

Habitat-based density model for beaked whales in the AFTT area

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October 1, 2016

This report documents the habitat-based density model for beaked whales in the Atlantic Fleet Testing and Training Area (AFTT) area. Information on the first stage of the modeling approach, including classification of ambiguous sightings, detection function fitting and $g(0)$ estimation can be found in individual taxon reports presented in Roberts et al. (2016) for the U.S. Atlantic and Gulf of Mexico.

Citation for this model: Mannocci L, Roberts JJ, Miller DL, Halpin PN (2016). Habitat-based density model for beaked whales in the AFTT area. 2016-10-01. Marine Geospatial Ecology Lab, Duke University, Durham, NC.

Citation for the related publication: Mannocci L, Roberts JJ, Miller DL, Halpin PN. Extrapolating cetacean densities to quantitatively assess human impacts on populations in the high seas. In review in Conservation Biology.

1- Available data

Table 1: Effort (km) and sightings per surveyed region (CAR: Caribbean, EC: East coast, EU: European Atlantic, GM: Gulf of Mexico, MAR: Mid-Atlantic ridge). Details on the origin of sightings used in this study can be found in Table 1 of the associated publication.

Region	Effort	Sightings
CAR	24264.473	16
EC	1044357.704	226
EU	27526.342	29
GOM	194715.349	116
MAR	2424.421	8
All regions	1293288.288	395

Table 2: Effort (km) and sightings per month.

Month	Effort	Sightings
January	77892.79	5
February	123591.37	9
March	117923.54	15
April	117929.72	9
May	149765.03	65
June	132713.99	27
July	162324.31	154
August	129660.43	86
September	71696.07	7
October	82560.18	5
November	69210.92	9
December	58019.93	4
All Months	1293288.29	395

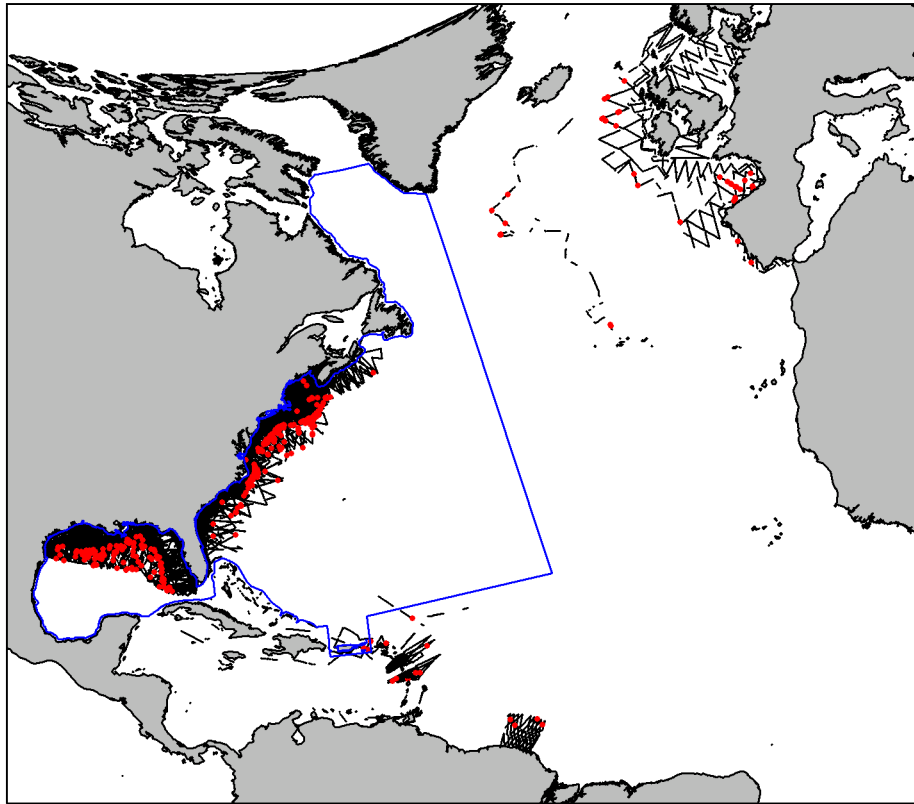


Figure 1: Map of segments (black lines) and sighting locations (red dots). An Albers equal area projection optimized for the AFTT area is used.

2- Methodological decisions

Methodological decisions reported in this section were made according to information available to us in the literature as well as feedback from a number of experts we consulted.

Modeled taxon

Beaked whales.

Since beaked whales are rarely differentiable at sea, leading to a high number of ambiguous sightings, we modeled them as a guild. Our beaked whale guild included Cuvier's beaked whale (*Ziphius cavirostris*) and 4 species of Mesoplodon -Blainville's beaked whale (*Mesoplodon densirostris*), Gervais' beaked whale (*Mesoplodon europaeus*), Sowerby's beaked whale (*Mesoplodon bidens*) and True's beaked whale (*Mesoplodon mirus*)- known to occur in the western North Atlantic (Macleod 2000). We did not include the northern bottlenose whale (*Hyperoodon ampullatus*) in our beaked whale guild because it is often distinguished from other beaked whale species in U.S. waters and its ecology largely differs from the ecology of *Ziphius* and *Mesoplodon spp.*

Modeled season

Our literature review did not yield any descriptions of seasonal movements for beaked whales at the scale of our study area; therefore, we fitted a year-round model.

Segments

We incorporated segments from the east coast, Gulf of Mexico, Caribbean and mid-Atlantic ridge where sightings were reported (Table 1). We excluded segments from the European Atlantic because we expected species composition to be different in this region compared to the western north Atlantic (for example, True's beaked whale is regular in the western North Atlantic but vagrant in the eastern North Atlantic (Waring et al. 2009); we expected this species to represent a significant proportion of the unidentified Mesoplodon sightings in the western north Atlantic but a negligible proportion in the eastern north Atlantic).

3- Best model

- **Predictors:** depth, distance to the nearest canyon or seamount (DistToCanyonOrSeamount), chlorophyll concentration (Chl), current speed
- **Model summary:**

```
##
## Family: Tweedie(p=1.358)
## Link function: log
##
## Formula:
## abundance ~ s(Depth, k = 4, bs = "ts") + s(DistToCanyonOrSeamount,
##      k = 4, bs = "ts") + s(Chl1, k = 4, bs = "ts") + s(CurrentSpeed,
##      k = 4, bs = "ts") + offset(log(area_km2))
## <environment: 0x1c93cbf4>
##
## Parametric coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)  -8.2844    0.1698  -48.79  <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##              edf Ref.df      F p-value
## s(Depth)      2.749     3 53.762 < 2e-16 ***
## s(DistToCanyonOrSeamount) 1.365     3 17.229 7.16e-14 ***
## s(Chl1)       2.766     3 14.697 1.92e-10 ***
## s(CurrentSpeed) 2.538     3  9.282 5.80e-07 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  -0.00276  Deviance explained = 42.8%
## -REML = 3370.6  Scale est. = 101.54    n = 124995
```

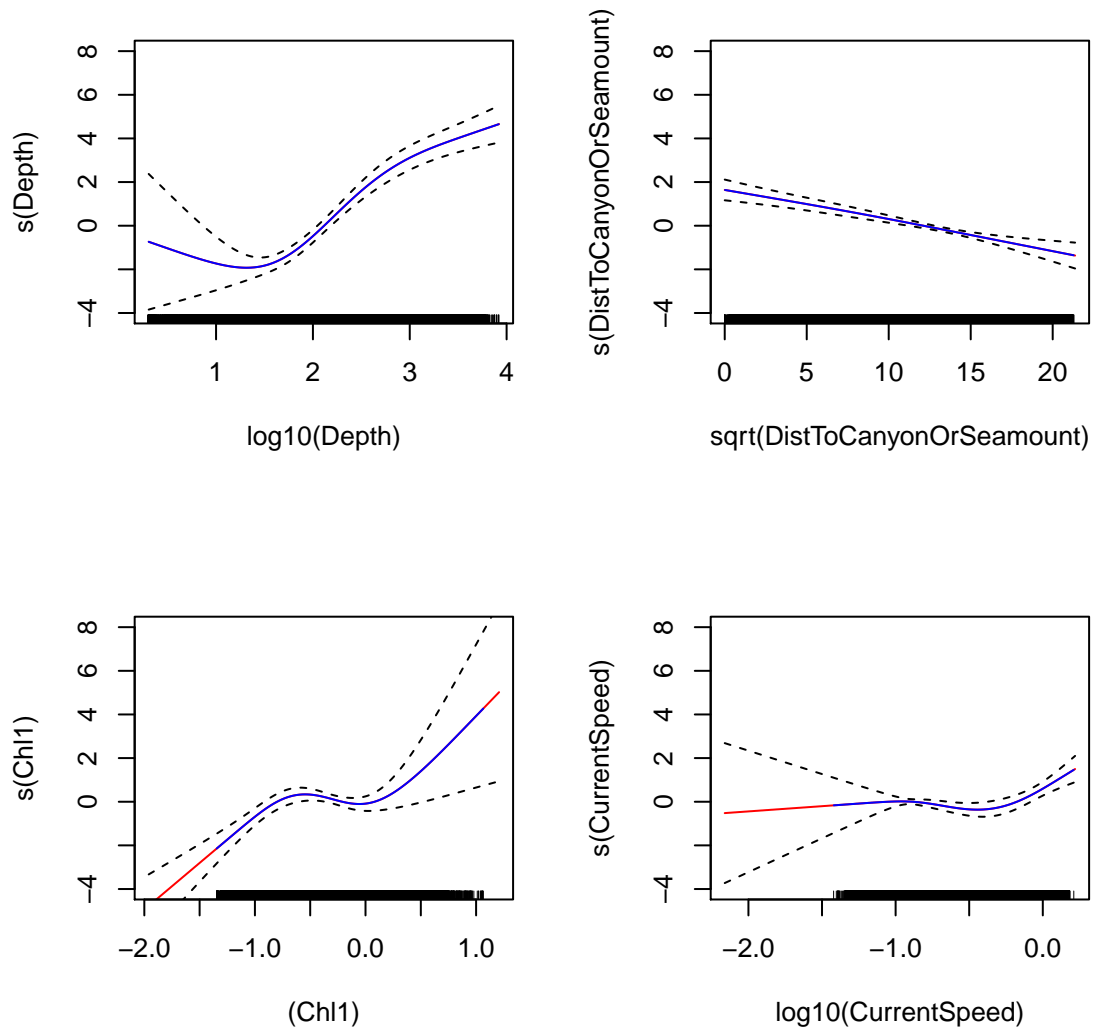


Figure 2: GAM term plots with the log-transformed abundance on the y axis. The solid blue line is the smooth function fitted to the data. The solid red line is the smooth function extrapolated to all covariate values in the prediction area. The dashed lines represent the approximate 95% confidence intervals. The rug plot on the x-axis shows covariate values sampled in the data. Note that transformations were used for some covariates.

4- Environmental envelopes

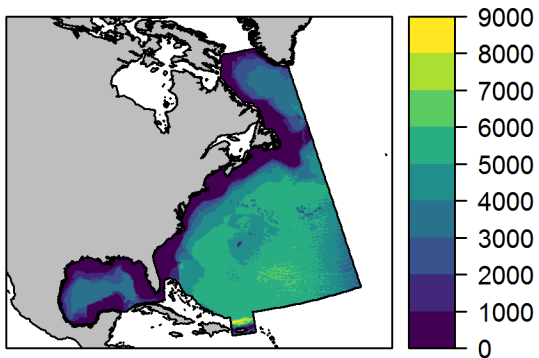


Figure 3: Environmental envelope for depth. White cells within the AFTT polygon indicate areas where covariate values fell beyond the range of covariate values sampled by the surveys.

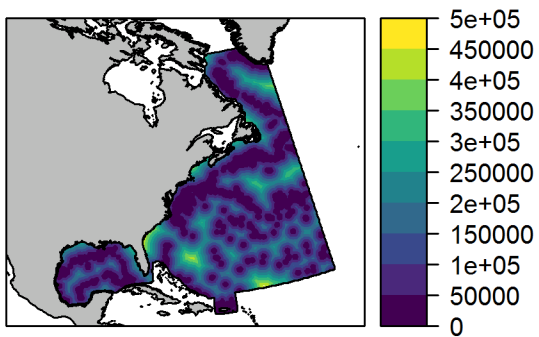
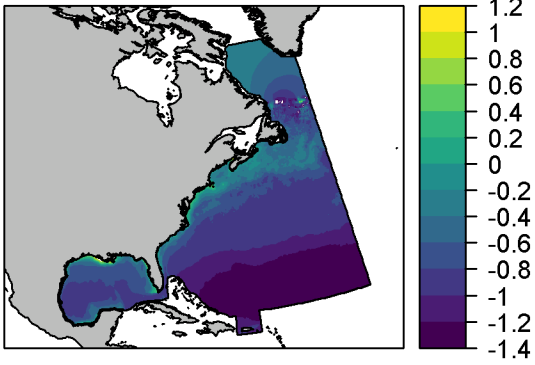
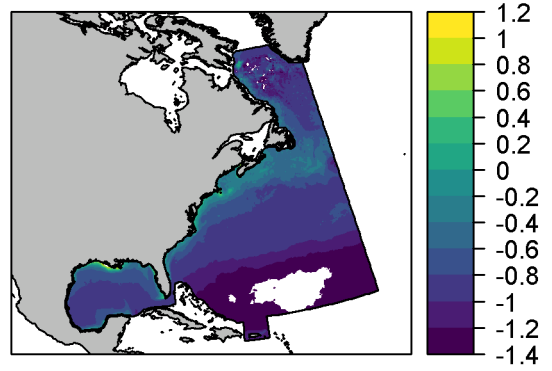


Figure 4: Environmental envelope for distance to the nearest canyon or seamount. White cells within the AFTT polygon indicate areas where covariate values fell beyond the range of covariate values sampled by the surveys.

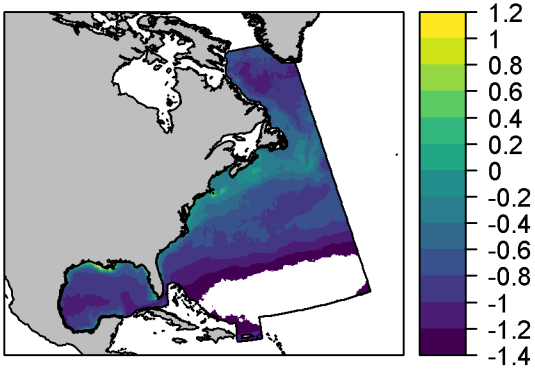
January



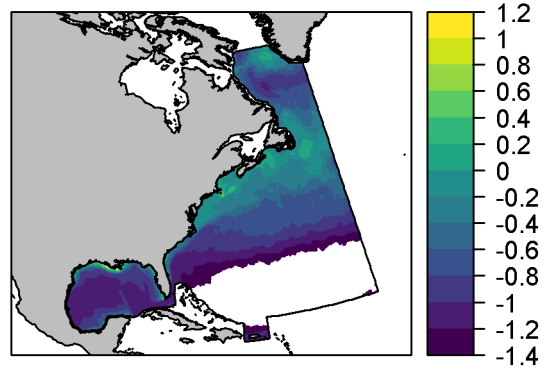
February



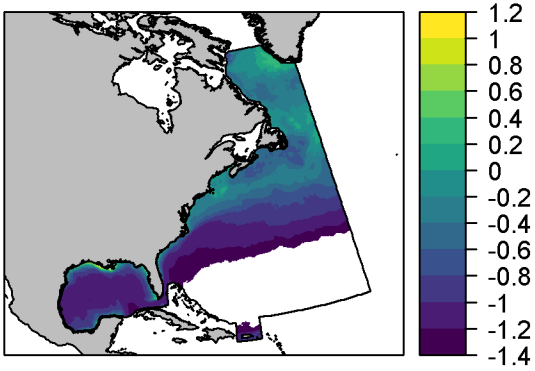
March



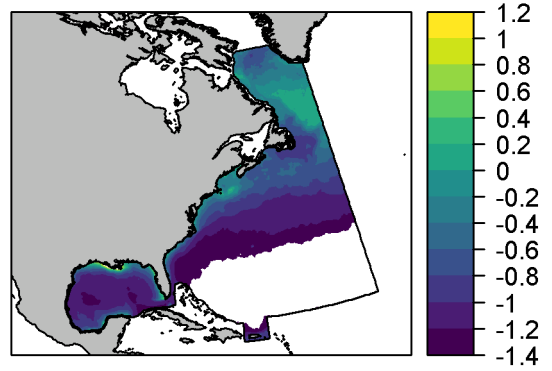
April



May



June



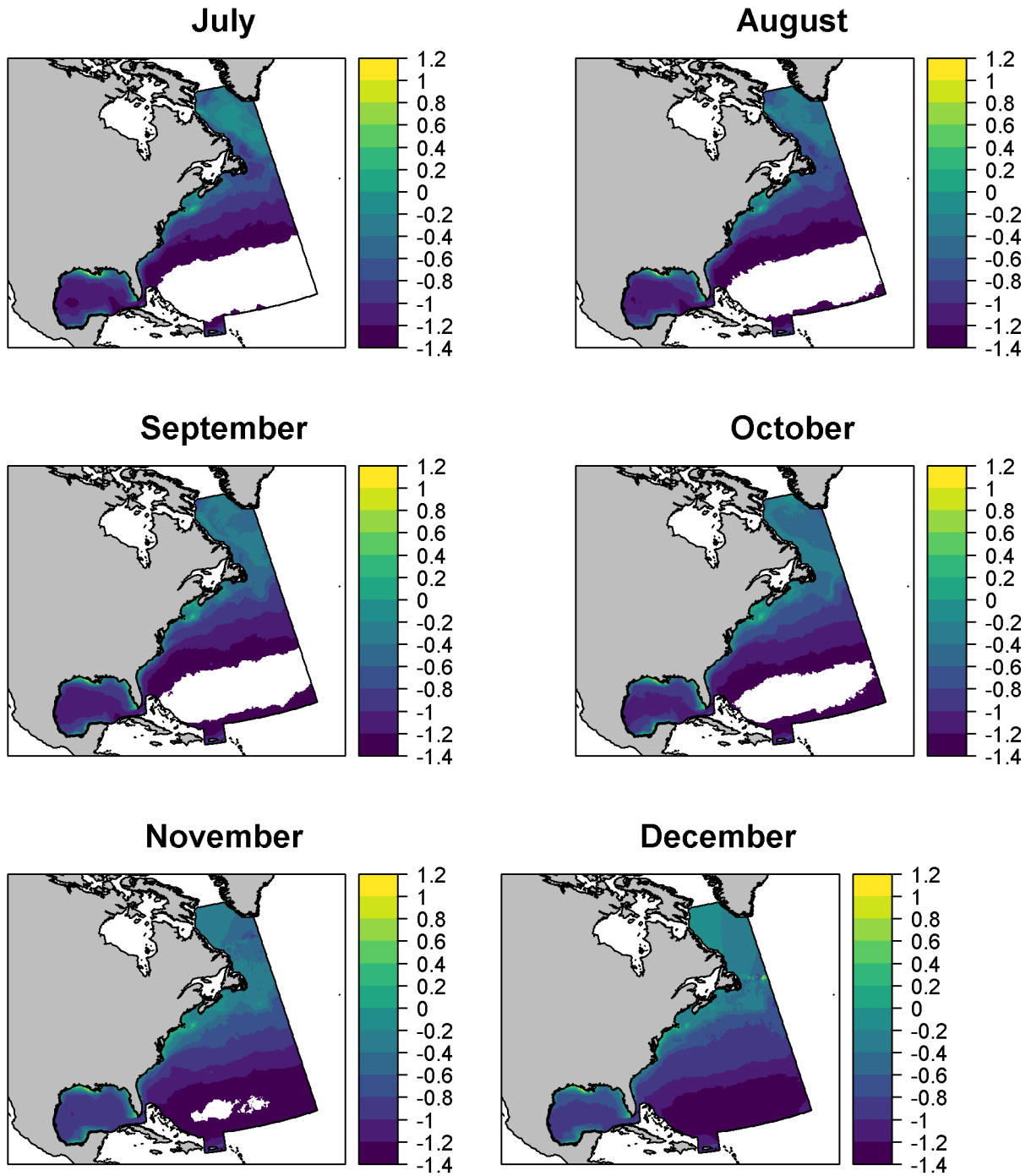
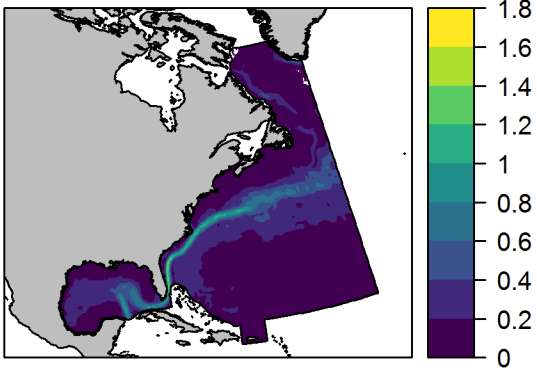
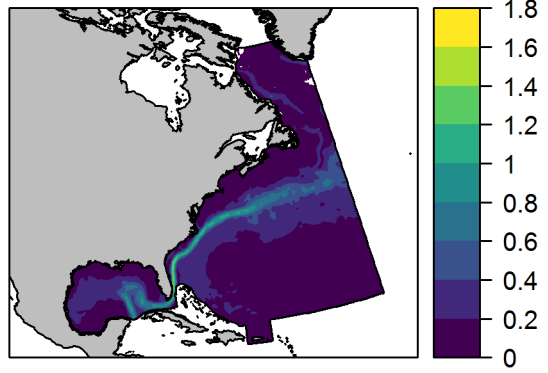


Figure 5: Monthly environmental envelopes for chlorophyll concentration. White cells within the AFTT polygon indicate areas where covariate values fell beyond the range of covariate values sampled by the surveys.

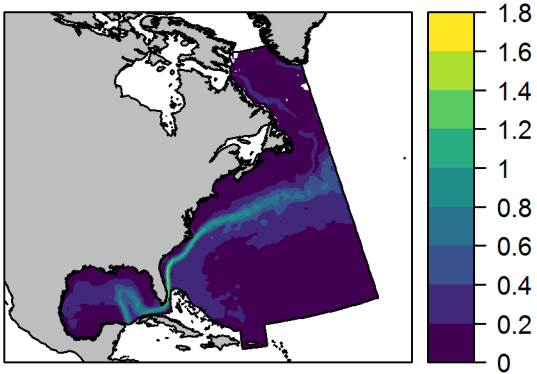
January



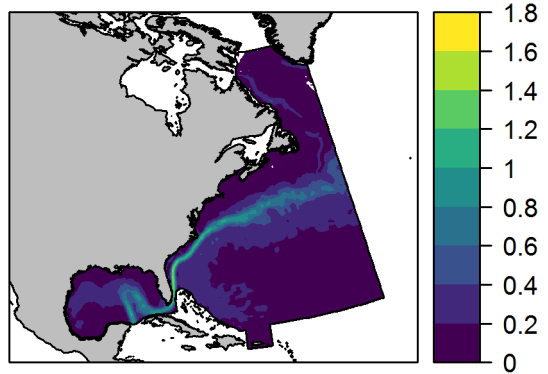
February



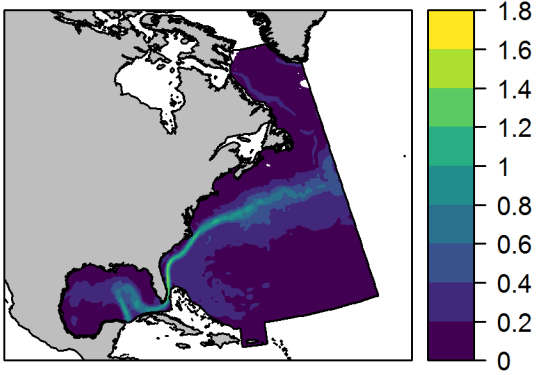
March



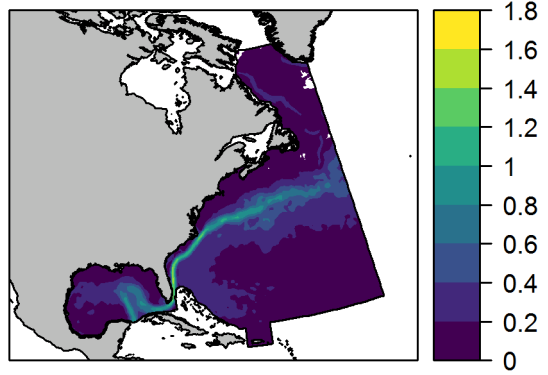
April



May



June



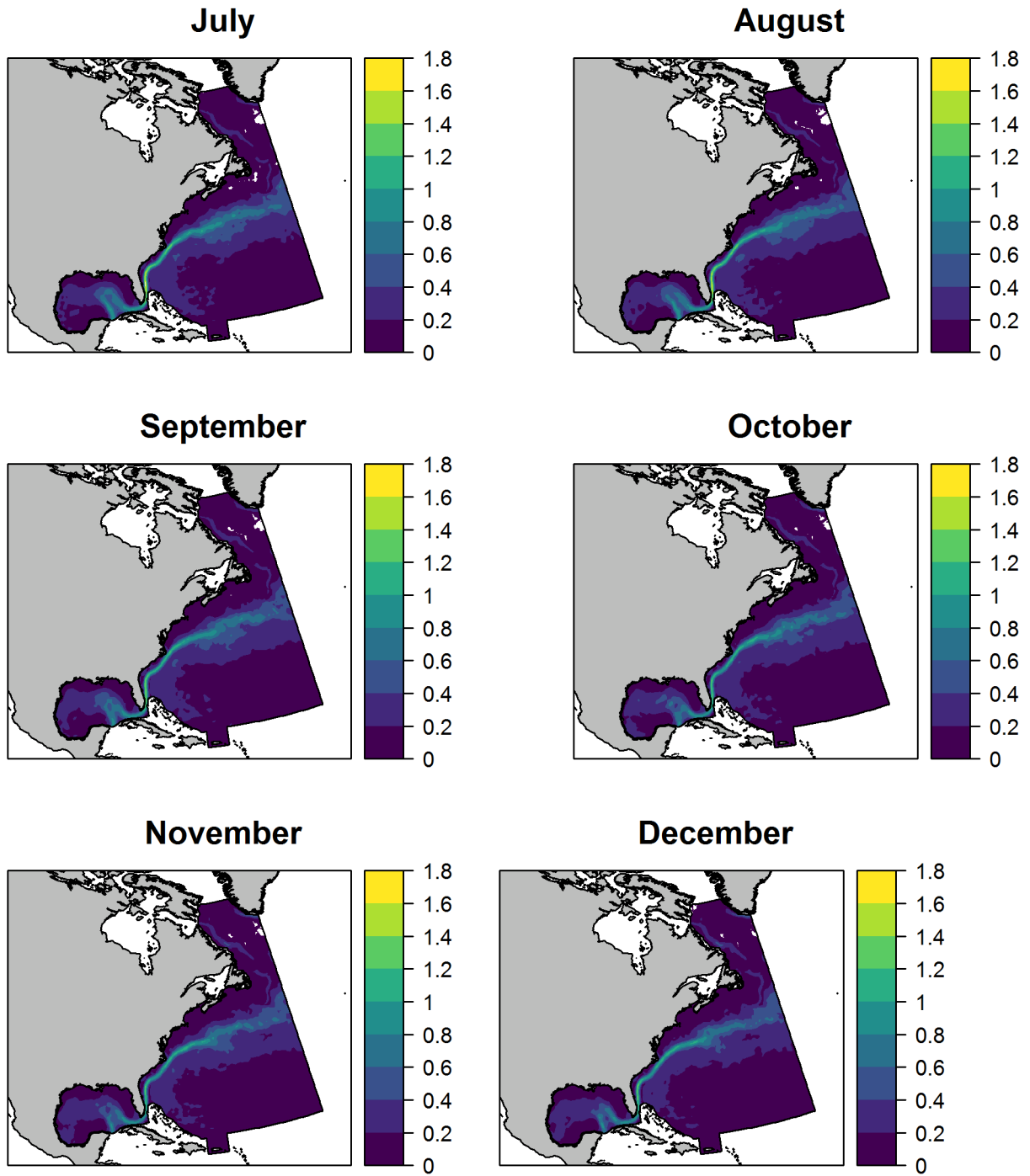


Figure 6: Monthly environmental envelopes for current speed. White cells within the AFTT polygon indicate areas where covariate values fell beyond the range of covariate values sampled by the surveys.

5- Predicted densities

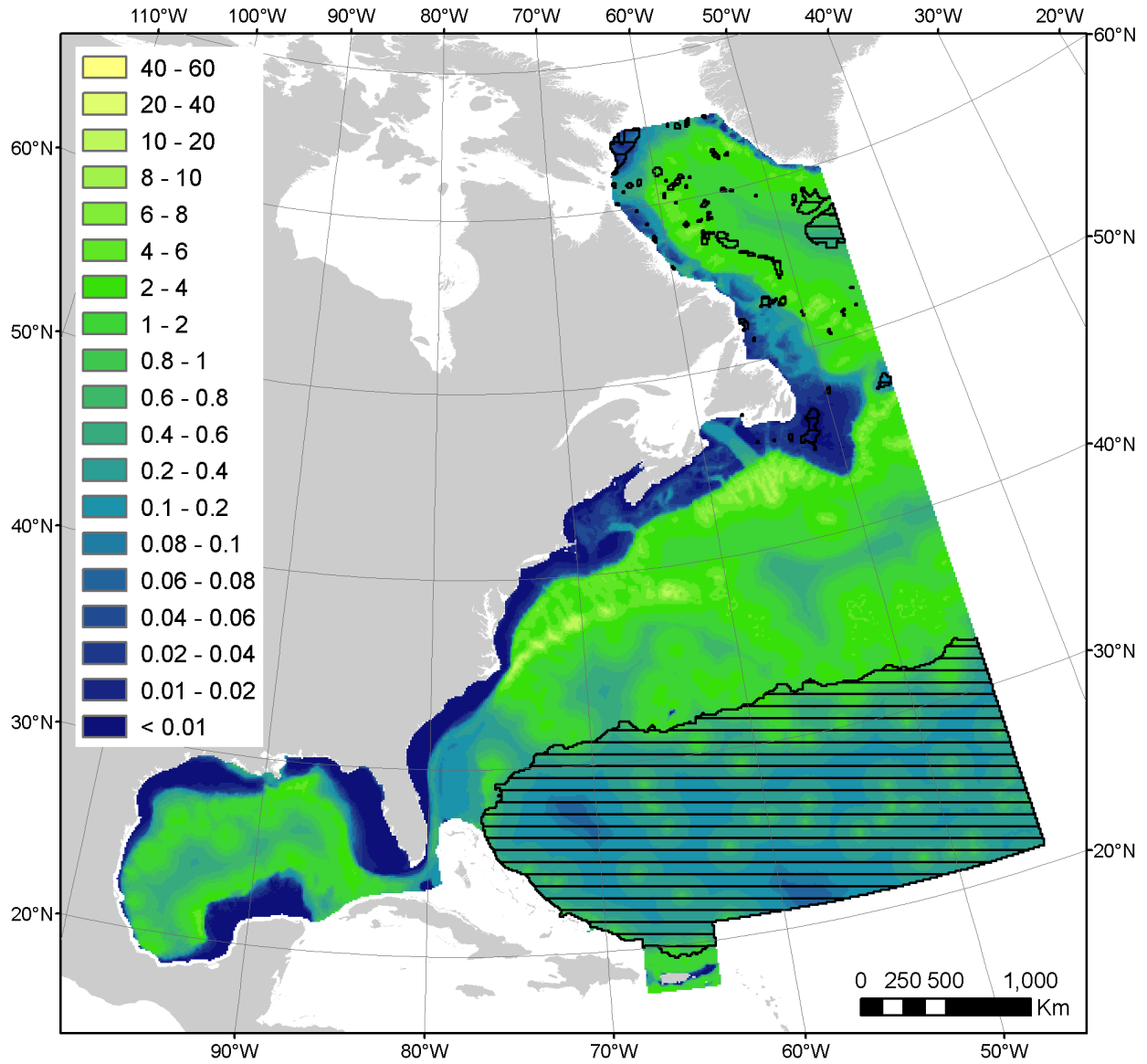


Figure 7: Mean predicted densities (individuals 100 km⁻²) in the AFTT area. Areas where we extrapolated beyond sampled predictor ranges and predicted densities should not be trusted are indicated with black crosshatches. An Albers equal area projection is used.

6- Coefficients of variation

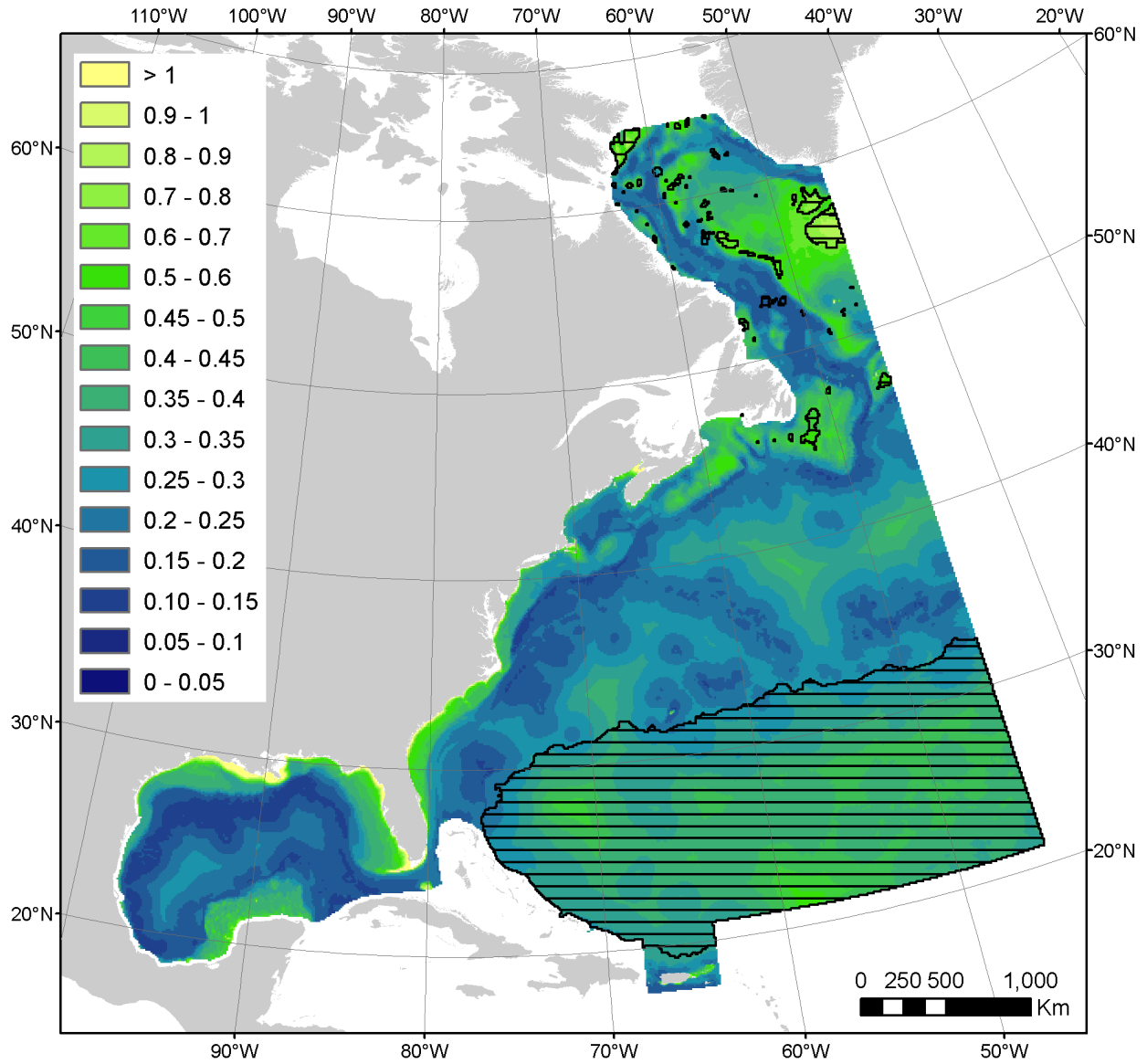


Figure 8: Mean predicted coefficients of variation derived from GAM parameters in the AFTT area. Areas where we extrapolated beyond sampled predictor ranges and coefficients of variation should not be trusted are indicated with black crosshatches. An Albers equal area projection is used.

7- Predicted densities per province

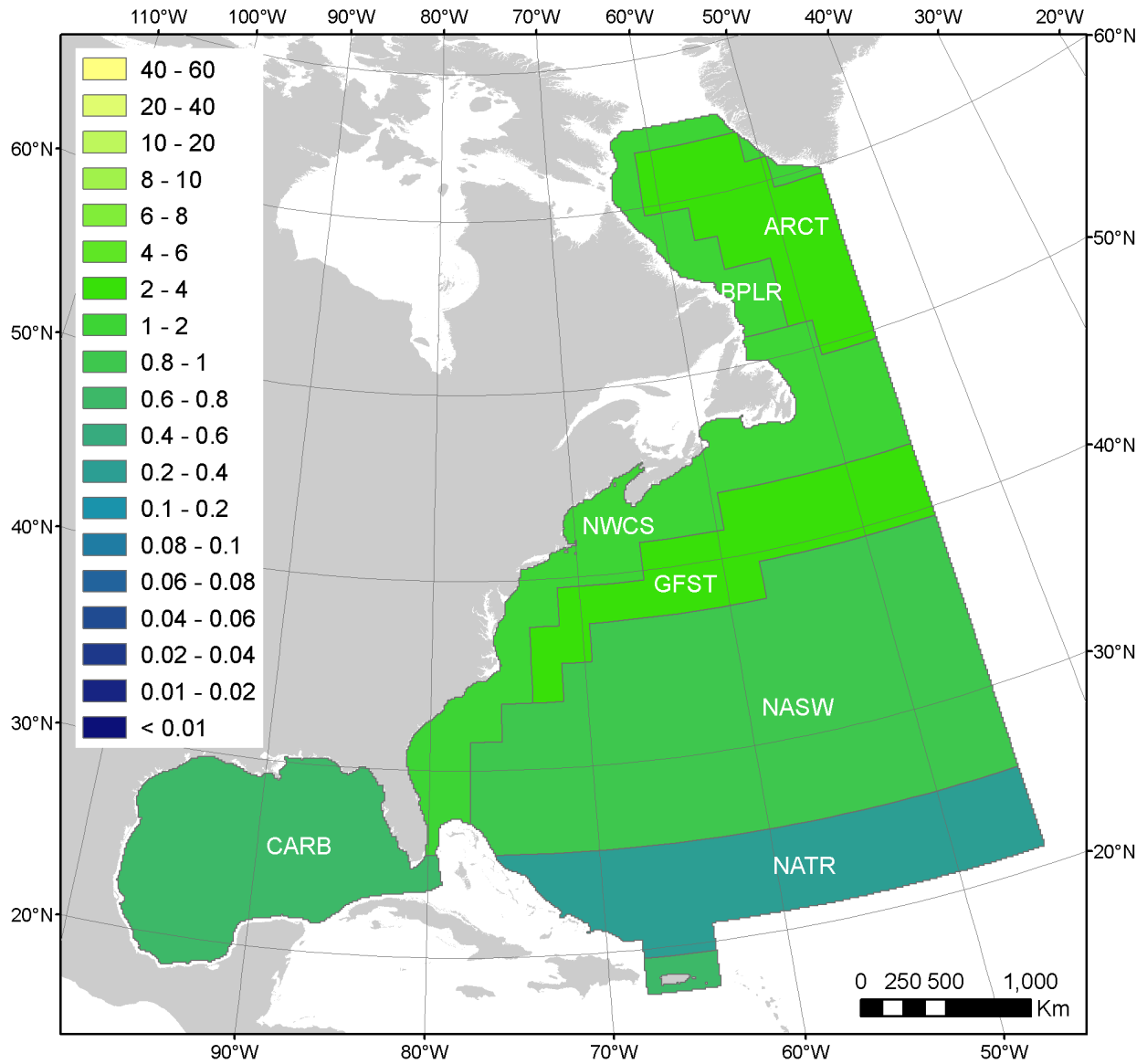


Figure 9: Predicted densities (individuals 100 km⁻²) averaged per Longhurst's biogeographical province. Note that the color scheme is the same as in Figure 7. Provinces: ARCT: Atlantic Arctic Province; BPLR: Boreal Polar Province; CARB: Caribbean Province; GFST: Gulf Stream Province; NATR: North Atlantic Tropical Gyral Province; NASW: North Atlantic Subtropical Gyral Province (West); NWCS: North West Atlantic Shelves Province.

8- Alternate models

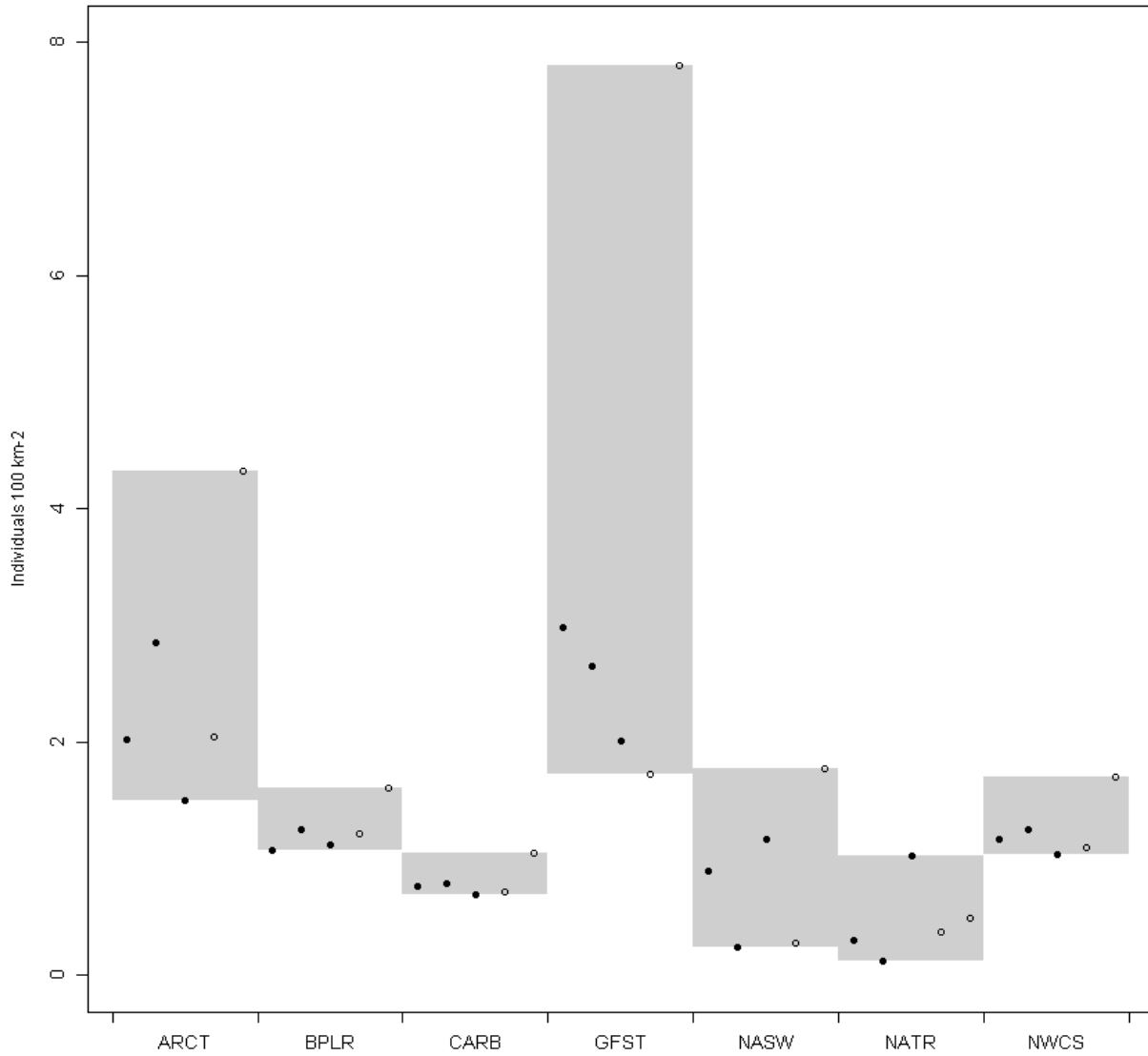


Figure 10: Sensitivity of densities predicted by the five top models per Longhurst's biogeographical province. Points represent predicted densities (individuals 100 km⁻²) for the five top models listed in Table 3, with the first to fifth models ordered from left to right. Filled points correspond to models with some support (sensu Burnham and Anderson (2002), i.e., $\Delta AIC < 2$) while hollow points correspond to models with little support (i.e., $\Delta AIC > 2$). The shaded areas indicate the range of densities predicted by the five top models for each province. Provinces: ARCT: Atlantic Arctic Province; BPLR: Boreal Polar Province; CARB: Caribbean Province; GFST: Gulf Stream Province; NATR: North Atlantic Tropical Gyral Province; NASW: North Atlantic Subtropical Gyral Province (West); NWCS: North West Atlantic Shelves Province.

Table 3: List of the five top models with lowest AIC values. Ns: non-significant. Predictor variables: EKE: eddy kinetic energy, SLAStDev: standard error of sea level anomaly, SST: sea surface temperature, PkPP: zooplankton production, PkPB: zooplankton biomass, EpiMnkPP: epipelagic micronekton production, EpiMnkPB: epipelagic micronekton biomass, VGPM: vertically generalized production model, CHL: chlorophyll-a concentration.

		Predictors		AIC	delta AIC
Depth	DistToCanyonOrSeamount	CurrentSpeed	Chl1	115361.4	0.0
Depth	DistToCanyon	CurrentSpeed	Chl1	115362.8	1.4
Depth	DistToCanyonOrSeamount	CurrentSpeed	DistToFront1	115363.0	1.6
Depth	DistToCanyon	CurrentSpeed	DistToFront1	115365.4	4.0
Depth	ns	Chl1	DistToFront1	115365.9	4.5

9- Residual diagnostics

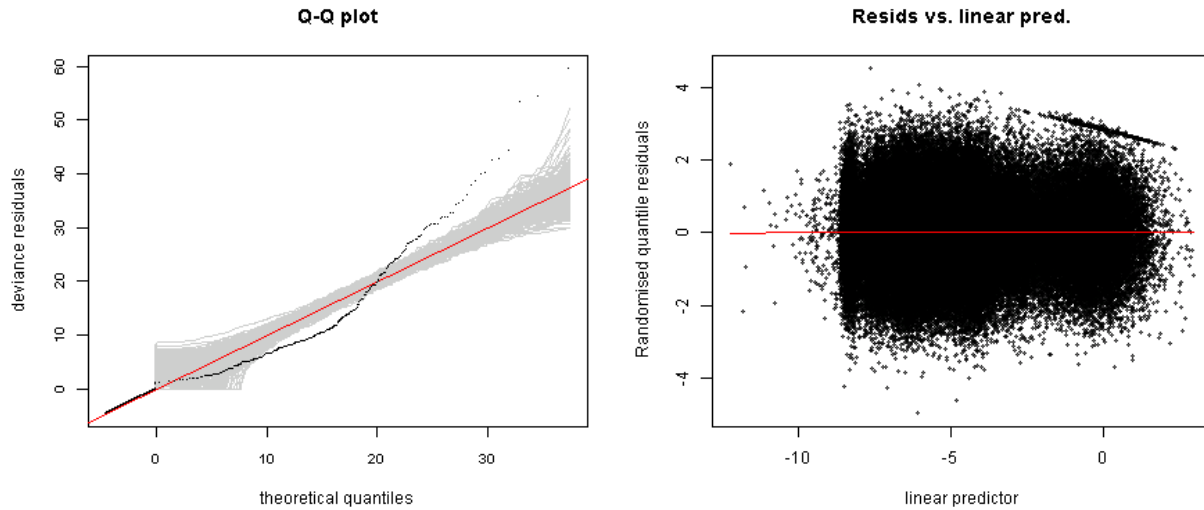


Figure 11: Diagnostic plots of residuals. Left: Quantile-quantile (Q-Q) plot of deviance residuals generated using the `qq.gam` function with 100 simulations (Augustin et al. 2012). Grey lines are possible simulated Q-Q plots under the assumption that the model is correct. The red reference line indicates perfect agreement between residual and theoretical residual distributions. Points lying away from the red line suggest poor model fit for the corresponding quantiles. Zeros appear to the left of the Q-Q plot in alignment with the reference line. Because, by design, models were not tightly fitted to the data (see discussion of the paper), deviations from the red line may be observed. Specifically, points far above the red line for large quantiles indicate that the model underestimates high abundances observed on some segments. Right: randomized quantile residuals vs. linear predictor. A LOWESS regression is shown as a red line to illustrate any trend in the points. This plot should be generally free of any pattern. Expanding y-range indicates non-constant variance (heteroskedasticity) in the model.

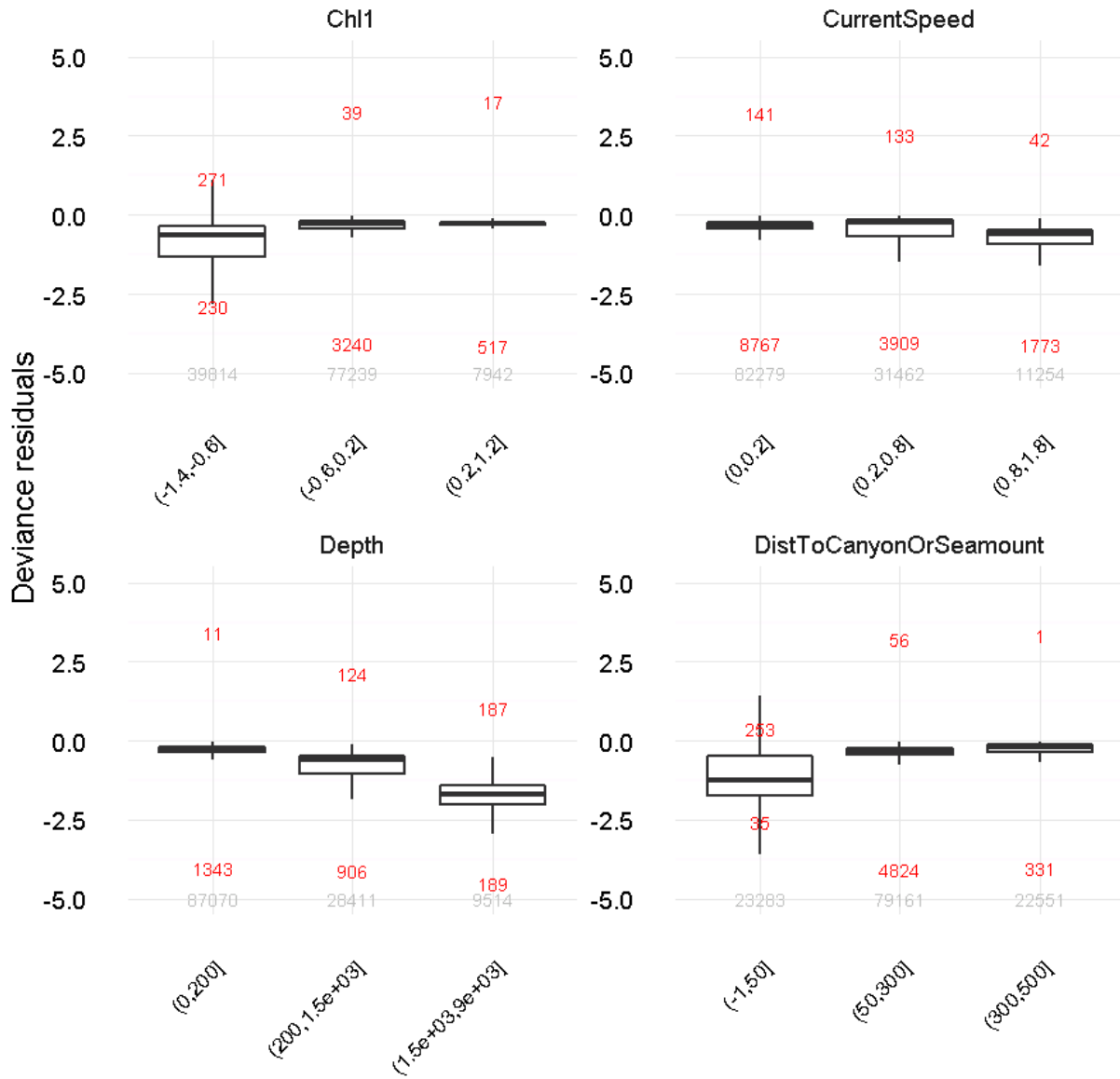


Figure 12: Boxplots of deviance residuals, binned for each predictor. The horizontal line represents the median, and the bottom and top of the box represent the first and third quartiles respectively. Whiskers extend 1.5 times the inter-quartile range following McGill et al. (1978). Total counts of outliers beyond the whiskers are indicated in red. Numbers of segments per bin are indicated in grey. Boxplots for the different bins of predictors should generally overlap. A boxplot having its median away from zero indicates poorer model fit for that predictor bin. Boxplots often have their medians close to zero and fewer outliers for predictor bins characterized by low abundances of the species, suggesting that model fit is generally better in low abundance areas. We believe this is an inherent feature of models applied to count data with numerous zeros.

10- Brief discussion and overall confidence in predictions

Description of confidence levels

We group taxa in three categories reflecting our relative level of confidence in predicted densities.

Level 1

This category includes tropical and warm temperate taxa for which survey data were available within most of the distributional range in the AFTT area. High/intermediate densities predicted beyond surveyed areas were supported by sightings available from OBIS-SEAMAP and the scientific literature. Very low densities predicted at northern latitudes were consistent with the described absence of these taxa. We have a reasonable confidence in predicted densities for these taxa.

Level 2

This category encompasses taxa for which a large part of the distributional range is in cold temperate and sub-polar waters. Models fitted to available survey data and extrapolated to cold temperate and sub-polar waters successfully predicted their occurrence, but predicted densities were largely speculative. The incorporation of line transect survey data from Canada and Greenland would be extremely useful to increase the reliability of predicted densities at northern latitudes. Unfortunately we were unable to obtain permission for using these data in our models. We remain hopeful that collaborations can be established in the future, and that the Canadian and Greenlandic surveys may be incorporated into a new version of our models. We have medium or low confidence in predicted densities for these taxa.

Level 3

This category includes taxa that are not known to primarily occur in cold temperate and sub-polar waters but were predicted in low/intermediate densities at higher latitudes. For these taxa, we believe predicted densities were likely overestimated at higher latitudes. However, predicted densities were supported by sightings available from OBIS-SEAMAP and the scientific literature within their core distributional range. The incorporation of line transect survey data from Canada and Greenland would be extremely useful to help correct the probable overestimation of densities at northern latitudes. We remain hopeful that collaborations can be established in the future, and that the Canadian and Greenlandic surveys may be incorporated into a new version of our models. We have medium or low confidence in predicted densities for these taxa.

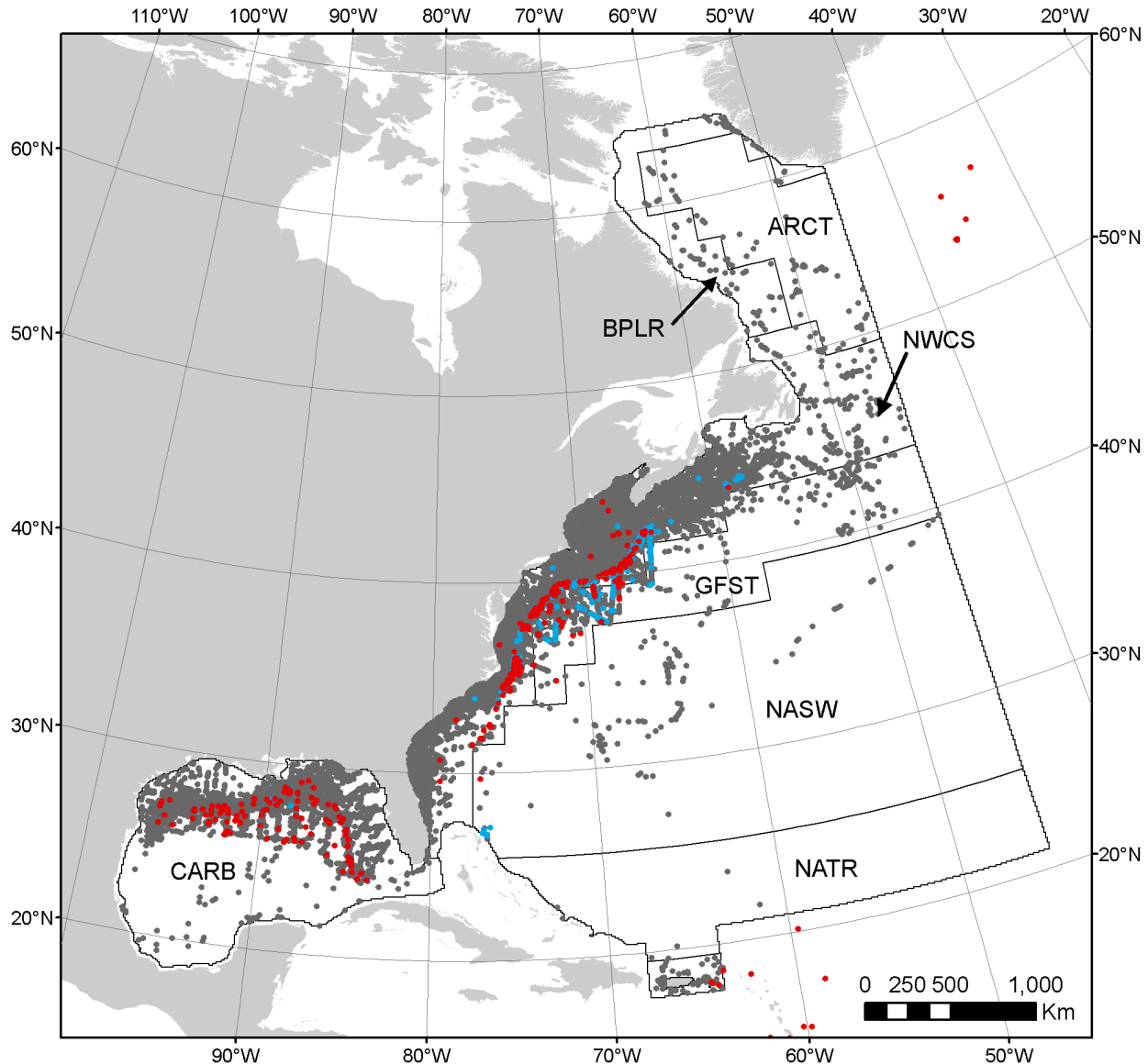


Figure 13: Red points are sightings of the taxon from line transect surveys used in this study. Blue points are sightings of the taxon reported by other datasets not used in our study for 1992-2016 (e.g., because they were not compatible with our methodology). Underlain grey points are sightings of other cetacean species, taken from these other datasets. Blue and grey points were extracted from OBIS-SEAMAP (accessible at <http://seamap.env.duke.edu/>) (Halpin et al. 2009); citations for individual datasets are provided at the end of this report. Longhurst's biogeographical provinces are shown as polygons. Dense patches of grey points without red or blue points suggest locations where the taxon of interest may be absent, under the presumption that observers who reported other cetacean taxa would have reported this one if sighted. However, important caveats apply: the map does not quantify observation effort, which was not available for all datasets and was very difficult to standardize across disparate sources (e.g., scientific surveys, whale watching logs, opportunistic sightings). The spatial distribution of effort was highly heterogeneous in both space and time. Only openly accessible datasets were considered; other cetacean datasets are known to exist for the AFTT area but have not been released for public use (e.g., the 2007 Trans North Atlantic Sightings Survey (TNASS) in Canada). The presumption that grey dots imply absence may not always hold; for example, if effort conducted in that area was directed towards particular species, sightings of our taxon of

interest may not have been recorded.

General

A total of 366 sightings were used to fit the habitat-based density model. The first or lowest AIC model included depth, distance to the nearest canyon or seamount, chlorophyll concentration and current speed (listed in decreasing order of importance according to F-scores) and had an explained deviance of 42.8%. All top five models included depth (Table 3). The second and third models had 3 predictors in common with the first model (depth and current speed), and a delta AIC < 2 indicating some statistical support sensu Burnham and Anderson (2002). The fourth and fifth model had little statistical support. Predicted densities from the top five models appeared relatively similar in the BPLR, CARB and NWCS provinces while they differed the most in the ARCT and GFST provinces (Figure 10). The fifth model (non statistically supported) predicted higher densities than the other models in most provinces and was responsible for most of the variation. The first, second and third model (statistically supported) predicted similar densities in the BPLR, CARB and NWCS provinces, and densities differing roughly by a factor 1.5 in the ARCT and GFST provinces and a factor 5 in the NASW and NATR provinces. The first best model had a lower AIC and explained 0.3-0.5% more deviance compared to the second and third models, suggesting it was slightly more suitable for modeling beaked whale densities.

Due to their cryptic behavior and occurrence in deep offshore waters, beaked whales are often difficult to observe at sea. This likely explains why few observations are reported beyond extensively surveyed areas (Figure 13).

Predictions in the AFTT area appeared broadly consistent with the known distribution of beaked whale species in a variety of deep waters from tropical to sub-polar waters. Cuvier's beaked whale has the most cosmopolitan distribution, ranging throughout tropical, sub-tropical, temperate and sub-polar waters worldwide (MacLeod et al. 2005). Sowerby's and True's beaked whales more commonly occur in cold temperate waters, whereas Blainville's and Gervais's beaked whales are more frequent in warm temperate waters (MacLeod 2000, MacLeod et al. 2005). We caution that beaked whales are mainly found in deep waters beyond the continental shelf break which received comparatively little survey effort compared to the continental shelf.

We now discuss the quality of predictions per biogeographic province by comparing them with available literature and observations from OBIS-SEAMAP.

Boreal polar (BPLR) and Atlantic Arctic (ARCT) provinces

Few dedicated or opportunistic observations were available to support predicted densities in the BPLR and ARCT provinces (Figure 13). Unidentified Mesoplodon were sighted on 8 occasions during the MAR-ECO survey, with the northernmost sighting around 57°N (Figure 13) (Waring et al. 2008). Macleod (2000) Sowerby's beaked whale sightings as far north as 71.5°N in the eastern North Atlantic. Although no sightings exist that far north in the western North Atlantic, it is not unlikely that Sowerby's beaked whale also occurs in this part of the basin. Cuvier's beaked whales have been sighted in various sub-polar and polar waters (notably in the Pacific Ocean) (Macleod 2000), and their presence in sub-polar and polar waters of the western North Atlantic does not seem unlikely. Until they are further validated with additional observations, predictions in the BPLR and ARCT provinces should be considered largely speculative. Moreover, extrapolation to lower current speed occurred in parts of these provinces and therefore predicted densities should be interpreted with a lot of caution.

North West Atlantic shelves (NWCS) and Gulf Stream (GFST) provinces

Relatively high densities were predicted in offshore waters beyond the continental shelf within the NWCS province as well as in the GFST province.

Beaked whales are often found in deep waters near high-relief bathymetric features, such as slopes, escarpments and canyons where their preferred prey are known to aggregate (Moors-Murphy 2014). The model predicted higher beaked whale densities near submarine canyons in the NWCS province. This appeared in line with the higher sighting rates of beaked whales in canyons compared to non-canyon habitats (Waring et al. 2001), as well as the known concentrations of Sowerby's and Cuvier's beaked whales in the Gully, Shortland and Haldimand canyons (Hooker & Baird 1999; Whitehead 2013) (Figure 13).

High predicted densities (maximum: 14 individuals 100 km⁻²) off Cape Hatteras, North Carolina, and in the western part of the GFST province were compatible with the concentration of sightings visible on Figure 13. Stanistreet et al. (2016) deployed High-frequency Acoustic Recording Packages off Cape Hatteras and recorded detections of Cuvier's beaked whales in 94% of the recording days and of Gervais' beaked whale in 42% of the days. When compared to two other locations in the western North Atlantic (the Norfolk canyon and the Gully canyon), Cape Hatteras had the highest detection rates. As far as our knowledge, the high predicted densities off Cape Hatteras are not incompatible with the findings of Stanistreet et al. (2016).

North Atlantic tropical gyral (NATR) and North Atlantic subtropical gyral (NASW) provinces

Limited line transect survey effort was available in offshore waters of the NATR and the NASW provinces. Yet, the model predicted relatively high densities of beaked whales in these provinces, notably around offshore seamounts. We warn that predictions in the NATR province and the southern part of the NASW province were derived from extrapolation to waters of lower chlorophyll concentration; they should be considered with extreme caution. We re-iterate that predicted densities from statistically supported models differed the most in these provinces.

Regarding the limited effort in offshore waters, we note that the highest densities of beaked whales were predicted in the western part of the Gulf Stream province where some survey effort did occur in offshore waters with depth > 4000m. Line transect surveys also occurred in offshore waters of the Caribbean Sea where beaked whale sightings were recorded as deep as 4900m. Finally, the MAR-ECO survey recorded beaked whale sightings further offshore than any other survey (Figure 13). Therefore, the relatively high predicted densities in offshore waters are supported by some survey effort.

In the extensively surveyed waters of the eastern tropical Pacific (ETP) that encompass a large proportion of abyssal plains, we note that Cuvier's beaked whales were sighted as deep as 5197m (mean depth 3445m) and Mesoplodon beaked whales as deep as 5749m (mean depth 3513m) (Ferguson et al. 2006). In addition, beaked whale observations in the ETP were often associated with offshore seamounts (Ferguson et al. 2006). Given these findings in the ETP, we believe predictions in the offshore western North Atlantic are not unrealistic.

Finally, we note that predictions to the north of the Bahamas (edge of the NASW province) are compatible with frequent observations of beaked whale species in the Great Bahamas and Little Abaco canyons (MacLeod & Zuur 2005; Claridge 2006) (Figure 13).

Caribbean (CARB) province

To our knowledge, no observation of live beaked whale is documented in the literature in the southern part of the Gulf of Mexico, but stranding records are documented for Cuvier's, Gervais' and Blainville's beaked whales (Jefferson & Schiro 1997; Ortega-Ortiz 2002). Until they are further validated with at-sea observations, predictions in the southern Gulf of Mexico remain speculative.

Predictions off Puerto Rico appeared compatible with opportunistic observations of Cuvier's beaked whales documented by Mignucci-Giannoni (1998).

Overall confidence: level 3

Predictions were in line with the occurrence of beaked whales in a variety of deep waters, from tropical to sub-polar waters. We believe the model may overestimate predicted densities in sub-polar waters where few records of beaked whales exist. The incorporation of line transect survey data from Canada and Greenland would help correct this possible overestimation. Unfortunately, we were unable to obtain permission for using these data in our model. We remain hopeful that collaborations can be established in the future, and that the Canadian and Greenlandic surveys may be incorporated into a new version of our model.

11- References

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