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**Supplemental Material**

# Cusk (*Brosme brosme*) and climate change: assessing the threat to a candidate marine fish species under the U.S. Endangered Species Act

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## Introduction

Two topics are covered in this supplemental material: details regarding iterative fitting of the species niche model and a list of research gaps identified during this study.

## Species Niche Model

Probabilities of cusk occurrence were most strongly related to bottom temperature and the structural complexity of the bottom measured with the TRI (Table S1). Cusk responses to solar elevation, salinity and residual salinity (derived from a nonlinear regression using depth as the independent variable) were weak or non-significant. Cusk distributions were related to bottom depth; cusk were likely to occur at depths ranging from 74 to 719 meters. However, bottom depth was not included in the final model since a direct physiological mechanism has not been proposed and to avoid constraining forecasts of the niche model to a specific range of depths.

The U.S. and Canadian trawl survey data were merged to construct the final model since cusk responses to bottom temperature and complexity were similar between surveys. The residual deviance and AIC of the models were reduced only slightly when survey dependent responses for bottom temperature and complexity were added (Table S1). Furthermore, temperature responses derived from the Canadian and U.S. trawl survey data had the same minimum threshold (4.2 $^{o}$C) and modal values differed by only a degree (Canada=8.2 $^{o}$C, US = 7.2 $^{o}$C). The upper threshold of the Canadian response was warmer (Canada = 12.4 $^{o}$C, US = 10.3 $^{o}$C). Adding a survey dependent response to bottom complexity had an even smaller impact on residual deviance and AIC than

temperature (Table S1). Regardless of the trawl survey, cusk were likely to be found in areas with TRI values greater than 3.

The final niche model used data collected in all seasons because shapes of cusk responses derived from the full dataset were similar to those derived from the separate summer and autumn dataset. The temperature responses derived from the summer and autumn datasets had modes and thresholds that differed by less than a degree (All surveys mode=7.8 $^{o}$C, max= 11 $^{o}$C, min=4.2 $^{o}$C; survey specific mode=7.6 $^{o}$C, max 11.4 $^{o}$C, min 3.5 $^{o}$C). The responses of cusk to bottom complexity did not vary in the two datasets.

The species niche model was projected using fixed temperature increases and output from an ensemble of Atmospheric-Ocean General Circulation Models. These results are described in the main paper. Here we also present the spatial distribution of cusk projected under fixed temperature increases (Figure S1). Cusk distribution is greatly reduced at increases $\geq 3^{o}$C. Our projections were based on the November-December period, which was chosen because this is the time of year of most spatially limited 'preferred-temperature). In May and June, potential thermal habitat covered much of the continental shelf area of the Northwest Atlantic (Figure 7 main text). The strong relationship between observed distributions and the climatology of November-December bottom temperatures within the "preferred range" indicates that cusk may not be capable of capitalizing on the seasonal expansion of habitat into shallower and southern portions of the region during the colder months. This hypothesis is consistent with information suggesting that cusk have small home ranges, limited movement capabilities, and spatially subdivided population structure (Collette & Klein-MacPhee 2002; Knutsen et al. 2009; Oldham 1972). At broad biogeographic scales, spatial processes like migration,

rather than species interactions, are believed to be primarily responsible for mismatches between realized distributions and potential habitats projected on the basis of a few abiotic niche dimensions (Araújo & Guisan 2006; Barve et al. 2011; Pulliam 2000).

The performance of the species-niche model was quantified using Receiver Operator Characteristic (ROC) analysis and a summary confusion matrix developed from 10-fold cross validation of the model (Fielding & Bell 1997). For the 10-fold cross validation the 39,858 observations were randomly partitioned into 10 nearly equally sized segments that served as independent test sets (Refaeilzadeh et al. 2009). Each test set was then used to predict probabilities of cusk presence using a model trained with remaining observations and habitat data. ROC was then applied to the test set predictions and observations to find an optimal probability threshold for classification of predictions of the niche model to construct a summary confusion matrix and binary habitat maps. To classify predictions, the minimum difference threshold was selected (Figure S2) (Jimenez-Valverde & Lobo 2007; Lobo et al. 2008). The difference between the sensitivity (the true positive predictions; i.e., presences) and specificity (the true negative predictions; i.e., absences) of the final statistical niche model was minimized at a probability of 0.075 (Figure S2).

**Identified Research Gaps**

This study identifies a number of information gaps in the consideration of the effect of climate change on cusk. Many of these information gaps apply to other species-

of-concern[1] and to other data-poor species. Here, we list these gaps in the hope that our work will stimulate future research.

- There are a number of detailed questions regarding the species niche modeling: for example the effect of different threshold methods, the shapes of the deviance functions (Figure 6 main text), and the use of presence / absence data vs abundance data. Future iterations should evaluate the uncertainty introduced through statistical "decisions" on climate projections (*sensu* Planque et al. 2011). These iterations could be used to refine the species niche model and the coupling to the environment.
- In our projections of climate change we only considered changes in temperature. We did not include the effect of ocean acidification on cusk. With increasing $CO_2$ concentrations, the ocean is expected to become more acidic in the future. Ocean acidification may affect cusk directly (e.g., metabolic scope, growth) or indirectly (affecting prey, predators, competitors) (Diaz Pulido et al. 2011; Munday et al. 2009; Pörtner & Farrell 2008; Pörtner et al. 2004). It is unclear if overall, a more acidic ocean would benefit or harm cusk, largely because research on this topic is in its infancy. The effects of ocean acidification on cusk, and more broadly on marine ecosystems, should be the focus of future investigations.
- A better measure of cusk abundance is needed. Fishery-independent trawl surveys show a dramatic decline in abundance. Davies and Jonsen (2011) argued that part of this decline can be explained by hyperdepletion of cusk in the trawl survey. Hyperdepletion can occur when fishing effort is concentrated on a subset of the population, while the remainder of the population remains unfished. This situation is

[1] http://www.nmfs.noaa.gov/pr/species/concern/

possible since cusk prefer complex habitats and at lower abundances, a greater proportion of the population may be in areas that are inaccessible to trawl gear. This result argues for a survey of cusk using gear that is more efficient in the complex bottom habitats (e.g., longline surveys, video surveys).

- Density-dependent effects on cusk distribution need to examined in more detail, especially since a density dependent catchability was also inferred by Davies & Jonsen (2011). The basin model described by MacCall (1990) is a useful theoretical construct for testing the application of such density dependent relationships and should be tested explicitly for cusk. Further, these ideas need to be better incorporated into species-niche modeling that is used in making climate projection.
- Our projections indicate that cusk habitat will become more fragmented, which may affect local population viability. To examine this effect in more detail, the movement of cusk needs to be quantified. Prior work suggests that cusk are sedentary (Collette & Klein-MacPhee 2002), but there is evidence for ontogenetic movements from shallow to deeper water (Figure S2). Also cusk spawn planktonic eggs and larvae, which might provide a mechanism for connecting spatially isolated populations of adults. Thus, the movement of cusk during all life stages must be described to better understand population connectivity (i.e., Pineda et al. 2007) in the context of increasingly isolated adult habitats.
- An improved understanding of the distribution of seafloor habitats would improve the spatial predictions of the model. TRI as a proxy for complex habitat is a very coarse grained measure. The improved resolution of multibeam bathymetry and backscatter not only can be used to delineate a range of complex topographies directly but can be

used measure variation in habitat patch size (e.g., variation in patch size of boulder ridges) that can be critical for assessing density dependent patterns and processes. Further, such data can facilitate studies of residency and movement patterns using approaches from landscape ecology.

- The projections are based on 40 year averages. This is necessary because the models do not capture the phasing of climate variability so year 2050 in the model, is not a prediction for the state of the climate in the year 2050. Thus, the projections were averaged to capture the average state of the climate over a 40 year period in the future. This approach results in conservative estimates of change. A mean change of 2 $^{o}$C will encompass years of greater change and years of lesser change. The effect of this shorter-term variability on the distribution of cusk needs to be examined and the potential for shorter term changes greater than the 40 year mean changes projected here need to be considered.
- There are a range of more complex ecological issues that are pertinent to evaluating the effect of climate change on cusk, but there is little information. Allele effects, depensation, recruitment processes, and metapopulation dynamics are basically unknown for cusk, but could play an important role in the ability of the species to sustain itself in the Gulf of Maine and Georges Bank region. An orchestrated ecological investigation would be required to begin to gather the type of data to consider these more involved processes.
- The physiological mechanisms responsible of the species niche distribution should be quantified. Temperature is a dominate factor affecting physiology; laboratory studies should be conducted and compared to the field-based estimates the temperature niche.

In addition, the physiological basis for depth-dependent distribution needs to be investigated. Many, if not all, benthic marine fish species exhibit some preference for specific depths (Gabriel 1992; Mahon et al. 1998). Several hypotheses have been proposed, but a clear mechanistic basis for depth preferences remains equivocal (Drazen & Seibel 2007; Sullivan & Somero 1980; Vetter et al. 1994).

- Another remaining question is the ability of cusk to adapt to climate warming. For cusk, which are long-lived and relatively stationary, there will be selective pressures to adapt to climate change. However, the capacity of cusk to adapt is unknown as is the possibility of local adaptation in a species with a planktonic larval stage. This latter issue again raises the need to understand population connectivity in cusk. The issue of evolutionary adaptation extends beyond cusk and applies to all species and remains a major source of uncertainty in projecting the response of a species to climate change.

Table S1. Results showing deviance, partial deviance, Akaike information criterion (AIC) and estimated degrees of freedom (DoF) of the smoother statistic from GAM analysis performed to construct the statistical niche model for cusk. Statistics from stage 3 analysis that examined differences in cusk responses to bottom temperature and complexity derived from full data set and a more conservative one are non-informative and not included.

Stage 1 Variable Selection

| Model | Deviance | Partial Deviance | AIC | Estimated Degrees of Freedom |
|---|---|---|---|---|
| Null | 17339.1 | | 14658.4 | |
| Bottom Temperature | 1735.7 | 1839.0 | 12960.4 | 4.7 |
| Bottom Ruggedness | 536.7 | 379.7 | 14151.0 | 8.5 |
| Bottom Temperature & Bottom Ruggedness | 2122.0 | | 12595.8 | |
| Solar elevation | | 161.5 | 12706.6 | 2.8 |
| Bottom depth | | 1070.8 | 11101.8 | 8.5 |
| Bottom salinity* | | 419.0 | | 4.4 |
| Bottom salinity residuals* | | 35.6 | | 3.6 |

* - In the dataset, there were many more observations of cusk that were accompanied only with temperature observations. In modeling salinity, a reduced dataset was used that only included cusk observations with both temperature and salinity.

Stage 2 Survey-dependent response

| Model | Deviance | Partial Deviance | AIC | Estimated Degrees of Freedom |
|---|---|---|---|---|
| Bottom Temperature | | 104.4 | 12505.6 | |
| Bottom Ruggedness | | 149.7 | 12454.8 | |

Stage 3 Density-dependent response

| Model | Deviance | Partial Deviance | AIC | Estimated Degrees of Freedom |
|---|---|---|---|---|
| Bottom Temperature | | 701.2 | 11910.8 | 4.4 |
| Bottom Ruggedness | | 100.2 | 12507.8 | 7.5 |

Figure S1. Binary maps of potential habitat for adult cusk classified from projections of the statistical niche model using bottom complexity and fixed bottom water temperature increases from the Nov-Dec bottom temperature climatology. (Will included as a movie if possible).

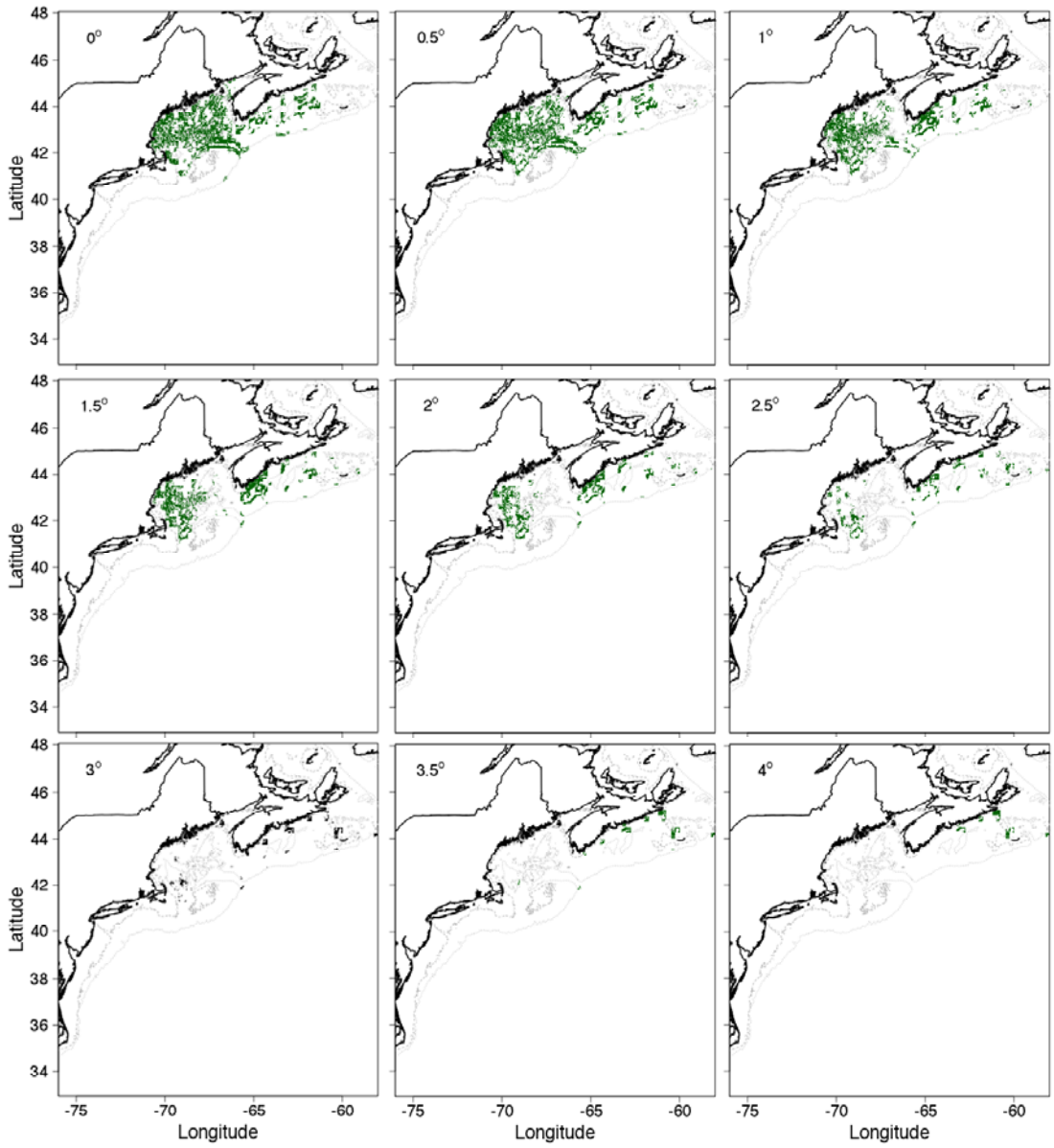


Figure S2. A) Sensitivity (the true positive predictions i.e. presences) and specificity (the true negative predictions i.e. absences) as a function of probability threshold for predicted presence from 10-fold cross validation of the GAM species niche model. The vertical line indicates the probability threshold where the difference between sensitivity and specificity was minimized (0.075). B) Reciever Operator Characteristic (ROC) curves derived from cross validated tests of the model. The point in panel B indicates location on the ROC curve where sensitivity and specificity values were minimized. The diagonal line indicates the region where true and false positives are equally likely by chance.

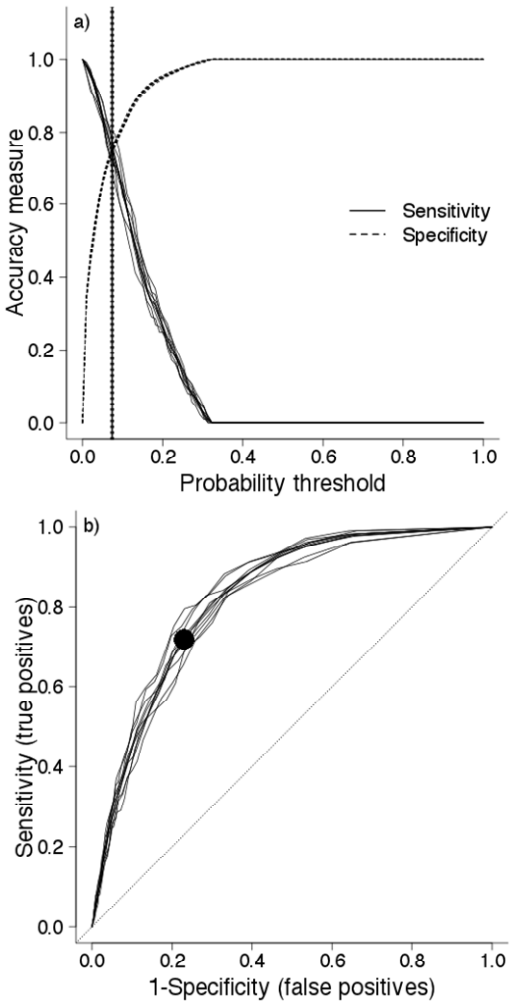
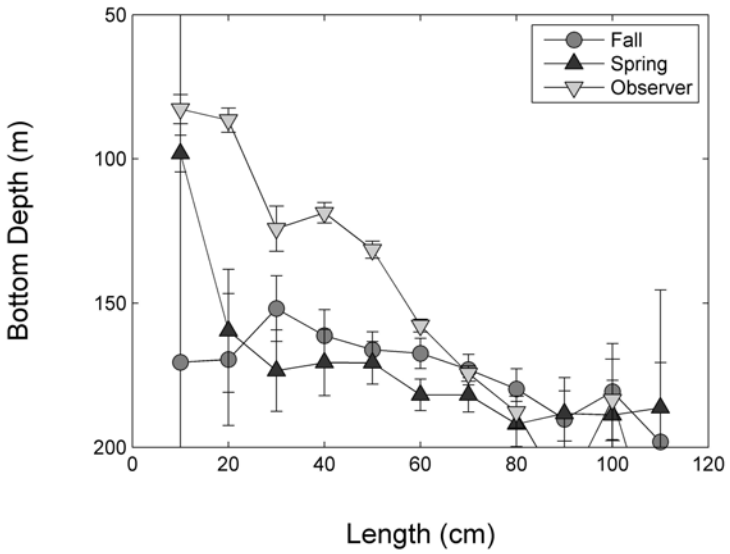


Figure S3. Mean (± 95% confidence intervals) depth of cusk by cusk length. Data from three sources are shown: the fall and spring fishery-independent trawl survey conducted by the Northeast Fisheries Science Center, and observer data from fishery-dependent sampling aboard commercial fishery vessels. The trawl survey data is described by (Azarovitz 1981). The observer data is described by (Rago et al. 2005).



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