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## Projecting regions of North Atlantic right whale, *Eubalaena glacialis*, habitat suitability in the Gulf of Maine in 2050

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Projecting regions of North Atlantic right whale,  
*Eubalaena glacialis*, habitat suitability in the Gulf of Maine  
in 2050

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May 18, 2020

A thesis submitted to the faculty of the Environmental Studies Program in  
partial fulfillment of the graduation requirements for the Degree of Bachelor  
of Arts with honors in Environmental Studies

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## ABSTRACT

North Atlantic right whales (*Eubalaena glacialis*) are endangered. Understanding the role environmental conditions play in habitat suitability is key to determining the regions in need of protection for conservation of the species, particularly as climate change shifts suitable habitat. This thesis uses three species distribution modeling algorithms, together with historical data on whale abundance (1993 to 2009) and environmental covariates to build monthly ensemble models of past *E. glacialis* habitat suitability in the Gulf of Maine. Then, the models are projected onto the year 2050 for a range of climate scenarios. Specifically, the distribution of the species was modeled using generalized additive models, boosted regression trees, and artificial neural networks, and the environmental covariates included sea surface temperature, bottom water temperature, bathymetry, a modeled *Calanus finmarchicus* habitat index, and chlorophyll. The 2050 projections used downscaled climate anomaly fields from RCP 4.5 and 8.5. The relative contribution of each covariate changed seasonally, with an increase in the importance of bottom temperature and *C. finmarchicus* in the summer when model performance was highest. Additionally, there was a negative correlation between model performance and sea surface temperature. The 2050 projections indicated decreased habitat suitability across the Gulf of Maine during the months assessed, with the exception of narrow bands of suitability along the Scotian Shelf in August, September, and October. The results suggest that regions outside of the current areas of conservation focus may become increasingly important habitats for *E. glacialis* under future climate scenarios.



## ACKNOWLEDGEMENTS

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## INTRODUCTION

Many species of baleen whales were hunted to near extinction in the last few centuries as a result of commercial whaling (Clapham et al. 1999). Of the Gulf of Maine species, the North Atlantic right whale (*Eubalaena glacialis*) suffered the greatest population loss due to high commercial demand and is currently one of the most endangered marine mammals on the planet (listed as ‘Endangered’ on the IUCN Red List; Cooke 2018; COSEWIC 2013), with an estimated population size of 408 (Pettis et al. 2019). Important *E. glacialis* habitats overlap with regions of high human activity, including heavily trafficked shipping lanes and fishing grounds (Kraus et al. 2005), which has inhibited post-whaling recovery (Clapham et al. 1999). The anthropogenic threats of vessel strikes and entanglement in fishing gear currently pose high risks to the species (Kraus 1990; Caswell et al. 1999; Knowlton and Kraus 2001; Kraus et al. 2005; Kenney 2018; Sharp et al. 2019). In 2010, *E. glacialis* appears to have experienced a regime shift that coincided with increases in deep water temperature and the biomass of *Calanus finmarchicus*, a crucial food source (Davis et al. 2017; Record et al. 2019b; Sorocean et al. 2019), suggesting that the species is vulnerable to the effects of climate change. The calving rate since 2010 has dropped roughly 40%, raising concern for the future of the species (Kraus et al. 2016).

Despite their rarity today, large whales, including *E. glacialis*, serve fundamental ecological roles. Prior to commercial whaling, large whales likely recycled more nitrogen than three times the atmospheric input to the ocean. Today, large whales still sustain productivity in ecosystems by bringing deep water nutrients to the surface despite lower population numbers (Roman and McCarthy 2010). When whales die and sink to the bottom of the ocean, they provide substrate for whale fall ecosystems. Whale falls are unique communities of organisms that have evolved to live off of the resources provided by whale carcasses. Up to 90% of all whale mortalities eventually become whale falls, allowing for these ecosystems to flourish and facilitating the recycling of nutrients (Smith and Baco 2003). Additionally, large whales served as a major carbon storage pool prior to commercial whaling. Due to their large biomass, whales efficiently sequester carbon in the ocean floor when they die, and rebuilding populations could be part of an effective strategy to manage carbon (Pershing et al. 2010).

For much of the year — summer through fall — *E. glacialis* heavily rely upon *C. finmarchicus*, a lipid-rich copepod that is abundant in the Gulf of Maine in the summer months (Baumgartner et al. 2003a; Runge et al. 2014). During the summer growing season, *C. finmarchicus* store lipids in order to survive overwintering (Ji et al. 2011), providing an energy-rich prey source for whales. *C. finmarchicus* mature within months in temperate waters like the Gulf of Maine (Ji et al. 2011), which has historically provided suitable habitat for this species of zooplankton. However, warming waters are likely affecting the suitability of the Gulf of Maine for *C. finmarchicus* (Plourde et al. 2009; Runge et al. 2014; Record et al. 2019a). The distribution of *E. glacialis* shifted around the year 2010 (Meyer-Gutbrod and Greene 2014; Davis et al. 2017; Pettis et al. 2019), with an increased presence in the mid-Atlantic region and a decreased presence in the Gulf of Maine, suggesting that *E. glacialis* habitat suitability may be directly affected by warming waters. As populations of copepods, namely *C. finmarchicus*, shift their distribution, *E. glacialis* will likely have to forage in new areas to find food (Pendleton et al. 2009). The current uncertainty in the seasonal patterns of *E. glacialis* feeding grounds and how they are likely to shift as climate change progresses confounds efforts to protect the species from anthropogenic threats, including ship strikes and entanglement in fishing gear. In order to conserve *E. glacialis*, assessing current knowledge of climate-driven regime shifts and the effectiveness of current management strategies is imperative (Record et al. 2019b).

Species distribution models (SDMs) are an important tool for modeling and predicting habitat suitability (Elith et al. 2006). They can also help to derive a more complete picture of the distributions of rare or elusive species (Guisan and Zimmermann 2000; Razgour et al. 2016; e.g., Bosso et al. 2018), such as *E. glacialis*. SDMs work by deriving relationships between species occurrence data (i.e. presence/absence) and relevant environmental covariates. These relationships can then be projected into different spatial and temporal domains. SDMs are important tools for understanding the potential present and future distributions of a species, which is an important component of long term resource management plans. Many SDM algorithms have been developed, and their relative performance compared (Elith et al. 2006). Selecting the best algorithm to model a species' distribution can be challenging. Ensemble modeling allows for the

merging of multiple different SDMs in order to combine the benefits of individual algorithms and help optimize model performance (Thuiller et al. 2009).

The focus of this thesis is on *E. glacialis* in the Gulf of Maine (Figure 1). This region has historically been a critical foraging ground for the species. Intensive marine mammal surveys in this region over the past 30+ years (Brown et al. 2007) have provided comprehensive knowledge of where and when to expect *E. glacialis*. Because the climate has been changing so rapidly in the Gulf of Maine (e.g., Mills et al. 2013; Pershing et al. 2015), my work represents an important case study in which a range shift is occurring for the species. Understanding possible future change is essential for effective resource management planning. To address these concerns, I built and projected monthly ensemble SDMs of *E. glacialis* habitat suitability in the Gulf of Maine using an extensive presence/absence dataset from multiple marine mammal surveys. I used output from a downscaled physical ocean model for moderate and extreme (i.e. high end of “business as usual”) warming scenarios, satellite-derived chlorophyll data, and modeled *E. glacialis* prey as environmental covariates. Because there is uncertainty surrounding the future state of the climate, as well as current knowledge of *E. glacialis* movement patterns, these projections do not represent forecasts. Instead, they constitute a synthesis of the current state of knowledge of the distribution of *E. glacialis* and represent an approach to understanding what some potential future habitat scenarios for this endangered species may look like.

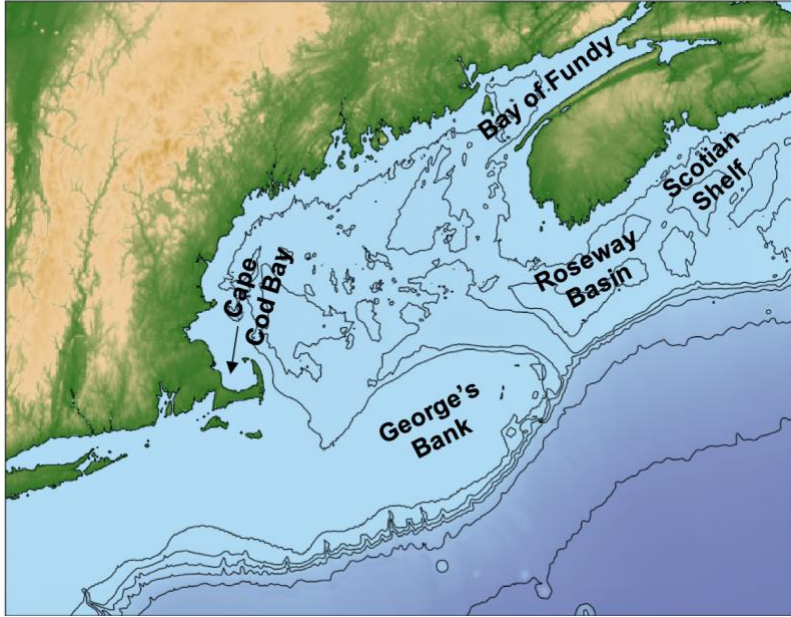
## **METHODOLOGY**

### **Study Area**

The study extent covers the Gulf of Maine from 39° – 45°N and 63° – 71°W (Figure 1a). This domain includes important historically recognized summer feeding grounds for *E. glacialis*, namely Cape Cod Bay (Mayo et al. 2004), the Great South Channel (CETAP 1982; Kenney and Wishner 1995), and the Bay of Fundy and Roseway Basin (Brown et al. 2009; Plourde et al. 2019). The study extend also includes areas known to host large numbers of right whales, but which have not been identified as primary feeding grounds, such as the area between the New York shipping lanes and Cape Cod (Leiter et al. 2017),

the deep basins of the Gulf of Maine, and the Scotian Shelf (Plourde et al. 2019; Figure 1a).

a)



b)

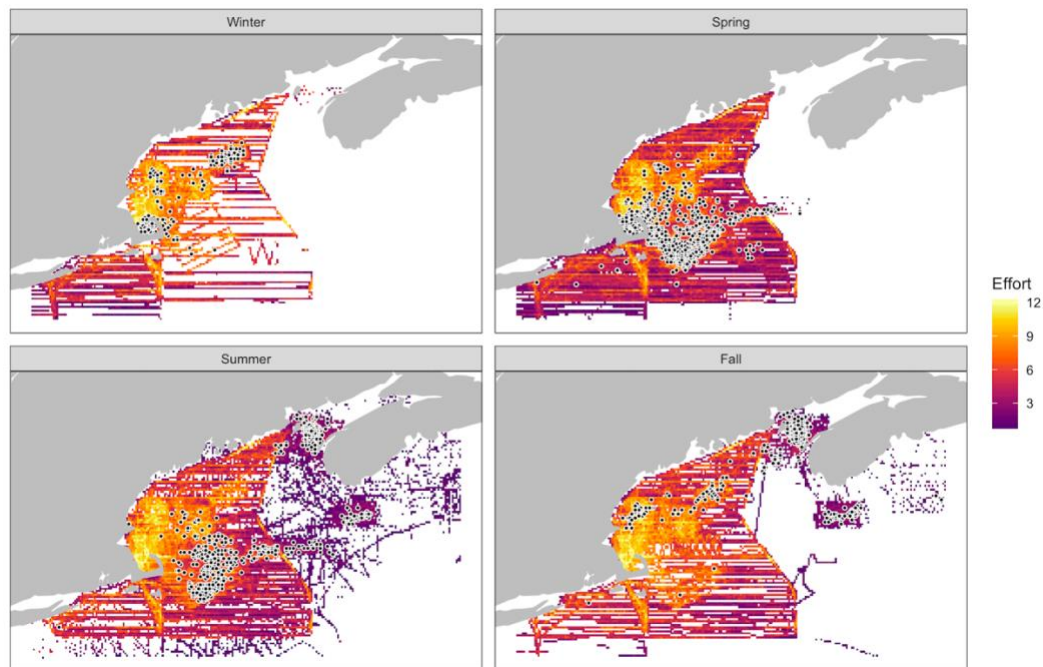


Figure 1. Effort in the study area for winter, spring, summer, and fall normalized to one visit to each location per month. The black dots with white outlines correspond to sightings in the study area during each of the seasons. Effort is cumulative, but each map only shows pixels in which there was effort during that season.

### **Species Presence/Absence Data**

I obtained marine mammal survey effort and associated sighting conditions from the North Atlantic Right Whale Consortium (NARWC) Sightings Database (NARWC, 2016). From this dataset, I extracted records of *E. glacialis* presence and absence (survey effort but *E. glacialis* not present) spanning the years 1993 to 2009 for my study area (Appendix I; Figure 1b). I selected this range of years to overlap with the years represented by the environmental covariate data, because of high survey effort, and because the data preceded the year during which *E. glacialis* began to shift their distribution in response to changes in the Gulf of Maine climate (i.e. 2010). Included in the dataset are survey and *E. glacialis* sighting information from numerous programs. Major data contributions to the dataset we used (> 5% of the dataset) came from shipboard and aerial surveys conducted by Center for Coastal Studies from 1997 - 2009 (Brown et al. 2007), the New England Aquarium from 1993 to 2009, and the National Marine Fisheries Service (Cole et al. 2007). My dataset included data from line-transect surveys and from platforms-of-opportunity, as described in Pendleton et al. (2009). We excluded records for which the Beaufort sea state was greater than 3 and visibility was less than or equal to 2 nautical miles, both of which are indicators of poor conditions.

### **Environmental Covariate Data**

Physical environmental covariate data was extracted from the present and future climate simulations from the BNAM high resolution ocean circulation model of the North Atlantic Ocean (Brickman et al. 2016), with the Gulf of Maine region being the focus of my thesis. The BNAM simulations use an average of six CMIP5 future climate atmospheric forcings to produce RCP 4.5 and RCP 8.5 climatologies for the periods centered on 2055 and 2075. In general, the model projections for the two RCPs are similar, with the main difference being that the RCP 4.5 scenario projects weaker temperature increases throughout the water column. The BNAM output includes temperature, salinity, and fluid dynamics fields for the entire water column, which have been used in numerous future climate studies (e.g. Beazley et al. 2018; Stanley et al. 2018; Le Corre et al. 2020; Mbaye et al. 2020).

I used monthly chlorophyll data from the Ocean Color Climate Change Initiative (OC-CCI; Sathyendranath et al. 2019), linearly interpolated to match the spatial grid of the BNAM model. My analysis took a climatological approach, using model averaged output representing the present climate period, centered around 1995. This period is representative of the conditions in the Gulf of Maine prior to the recent rapid climate shift (e.g. Pershing et al. 2015). The *C. finmarchicus* field was calculated using a life history model with sea surface temperature and surface chlorophyll as inputs (Ji et al. 2011). This model uses the seasonally varying conditions and provides a good index of the suitability of a location for diapause that can be estimated from available environmental data (Record et al. 2018). The bathymetry layer for the study extent was the NOAA ETOPO1 relief model (Amante and Eakins 2009), downsampled to match the grid of the other data layers.

### **Data Processing**

Presences and absences were extracted from the NARWC sightings database. Latitude and longitude values for each record were collated to a raster grid with 0.058km by 0.089km spatial resolution. The grid was defined by the native grid of the environmental covariate data as described above — specifically that of the BNAM physical ocean model. Duplicate records in one pixel on the same day were reduced to a presence if at least one record contained a presence and converted to an absence if there was survey effort in that pixel, but no presences were recorded. The environmental covariate values at each pixel containing a presence or absence were appended to the sightings and effort data. The newly formatted data was cross-checked with the original environmental covariate and sightings data to ensure correct matching.

I tested additional covariates in preliminary runs and excluded those that appeared to have very low explanatory power (e.g. Lyapunov exponent derived from flow fields). Correlation coefficients were computed between the covariates chosen to determine which should be included in the model. Despite a high correlation between sea surface temperature and bottom temperature ( $r = 0.92$ ), I decided to include both covariates due to differing biological significance — in particular, the importance of deep water temperatures to *C. finmarchicus* distributions.

## Building the Model

Monthly individual and ensemble models were built using the ‘*biomod2*’ package in R (Thuiller et al. 2009; R Development Core Team 2019). The package contains 10 inbuilt statistical species distribution models. I implemented generalized additive models (GAMs), binary regression trees (BRTs), and artificial neural networks (ANNs). Each algorithm has strengths and weaknesses. While GAMs are often accurate explanatory models, they tend to have low predictive capabilities (Roloff and Kernohan 1999; Pearce et al. 2000; Guisan et al. 2002). GAMs serve as good baseline models that tend to capture general trends in the data. Despite potential for overfitting, BRTs learn the data in detail and generally have higher predictive performance than other models (Leathwick et al. 2006; Elith et al. 2008). ANNs generally perform better than other models when the environmental covariates are strongly correlated (Li and Wang 2013).

For each modeling approach, I built a separate model for every month of the year, working under the assumption that the relationship between whale distribution and environmental covariates is different at different times of year. For all models, the covariates used were sea surface temperature, bottom water temperature, bathymetry, modeled *C. finmarchicus*, and chlorophyll. The individual models were built using 10-fold cross-validation with random 70% - 30% data splits for each fold. Response curves for each model were plotted to include all ten cross-validation folds.

Area under the receiver operator characteristic curve (AUC) and the true skill statistic (TSS) were used to compare ensemble and individual models, as both are robust methods to compare SDMs statistically (Fielding and Bell 1997; Allouche et al. 2006; Liu et al. 2011). AUC compares the proportion of correctly classified presences to the proportion of incorrectly classified absences between the threshold values of 0 and 1. An AUC above 0.5 indicates better performance than a random model (Fielding and Bell, 1997). AUC is useful when there is true absence data available and the goal of the model is to estimate the actual distribution of a species (Jiménez-Valverde, 2012), as is the case in this thesis. TSS compares the model output to a hypothetical validation dataset that perfectly predicted the distribution, which is then used to compute the proportion of true positives for both presences and absences. Scores range between -1 and +1, with a score of above zero indicating better performance than a random model (Allouche et al.



2006). Both AUC and TSS were computed using an inbuilt *biomod2* function (Thuiller et al. 2009). An ensemble model was created using individual models with an AUC score of greater than or equal to 0.75. The ensemble and the individual models were projected back onto the environmental covariates to create one habitat suitability prediction map for each month.

For the 2050 projections, the ensemble and each of the individual models were projected onto the future climatological covariates. For all covariates except for chlorophyll, I used the projected climatologies for RCP 4.5 and RCP 8.5. For chlorophyll, there is not yet a downscaled climate projection product for this region, so I ran each climate scenario with three chlorophyll climatologies: half of present-day levels (HC), present-day levels (SC), and double present-day levels (DC). This gave six projected climate change scenarios for each month, and for each model.

## RESULTS

### Model performance

The ensemble models consistently performed better than the individual model algorithms, with AUC as the performance metric (Figure 2). I also assessed TSS, which yielded similar results and is included in the supplements (Appendix II).

The individual models performed similarly to one another, with the evaluation scores varying seasonally. BRTs performed worse than ANNs and GAMs in the winter months, but performed better than ANNs and the same as GAMs in the fall, though these differences were within the range of variation for each method (Figure 2). The best performing models were consistently in the late summer and early fall (July, August, September, and October; ensemble  $AUC \geq 0.9$ ). The late winter, early spring, and November models performed the worst, relatively (individual models:  $0.7 \leq AUC \leq 0.8$ ; ensembles:  $0.8 \leq AUC \leq 0.9$ ). For the remainder of the results shown below, I focused on the July-October period, where model performance was consistently highest.

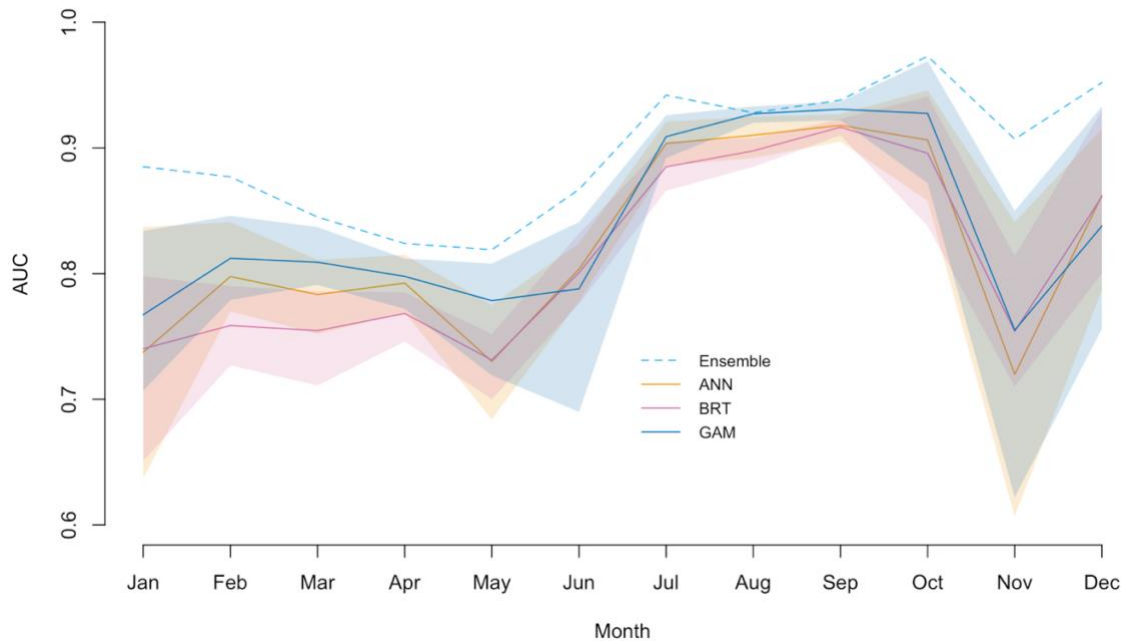


Figure 2. Evaluation score for each model algorithm for each month. The lines represent the mean evaluation score over the 10 cross-validation runs. Ranges for individual models are represented by the shaded areas.

### Covariate contribution

Chlorophyll and sea surface temperature had the highest contribution of the covariates to the individual models on average (Figure 3). Covariate contributions varied seasonally, especially in the GAM and BRT models. A spring-bloom-like pattern is evident in March and April for both GAM and BRT models based on the increased chlorophyll contribution. *C. finmarchicus* appears to have a high level of seasonality, especially in the BRTs where *C. finmarchicus* only contributed in the summer months (Figure 3c). The contribution of *C. finmarchicus* appeared to vary inversely with the contribution of bathymetry. This seasonality is less apparent in other models, especially ANNs where the contribution of covariates appears to vary little across the months (Figure 3a). In the winter, sea surface temperature contributes more in comparison to bottom temperature. In the summer months, bottom temperature tends to dominate over sea surface temperature.

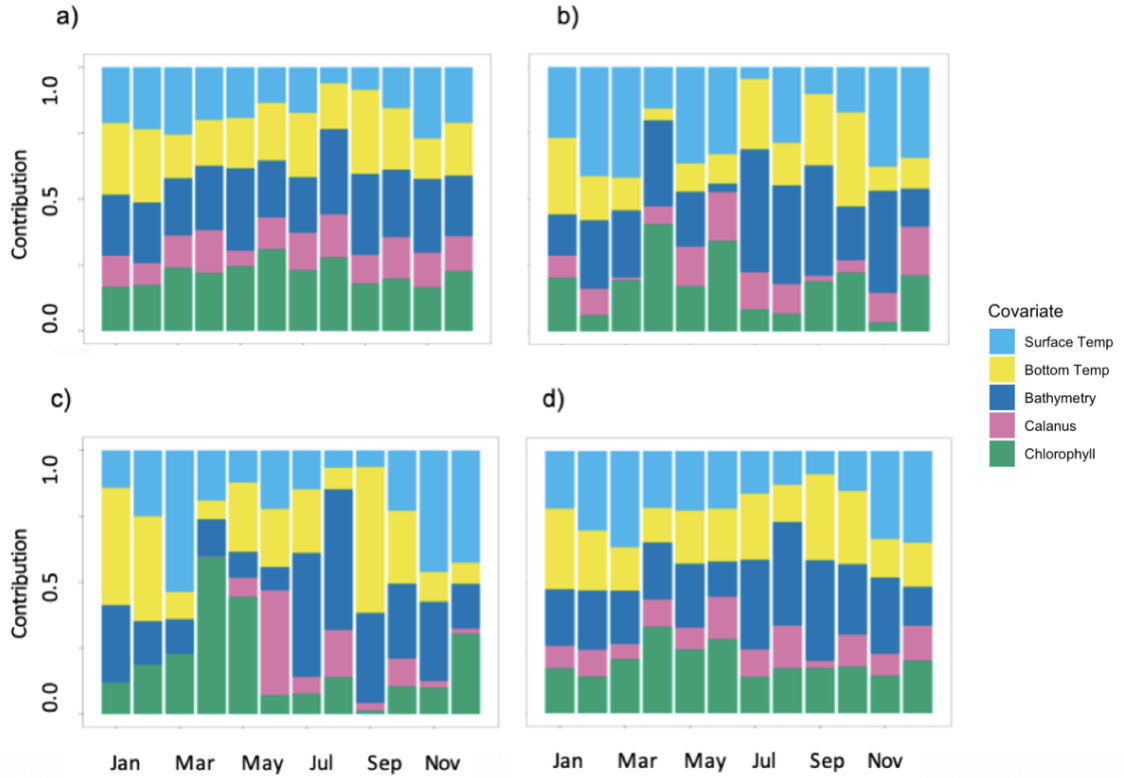


Figure 3. Covariate contribution across the individual models, a) ANNs, b) GAMs, and c) BRTs; and d) averaged over the individual models, excluding the ensembles.

Model performance varies with the relative contributions of some of the environmental variables. There is a significant negative correlation between sea surface temperature and AUC for the three individual models ( $p < 0.01$ ; Table 1). There is a significant positive correlation between bottom temperature and AUC in the ANN and GAM models ( $p < 0.05$ ; Table 1a-b). There is also a significant positive correlation between *C. finmarchicus* and AUC in the ANN models ( $p < 0.05$ ; Table 1a) and a near significant positive correlation in the BRT models ( $p = 0.066$ ; Table 1c).

Table 1. Correlation coefficients and p-values between each of the covariates and the individual model AUCs for all twelve monthly a) ANN, b) GAM, and c) BRT models. \* p-value < 0.05, \*\* p-value < 0.01, \*\*\* p-value < 0.001.

a)

Covariate	Corr. coeff.	P-value
Sea surface temperature	-0.52	1.2e-09 ***
Bottom temperature	0.23	0.013 *
Bathymetry	0.23	0.18
<i>C. finmarchicus</i>	0.22	0.015 *
Chlorophyll	0.18	0.056

b)

Covariate	Corr. coeff.	P-value
Sea surface temperature	-0.50	5.9e-09 ***
Bottom temperature	0.48	3.1e-08 ***
Bathymetry	0.37	3.4e-05 ***
<i>C. finmarchicus</i>	-0.089	0.33
Chlorophyll	-0.18	0.052

c)

Covariate	Corr. coeff.	P-value
Sea surface temperature	-0.28	0.0017 **
Bottom temperature	0.080	0.39
Bathymetry	0.55	6.6e-11 ***
<i>C. finmarchicus</i>	0.17	0.066
Chlorophyll	-0.43	1.0e-06 ***

### Response curves

I chose to include response curves for the BRT models as an example, with the ANN and GAM response curves included in the appendices (Figure 4; Appendix III). Habitat

suitability decreases with increased sea surface temperature and bottom temperature. Deeper bathymetry is associated with more suitable habitat than shallow bathymetry. Increased *C. finmarchicus* and chlorophyll are associated with higher habitat suitability.

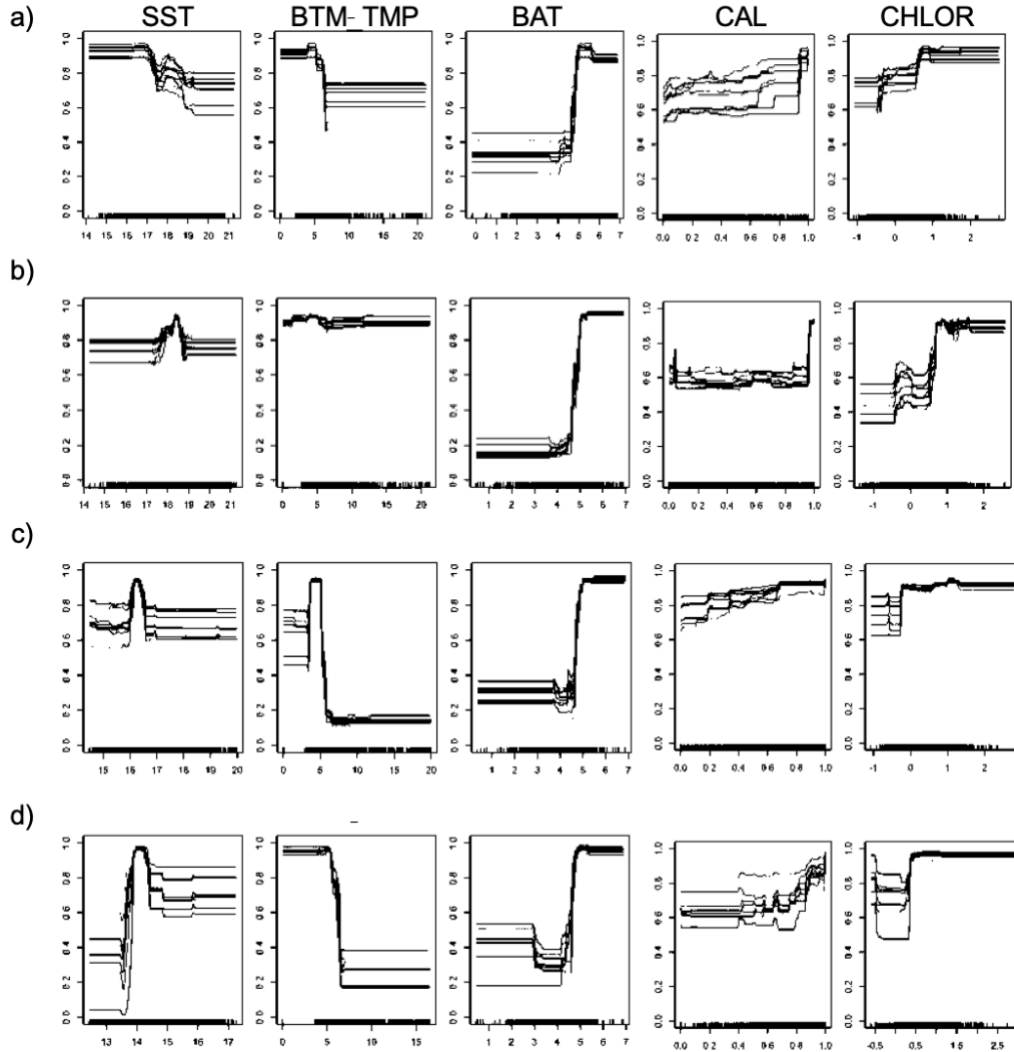


Figure 4. Response curves for the 10 cross-validation runs of the BRT models in a) July, b) August, c) September, and d) October.

The different cross-validation runs appear to result in similar response curves with the exception of some extreme values of covariates (e.g. low sea surface temperature and high bottom temperature; Figure 4). The response curves also appear similar across the months. Bottom temperature appears to have little effect on habitat suitability in August (Figure 4b). As the season progresses, lower sea surface temperature and high *C.*

*finmarchicus* appear to lead to high habitat suitability (Figure 4). Higher chlorophyll appears to lead to higher suitability in July and August, but appears less important in September and October (Figure 4).

### Climatological Hindcasts

The ensemble model hindcasts align well with the 1993 to 2009 sightings data for the months selected. In July, the hindcasts indicate high habitat suitability in the central Gulf of Maine, especially off the northwestern edge of George's Bank and in Grand Manan Basin, Bay of Fundy (Figure 5a). The hindcast also indicates relatively high suitability along the Scotian Shelf and in Roseway Basin, despite a lack of sightings in that region.

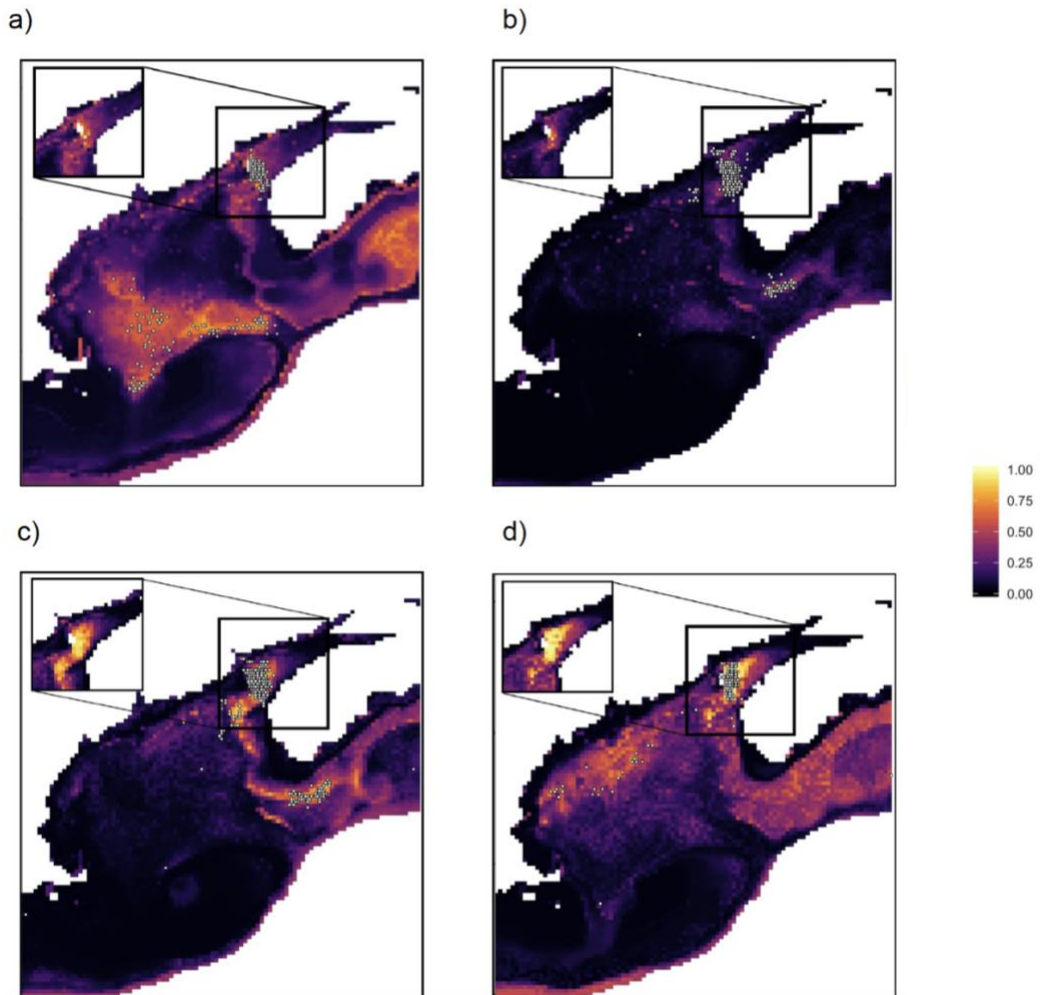


Figure 5. Climatological hindcasts of the ensemble models mapped onto the domain, with whale presences overlaid. The inset shows habitat suitability in the Bay of Fundy without presences marked for easier visibility. The maps correspond to a) July, b) August, c) September, and d) October.

In August, the model hindcasts indicate a high level of habitat suitability to the south of Grand Manan Basin, which is consistent with the relatively high number of sightings in this region of the Bay of Fundy (Figure 5b). The August hindcast indicates moderate levels of habitat suitability along Roseway Basin, which overlaps with a cluster of sightings (Figure 5b). In September, the model hindcasts are similar to those in August, but with much higher suitability both in the Bay of Fundy and along the Scotian Shelf, suggesting that the conditions in these regions become more suitable in the early fall (Figure 5c). In October, the model hindcasts suggest that the Bay of Fundy and the western Gulf of Maine are highly suitable, similar to July (Figure 5d).

### **2050 projections**

The 2050 projections suggest decreased habitat suitability in 2050 under both the RCP 4.5 and RCP 8.5 scenarios. The overall pattern indicates a decline in habitat suitability in historical foraging areas, such as the Bay of Fundy and Cape Cod Bay and an increase in habitat suitability in the eastern part of the domain, along the Scotian Shelf and in Roseway Basin. Beyond this general pattern, there are some interesting nuances.

In July, the central Gulf of Maine and Roseway Basin became less suitable relative to the hindcasts (Figure 6a). The Bay of Fundy became unsuitable in all of the RCP 8.5 scenarios and in the HC scenario for RCP 4.5, and slightly less suitable in the SC and DC scenarios (Figure 6a). The July projections suggest a large decrease in habitat suitability in the central Gulf of Maine, specifically off of the northwestern edge of George's Bank (Figure 6a). There is also a decrease in the Bay of Fundy and along Roseway Basin and the Scotian Shelf, though these decreases appear to be less drastic.

In August, the entire Gulf of Maine appears unsuitable under all six scenarios with the exception of slight suitability along the southwestern tip of Nova Scotia (Figure 6b). This is apparent particularly in the RCP 4.5 and RCP 8.5 DC scenarios.

In September, there appears to be a northeastward shift in habitat suitability, with the most suitable habitat along the Scotian Shelf in all six scenarios (Figure 6c). There is decreased suitability in the western Gulf of Maine, with the exception of a slight increase in suitability off the northwestern edge of George's Bank in both of the HC scenarios, relative to the hindcasts (Figure 6c). There is higher suitability relative to the present in

the central Gulf of Maine in the SC and DC scenarios for RCP 4.5 and RCP 8.5 (Figure 6c).

In October, there is decreased habitat suitability in the western Gulf of Maine in all six scenarios (Figure 6d). In the HC and DC scenarios for both RCP 4.5 and RCP 8.5, there is an increase in habitat suitability in Roseway Basin and along the Scotian Shelf (Figure 6d). The HC scenario under both RCP 4.5 and RCP 8.5 predict more widespread suitability relative to the other scenarios, while the SC and DC scenarios indicate smaller regions of relatively high suitability.

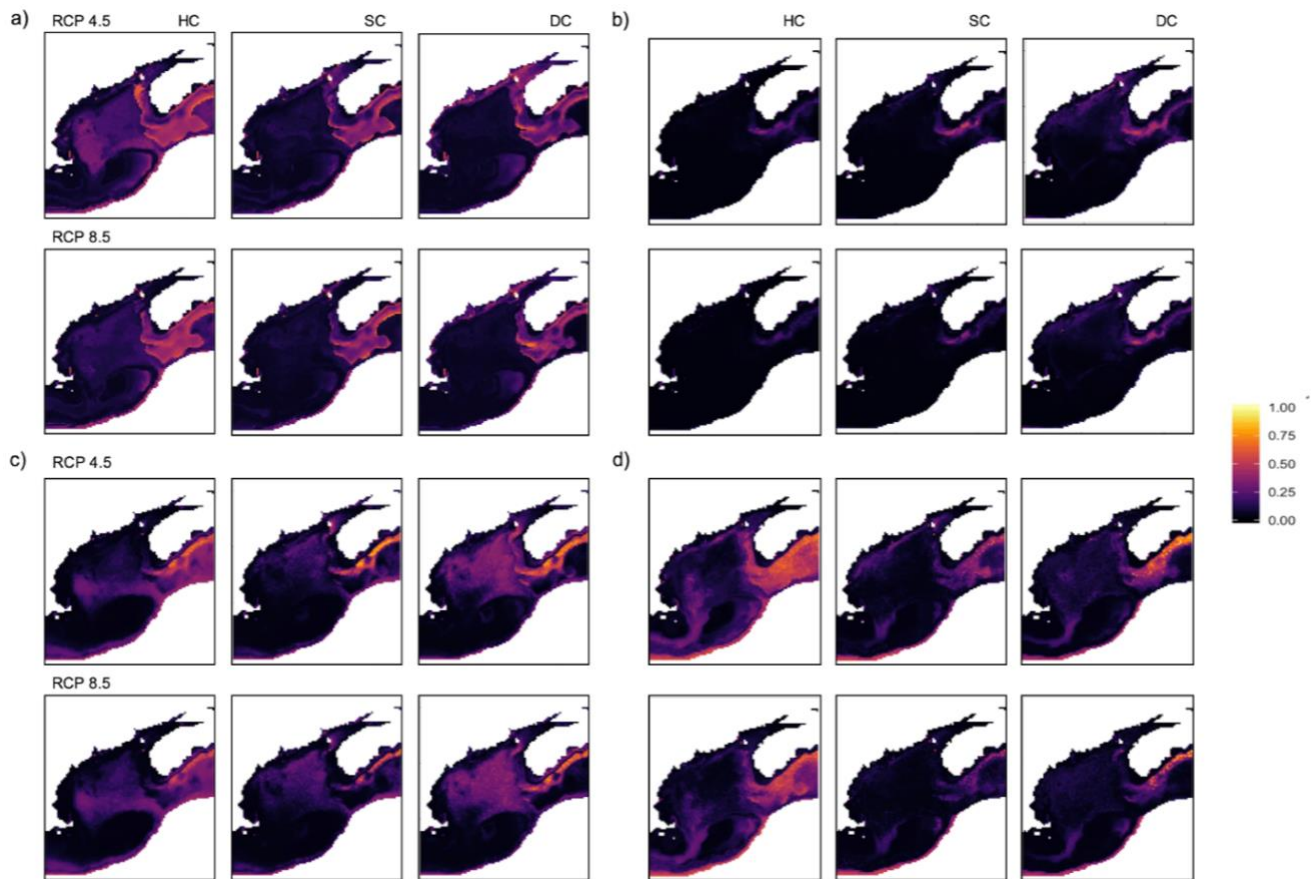


Figure 6. Habitat suitability projections under six potential year-2050 scenarios for a) July, b) August, c) September, and d) October. For each month, I projected the models into scenarios with half of the present chlorophyll levels (HC), the same present chlorophyll levels (SC), and double the present chlorophyll levels (DC) for both the projected RCP 4.5 and RCP 8.5 climate scenarios (Brickman et al. 2016; Sathyendranath et al. 2019).



## DISCUSSION

Understanding the distribution of *E. glacialis* is imperative to their conservation (Pendleton et al. 2009; Pershing et al. 2009; Pendleton et al. 2012; Monsarrat et al. 2015; Gomez et al. 2017; Plourde et al. 2019; Record et al. 2019b). Mortality rates for *E. glacialis* have increased markedly over the past few years as a byproduct of changing foraging patterns (Meyer-Gutbrod and Greene 2014; Davies and Brilliant, 2019; Record et al. 2019b). So far, the management response has been reactive to these changes, making adjustments only after spatiotemporal foraging patterns have changed and often after mortalities have occurred. Using forward-looking projections of changes in habitat suitability could help inform a more proactive approach to reducing mortality. To begin with, projections could aid in choosing which regions may warrant increased survey effort. There are substantial regions in both the hindcasts and the projections that show high habitat suitability but have not been the focus of historic survey effort. Rather than focusing most survey effort in the same regions each year, projections could potentially guide where to look to find new aggregation areas before large mortality events occur.

In this thesis, I modeled *E. glacialis* habitat suitability using ensemble SDMs. By using ensembles, I combined the benefits of the individual models to optimize performance (Thuiller et al. 2009; Figure 2) and utilized only the models that performed well (i.e.  $AUC \geq 0.75$ ). I applied HC, SC, and DC chlorophyll levels under the RCP 4.5 and RCP 8.5 physical oceanographic climate anomaly fields (Brickman et al. 2016) to create six projected 2050 climate scenarios. Due to the inherent uncertainty in SDMs, projecting the models onto multiple future scenarios widened my view into a few of many possible futures for *E. glacialis*. Because there are currently no studies that project chlorophyll this far into the future, I used three different chlorophyll scenarios to account for a breadth of possible futures. Despite this widened view, there was some degree of consistency between the projected whale distributions. The model results suggest a decrease in habitat suitability throughout the Gulf of Maine under most of the projections (Figure 6). In the cases where suitable habitat remained, the projections suggested a northeastward shift in suitability (Figure 6). This is consistent with the results of previous studies that suggested *E. glacialis* are susceptible to the effects of climate change (Meyer-Gutbrod and Greene 2014; Davis et al. 2017; Pettis et al. 2019; Record et

al. 2019b), as the projections show a possible prey-driven shift of the distribution of the species into colder waters.

The evaluations suggest that the ensemble models performed better than the individual ANN, GAM, and BRT models, which is consistent with expectations (Pearce and Ferrier 2000; Thuiller et al. 2009). The individual models and the ensembles performed best in July, August, September, and October relative to other months, with ensemble AUCs ranging from 0.92 to 0.95 (Figure 2), demonstrating strong performance (Pearce and Ferrier 2000). This indicates that the models predicted habitat suitability best in the months during which the Gulf of Maine is an important foraging ground for *E. glacialis* (Murison and Gaskin 1989; Kenney and Wishner 1995; Baumgartner et al. 2003b; Brown et al. 2009, Patrician and Kenney 2010; Pendleton et al. 2012), and in particular, when they are feeding on the lipid-rich stages of *C. finmarchicus* (Davies et al. 2014; Plourde et al. 2019); this suggests that the models are able to accurately capture this aspect of *E. glacialis* phenology. The ensemble models performed the worst between November and June, with the exception of December, which performed relatively well. However, the low number of sightings in December relative to the months selected suggests that it is possible that the rarity of sightings lead to a falsely inflated AUC score (Appendix I). November through June, again with the exception of December, also had the largest discrepancy between individual model evaluations and the ensemble evaluations. Some of the winter and spring months are historically important foraging times, particularly in Cape Cod Bay. During these months, other copepod species (*Pseudocalanus* spp, *Centropages* spp) can be more important than *C. finmarchicus* for periods of time (Stamieszkin et al. 2010). Including these species as prey data layers can improve model performance; previous modeling work using these species successfully predicted a winter range expansion into waters south of Nantucket (Pendleton et al. 2012). The ability to project these other copepod species onto 2050 conditions would likely improve my projections of *E. glacialis* habitat suitability in the winter and spring months.

The environmental covariates each contributed in different ratios to the individual models. On average, chlorophyll and sea surface temperature had the highest contribution of the covariates. However, there was high seasonal variability, and during months when model performance was highest, bottom temperature and *C. finmarchicus*

had higher contributions. Of the covariates, the highest seasonal variability appears to be in the contribution of sea surface temperature and bottom temperature. The ANN model did not capture seasonality, unlike the other two algorithms (Figure 3a). This may be due to the way ANNs balance correlated covariates; they are highly flexible and able to find a smooth fit for many inter-correlated variables (Li and Wang, 2013). An increase in the contribution of chlorophyll in March and April in both the GAM and BRT models corresponds to the timing of the spring bloom; chlorophyll could be acting as a proxy in the models for copepod production during non-diapause months (Record et al. 2019a). The *C. finmarchicus* covariate used a model that focuses on diapause as an index of the lipid-rich prey resource. The contribution seasonality of this covariate reflects this choice: for example, this covariate only contributed in and adjacent to the summer months in the BRT models (Figure 3c). This is consistent with the time period during which *C. finmarchicus* begins to enter diapause, and when *E. glacialis* feed on this prey species in the Gulf of Maine (Plourde et al. 2019).

The relationship between covariate contribution and model performance can be instructive as to the different roles of the covariates. A significant negative correlation between sea surface temperature and AUC for the three individual models suggests that a high reliance on sea surface temperature decreases model performance (Table 1). On the contrary, bottom temperature appears to be positively correlated with model performance in two of the three individual models (Table 1a-b). While sea surface temperature is often a major driver of marine species distribution models (e.g. Pershing et al. 2009a; Nye et al. 2009; Pendleton et al. 2012; Abrahms et al. 2019), these results suggest that bottom temperature, or some subsurface temperature, should be included in *E. glacialis* species distribution models. The results also suggest a significant positive correlation between *C. finmarchicus* and model performance in the ANNs and a near-significant positive correlation in the BRTs (Table 1a and Table 1c). This relationship underscores the importance of including prey fields in *E. glacialis* SDMs.

The ensemble model hindcasts align well with the 1993 to 2009 sightings data for the months selected, suggesting that the models successfully captured the trends of past *E. glacialis* habitat suitability. The July hindcast indicates the regions along the Scotian Shelf and in Roseway Basin are suitable *E. glacialis* habitat, despite a lack of sightings.

This result is consistent with the findings of Plourde et al. (2019), which suggested based on a preyscape model that the Scotian Shelf and Roseway Basin are likely key summer foraging grounds for *E. glacialis*. In August, September, and October, the model hindcasts indicate a high level of habitat suitability to the south of Grand Manan Basin, which is consistent with the relatively high number of sightings in this region of the Bay of Fundy (Figure 5b). The Bay of Fundy is a crucial feeding ground for *E. glacialis* in July and August (Brown et al. 2009; Pendleton et al. 2012; Plourde et al. 2019), and both hindcasts highlight this importance.

In the 2050 projections, the lack of habitat suitability in the Bay of Fundy and the general northeastward shift in suitability suggests that *E. glacialis* is unlikely to return to its historical foraging patterns, potentially as a result of prey resources shifting northward into colder waters due to climate change (e.g. Record et al. 2019b; Sorochan et al. 2019). The September and October projections show an increase in habitat suitability along Roseway Basin and the Scotian Shelf, indicating a shift to a narrower region of high suitability in comparison to the hindcasts (Figure 6c-d). While suitability decreased in the rest of the Gulf of Maine, this increase along Roseway Basin and the Scotian Shelf suggests that there may still be suitable habitat for *E. glacialis* just outside of the Gulf of Maine in 2050. The probability of high suitability generally increased with chlorophyll and was higher in the RCP 4.5 scenario than in the RCP 8.5 scenario, suggesting that lower water temperature and higher chlorophyll may be strong future predictors of habitat suitability, a finding consistent with previous studies that have suggested a sensitivity of *E. glacialis* to warming waters due to a shift in prey abundance (e.g. Meyer-Gutbrod and Greene 2014; Meyer-Gutbrod et al. 2015; Record et al. 2019b; Sorochan et al. 2019).

Despite an increase in the *E. glacialis* population size prior to 2010, the species experienced a regime shift that has led to decreasing population numbers and higher rates of mortality ever since (Meyer-Gutbrod and Greene 2014; Davis et al. 2017; Pettis et al. 2019; Record et al. 2019b; Sorochan et al. 2019). The ability to model and predict regions of present and future habitat suitability for this species is crucial for management (Pendleton et al. 2009; Pershing et al. 2009; Pendleton et al. 2012; Monsarrat et al. 2015; Plourde et al. 2019; Record et al. 2019b). While species distribution models are inherently uncertain (Pearson et al. 2006), the 2050 projections produced can provide

insight into possible future scenarios for *E. glacialis* habitat suitability. Some biological inconsistencies in the models, like the lack of seasonality in the covariate contributions of the ANNs (Figure 3a), suggest that further tuning and research into different modeling techniques would be beneficial. These differences also highlight the utility of applying multiple modeling algorithms as one way to represent the uncertainty in current knowledge of species distribution changes. The hindcasts suggest that the models were able to capture the habitat of *E. glacialis* with relatively high performance, suggesting that this thesis can provide a window into one version of a possible future. As current understanding of processes improves — such as the physical mechanisms that aggregate prey, or the drivers of whale movement beyond direct foraging — this understanding can be used to refine projections.

This thesis can be viewed as a foundation upon which future studies can build with the ultimate goal of better understanding the past and future distributions of *E. glacialis* for the purpose of conservation. These models can aid in current understanding of the movement patterns and habitat preferences of the species under possible future climate scenarios, ultimately helping to inform conservation measures, as long as they are cautiously used with an understanding of the level of uncertainty in the projections. The future shift of *E. glacialis* distributions out of the Gulf of Maine that is suggested by these projections is not a reason to disrupt conservation efforts in historical foraging grounds. Instead, the high level of uncertainty is a compelling reason to keep current conservation efforts in place, while potentially investigating regions like the Scotian Shelf as possible future foraging grounds for the species. Evidence of past regime shifts and the mechanisms suggested (e.g. Meyer-Gutbrod and Greene 2014; Record et al. 2019b; Sorochan et al. 2019) indicate that future regime shifts are a strong possibility for *E. glacialis*. The sooner and the better we are able to understand the distributions of this endangered species, the more precise and successful conservation efforts will be.

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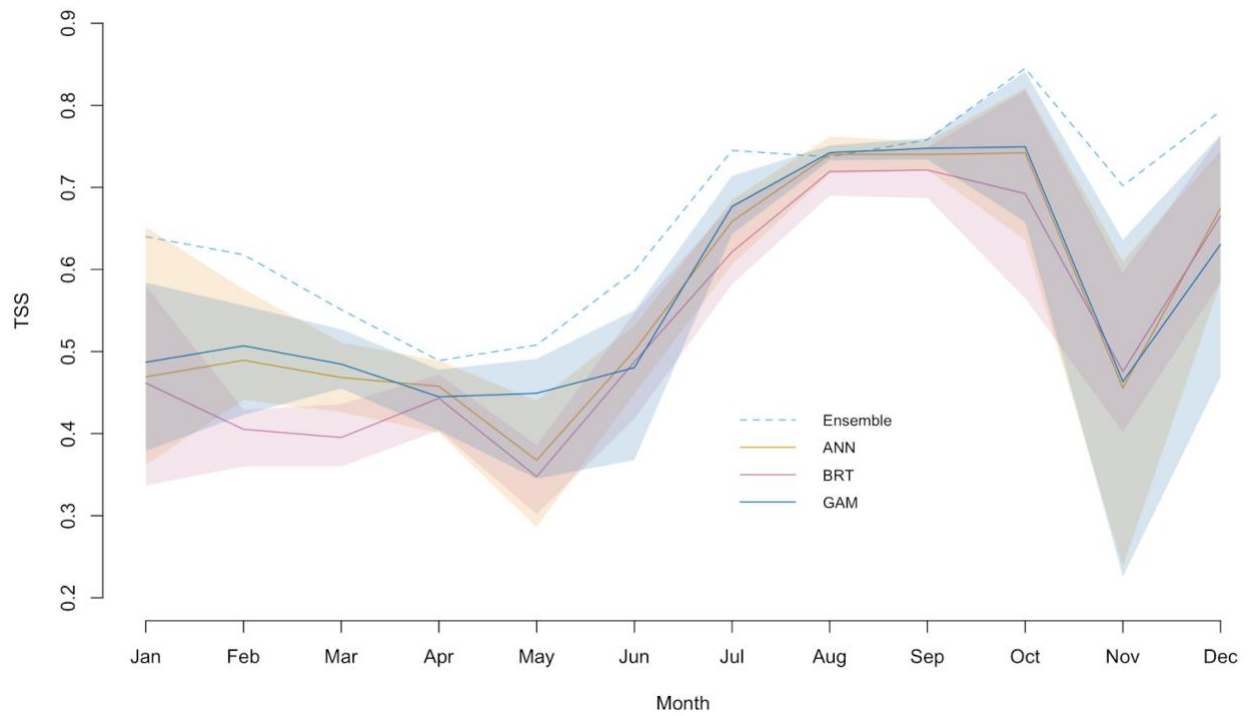
## APPENDICES

### Appendix I

Number of presences and absences used in monthly models of *E. glacialis* habitat suitability. Presence-absence data were drawn from the years 1993 and 2009. Duplicate records for the same day and location were discarded.

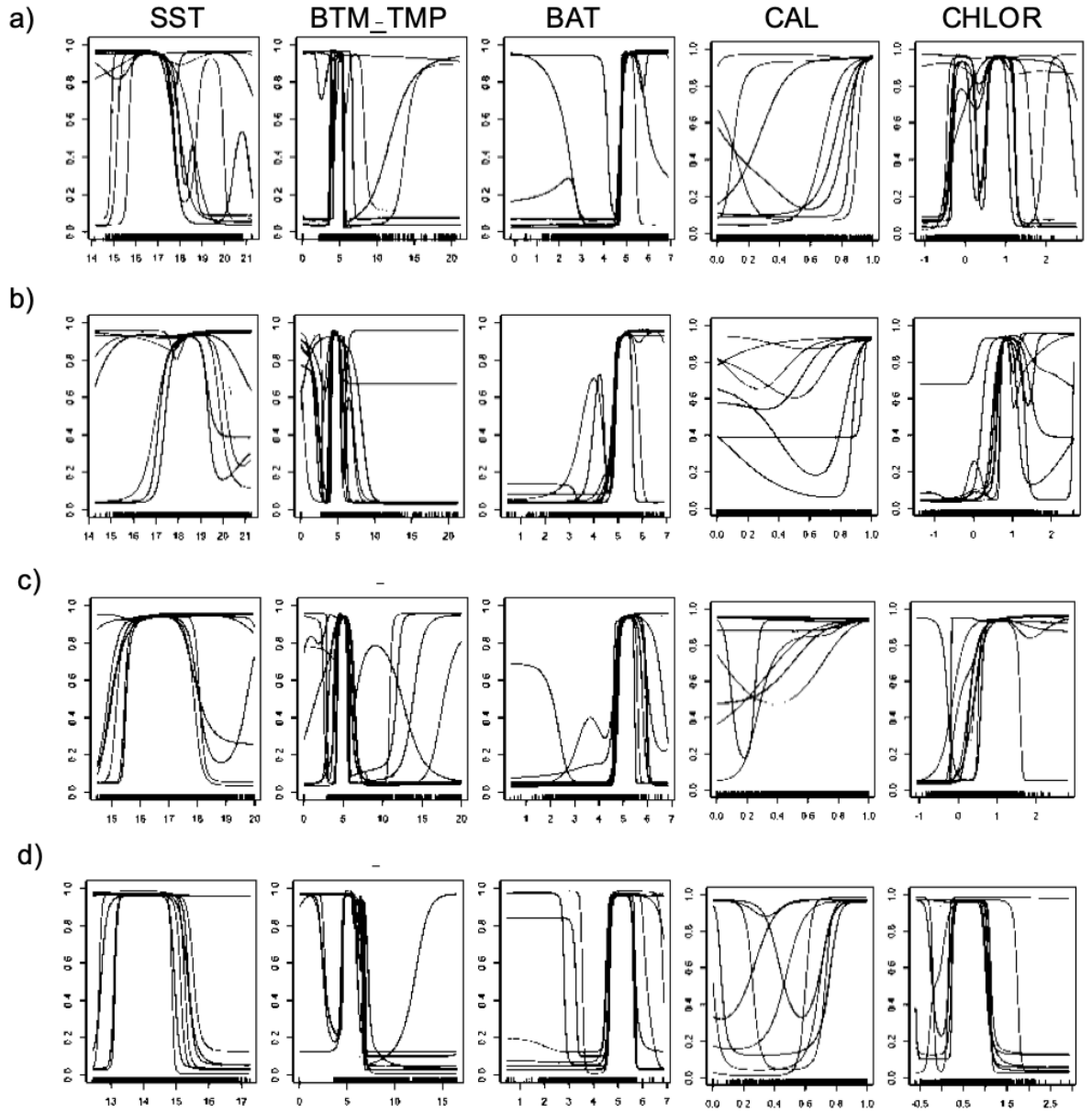
	<b>Presences</b>	<b>Absences</b>
<b>January</b>	92	5,902
<b>February</b>	273	9,805
<b>March</b>	556	13,379
<b>April</b>	685	21,476
<b>May</b>	500	25,153
<b>June</b>	299	19,817
<b>July</b>	435	13,527
<b>August</b>	1,371	12,863
<b>September</b>	1,031	10,225
<b>October</b>	160	7,065
<b>November</b>	60	6,612
<b>December</b>	59	3,930

## Appendix II

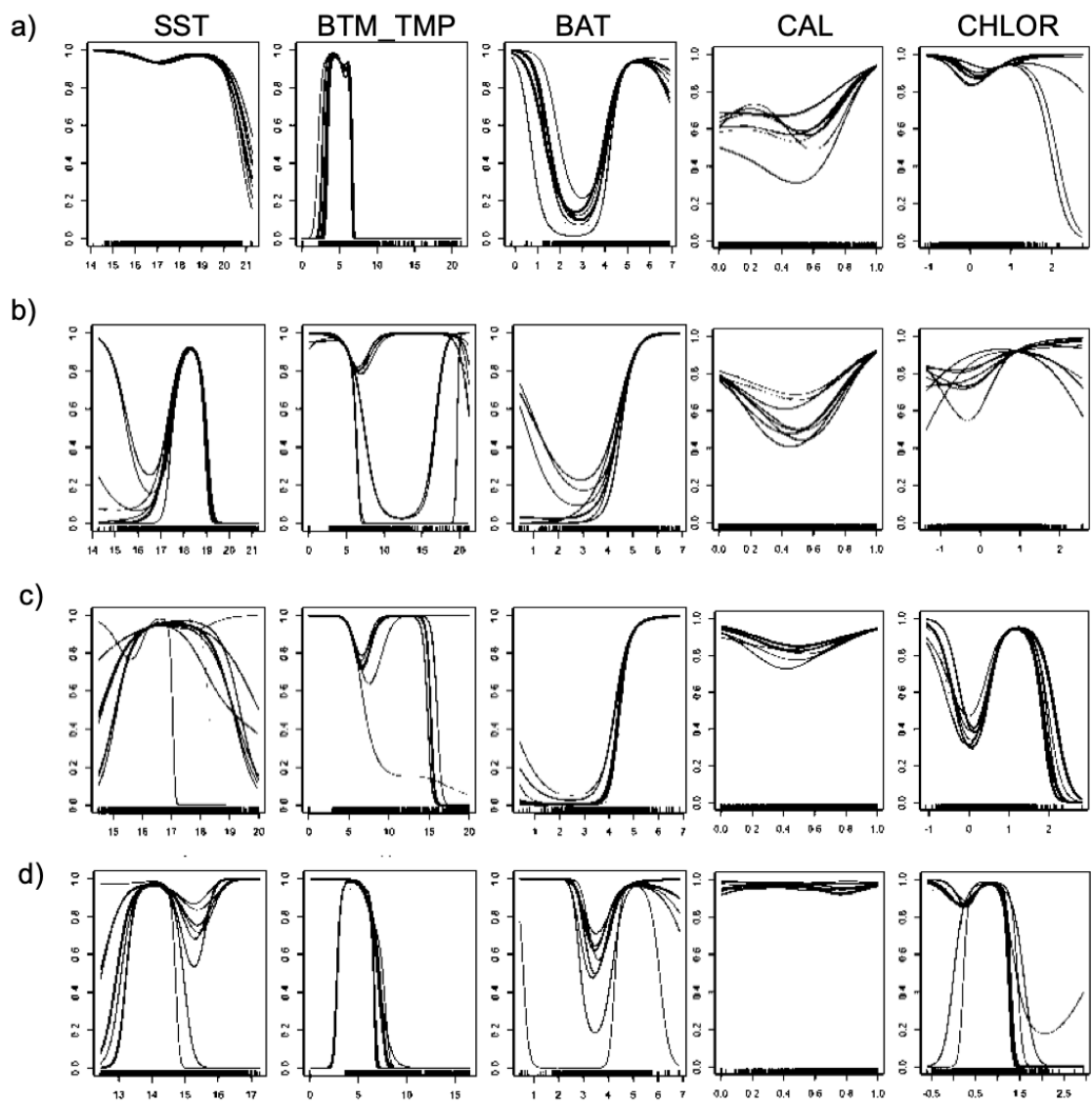


Evaluation score for each model algorithm for each month using TSS. The lines represent the mean evaluation score over the 10 cross-validation runs. Ranges for individual models are represented by the shaded areas.

### Appendix III



Response curves for the 10 cross-validation runs of the ANN models in a) July, b) August, c) September, and d) October.



Response curves for the 10 cross-validation runs of the GAM models in a) July, b) August, c) September, and d) October.