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

Laura Mannocci, Jason J Roberts, David L Miller, Patrick N Halpin

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This report documents the habitat-based density model for Humpback 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 Humpback 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
EC	723085.104	2578
MAR	2424.421	1
All regions	725509.524	2579

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

	Month	Effort	Sightings
4	April	105121.39	261
5	May	107303.24	465
6	June	118927.77	637
7	July	113904.31	512
8	August	110040.12	231
9	September	52584.62	79
10	October	57619.14	250
11	November	60008.94	144
12	All Months	725509.52	2579

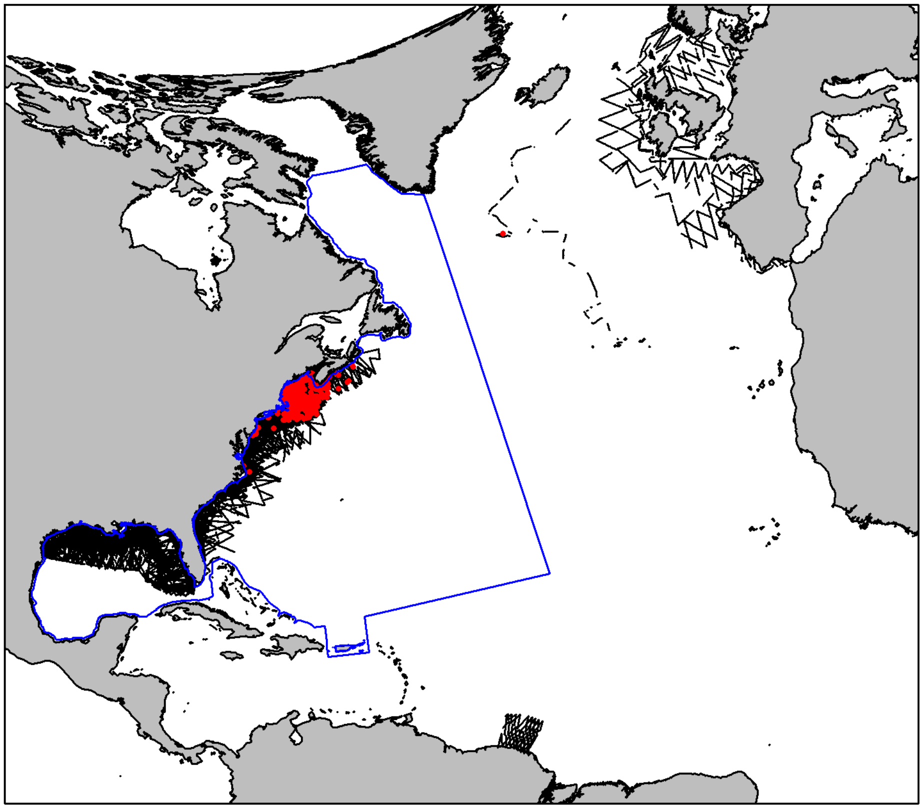


Figure 1: Map of segments (black lines) and sighting locations (red dots). An Albers equal area projection optimized for the AFTT area is used.

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

Humpback whale (*Megaptera novaeangliae*)

Modeled season

Humpback whales travel thousands of kilometers between high-latitude summer feeding grounds and low-latitude winter breeding grounds (in the North Atlantic, mainly located in the West Indies) (Stevick et al. 1998, Kennedy et al. 2014, Mattila et al. 1989, 1994). In the western North Atlantic, humpback whales feed during spring, summer, and fall. Here, we present a habitat-based density model corresponding to an extended summer season, when humpback whales typically feed at high latitudes. We defined the extended summer season from April to November, representing the months when humpback whales mostly occur in the Gulf of Maine (Robbins 2007). April was also the month when humpback whales tagged in the Caribbean initiated their northward migration to high-latitude feeding grounds (Kennedy et al. 2014). We presumed that most individuals present in our study area during this extended summer season were feeding (some individuals were also migrating from/to breeding grounds).

Segments

We incorporated segments from the western North Atlantic (east coast, Gulf of Mexico and Caribbean). Only one sighting was reported at the mid-Atlantic ridge and none were reported in the European Atlantic where humpback whale is described as rare (Waring et al. 2009).

Special treatment in the Gulf of Mexico

Since there were no humpback whales sighted during the Gulf of Mexico surveys and the species is only considered of accidental occurrence in the Gulf of Mexico (Jefferson and Schiro 1997), we assigned zero densities to the entire Gulf of Mexico rather than leaving the low densities predicted by the model.

3- Best model

- **Predictors**: Depth, chlorophyll concentration (Chl), distance to sea surface temperature fronts (DistToFront), standard deviation of sea level anomaly (SLAStDev)
- **Model summary**:

```
##
## Family: Tweedie(p=1.298)
## Link function: log
##
## Formula:
## abundance ~ s(Depth, k = 4, bs = "ts") + s(Chl1, k = 4, bs = "ts") +
##     s(DistToFront1, k = 4, bs = "ts") + s(SLAStDev, k = 4, bs = "ts") +
##     offset(log(area_km2))
## <environment: 0x2422c92c>
##
## Parametric coefficients:
##             Estimate Std. Error t value Pr(>|t|)
## (Intercept) -11.2128     0.4102  -27.34   <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)        2.990      3 182.44  <2e-16 ***
## s(Chl1)         2.905      3  95.07  <2e-16 ***
## s(DistToFront1) 2.627      3  62.53  <2e-16 ***
## s(SLAStDev)     2.926      3  76.02  <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.0284   Deviance explained = 36.6%
## -REML =  11669  Scale est. = 19.76     n = 87948
```

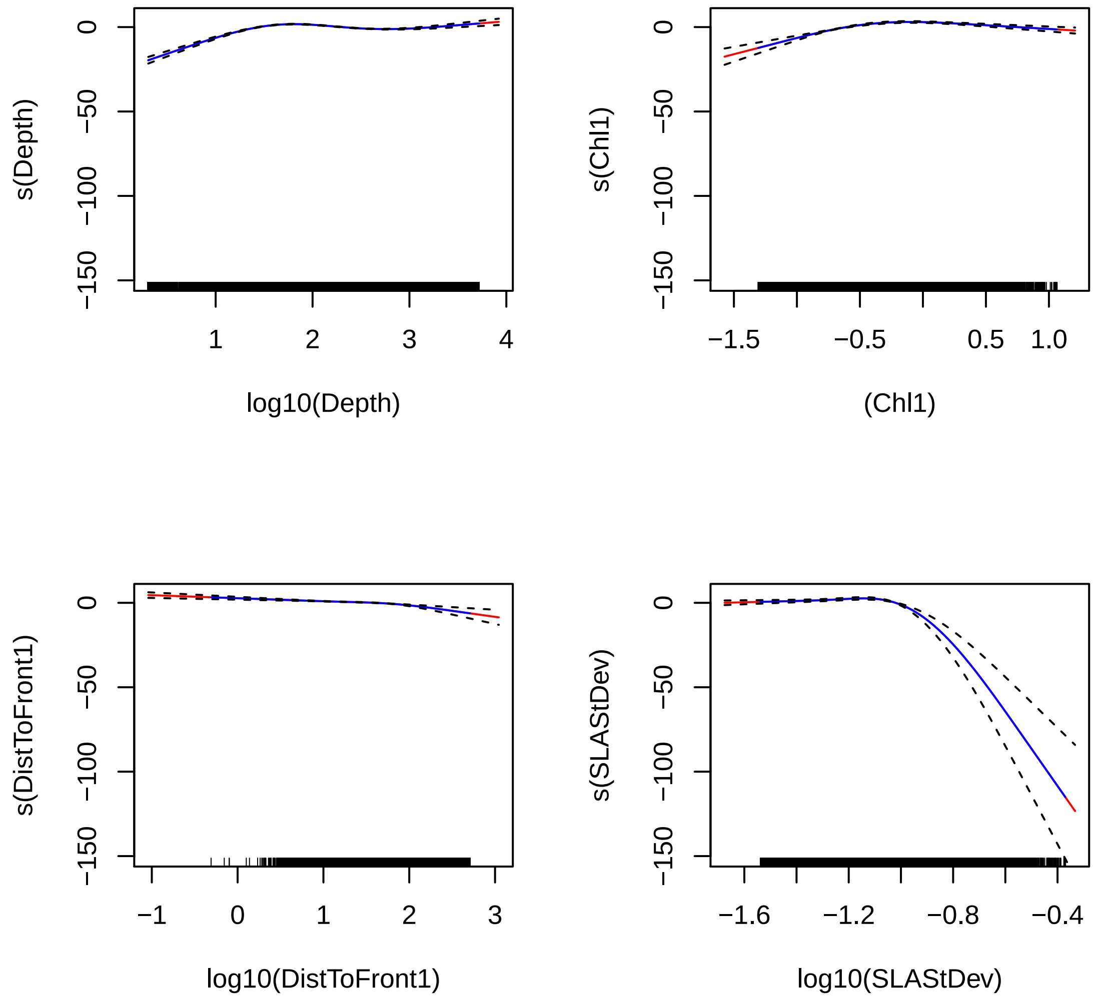


Figure 2: GAM term plots with the log-transformed abundance on the y axis. The solid blue line is the smooth function fitted to the data. The solid red line is the smooth function extrapolated to all covariate values in the prediction area. The dashed lines represent the approximate 95% confidence intervals.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

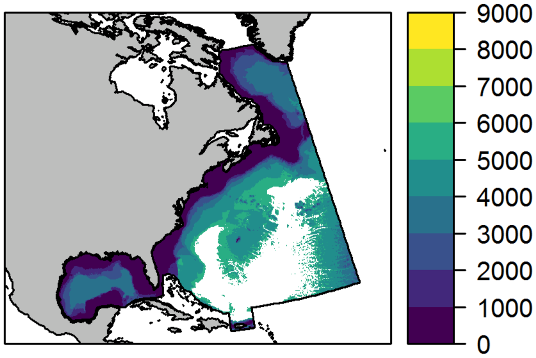
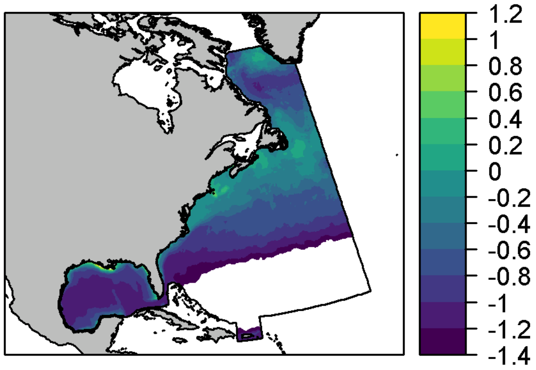
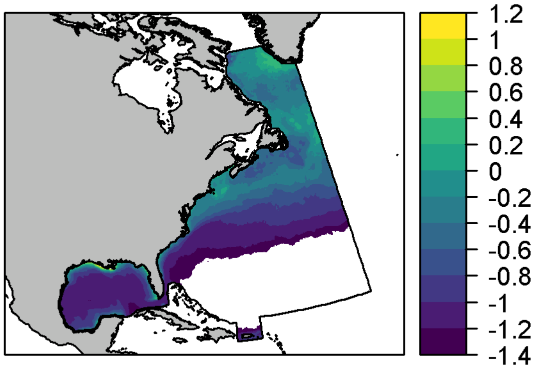


Figure 3: Environmental envelope for depth. White cells within the AFTT polygon indicate areas where covariate values fell beyond the range of covariate values sampled by the surveys.

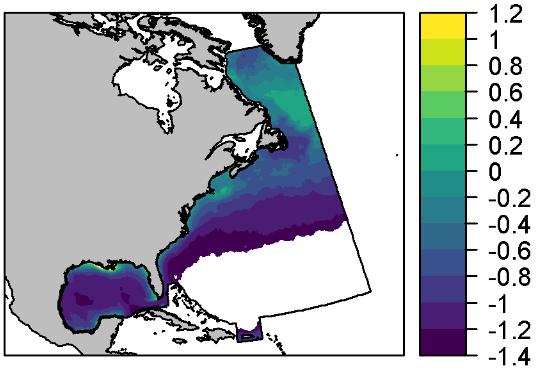
April



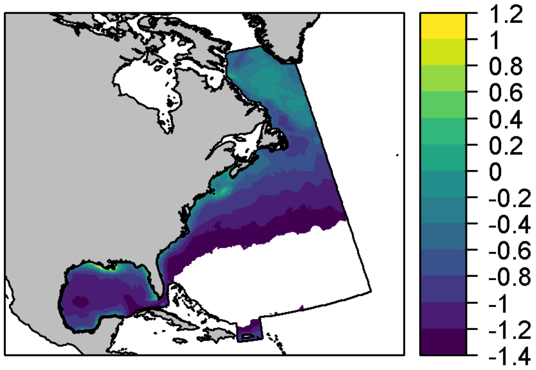
May



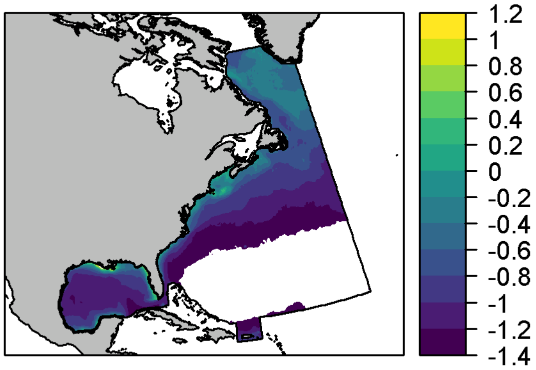
June



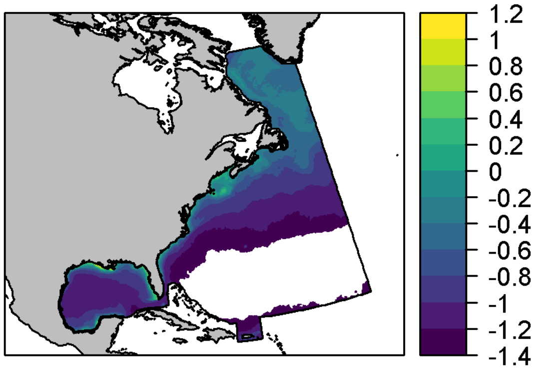
July



August



September



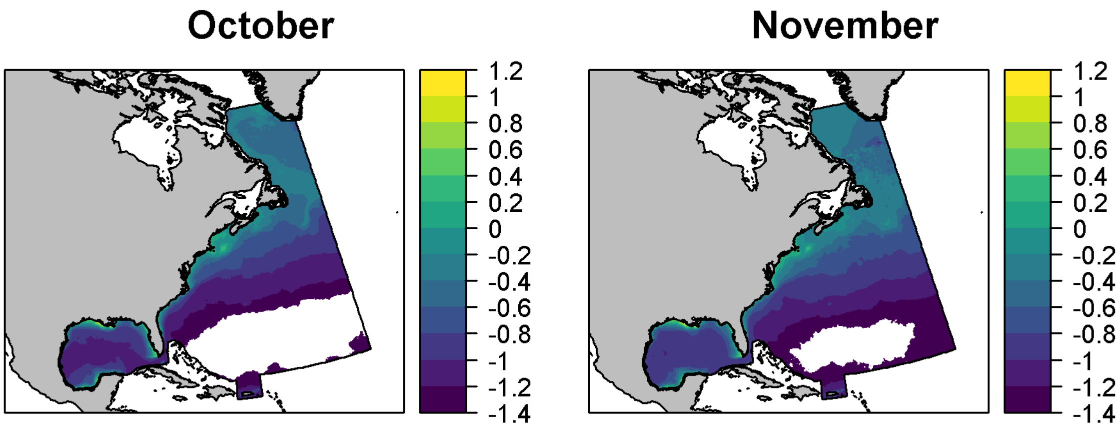
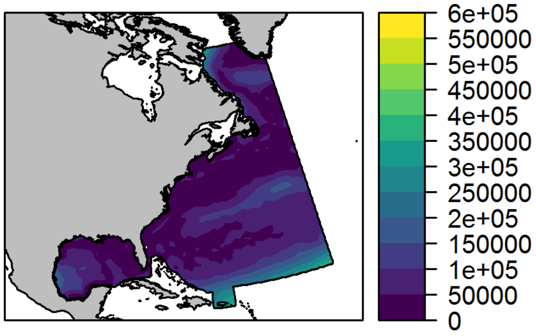
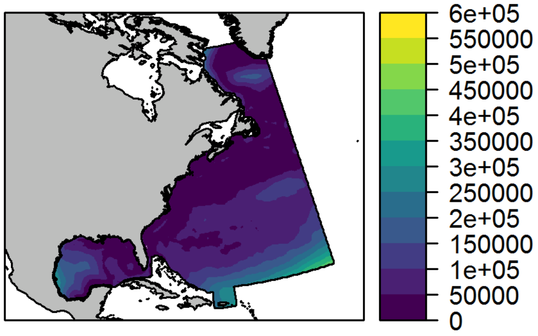


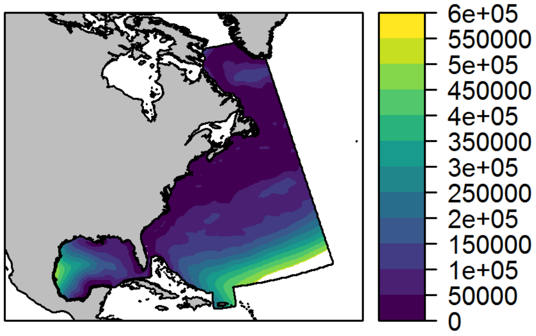
Figure 4: Monthly environmental envelopes for chlorophyll concentration. White cells within the AFTT polygon indicate areas where covariate values fell beyond the range of covariate values sampled by the surveys.



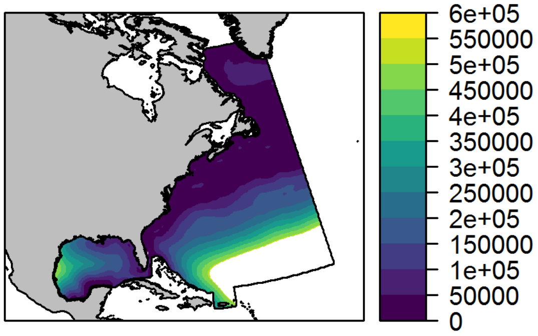
April



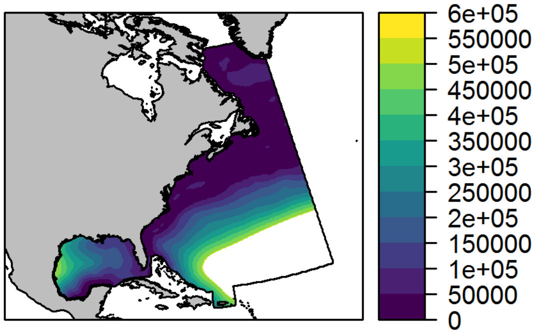
May



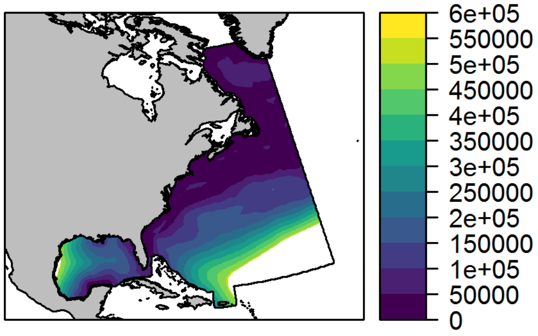
June



July



August



September

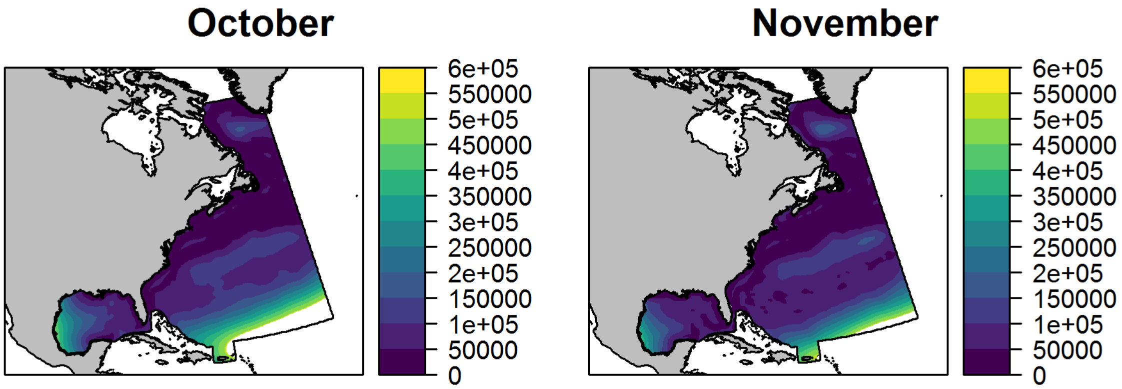
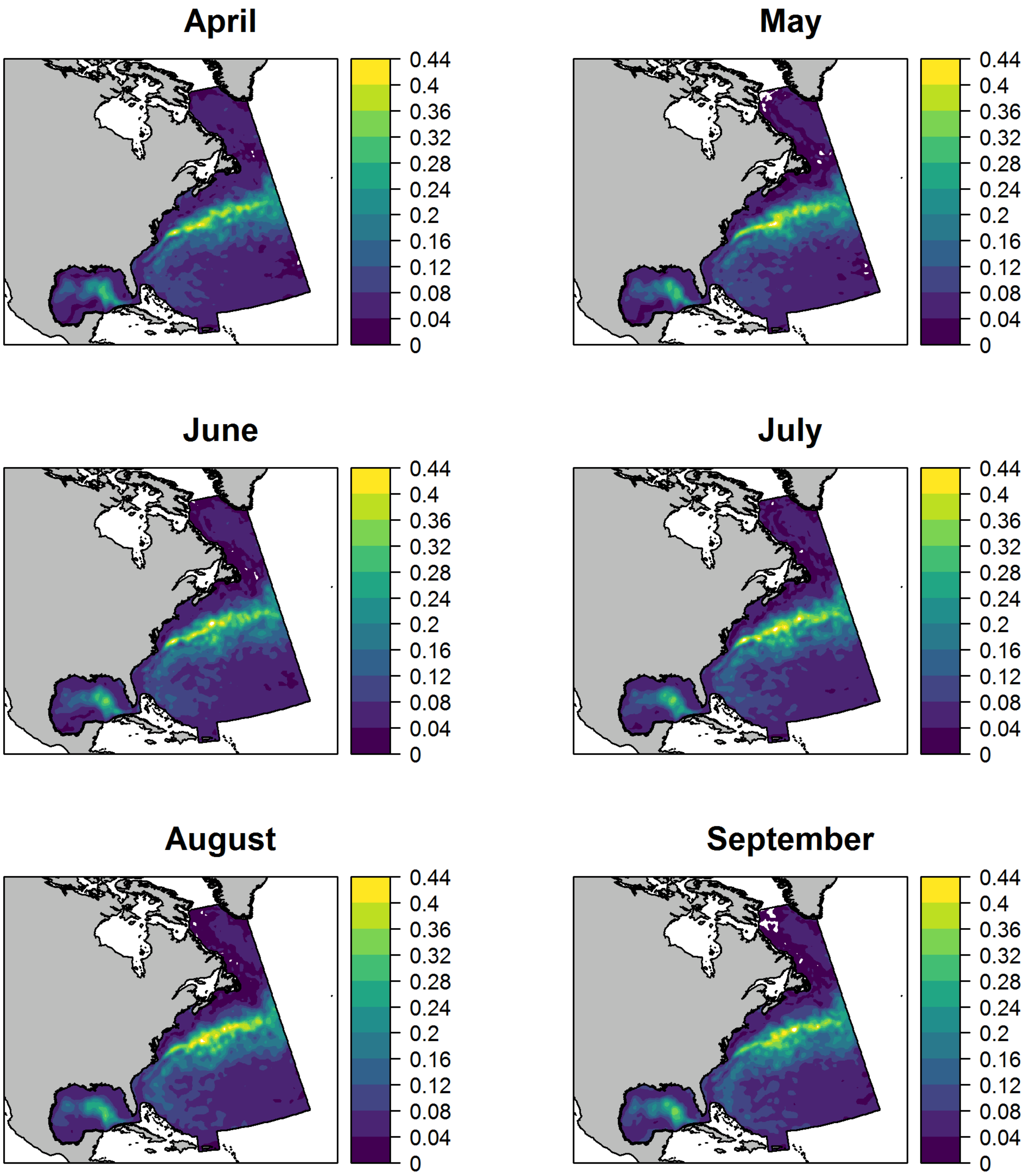


Figure 5: Monthly environmental envelopes for distance to distance to sea surface temperature fronts. White cells within the AFTT polygon indicate areas where covariate values fell beyond the range of covariate values sampled by the surveys.


April
0.44
0.4
0.36
0.32
0.28
0.24
0.2
0.16
0.12
0.08
0.04
0
May
0.44
0.4
0.36
0.32
0.28
0.24
0.2
0.16
0.12
0.08
0.04
0
June
0.44
0.4
0.36
0.32
0.28
0.24
0.2
0.16
0.12
0.08
0.04
0
July
0.44
0.4
0.36
0.32
0.28
0.24
0.2
0.16
0.12
0.08
0.04
0
August
0.44
0.4
0.36
0.32
0.28
0.24
0.2
0.16
0.12
0.08
0.04
0
September
0.44
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0

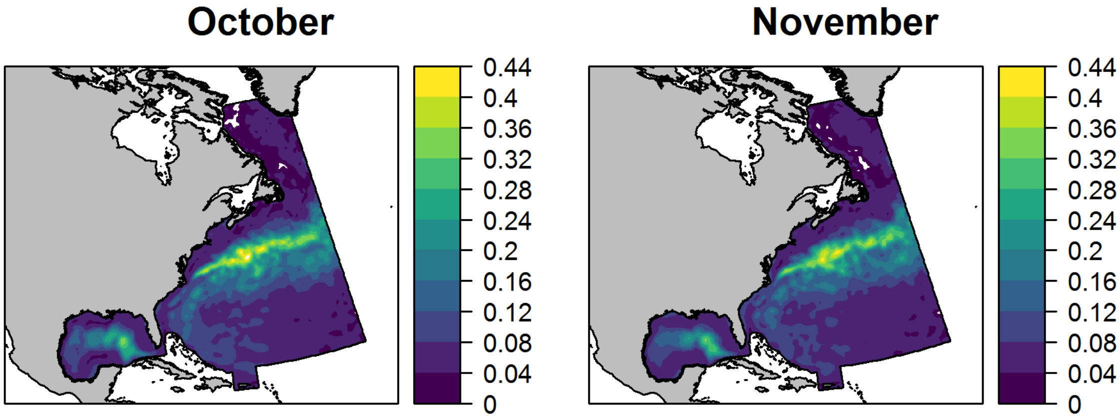

Figure 6: Monthly environmental envelopes for standard deviation of sea level anomaly. White cells within the AFTT polygon indicate areas where covariate values fell beyond the range of covariate values sampled by the surveys.

5- Predicted densities

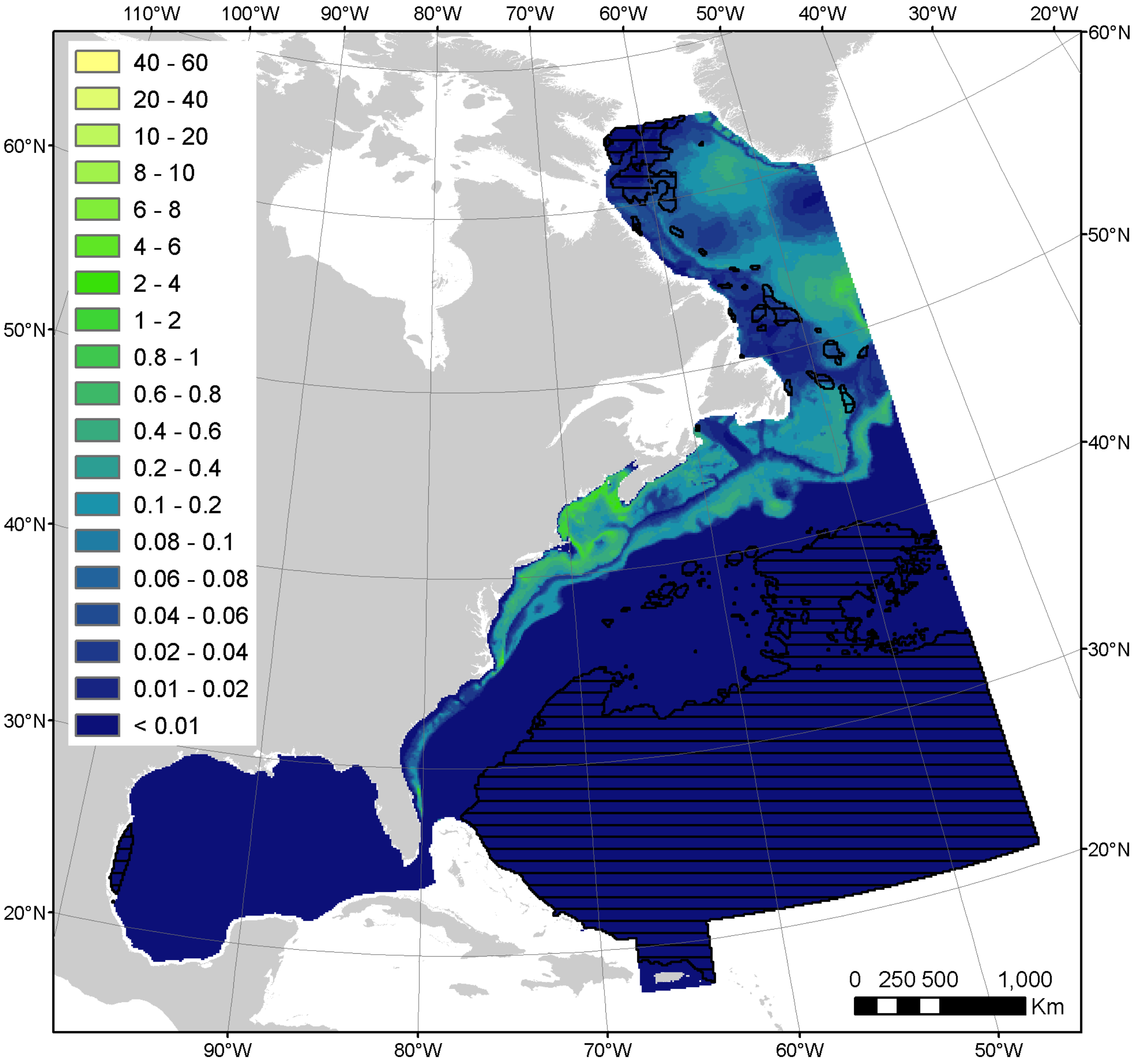

Figure 7: Mean predicted densities (individuals 100 km-2) in the AFTT area. Areas where we extrapolated beyond sampled predictor ranges and predicted densities should not be trusted are indicated with black crosshatches. An Albers equal area projection is used.

6- Coefficients of variation

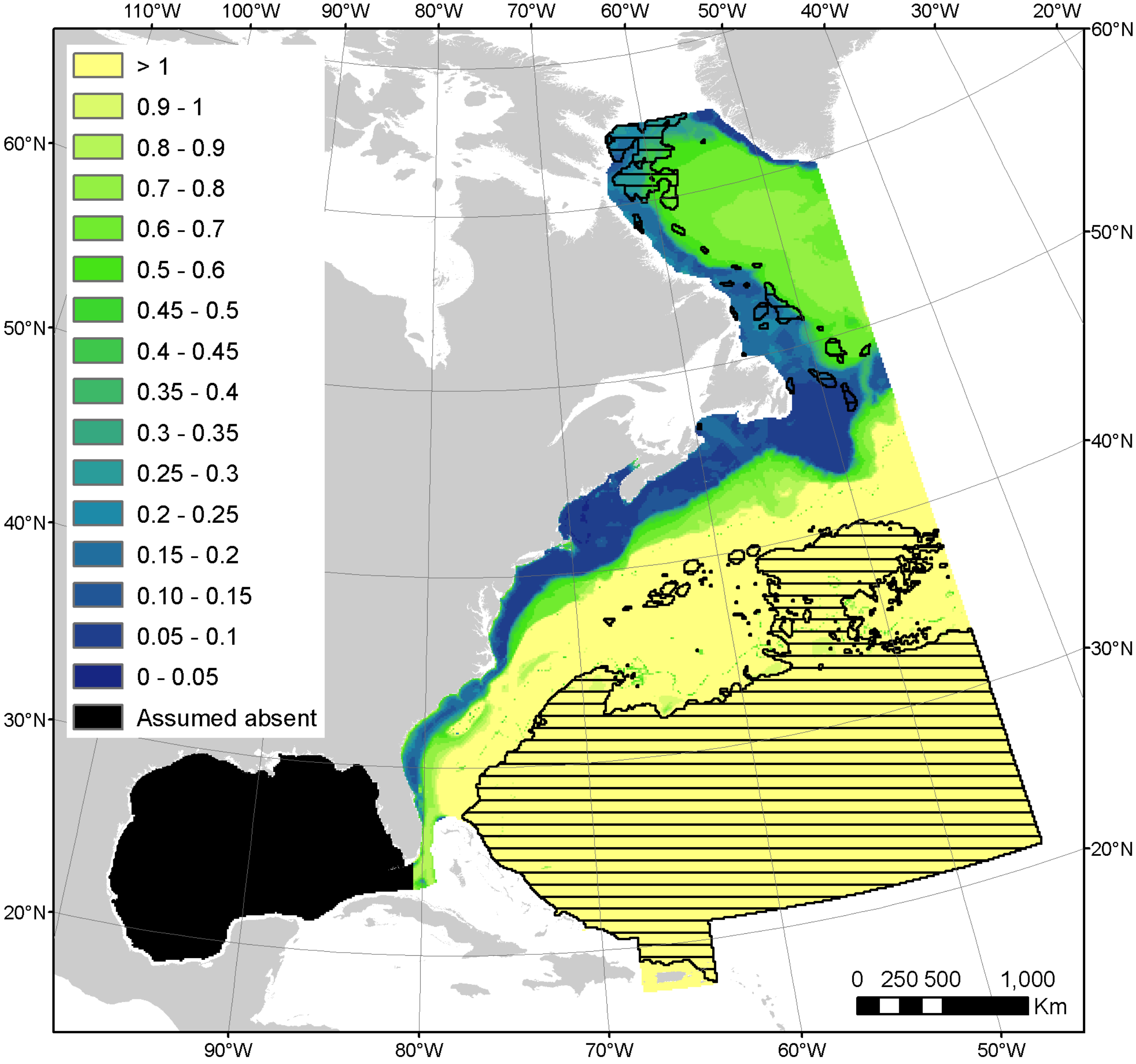

Figure 8: Mean predicted coefficients of variation derived from GAM parameters in the AFTT area. Areas where we extrapolated beyond sampled predictor ranges and coefficients of variation should not be trusted are indicated with black crosshatches. An Albers equal area projection is used.

7- Predicted densities per province

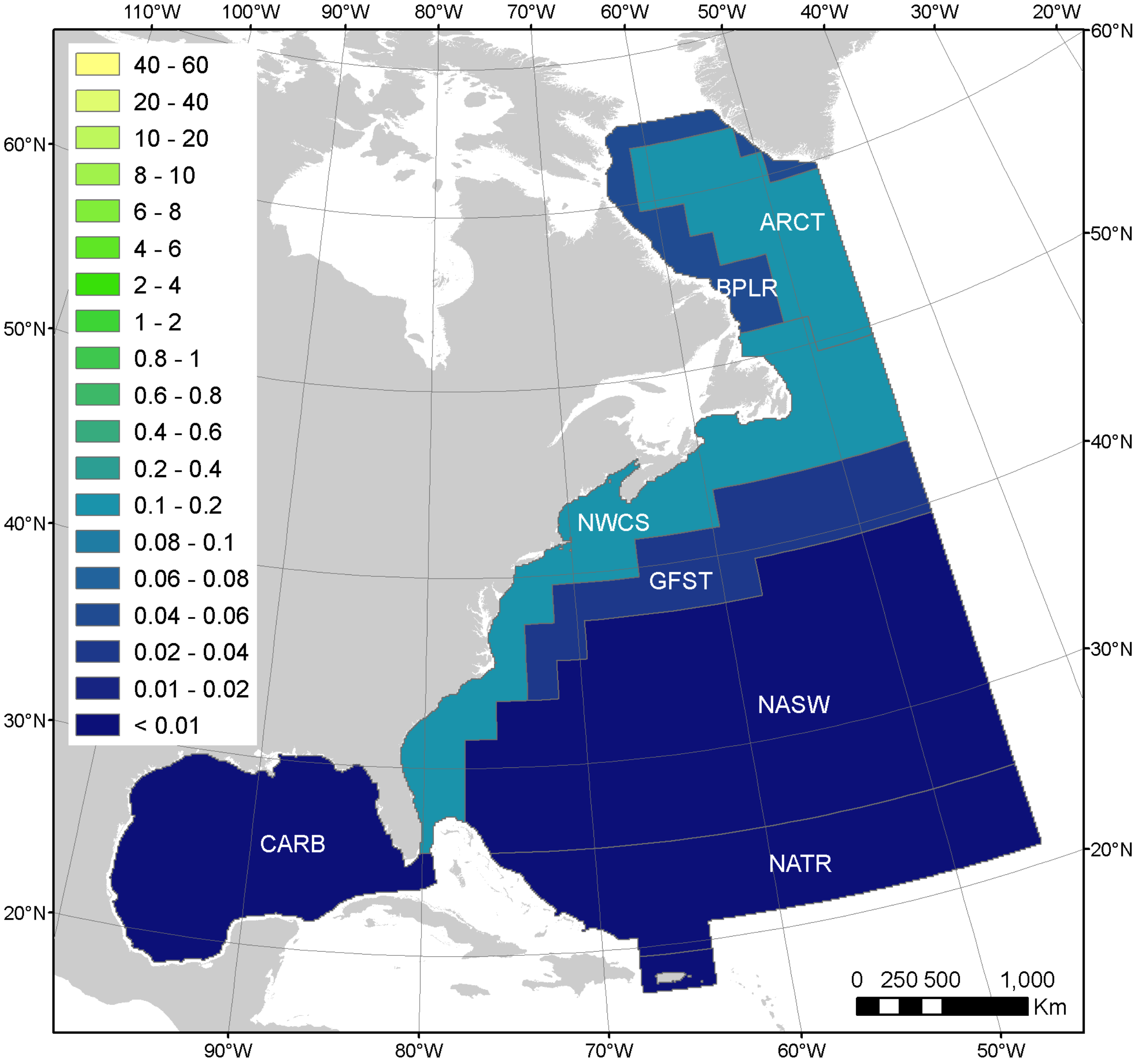

Figure 9: Predicted densities (individuals 100 km-2) averaged per Longhurst's biogeographical province. Note that the color scheme is the same as in Figure 7. Provinces: ARCT: Atlantic Arctic Province; BPLR: Boreal Polar Province; CARB: Caribbean Province; GFST: Gulf Stream Province; NATR: North Atlantic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

8- Alternate models

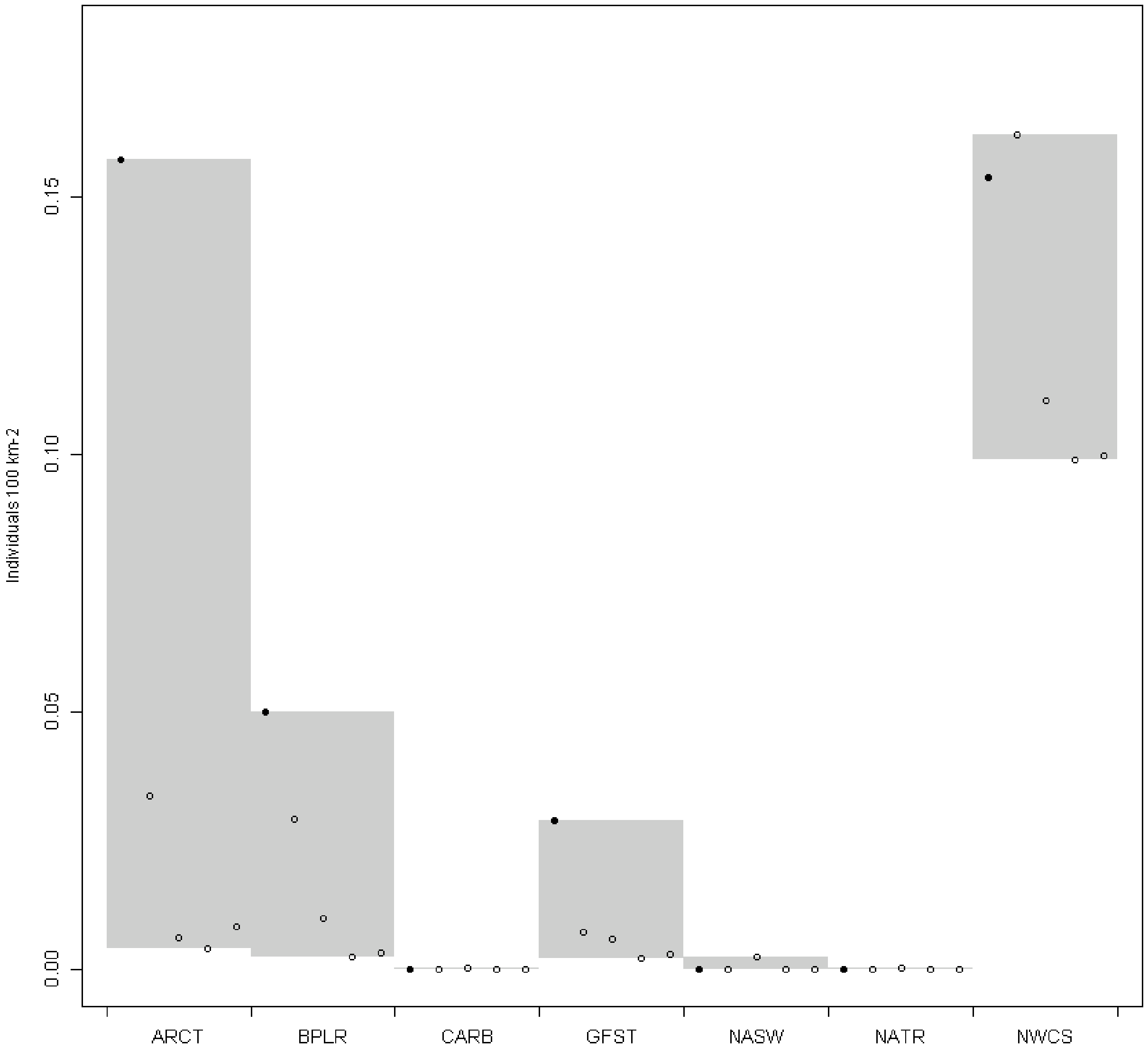

Figure 10: Sensitivity of densities predicted by the five top models per Longhurst's biogeographical province. Points represent predicted densities (individuals 100 km-2) for the five top models listed in Table 3, with the first to fifth models ordered from left to right. Filled points correspond to 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	DistToFront1	SLAStDev	Chl1	89022.37	0.00
Depth	DistToFront1	SLAStDev	PkPB	89038.87	16.50
Depth	DistToFront1	EKE	EpiMnkPP	89054.34	31.97
Depth	DistToFront1	SLAStDev	VGPM	89058.66	36.29
Depth	DistToFront1	SLAStDev	PkPP	89060.64	38.27

9- Residual diagnostics

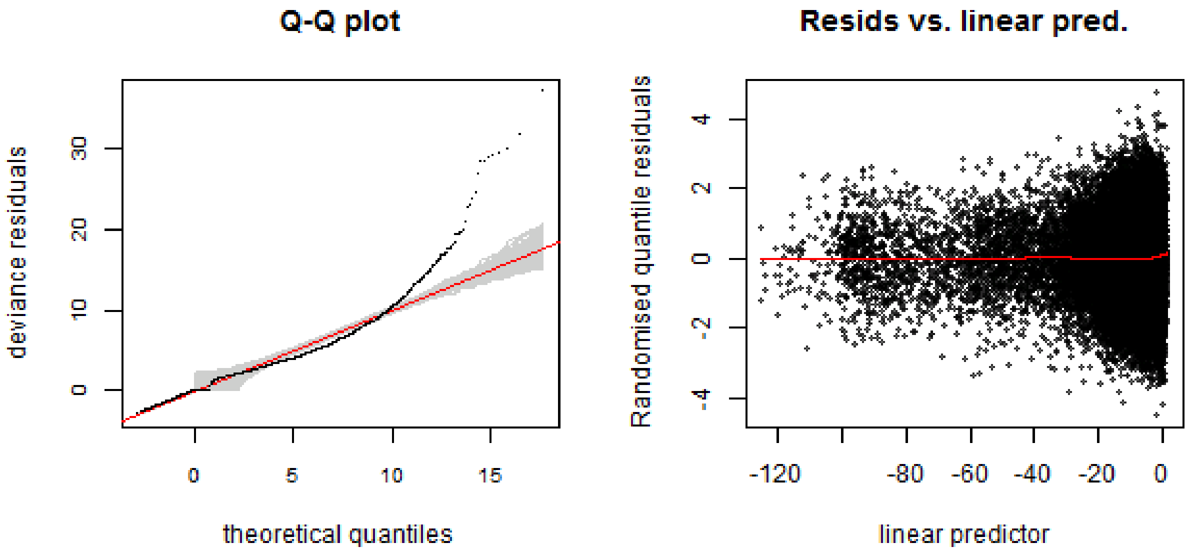

Figure 11: Diagnostic plots of residuals. Left: Quantile-quantile (Q-Q) plot of deviance residuals generated using the qq.gam function with 100 simulations (Augustin et al. 2012). Grey lines are possible simulated Q-Q plots under the assumption that the model is correct. The red reference line indicates 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.

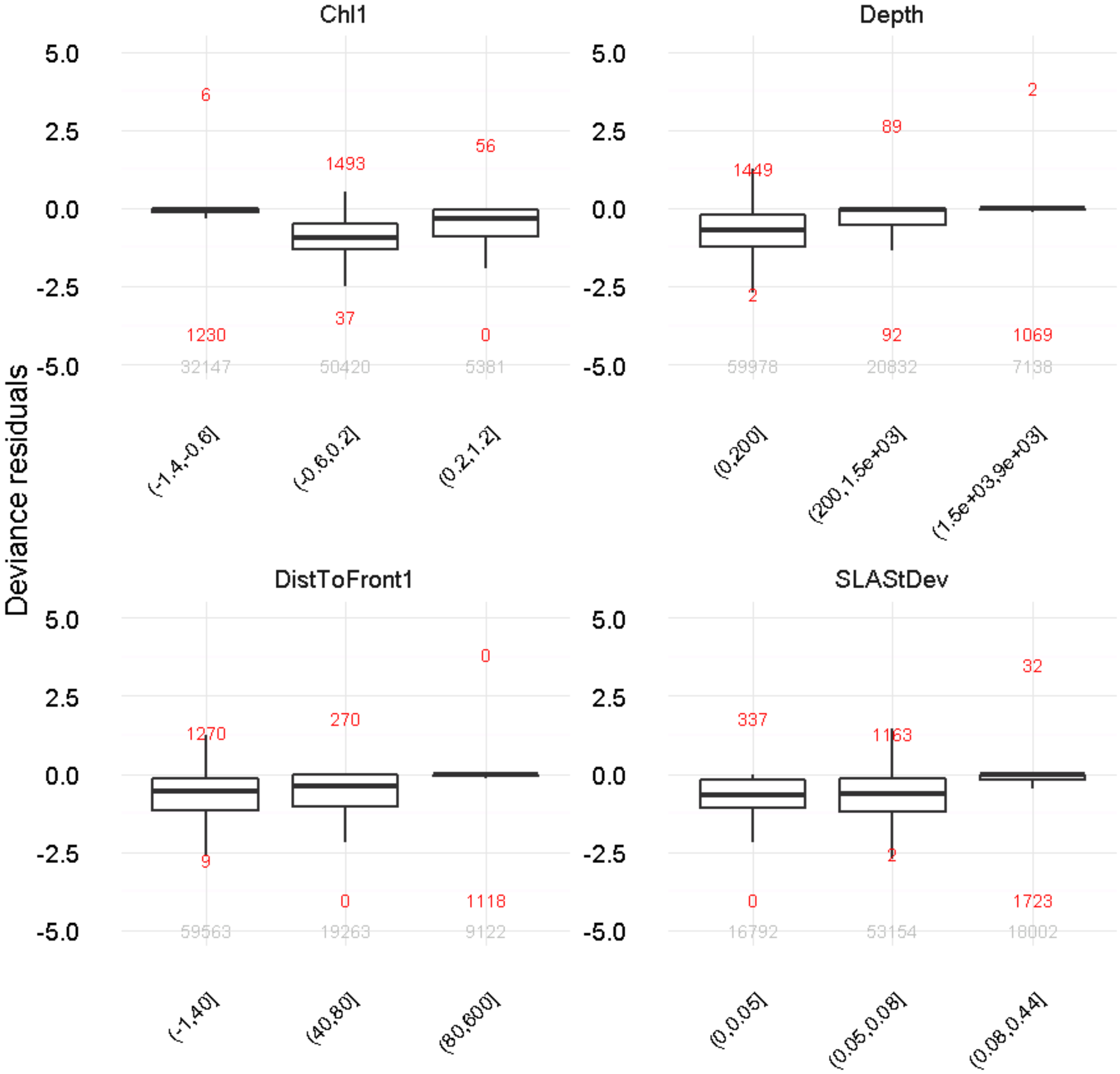

Figure 12: Boxplots of deviance residuals, binned for each predictor. The horizontal line represents the median, and the bottom and top of the box represent the first and third quartiles respectively. Whiskers extend 1.5 times the inter-quartile range following McGill et al. (1978). Total counts of outliers 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.

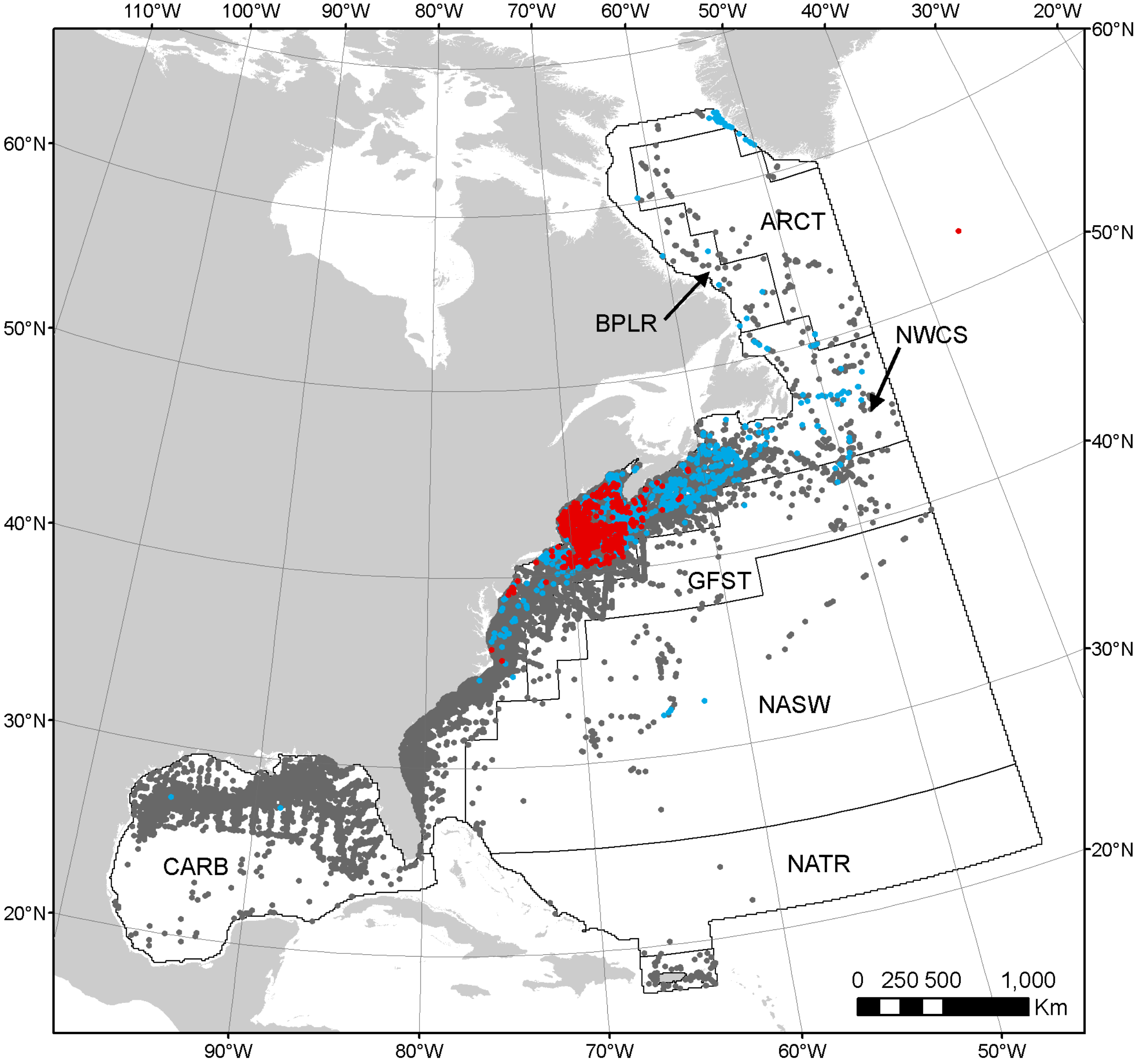

Figure 13: Red points are sightings of the taxon from line transect surveys used in this study. Blue points are sightings of the taxon reported by other datasets not used in our study for 1992-2016 (e.g., because they were not compatible with our methodology). Underlain grey points are sightings of other 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 large sample size of 2578 sightings was available to fit the habitat-based density model. The lowest AIC model included depth, chlorophyll concentration, standard error of sea level anomaly and distance to fronts (listed in decreasing order of importance according to F-scores) and had an explained deviance of 36.6%. It was the only statistically supported model sensu Burnham and Anderson (2002) (Table 3). All top five models included depth and distance to fronts. Predicted densities from the top five models were close to zero in the CARB, NASW and NATR provinces. They differed by a factor 1.7 in the NWCS province and dramatically in the ARCT, BPLR and GFST provinces (Figure 10). The third, fourth and fifth models predicted very low densities (< 0.2 individuals 100km-2) in the ARCT and BPLR provinces. Since humpback whale feeding grounds are described in Labrador and Greenland, we believe these low predicted densities are unrealistic. When examining these results it should be kept in mind that the second, third, fourth and fifth models had little statistical support sensu Burnham and Anderson (2002).

In spring, summer and fall, humpback whales mostly feed in coastal and shelf waters of high latitudes (Clapham 2009), although feeding is also suspected in offshore waters (Heide-Jørgensen and Laidre 2007). In our study area, feeding grounds are situated in the Gulf of Maine, Newfoundland, Labrador and West Greenland. Because most of the survey data available to us came from the Gulf of Maine feeding ground, predictions in other feeding grounds were derived from a broad geographic extrapolation.

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

Predicted densities were on average higher in the offshore waters of the ARCT province than in the BPLR province. In the BPLR province, predicted densities were higher near West Greenland.

In West Greenland, humpback whales were sighted on 21 occasions during an aerial survey in September 2005 (Heide-Jørgensen et al. 2008), and on 30 occasions during a shipboard survey at the same period (Heide-Jørgensen et al. 2007). Sightings were distributed in coastal as well as offshore areas. Abundance estimates derived from these surveys seemed relatively high compared to those derived from older surveys. According to the authors, this may be due to a growth of the population, as observed in the eastern North Atlantic, or an increased affinity to the West Greenland feeding grounds.

Photo-identification surveys conducted from 1988-1993 in West Greenland out to the 200 m isobath found large concentrations of humpback whales (Larsen and Hammond 2004) (sightings from the last 2 years of these surveys, coordinated with the YoNAH program and contributed to OBIS-SEAMAP, are visible on Figure 13).

Humpback whales tagged in West Greenland showed a high affinity for coastal waters where major prey aggregations are known to occur (Heide-Jørgensen and Laidre, 2007). Individuals also used some offshore waters where they presumably foraged on sandeel concentrations. The satellite tracking data revealed long-distance movements (one individual crossed Baffin Bay all the way to Canada).

No survey data are currently available to support the relatively high predicted densities in offshore waters of the ARCT province (notably the area between 50°N and 55°N). Given the findings reported above, we believe such offshore concentrations are not unlikely. Until they are validated with further data, these high predicted densities will remain largely speculative.

A few sightings were reported on the Canadian continental shelf (Figure 13) where the model predicted overall low densities. Benjamins et al. (2012) reported large numbers of humpback whales entangled in commercial fisheries operating off Labrador, predominantly inshore. Extrapolation beyond predictor ranges occurred in parts of the BLPR province; therefore, these predictions should be considered with due caution.

North West Atlantic shelves (NWCS) province

Highest densities were predicted on the inner continental shelf within the Gulf of Maine where numerous sightings were reported by surveys (Figure 13).

Intermediate densities were predicted on the continental shelf from Nova Scotia to Newfoundland. During the Canadian TNASS survey in summer 2007, humpback whales were sighted on 59 occasions east of Newfoundland, 85 occasions south of Newfoundland and 51 occasions on the Scotian shelf (Lawson and Gosselin 2009) (these sightings were not contributed to OBIS-SEAMAP and therefore not shown on Figure 13). Sightings available from OBIS-SEAMAP were concentrated on the Scotian shelf, as well as the continental shelf and shelf break further north (observation effort was comparatively lower) (Figure 13). Humpback whales are known to occur in the Gully canyon, on the Scotian shelf break, mostly in late summer (Hooker et al 1999). Benjamins et al. (2012) documented large numbers of humpback whales entangled in commercial fisheries operating off Newfoundland, predominantly inshore. Medium predicted densities in the northern part of the NWCS province appeared compatible with these results.

The model predicted overall low densities in coastal waters from North Carolina all the way to 27°N off Florida. Humpback whale sightings were reported by surveys as far south as North Carolina in April and May (Figure 13) and strandings were documented in North Carolina, Georgia and Florida between 1989 and 1992 (Wiley et al. 1995). Although these predictions are supported by relatively few records of the species, we believe they are not unrealistic and could potentially correspond to individuals following a coastal route on their migration from/to low-latitude breeding grounds.

Gulf Stream (GFST) province

Overall low densities were predicted in offshore waters beyond the continental shelf within the GFST province. A few sightings were reported in OBIS-SEAMAP on the continental slope (Figure 13). We warn that extrapolation beyond predictor ranges occurred in parts of the GFST provinces and therefore these predictions should be considered with due caution.

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

Very low densities were predicted in the NASW and NATR provinces. We caution that extrapolation to deeper waters occurred in large parts of these provinces, leading to speculative predictions.

Humpback whales are known to transit through these provinces during their northward migration from Caribbean breeding grounds (Kennedy et al. 2014). In particular, it has been suggested that waters surrounding Bermuda constitute a mid-ocean habitat for individuals migrating north (Stone et al. 1987; Kennedy et al. 2014). Furthermore, hydrophone arrays from the Integrated Undersea Sound Surveillance System detected humpback whales to the east of Bermuda, with a peak in late spring (Clark & Gagnon 2004). Several sightings, presumably of individuals migrating, were reported to the east of Bermuda in April, May and November (Figure 13).

Together, these findings suggest that the model may underestimate densities of individuals migrating across the NATR and NASW provinces.

Caribbean (CARB) province

No humpback whale sightings were reported during the Gulf of Mexico surveys but two sightings were documented in OBIS-SEAMAP (Figure 13). We believe these sightings are extralimital as the species is described as accidental in the Gulf of Mexico (Jefferson and Schiro 1997).

Very low predicted densities near Puerto Rico were consistent with the absence of humpback whale sightings in summer months (sightings are mainly reported from January to March) (Mignucci-Giannoni 1998).

Overall confidence: level 2

Large amounts of survey data were available in the Gulf of Maine feeding ground and predictions in northern waters were largely derived from these data. Predictions were in line with the occurrence of humpback whales at high latitudes where they are known to feed in summer but predicted densities in northernmost waters remain speculative. The incorporation of line transect survey data from Canada and Greenland would be critical to increase the reliability of predicted densities at high latitudes. 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 models.

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