Habitat-based density model for sperm whale in the AFTT area

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This report documents the habitat-based density model for sperm whale 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 sperm whale 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	34
EC	1044357.704	501
EU	27526.342	34
GOM	194715.349	357
MAR	2424.421	49
All regions	1293288.288	975

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

Month	Effort	Sightings
January	77892.79	9
February	123591.37	26
March	117923.54	27
April	117929.72	46
May	149765.03	162
June	132713.99	137
July	162324.31	352
August	129660.43	169
September	71696.07	18
October	82560.18	7
November	69210.92	7
December	58019.93	15
All Months	1293288.29	975

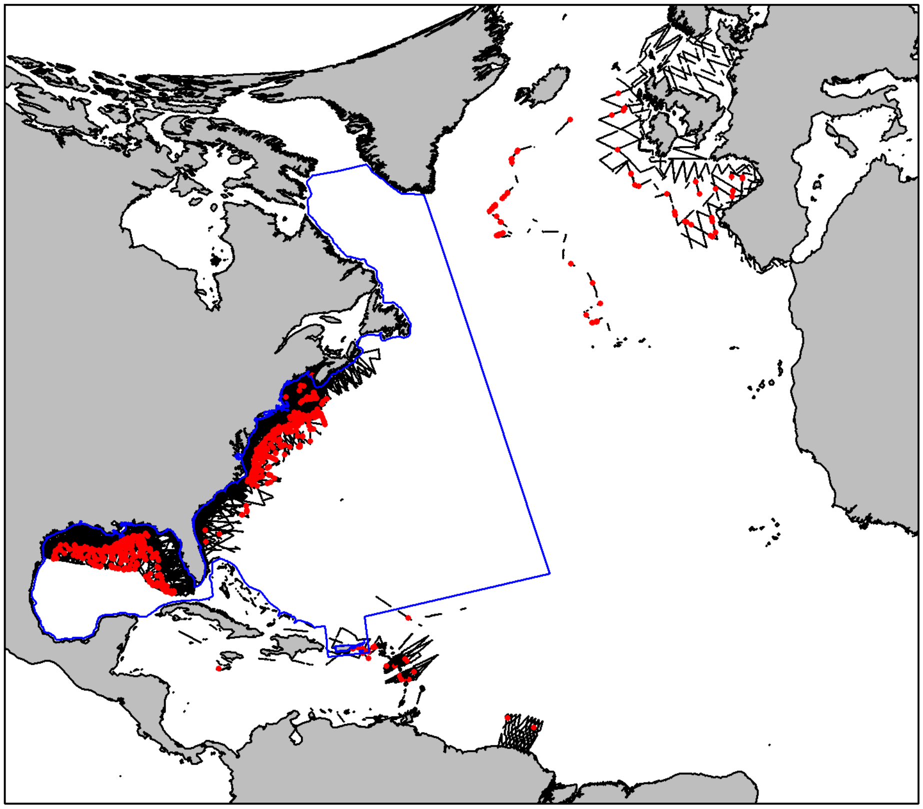


Figure 1: Map of segments (black lines) and sighting locations (red dots). An Albers equal area projection optimized for the AFTT area is used.

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

Sperm whale (*Physeter macrocephalus*)

Sperm whales exhibit complex social dynamics that affect both their distribution and migration patterns (Whitehead 2009). Since our survey data lacked the data attributes (sex in particular) to address this, we fitted a single model that incorporated all available sightings.

Modeled season

Sperm whales are reported year-round in U.S Atlantic and Gulf of Mexico waters. In addition, satellite tracks of 52 individuals in the Gulf of Mexico revealed no discernible seasonal migrations (Jochens et al. 2008). Based on their described year-round presence, it seemed reasonable to fit a year-round model incorporating all available survey data.

Segments

We incorporated segments from the east coast, Gulf of Mexico, Caribbean and mid-Atlantic ridge. Incorporating segments from the European Atlantic seemed to excessively increase predicted densities near canyons and seamounts in the western North Atlantic. Based on this result and the presumption that sperm whales may respond differently to environmental drivers in the eastern North Atlantic, we excluded segments from the European Atlantic.

3- Best model

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

```
##
## Family: Tweedie(p=1.267)
## Link function: log
##
## Formula:
## abundance ~ s(Depth, k = 4, bs = "ts") + s(Chl1, k = 4, bs = "ts") +
##     s(DistToCanyonOrSeamount, k = 4, bs = "ts") + offset(log(area_km2))
## <environment: 0x0f33a0c4>
##
## Parametric coefficients:
##             Estimate Std. Error t value Pr(>|t|)
## (Intercept)  -8.7837     0.1301   -67.5   <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)                   2.220      3 104.62  < 2e-16 ***
## s(Chl1)                    2.192      3  17.76 1.19e-13 ***
## s(DistToCanyonOrSeamount) 2.222      3  73.66  < 2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.0181   Deviance explained =   42%
## -REML = 5924.3  Scale est. = 30.307    n = 124995
```

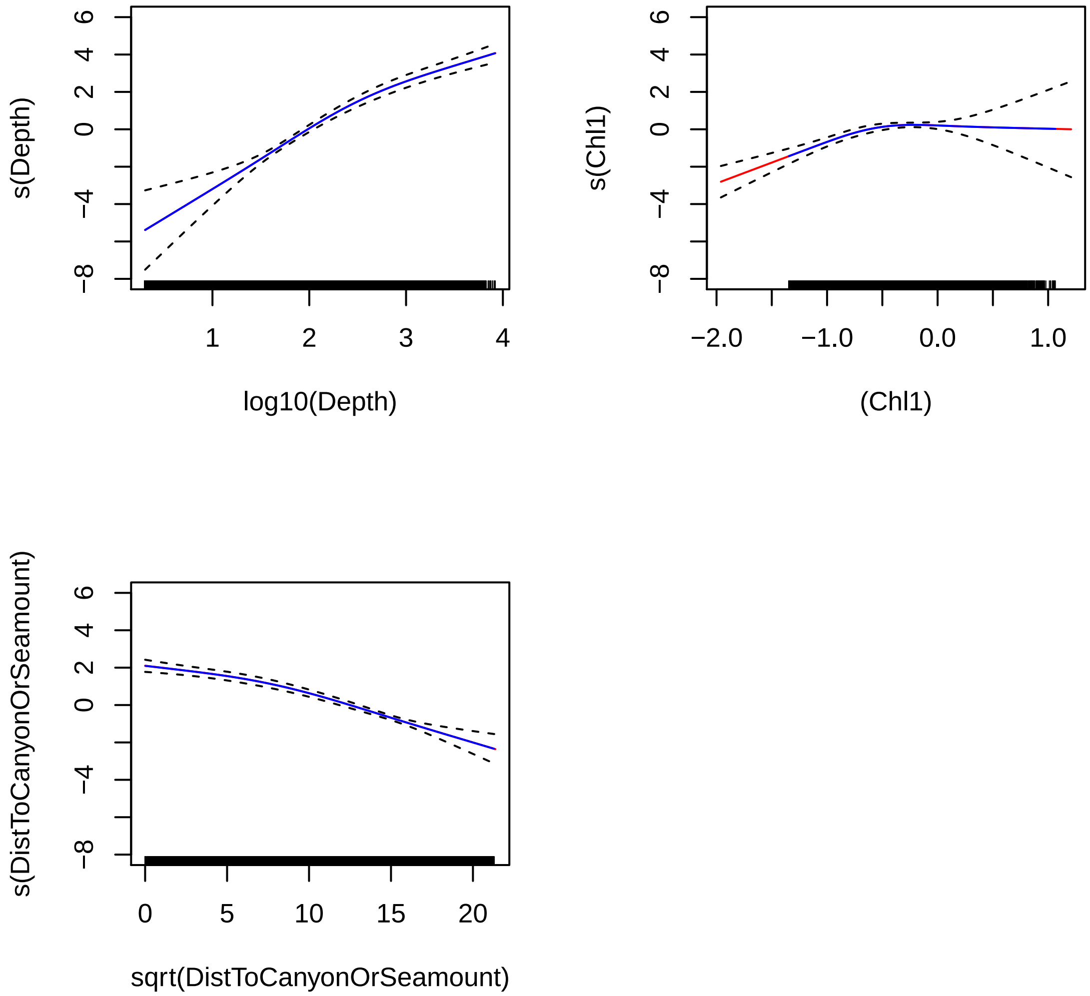


Figure 2: GAM term plots with the log-transformed abundance on the y axis. The solid blue line is the smooth function fitted to the data. The solid red line is the smooth function extrapolated to all covariate values in the prediction area. The dashed lines represent the approximate 95% confidence intervals. 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

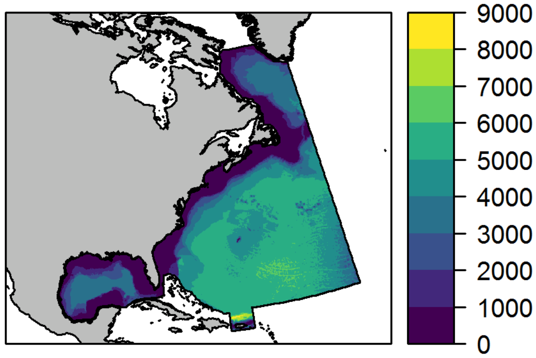
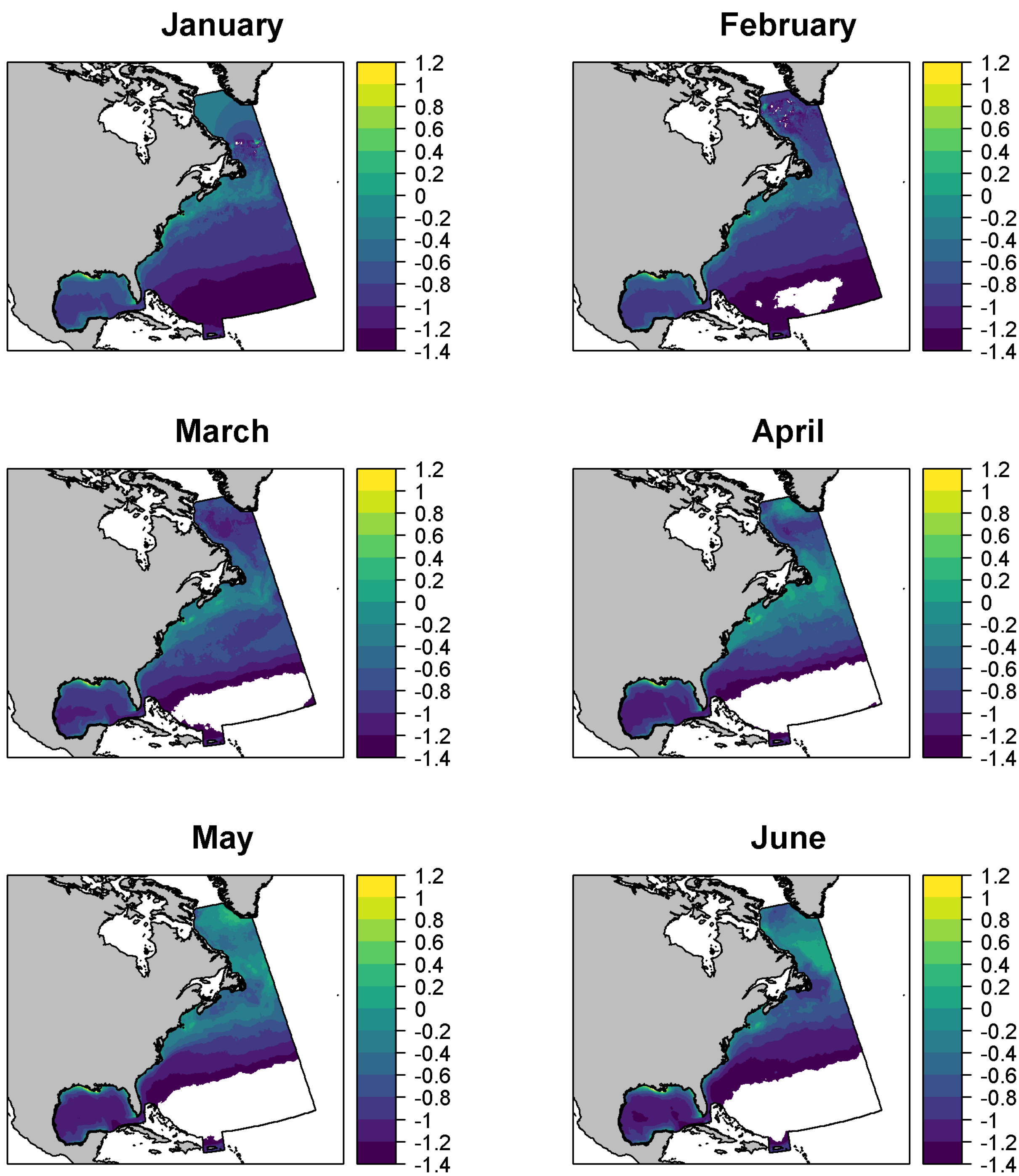


Figure 3: Environmental envelope for depth. White cells within the AFTT polygon indicate areas where covariate values fell beyond the range of covariate values sampled by the surveys.


January
February
March
April
May
June
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
-1.2
-1.4

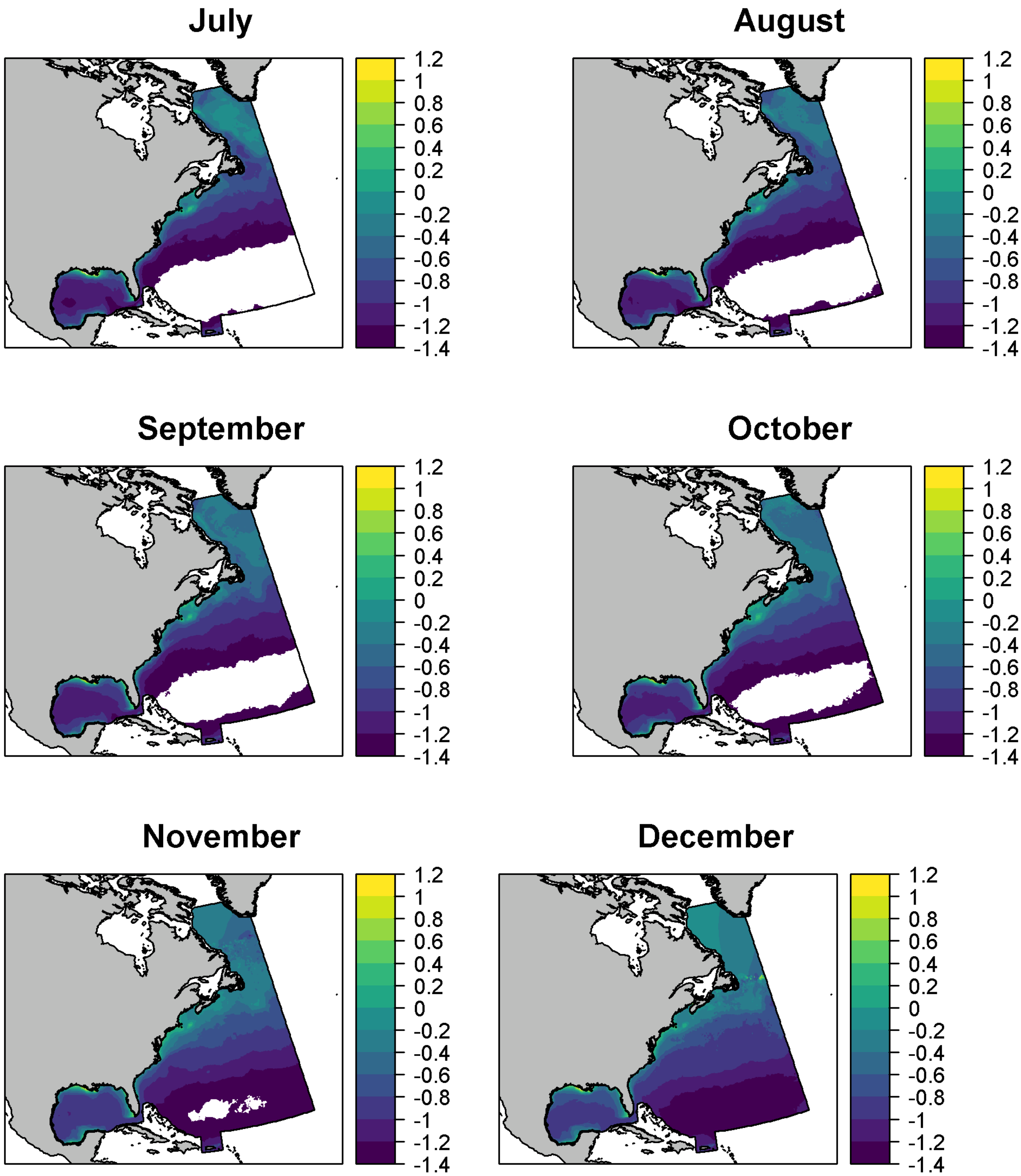


Figure 4: Monthly environmental envelopes for chlorophyll concentration. White cells within the AFTT polygon indicate areas where covariate values fell beyond the range of covariate values sampled by the surveys.

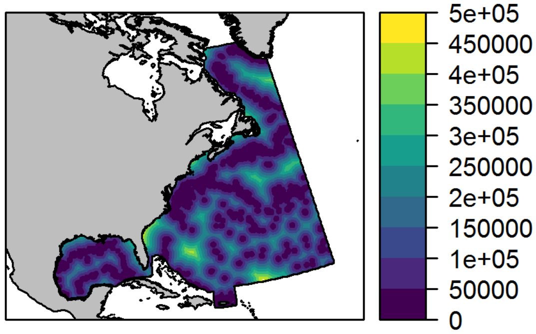


Figure 5: Monthly environmental envelopes for distance to the nearest canyon or seamount. White cells within the AFTT polygon indicate areas where covariate values fell beyond the range of covariate values sampled by the surveys.

5- Predicted densities

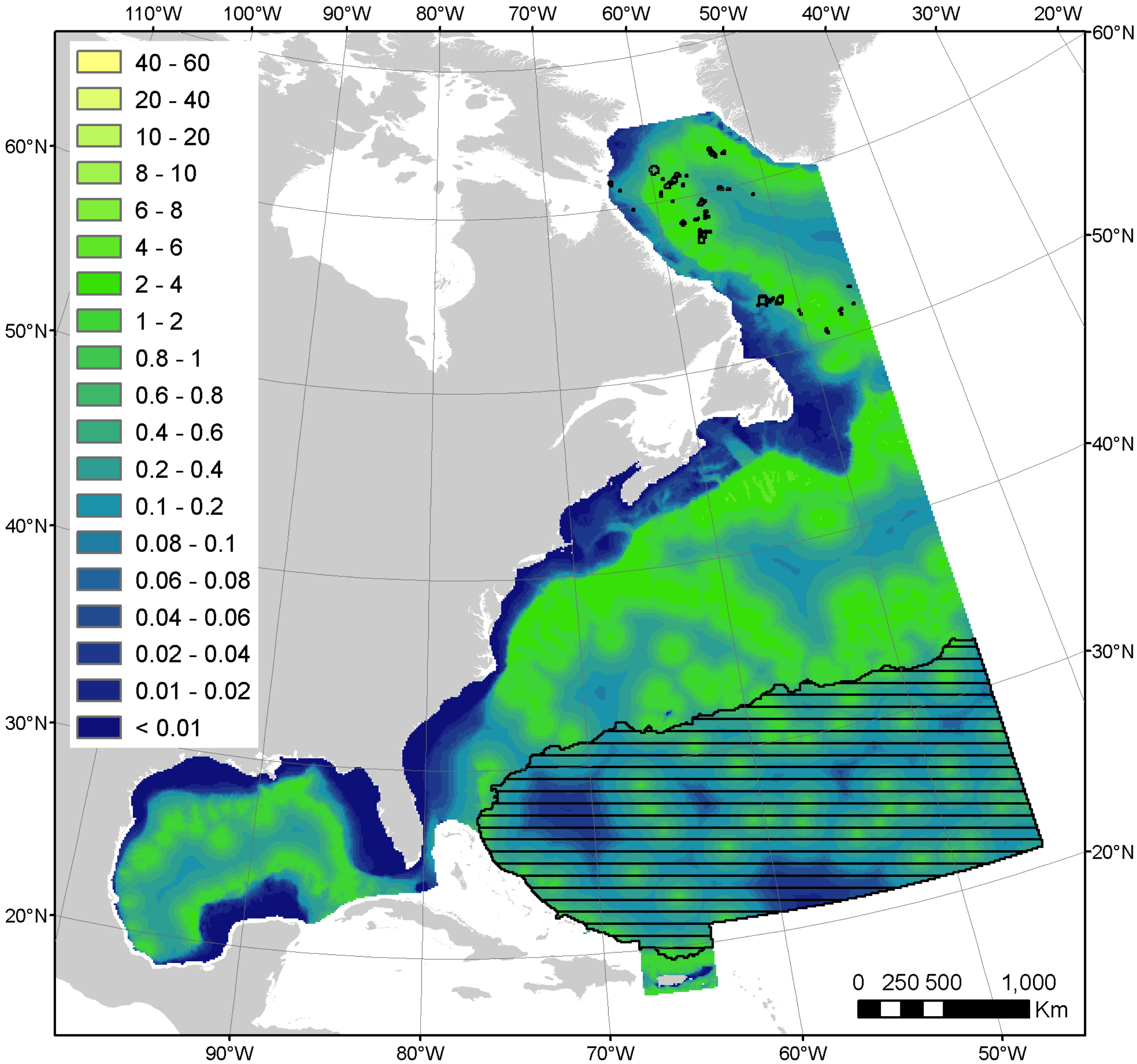


Figure 6: Mean predicted densities (individuals 100 km-2) in the AFTT area. Areas where we extrapolated beyond sampled predictor ranges and predicted densities should not be trusted are indicated with black crosshatches. An Albers equal area projection is used.

6- Coefficients of variation

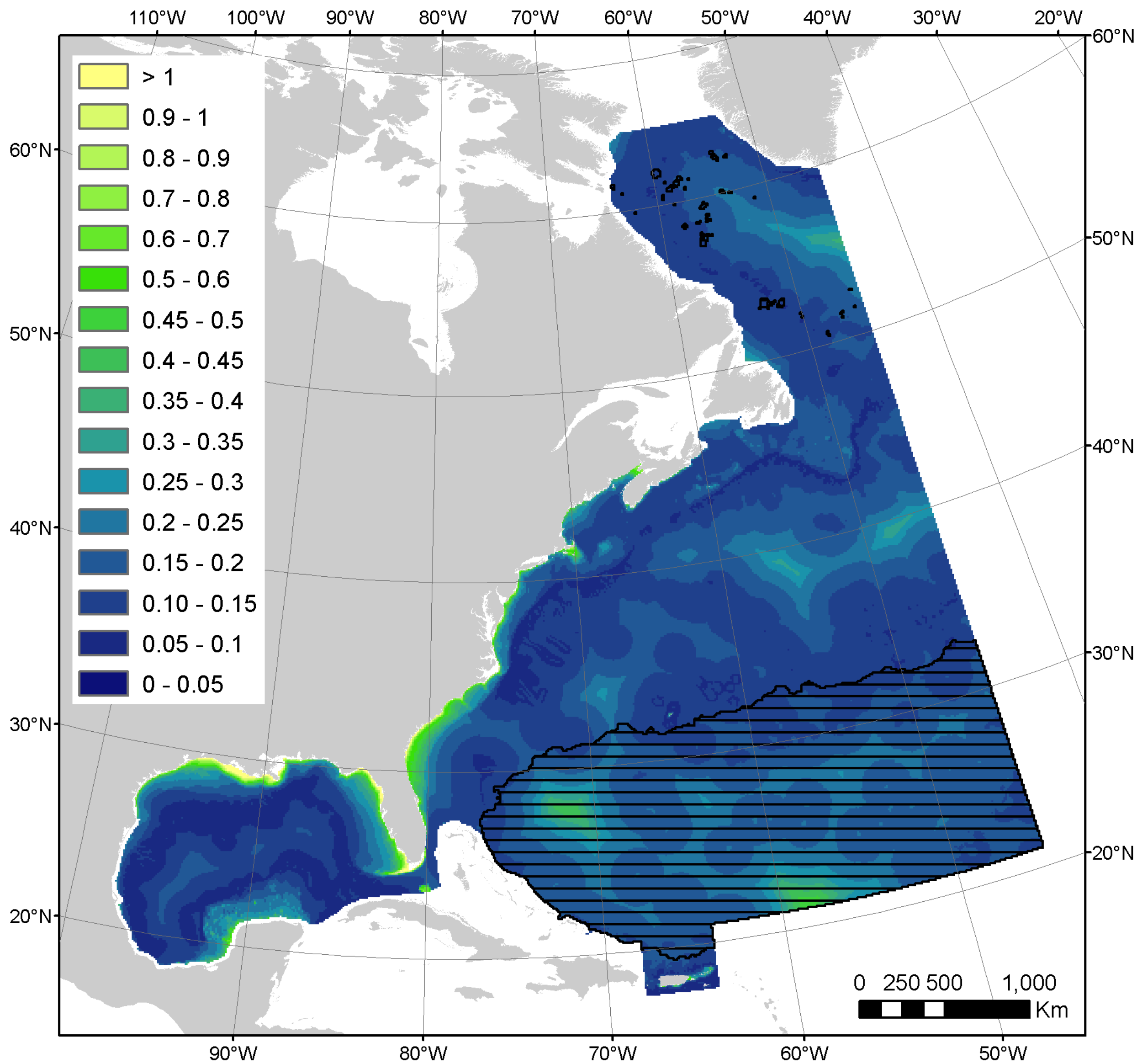


Figure 7: Mean predicted coefficients of variation derived from GAM parameters in the AFTT area. Areas where we extrapolated beyond sampled predictor ranges and coefficients of variation should not be trusted are indicated with black crosshatches. An Albers equal area projection is used.

7- Predicted densities per province

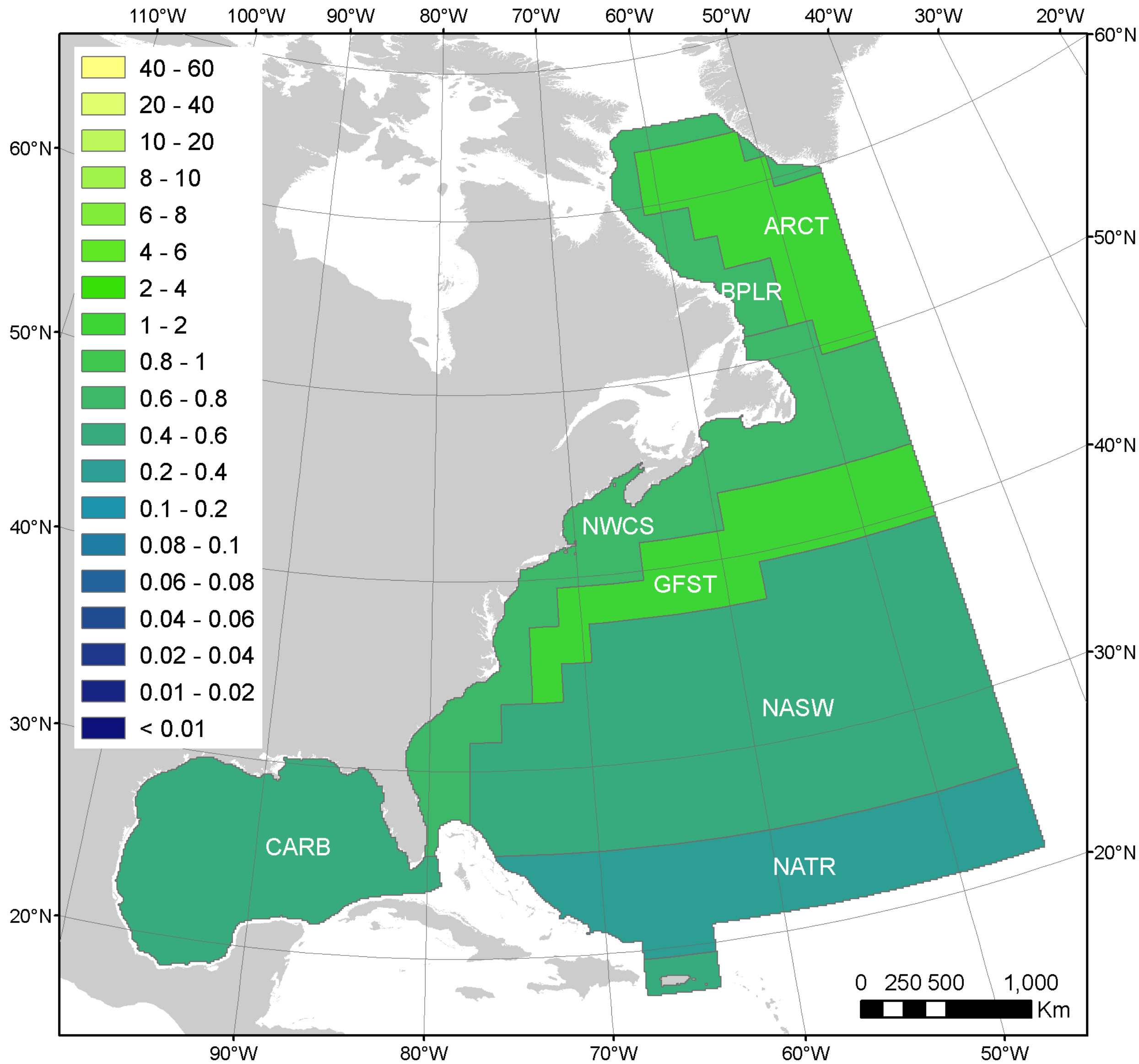


Figure 8: Predicted densities (individuals 100 km-2) averaged per Longhurst's biogeographical province. Note that the color scheme is the same as in Figure 7. Provinces: ARCT: Atlantic Arctic Province; BPLR: Boreal Polar Province; CARB: Caribbean Province; GFST: Gulf Stream Province; NATR: North Atlantic Tropical Gyral Province; NASW: North Atlantic Subtropical Gyral Province (West); NWCS: North West Atlantic Shelves Province.

8- Alternate models

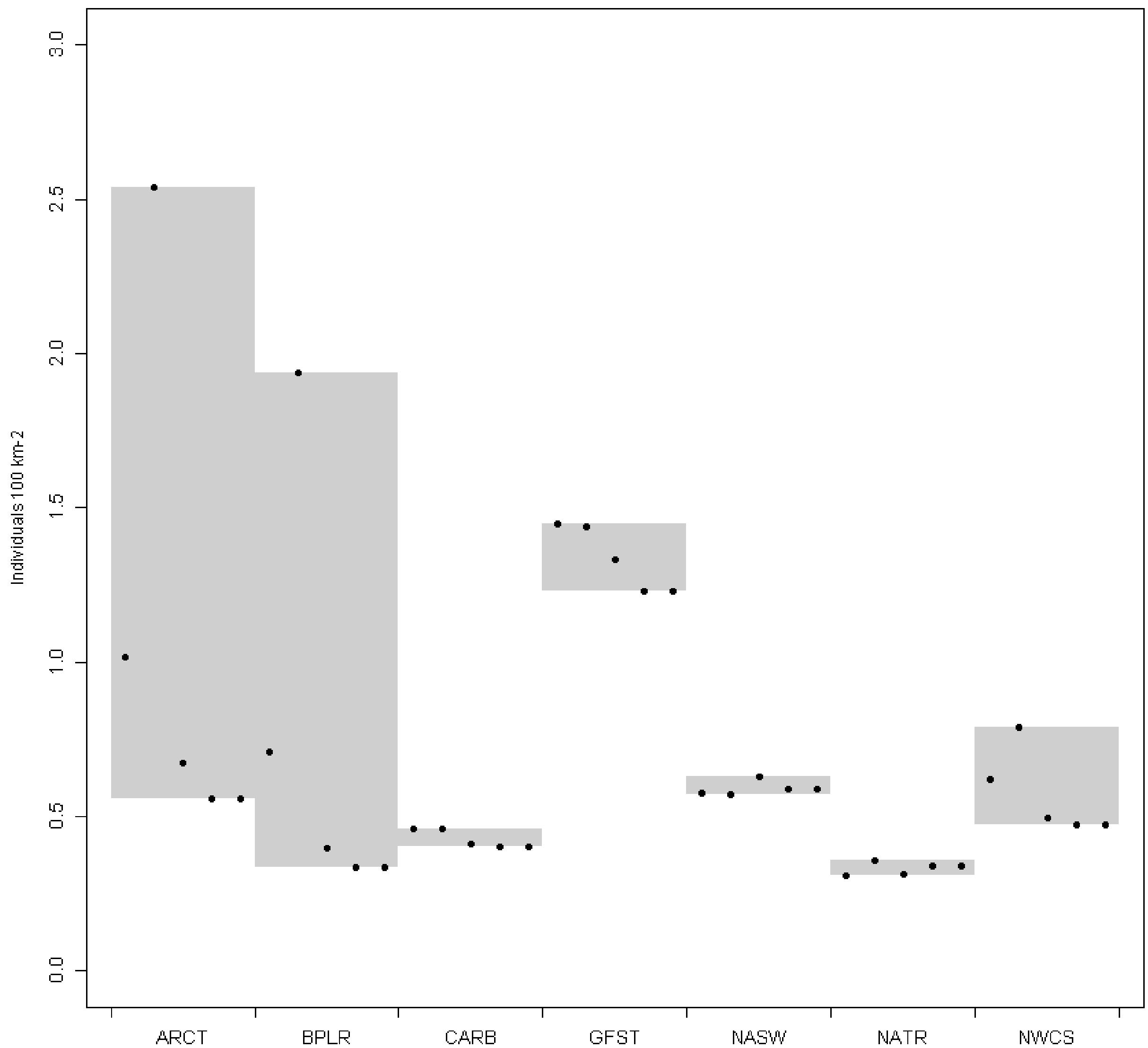


Figure 9: Sensitivity of densities predicted by the five top models per Longhurst's biogeographical province. Points represent predicted densities (individuals 100 km-2) for the five top models listed in Table 3, with the first to fifth models ordered from left to right. Filled points correspond to models 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	Chl1	CurrentSpeed	116692.2	0.0
Depth	DistToCanyonOrSeamount	Chl1	EKE	116692.4	0.2
Depth	DistToCanyonOrSeamount	PkPP	EpiMnkPP	116693.1	0.9
Depth	DistToCanyonOrSeamount	PkPP	DistToFront1	116693.4	1.2
Depth	DistToCanyonOrSeamount	PkPP	CurrentSpeed	116693.4	1.2

9- Residual diagnostics

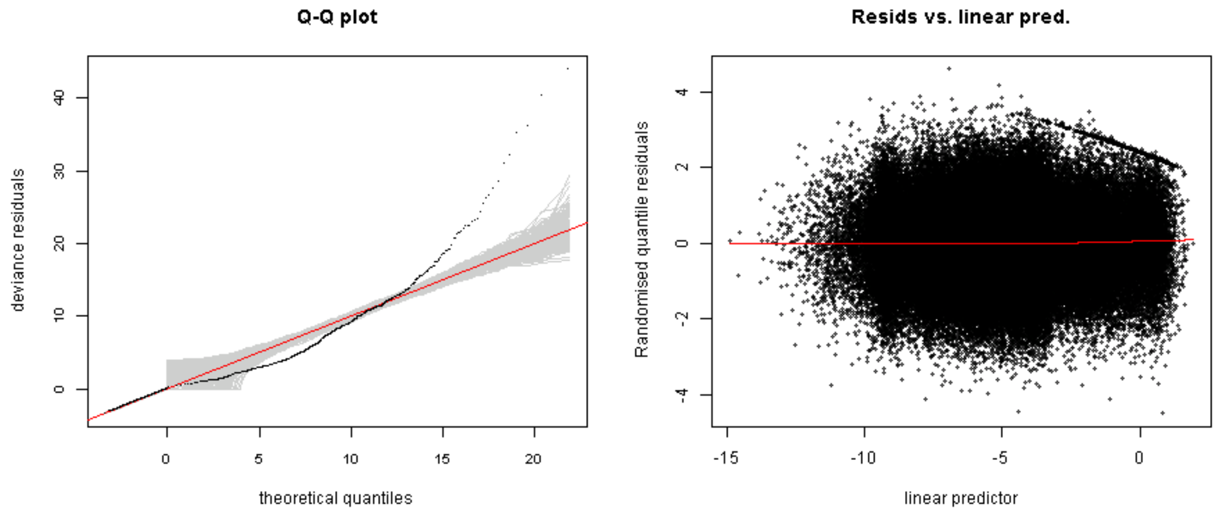


Figure 10: Diagnostic plots of residuals. Left: Quantile-quantile (Q-Q) plot of deviance residuals generated using the qq.gam function with 100 simulations (Augustin et al. 2012). Grey lines are possible simulated Q-Q plots under the assumption that the model is correct. The red reference line indicates 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.

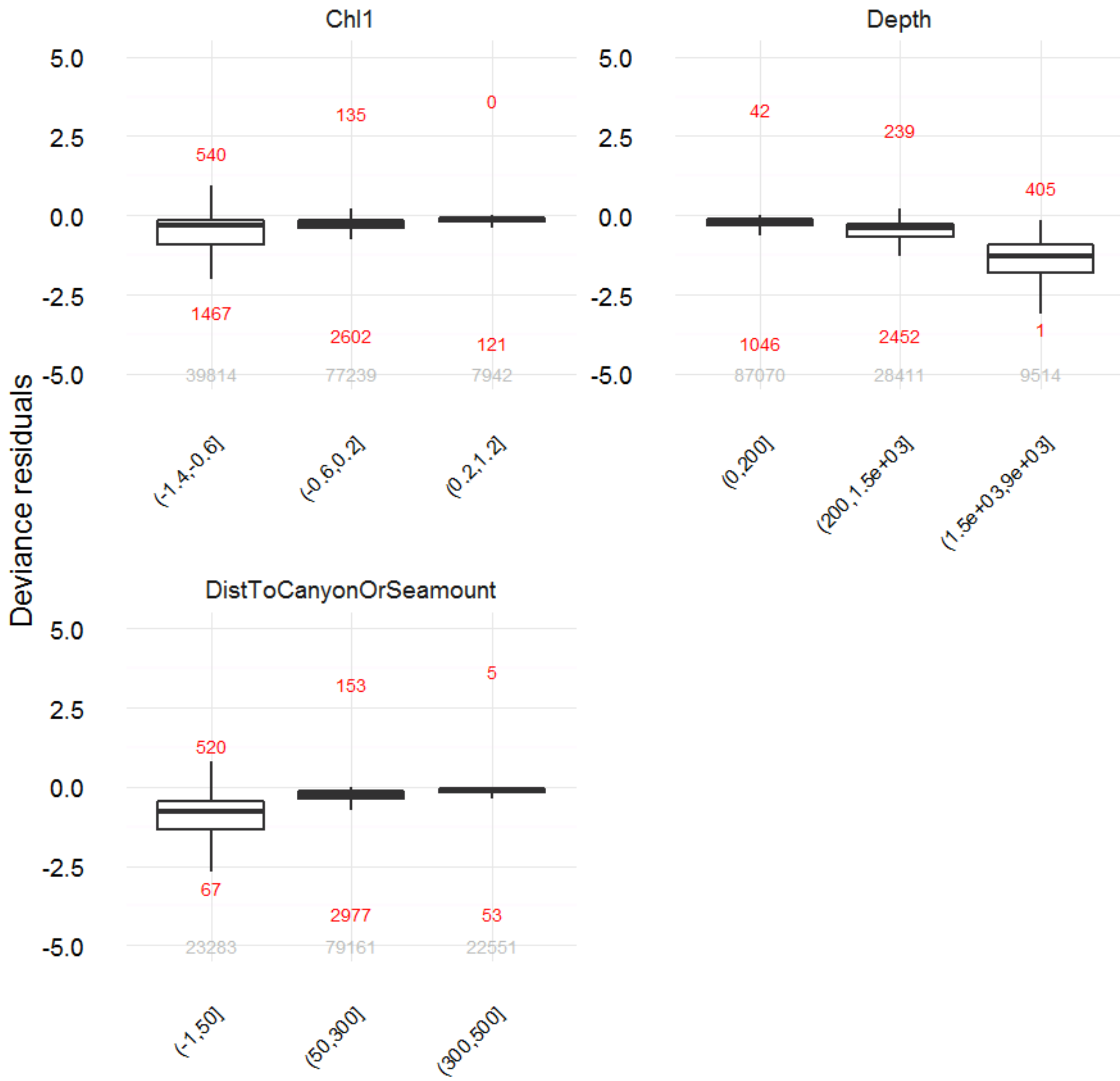


Figure 11: Boxplots of deviance residuals, binned for each predictor. The horizontal line represents the median, and the bottom and top of the box represent the first and third quartiles respectively. Whiskers extend 1.5 times the inter-quartile range following McGill et al. (1978). Total counts of outliers 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.

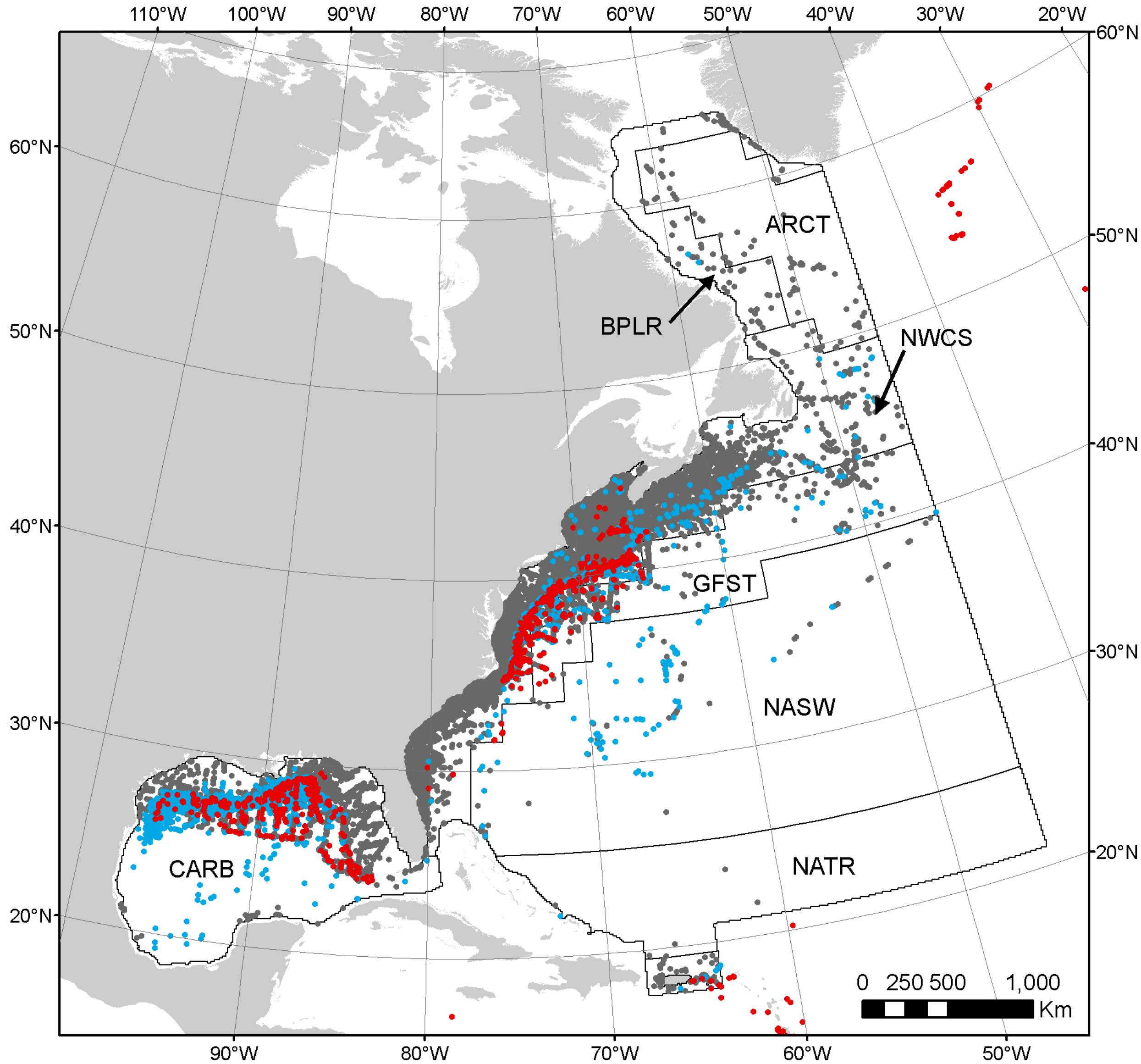


Figure 12: Red points are sightings of the taxon from line transect surveys used in this study. Blue points are sightings of the taxon reported by other datasets not used in our study for 1992-2016 (e.g., because they were not compatible with our methodology). Underlain grey points are sightings of other 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 941 sightings were used to fit the habitat-based density model for this species. The lowest AIC model included depth, distance to the nearest canyon or seamount and chlorophyll concentration (listed in decreasing order of importance according to F-scores) and had an explained deviance of 42%. We briefly discuss modeled relationships in comparison with the literature.

We found that depth was an important predictor of sperm whale densities, in accordance with other habitat modeling studies (e.g., Praca et al. 2009; Becker et al. 2010). Sperm whale densities showed an increasing relationship with depth (Figure 2), consistent with their described presence in waters generally > 1000 m (Rice 1998; Whitehead 2009).

Sperm whale densities showed a decreasing relationship with distance to the nearest canyon or seamount (Figure 2). As a result, predictions looked "patchy" as they were largely influenced by the locations of these underwater features. High predicted densities near submarine canyons seemed consistent with their year-round presence in submarine canyons, including the Gully canyon off the Scotian shelf (Reeves and Whitehead 1998; Hooker et al. 1999), the Mississippi Canyon in the Gulf of Mexico (Baumgartner et al. 2001) and the Great Bahamas canyon (Claridge et al. 2012). Although they were supported by limited survey effort, we believe higher predicted densities near offshore seamounts are not unrealistic. Indeed, sperm whales have been observed in association with offshore seamounts in various regions including the Mediterranean Sea (Moulins & Würtz 2005) and the mid-Atlantic ridge (Waring et al. 2008). Wong & Whitehead (2013) recorded sperm whale echolocation clicks over Kelvin Seamount in the New England seamount chain, with a higher prevalence in the spring. Wong (2012) found that the probability of detecting sperm whales decreased with distance to seamounts. These findings seemed in agreement with the results of our study. Finally, it is worth noting that our model predicted sperm whale distribution mostly offshore, consistent with their presumed historical distribution, but in closer association with seamounts than suggested by whaling logbooks data (Smith et al. 2012) (we note, however, that important caveats apply to logbooks data, e.g., inaccuracies of positions and errors in species identifications).

Sperm whale densities showed a weaker but significant increasing relationship with chlorophyll concentration, reaching a plateau around 0.30 mg m-3 (Figure 2). As a result, our model predicted higher sperm whale densities in chlorophyll-rich waters of high latitudes where mature males mostly distribute (Whitehead 2009). Previous studies found that chlorophyll concentration was a good indicator of the distribution and densities of sperm whales at large spatial scales (Jaquet et al. 1996; Jaquet & Whitehead 1996). Wong (2012) found that chlorophyll concentration was an important predictor of sperm whale presence in the Sargasso Sea and suggested that their higher abundance in the northern compared to the southern Sargasso Sea was related to the higher chlorophyll concentration. A model including only static predictors would likely require less extrapolation than a model including dynamic predictors, but would fail to explain latitudinal trends in sperm whale densities.

All top five models included depth and distance to the nearest canyon or seamount and had a delta AIC < 2 (Table 3), indicating some statistical support sensu Burnham and Anderson (2002). Predicted densities from the top five models were very similar in the CARB, NASW and NATR provinces, relatively similar in the GFST and NWCS provinces while they differed roughly by a factor 5 in the ARCT and BPLR provinces (Figure 10). In these provinces, the second model predicted the highest densities, while the third, fourth and fifth models predicted the lowest densities. The first model predicting intermediate densities was situated in between. The first model including depth, distance to the nearest canyon or seamount and chlorophyll concentration (detailed above) had a slightly lower AIC and explained slightly more deviance than the other four models, suggesting it was slightly more suitable for modeling sperm whale densities.

Overall, model predictions appeared consistent with the cosmopolitan distribution of sperm whales in offshore waters generally deeper than 1000m, from the equator to the ice edge (only large mature males occur at high latitudes) (Rice 1998; Whitehead 2009).

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

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

Model uncertainty was the highest in the BPLR and ARCT provinces, resulting in a relatively large range of predicted densities (densities predicted by the best supported model were situated within this range). Relatively high sperm whale densities were predicted on the continental slope to the northern extent of the AFTT area. Overall, predictions seemed plausible as mature males are known to inhabit deep waters as far north as the ice edge, but we note that few sightings were available to support the high predicted densities. Two sperm whale sightings were reported in OBIS-SEAMAP in the BPLR province and none was reported in the ARCT province (Figure 12). During an aerial survey in summer 2005 in West Greenland, sperm whale were recorded on 2 occasions in the deepest waters (Heide-Jørgensen et al. 2007) (sightings not publically shared in OBIS-SEAMAP). We believe the paucity of sightings reflects the very sparse observation effort and that sperm whales widely occur in these northern offshore waters. Sperm whale was the most commonly sighted odontocete during the MAR-ECO survey along the mid-Atlantic ridge where it was recorded on 48 occasions as far north as 61°N (Waring et al. 2008). We warn that extrapolation beyond predictor ranges occurred in parts of the ARCT and BPLR provinces and predictions should be considered with caution.

North West Atlantic shelves (NWCS) provinces

Highest densities were predicted off the continental shelf from North Carolina to Newfoundland in associations with submarine canyons (see also general discussion). Lower predicted densities from Florida to South Carolina (where the continental shelf, known as the Blake plateau, is wider) seemed consistent with the paucity of sightings. Relatively high predicted densities north of 42°N, where survey effort was much more limited, appeared supported by numerous sightings available in OBIS-SEAMAP on the shelf break and continental slope from Nova Scotia to Newfoundland. Sperm whales are known to concentrate on the Scotian shelf edge and occur year-round in the Gully submarine canyon (Whitehead et al. 1992; Reeves and Whitehead 1998; Hooker et al. 1999). During the Canadian TNASS aerial survey in summer 2007, sperm whales were sighted on 2 occasions east of Newfoundland, 9 occasions south of Newfoundland and 11 occasions on the Scotian shelf (Lawson & Gosselin 2009) (sightings not publically shared in OBIS-SEAMAP).

Gulf Stream (GFST) province

The relatively high predicted densities in offshore waters of the GFST province appeared compatible with multiple sperm whale sightings reported throughout this province (Figure 12). Previous studies have found that sperm whales associate with the north wall of the Gulf Stream (Waring et al. 1993), as well as temperature fronts and warm-core eddies (Griffin 1999; Waring et al. 2001).

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

Extrapolation to waters of lower chlorophyll concentration occurred throughout the NATR province and most of the NASW province; therefore predicted densities were largely speculative and should be considered with extreme caution. Sperm whales were predicted in tight association with offshore seamounts (see also general discussion). Overall, relatively high predicted densities in the NASW province did not appear unrealistic as they were supported by numerous sightings, some of them reported near offshore seamounts where the model predicted the highest densities (Figure 12).

Wong & Whitehead (2013) recorded sperm whale echolocation clicks over Kelvin Seamount, in the New England seamount chain, where our model predicted high sperm whale densities. Recent acoustic surveys conducted by the latter researchers found large numbers of sperm whales in the Sargasso Sea (Wong 2012). According to Wong's dissertation, densities of sperm whales in the northern Sargasso Sea may be among the highest globally. Our results are not incompatible with her findings. Finally, we note that sperm whales were historically common in offshore waters surrounding Bermuda where they used to be hunted for their oil (Reeves et al. 2006). No sightings were reported in OBIS-SEAMAP for the NATR province (except for one sighting reported close to the Bahamas at the edge of the AFTT area), but observation effort was extremely sparse (Figure 12).

Caribbean (CARB) province

In the Gulf of Mexico, highest densities were predicted near the continental slope, in association with submarine canyons. The Mississippi canyon has been described as an important year-round habitat for sperm whales (Davis et al. 1998). According to O'Hern and Bigs (2009), loop current eddies and cyclones spinning into the Mississippi Delta Canyon region may create pockets of concentrated secondary mesopelagic productivity, providing foraging opportunities for sperm whales.

Predictions in the southern Gulf of Mexico appeared supported by numerous sperm whale sightings (from tagged individual locations), mainly off the continental shelf (Figure 12) (Jochens et al. 2008). Ortega-Ortiz (2002) reported a dozen sperm whale sightings during a shipboard survey in the southern Gulf of Mexico and noted their frequent association with the continental slope, apparently in line with our predictions.

Predicted densities near Puerto Rico and the Virgin Islands appeared compatible with 43 opportunistic sightings, often in areas with high bottom relief, documented by Mignucci-Giannoni (1998), as well as sightings visible on Figure 12.

Overall confidence: level 2

Available survey data did not span the wide range of sperm whales (specifically, large mature males) throughout cold temperate and sub-polar waters. The model successfully predicted their occurrence in northern waters but predicted densities remain largely speculative. Predicted densities in northern waters were supported by comparatively few sightings and characterized by a larger model uncertainty, but in our opinion, were not unrealistic. Unfortunately we were unable to obtain permission for using line transect survey data from Canada and Greenland 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. The relatively high densities predicted in the North Atlantic gyre were derived from an extrapolation beyond sampled predictor ranges and should be interpreted with great caution. Nevertheless, they appeared supported by numerous offshore sightings.

11- References

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