

## RESEARCH ARTICLE

# Predicting the foraging patterns of wintering Auks using a sea surface temperature model for the Barents Sea

Samuel Hodges<sup>1</sup>  | Kjell Einar Erikstad<sup>2</sup> | Tone Kirsten Reiertsen<sup>2</sup>

<sup>1</sup>Independent Researcher, Leeds, UK

<sup>2</sup>Norwegian Institute for Nature Research, FRAM Centre, Hjalmar Johansen's Gata, Tromsø, Norway

## Correspondence

Samuel Hodges, 41 St. Ann's Lodge, St. Ann's Lane, Kirkstall, Leeds, United Kingdom, LS4 2SJ.

Email: [sam.jir.hodges@btinternet.com](mailto:sam.jir.hodges@btinternet.com)

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## Abstract

1. The conservation of seabirds is increasingly important for their role as indicator species of ocean ecosystems, which are predicted to experience increasing levels of exploitation this century. Safeguarding these ecosystems will require predictive, spatial studies of seabird foraging hotspots. Current research on seabird foraging hotspots has established a significant relationship between probability of presence and several environmental variables, including Sea Surface Temperature (SST). However, inter-annual, basin-wide variation has the potential to invalidate these models, which depend on seasonal mesoscale variability.
2. In this study, we present a novel solution to predict presence from spatially and temporally variable environmental predictors, while reducing the influence of large-scale basin-wide variation. We model the Maximum Entropy (MaxENT) Model-derived relationship between Standardized Monthly SST (StdSST) and Habitat Suitability using Gaussian curve models, and then apply these models to independent StdSST data to produce heatmaps of predicted seabird presence.
3. In this study, we demonstrate StdSST to be a functional environmental predictor of seabird presence, within a Gaussian curve model framework. We demonstrate accurate predictions of the model's training data and of independent seabird presence data to a high degree of accuracy (area under the receiver operator characteristic curve > 0.65) for four species of Auk: Common Guillemots (*Uria aalge*), Razorbills (*Alca torda*), Atlantic Puffins (*Fratercula arctica*) and Brunnich's Guillemots (*Uria lomvia*).
4. We believe that the methodology we have developed and tested in this study can be used to guide ecosystem management practices by converting coupled-climate model predictions into predictions of future presence based on Habitat Suitability for the species, allowing us to consider the possible effects of climate change and yearly variation of SST on foraging seabird hotspots in the Barents Sea.

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## KEYWORDS

Atlantic Puffin, Barents Sea, Brunnich's Guillemot, Common Guillemot, ecological modelling, MaxENT, Razorbill, spatial ecology

## 1 | INTRODUCTION

The Barents Sea is an important ecological region for seabirds which has come under increasing threat from mineral exploitation (Erikstad et al., 2016; Moreno et al., 2013). Scientists have expressed concerns of possible oil spills and the long-term damage this could cause to the Barents Sea ecosystem (Erikstad et al., 2016; Husson et al., 2020; Jakobsen & Ozhigin, 2011; Skov et al., 2021).

Seabirds are of special interest to marine and coastal conservation as they are usually *k*-selected species, with a low reproductive rate and high mortality at the juvenile stage, when they undergo transition from parental care to independent foraging (Schreiber & Burger, 2001; Hamer et al., 2001). They also subsist at the upper trophic levels of the Barents ecosystem, which are the most affected by ecosystem instability (Thorne, 2010; Cox et al., 2016). This makes their populations vulnerable to extreme events, both natural (Fayet et al., 2017; Grémillet et al., 2015) and anthropogenic (Krüger et al., 2017).

Of the seabirds present in the Barents Sea, four species of the Auk family are particularly vulnerable to an oil spill disaster: Common Guillemots (*Uria aalge*), Razorbills (*Alca torda*), Atlantic Puffins (*Fratercula arctica*) and Brunnich's Guillemots (*Uria lomvia*) (Figure 1) (Fauchald et al., 2015; Jakobsen & Ozhigin, 2011). This is because during the non-breeding season (wintering season), these birds are foraging at sea while supporting a single, flightless chick (Jakobsen & Ozhigin, 2011; Harris et al., 2015). They forage during this period for small fish such as Capelin (*Mallotus villosus*) and Sandeel (*Ammodytes marinus*) by pursuit diving (Anderson et al., 2014; Waggitt et al., 2016).



**FIGURE 1** The Auk species used in this study: from left to right, top to bottom—Common Guillemot, Razorbill, Puffin and Brunnich's Guillemot. These are pelagic diving birds with excellent swimming skills and limited capacity for flight. They are semi to fully colonial breeders and lay a single egg per season (Gaston & Jones, 1998).

Oil spill pollution events can cause their wings to become oiled and prevent flight or diving, which leaves individuals unable to forage: resulting in catastrophic increases in adult and juvenile mortality rate (Riffaut et al., 2005; Troisi et al., 2006).

Oiling can occur as a result of industrial and shipping accidents, for example during extraction or transport (Troisi et al., 2006). It would be useful for future policymakers to be aware of seabird occupancy ranges when planning mineral exploitation and shipping lanes in order to minimize the ecological risks of these activities and support sustainable use of the Barents Sea ecosystem (Fifield et al., 2017; McGowan et al., 2013). Spatial modelling is essential to establish occupancy ranges over the non-breeding period, as direct observations of seabirds are limited due to their dispersal over wide ranges and field research at sea is too infrequent over the winter period (Humphries, 2015; Burger & Shaffer, 2008). Relying on observational data would result in biased sampling toward areas with a higher observer count (e.g. coastline, shipping lanes, oil rigs).

A technique that has been widely used in previous studies is to combine remote logging with presence-only modelling (Boyd et al., 2015; Skov et al., 2016; Phillips & Dudik, 2008). In this method, Geo-Location Sensors (GLS) are used to record daily seabird positions (Wakefield et al., 2009; Burger & Shaffer, 2008). After retrieval, these records can then be combined with ocean conditions obtained from observations, an ocean model or a combination of both to explore covariance of presence with physical oceanography (de Grissac et al., 2017; Gomez & Cassini, 2015; Thorne, 2010). This is consistent with the known ecology as the spatial distributions of Salinity and Sea Surface Temperature (SST) have been linked to the formation of plankton concentrations by previous studies (Sarma et al., 2018; McManus & Woodson, 2012), which in turn impact species distributions at higher trophic levels (Thorne, 2010; McGowan et al., 2013).

Previous studies have used the presence-only program MaxENT to analyse presence and environment data to produce landscapes of Habitat Suitability, which is a transformation of the Relative Occurrence Rate (ROR) of an organism across a given domain (Merow et al., 2013). MaxENT has been used in previous studies to determine species ranges in data-deficient regions (Royle et al., 2012; Çoban et al., 2020), including at sea (Shahparian et al., 2017; Nachtsheim et al., 2017). MaxENT has been the preferred choice for some studies thanks to its user-friendly output and low requirements of user scripting knowledge (Yackulic et al., 2013; Merow et al., 2013).

A particularly noteworthy set of previous studies have proposed a new type of presence model in order to assess the risks to seabirds from possible oil spills in the arctic (Skov et al., 2016; Skov et al., 2021) using a combination of hydrodynamic, dynamic Habitat Suitability and agent-based modelling. However, we remain concerned around their use of raw oceanographic variables such as SST inside these models.

Salinity and SST are environmental predictors that are prone to large inter-annual variation at the basin scale (Serykh & Kostianoy, 2019). This effect can mask spatial variability associated with mesoscale fronts and underwater topography (Warwick-Evans et al., 2016), which frequently form the basis for Habitat Suitability modelling at sea (Scales et al., 2014; Thorne, 2010). This is because ocean fronts promote nutrient mixing and plankton formation which attracts organisms from higher trophic levels, including our study species (Thorne, 2010; McManus & Woodson, 2012). As climate change progresses, particularly as the Arctic sea ice cover declines, it is likely that inter-annual change in Salinity and SST will become more pronounced over time (Long & Perrie, 2017; Oziel et al., 2016; Serykh & Kostianoy, 2019), potentially invalidating models which do not account for this variation in their environment data input.

The hypothesis of this study is that Spatially Standardized SST (StdSST) is a better environment predictor of Habitat Suitability than raw SST. To test this, we have the following two aims.

The first aim is to explore the prediction capabilities of Habitat Suitability models, based on response curves generated by Maximum Entropy Modelling using the MaxENT software and raw SST and StdSST as the environment predictors and whether spatial standardization removes the effect of inter-annual variability in the SST data, improving the performance of the Habitat Suitability models.

Our second aim is to develop a tool to produce predictive models from MaxENT-generated response curves that can be used to make dynamic predictions of monthly seabird presence from independent SST data. This tool will allow us to test the accuracy of models based on raw SST or StdSST (code listed in File S1) and generate maps of future seabird occupancy ranges (code listed in File S2).

## 2 | MATERIALS AND METHODS

### 2.1 | Seabird geolocation data

The species used in this study were Common Guillemots (*Uria aalge*), Razorbills (*Alca torda*), Atlantic Puffins (*Fratercula arctica*) and Brunnich's Guillemots (*Uria lomvia*) (Figure 1). All four species are members of the Auks, a family of pursuit-diving seabirds which spend the majority of their lives at sea (Gaston & Jones, 1998). While these species are ecologically distinct in prey choice and foraging habitat in the Barents Sea, all are mutually threatened from ecological stress caused by human activity, such as oil spills and overfishing (McGowan et al., 2013; Fifield et al., 2017). We also believe that SST significantly influences the foraging habitat of all four species, although we recognize the independence of their niches in this study by constructing species-specific models (St. John Glew et al., 2019).

Whilst GLS data could be used from SEATRACK, due to issues of licensing, we were only able to work with data produced directly by the Norwegian Institute for Nature Research (NINA; SEAPOP, 2014). Further, the analytical experiment needed to be kept as simple as possible while we established our basic model structure and dataflow. For these

reasons, the study was restricted to studying data from the Hornøya colony (70.39N, 31.56E).

The geospatial data for each seabird species (Figure 1) used in this study were obtained using GLS: these approximately determine positions using established knowledge of sunrise and sunset (Burger & Shaffer, 2008; Christensen-Dalsgaard et al., 2018; Wakefield et al., 2009). GLS are used extensively by organizations undertaking seabird spatial studies, including NINA, which forms a part of the SEATRACK program to bring together seabird tracking data sets from across the northern polar regions (SEAPOP, 2014). A summary of the presence data used in this study is provided in Table S1, which shows the number of records by species and month.

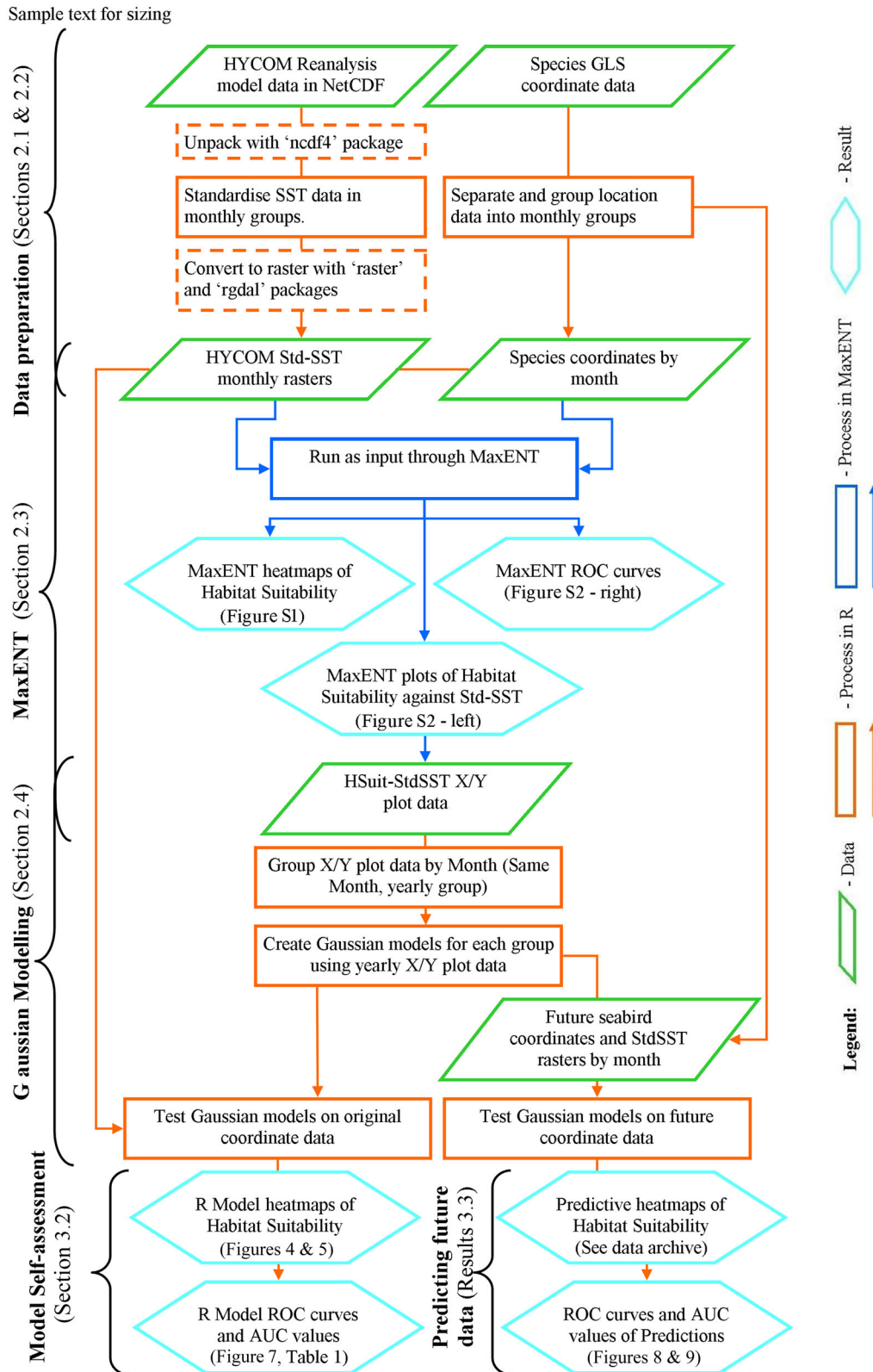
GLS have advantages over GPS trackers in presence studies because they are easier to miniaturize and do not consume power as rapidly as a GPS system (Humphries, 2015; Burger & Shaffer, 2008). This allows for measurements to be taken over an extended period of time (up to 3 years or more) and can be easily attached and retrieved from individual birds, with no significant impairment of their flight or swimming abilities (Wakefield et al., 2009; Burger & Shaffer, 2008). The drawbacks of GLS are their reduced accuracy compared to GPS, and they require manual retrieval of data from the loggers (similar to mark-recapture studies) (Burger & Shaffer, 2008). The mean and standard deviation of GLS error was estimated to be  $186 \pm 114$  km (1.66 degrees of Latitude) in a previous study (Phillips et al., 2004). While imprecise for a fine-scale foraging study, this is thought to be of low impact for a broad study of spatial Habitat Suitability (Phillips et al., 2004), given that the analysis is primarily influenced by presence clusters.

The GLS data were sorted into monthly groups to account for limited daily data and to reduce the computational complexity in our later modelling (Figure 2, Data Preparation). The GLS data contained all months from August to April, excluding September and March, as the differences in time between sunrise and sunset over latitude is greatly reduced, causing small errors in the logger's light detection to create increasingly larger errors in positioning before and after the equinoxes (Wakefield et al., 2009; Bindoff et al., 2018).

As the seabird wintering period lasts from August to April (time of leaving the colony to the time of return for nesting), we find it more useful to discuss our data and results in terms of 'Cycles' instead of years (e.g. 2011/2012, not 2011 or 2012), to more accurately reflect the seasonal patterns of the study species. Where single years are noted, it is only for a specific month in the cycle (e.g. August 2013 is the first month of cycle 2013/2014).

### 2.2 | Environmental data and standardization

The environment data used in this study come from the Hybrid Coordinate Ocean Model (HYCOM) database: HYCOM reanalysis/analysis data are a homogeneous physical oceanography global data set in space and time (Dobrynin & Pohlmann, 2015; Wallcraft et al., 2009; HYCOM, 2022). HYCOM reanalysis/analysis data are produced by combining inhomogeneous observations with a short-range forecast from a global ocean model at 1/12 degree horizontal resolution



**FIGURE 2** A flowchart describing our methodology. References to other figures, tables and sections of this paper are included in this figure to highlight where this stage of the processing chain is relevant. The data used in each stage of the process are wholly reproduced in our data archive (link included in the DATA AVAILABILITY STATEMENT).

using data assimilation (Wallcraft et al., 2009). Observations assimilated include surface observations from satellites, XBTs (expendable bathythermographs), CTDs (conductivity temperature depth), Argo floats and moored buoys for temperature and salinity (Wallcraft et al., 2009).

We used both re-analysis and analysis SST and Salinity data on a 0.08-degree uniform interpolated grid from the GLBu0.08 database (HYCOM, 2022). Re-analysis data were used from the beginning of 2011 to the end of 2012 and after this point only operational analysis data were available. We used these data to produce ASCII rasters of the monthly averages for each variable to correspond with our seabird tracking data (Figure 2, Data Preparation). The suitability of both variables for presence modelling was evaluated during MaxENT model exploration.

To address the problem of inter-annual basin-wide variation in SST, in this study we consider Spatially Standardized SST (StdSST) over a fixed space representing the Barents Sea. This is calculated by subtracting the spatial mean and dividing by the spatial standard deviation computed over the selected domain for each data point for each month. The domain (65N–77N, 10E–60E) was chosen to encompass the Barents Sea and the majority of the seabird presence data available, excluding a small number (<20 per species per month) of points that were outside the domain.

### 2.3 | Application of MaxENT

MaxENT is probabilistic spatial modelling software that is used in ecological studies to determine species occupancy ranges when working with limited observational data (Morales et al., 2017; Merow et al., 2013; Royle et al., 2012). It is an input–output program that analyses the covariance of environmental data with species presence data to produce probability of presence outputs; this is done by comparing points of known presence against a randomly sampled set from the data (BCCVL, 2019; Merow et al., 2013).

We used MaxENT to produce response curves of the Relative Occurrence Rate (ROR, Raw output) and Habitat Suitability (ClogLog output) against SST and StdSST (Figure 2, MaxENT). The ROR functions as an estimate of the probability of a presence record appearing in a given raster square out of the whole domain, whereas Habitat Suitability is a complementary log–log transformation of ROR that approximates the probability of presence independently from the rest of the domain (Merow et al., 2013).

MaxENT also produces Receiver Operator Characteristic (ROC) curves and raster plots of Habitat Suitability, which are useful for MaxENT model assessment (Figures S1 and S2). These are also useful for comparison with the corresponding output of the R tool developed in this study, to check for loss of accuracy. While ROC curves are traditionally associated with presence–absence data in biological studies (Lobo et al., 2008), they functionally represent the true positive to false positive rate of Habitat Suitability predictions, and therefore do not require absence data (Robin et al., 2011).

Multiple MaxENT runs were performed based on the settings we have summarized in File S3 (Final MaxENT settings). The settings were chosen based on previous studies (Merow et al., 2013; Royle et al., 2012; Morales et al., 2017) and early findings from our exploration of model types. MaxENT offers a range of feature classes to model background–presence response curves. Feature classes are mathematical transformations of the environment variable prior to MaxENT's response curve model fitting, which affect the shape and complexity of the response curve output (Phillips & Dudík, 2008). MaxENT provides Linear (L), Quadratic (Q), Product (P), Threshold (T) and Hinge (H) as selectable features, which can be used alone or in any combination (Phillips & Dudík, 2008; Merow et al., 2013). To decide which combination of MaxENT features is most appropriate for modelling seabird presence with SST or StdSST, we performed model runs for all possible MaxENT feature combinations, using a sample of the 3 months with the greatest number of seabird presence records per species. We found that of the possible combinations, Threshold-features-only was the most frequent best-fit for the model, in terms of area under the curve (AUC) of the ROC curve (Sonego et al., 2008). The exceptions where Threshold-features-only was not the best-fit according to AUC always contained Threshold features as a component and Threshold-features-only always appeared in the top 10 combinations for every month sampled (Tables S2 and S3).

MaxENT can also produce models using multiple environment predictors, and in the beginning of the study we considered using models based on Salinity and SST; however, Salinity was found to only play a significant role in foraging zone selection when SST was a poor predictor. This was established through jackknife tests in MaxENT using the same sampling method we used in feature testing (Figure S3) (Gomez & Cassini, 2015; Baldwin, 2009). Salinity-dominant models were also found to be infrequent in these tests, so we decided to focus the study on a comparison of StdSST and SST models.

### 2.4 | Gaussian modelling of habitat suitability

#### 2.4.1 | Hindcast and forecast modelling

The MaxENT model outputs are suitable for assessing species occupancy ranges if we assume that the spatial patterns of the environmental predictors are stable over time; however, the variation of SST is highly dynamic (Wege et al., 2021; Kowalczyk et al., 2015; Pendleton et al., 2020). This means that MaxENT models can only provide reliable estimates of occupancy in the same period as their training data. However, the relationship between the environmental predictor and Habitat Suitability remains relevant if a consistent pattern over time can be found. The response curve data can then be extracted from the model output and used to determine Habitat Suitability in independent environment data.

We created an R tool to produce models of the response curve data (Files S1 and S2), by computing fits to a Gaussian function which can then be used to produce Habitat Suitability rasters from independent

SST or StdSST data (Figure 2, Gaussian Modelling). The function can then be used with environmental data where seabird presence data are unavailable to make predictions of species occupancy ranges (File S2). We decided from a visual inspection of the response curve shapes to use a Gaussian model for our R tool (Figure S4).

We explored two principle approaches for how to apply the modelling technique: monthly groups (e.g. all Augusts) and cycle groups (e.g. all August to April periods). Cycle groups appeared to have low coherence in the location of their response curves in terms of SST/StdSST; however, monthly groups showed good coherence across cycles (Figure S5) and are therefore easier to model. This also suited the aims of the study to explore spatial variability of Habitat Suitability over inter-annual periods. We tested this tool on single-response curves first. However, we found through statistical analysis, that is Analysis of Covariance (ANCOVA), that the resulting predictions could be sensitive to our choice of response curve to produce the model (ANCOVA, StdSST  $p = 0.055$  and SST  $p = 0.005$ ); thus, we decided to group response curve data by month and to produce a single best-fit response curve.

Hindcasting used monthly groups of response curve data to solve for the Gaussian model coefficients and then used the resulting model to predict the original seabird presence data used in MaxENT model training. This was done by generating a Habitat Suitability landscape using the R model and then comparing against records of seabird presence. The model output contained a Habitat Suitability raster plot with seabird presence data overlaid, an ROC based on the raster and an AUC value that summarizes the ROC curve, which are used to evaluate the performance of the model (Figures S1 and S2). These were produced for each month contributing a response curve. Model AUCs were tabulated and given a colour grade according to value.

Forecasting then followed on from the hindcast evaluation to test the model prediction capability using independent environment and species presence data; these were sourced from future cycles to those used in the model construction. The methods were otherwise similar to those used in hindcasting, with ROC curves and AUCs used as the main assessment statistic for model prediction accuracy. We were unable to test all species presence data in forecasting mode due to the aforementioned limited availability of seabird presence data for some species (no access to SEATRACK). For this reason, Common Guillemots and Razorbills were the only two species that have been tested in forecasting mode. We also conducted a series of statistical tests to assess any significant difference in AUC values between models produced using SST and StdSST, and the possible correlation of AUCs with several key model parameters, including Prediction Lag (length of time to time of prediction), Number of Model Response Curves used to train the model, Species and the Monthly Group. These were tested using paired  $T$ -tests (after an  $F$ -test to confirm homoscedasticity) and ANCOVA, respectively. Fligner–Killeen tests for homoscedasticity between non-parametric groups were used to test specifically for variability in AUC results, which would indicate that differences in model accuracy were linked to one or more dependent variable.

## 2.4.2 | R tool ‘GaussNpROC’

The R tool (Files S1 and S2) was written in R 4.0.5 with packages ggplot, pROC and sp (Wickham, 2009; R Core Team, 2019; Robin et al., 2011; Bivand et al., 2013). The tool fits a Gaussian model curve to a given monthly group of MaxENT response curves using the following equation:

$$f(x) = a \times \exp\left(-\frac{(x-b)^2}{2c^2}\right).$$

The above equation represents a standard function for a Gaussian curve or normal distribution. There are three coefficients:  $a$  (maximum value of  $f(x)$ ),  $b$  (the mean and median of  $x$ ,  $f(b) = a$ ) and  $c$  (standard deviation, controls the shape of the curve).

The three coefficients were calculated as follows: ‘ $a$ ’ was taken from the maximum of each response curve for Habitat Suitability and ‘ $b$ ’ from the corresponding values of SST/StdSST, both were then averaged. ‘ $c$ ’ was then calculated using a least squares approach to fit the model curve to the monthly group of response curves. Using this method with our monthly groups, we were able to generate models that described the relationship of SST or StdSST to Habitat Suitability for each month in the non-breeding season for each of our four species. We made the following assumptions when calculating model coefficients:

1. The MaxENT response curves all approximate a Gaussian function.
2. The MaxENT response curves in each monthly group are similar in height and width; that is there is no significant variation in coefficients between cycles for a particular month.
3. The mean of each MaxENT response curve is not significantly different to the median (minimal skew).

If the first assumption is violated, we would expect the model to be a poor fit to the true shape of the response curves and hence we would expect the prediction accuracy to be near random. This is the most serious assumption that might be violated, but the likelihood of this happening in biological response curves is low, unless a sampling intensity problem is present (Coudun & Gégout, 2006; Pepler-Lisbach, 2008). An exception to this is when the response curve is multimodal, which we discuss in Section 4. Violation of the second assumption can produce a similar effect, due to the model fit having large residuals, resulting in poor prediction quality (see Figure S4, SST). While this is not as serious a violation as the first assumption, it is more frequent and large violations were often responsible for poor model performance. The third assumption is equivalent to assuming that skew is insignificant. While it is theoretically possible to accommodate skew into the model, this has not been done at this stage and is left for future work. Skew can produce a noticeable impact in least squares fitting by causing under- and overshoot of the model on either side of the maxima. In practice, this produces similar results to a violation of the second assumption when considering residuals. However, the effects of skew were found to be limited in this study. Large differences between skew

in the monthly response curves would produce an impact, but this is more related to a violation of the second assumption. Ecological data are likely to produce some limited violations of these assumptions; however, as long as these violations remain small, we consider this to be tolerable.

## 2.5 | Model assessment using ROC curves and AUCs

To quantify the accuracy of MaxENT and the Gaussian models developed using the R tool, we have used ROC curves and their AUC values throughout this study (Phillips & Dudík, 2008; Sonogo et al., 2008). The quality of the models was assessed in the hindcast phase using the following thresholds:  $AUC < 0.65$  is considered to indicate near-random association between predicted Habitat Suitability and seabird presence data,  $AUC > 0.80$  is considered to indicate that they are highly correlated and  $0.65 < AUC < 0.80$  indicates an imperfect but still correlative association. These AUC values were tabulated and colour coded corresponding to their threshold group in Table 1. We also used this framework to inform our interpretation of the forecasting results, though this part of the analysis was more focused on exploring correlations between AUC and the dependent variables of the model predictions defined earlier.

To make the ROC curves using the R tool, we paired the predicted Habitat Suitability with a Boolean variable that indicates species presence (Robin et al., 2011). The ROC curves are then produced by varying the discrimination threshold, or the minimum Habitat Suitability required for a positive identification of seabird presence (Robin et al., 2011). This is then compared with the Boolean of confirmed presences to produce the ratio of true positive to false positive identification for a single threshold, which corresponds to a single point on the ROC curve (Robin et al., 2011). The true positive rate corresponds to the Sensitivity axis on a ROC curve and the false positive rate corresponds to  $1 - \text{Specificity}$  (Robin et al., 2011). The latter would theoretically require the true negative rate; however, it can be calculated empirically from the observed false positive rate (Robin et al., 2011).

The AUCs are calculated from the resulting ROC curve using trapezoids, and approximate the probability of finding a true positive event associated with higher values of Habitat Suitability (Robin et al., 2011). While AUCs have been traditionally employed in bioinformatics to assess model performance (Sonogo et al., 2008; Hanczar et al., 2010), they must be interpreted with care, as the AUC value represents an integral of all possible discrimination thresholds (Lobo et al., 2008), but a single threshold will likely be used to interpret the model output (Lobo et al., 2008). However, we argue that this does not make AUCs unusable as suggested by some (Lobo et al., 2008), instead we suggest interpreting AUC as the prediction efficiency of the model. Higher efficiency is indicated by the appearance of high true positive to false positive rate under the lower end of the range of discrimination threshold values.

## 3 | RESULTS

### 3.1 | Standardization of SSTs and the effects on basin-wide inter-annual variation of cycle data

In comparison to SST, StdSST shows a reduced inter-annual variability, which we later show impacts this variable's ability to predict AUC values, especially when introducing time lags into the model for prediction (see Section 3.3). This is shown in Figure 3 where the StdSST can be seen to reduce the impact of inter-annual variability on cycle dissimilarity compared to SST by centring values associated with seabird presence within a consistent range between cycles.

### 3.2 | Hindcasting and model testing

Our initial hypothesis that seabird occurrence is better explained by a regionally standardized form of SST is highlighted by our results shown in Figures 4–6, which shows the difference in Habitat Suitability between StdSST and SST for August 2013 overlaid with presence for our four species. This shows that presence records are more likely to be found in regions of high Habitat Suitability produced by models using StdSST (Figure 4), whereas models using SST omit a large quantity of the records (Figure S6). This appears to be due to inter-annual variability caused by abnormal warming of the Barents Sea, which in raw SST models causes a poleward shift in predicted Habitat Suitability that is not reflected by the spatial distribution of the presence data (Figure 5).

Hindcasts using Gaussian models based on StdSST response curves produce significantly higher AUC values than models based on SST (one-way paired *t*-test,  $p = 0.007$ ; *F*-test,  $p = 0.540$ ). The mean difference between SST- and StdSST-produced AUCs is approximately 0.01; however, differences between the paired AUCs ranged up to 0.27 in favour of StdSST (see Table S4). The case for StdSST is further supported through comparison of ROC curves generated by StdSST and SST models during anomalous years (Figure 6), which show that models based on StdSST have a higher true positive to false positive rate for lower discrimination thresholds.

Of the AUC values produced, neither SST or StdSST was commonly found to drop below the near-random threshold ( $AUC < 0.65$ ) that we set except for Brunnich's Guillemot models (Table 1). In several cases, higher AUC values were obtained ( $AUC > 0.80$ ) indicating a strong relationship between predicted Habitat Suitability and seabird presence (Table 1). This confirms that temperature is a critical component of species prediction.

Of the four species studied, the Common Guillemot and Razorbill spatial distributions seem to work best with our modelling technique (Table 1), Puffin models perform less well but are still useful and Brunnich's Guillemot models frequently produce poor AUCs. Although Razorbill models perform well, their response curves were occasionally found to be multi-modal, which possibly indicates that these species split into a number of foraging sub-groups that select for different

**TABLE 1** AUC evaluation values (model accuracy) of ROC curves for hindcast Habitat Suitability from our response curve models compared against seabird presence

<b>Sea Surface Temperature</b>							
<b>Common Guillemot</b>							
Cycle	August	October	November	December	January	February	April
2011/2012	0.805	0.765	0.819	0.811	0.864	0.889	0.920
2012/2013	0.772	0.782	0.808	0.787	0.811	0.843	0.853
2014/2015	0.624	0.825	0.786	0.780	0.827	0.888	0.921
<b>Razorbill</b>							
Cycle	August	October	November	December	January	February	April
2012/2013	0.815	0.869	0.884	0.769	0.751	0.834	0.739
2013/2014	0.474	0.877	0.857	0.744	0.720	0.851	0.918
2015/2016	0.673	0.862	0.830	0.791	0.729	0.823	0.852
<b>Puffin</b>							
Cycle	August	October	November	December	January	February	April
2012/2013	0.741	0.706	0.753	0.742	0.709	0.604	0.829
2013/2014	0.650	0.737	0.756	0.724	0.763	0.625	0.926
<b>Brunnich's Guillemot</b>							
Cycle	August	October	November	December	January	February	April
2012/2013	0.725	0.584	0.541	0.569	0.553	0.725	0.819
2013/2014	0.573	0.634	0.703	0.655	0.616	0.715	0.894
<b>Standardised Sea Surface Temperature</b>							
<b>Common Guillemot</b>							
Cycle	August	October	November	December	January	February	April
2011/2012	0.829	0.757	0.816	0.820	0.875	0.914	0.886
2012/2013	0.818	0.812	0.811	0.785	0.819	0.861	0.903
2014/2015	0.715	0.826	0.758	0.784	0.850	0.898	0.921
<b>Razorbill</b>							
Cycle	August	October	November	December	January	February	April
2012/2013	0.862	0.856	0.886	0.769	0.752	0.829	0.860
2013/2014	0.740	0.890	0.857	0.735	0.721	0.853	0.905
2015/2016	0.678	0.862	0.824	0.787	0.726	0.814	0.845
<b>Puffin</b>							
Cycle	August	October	November	December	January	February	April
2012/2013	0.774	0.707	0.764	0.711	0.719	0.607	0.874
2013/2014	0.756	0.733	0.760	0.735	0.759	0.621	0.914
<b>Brunnich's Guillemot</b>							
Cycle	August	October	November	December	January	February	April
2012/2013	0.674	0.598	0.543	0.571	0.552	0.729	0.865
2013/2014	0.638	0.627	0.706	0.657	0.619	0.709	0.858

Note: Blue shaded cells indicate models that made particularly accurate predictions, whereas red shaded cells indicate near-random association between Habitat Suitability and seabird presence, as indicated by the legend. Organized by model type, species, predicted cycle and the month of that cycle.

Legend	
>0.80	
>0.65	
<=0.80	
<=0.65	





**FIGURE 3** The effects of Spatially Standardizing Sea Surface Temperature (StdSST) data associated with Common Guillemot presence; blue-dashed bars represent mean upper and lower quartiles for Sea Surface Temperature (SST)/StdSST at locations where Common Guillemots are present during August. Left panel for SSTs and right panel for StdSSTs. The effect of standardization is to reduce inter-annual variability in SST between cycles, which increases the weight of spatial variability in response curve modelling.

regions with different temperature characteristics (see Hestem, 2019). Brunnich's Guillemot response curves contained a large degree of skew and some multimodality, probably due to the spread of their presence data; we believe that this violation of the first and third assumptions of our modelling is the cause of their low AUC values.

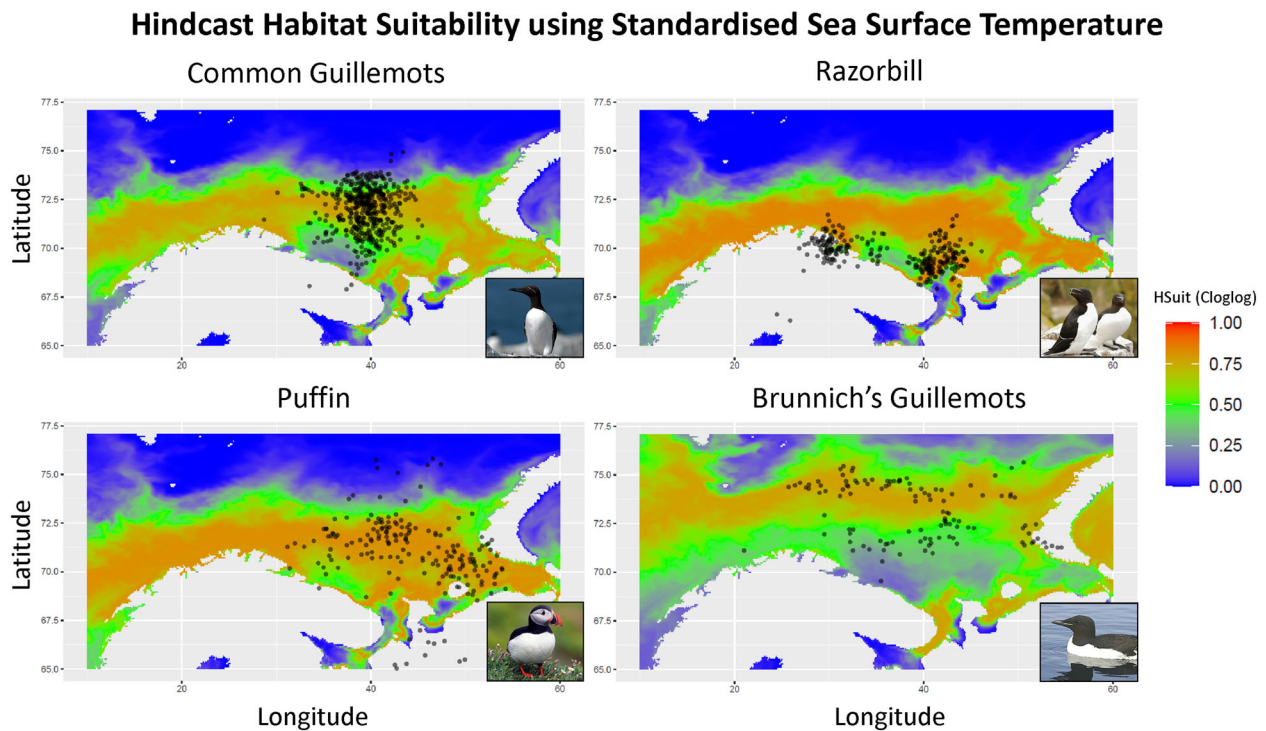
Due to these characteristics in response curve shape and presence clustering between species (Figures 4–6), this would indicate ecologically that Common Guillemots and Puffins are specialized foragers, repeatedly selecting regions with similar ecological and physical features to forage in. On the other hand, Brunnich's Guillemots and Razorbills behave opportunistically as evidenced by prevalence of multi-modality and skew (this behaviour was later verified for Razorbills by Hestem, 2019); however, this has a limited impact on Razorbill models owing to their coastal distribution, which is localized to the Norwegian Coastal Current.

### 3.3 | Forecasting

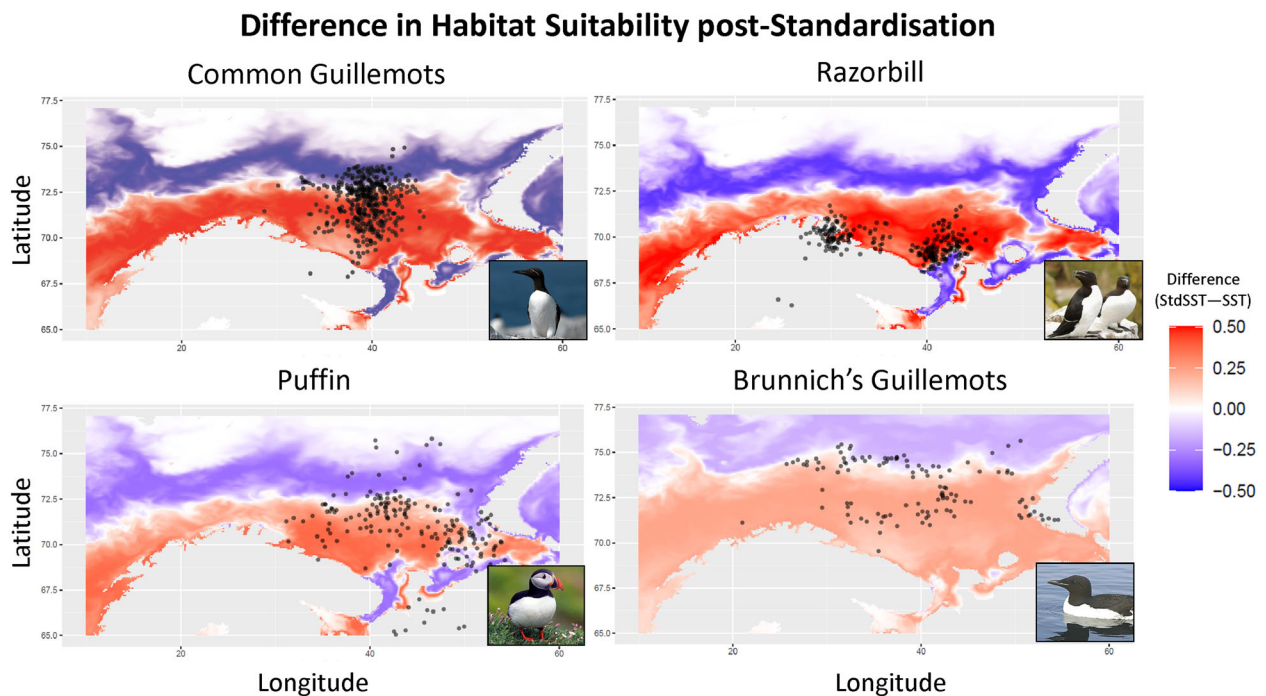
The AUC values from forecasting are high for all of StdSST (98.8% AUCs > 0.65) and a majority of SST models (81.0% AUCs > 0.65) (Table S5); therefore, the response curve model we are using is also capable of predicting future distributions of seabird presence. Forecast AUC

values were also found to be significantly different between StdSST and SST models (one-way paired *t*-test,  $p < 0.001$ ; *F*-test,  $p = 0.33$ ), with a greater mean difference compared to hindcasts (0.10 vs. 0.01 in favour of StdSST; Figure 7). Our analysis of covariance between AUCs and the dependent variables used in model construction (see Section 2) found no significant difference between Common Guillemots and Razorbills in StdSST forecasts (ANCOVA,  $p = 0.423$ ); however, significant difference did appear between these species for SST forecasts (ANCOVA,  $p < 0.001$ ). It was also found that the number of Model Cycles (MaxENT response curves) used did not produce any significant difference in AUC output in SST models (ANCOVA,  $p = 0.435$ ), although for StdSST models AUC difference was found to be close to significant (ANCOVA,  $p = 0.093$ ).

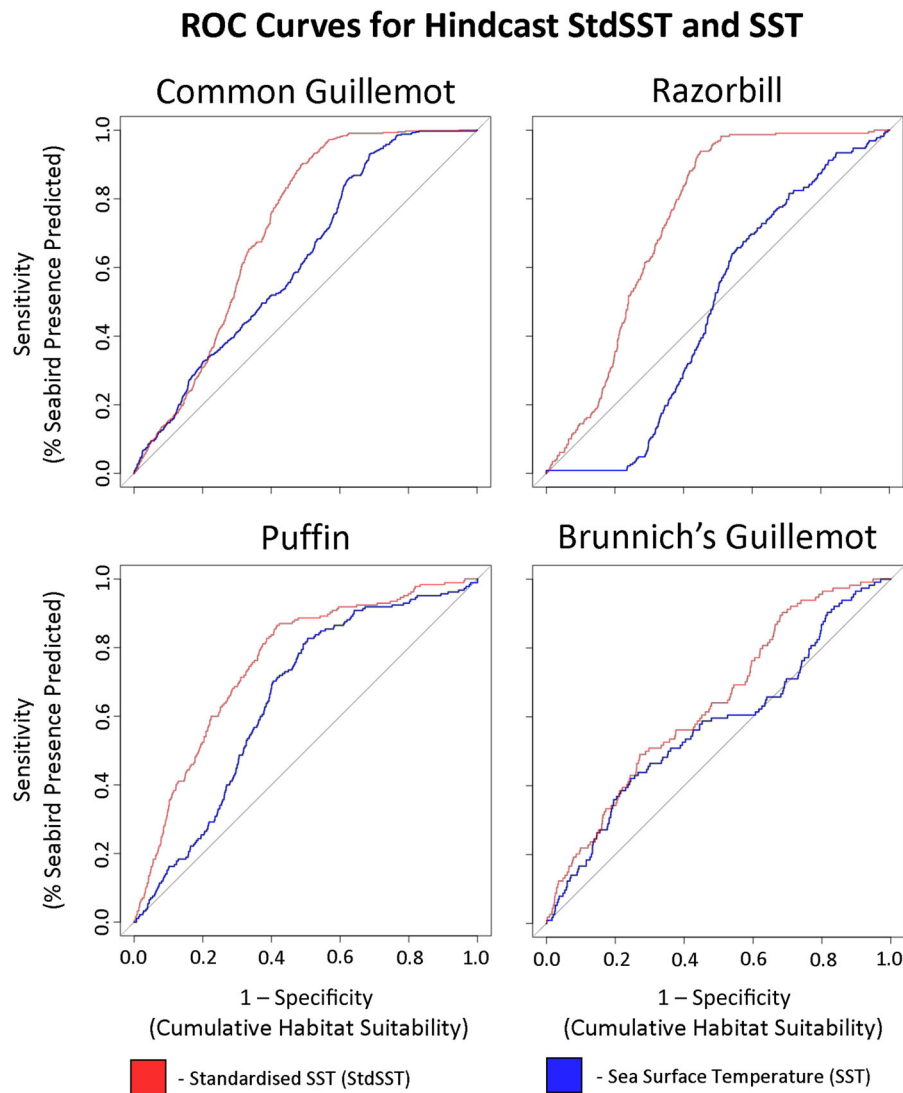
Time to Prediction (forecast lag) did not produce significant difference in median AUC values for StdSST models (ANCOVA,  $p = 0.693$ ); however, models based on SST experienced a significant loss in median AUC over time (ANCOVA,  $p = 0.040$ ) (Figure 7). There appeared to be a significant effect on the variance of StdSST AUCs due to quartile expansion with increasing Time to Prediction (Figure 7); however, both a variance test (Fligner–Killeen,  $p = 0.233$ ) and linear models of the upper and lower quartiles returned inconclusive results (Linear Model, Q1  $p = 0.100$  and Q3  $p = 0.213$ ). This indicates that the average quality of the predictions is preserved over time in StdSST models, while



**FIGURE 4** Heatmaps of hindcast Habitat Suitability using independently generated Spatially Standardizing Sea Surface Temperature (StdSST) models for each of the four study species. Influx of warm water from the North Atlantic Current appears to be the most important determinant of Habitat Suitability, closely followed by the Norwegian Coastal Current. The predicted month is August 2013, part of an anomalous cycle (2013/2014) of SST data. Dots represent Geo-Location Sensors (GLS) data for each species.



**FIGURE 5** Difference of Habitat Suitability between using Spatially Standardizing Sea Surface Temperature (StdSST) and Sea Surface Temperature (SST) (StdSST Cloglog - SST Cloglog). The StdSST models place greater importance on the southern regions of the Barents Sea, which tend to contain the centres of seabird Geo-Location Sensors (GLS) distributions. Predicted Month is August 2013, part of an anomalous cycle (2013/2014) of SST data. Dots represent GLS data for each species.



**FIGURE 6** Receiver Operator Characteristic (ROC) curves corresponding to the heatmaps shown in Figures 6–7. While both ROC curves based on using Spatially Standardizing Sea Surface Temperature (StdSST) (red lines) and Sea Surface Temperature (SST) (blue lines) response curve models indicate sufficient non-randomness for all species except Brunnich's Guillemots in this example, the StdSST curve performs better in all cases as it shows a greater rate of Sensitivity to 1 – Specificity at multiple positions on the graphs.

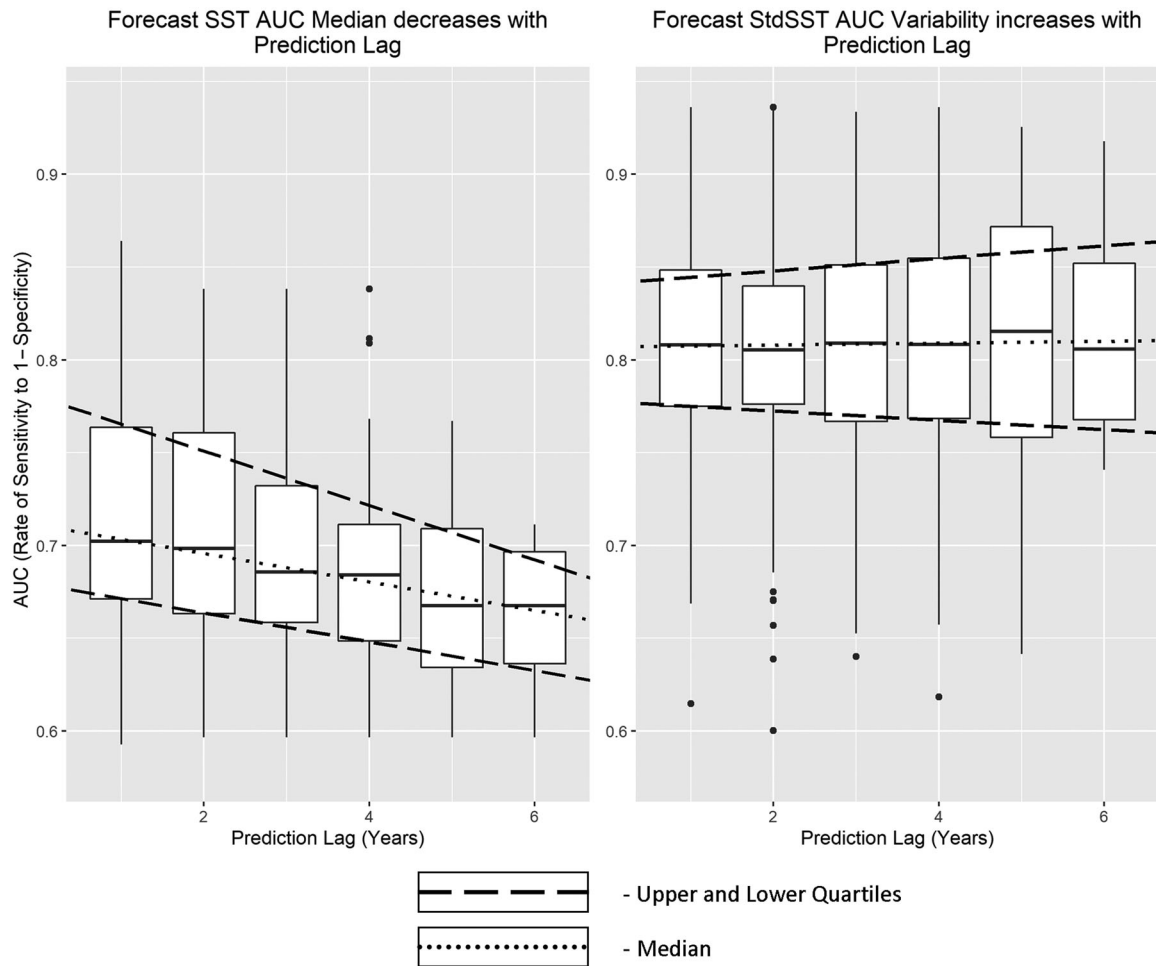
prediction quality in SST models decays significantly with every year of forecast lag.

We also discovered that the prediction capability increases rapidly toward the end of the wintering season in our forecast models (ANCOVA, StdSST and SST  $p < 0.001$ ). This is due to the birds migrating back to the colony to end their wintering season, which causes their presence distribution to be more clustered around the Hornøya colony. The quartiles of AUCs in StdSST forecasting models are wider in October and November (Figure S7) as this is during the middle of the wintering season, where presence clusters are most spread out across the Barents Sea. We observe an increase in median AUC over time in a cycle due to gradual localization and contraction of the GLS clusters to the immediate vicinity of Hornøya (see Data Availability Statement). Unequal variance was confirmed using the Fligner–Killeen

test for homoscedasticity across all the monthly groups of AUC in our forecasting (Fligner–Killeen,  $p < 0.001$ ).

## 4 | DISCUSSION

This study has shown that spatially standardized SST is a stronger environmental predictor than raw SST in predicting species presence for three of the four Auk species in our novel analytical framework, confirming our hypothesis. The study has produced response curve models for both StdSST and SST, for each individual species, and has demonstrated that StdSST is a better environmental predictor than SST (except for Brunnich's Guillemots). We believe that the main reason for the better performance of the StdSST models is their reduced susceptibility to inter-annual variability compared to raw SST



**FIGURE 7** The role of prediction lag in area under the curve (AUC) variability for Sea Surface Temperature (SST) (left) and Spatially Standardizing Sea Surface Temperature (StdSST) (right) models. Prediction lag is equivalent to the time in years from the last year used for model training to the year of the model prediction. We observe a stable trend in AUC for StdSST models and a decay in the quality of SST models. Dashed and dotted lines represent linear models of the quartiles and median of the AUC boxplots over time.

models. Inter-annual variability can affect the quality of predictions in models that do not account for it, as large temporal variability in the environmental training data can invalidate the response curves and impact the predictive power for anomalous months (Trevail et al., 2019; Kowalczyk et al., 2015; El-Gabbas et al., 2021). Inter-annual basin wide variability is particularly noticeable for cycles 2013/2014 and 2016/2017, which we identify as anomalous. This finding is confirmed by an oceanographic study of the region during spring 2014 which found that inflow from the North Atlantic Current was characterized by warmer and more saline conditions compared to historical observations (Dobrynin & Pohlmann, 2015). However, our generalized response curves are species dependent and in some cases show multimodality, causing a drop in AUC value. This is particularly common for Brunnich's Guillemots, rarely in Razorbills and occasionally for the other two species. It is possible that there is a better choice of function that can account for multi-modality and response curve skew, for example mixed gaussian models or *b*-splines.

The SST-Habitat Suitability models in our study show northward shifts under heightened SSTs (Figure S6). This might be in accor-

dance with long-term expectations for changing species ranges under climate change (Husson et al., 2020); however, the northward shift is poorly reflected in contemporary GLS distributions, which cluster around lower Latitudes, with the possible exception of Brunnich's Guillemots. This might indicate a decoupling or delayed response of species distributions to shifting climate zones.

Whilst we have used MaxENT to derive our response curves, it must be stressed that MaxENT itself does not make predictions (Merow et al., 2013; Guillera-Aroita et al., 2014). In fact, the use of SST or StdSST with MaxENT does not affect the shape of the generated MaxENT response curves, but does affect their location on a shared scale, and hence the Gaussian fitting of a generalized response curve (Figure S4). Standardization also does not generally affect the MaxENT AUC values, because there is no comparison of data across months, so inter-annual basin-wide variation does not appear in the MaxENT process, and standardization only affects the scale of the environment variable. Once predictions take place, in hindcasting or forecasting, standardization can have a noticeable effect by reducing the impact of inter-annual variation. Using StdSST for modelling and prediction

using these response curves results in better predictive power than an SST range taken directly from MaxENT due to the reduced influence of inter-annual variability. It should also be stressed that in presence-only models, a low Habitat Suitability value does not imply an absence of species presence, just a low probability-of-presence/preference.

Although the prediction models performed well, uncertainty is introduced through both the environmental data and the seabird geo-location in both the model training of MaxENT and the R tool models. The uncertainty in the environment variables comes from the HYCOM reanalysis/analysis, which provides our best four-dimensional view of the ocean state over a recent historical time period (Poli et al., 2017; Dobrynin & Pohlmann, 2015). The quality of the reanalysis is strongly influenced by how observations from multiple sources are distributed in space and time, as well as the ocean model and data assimilation which combines the observations with the model (Wallcraft et al., 2009; Dobrynin & Pohlmann, 2015). Limited sampling and geo-location error also contribute to uncertainty in our seabird data: geo-location errors can result from aberrant light-level recordings, and small variations in light level can translate to large deviations in position, especially around the time of the equinoxes, which is why March and September have been excluded from the analysis (Phillips et al., 2004; Bindoff et al., 2018). Uncertainty in our modelling is also related to minor violations of the three assumptions used in this study and most frequently appears as an imbalance in the residuals produced by the least-squares fitting.

This methodology has been applied solely to Auk species using the Barents Sea as a closed domain; however, it could also be applied to other species and other regions, including vulnerable marine mammals such as Baleen Whales, Ross Seals (*Ommatophoca rossi*) and dolphins in the Southern Ocean: several previous studies have demonstrated the importance of ocean thermal conditions to these species when seeking prey at depth by using MaxENT to model their occupancy ranges (El-Gabbas et al., 2021; Pendleton et al., 2020; Wege et al., 2021). These studies also benefit from the use of multiple environment variables which is not the case for this study (see Skov et al. [2021] and Krüger et al. [2017] for further examples of multiple environment variables in MaxENT model training). However, these studies do not consider the impact of inter-annual variability or long-term changes in the environment variables. Future work will also explore the use of salinity and temperature profiles in the type of model presented in this study, since these have been implicated in the distribution of fish shoals and plankton concentrations (de Grissac et al., 2017; Thorne, 2010; Cox et al., 2016), which directly impact the birds' foraging habits.

The potential for incorporating MaxENT output into further analytical stages has been made clear by another notable study (Krüger et al., 2017). While also oriented toward conservation study, the aims of the Krüger et al. (2017) study are divergent from our own, leading to clear differences in post-processing of MaxENT output. In particular, their study does not consider the impact of inter-annual variability on their models or conduct forecasts and instead focuses on moderating the value of Habitat Suitability with respect to the spatial variability of anthropogenic impacts across a wide range of species.

Our study confirms several reported characteristics of seabird wintering movements from past studies, including reliable repetition of monthly spatial patterns, species-specific site selection and gradual clustering of the population as the wintering season comes to an end (Scales et al., 2014; Cox et al., 2016; McGowan et al., 2013; Fauchald et al., 2015). It is unfortunate that there remains a large amount of variance in forecast model prediction capability during October and November, during the height of the wintering season and when the birds are ecologically most vulnerable (St. John Glew et al., 2019; Fauchald et al., 2015). This is likely due to their more dispersed distribution (Figure S7) and opportunistic foraging and avoidance of competition during these periods (Hestem, 2019).

We aim to reduce this problem in future work by refining our R tool with more complex modelling techniques to account for non-normal behaviour of the response curves, as described above. Addition of further seabird presence records to create a larger data range is also desirable to further explore the effect of more extended forecast lags on models based on raw SST and StdSST. We could also use the R tool developed in this study to look at a wider array of environment variables that are commonly used in modelling Habitat Suitability for upper trophic levels, such as sea ice extent and salinity, which have been used in marine mammal studies (El-Gabbas et al., 2021; Pendleton et al., 2020; Wege et al., 2021).

Past events have demonstrated the severe ecological impacts of oil spills from rigs and tankers on seabird populations (Fauchald et al., 2015; Fifield et al., 2017). The tool that has been developed in this study and evaluated for Auk species in the Barents Sea can also be used to inform marine protected area planning to protect such vulnerable species against the possibility of industrial disasters (Krüger et al., 2017; Fifield et al., 2017).

## AUTHOR CONTRIBUTIONS

Samuel Hodges was responsible for the design of the experiment and study methodology, carried out the analysis and scripting, and drafted this article. Kjell Einar Erikstad and Tone Kirsten Reiertsen were responsible for data collection and critical review of the manuscript.

## STATEMENT ON INCLUSION

Our study was a collaborative work between a visiting scientist and local researchers, who all operated under the oversight of a national institute. Our data collection also involved collaboration with researchers from other European nations. References are drawn from across the global scientific community but citations of local work are included where suitable. We recognize a bias toward English language articles; we will endeavour to address this in future research.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data for this study—including HYCOM reanalysis SST data (in R dataframes and ASCII raster formats) by month and year, GLS coordinate data for all four Auk species by month and year, full MaxENT output, results from Gaussian modelling and R scripts for data preparation and analysis—are all freely available in Zenodo: <https://zenodo.org/record/6643359> (Hodges et al., 2022). For further inquiries, please contact Samuel Hodges at [sam.jir.hodges@btinternet.com](mailto:sam.jir.hodges@btinternet.com).

## ORCID

Samuel Hodges  <https://orcid.org/0000-0002-3280-7840>

## PEER REVIEW

The peer review history for this article is available at: <https://publons.com/publon/10.1002/2688-8319.12181>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1:** An example of MaxEnt's output; a geographical representation of Habitat Suitability as predicted by the model, with heat map colouring for probable location and white squares representing the GLS coordinates fed into the program

**Figure S2:** An example of our output from MaxEnt

**Figure S3:** Comparison of MaxENT Jackknife tests for August 2012 (top, a typical year) with August 2013 (bottom, an anomalous year)

**Figure S4:** A visual demonstration of how the Gaussian modelling works

**Figure S5:** Assembled plots of MaxENT response curves for Habitat Suitability to Standardized Sea Surface Temperature

**Figure S6:** Heatmaps of hindcast Habitat Suitability using SST models.

**Figure S7:** Forecast AUC variability across the non-breeding cycle

**Table S1:** Sample size of GLS logger data, sorted by Species, Month and Cycle.

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