Predicting at-sea distribution of Razorbill in the St. Lawrence Gulf and Estuary, Québec, Canada during the breeding period using GPS telemetry

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ABSTRACT. Seabirds in the St. Lawrence Gulf and Estuary are vulnerable to anthropogenic threats such as oil spills and fisheries bycatch. A better understanding of their at-sea distribution is needed to determine occurrence and abundance hotspots where protection and conservation efforts should be concentrated. The goal of this study was to develop an at-sea distribution map of Razorbills (Alca torda) during the breeding period throughout the St. Lawrence to respond efficiently in the event of an environmental emergency. We tracked and recorded Razorbills using GPS transmitters (n = 58) in six colonies located in the province of Québec along the St. Lawrence between 2015 and 2018. Two sets of models and maps (habitat suitability and density) were developed for Razorbills from GPS locations and a set of eight environmental covariates using a machine-learning approach (boosted regression trees). We then predicted at-sea habitat suitability and density around all known and active Razorbill colonies throughout the St. Lawrence (n = 85). The main covariates affecting habitat suitability and density of Razorbills were distance to the colony and distance to shore. Sea surface temperature and chlorophyll-a concentration were also important for habitat suitability. The model allowed generating at-sea maps for the entire targeted area during the breeding period. We identified large areas of high suitability (hotspots) to determine locations where Razorbills are most at risk and where conservation efforts should be focused. This work will be important to assess risk and minimize impacts in the case of an environmental emergency such as oil spills occurring in the St. Lawrence.

Prédiction de la répartition en mer du Petit Pingouin pendant la période de reproduction dans le golfe et l’estuaire du Saint-Laurent, Québec, Canada, à l’aide de la télémétrie GPS

RÉSUMÉ. Les oiseaux marins du golfe et de l’estuaire du Saint-Laurent sont vulnérables aux menaces anthropiques tels les déversements d’hydrocarbures et les prises accidentelles par les pêcheurs. Une meilleure compréhension de leur répartition en mer est nécessaire pour qu’on détermine les points chauds d’occurrence et d’abondance, où les efforts de protection et de conservation devraient être concentrés. L’objectif de la présente étude était d’élaborer une carte de répartition en mer des Petits Pingouins (Alca torda) pendant la période de reproduction dans le Saint-Laurent, afin qu’on puisse réagir efficacement en cas d’urgences environnementales. Nous avons suivi des Petits Pingouins nicheurs à l’aide d’émetteurs GPS (n = 58) dans six colonies situées dans la province de Québec, le long du Saint-Laurent, entre 2015 et 2018. Deux ensembles de modèles et de cartes (caractère propice de l’habitat et densité) ont été élaborés pour les pingouins à partir des positions GPS et d’un jeu de huit covariables environnementales, au moyen d’une approche d’apprentissage automatique (technique de boosting d’arbres de régression). Nous avons ensuite prédit la qualité de l’habitat et la densité en mer autour de toutes les colonies de pingouins connues et actives dans le Saint-Laurent (n = 85). Les principales covariables qui ont affecté le caractère propice de l’habitat et la densité des pingouins étaient la distance à la colonie et la distance à la côte. La température de surface de la mer et la concentration de chlorophylle-a étaient également importantes pour la qualité de l’habitat. Le modèle a permis de générer des cartes en mer pour l’ensemble de la zone ciblée pendant la période de reproduction. Nous avons défini de grandes zones dans lesquelles l’habitait était très propice (points chauds), afin de déterminer les endroits où les pingouins sont les plus menacés et où les efforts de conservation devraient être concentrés. Les résultats de cette étude sont importants pour nous permettre d’évaluer le risque et de minimiser les impacts advenant une urgence environnementale, tel un déversement d’hydrocarbures, dans le Saint-Laurent.

Key Words: alcids; conservation; geographic information system; marine threats; foraging range

INTRODUCTION

The St. Lawrence is a vast and complex ecosystem where biological productivity is high. It is a major transportation corridor for international commercial vessels subjected to high anthropogenic pressure resulting in cumulative exposure and environmental changes (Beauchesne et al. 2020, Blais et al. 2021). Few areas of the St. Lawrence are free from stressors such as pollution, acidification, fisheries, invasive species, and ship traffic (Beauchesne et al. 2020). Approximately 4000 vessels per year transit through the seaway, transporting various commodities including over 3 million metric tonnes of petroleum products (St. Lawrence Seaway Corporation Management 2019). Oil spills from oil tankers, ship-to-ship transfer, and oil handling facilities
are of particular concern because they could have major detrimental effects on this ecosystem and its biological communities (Roberge and Chapdelaine 2000, Archambault et al. 2017). Biological diversity is impressive in the St. Lawrence and protected areas have been created by federal and provincial governments to protect biodiversity and promote wildlife conservation (Desgranges and Jobin 2003). Some examples include several National Wildlife Areas and Migratory Bird Sanctuaries as well as the Saguenay-St. Lawrence Marine Park, which offer refuge to many species during vulnerable stages of their life cycle. Migratory Bird Sanctuaries are especially important for the protection of birds during their reproduction period (Rail 2021). Overall, the St. Lawrence provides critical foraging habitats during the breeding, migratory, and overwintering periods for over a million seabirds (Desgranges and Jobin 2003, ECC 2016, 2020, 2022).

Seabirds are sensitive to threats such as fisheries bycatch, climate change, diseases, invasive species, and pollution (Dias et al. 2019, NACBI-Canada 2019). On a global scale, population trends of seabirds are decreasing at an alarming rate (Paieczny et al. 2015): 60% of species that use Canadian waters are of conservation concern and 34% are at risk of extinction (Partners in Flight 2019). In the St. Lawrence, population trends of the 19 breeding seabird species in the last two decades increased for 21% of species, decreased for 32% of species, whereas trends were not significant for 47% of species (J.-F. Rail 2019, personal communication). Among the species with positive demographic trends, Razorbill (Alca torda) showed a three-fold increase (Chapdelaine et al. 2001, Rail and Cotter 2015, Rail 2021; J.-F. Rail 2019 personal communication). Approximately 12% of the world Razorbill population is found in Canada, 63% of which is found in the St. Lawrence Gulf and Estuary in the province of Québec (ECC 2019, Partners in Flight 2019; J.-F. Rail, 2019 personal communication). This large proportion highlights the importance of this species in Québec in terms of responsibility from a conservation standpoint. Razorbills are vulnerable to environmental threats such as oil spills, bioaccumulation of contaminants, and fisheries bycatch (Lavoie et al. 2010, Ellis et al. 2013). Given its abundance and ubiquity in the St. Lawrence and sensitivity to disturbance, the Razorbill is an ideal species to monitor the state of the St. Lawrence and to use as proxy to determine areas of higher occurrence and abundance where conservation efforts should be focused.

To properly address conservation issues for seabirds, it is imperative to characterize the areas of high use and identify sites of importance. Several seabird monitoring programs have been developed in Canada to monitor breeding colonies (ECC 2016, 2020) as well as offshore distribution and abundance (ECC 2022). These long-term standardized programs provide a strong basis for population trends and biodiversity hotspots. However, large-scale aerial or boat surveys can be costly and provide a snapshot at the time of the survey only. Alternatively, or in tandem, seabirds can be tracked with GPS transmitters to determine their at-sea distribution over the course of the breeding season. Tracking data from individuals can provide information on important areas based on frequency of use (Irvine et al. 2014). However, it is often not realistic to deploy GPS transmitters on a large number of bird colonies because of the high cumulative cost and the inaccessibility to some of them (e.g., cliff-nesting individuals). Deploying transmitters on individuals from a subset of colonies is therefore more appropriate. Predictive spatial analyses can then be used to extrapolate seabirds’ distribution to other colonies based on a set of environmental variables (Lieske et al. 2020). For instance, the foraging range of breeding colonial seabirds is constrained around their nest (Elliott et al. 2009) and the distance to the colony is typically strongly limiting. Other variables such as prey density, environmental variability, bathymetry, and sea surface temperature can also explain seabirds’ foraging behavior around their colony (Burke and Montevecchi 2009, Kowalczyk et al. 2015, Soanes et al. 2016, Delord et al. 2020, Perez-Correa et al. 2020). Recent advances in GPS tracking technologies and associated mathematical models have allowed researchers to: (1) identify environmental variables with the most explanatory power based on a subset of prior information (e.g., GPS positions of tracked individuals), (2) identify optimal values for these environmental variables, and (3) generate spatial predictions for non-sampled areas (e.g., bird distribution; Elith et al. 2008, Lieske et al. 2020). The resulting distribution maps can show where areas of high occurrence and density are located and where conservation actions are required.

The goal of this study was to develop at-sea habitat suitability and density maps of Razorbills during the breeding period for 85 colonies located in the St. Lawrence based on tracked individuals from six colonies. We also aimed to identify the location of the largest habitat suitability hotspots. The at-sea distribution maps of the St. Lawrence produced in this study will provide valuable information on their range during the breeding season, which will help better inform management and conservation agencies. In addition, the results will be an important resource in case of environmental emergency events (e.g., oil spill) for preparedness, planning, to direct intervention efforts, to minimize impacts, and for damage assessment.

**METHODS**

**Study area and tracking data**

We captured Razorbills on six breeding colonies located in the province of Québec (Canada) along the St. Lawrence Estuary and Gulf (Table 1; Fig. 1). We deployed 85 GPS transmitters (URIA series, Ecotone Telemetry Inc., Gdynia, Poland) on breeding adult Razorbills between 26 May and 25 July from 2015 to 2018. We captured individuals at their nest site during the incubation period using nest boxes equipped with a remote-triggered door system. Transmitters were programmed to acquire GPS locations at fixed intervals (5–30 minutes depending on colony and year of sampling). GPS fixes were logged on the transmitter until they were automatically downloaded on a base-station located near the nest.

**Data processing**

We discarded all GPS locations recorded between the capture and the first time the bird came back to the colony to avoid the inclusion of erratic movements caused by post-capture stress. We excluded all locations at the nest using a 20 m buffer around the colony to take into account the theoretical accuracy of the GPS module (L. Iliszko, Ecotone Telemetry Inc. 2020 personal communication). To reduce the variability in sampling effort among individuals, all tracks were standardized to 30 minute
Fig. 1. Location of six Razorbill (*Alca torda*) colonies from the St. Lawrence where birds were equipped with a GPS transmitter during breeding seasons of 2015–2018 (n = 85 deployed; 58 kept in the model; gray circles). These colonies were used to model and predict the spatial distribution of all known and active Razorbill colonies (white circles) in Québec, Canada (gray background). The dividing line shows the limit between Estuary (west) and Gulf (east). Individual bird tracks are shown for the six colonies in insets A to C (letters correspond to the boxes in the top left panel).

### Table 1. Names and coordinates of the six Razorbill (*Alca torda*) colonies in the St. Lawrence where GPS transmitters were deployed during breeding seasons of 2015–2018. Sample sizes of GPS that were deployed (n = 85) and kept for the model (n = 58) are shown for each colony.

| Breeding colonies | Coordinates (dd°mm') | Number deployed | Number kept for the model |
|-------------------|-----------------------|-----------------|---------------------------|
| Estuary           |                       |                 |                           |
| Gros Pèlerin Island | 47°44'N, 69°41'W | 20              | 17                        |
| Gros Pot Island   | 47°52'N, 69°41'W | 9               | 4                         |
| Bicquette Island  | 48°24'N, 68°53'W | 13              | 11                        |
| Gulf              |                       |                 |                           |
| Corossol Island   | 50°05'N, 66°23'W | 10              | 5                         |
| Betchouane Island | 50°11'N, 63°12'W | 18              | 11                        |
| Îles Sainte-Marie | 50°18'N, 59°39'W | 15              | 10                        |
| Total             |                       | 85              | 58                        |

individual within the 5–95 percentiles (i.e., 23–367 positions), considering this a reasonable trade-off between standardization of sampling effort and data loss. Because Razorbills rarely spend time on land other than at the colony, locations occurring on land were discarded (n = 221). After data processing, a total of 9803 locations from 58 GPS transmitters were kept for the analysis (Fig. 1).

Razorbill space use was modeled to relate the occurrence and density of GPS locations to a set of biologically relevant environmental covariates (Lieske et al. 2020). For the purpose of this study, we assumed that the occurrence and density of GPS locations in a given area were considered a good proxy of the occurrence and density of individuals in that area. To estimate density of birds in an area, we first binned GPS locations of each individual into a 1 x 1 km resolution grid centered on the breeding colony. The extent of each individual grid was determined using the mean of maximum foraging distances recorded across all colonies (mean ± SD; 79 ± 46 km). To determine spatial at-sea distribution, we also gave a binary (0, 1) occurrence value to each individual grid cell. For occurrence, the goal was to produce a probability map of the potential distribution, hereafter called habitat suitability index, ranging from 0 to 1 (Hazen et al. 2021). Only grid cells occurring over seawater were kept for further analysis (inland values were set to not available [NA]).
Environmental data
We modeled density and a habitat suitability index for Razorbills using a set of environmental covariates that have been shown or hypothesized to influence the distribution of colonial alcids: distance to the colony, distance to the nearest shoreline, depth, seafloor slope, rugosity, chlorophyll-α concentration, and sea surface temperature (SST; McDuie et al. 2018, Lieske et al. 2020, Perez-Correa et al. 2020). Satellite imagery of chlorophyll-α concentrations has been successfully used as a proxy for productivity and presence of prey to examine spatio-temporal variations of seabird and whale densities (Suryan et al. 2012, McDuie et al. 2018, Abrahms et al. 2019). Similarly, SST has been found to explain seabirds’ occurrence and abundance (Domalik et al. 2018, McDuie et al. 2018, Delord et al. 2020, Perez-Correa et al. 2020). All covariates were extracted as spatial raster from various sources (Table A1.1; Fig. A1.2; A1.1). For covariates with temporal variation (i.e., chlorophyll-α concentration and SST), we extracted monthly composite from June and July of 2015 to 2018 and calculated an average of all rasters (A1.1).

All individual occurrence and density grids were then stacked with colony-specific environmental rasters. As a final data processing step, individual raster stacks were combined (concatenated) to form a single data set containing occurrence, density, and environmental covariates values. Using the resulting final data set, we tested spatial autocorrelation for each colony using Moran’s I (Moran 1950) and Geary’s C (Geary 1954; A1.2). A sensitivity analysis of the effect of pseudo-absence sampling on the models outputs is presented in Figure A1.1.

Modeling process
Razorbill habitat suitability and density were modeled using boosted regression tree models predicting the habitat suitability and density of Razorbills (Alca torda) around their colony in the St. Lawrence Gulf and Estuary, Quebec, Canada. Variables names are distance from the colony (distcol), sea surface temperature (sst), distance from the shore (distshore), depth, and region. Detailed description of each variable is presented in Table A1.1 and Figure A1.3.

Table 2. Relative strength (interaction size) showing the magnitude of the second order pairwise interaction detected for boosted regression tree models predicting the habitat suitability and density of Razorbills (Alca torda) around their colony in the St. Lawrence Gulf and Estuary, Quebec, Canada. Variables distances are names distance from the colony (distcol), sea surface temperature (sst), distance from the shore (distshore), depth, and region. Detailed description of each variable is presented in Table A1.1 and Figure A1.3.

| Model               | Variable 1 | Variable 2 | interaction size |
|---------------------|------------|------------|------------------|
| Habitat suitability | distcol    | sst        | 985              |
|                     | region     | sst        | 439              |
|                     | distcol    | distshore  | 357              |
| Density             | sst        | depth      | 483              |
|                     | sst        | distcol    | 72.2             |
|                     | depth      | distcol    | 31.1             |

Model validation
Density and habitat suitability models were validated using a 10-fold cross-validation where the data set comprising all the grid cells of the sampled colonies was randomly divided in 10 fold with 90% of the data set used as training data, which was then used to predict values on the remaining test fold (i.e., 10% of the data set). This procedure was repeated nine times with a different fold until all folds were used as test data set.

Performance of the habitat suitability model was assessed using discrimination and calibration (Pearce and Ferrier 2000). Discrimination performance was reported using the area under the receiver operating characteristic curve (AUC; Fielding and Bell 1997). AUC values range between 0 and 1, with values between 0.7 and 0.9 considered as good for prediction purpose, and values > 0.9 considered as excellent. A linear regression of the relative frequency of observed presences over 10 bins of predicted habitat suitability was used to determine the model calibration (slope) and bias (intercept; Phillips and Elith 2010). A perfect model is represented by calibration = 1 and bias = 0 (Phillips and Elith 2010, Oppel et al. 2012). For the density model, predictive accuracy was reported using the root mean square error (RMSE) and Pearson’s correlation coefficient between predicted and observed counts. Calibration and bias were assessed using the slope and intercept of a major axis regression of observed over predicted counts (Potts and Elith 2006, Piñeiro et al. 2008). The coefficient of determination (R²) of this regression was also

2010, Oppel et al. 2012, Hazen et al. 2021). Random selection of pseudo-absences (“background”) is the most commonly used technique and was chosen to match the goal of our study (Iturbide et al. 2015, Hazen et al. 2021). Based on recommendations of Barbet-Massin et al. (2012), we selected the same number of pseudo-absences as presences. For each individual, we sampled pseudo-absence grid cells for both occurrence and density inside a radius equal to its maximum distance from the colony, but no longer than the chosen grid extent (79 km). The median percent coverage of pseudo-absences or presences in the area was 3% (5th–95th percentiles; 1–15%). A sensitivity analysis of the effect of pseudo-absence sampling on the models outputs is presented in Figure A1.1.
Table 3. Validation statistics of boosted regression trees used to predict the occurrence and density of Razorbills (Alca torda) around their colony in the St. Lawrence Gulf and Estuary, Québec, Canada. Statistics were calculated on test data set using 10-fold cross-validation and presented as average ± standard deviation over the 10 folds. AUC = area under the receiver operated characteristic curve. COR = point biserial correlation (habitat suitability model) or Pearson’s correlation coefficient (density model). For the habitat suitability model, we present calibration and bias as the slope and intercept of a binned calibration plot (see Model validation in the Methods section for more information). For the density model, we present calibration, bias and R² as the slope, intercept, and coefficient of determination of a major axis regression of observed vs. predicted counts. RMSE = root mean square error.

| Model          | AUC    | COR | Calibration | Bias         | R²    | RMSE  |
|----------------|--------|-----|-------------|--------------|-------|-------|
| Habitat suitability | 0.85 ± 0.01 | -   | 0.93 ± 0.02 | 0.039 ± 0.020 | -     | -     |
| Density        | -      | 0.74 ± 0.12 | 1.5 ± 1.0  | -0.16 ± 0.72 | 0.56 ± 0.17 | 2.08 ± 0.83 |

Predictions

Final models were fitted on the entire data set to predict the habitat suitability and density of Razorbills on a radius of 79 km around each independent colony from the St. Lawrence Gulf and Estuary. Information on colonies (i.e., name, location, estimated number of birds) were obtained from the Computerized Database of Québec Seabirds (ECCC 2020) as part of the Québec Seabird Colony Monitoring Program led by Canadian Wildlife Service, Environment and Climate Change Canada. All colonies that were active (i.e., at least one bird detected) during the last survey (excluding surveys older than 1986) were included (J.-F. Rail 2019, personal communication). Similarly to the colony-grid used for modeling, prediction grids were built around all colonies (n = 85) using the same extent and environmental covariates as described above. Habitat suitability index around the colony was predicted for each grid cell using the habitat suitability (occurrence) model. Predicted bird density around the colony (birds/km²) were obtained by re-scaling predicted counts (number of GPS locations in a grid cell) between 0 and 1 (i.e., a utilization distribution):

$$\hat{D}_{i,j} = \frac{\text{count}_{i,j}}{\text{sum}(\text{count}_{i,j})}$$

where $i$ = a given grid cell and $j$ = a given colony. We then multiplied by colony size (C) for each colony to obtain bird density (birds/km²):

$$\hat{BD}_{i,j} = \hat{D}_{i,j} * C_j$$

for grid cell $i$ and colony $j$. We obtained colony size estimates (number of breeding individuals) from the Computerized Database of Québec Seabirds (ECCC 2020). We divided the number of individuals by two to obtain the number of pairs; we assumed that half of the individuals were at-sea while the other half (the partners) were at the colony. To produce an estimate of bird density for the entire study area, we combined each prediction grid and overlapping cells using the mosaic function in the raster package (Hijmans and van Etten 2012). For the habitat suitability mosaic, overlapping values were combined based on the probability of a union of events (DeGroot and Schervish 2012):

$$P = 1 - \prod_{i=0}^{I} (1 - p_i)$$

where $p_i$ is the habitat suitability index for a pixel of one colony and $P$ is the number of overlapping pixel of different independent colonies.

This resulted in a raster of habitat suitability index ranging between 0 and 1. For the density mosaic, overlapping values were summed. Largest areas of high habitat suitability index (i.e., hotspot) were determined by keeping cells with a habitat suitability index higher than 0.75 and merging contiguous cells.

RESULTS

Average trip distance for all colonies was 15.2 ± 18.5 km (range 0.04–156 km) and varied from 6.0 ± 9.3 km (range: 0.04–50.3 km) at Gros Pot Island (number of positions = 421, number of loggers = 4) to 31.4 ± 27.9 km (range: 0.05–106 km) at Iles Sainte-Marie (number of positions = 1145, number of loggers = 10; Table A1.3).

Model performance

The habitat suitability model was good at discriminating between absences and presences (AUC = 0.85; Table 3) and was well calibrated (calibration: 0.93, bias: -0.039). For the density model, bias (-0.16), RMSE (2.08 ± 0.3), and calibration (1.5) were satisfactory. Predicted density values were correlated to observed values (Pearson correlation, $r = 0.74$). The density model explained 56% of the variation.

Effect of environmental covariates

Distance to the colony was the main covariate affecting habitat suitability and density of Razorbills with a relative influence of 20% and 48%, respectively (Fig. 2). Habitat suitability and density decreased drastically as distance to the colony increased (Fig. A1.3). In general, habitat suitability index and density were higher near the coast and in shallower depths. The relative influences of SST and chlorophyll-$a$ were in the second (18%) and third (15%) ranks, respectively, after distance from the colony in the habitat suitability model, but only 6% and 7%, respectively in the density model (Fig. 2). Both metrics decreased with SST and peaked at a chlorophyll-$a$ concentration near 5 mg/m³ (Fig. A1.3).

Predictions

Density and habitat suitability maps for all colonies are presented in Figures 3 and 4, respectively, and in raster formats in Appendix 2 and 3, respectively. The five largest habitat suitability hotspots were: (1) North Shore of the St. Lawrence (near Iles Sainte-Marie; 6043 km²), (2) Saguenay-St. Lawrence Estuary confluence...
Fig. 2. Relative influence of nine environmental covariates affecting (a) the habitat suitability, and (b) density of Razorbills (*Alca torda*) around their colony in the St. Lawrence Gulf and Estuary, Québec, Canada. Variables are distance from the colony (distcol), sea surface temperature (sst), chlorophyll-a concentration (chloro), distance from the shore (distshore), depth, slope, rugosity, and region. Detailed description of each covariate is presented in Table A1.1 and Figure A1.3.

Fig. 3. Razorbill (*Alca torda*) density (birds/km²) during the breeding season predicted for all active colonies (n = 85), based on 58 GPS-tracked individuals from six colonies. The resolution of the raster is 1 x 1 km. Predictions beyond a radius of 79 km around colonies were set as NAs (hatched areas).

Fig. 4. Razorbill (*Alca torda*) habitat suitability index (0 to 1) during the breeding season predicted for all active colonies (n = 85), based on 58 GPS-tracked individuals from six colonies. The five largest habitat suitability hotspots are shown (black solid contour line): (1) North Shore of the St. Lawrence, (2) Saguenay-St. Lawrence Estuary confluence, (3) Anticosti Island, (4) Gaspé Peninsula, and (5) Mingan Archipelago National Park Reserve. The resolution of the raster is 1 x 1 km. Predictions beyond a radius of 79 km around colonies were set as NAs (hatched areas).

(4844 km²), (3) Anticosti Island (1269 km²), (4) Gaspé Peninsula (1212 km²), and (5) Mingan Archipelago National Park Reserve (1032 km²; Fig. 4).

**DISCUSSION**

Razorbill habitat suitability and density were successfully predicted for the 85 monitored colonies throughout the St. Lawrence during the breeding season. Using BRT modeling, we determined hotspots of high-habitat suitability, which can be used for conservation efforts. The relative influence of environmental covariates differed between habitat suitability and density models, but distance from the colony ranked first in both models. This latter result was expected, because Razorbills are central place foragers during the breeding period, which forces them to return to the colony to incubate their egg or feed their chick. The foraging
range of Razorbills is usually closer to the colony than other sympatric alcids in the North Atlantic (Lavers et al. 2020). In the Mingan Archipelago (Gulf of St. Lawrence), Razorbills traveled on average 7.2 ± 0.1 km from their colony during a foraging trip compared to 30.7 ± 0.6 km for Common Murres (Uria aalge) and 56.7 ± 0.5 km for Black-legged Kittiwake (Rissa tridactyla; Petalas et al. 2021). Breeding Razorbills tracked with GPS in Saint Pierre and Miquelon Archipelago (northwestern Atlantic) foraged at a maximum distance from the colony of 11 ± 10 km (Delord et al. 2020). Distance from the colony was among the principal factors influencing foraging of breeding Wedge-tailed Shearwaters (Ardenna pacifica) in Australian marine waters using a similar statistical approach (i.e., BRT on GPS-tracked adults; McDuie et al. 2018).

Distance to shore was the fourth and second most important predictor for habitat suitability and density models, respectively. In addition, the combined bathymetry metrics (slope, rugosity, and depth) had a moderate relative influence in both models. The foraging habitat of Razorbill is generally found in relatively shallow waters, close to shore, and where feeding conditions (often at fronts and upwellings) and concentrations of their prey are predictable (Huettmann et al. 2005, Lavers et al. 2020). Razorbills are more selective in the choice of their foraging habitat than other sympatric alcids (Wanless et al. 1990, Huettmann et al. 2005). In the Gulf of St. Lawrence, Razorbills are known to forage almost exclusively on capelin (Mallophus villosus) and sand lance (Ammodytes sp.) during the chick-rearing period (Chapdelaine and Brousseau 1996, Lavoie et al. 2012, Petalas et al. 2021). Razorbills use waters closer to shore compared with many other sympatric seabirds (Gaston and Jones 1998, Thompson et al. 1999, Huettmann et al. 2005).

Dynamic variables such as chlorophyll-α concentration and SST had a clear effect on the habitat suitability model, but not on the density model. Previous studies found that dynamic variables explained foraging locations of seabirds during the chick-rearing period (Domalik et al. 2018, McDuie et al. 2018). Foraging areas of seabird species can be predicted by low SST and high chlorophyll-α concentrations, which are indicative of upwelling and primary productivity (Grecian et al. 2016). For Razorbills, Delord (2020) found that SST explained the behavioral state (transit vs. foraging) of breeding adults in the Saint Pierre and Miquelon Archipelago. Areas where mixing of water masses occurs (with different temperatures and salinities) have also been found to favor Razorbill aggregation (Begg and Reid 1997, Camphuysen and Webb 1999). In our study, habitat suitability decreased with temperature, which is consistent with their preferred prey (capelin and sand lance) that are found in cold waters (Scott and Scott 1988).

Razorbill habitat suitability hotspots were found in five main areas (Fig. 4), which are known colonial seabird diversity and abundance hotspots. The North Shore, near Iles Sainte-Marie, is notable for its large numbers of Razorbill colonies and other alcid species such as Common Murres and Atlantic Puffins (Fratercula arctica; Rail and Cotter 2015). In addition, primary and secondary productivity is notably high in the Saguenay-St. Lawrence Marine Park where large numbers of marine mammals and seabirds can be found (Bédard et al. 1997, Rail 2018). The Gaspé Peninsula region supports several seabirds including a large Northern Gannet (Morus bassanus) colony, which heavily feeds on capelin, sand lance, Atlantic Mackerel (Scomber scombrus), and Atlantic Herring (Clupea harengus; Rail et al. 2013, Pelletier and Guillemette 2022). The Mingan Archipelago National Park Reserve is also an area of high seabird biodiversity and abundance. The five largest habitat suitability hotspots found in our study were corroborated by the results of the Atlas of Seabirds at Sea in Eastern Canada 2006–2020 (ECCC 2022) during the breeding season. The Atlas is a series of maps based on the Eastern Canada Seabird at Sea (ECSAS) survey conducted annually by the Canadian Wildlife Service in the Quebec and Atlantic regions. This survey is conducted by recording seabirds at sea from ships using line and point transects followed by a distance sampling approach to estimate bird density (Gjerdrum et al. 2012). Although the maps generated were of lower resolution (100 x 100 km) than the current study (1 x 1 km), these two independent assessment methods captured a very similar spatial pattern throughout the St. Lawrence during the breeding season, which increases the confidence in the validity of our model. The hotspot areas presented in this study also correspond to zones of high cumulative threats (ship-source oiling, marine traffic, bycatch, and light pollution) according to the assessment of Lieske (2020) for seabirds in general, and more specifically for alcids. Finally, each hotspot area identified in our study overlaps with one or more Important Bird Areas (http://www.ibacanada.com). The areas presented here will help to rapidly and efficiently communicate with response agencies the level of threat that Razorbills are facing in the event of an environmental emergency such as an oil spill. They will be useful to designate areas of special concern to prioritize and direct response strategies.

The BRT model performed well for the studied environment and led to comprehensive maps of the Razorbill’s at-sea distribution in the St. Lawrence. A similar BRT model to ours was used on the Atlantic Coast of Canada for 13 species/groups of seabirds from over 5000 species-specific colonies to predict abundance (Lieske et al. 2020). The authors used seabird abundance and anthropogenic threats (e.g., ship-source oil pollution) as well as a sensitivity index to those threats to map cumulative risks. Our study incorporated additional environmental covariates in the model and presented maps of finer resolution. BRT models have been used on GPS-tracked marine mammals, sharks, turtles, and seabirds in various marine systems to identify or to predict foraging patches, sensitive areas, or densities at various stages of the animals’ life cycle (Hazen et al. 2017, Hazen et al. 2018, Lieske et al. 2020) and shows the wide applications of this method.

The maps presented here will help with conservation efforts, monitoring, risk mitigation associated with anthropogenic activities, and scientific purposes. Seabirds are vulnerable to fisheries bycatch and it is estimated that between 2679 to 45,586 birds die annually across Canada as a result (Ellis et al. 2013). In the St. Lawrence, approximately 464 birds die annually (range: 26–2082; Ellis et al. 2013). These are likely underestimated numbers because of carcasses lost at sea and spatial data gaps due to low observer coverage on fishing boats (Ellis et al. 2013). A better understanding of birds’ at-sea distribution may help in identifying ways to mitigate the mortality rate. For instance, certain key areas presented here could be avoided by fisheries activities during critical times such as the breeding period. In
addition, seabirds are vulnerable to oil spills because they spend most of their time at sea and any exposure to oil can lead to adverse health effects and death. Spills at sea can occur from accidental or deliberate discharge. As an example, between 1000 and 4000 birds died as a result of an oil spill from the ship the Gordon C. Leitch that occurred during the non-breeding period in 1999 near Havre-Saint-Pierre (Roberge and Chapdelaine 2000), an area used by some of our tagged Razorbills from the Betchouane Migratory Bird Sanctuary. Such an event occurring during the breeding season would undeniably have more serious consequences on the avian community. At-sea distribution of seabirds that are susceptible to oiling like Razorbills can help to assess risk and develop a response strategy to prevent adverse situations (IPIECA 2014). Decisions need to be made quickly in order to mitigate risk to wildlife and prior knowledge on areas of greater or lower risk are needed for a successful operation and an efficient use of resources (ECCC, in press). In the St. Lawrence, higher boat traffic, marine pollution, and overall greater risk occurs in the narrower and southern sections (Beauchesne et al. 2020). Our analysis shows that Razorbills in the Saguenay-St. Lawrence Estuary confluence and in the Gaspé Peninsula face greater oiling and cumulative risk factors (Fig. 4).

The maps presented in this study will be a good tool to help governmental bodies (e.g., Canadian Wildlife Service) to better prepare and respond to environmental emergencies. For instance, rapid estimates of birds’ occurrence and density will be readily available to efficiently communicate information to, and properly advise governments, Indigenous organizations, industry, response organizations, and other stakeholders. These estimates are important to identify wildlife and their key habitats that are expected to be affected (ECCC, in press). Appropriate actions can then be planned proportionally to the potential impact on birds. Efforts are currently underway to use this model template on other species and obtain a more complete overview of seabirds’ at sea across the St. Lawrence. A better general understanding of at-sea distribution will help with conservation efforts and mitigate impacts in case of environmental emergencies.

Responses to this article can be read online at: https://www.ace-eco.org/issues/responses.php/2188

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Appendix 1. Supporting Text, Tables, and Figures.

Text A1.1. Environmental data

During the breeding season, the distance and duration of Razorbills’ foraging trips are constrained by the need to make round trips to the nest (i.e. central place) to incubate their egg or feed their chick. Hence, the distance to any foraging location from the colony becomes an important environmental feature that will affect the space use of birds during nesting. Since Razorbills avoid flying over large patches of land, we reported distance to the colony as the effective geographical distance (Michels et al., 2001), defined here as the Euclidean distance from each grid cell to the colony, avoiding travel through land. Using functions from the gdistance package in R (van Etten, 2017), we performed a least-cost path analysis (Adriaensen et al., 2003) using a colony-centered resistance layer with terrestrial grid cells having a high resistance cost (i.e., 999999) and water cells having a low resistance cost (i.e., 1). The parameter to determine which adjacent pixels are used to determine cumulative cost values was set to 8 as a tradeoff between a more circular aspect around colonies (when using a parameter of 16) and computing time. Moreover, a parameter of 8 is the most common way to connect grids in GIS software (van Etten, 2017). The resulting least-cost path raster was a continuous variable of cumulative distance from the colony, avoiding any land surface. To adjust each analysis grid to a biologically meaningful extent, we excluded from further analysis all grid cells with a distance to the colony value larger than the mean of maximum foraging distances recorded across all colonies (79 km). For each grid cell, we also calculated the minimum distance to the nearest shoreline using a coastline feature (1:250 000 scale) and Euclidean distance tool in ArcGIS 10.2.2 (ESRI).

Bathymetric data were extracted from a 30 arc-second global grid of elevation on the British Ocean Data Centre database (BODC; https://www.bodc.ac.uk). Depth was defined as the below-zero (sea-level) values of elevation. After removing mainland values, there were still some raster cells containing small islands with non-negative values, thus creating a bias of “available” depth for Razorbills. All remaining non-negative values were set to zero and considered as not available. Slope and rugosity of seabed floor were extracted from depth, calculated in a 3 x 3 km roving window so that the value of each cell was calculated from the values of its surrounding cells (Horn, 1981). Both metrics were calculated with the terrain function of the raster package (Hijmans and van Etten, 2012).

We used chlorophyll-a concentration (mg/m³) as a proxy for primary productivity estimated from Visible Infrared Imaging Radiometer Suite (VIIRS). Chlorophyll monthly composite maps (0.0375 degree resolution) were obtained from the National Oceanic and Atmospheric Administration (NOAA) ERDDAP data server (https://coastwatch.pfeg.noaa.gov) for June and July from 2015 to 2018. Each monthly georeferenced data sets where transformed into a raster using NetCDF Raster Layer tool in ArcGIS 10.2.2.
Sea surface temperature (SST; °C) data for the St. Lawrence Gulf and Estuary was extracted as monthly composite maps for June and July from 2015 to 2018 from Galbraith et al. (2018) at a resolution of 0.01 degree of latitude and 0.015 degree of longitude.

Dynamic oceanographic data such as SST and chlorophyll-α concentration can vary temporally. Between-years Pearson’s correlation coefficients for chlorophyll-α concentration monthly composites were 0.67 ± 0.10 (±SD) for June and 0.67 ± 0.10 for July and correlations for SST were 0.85 ± 0.04 for June and 0.87 ± 0.11 for July. Between-months correlation coefficients ranged from 0.65 to 0.81 for chlorophyll-α concentration monthly composites and from 0.66 to 0.83 for SST. For prediction purpose, we averaged years (2015–2018) and months (June and July) and used the resulting rasters for both covariates in the boosted regression tree (BRT) model. Climatological covariates are preferred since they represent the long-term state (i.e., 4 years in this case) of the environment at a given location during moment of interest (i.e., breeding season in this case (Mannocci et al., 2017)). This monthly scale was considered a good trade-off to capture coarse dynamic marine features, while reducing gaps in maps (Derville et al., 2018, Perez-Correa et al., 2020). The spatial coverage of the SST layer was incomplete in some areas with a complex shoreline. We interpolated data from an 5 x 5 km roving window to fill those gaps (i.e., NAs) using the function `focal` implemented for R package `raster` (Hijmans, 2019). Each grid cell with missing values at the center of a non-empty roving window was assigned a value equal to the average of the non-empty pixel values within the window as described in Jaafar and Ahmad (2020), which used Landsat 7 images: thermal, red, near-infrared, and surface reflectance shortwave bands.

Text A1.2 Spatial autocorrelation

Spatial autocorrelation is an inherent problem in ecological sampling and must be accounted for in distribution models (Dormann, 2007). For each colony grid, we calculated Moran’s I (a measure of global spatial autocorrelation (Moran, 1950)) and Geary’s C (a measure of local spatial autocorrelation (Geary, 1954)). Values of Morans’s I range between -1 and 1 while Geary’s C range from 0 to 2. Values near 0 and 1 for Moran’s I and Geary’s C, respectively, indicate random spatial patterns and thus, no spatial autocorrelation. Both metrics were calculated for the 50 nearest neighbouring grid cells using functions `moran.test` and `geary.test` implemented in the package `spdep` (Bivand et al., 2013, Bivand and Wong, 2018) using the software R (R Core Team, 2019). Our data provided low evidence of spatial autocorrelation for both habitat suitability (Moran’s $I = 0.002 \pm 0.006$ SD; Geary’s C: 0.997 ± 0.006 SD, n = 6) and density (Moran’s $I = 0.13 \pm 0.10$ SD; Geary’s C: 0.91 ± 0.08 SD, n = 6) grids. Therefore, no additional measures were taken to account for spatial autocorrelation in the modelling process.
Table A1.1. List of environmental covariates used to predict the habitat suitability and density of Razorbill in Quebec using boosted regression trees.

| Covariate (abbreviation) | Unit       | Original resolution | Description                                                                                                                                 |
|--------------------------|------------|---------------------|---------------------------------------------------------------------------------------------------------------------------------------------|
| Distance from the colony (distcol) | m          | 1 km                | Minimum distance by sea from the centroid of each grid cell to the colony location                                                          |
| Distance to the nearest shoreline (distshore) | m          | 1 km                | Euclidean distance from the centroid of each grid cell to nearest shoreline                                                                  |
| Depth                    | m          | 30 arc-second       | Depth at centroid of each grid cell                                                                                                          |
| Rugosity                 | m          | 30 arc-second       | Standard deviation in depth in a 3 x 3 km roving window from the centroid of each grid cell                                                   |
| Slope                    | º          | 30 arc-second       | Slope from a 3 x 3 km roving window from the centroid of each grid cell                                                                      |
| Chlorophyll $a$ concentration (chloro) | mg/m$^3$ | 0.0375º             | Average of monthly composite in chlorophyll $a$ concentration calculated for June and July 2015-2018                                           |
| Sea surface temperature (sst) | ºC         | 0.01º lat * 0.015º long | Average of monthly composite in sea surface temperature calculated for June and July 2015-2018                                               |
| Region                   | -          | -                   | Region of the St. Lawrence river where the colony is present; either Gulf or Estuary                                                        |
Table A1.2. Cross-validation results to find optimal parameters of boosted regression trees used to predict the habitat suitability and density of Razorbills around their colony in the St. Lawrence Gulf and Estuary, Québec, Canada. Multiple combinations of learning rate (\(lr\)) and tree depth (\(td\)) were tested to find the optimal number of trees (\(nt\)) for a given combination. A first BRT model is built using \(nt = 50\), and average cross-validation deviance over 10 folds ± standard deviation (CV dev. ± SD) is recorded. The next BRT is built by adding 50 trees and so on, until the minimization of cross-validation deviance. Here we present the optimal number of trees (optimal \(nt\)) for each combination, for both models. The combination used to fit each model is in bold.

| Tree parameters | Habitat suitability \(^a\) | Density \(^a\) |
|-----------------|-----------------------------|--------------|
|                 | \(lr\) \(td\) \(nt\) \(CV\) dev. ± SD | \(nt\) \(CV\) dev. ± SD |
| 0.001           | 3  10000  0.068 ± 0.001 | 6150  4.59 ± 0.379 |
| 0.001           | 4  10000  0.067 ± 0.001 | 5400  4.58 ± 0.432 |
| 0.001           | 5  10000  0.066 ± 0.001 | 5150  4.50 ± 0.298 |
| 0.001           | 6  NA  NA | 5500  4.47 ± 0.459 |
| 0.001           | 7  NA  NA | 5350  4.50 ± 0.359 |
| 0.001           | 8  NA  NA | 4850  4.57 ± 0.285 |
| 0.005           | 3  7700  0.065 ± 0.001 | 2000  4.53 ± 0.317 |
| 0.005           | 4  6350  0.064 ± 0.001 | 1600  4.51 ± 0.283 |
| 0.005           | 5  5900  0.064 ± 0.001 | 1250  4.49 ± 0.227 |
| 0.005           | 6  5100  0.064 ± 0.001 | 1400  4.43 ± 0.321 |
| 0.005           | 7  4850  0.064 ± 0.001 | 1350  4.56 ± 0.345 |
| 0.005           | 8  5000  0.063 ± 0.001 | 1350  4.51 ± 0.415 |
| 0.01            | 3  5950  0.064 ± 0.001 | 850  4.52 ± 0.353 |
| 0.01            | 4  4650  0.064 ± 0.001 | 1250  4.44 ± 0.285 |
| 0.01            | 5  4450  0.064 ± 0.001 | 750  4.45 ± 0.323 |
| 0.01            | 6  4350  0.063 ± 0.001 | 750  4.45 ± 0.288 |
| 0.01            | 7  4000  0.063 ± 0.001 | 500  4.53 ± 0.203 |
| 0.01            | 8  3250  0.063 ± 0.001 | 500  4.50 ± 0.366 |
| 0.05            | 3  3050  0.064 ± 0.001 | NA  NA |
| 0.05            | 4  2600  0.063 ± 0.001 | NA  NA |
| 0.05            | 5  2100  0.063 ± 0.001 | 200  4.45 ± 0.377 |
| 0.05            | 6  1850  0.063 ± 0.001 | NA  NA |
| 0.05            | 7  1600  0.063 ± 0.001 | NA  NA |
| 0.05            | 8  1550  0.063 ± 0.001 | NA  NA |

\(^a\) The habitat suitability model and the density model were fitted using a Bernoulli and a Poisson distribution, respectively (\(n = 9064\) grid cells).
Table A1.3 Distance from the colony (min, max, mean ± sd; km), sample size (positions and individuals) and date range (min, max).

| Colony                | min  | max  | mean | sd   | n positions | n individuals | min date | max date |
|-----------------------|------|------|------|------|-------------|--------------|----------|----------|
| Betchouane Island     | 0.05 | 43.8 | 7.8  | 7.9  | 1757        | 11           | June 7   | July 14  |
| Bicquette Island      | 0.05 | 37.4 | 7.4  | 8.0  | 2350        | 11           | June 6   | July 9   |
| Corossol Island       | 0.08 | 156  | 22.3 | 20.1 | 1326        | 5            | June 6   | July 21  |
| Gros Pèlerin Island   | 0.04 | 79.5 | 17.7 | 18.6 | 2804        | 17           | May 26   | July 4   |
| Gros Pot Island       | 0.04 | 50.3 | 6.0  | 9.3  | 421         | 4            | June 10  | June 29  |
| Iles Sainte-Marie     | 0.05 | 106  | 31.4 | 27.9 | 1145        | 10           | July 4   | July 25  |
| All                   | 0.04 | 156  | 15.2 | 18.5 | 9803        | 58           | May 26   | July 25  |
Figure A1.1 Sensitivity analysis of the effect of pseudo-absence sampling on the relative influence of covariates on models. Habitat suitability (left) and density (right) models were run 1,000 times with a random set of pseudo-absences for each iteration. Violin plots (gray) show the distribution of the relative influence of each covariate with means (black points) and standard deviations (black lines). Red points refer to the values computed by the model reported in the paper.
Figure A1.2. Spatial variation maps of six out of eight covariates used to predict Razorbill distribution and density in the St. Lawrence Gulf and Estuary. Here we present the distribution of (a) distance to the nearest shoreline (m), (b) depth (m), (c) rugosity (m), (d) slope (degree), (e) sea surface temperature (°C) averaged for June and July 2015–2018, and (f) chlorophyll-a concentration (mg/m³) averaged for June and July 2015–2018. See Table A1.1 for detailed descriptions and abbreviations of covariates.
Figure A1.3. Partial dependence plots showing the relationship between environmental covariates and predicted habitat suitability index (HSI; black line) and density (red line) of Razorills around their colony in the St. Lawrence Gulf and Estuary, Québec, Canada. Partial dependence fitted functions (lines) show the effect of a variable on the response after accounting for the average effects of all other variables in the model. Rug plots at inside top of plots show distributions across that variable, in deciles. See Table A1.1 for detailed descriptions of covariates.
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Appendix 2. Raster file of bird density (bird/km2).

Please click here to download file 'appendix2.tif'.
Appendix 3. Raster file of habitat suitability index.

Please click here to download file ‘appendix3.tif’.