grabs and corers, which do not distinguish boulder or bedrock habitat, and as a result, these habitat types are implicitly excluded from our analysis. The grain

Table 2. Habitat variables evaluated for application in models of potential skate egg nursery habitat in the eastern Bering Sea slope and outer shelf. The 10 variables listed in **bold** were used in model development and testing. AFSC: Alaska Fisheries Science Center; ROMS: Regional Ocean Modeling System

Variable	Unit	Definition	Interpolation method	Source
Depth	m	Bathymetry of the seafloor based on digitized and position corrected National Ocean Service (NOS) charts	Linear interpolation	Digitized NOS smooth sheets (S. Lewis pers. comm.)
Slope	%	Maximum difference between a depth measurement and its adjoining cells	–	Calculated from depth layer
Distance from shelf break	km	Linear distance to the closest point along the shelf break defined as the 1° slope contour as in Sigler et al. (2015)	–	Calculated from depth layer
Sediment grain size	phi	Negative $\log_2$ transform of mean grain size (mm)	Ordinary kriging	Richwine et al. (2018)
Sediment sorting	–	Variability (standard deviation) of grain size	Ordinary kriging	Richwine et al. (2018)
Maximum tidal current	cm s^{-1}	Maximum of the predicted tidal current at each bottom trawl location over a 1 yr cycle	Ordinary kriging	Egbert & Erofeeva (2002)
Mean bottom ocean current	m s^{-1}	Seafloor ocean current speed predicted from the Regional Ocean Modeling System (ROMS) model during the years 1975–2010 and averaged on a 100 km^2 grid	Inverse distance weighting	Danielson et al. (2011)
Variability in bottom ocean current	–	Standard deviation of seafloor ocean current speed predicted from the ROMS model during the years 1975–2010 and averaged on a 100 km^2 grid	Inverse distance weighting	Danielson et al. (2011)
Aspect relative to mean current	degrees	Absolute difference between the direction of the current and the aspect of the bathymetry	–	Derived from mean current variable and bathymetry variable
Bottom temp.-AFSC	°C	Mean summer bottom temperature for the region measured during bottom trawl surveys from 1996–2013	Ordinary kriging	Temperature data collected at bottom trawl hauls
Bottom temp.-ROMS	°C	Seafloor temperature from the ROMS model during the years 1975–2010 and averaged on a 100 km^2 grid	Inverse distance weighting	Danielson et al. (2011)
Bottom temperature variability	–	Standard deviation of seafloor temperature predicted from the ROMS model during the years 1975–2010 and averaged on a 100 km^2 grid	Inverse distance weighting	Danielson et al. (2011)
O_2	ml l^{-1}	Mean bottom oxygen concentration measured at bottom trawl survey hauls (2012 & 2016) and International Pacific Halibut Commission (IPHC) stations (2009–2013)	Ordinary kriging	IPHC and bottom trawl survey data
O_2 variability	–	Variability in oxygen concentration (standard deviation) fixed IPHC stations with multiple measurements across years	Ordinary kriging	IPHC data

size and sorting values from the sediment data (n = 803) were kriged using an exponential model (Venables & Ripley 2002), which was the best fit to the semi-variogram of both grain size and sorting values.

Four measures of ocean currents were used in the modeling: maximum tidal current speed, mean current speed, variability in current speed and the directional alignment (aspect) of currents and slope (Table 2). The first variable was the maximum speed estimated for a lunar year (368 consecutive days from 1 January 2009 to 3 January 2010) using a tidal inversion program parameterized for the eastern Bering Sea (Egbert & Erofeeva 2002). The maximum tidal speed was estimated for each point on a 1 km^2 grid overlaid on the eastern Bering Sea slope and shelf, which was then converted into a raster coverage.

The second water movement variable was the predicted bottom water layer current speed from the Northeast Pacific (NEP) Regional Ocean Modeling System (ROMS) model runs from 1970–2004 (Danielson et al. 2011). Long-term current speed and direction were available as points on a 100 km^2 grid. The ROMS model was based on a 3-dimensional grid with 60 depth bins for each grid cell. The current speed and direction for the deepest depth bin at each point (closest to the seafloor) were used in this analysis. This regularly spaced data was interpolated to a 1 km^2 resolution raster covering the eastern Bering Sea shelf and slope using inverse distance weighting (Hijmans & van Etten 2012, R Core Development Team 2016). Similarly, the variation (standard deviation) in current speed at each ROMS model point over the time series was computed and interpolated to a 1 km^2 resolution raster.

The final water current variable used in the modeling was the aspect of the seafloor relative to the mean current direction. Aspect of the seafloor identifies the compass direction of the maximum gradient of slope (angle the seafloor faces) in degrees relative to north (0°). Aspect was computed from the 1 ha bathymetry raster grid using the 'raster' package in R software (Hijmans & van Etten 2012, R Core Development Team 2016). The current direction used was the mean current direction from the long-term model output from the ROMS model (Danielson et al. 2011) on a 1 km^2 grid. The absolute value of the difference between the current direction, and the aspect of the seafloor at the position of each bottom trawl haul was used as a habitat variable in the modeling. This value ranged from 0° (where the currents were flowing in the same direction the seafloor was facing) to 180° (where the mean current was flowing directly opposite the aspect of the seafloor) and was produced on a 1 km^2 raster.

We considered 2 sources of bottom temperature data for the modeling: field-collected and modeled data (Table 2). Summertime bottom trawl surveys have collected measurements of bottom temperature (n = 1381) for tows since 1996 (Hoff 2013, Conner & Lauth 2017) using a Seabird SBE19 or similar temperature–depth recorder. These data were kriged using a spherical semi-variance model; the resulting grid represents the long-term average of summer conditions in the eastern Bering Sea since 1996. Temperature values from the model-based reconstruction of bottom temperature from 1975–2010 were derived from the NEP ROMS (Danielson et al. 2011), averaged across years and interpolated to a 1 km^2 grid for an alternative long-term mean bottom temperature.

In 2012 and 2016, oxygen concentration measurements were collected during the bottom trawl surveys of the eastern Bering Sea slope (Table 2). Oxygen concentration data were collected with a SeaGuard CTD IW (Aanderaa Data Instruments) deployed on the headrope of each trawl during survey tows. Data were recorded every 7 s (2012 survey) or every 2 s (2016 survey), and a mean value was computed for oxygen concentration for each station by averaging all values collected for each trawl between the footrope making bottom contact and lifting off the bottom at the end of the tow. In addition, we used O_2 measurements collected by the International Pacific Halibut Commission (IPHC) at a series of fixed stations between 2009 and 2013 using a SBE19plusV2 with an auxiliary SBE43 Oxygen sensor. The bottom trawl and IPHC bottom oxygen concentration data were combined across years and kriged to a 1 km^2 grid (as with the bottom trawl survey temperature above). Variability for oxygen concentration was computed for the IPHC data only (Table 2), since these data came from fixed stations that were revisited in each of the 5 yr (2009–2013). Because the bottom trawl survey stations were not fixed over time, variability in oxygen across years could not be computed. The variability in IPHC bottom and oxygen concentration (measured by the standard deviation) was kriged to a 1 km^2 grid for evaluation in the modeling.

Although multicollinearity is less of a problem for maximum entropy (MaxEnt) (and other machine learning programs) than for statistical methods (Elith et al. 2011), we minimized correlation among predictors prior to analysis (Merow et al. 2013). The 14 initial habitat variables were examined for multicollinearity by randomly selecting 10 000 points from each of the interpolated raster grids. These were regressed against each other and pairwise Pearson's correlation coefficients (r) were calculated. Variance inflation factors (VIFs) were also calculated using the method of Zuur et al. (2009). Raw predictor values were used in the analyses, as MaxEnt requires no data transformation for explanatory variables.

2.4. Modeling and cross-validation

Habitat suitability modeling was conducted using MaxEnt methods (Phillips et al. 2006, Elith et al. 2011). This modeling was performed using the 26 skate egg nursery sites as presence data (Table 1) and 10 of the 14 habitat variables (Table 2) determined to be satisfactory using the VIF scores. Instead of using a random selection of background points as pseudo-absence data (the default settings), which is the regular procedure in MaxEnt modeling, we specified the absence data (n = 1639) from the camera (n = 248) and bottom trawl (n = 1391) surveys as pseudo-absences for model parameterization and testing. MaxEnt modeling was carried out using the 'dismo' package in R (Hijmans et al. 2007).

Maximum entropy models can be sensitive to the choices for model regularization and feature classes (Warran & Seifert 2011, Merow et al. 2013, Morales et al. 2017). Regularization in MaxEnt models is used to effectively penalize complexity in the modeled relationships between presence and habitat features and can constrain over-parameterization. Feature classes define the potential range of shapes of the relationship between presence and habitat features. During initial data exploration, the regularization parameter and feature classes used in the MaxEnt modeling were varied systematically to choose the best settings for analysis. The regularization was varied across values from 0.6–4.0, and models with feature classes excluding quadratic, hinge and both quadratic and hinge were compared to those containing all potential feature classes. For this exercise, a 5-fold division of data was randomly selected (for each replicate fold, 80% of the data was used as training and 20% reserved for testing). The average area under the receiver operating curve (AUC) for the training data (AUC_{train}), test data (AUC_{test}), the difference between AUC_{train} and AUC_{test} (ΔAUC) and Akaike's information criterion corrected for small sample sizes (AIC_c; Akaike 1992, Burnham & Anderson 2002) were computed across replicate folds of the data for each combination of regularization and feature class values. The joint rank of the AUC_{test}, ΔAUC and AIC_c was computed for each combination of regularization and feature class for evaluation. The 3 statistics (AUC_{test}, ΔAUC, AIC_c) were ranked from best to worst, and these ranks were averaged for each model. In this case, the highest AUC_{test} was the best, while the smallest values for ΔAUC and AIC_c were best. For the skate egg nursery data, a regularization parameter of 3.4 with inclusion of all feature classes (linear, quadratic and hinge) was found to have the best average rank across the 3 test criteria and still maintain an adequate model fit to the training data ($AUC_{train} > 0.70$; Hosmer & Lemeshow 2000). These were the settings used for further modeling.

An initial MaxEnt model of skate egg nursery habitat containing 10 environmental variables was reduced by sequential, backwards step-wise elimination of unimportant variables, as determined by jackknife analysis of variable contribution to model fit. The process began by fitting the full model containing all variables to the 5-folds of presence and absence data. The least important variable was identified from the full model as the variable contributing the smallest amount of explanatory power to the model (averaged across the 5-folds) and was removed from the model, and the model was re-run. This process was repeated until only a single environmental variable remained in the model. The joint rank of the AUC_{test}, ΔAUC and AIC_c was computed for each model and was then used to determine the model with the best combination of environmental variables for predicting skate egg nursery habitat.

Finally, a MaxEnt model using the best combination of variables was run for the entire data set including all presence and absence data. This final model was used to generate a map of predictions of probability of suitable habitat for skate egg nursery sites for the eastern Bering Sea slope and outer shelf on a 1 km^2 raster grid. The 5-fold cross-validation for this model was used to construct replicate prediction maps and compute a standard error for prediction at each raster grid cell on the map. To determine the potential area of skate egg nursery habitat in the eastern Bering Sea, a threshold probability of suitable habitat was generated using the 'PresenceAbsence' package in R (Freeman & Moisen 2008). We initially chose the threshold to match the prevalence of skate egg nursery habitat in the camera survey (2 of 250), since this survey generated randomly selected presence and absence data that was the most reliable. However, this resulted in predictions of absence of suitable habitat for the majority of known egg nursery locations. Thus, as a more conservative measure we used a threshold that allowed no more than 10% of predictions of presence to be misclassified (thus maximizing the area of suitable habitat) for the final model. The threshold-dependent metrics: sensitivity (the proportion of observed presences of suitable skate egg nursery habitat that are correctly predicted), specificity (the proportion of actual absences of suitable skate egg nursery habitat that are correctly predicted), and the true skill statistic (sensitivity + specificity − 1, Allouche et al. 2006, Jiménez-Valverde et al. 2013) were calculated using the conservative threshold and the 'PresenceAbsence' package in R (Freeman & Moisen 2008).

3. RESULTS

Based on the VIF cutoff for inclusion (VIF ≥ 5), mean current speed, sediment grain size (phi) and distance from the shelf break were eliminated from the modeling. Of the remaining 11 variables, depth was highly correlated with oxygen concentration and slope (0.71). Because of this, depth was eliminated from the modeling exercise, leaving 10 variables available for analysis (Fig. 2). In total, 7 of the 10 variables were found to be important when used in predicting the 5-folds of training and testing data (Table 3).

In the final model using all the presence and absence points, seafloor slope was the most important variable (measured by both percent contribution and permutation importance) and probability of suitable skate egg nursery habitat increased with increasing slope to ~2 degrees and then declined (Fig. 3). The variability in bottom temperature (from the ROMS model) was the second most important variable in the final MaxEnt model. The probability of suitable skate egg nursery habitat declined with increasing temperature variability, indicating that low to moderate levels of variability in temperature were preferred (Fig. 3). Oxygen concentration was the next most important variable, with probability of suitable habitat increasing with increasing oxygen concentration (Fig. 3). Increasing variability in oxygen concentration was associated with a slight increase in the probability of suitable skate egg nursery habitat. Bottom temperature averaged across years, maximum tidal current and current variability had little or no impact on the probability of suitable skate egg nursery habitat, but were included in the final model because they were important for one or more folds of the variable selection analysis.

Models developed for each of the 5 randomly selected divisions of the data had similar performance to each other (Fig. 4). The mean prevalence of skate nursery sites in each of the 5 randomly selected data divisions was 0.159 (ranging from 0.009 to 0.021). All the models predicted the highest probability of suitable habitat for skate nurseries along the outer shelf and shelf break zone, with higher probabilities in large canyons. These individual models were also similar to the final model with all data included (Fig. 5). The final model indicated that areas of high probability of suitable skate egg nursery habitat were found along the western edge of Bering Canyon, in the arms of Pribilof and Zhemchug canyons and throughout Pervenets and Navarin canyons. Skate egg nursery habitat was also predicted to occur in a relatively narrow band along most of the upper continental slope (Fig. 5). The standard error of the predictions indicated that prediction error was highest around Navarin Canyon and uniformly low throughout the rest of the region (Fig. 6). In Fig. 4, it appears that 1 or perhaps 2 of the models (based on data folds 2 and 5) had slightly different spatial patterns in predictions around Navarin Canyon, while predictions throughout the rest of the study area were similar across data folds. This caused the elevated error near Navarin Canyon and could indicate that additional sampling may be needed in this area (it tended to have the lowest density of bottom trawl survey tows of any of the canyons or continental slope and did not have any underwater camera samples).

Based on a threshold value of 0.60 (the threshold that results in a misclassification rate of <10 % of the observations), 54 202 km^2 of probable skate egg nursery habitat exists along the eastern Bering Sea slope. The sensitivity of the model using this threshold was 0.923 and the specificity was 0.600, reflecting the conservative nature of the chosen threshold (resulting in predictions of presence of suitable habitat in areas where skate egg nurseries were not observed, resulting in a lower specificity). The true skill statistic of the model was 0.524. Using the prediction error to calculate confidence intervals on the predictions, the amount of suitable habitat is predicted to range from 41 878–62 134 km^2. The predicted suitable skate egg nursery habitat based on this threshold occurs extensively throughout the eastern Bering Sea slope and some of the outer shelf (Fig. 7). The proportion of suitable habitat declines with increasing depth after about 200–400 m for most regions (Fig. 8). In both Bering Canyon and the intercanyon area between Bering and Pribilof canyons, the suitable habitat for skate egg nursery areas extends deeper than in other regions along the outer shelf and slope.

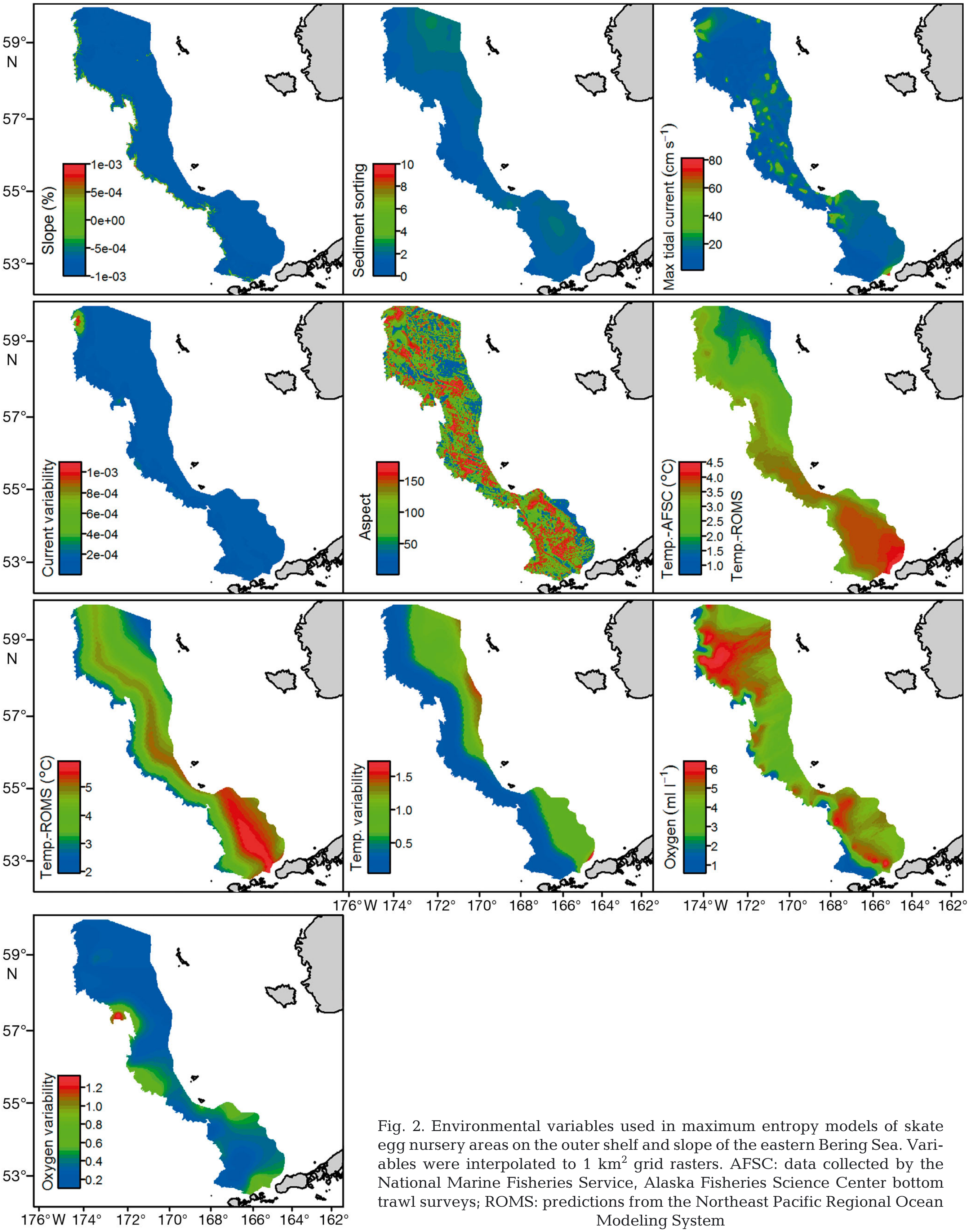

Fig. 2. Environmental variables used in maximum entropy models of skate egg nursery areas on the outer shelf and slope of the eastern Bering Sea. Variables were interpolated to 1 km^2 grid rasters. AFSC: data collected by the National Marine Fisheries Service, Alaska Fisheries Science Center bottom trawl surveys; ROMS: predictions from the Northeast Pacific Regional Ocean Modeling System

Table 3. Alternative maximum entropy models developed for skate egg nursery habitat using backwards step-wise elimination of the least important environmental variables. The full model used 10 environmental variables. Variables are listed in the order of importance for the model and the best-ranked model is highlighted in **bold**. AFSC: data collected by the National Marine Fisheries Service, Alaska Fisheries Science Center bottom trawl surveys; ROMS: predictions from the Northeast Pacific Regional Ocean Modeling System; AUC: area under the receiver operating curve for training data (AUC_{train}), test data (AUC_{test}) and the difference between AUC_{train} and AUC_{test} (ΔAUC); AIC_c: Akaike's information criterion corrected for small sample sizes

Model variables	AUC_{train}	AUC_{test}	AIC_c	ΔAUC	Ave. rank
Slope, bottom temperature variability, bottom temperature (AFSC), bottom current variability, maximum tidal current, O_2 variability, aspect, O_2, bottom temperature (ROMS), sediment sorting	0.788	0.757	476.7	0.031	4.00
Slope, bottom temperature variability, bottom current variability, bottom temperature (AFSC), O_2 variability, maximum tidal current, O_2, aspect, bottom temperature (ROMS)	0.790	0.758	475.2	0.032	4.00
Slope, bottom temperature variability, bottom current variability, maximum tidal current, bottom temperature (AFSC), O_2 variability, O_2, aspect	0.784	0.752	471.3	0.032	6.67
Slope, bottom temperature variability, bottom current variability, bottom temperature (AFSC), maximum tidal current, O_2 variability, O_2	**0.786**	**0.762**	**472.4**	**0.025**	**2.67**
Slope, bottom temperature variability, bottom current variability, maximum tidal current, bottom temperature (AFSC), O_2 variability	0.786	0.753	472.3	0.033	6.33
Slope, bottom temperature variability, bottom current variability, bottom temperature (AFSC), maximum tidal current	0.782	0.751	467.2	0.031	6.67
Slope, bottom temperature variability, bottom current variability, bottom temperature (AFSC)	0.779	0.760	464.5	0.019	4.00
Slope, bottom temperature variability, bottom current variability	0.774	0.748	464.6	0.026	7.00
Slope, bottom temperature variability	0.768	0.769	465.6	−0.002	3.67

4. DISCUSSION

The most important habitat variable determining the presence of suitable habitat for skate nurseries was slope. In general, the probability of suitable habitat peaked at low slopes (~1–3 % gradient). This is consistent with the definition of the shelf break in the eastern Bering Sea, which has previously been defined at slopes of 1 % gradient (Sigler et al. 2015 and references therein). In combination with the finding that suitable habitat declines above 200 m and below 400 m (Fig. 8), this indicates that the areas with probable suitable habitat for skates are located along the upper continental slope. Oxygen concentration was also an important variable, as the probability of suitable habitat for skate egg nursery areas increased with increasing O_2 concentrations. The eastern Bering Sea showed very few areas of hypoxia (dissolved oxygen concentration <1.43 ml l^{-1}) and most of the region had oxygen levels from 4–6 ml l^{-1}. This would correspond to saturation levels from 54–81 % based on a temperature of 3.5°C and salinity of 32.5 ppt (Benson & Krause 1984). Other studies of groundfish distributions have indicated that adult demersal fish distributions can be affected by low dissolved oxygen (Craig et al. 2001, Palsson et al. 2008, Keller et al. 2010, 2015); however, it is unknown what the oxygen requirements for elasmobranch egg cases might be. Within these slope areas, suitable skate egg nursery habitat appeared to be highest where there was a relatively stable environment for egg incubation (measured in this case by temperature variability). Other studies have found elevated currents were associated with higher probability of suitable habitat, consistent with the biology requirements of skate egg development, where there needs to be sufficient water flow and O_2 enrichment for metabolic purposes, but not so much so that there is a risk of scattering eggs out of the egg nursery habitat (Leonard et al. 1999, Hoff 2007, 2008). We did not find that higher currents were associated with higher probability of suitable habitat for either tidal or mean currents predicted by the ROMS model. This may be because of the relatively constant and low tidal currents and current variability found along the outer shelf and slope. The current conditions may be adequate for skate egg metabolism throughout the study area.

Although this analysis incorporated a group of environmental variables thought to be important for successful development in skate egg nurseries, other factors could also influence the distribution of egg

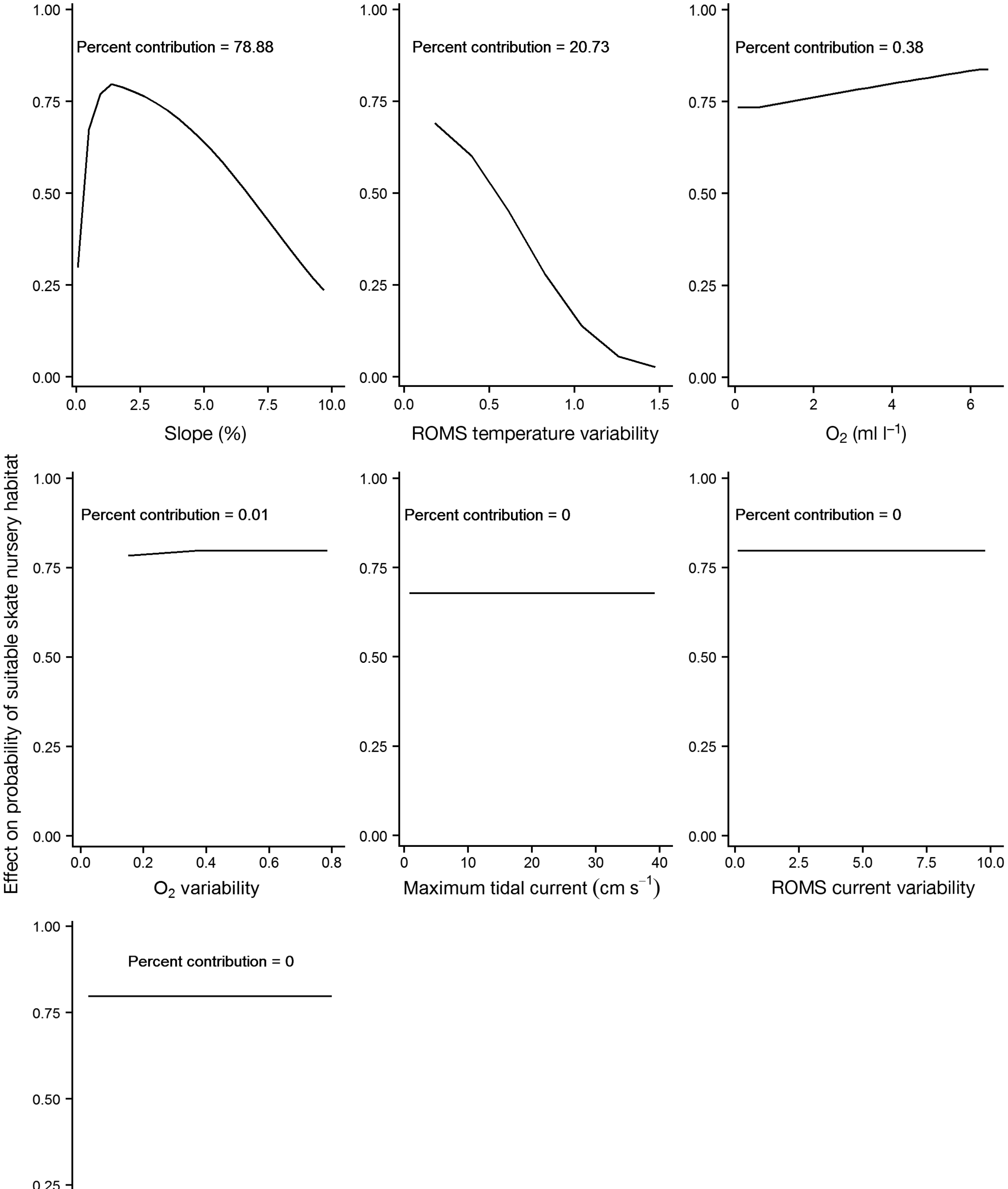

Fig. 3. Effects on the predicted probability of suitable skate egg nursery habitat by habitat variables from the best fitting model in decreasing order of contribution to model performance. AFSC: data collected by the National Marine Fisheries Service, Alaska Fisheries Science Center bottom trawl surveys; ROMS: predictions from the Northeast Pacific Regional Ocean Modeling System

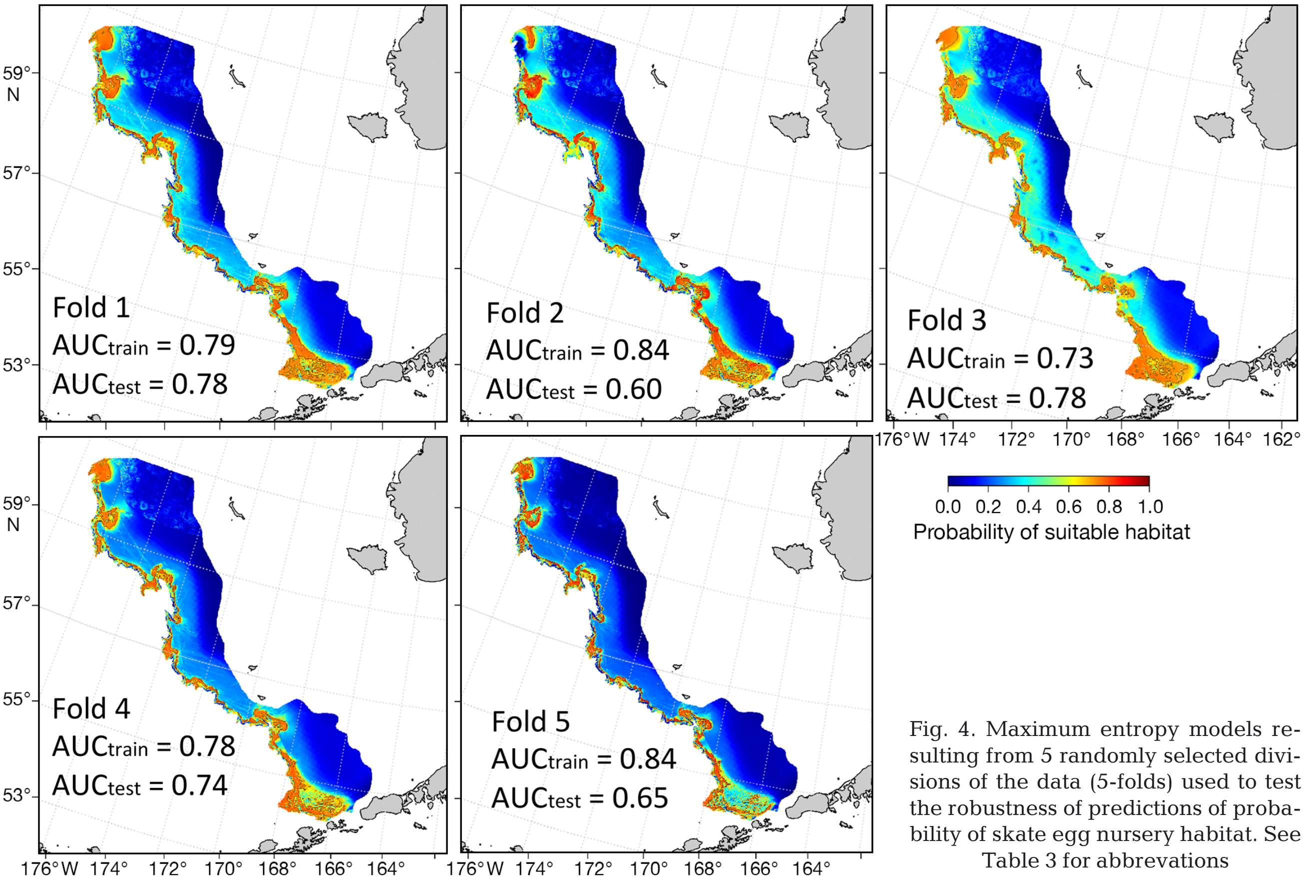

Fig. 4. Maximum entropy models resulting from 5 randomly selected divisions of the data (5-folds) used to test the robustness of predictions of probability of skate egg nursery habitat. See Table 3 for abbrevations

nurseries. These include the local abundance of egg predators such as gastropods (Cox et al. 1999, Lucifora & Garcia 2004, Hoff 2007), as well as nearby access to deeper and shallower areas where hatching juveniles are less likely to be depredated by large fish (Hoff 2010). Relatively little is known of the distribution of predatory gastropods in the eastern Bering Sea and which species might be responsible for consuming skate egg cases in egg nursery areas. Much more is known about the distribution of predatory fishes, and previous studies have suggested that newly hatched juvenile skates are susceptible to predation by species such as Pacific cod *Gadus macrocephalus* and Pacific halibut *Hippoglossus stenolepis*, which are common on the eastern Bering Sea slope (Hoff 2010). Seasonality in the biotic

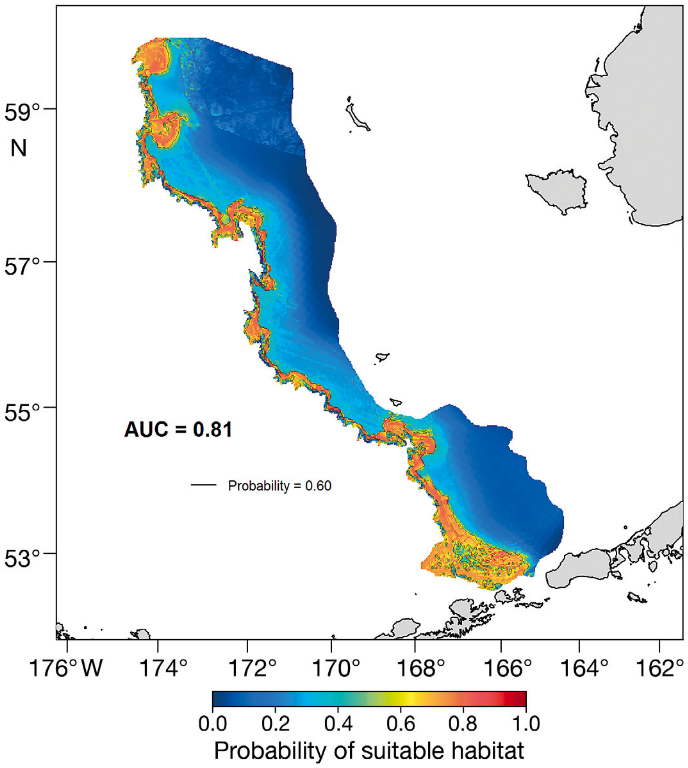

Fig. 5. Map of the best model of probability of suitable habitat for skates based on environmental variables, presence observations (n = 26) and absences for the eastern Bering Sea outer shelf and slope. Contour line: threshold probability (0.60) at which presence of suitable habitat was determined

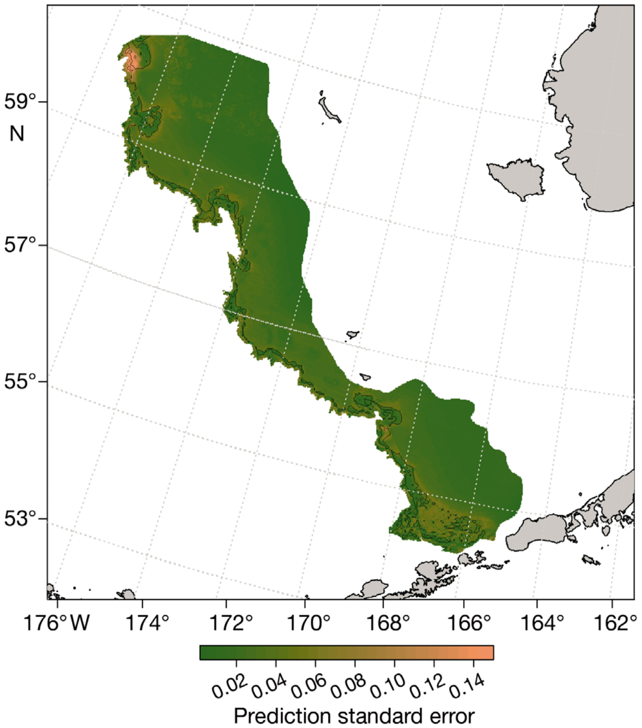

Fig. 6. Map of prediction error for models of probability of suitable habitat for skate nurseries. Prediction error was calculated as the standard error of the random 5-folds of data that were modeled

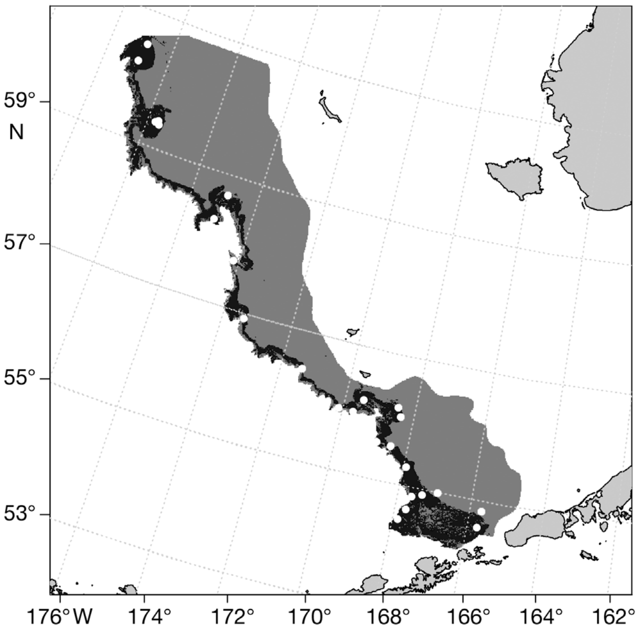

Fig. 7. Area of predicted suitable habitat for skate egg nursery areas based on a probability threshold of 0.60 (the probability where <10 % of observations of skate nurseries were misclassified). White circles: observed skate egg nursery areas; black area: predicted suitable habitat; dark grey area: predicted unsuitable habitat

interactions with other predatory species was also not considered in this analysis, because these data are not typically available on the scale of the eastern Bering Sea. Studies that address seasonal and stage-specific biotic interactions between skate eggs and their predators could be important to determining where successful skate egg nurseries are located.

There are few comparable observations or modeling studies of deep-water skate egg nursery habitats. Skate egg nursery sites have been found throughout the world's oceans in a wide range of seafloor conditions. Previously described egg nursery areas have been found to occur both on sandy substrates (Hoff 2008, 2010, Chembian 2010, Amsler et al. 2015), similar to the dominant sediment in the eastern Bering Sea slope (Rooper et al. 2016), and on rocky or hard-bottom substrates (Ross & Quattrini 2007, Love et al. 2008, Hunt et al. 2011). Skate egg nursery sites have

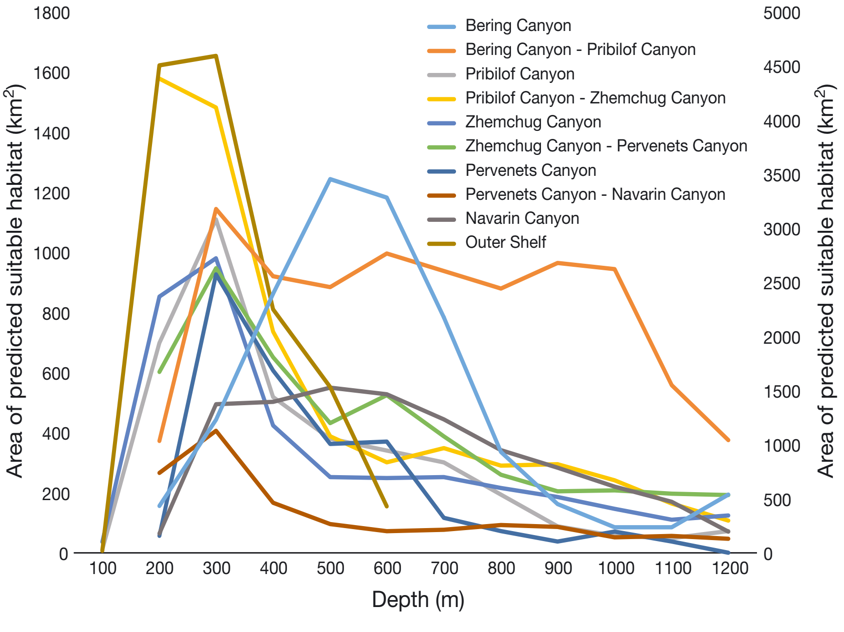

Fig. 8. Area of the eastern Bering Sea slope and outer shelf that is predicted to contain suitable habitat for skate nurseries by depth. The outer shelf area is plotted on the secondary axis. Lines refer to areas defined as in a canyon or between canyons. For example, 'Bering Canyon' is the area highlighted as Bering Canyon on Fig. 1 and 'Bering Canyon–Pribilof Canyon' is the area between Bering Canyon and Pribilof Canyon on the continental slopein Fig. 1

been found over a wide range of depths, from < 200 m (Chembian 2010) to even deep-water cold-seep sites > 700 m (Truede et al. 2011). In this study, only 1 of the 26 known egg nursery sites in the eastern Bering Sea occurred in substrates other than sand. However, sediment type was not found to be significant in our model, suggesting both that other sediment types are rare and possibly that the effect of sediment is less important than other habitat characteristics in the study area. Other studies of egg nursery sites for skates tend to be reports of singular occurrences of large skate egg concentrations (e.g. Love et al. 2008, Truede et al. 2011, Amsler et al. 2015). As such, we have found no large-scale modeling efforts such as performed in this study to which comparisons can be made.

One of the drawbacks of this modeling effort was the small sample size of known egg nursery sites. The small sample size forced us to combine presence records across species. The effect on the results of the analysis was largely in the broadening of the predictions of where suitability for skate egg nursery habitat was probable. For example, 2 of the species, the deep-sea skate *Bathyraja abyssicola* and the roughtail skate *B. trachura*, had nurseries that all occurred deeper than 600 m. These were deeper than the other skate species with egg nursery observations. Since most of the deep-sea and roughtail skate nurseries occurred between Bering and Pribilof canyons, the predicted depth distribution for potential egg nursery habitat in this region was generally deeper than in the rest of the regions (see Fig. 8). If these 2 species' nurseries were eliminated, the predicted area of total suitable egg nursery habitat was reduced by 36%, with the reduction coming almost entirely from deeper waters. Although some skate species in Alaska have been found to share common egg nursery areas (Hoff 2010), each egg nursery site appears to be dominated by a single species (Hoff 2008, 2010). Thus, combining across species undoubtedly reduced the accuracy of model predictions for any single species in the skate assemblage in the eastern Bering Sea. In interpreting the results of this study, this likely means that the overall distribution of skate egg nurseries may be over-predicted since species with deeper and shallower observed egg nurseries were combined in the modeling. Similarly, the variables available for modeling were generally derived from large-scale models or interpolations (e.g. the ROMS model outputs), and were not collected at the specific egg nursery sites. Interpolation of these variables to the skate egg nursery sites probably resulted in some error in model predictions and over-generalization of the conditions where skate egg nurseries were likely to occur. The prediction of the extent of suitable habitat for skate egg nursery sites in the eastern Bering Sea would benefit from an independent *in situ* survey to validate the model results.

Maximum entropy models are designed to utilize presence-only data (Phillips et al. 2006, 2017), and perform well in cases where the data do not strictly adhere to a sampling design (Elith et al. 2006). MaxEnt modeling has also been found to work well with small sample sizes of presence observations (Wisz et al. 2008, Piechaud et al. 2015), as is the case with skate egg nursery areas in the eastern Bering Sea. In this modeling effort, there were too few cases to fully evaluate the models using independent data, but by conducting model validation using random subsets of the data, we were able to portray uncertainty of predicted suitable habitat in space and evaluate model variable importance. During initial data exploration, statistical models (generalized additive models and general linear models) were fit to the presence–absence data; however, the residual patterns and fits even with a single explanatory variable (e.g. slope) were unacceptable. Two other approaches (random forest and boosted regression trees) were also attempted during data exploration. The model fits were similar and sometimes better than the MaxEnt fits for training data, but the models did not perform well in predicting out of sample data (during 5-fold cross-validation). Average AUC_{test} values were 0.546 for boosted regression tree models and 0.724 for random forest models, compared to 0.762 for MaxEnt (from Table 3). This would indicate that the random forest and boosted regression tree models overfit the training data, likely due to the small number of presence observations in the data set (Elith et al. 2006, Moore et al. 2016). In an evaluation by Wisz et al. (2008), it was found that MaxEnt was one of the best performers at small sample sizes (even compared to tree-based techniques). In addition to the low number of presence observations and disparate survey sampling designs, one of the reasons for utilizing MaxEnt modeling for this data set was the relative difference in detectability of skate egg nursery areas between the bottom trawl gear and the 3 underwater camera surveys. The bottom trawl survey and the Rooper et al. (2016) camera survey both utilized stratified random sampling designs, but the strata were different. The Miller et al. (2012) survey had a haphazard design that focused on areas with presumed higher probability of deep water coral and sponge presence. In addition, the detectability of skate egg nursery areas for the camera surveys is likely equal to 1, as the seafloor is directly examined for skate egg cases. However, the detectability of skate egg cases for the bottom trawl is probably somewhat less than 1. Combining these different types of data required a modeling method such as MaxEnt that is less sensitive to zero-inflation (than a generalized linear model or other statistical method), detectability differences among gear types and sampling design. These characteristics of the data, as well as the predilection of maximum entropy modeling to overpredict the area of suitable habitat and the conservative probability threshold used in this study, should all be considered when interpreting these results.

Skates in the eastern Bering Sea are captured as bycatch in commercial fisheries (Stevenson & Lewis 2010) and skate egg cases are regularly encountered in commercial trawl and longline fisheries (Stevenson et al. 2019). Although overall, populations of skates have been stable over recent times (Ormseth 2017), their interactions with changing spatial patterns of fishing is a potential concern. The results of this study could be useful for identifying areas where management measures to protect skate egg nursery habitat could be effectively applied through fishing closures or exclusion zones. Evidence from previous skate egg nursery studies shows that they are persistent across years in the same locations along the continental slope (Hoff 2008, 2010). These canyons along the eastern Bering Sea slope tend to be areas of high productivity (Springer et al. 1996) and concentrated commercial fishing activity, with ~35–40% of total US landings taken from this area in terms of walleye pollock *Gadus chalcogrammus* alone (Voorhees et al. 2016). The most important implication of this modeling study for conservation of skates in the eastern Bering Sea is that there is a fairly limited area of the upper continental slope where conditions would support potential skate egg nursery areas relative to the broader expanse of the eastern Bering Sea continental shelf and slope. However, within the upper slope, the model predicts that potential skate egg nursery habitat is broadly distributed in a narrow band at depths from about 200–400 m. Areas with the highest probability of suitable skate egg nursery habitat tend to occur in isolated areas at the heads of underwater canyons. Spatial management for existing skate egg nursery areas has included identification of HAPC sites, with no protection measures implemented. A recent analysis of bycatch data indicated that fishing gear is being deployed in and near skate nursery sites, including those designated as HAPC (Stevenson et al. 2019). The interaction of the spatial footprint of commercial fishing and the potentially limited areas for successful reproduction and recruitment for skate species should be considered for future management of the eastern Bering Sea.

As a corollary, more egg nursery areas will likely be found in future years, as the upper continental slope is relatively unexplored by bottom trawl or underwater camera surveys. To date, only 2 underwater camera surveys have been conducted in the area that could potentially encounter skate egg nursery areas (Miller et al. 2012, Rooper et al. 2016), and both of these camera surveys found new skate egg nursery areas. In a typical survey year only about 130 bottom trawl survey stations are sampled on the eastern Bering Sea slope at depths from 200–500 m, each covering about 0.45 km^2. This equates to about 900 yr of bottom trawl surveys required to explore the entire area of potential skate egg nursery habitat identified in this modeling. For camera surveys, the area covered to date has only been 0.28 km^2 (in a 28 d survey), which equates to about 5.4 million d (>14 500 yr) of camera surveys necessary to cover the area of potential skate egg nursery habitat. Further research that can be used to refine the boundaries of potential skate egg nursery habitat by species is clearly needed. The methodologies and models used here can easily be transferred to management issues arising from the need to conserve fish and invertebrate habitat in other regions of the globe where limited data are available to guide decision making.

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