PREDICTING SUITABLE MARINE HABITAT FOR PINK-FOOTED SHEARWATERS *ARDENNA CREATOPUS* IN THE WATERS ALONG THE PACIFIC COAST OF CANADA

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ABSTRACT

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Anthropogenic activities are threatening global marine ecosystems, with seabirds representing a vulnerable group that has experienced pronounced population declines in recent decades. The ability to identify important marine areas for vulnerable seabirds is fundamental to conservation initiatives. The Pink-footed Shearwater *Ardenna creatopus* (listed as Endangered in Canada) breeds only in Chile, but during the non-breeding season, it ranges northward to waters off Canada's Pacific coast and the northern Gulf of Alaska. Using at-sea survey data spanning from 1992 to 2019, we examined the relationship between the species' distribution and environmental variables using a two-step generalized additive model approach. Cross-validation with out-of-sample testing showed high predictive accuracy for shearwater occurrence (area under receiver operating characteristic curve [AUC] = 0.94) and moderate performance for relative abundance predictions (Spearman's rank correlation = 0.32, root mean square error = 3.92, mean absolute error = 0.45) at a 4-km² resolution. The results give us confidence in the model's ability to identify areas suitable for Pink-footed Shearwaters. Distribution was strongly associated with several oceanographic and geographic factors, particularly latitude and distance to the continental shelfbreak. The findings of this study may help inform marine conservation efforts within Canada's Pacific exclusive economic zone and beyond.

Key words: at-sea survey, seabirds, generalized additive model, habitat modelling, habitat suitability model, Pacific Ocean

INTRODUCTION

According to the International Union for Conservation of Nature Red List criteria, 31% of all seabird species are globally threatened (Dias et al., 2019), and 47% of seabird species are exhibiting population declines, primarily from anthropogenic causes (e.g., climate change and fisheries bycatch; Dias et al., 2019; Paleczny et al., 2015; Schreiber & Burger, 2002). The decline in biodiversity of marine birds and other taxa influences the structure and stability of ocean ecosystems. The Pink-footed Shearwater *Ardenna creatopus* is a procellariid that nests on only three islands in Chile and spends the non-breeding season (May through October) in the eastern Pacific between Chile and the Gulf of Alaska and occasionally in the Bering Sea (Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2016; Felis et al., 2019; Guzman & Myres, 1983). COSEWIC has reassessed the conservation status of the Pink-footed Shearwater as Endangered (COSEWIC, 2016), after it was originally assessed by COSEWIC in 2004 as Threatened. This status was amended on Schedule 1 of the Species at Risk Act as of May 2019.

At their breeding colonies, Pink-footed Shearwaters are threatened by illegal harvesting of chicks, invasive species, light pollution, and habitat degradation and loss (Carle et al., 2019; COSEWIC, 2016). In addition, the species is taken as fisheries bycatch in most waters throughout its at-sea range and is believed to be vulnerable to marine oil and plastic pollution and to collisions with offshore wind farms and oil platforms (Carle et al., 2022; COSEWIC, 2016). Pink-footed Shearwaters capture prey (primarily fishes, squids, and crustaceans) by scavenging, surface seizing, pursuit-plunging, and shallow wing-and-foot-propelled diving (Adams et al., 2019; Prince & Morgan, 1987). Although their foraging behavior in Canada has not been studied, they have been observed scavenging and surface seizing in this region (KM, unpublished observations from 2010).

Pink-footed Shearwaters are present annually as non-breeders in Canadian waters (May through October; Guzman & Myres, 1983), where it is estimated that between 10,000 and 20,000 occur annually (COSEWIC, 2016). However, the locations and characteristics of critical habitat in Canadian waters remain unknown and are not described in the current Canadian recovery strategy for the species (Environment Canada, 2008).

Studying how offshore seabirds (such as this species) relate to their marine environment is challenging for several reasons. First, because surveys are logistically difficult and expensive to organize and conduct, coverage in time and space is often restricted. Second, these birds are highly mobile and often occur in transit in suboptimal areas. These limitations highlight the importance of accurately predicting a species' distribution and abundance and creating general models that rely on ecological relationships (rather than just observations), which are vital when describing areas of importance.

Toward that end, habitat suitability models (HSMs) are valuable for understanding species' spatial and temporal relationships with their environment. These models estimate the statistical relationship between environmental factors and a species' presence and abundance, and they have predictive capabilities (Hirzel et al., 2006). For example, HSMs can predict the probability of presence and abundance for unsurveyed areas and specific time periods. Over the past decade, researchers have increasingly used HSMs to assess relationships between seabirds and marine environments (Baines & Weir, 2020; Bonnet-Lebrun, 2020; Mannocci et al., 2014). The usual technique for collecting data for marine birds is at-sea surveys, where researchers collect vessel-based observations and identify and georeference locations where species were encountered. Using inputs like at-sea survey data, the goal of HSMs is to create models encompassing general ecological relationships so that they can be spatially and temporally transferable. A challenge when creating these models is to account for how birds are distributed at sea. The response variable (i.e., seabird numbers) tends to be non-normally distributed and zero-inflated, and its relationship with the environment is often nonlinear.

The creation of a model framework that is flexible enough to deal with these issues has extensive value and could help contribute to an array of conservation initiatives. Generalized additive models (GAMs) are flexible in relating a response variable to one or more predictor variables (Wood, 2017). GAMs do not require the distributional assumptions of traditional parametric approaches and can fit nonlinear response curves to individual predictor variables (Wood, 2017). Functions are specified for each predictor variable, which allows for response curves specific to the individual predictors (partial predictions). A "two-step" GAM uses a two-step fitting process to account for zero inflation when regular count models, such as Poisson or negative binomial, are unrealistic (Feng, 2021; Heinänen et al., 2017). The first part of two-step GAMs can be used to determine why a species occurs in specific areas, and the second part addresses what influences the frequency of use within these spaces (Heinänen et al., 2017; Jensen et al., 2005).

Using models based on at-sea survey data collected in the Canadian Pacific between 1992 and 2019, this study's objectives were to (1) predict the distribution and relative abundance of Pink-footed Shearwaters and (2) understand the underlying environmental associations that may be driving these patterns. We used both presence–absence data and relative abundance information to create a two-step GAM to describe and predict species distribution and relative abundance. Subsequently, we evaluated the transferability of our models by implementing out-of-sample testing (cross-validation).

Predicting spatial areas of importance and identifying the underlying causes of high seabird abundance is a component of marine spatial planning and the designation of marine protected areas. These actions can aid in mitigating potential conflicts between human activities and marine species. Canada's coastal areas have been subjected to intense anthropogenic changes (Singh et al., 2020), which makes conservation initiatives critical to this region's ocean sustainability. Policymakers employing strategies that prevent seabird decline and promote environmental stability can support these initiatives. Our results are intended to inform seabird management and conservation efforts on the Canadian Pacific coast and support broader global conservation movements.

METHODS

Data Collection and Study Extent

To build HSMs, we used at-sea survey data collected throughout Canada's Pacific waters (Fig. 1) between 1992 and 2019. At-sea survey data were assembled from two sources (Fig. 2). The first source, which provided the majority of the observations, was the Canadian Wildlife Service (CWS). We accessed CWS's datasets via the North Pacific Pelagic Seabird Database (Drew et al., 2015). At-sea seabird observers collected data on a variety of ships of opportunity, using strip transect methodology (Ronconi & Burger, 2009). Due to surveys being conducted aboard ships of opportunity, the data collected are spatially and temporally inconsistent. Recorded information on transect length and width are used to calculate the area of effort applied per transect. We define a transect as a strip of continuous survey effort, with information saved to the segment centroid point.

The Raincoast Conservation Foundation (RCF) was the second source of data, with voyages throughout the Queen Charlotte Sound and Hecate Strait between 2005 and 2008 (Fox et al., 2017). From these data, information recorded for each transect was used at the transect's centroid point. The data were downloaded from the Ocean Biogeographic Information System Spatial Ecological Analysis of Megavertebrate Animal Populations (OBIS-SEAMAP) database (Fox & Raincoast Conservation Foundation, 2016). The RCF surveys were conducted using a distance sampling design with random starting points (for further details see Fox et al., 2017). To make this dataset compatible with the CWS strip transect data, using the raw observations, we limited shearwater sightings to those seen within 300 m on either side of the vessel (Barbraud & Thiebot, 2009). Then, we incorporated the given segment length to calculate the survey area effort and thereby mimicked the strip transect survey data format.

We combined both datasets using the merge tool in ArcGIS Pro 2.3.0 and then aggregated centroid segment points by survey identification (Survey ID) to a standardized 4-km^2 grid cell. We used only those surveys run between May and October to reflect the Pink-footed Shearwater's non-breeding season and when we would expect the species to be present in Canada's Pacific exclusive economic zone (EEZ).

To better enable the detection of environmental variables of interest, our study extent was restricted to the inferred distribution boundaries of the species in Canada's Pacific EEZ (COSEWIC, 2016). We excluded inlets along the British Columbia mainland, Haida Gwaii, and Vancouver Island. We also excluded most of the Salish Sea and Queen Charlotte Strait and restricted the western boundary of the study area to 100 km seaward of the 1,000-m isobath (Fig. 1). Areas with grids cells that had insufficient environmental data were also excluded.

Environmental Variables

We selected candidate environmental variables (Table 1) by considering their biological relevance to shearwaters and other related seabirds (e.g., Ainley et al., 2005; O'Hara et al., 2006; Vilchis et al., 2006). These variables included the following: latitude (Lat); depth (Depth); slope (Slope); ruggedness (Rugg); tidal current speeds averaged over cycles (Tidal); distance to the

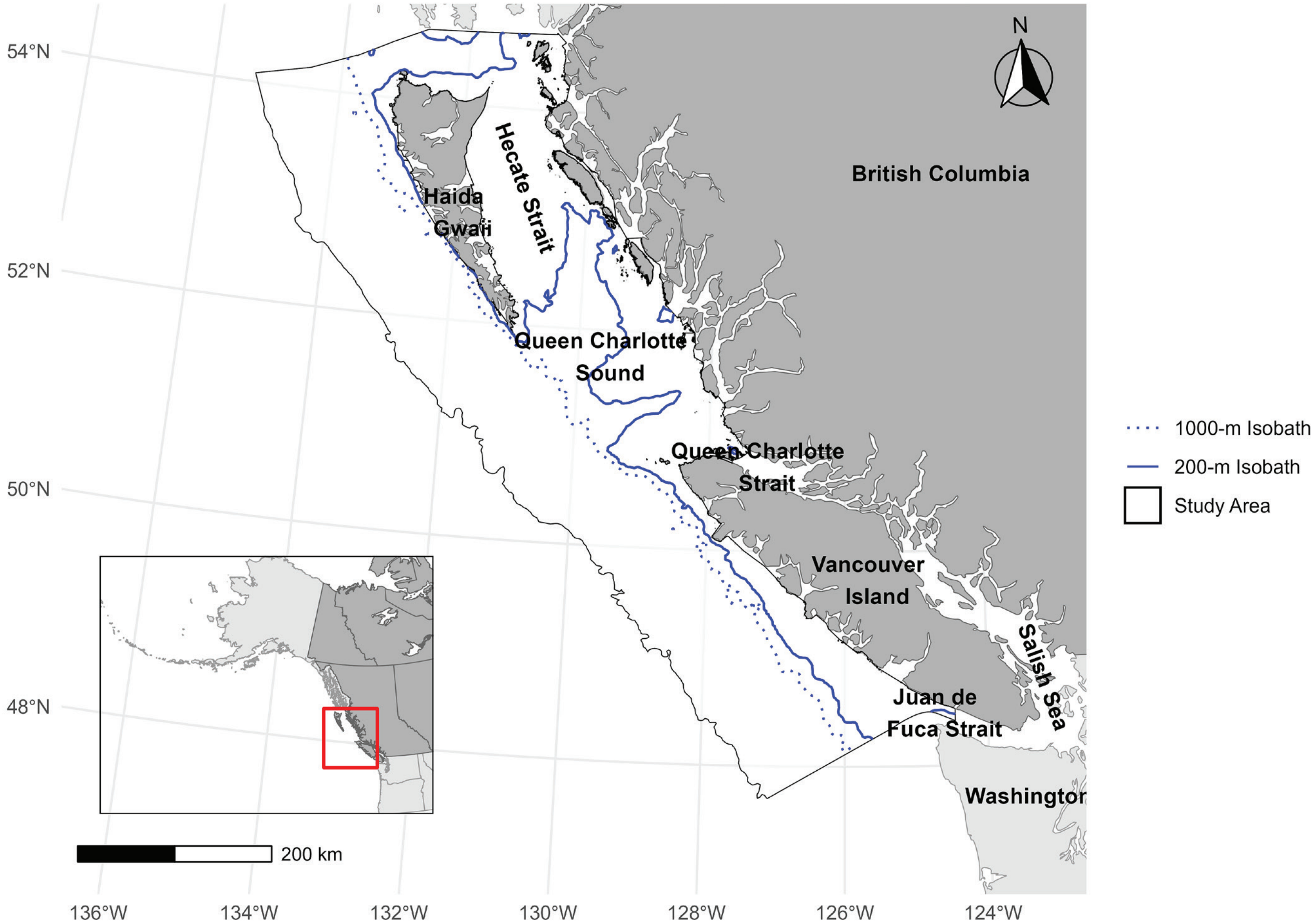

Fig. 1. Map of the British Columbia coast, western Canada. Major areas labeled include Haida Gwaii, Hecate Strait, Queen Charlotte Sound, Queen Charlotte Strait, Juan de Fuca Strait, and the Salish Sea. The solid blue line represents the 200-m isobath, and the dashed blue line indicates the 1,000-m isobath. The solid black boundary represents the study area boundary.

shelfbreak, defined here as the 200-m isobath (ISO_{dist}); being on or off the continental shelf (SHELF); annual monthly average sea surface temperatures (SST_{month}); long-term sea surface temperatures ($SST_{average}$); distance to annual monthly average SST fronts ($FRONTS_{month}$); distance to SST fronts averaged over the study period ($FRONTS_{average}$); distance to marine canyons ($CANYON_{dist}$); and month (Month). See Appendix 1 (available on the website) for an extended description of variables, including how they were selected, extracted, and formatted.

Processing Survey Data

Initially, survey observations were saved as segment centroid points. However, to help decrease zero inflation and have environmental layers and observations on comparable scales, we aggregated these observation points (grouped by unique survey) to the standardized 4-km^2 grid (see above). The survey effort information (area surveyed; m^2) was also aggregated and saved at this scale. Many marine birds sit on the water when resting and, in the case of surface seizers, foraging and are seen in flight only when transiting locations. Flying Pink-footed Shearwaters should not be considered merely transiting birds, as they frequently forage while airborne, using wind to enhance search efficiency (Raymond et al., 2010) and exhibiting the characteristic low-altitude "surface-shearwater" flight style described by Spear and Ainley (1997a, 1997b). As surface foragers, they fly close to the water to take prey driven upward by subsurface predators while relying on wind to maintain efficient on-the-wing foraging (Spear & Ainley, 1997a, 1997b). Therefore, we needed to considered birds on the water and birds in flight when considering marine habitat use and, thus, combined these counts. We assumed 100% detection within the 300-m distance limit, as this has been measured as a reasonable observation limit for large shearwaters during ideal marine conditions (Barbraud & Thiebot, 2009; Spear et al., 2004).

Data Analysis

Two-Step GAM

We used a two-step GAM approach due to its simplicity and flexibility when exploring nonlinear relationships with data that are zero-inflated, which is often the case in marine environments (e.g., Jensen et al., 2005; Skov et al., 2016). The basic setup of the two-step GAM is as follows: begin by creating a model using presence–absence data, followed by a model of the nonzero observations (presence-only) as a continuous or count variable. For our setup, after the initial data processing, we ran a binomial distribution (logit-linked) GAM model using the presence–absence

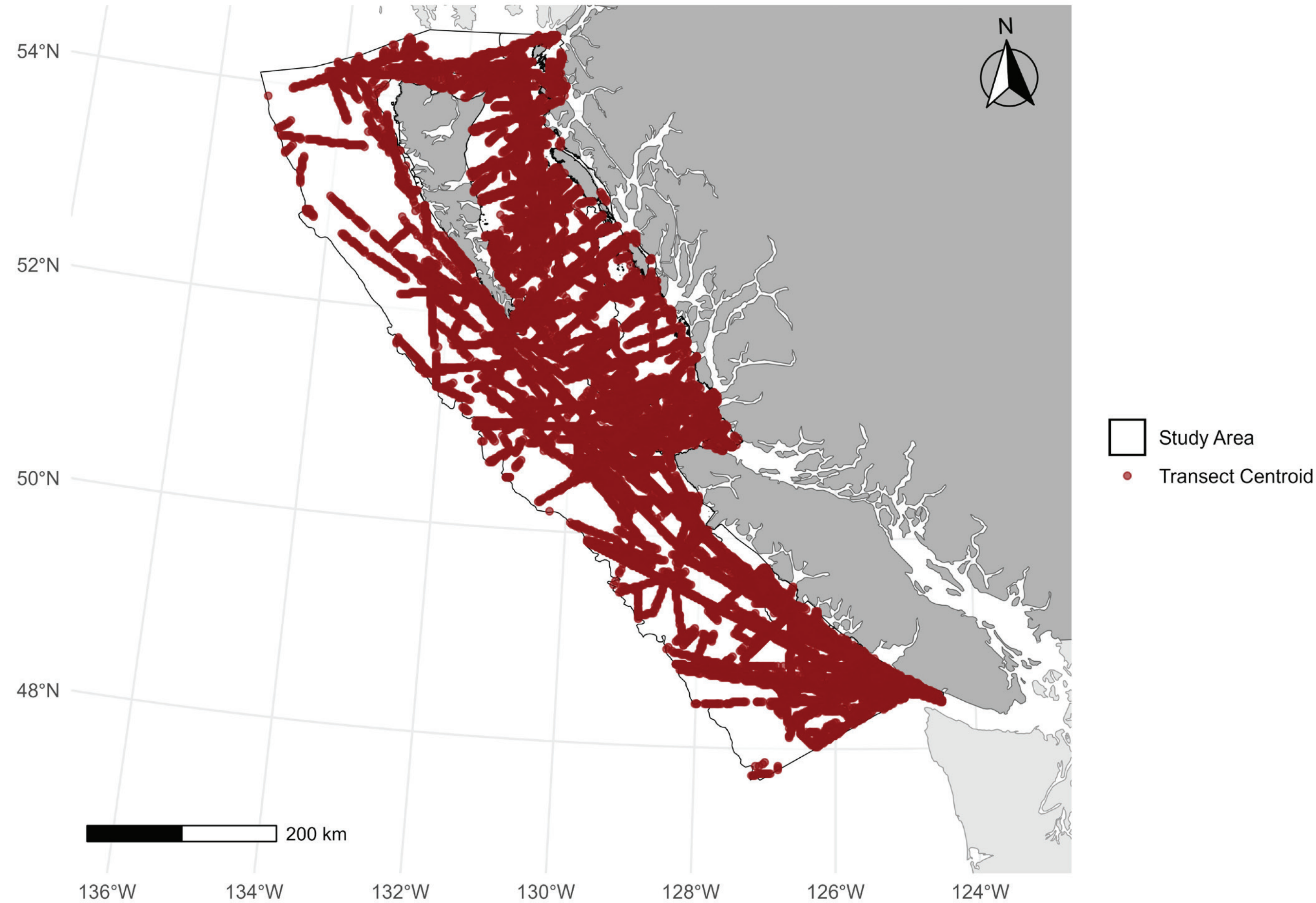

Fig. 2. At-sea survey segment centroids used to represent survey effort throughout the study area, with data collected opportunistically between 1992 and 2019.

data. Thereafter, we used the count data from the positive-only observations to build a negative binomial GAM model (log-linked). GAMs were fitted using the "mgcv" package in R version 4.4.3 (Wood, 2017). A restricted maximum likelihood estimation (REML) was used for the smoothing parameter. We used REML because it outperforms the more commonly used generalized cross-validation/Akaike information criterion smoothness selection process and allows for better smoothing parameter estimation (Wood, 2011). The basis dimension parameter, *k*, was limited to 5 to avoid overfitting and ensure computational efficiency while still allowing sufficient flexibility to capture nonlinear patterns. Since survey effort varied, we used an offset term within the GAM model (Wood, 2017) to account for transect area, with the model output reflecting effort-corrected conditional abundance (counts/area). Finally, we included survey ID and year as random effects to account for survey variability (Wood, 2017).

We used a preliminary "full model" that contained all terms and cross-checked paired variables' concurvity values to check whether one variable's smooth curve significantly correlates to another's (Table 2). We then removed covariates that indicated collinearity levels above 0.75, as their inclusion can cause substantial bias in coefficient estimates (Yoo et al., 2014). After model construction, we tested for evidence of spatial autocorrelation using a correlogram test, which calculates Moran's *I* value over increasing spatial lags (Fortin et al., 2002). We ran the correlogram test on the raw counts, the model residuals, and the model residuals of a GAM that used coordinates as interacting predictors (Wood, 2017; Fig. 3). We concluded that our model adequately accounted for spatial autocorrelation (Fletcher & Fortin, 2018), even without incorporating the interactive effects of latitude and longitude. Hence, it was deemed reasonable to proceed without including the coordinates together but to retain latitude as a variable of interest.

We implemented a double-penalty shrinkage approach (Marra & Wood, 2011) for model selection. This method adds an extra penalty to a smooth term, penalizing functions in both the null and range space. Shrinkage techniques, such as the double-penalty approach, carry out model selection in a single step (Marra & Wood, 2011). The double-penalty shrinkage step was added to the model, using the function *select=T* in the "mgvc" package, which essentially removes terms during fitting and results in a parsimonious final model. Terms that are "shrunk" out of the model are labeled with zero degrees of freedom within the smoothing terms.

We evaluated the significance of predictor variables in our GAM using the *summary()* function in R. To assess the significance of each variable, we examined the *P*-value, which indicates the level of statistical significance of the variable's association with the response. We considered variables with a *P*-value less than .05 to be significant, indicating a strong association with the response variable. Finally, we quantified the range of values depicted in the partial plots, as well as the precision of the corresponding

TABLE 1
Variables used as covariates with respect to Pink-footed Shearwaters' *Ardenna creatopus* distribution or relative abundance in Canadian Pacific coastal waters

Variable[a]	Type	Working name	Unit	Significance
Latitude	Spatial	Lat	metres	Canada occurs in the shearwaters' more northern range and, therefore, latitude is an important consideration (COSEWIC, 2016).
Distance to 200-m isobath	Spatial	ISO_{dist}	metres	The shelfbreak is a highly productive area, with many pelagic species tied to its location (Serratosa et al., 2020).
On or off shelf	Spatial	SHELF	–	Many related species have a stronger affinity to occur on the continental shelf (Felis et al., 2019).
Sea surface temperature (annual monthly average)	Spatio-temp	SST_{month}	degrees C	Cooler SST has been linked to nutrient enhancement and prey aggregations (Deser et al., 2010).
Long-term averaged sea surface temperature	Spatial	$SST_{average}$	degrees C	Long-term average SST can help predict general productive zones for marine species (O'Hara et al., 2006).
Distance to fronts	Spatio-temp	$FRONTS_{month}$	metres	Fronts have been found to aggregate seabirds and their prey (Hoefer, 2000).
Average distance to fronts	Spatial	$FRONTS_{average}$	metres	Areas that consistently form fronts may be seen as reliable foraging locations for marine species (Hoefer, 2000).
Depth	Spatial	Depth	metres	Shallow waters are often productive (Serratosa et al., 2020).
Slope	Spatial	Slope	degrees	The slope of the seafloor can influence nutrient mixing (Serratosa et al., 2020).
Ruggedness	Spatial	Rugg	proportion	Similar to slope, ruggedness can affect nutrient mixing (Fox et al., 2017).
Distance to marine canyons	Spatial	$CANYON_{dist}$	metres	Marine canyons provide conditions for productive zones (Harris & Whiteway, 2011).
Tidal current speed	Spatial	Tidal	metres per second	Tidal currents influence productivity and biodiversity (Foreman et al., 2000).
Month	Temporal	Month	month	Pink-footed Shearwaters occur in Canada during their non-breeding season. Months are restricted to between May and October (COSEWIC, 2016).

[a] Not all variables listed were considered in the final modelling process.

TABLE 2
Concurvity correlation coefficients between all pairs of environmental variables[a,b]

	Lat	**Tidal**	**Slope**	**Rugg[c]**	**ISO_{dist}**	**$CANYON_{dist}$**	**SST_{month}**	**Depth**	**$FRONTS_{month}$**	**$SST_{average}$**	**$FRONTS_{average}$**
Lat	1	0.17	0.11	0.12	0.07	0.48	0.06	0.13	0.12	0.74	0.08
Tidal	0.17	1	0.64	0.75	0.45	0.64	0.20	0.59	0.57	0.29	0.45
Slope	0.11	0.64	1	**0.87**	0.46	0.56	0.23	0.60	0.60	0.22	0.27
Rugg	0.12	0.75	**0.87**	1	0.54	0.68	0.26	0.48	0.70	0.27	0.36
ISO_{dist}	0.07	0.45	0.46	0.54	1	0.44	0.20	0.58	0.36	0.35	0.34
$CANYON_{dist}$	0.48	0.64	0.56	0.68	0.44	1	0.15	0.24	0.50	0.57	0.39
SST_{month}	0.06	0.20	0.23	0.26	0.20	0.15	1	0.18	0.32	0.13	0.07
Depth	0.13	0.59	0.60	0.48	0.58	0.24	0.18	1	0.30	0.36	0.14
$FRONTS_{month}$	0.12	0.57	0.60	0.70	0.36	0.50	0.32	0.30	1	0.17	0.37
$SST_{average}$	0.74	0.29	0.22	0.27	0.35	0.57	0.13	0.36	0.17	1	0.19
$FRONTS_{average}$	0.08	0.45	0.27	0.36	0.34	0.39	0.07	0.14	0.37	0.19	1

[a] See Table 1 for full variable names and associated information.
[b] Significant correlations (> 0.80) are highlighted in bold.
[c] Ruggedness (Rugg) was discarded before final model construction.

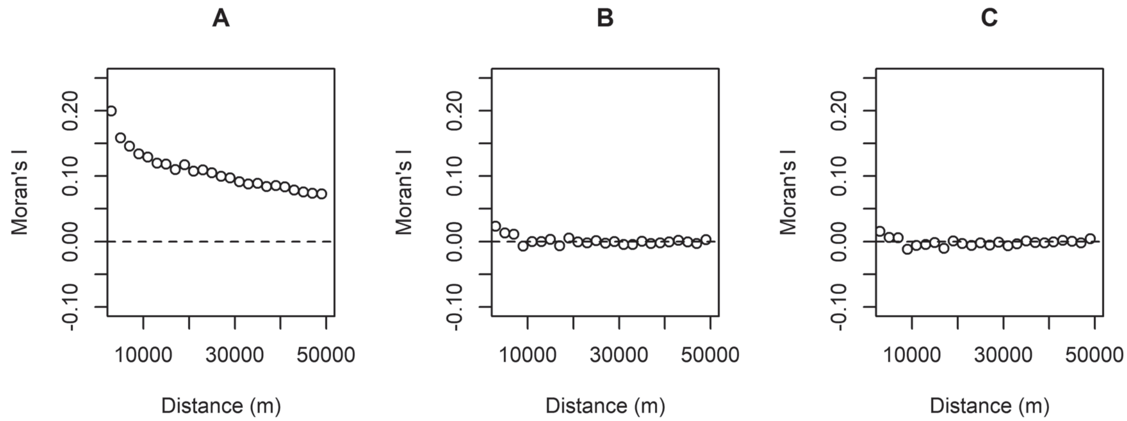

Fig. 3. Correlograms showing Moran's *I* values over a range of distance lags (at 2,000-m intervals) for (A) raw counts, (B) spatial model residuals, and (C) coordinate model residuals for Pink-footed Shearwater *Ardenna creatopus* counts collected between 1992 and 2019. Higher positive Moran's *I* values indicate increasing spatial autocorrelation.

confidence intervals, to determine the relative importance of the predictor variables.

Predictions

Our final models, which we fitted using all available data, were used to predict the distribution and relative abundance of the Pink-footed Shearwater onto the smooth standardized 4-km^2 spatiotemporal dataset. We made predictions using the *predict.gam* function from the "mgcv" package in R version 4.4.3.

We ran these predictions over a smooth grid for every month-year that fell within the temporal parameters for which data were collected. Two map types were visualized: the first was the averaged probability of occurrence over time, and the second was the predicted integrated relative abundance over time (predicted occurrence × conditional abundance). We also plotted predicted occurrences by month to visualize how areas of importance vary temporally.

Model Assessment

We assessed the amount of variation explained by the model by the percent deviance explained for both model parts. We then evaluated the predictive accuracy using an out-of-sample (cross-validation) test. We fitted each model using 70% of the data, randomly selected, as training data, with the products of those models used to predict onto the remaining 30% of the dataset as testing data. The presence–absence model, predicting the probability of occurrence, was then assessed using a threshold independence measure, the area under the receiver operating characteristic curve (AUC). These curves are simply a plot of sensitivity (the fraction of correctly predicted presences) against specificity (the fraction of correctly predicted absences). An AUC value of 0.9 indicates that the model can discriminate between occupied and unoccupied cells 90% of the time (Pearce & Ferrier, 2000). In contrast, an AUC of 0.5 indicates that the model has randomly selected its values and has no predictive power (Pearce & Ferrier, 2000). We evaluated effort-corrected relative abundance predictions using Spearman's rank correlation. This test indicates whether the predicted counts are of the right order of magnitude compared to the observed counts (Schober et al., 2018). To further evaluate model performance, we calculated both the root mean square error (RMSE) and the mean absolute error (MAE). RMSE provides a measure of the average magnitude of prediction error, giving greater weight to large errors, while MAE offers a more robust estimate of typical prediction error by averaging the absolute differences between predicted and observed values. Lower RMSE and MAE values indicate better model performance, though the interpretation is context dependent and influenced by the scale of the response variable. In general, values approaching zero suggest strong predictive accuracy, while values nearing or exceeding the range of the observed data reflect weak performance (Chai & Draxler, 2014; Willmott & Matsuura, 2005). We visually compared the mapped predicted effort-corrected relative abundance against the observed counts to speak to the spatial patterns' reliability (Fig. A1, Appendix 1). As another form of evaluation, we compared our presence–absence GAM outputs to the results of a Maxent model, which is another type of HSM (Appendix 2).

All data and code used for the analysis are publicly available on Figshare (Pastran et al., 2025).

RESULTS

After grouping unique surveys into the standardized 4-km^2 grid cells, there were 16,829 observation points, with 842 of those points containing positive observations. Between 1992 and 2019, the counts within these grid cells ranged from 0 to 162. Only 3% of positive observations contained counts higher than 50 within a grid cell. The overall density varied between months (Fig. 4). The lowest total survey effort occurred in October (1,032 km^2), and the highest total survey effort took place in June (4,645 km^2). The highest density of birds occurred in August (Fig. 4), and the lowest density was in May (Fig. 4).

Model Development

We found high correlations (> 0.75) between Slope and Ruggedness (Table 2). As slope has previously been found to be associated with other pelagic seabird species (Fox et al., 2017), ruggedness was discarded. Other variables had somewhat high correlations but not high enough to discard from model consideration. We examine the implications of these correlations in the Discussion section. We ran the remaining explanatory variables as main effects (Table 3).

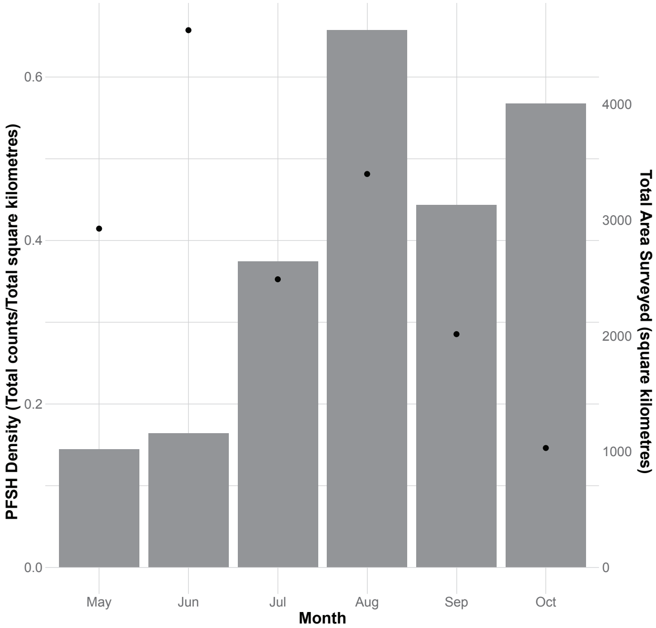

Fig. 4. Total monthly density of Pink-footed Shearwaters *Ardenna creatopus* (PFSH) recorded (solid bars) and total area surveyed (points) for the cumulative survey effort from 1992 to 2019.

The double-penalty shrinkage term further removed the main effects of Tidal, Slope, and $CANYON_{dist}$ from the first part of the model (presence–absence), and $CANYON_{dist}$, SST_{month}, Depth, and $FRONTS_{average}$ from the second part of the model (presence-only) (Table 3).

Environmental Relationships and Mapped Predictions

The response curves for both predicted distribution and effort-corrected relative abundance were the product of the final models (Figs. 5, 6). Double-penalty shrinkage caused inconsequential variables to have the smooth term degrees of freedom listed as zero (Figs. 5, 6; Table 3).

We found that Latitude was significant in both models; the probability of occurrence declined and predicted relative abundance decreased with increasing latitude. Pink-footed Shearwaters were far more likely to occur and reach higher densities in southern waters, with strong declines toward northern regions of the Canadian Pacific coast. Slope was significant in the relative abundance model. Predicted relative abundance increased as the slope gradient values increased, suggesting shearwaters are more likely to concentrate in areas with steeper bathymetric gradients. $SST_{average}$ (long-term SST) was significant in both models. In the presence–absence model, occurrence had a peaked response to SST, with highest occurrence at intermediate SSTs. In contrast, relative abundance declined steadily with temperature. This suggests shearwaters are more likely to occur in moderate-temperature waters, but their densities are highest in cooler SST zones. $FRONTS_{month}$ (short-term proximity to SST fronts) was significant in the presence–absence model. Occurrence increased as the distance to fronts increased, indicating shearwaters are present farther away from local monthly fronts. $FRONTS_{average}$ (long-term frontal proximity) was significant in the presence–absence model. Occurrence was higher closer to frontal features and then declined sharply farther away, indicating Pink-footed Shearwaters may associate closer to persistent frontal features.

TABLE 3
Generalized additive model (GAM) results relating distribution and relative abundance of Pink-footed Shearwaters *Ardenna creatopus* for the presence–absence and presence-only models that utilized data from between 1992 and 2019[a,b,c]

Predictors[d]	Presence–absence GAM	Presence-only GAM
Latitude	**s(3.01e+00)**	**s(9.72e–01)**
Tidal	-	s(5.71e–01)
Slope	-	**s(7.61e–01)**
$SST_{average}$	**s(2.52e+00)**	**s(1.79e+00)**
$FRONTS_{month}$	**s(1.84e+00)**	s(7.54e–01)
$CANYON_{dist}$	-	-
SST_{month}	s(3.23e+00)	-
$FRONTS_{average}$	**s(2.37e+00)**	-
ISO_{dist}	**s(2.38e+00)**	**s(3.61e+00)**
Depth	**s(8.45e–01)**	-
SHELF	**F**	**F**
Month	**F**	F
% deviance explained	50.1	54.1
Adjusted R^2	0.38	0.11

[a] The selected explanatory variables are smooth functions (s) and factors (F), along with their estimated degrees of freedom in parentheses.
[b] Terms labeled as significant ($P < .05$) are highlighted in bold.
[c] The empty spaces correspond to variables shrunk out of the model.
[d] See Table 1 for full variable names and associated information.

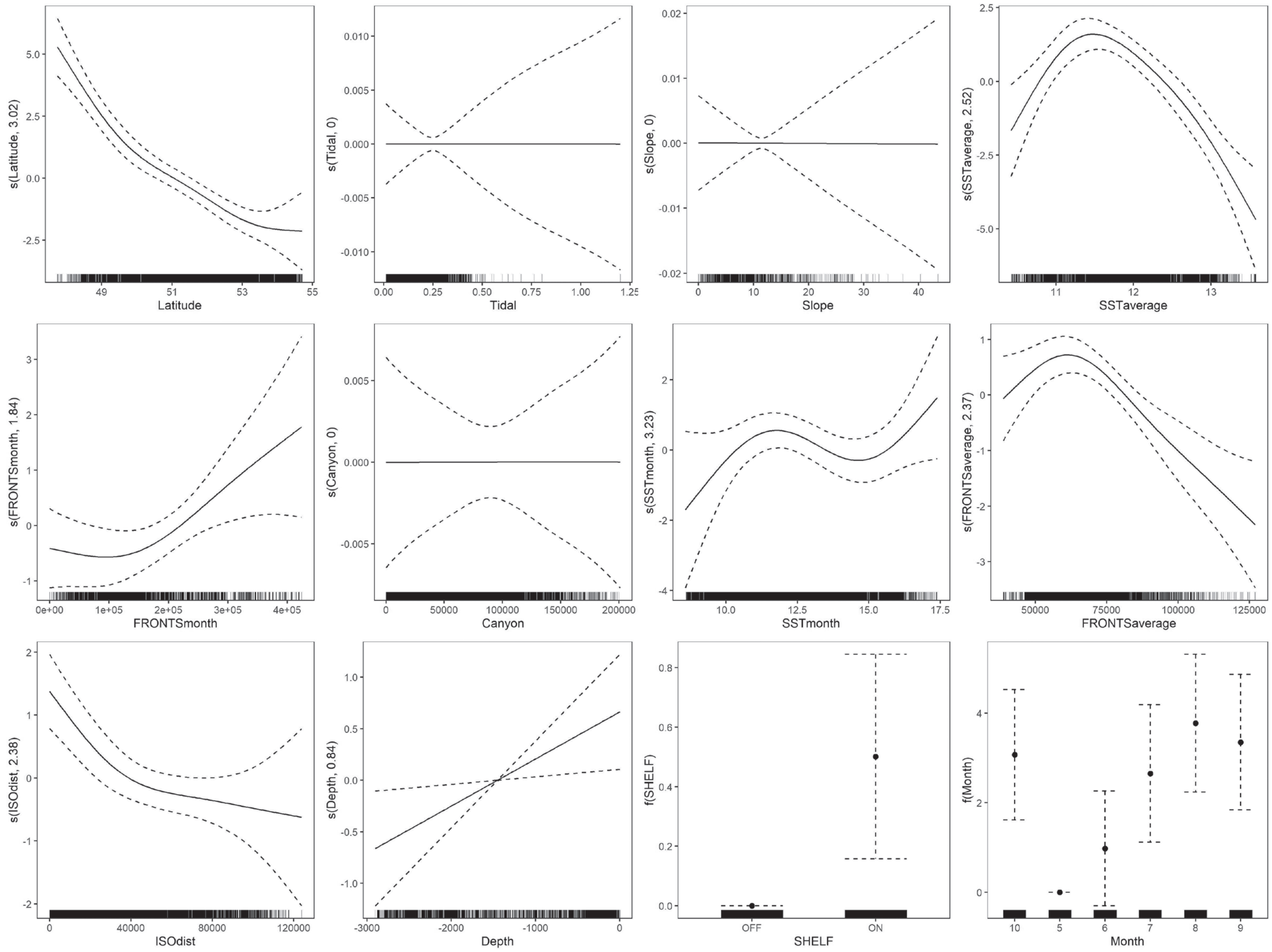

Fig. 5. Model terms for the presence–absence (GAM) of Pink-footed Shearwater *Ardenna creatopus* occurrence probability. Estimated smooth functions (solid lines) with confidence intervals (dashed lines) are shown for each explanatory variable. The x-axes represent the range of each predictor variable (on the original, untransformed scale), and the y-axes represent the partial effect of each predictor on the logit scale of occurrence probability, centered around zero. Numbers shown in parentheses in the y-axis labels represent the estimated degrees of freedom for each smooth term. Tick marks along the x-axes indicate the distribution of observed data. A flat relationship indicates the term was shrunk out of the model. Latitude, $SST_{average}$, $FRONTS_{month}$, $FRONTS_{average}$, ISO_{dist}, Depth, SHELF, and Month were found to be significant. Untransformed values are shown for ease of interpretation.

ISO_{dist} (distance to the continental shelfbreak) was significant in both the presence–absence and relative abundance models. Both the presence–absence (Fig. 5) and relative abundance (Fig. 6) models indicated higher values near the shelfbreak, with occurrence probability and predicted relative abundance increasing as distance decreased. These patterns suggest that Pink-footed Shearwaters are more likely to occur and aggregate in higher numbers closer to the continental shelfbreak.

Depth was significant in the presence–absence model. In the presence–absence model, occurrence increased as waters became shallower. However, their local abundance did not increase in shallower areas, suggesting that different processes, such as prey availability or bathymetric complexity, may drive presence and density. Being on the continental shelf (SHELF) was found to be significant for both the presence–absence and relative abundance models. Month was found to significantly influence the presence–absence of shearwaters but not their relative abundance (Figs. 5, 6).

The predicted distribution map of Pink-footed Shearwaters indicates that they are most likely to occur off the entrance to the Juan de Fuca Strait and along most of the west coast of Vancouver Island, near the shelfbreak (Fig. 7). The predicted counts are highest off the southern half of the west coast of Vancouver Island (Fig. 8). Monthly predicted distribution maps show that Pink-footed Shearwater distribution is restricted during the early non-breeding season (May and June) but later becomes more dispersed, especially between August and October (Appendix 1, Fig. A2).

Model Evaluation

The presence–absence component of the model explained 50.1% of the deviance, while the relative abundance (presence-only) component explained 54.1%, reflecting moderate to strong explanatory power across both stages of the two-step model. When evaluated against a 30%-withheld test dataset, the presence–absence model demonstrated excellent discriminatory ability, with an AUC of 0.94. Effort-corrected predicted relative abundance values from

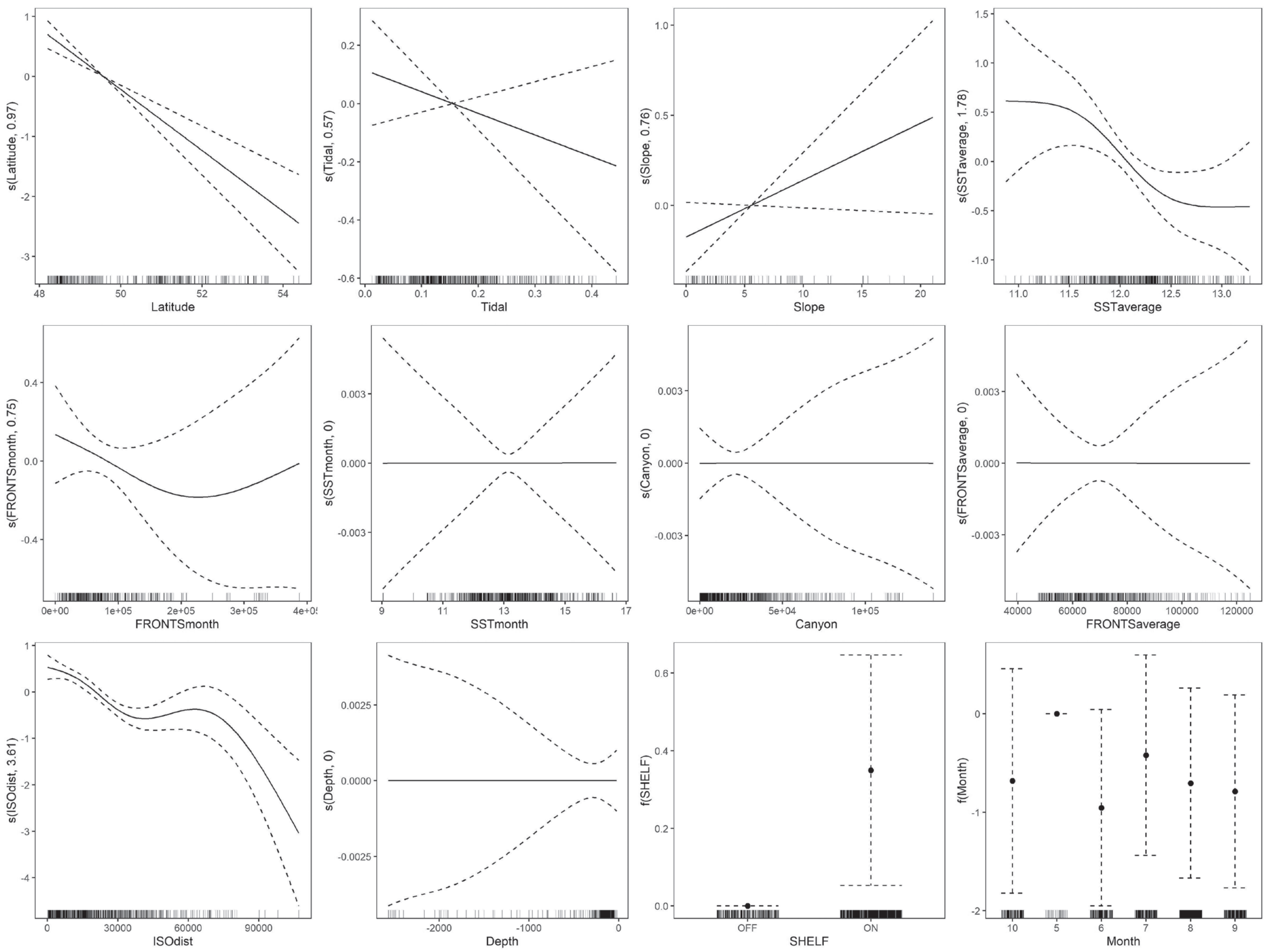

Fig. 6. Model terms for the presence-only GAM of Pink-footed Shearwater *Ardenna creatopus* predicted conditional abundance. Estimated smooth functions (solid lines) with confidence intervals (dashed lines) are shown for each explanatory variable. The x-axes represent the range of each predictor variable (on the original, untransformed scale), and the y-axes represent the partial effect of each predictor on the logit scale of occurrence probability, centered around zero. Numbers shown in parentheses in the y-axis labels represent the estimated degrees of freedom for each smooth term. Tick marks along the x-axes indicate the distribution of observed data. A flat relationship indicates the term was shrunk out of the model. Latitude, Slope, $SST_{average}$, ISO_{dist}, and SHELF were found to be significant. Untransformed values are shown for ease of interpretation.

the relative abundance model were moderately correlated with observed counts, with a Spearman's rank correlation of 0.32, a RMSE of 3.92, and a MAE of 0.45. Observed values in the test dataset ranged from zero to 150 birds per 4-km² grid cell, while hurdle-adjusted predicted relative abundance values ranged from zero to 41. Although predicted values did not reach the highest observed counts, the majority fell within the same order of magnitude (Fig. 9). Finally, visual comparison of predicted surfaces and point observations confirmed strong spatial agreement, with the majority of observed presence data and higher counts occurring in areas predicted to have elevated probability of occurrence and relative abundance (Appendix 1, Fig. A1).

DISCUSSION

Predictive Accuracy

Our primary goal was to create models capable of accurately predicting the relative abundance and distribution of Pink-footed Shearwaters. We had a high amount of variance explained for both the presence–absence and the presence-only models. The deviance explained is the proportion of null deviance explained by the model, which is more appropriate to use with non-normal data than R^2 and preferred over R^2 as a measure of model fit for non-Gaussian response distributions (Wood, 2017). From the deviance explained, we found that over 50% of the variance was explained by each model. Our models also had a high transferability at the 4-km^2 spatial scale. The AUC value of 0.94 indicated the presence–absence portion of the model had an excellent ability to distinguish which conditions would likely be occupied or not (Pearce & Ferrier, 2000). An HSM for Pink-footed Shearwaters in Washington, USA, used similar GAM techniques and also yielded high predictive accuracy when modelling shearwater distribution (Menza et al., 2016). Our presence–absence model's ability to predict the probability of presence was higher than the Maxent model we built (Appendix 2). This was expected, as our GAM had the ability to incorporate temporal variables, whereas the Maxent standalone software restricts the uses to inputting

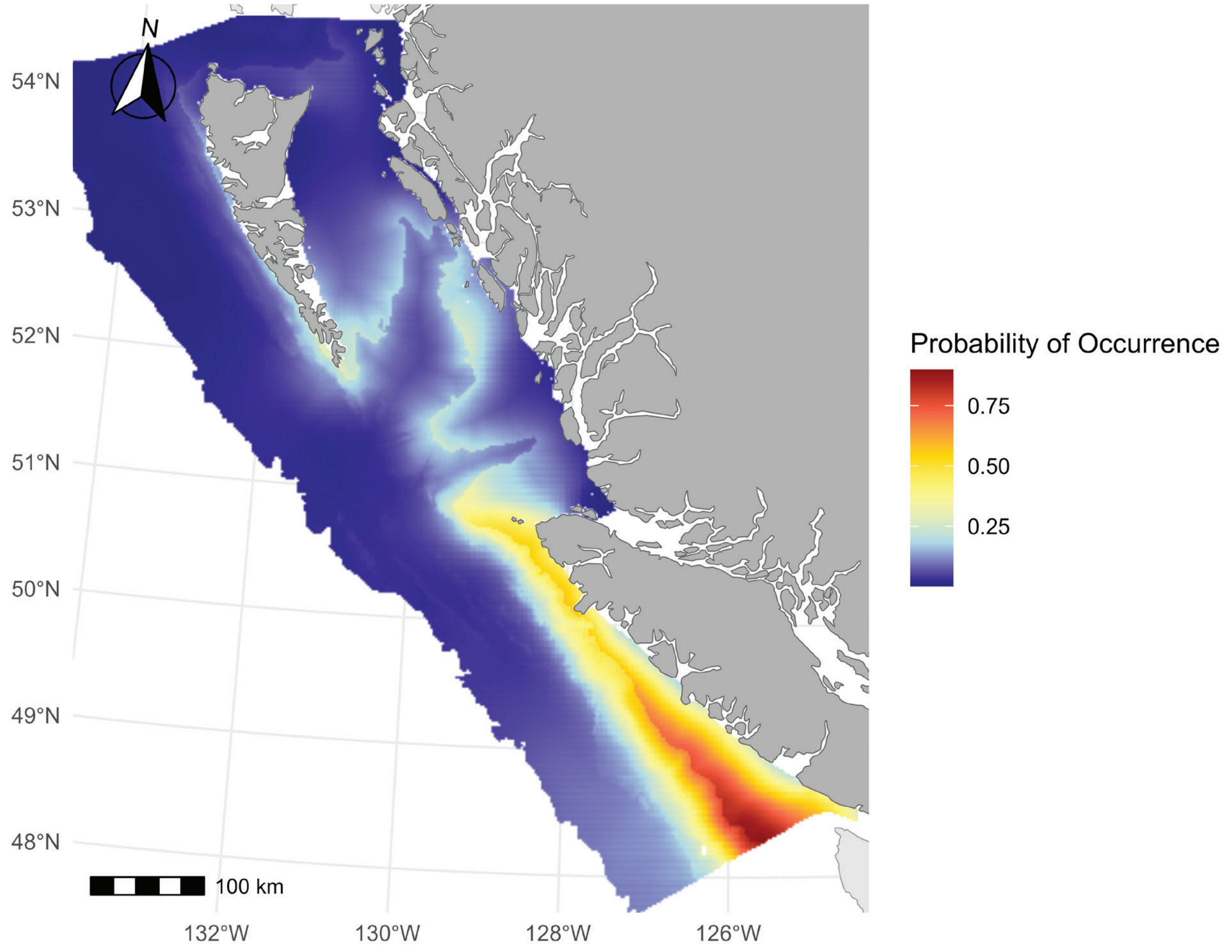

Fig. 7. Average predicted probability of Pink-footed Shearwater *Ardenna creatopus* occurrence, derived from the presence–absence GAM model and projected onto a 4-km^2 grid for the study area, off the Pacific coast of Canada.

only spatial predictors (Merow et al., 2014). However, even with these restrictions, the Maxent results showed a high predictability (AUC = 0.87), reinforcing the importance of our selected spatial predictor variables for this species. The full results and a discussion of the Maxent model can be found in Appendix 2.

Given the large spatial scale of our dataset, we found the two-step GAM's ability to accurately predict effort-corrected relative abundance was satisfactory (Schober et al., 2018). The predicted means were similar to observed relative abundances and spatial distribution (Fig. A1, Appendix 1), with a correlation value of 0.32, RMSE of 3.92, and MAE of 0.45. However, our model generally predicted counts lower than what was observed and was unable to predict peak abundances. A factor that may be contributing to consistently lower predicted counts is that our model may not have incorporated the temporal resolution to detect peak migration times. Another factor influencing high numbers of birds is likely related to the spatiotemporal abundance of prey, for which our model did not account. Though we used environmental predictors to forecast highly productive areas, the temporal scale we were able to use undoubtedly did not always capture the productive events. Additionally, we did not account for anthropogenic influences such as fishing vessels, which often attract large mixed flocks of pelagic birds (Boswall, 1960; Skov & Durinck, 2001). Additionally, detectability during ship-based surveys may be influenced by wind-driven flight behaviour. Shearwaters change their flight height, ground speed, and mode (gliding vs. flapping) in relation to wind strength and direction (Ainley et al., 2015; Spear & Ainley, 1997a, 1997b), which can alter their visibility to observers and bias counts either upward or downward depending on conditions.

Though expected, it should also be noted that the presence-only portion of the model had a limited numeric range of associated environmental predictors compared to the presence–absence model, due to the availability of fewer data points. However, we still captured the differences in relative abundance among locations even with these limitations. This is supported by our model evaluations, which showed that the predicted and observed counts were generally within the same order of magnitude (Fig. 9). The RMSE of 3.92 indicates that, on average, predicted values deviated from observed counts by approximately four birds per 4-km² grid cell, while the MAE of 0.45 suggests that most errors were relatively small, with many predictions closely matching observed values. These metrics support the interpretation that, despite underpredicting peak values, the model performed well in capturing broad-scale patterns in relative abundance.

Model Interpretations and Area Highlights

Our secondary goal was to accurately describe the modelled relationships between the species and the environmental predictors.

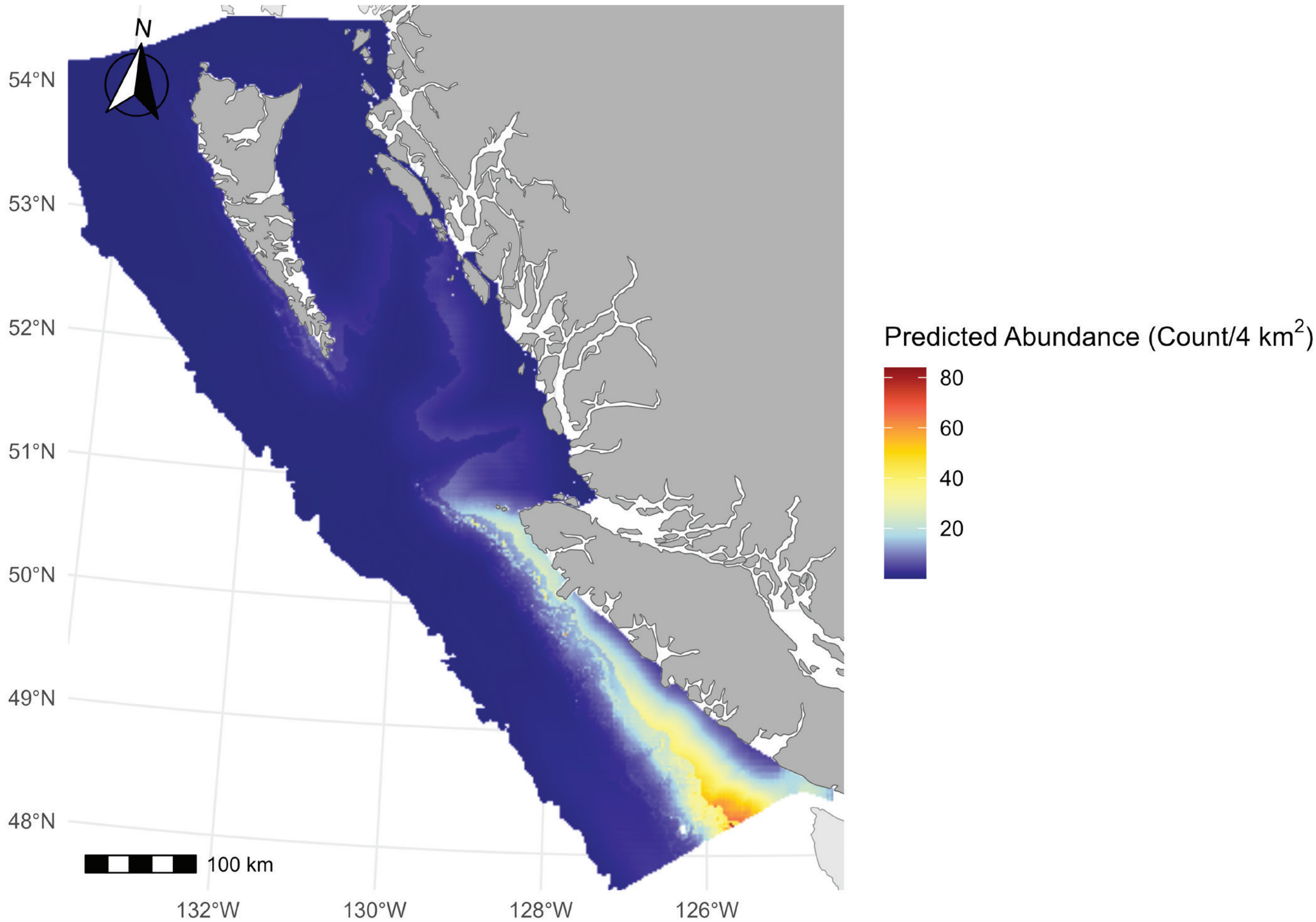

Fig. 8. Average predicted relative abundance of Pink-footed Shearwater *Ardenna creatopus* presence, based on the two-step GAM products, projected onto a 4-km^2 grid for the study area, off the Pacific coast of Canada.

Although studies explicitly testing environmental relationships to Pink-footed Shearwaters in Canadian waters are limited (COSEWIC, 2016), our results generally support findings from other regions (Ainley et al., 2005, 2009; Leirness et al., 2021; Russell et al., 2023). These patterns align with well-known biogeographic trends in seabird foraging modes, where water temperature, turbidity, and productivity structure the distribution of pursuit-diving species (Ainley, 1977). Consistent with these expectations, Pink-footed Shearwaters showed a strong association with the continental shelfbreak, an area typically influenced by productive mixed-layer dynamics, indicating that our results reflect these broader biogeographic patterns.

Latitude was a substantial predictive factor, and this result highlights the importance of shearwater habitat use of lower latitudes within Canadian waters. We attribute the strength of this relationship to two causes. First, the shelf waters off the northern end of Vancouver Island approximate the northern extent of the core non-breeding range of the Pink-footed Shearwater (Carle et al., 2022), and therefore, a stronger relationship to the south was expected within Canadian waters. An additional and related factor is the highly productive nature of the Juan de Fuca Eddy (Burger, 2003), which occurs off the southern end of the west coast of Vancouver Island. This eddy, reaching up to 50 km in diameter, generally begins in June and ends in early December. Upwelling, caused partially by the eddy, creates nutrient-rich water that mixes with water from the Juan de Fuca Strait and thereby enhances coastal productivity in water that flows westward (Burger, 2003). Modelling the distribution of Pink-footed Shearwaters throughout Washington's marine areas, Menza et al. (2016) found that the area adjacent to the Juan de Fuca Strait had the highest predicted relative abundance. This relationship to the deep zones occurring outside of the Juan de Fuca Eddy, where upwelling occurs and production is high, is reflected in the significant interaction that was found between cooler SSTs and deep waters.

The other key environmental factor that has defined the distribution of Pink-footed Shearwaters in our study is the distance to the continental shelfbreak. It is well known that the continental shelfbreak is a key foraging area for many seabird species, including shearwaters (e.g., Bonnet-Lebrun et al., 2020; Guzman & Myres, 1983). The area is characterized by the upwelling of cold, nutrient-rich waters from the ocean depths that become mixed with warmer surface waters (Yoder et al., 1983). Moreover, the shelfbreak also acts as a barrier that accumulates and concentrates nutrients, such as nitrogen and phosphorus, from land runoff and deep ocean currents (Jacox & Edwards, 2011). This concentration of nutrients further enhances the productivity of the area and creates a rich feeding ground for marine life. Key environmental factors that have defined the distribution of Pink-footed Shearwaters in

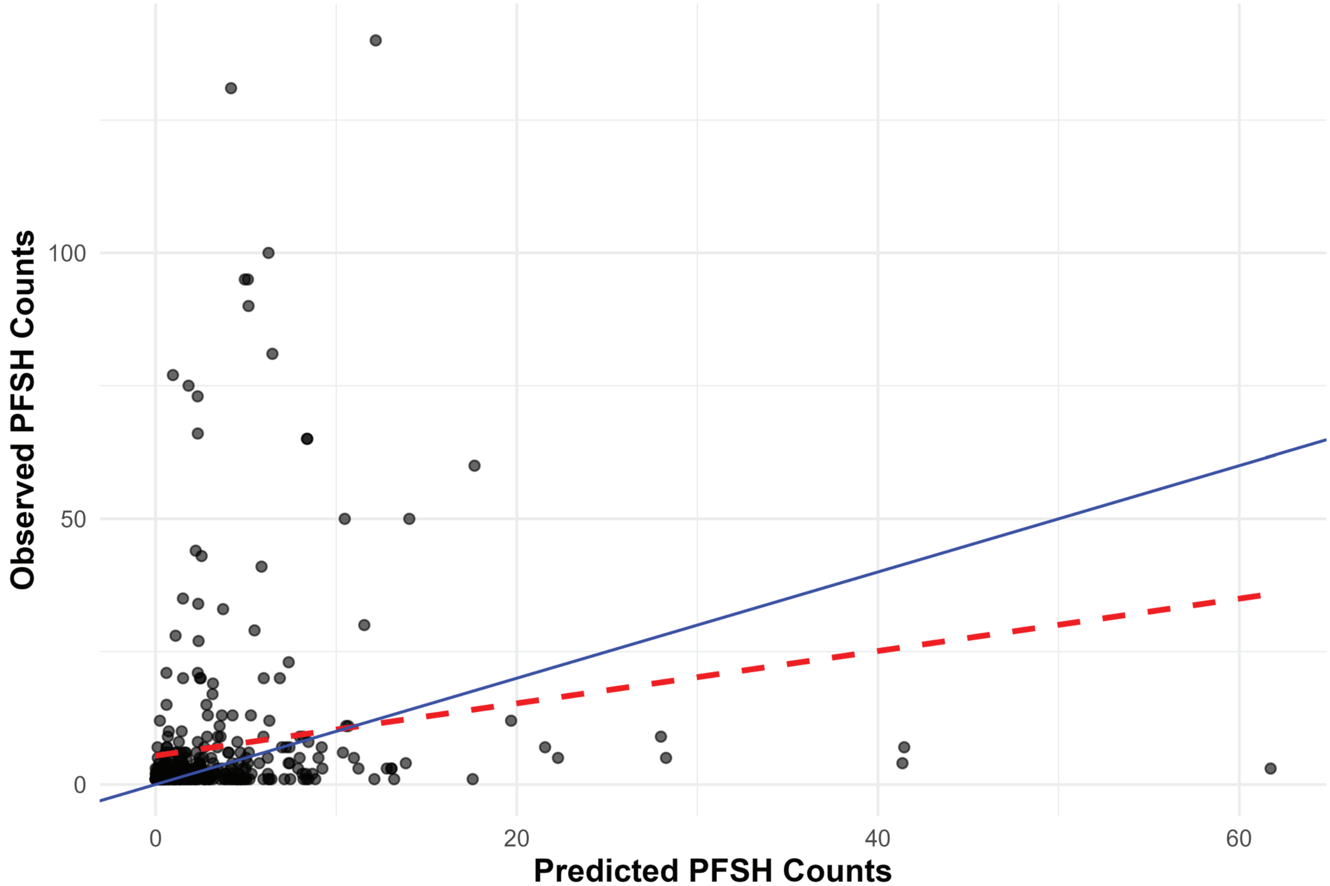

Fig. 9. Cross-validation plot showing the relationship between predicted and observed Pink-footed Shearwater *Ardenna creatopus* (PFSH) counts within grid cells based on the training dataset (including zero counts). Each point represents a grid cell in the study area. The solid blue line indicates the 1:1 line (perfect prediction), while the dashed red line shows the best-fit linear trend between predicted and observed values.

California are depth, the continental shelf, and temperature fronts (Ainley et al., 2005, 2009). Since most of these birds are likely to occur on the continental shelf and close to the shelfbreak (Felis et al., 2019), it logically follows that their probability of presence increases as depth decreases, which is what we found.

The SST relationship to the distribution and abundance of Pink-footed Shearwaters differed depending on whether we examined long-term averages or monthly values. Relationships with SST have commonly been detected in other pelagic seabird studies (Fox et al., 2017; O'Hara et al., 2006; Vilchis et al., 2006; Wakefield et al., 2009). Although we detected a large effect of the long-term average SST, we caution that this effect may be influenced by latitude, as these factors have a somewhat high correlation. Although both long-term and short-term SST front metrics were included as covariates, they had distinct effects on Pink-footed Shearwater occurrence and relative abundance. $\text{FRONTS}_{\text{average}}$, which reflects the average distance to SST fronts across multiple years (1992–2019), was significantly associated with shearwater occurrence. Birds were more likely to occur in areas that were consistently closer to long-term frontal zones, suggesting a preference for regions with persistent hydrographic features where predictable prey aggregations may form over time. This aligns with other studies linking recurrent fronts to stable foraging opportunities for pelagic seabirds (Ainley et al., 2009; Hoefer, 2000). Both frontal covariates were statistically significant in the occurrence model but exhibited opposite relationships. Pink-footed Shearwaters were more likely to occur near long-term frontal zones ($\text{FRONTS}_{\text{average}}$), suggesting that persistent frontal features may provide predictable foraging conditions or long-term prey aggregations. In contrast, occurrence probability decreased with proximity to short-term frontal features ($\text{FRONTS}_{\text{month}}$), indicating birds were less likely to be found near transient or recently formed fronts. This seemingly contradictory pattern may reflect differing ecological functions of these features. Persistent fronts, as described by Xing et al. (2024), represent recurring oceanographic features that maintain stable conditions over time, whereas ephemeral fronts are more variable. This contrast in predictability may help explain the observed pattern, with persistent fronts offering more consistent foraging conditions than transient ones.

The mouth of the Juan de Fuca Strait is highlighted in this study as a priority for protecting Pink-footed Shearwaters (Figs. 7, 8). This spatial relationship remains relatively consistent for the months the birds are in Canadian waters (Appendix 1, Fig. A2). Although the Juan de Fuca Eddy and nearby areas have been identified as being highly productive and vital for many species (e.g., Burger, 2003; Guzman & Myres, 1983; Menza et al., 2016), no Marine Protected Areas exist within these zones (Fisheries and Oceans Canada, 2025).

Study Limitations and Future Directions

Studying the marine habitat of seabirds is inherently challenging with respect to both data collection and analysis. Available surveys were not systematically collected, so detecting shifts in distributions within and across years was not possible. The spatial scale at which modelling was conducted also played a prominent role in determining outcomes. Our results would likely shift had we focused on a particular region within Canada's Pacific waters. We also focused on abiotic environmental variables rather than biotic factors (e.g., potential prey concentrations).

We hope that the results of this study will help identify important habitat for the Pink-footed Shearwater in Canada. Recommended additional work includes identifying areas and timing of the highest potential anthropogenic threats to the species, as these threats are poorly understood in Canadian waters (Carle et al., 2022; COSEWIC, 2016).

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