Extrapolating cetacean densities to quantitatively assess human impacts on populations in the high seas

Laura Mannocci[1*], Jason J. Roberts[1], David L. Miller[2,3,4], Patrick N. Halpin[1]

[1]Marine Geospatial Ecology Laboratory, Nicholas School of the Environment, Duke University, Durham NC 27708, U.S.A.

[2]Integrated Statistics, 16 Sumner Street, Woods Hole, MA 02543, U.S.A.

[3]Centre for Research into Ecological and Environmental Modelling and School of Mathematics and Statistics, University of St Andrews, The Observatory, Buchanan Gardens, St Andrews, Fife, KY16 9LZ, Scotland

[4]Woods Hole Oceanographic Institution, Woods Hole, MA 02543, U.S.A.

[*]Corresponding author: laura.mannocci@duke.edu

Running head: Cetacean densities

Keywords: extrapolation, habitat-based density models, survey coverage

Word count: 6012

Abstract

As human activities expand beyond national jurisdictions to the high seas, there is increasing need to consider anthropogenic impacts to species that inhabit these waters. The current scarcity of scientific observations of cetaceans in the high seas impedes the assessment of population-level impacts of these activities. This study is directed towards an important management need in the high seas—the development of plausible density estimates to facilitate a quantitative assessment of anthropogenic impacts on cetacean populations in these waters. Our study region extends from a well-surveyed region within the United States Exclusive Economic Zone into a large region of the western North Atlantic sparsely surveyed for cetaceans. We modeled densities of 15 cetacean taxa using available line transect survey data and habitat covariates and extrapolated predictions to sparsely surveyed regions. We formulated models carefully to reduce the extent of extrapolation beyond covariate ranges, and constrained them to model simple and generalizable relationships. To evaluate confidence in the predictions, we performed several qualitative assessments, such as mapping where predictions were made outside sampled covariate ranges, and comparing them with maps of sightings from a variety of sources that could not be integrated into our models. Our study

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/cobi.12856.

revealed a range of confidence levels for the model results depending on the taxon and geographic area, and highlights the need for additional surveying in environmentally distinct areas. Combined with their explicit confidence levels and necessary caution, our density estimates can inform a variety of management needs in the high seas, such as the quantification of potential cetacean interactions with military training exercises, shipping, fisheries, deep-sea mining, as well as delineation of areas of special biological significance in international waters. Our approach is generally applicable to other marine taxa and geographic regions for which management will be implemented but data are sparse.

Introduction

During the past century, technological developments have allowed humans to exploit ocean waters farther from shore. Offshore waters beyond national jurisdiction, known as the high seas, are increasingly used for fishing, shipping, military training and other purposes (Ramirez-Llodra et al. 2011). These activities are known to be incidentally harmful to cetaceans but cetacean abundance and density data for the high seas are often very sparse and thus population-level impacts are poorly known.

Line transect surveys (LTS) are frequently used to estimate the abundance and density of cetacean populations. They involve a ship or aircraft with observers onboard recording sightings using distance sampling to control for the decrease in detection probability with increasing distance from the transect line (Buckland et al. 2001). Line transect methods are traditionally used to provide stratified estimates for a surveyed area (*e.g.,* Hammond et al. 2013), or develop “habitat-based density models” that relate cetacean densities to environmental covariates (*e.g.*, Ferguson et al. 2006). Modeled relationships can then be used to predict cetacean densities in fine-resolution spatial grids spanning surveyed areas (Miller et al. 2013). LTS have been conducted within Exclusive Economic Zones (EEZs) of many countries (extending 200 nmi from shore), but comparatively few have occurred in the high seas (Kaschner et al. 2012).

Density estimates may be derived for unsurveyed areas by fitting habitat models in extensively surveyed areas and carefully extrapolating them (Conn et al. 2015; Mannocci et al. 2015). But extrapolation is inherently risky because of the lack of observations for evaluating model predictions. Extrapolation in geographic space, *i.e.,* beyond surveyed areas but within the sampled ranges of covariate values, can lead to accurate predictions if relationships between species densities and covariates hold in extrapolated areas (Wenger & Olden 2012). Extrapolation in environmental space, *i.e.,* beyond the ranges of covariate values sampled in the surveyed areas, may lead to more speculative predictions because relationships between species densities and covariates are unknown in the new environments (Elith et al. 2010).

Despite these risks, the spatiotemporal coverage of LTS surveys for cetaceans is likely to remain patchy for the foreseeable future, owing to high logistical and financial costs (Kaschner et al. 2012). As ocean users, regulators, and conservation practitioners negotiate the expanding use of the high seas, more decisions are likely to be based on extrapolative models. In this paper, we consider a case study of this problem: the development of extrapolated density estimates to facilitate a quantitative assessment of the impacts of naval training exercises on cetacean populations.

Active sonar and other in-water devices used in military training are of particular concern for cetaceans. The intense sounds they produce have been shown to disrupt diving behavior (DeRuiter et al. 2013), alter acoustic communication (Henderson et al. 2014) and cause displacements from productive habitats (Goldbogen et al. 2013). There is also growing evidence for a link between military sonar exercises and atypical mass strandings of cetaceans (Jepson et al. 2003). In the United States, the Marine Mammal Protection Act regulates the “take” (defined as “to harass, hunt, capture, or kill, or attempt to harass, hunt, capture, or kill”) of marine mammals by U.S.-based organizations anywhere in the world, including the high seas. The U.S. Navy is required to estimate incidental takes resulting from naval training exercises, and seek permits to conduct these activities. To do so, the U.S. Navy developed a model that simulates propagation of sound from planned exercises across cetacean density maps and tallies the individual cetaceans affected (Ciminello et al. 2013).

Using as our area of interest the U.S. Navy Atlantic Fleet’s training and testing area, spanning large regions of the western North Atlantic never surveyed for cetaceans, we modeled densities of 15 taxa using available LTS data and habitat-based covariates and extrapolated predictions to unsurveyed regions. We formulated and constrained models carefully to reduce the chance of errant extrapolations and used a variety of diagnostics to evaluate confidence in the predictions, urging caution in poorly surveyed, environmentally unique areas. Our study revealed a range of confidence in what we can currently infer about cetacean densities in the area, and highlights the need for additional surveying in particularly distinct areas. While we demonstrate our approach for a particular management need, it is generally applicable to other geographic areas, marine taxa and management requirements in areas of sparse survey effort.

Methods

Study area and LTS data

The spatial extent for this study corresponded to the U.S. Navy Atlantic Fleet Training and Testing (AFTT) area. The AFTT area spans 11 million km^2 of the western North Atlantic Ocean, extending from the coast of North America to 45°W, and from approximately 20°N to 65°N, and includes the Gulf of Mexico and U.S. waters surrounding Puerto Rico, spanning Longhurst’s Atlantic coastal, trades, westerlies and polar biomes (Longhurst 2007) (Fig. 1a). Major oceanographic features include the Loop Current, the Gulf Stream, the Labrador Current and the North Atlantic gyre (Fig. 1b). The study area was projected to an Albers equal area projection to minimize spatial error, and gridded into 10x10 km cells, the requested spatial resolution for this management application.

We considered LTS that used two or more observers and met the assumptions of distance sampling methodology (Buckland et al. 2001). We included shipboard and aerial surveys conducted between 1992 and 2014 along the U.S. east coast (887,963 km of effort) and in the northern Gulf of Mexico (194,715 km) by multiple U.S. organizations (see Roberts et al. (2016) for more details), as well as various surveys from the Caribbean, mid-Atlantic ridge and European Atlantic (Table 1).

Incorporating surveys from these other North Atlantic regions increased the representativeness of biomes encompassed by the study area but that were poorly covered by U.S. surveys (Fig. 1a), and increased the sample sizes available for fitting detection functions and developing density models (see below).

Group size (number of sighted individuals), taxonomic identification, perpendicular distance and the observer's assessment of detection conditions (*e.g.,* Beaufort sea state) were available for all the surveys.

We divided survey transects into (approximately) 10 km segments following the procedure described in Roberts et al. (2016). This segment length corresponded to the requested spatial resolution of predictions and was a reasonable compromise between the resolutions of environmental data available (4 km to 0.25°; Appendix S1).

Environmental covariates

To reduce the extent of environmental extrapolation, we used covariates for which broad ranges of values were sampled by the surveys. Hence, we excluded longitude, latitude, distances to the shore and ecologically relevant isobaths; these are commonly used in cetacean habitat modeling studies (*e.g.,* Ferguson et al. 2006), but would result in extrapolating far beyond the range of sampled values in the study area. To increase the success of model transferability to new regions, we considered biological covariates expected to be directly related to cetacean densities (Wenger & Olden 2012), namely biomass and production of epipelagic micronekton and zooplankton predicted with the Spatial Ecosystem and Population DYnamics Model (SEAPODYM) (Lehodey et al. 2010). Zooplankton and epipelagic micronekton, encompassing squid, crustaceans and fish, constitute potential prey for many of the cetaceans modeled in this study (in particular, dolphins and mysticetes (Pauly et al. 1998)). All covariates used in this study were previously shown to be correlated with cetacean distributions (e.g., Ferguson et al. 2006; Doniol-Valcroze et al. 2007; Lambert et al. 2014).

We derived covariates from remote sensing and ocean models (Appendix S1) and resampled them to the 10x10 km grid of the study area. For dynamic covariates, we prepared monthly climatologies by aggregating and summarizing the available time series. Although monthly climatologies smoothed out inter-annual variations in oceanographic conditions, they successfully captured important seasonal variations. We obtained covariate values for the survey segments by interpolating the 10x10 km grid at the segment centroids. We used ArcGIS 10.2.2 and the Marine Geospatial Ecology Tools software (Roberts et al. 2010) to prepare all covariates.

Habitat-based density models

We relied on the two-stage density modeling approach (Hedley & Buckland 2004; Miller et al. 2013) described hereafter.

Detection function fitting and per-segment abundance estimation

We fitted taxon-specific detection functions using the single-observer methodology (Buckland et al. 2001). For each taxon, we pooled multiple surveys with similar observation platforms and protocols or used "proxy" species with similar detectability to obtain sufficient sightings to fit detection functions (Roberts et al. 2016). Before fitting each detection function, we right-truncated the most distant sightings and applied left truncation for aerial surveys that suffered from an inadequate view of the survey trackline (Buckland et al. 2001). We compared a number of detection function formulations, using both Conventional Distance Sampling (CDS; Buckland et al. 2001) and Multiple Covariate Distance Sampling (MCDS; Marques & Buckland 2004) and selected the model with the lowest Akaike information criterion (AIC) (see Roberts et al. (2016) and the accompanying reports). We fitted all detection functions in R using the *mrds* package version 2.1.10 (Laake et al. 2014).

The probability of detecting an animal on the trackline, or *g(0)*, is affected by both availability bias (when observers fail to detect animals because they are submerged) and perception bias (when observers fail to detect animals that are present at the surface) (Pollock et al. 2006). We corrected for availability and perception bias by obtaining estimates of *g(0)* from the literature that incorporated these biases. We obtained separate *g(0)* estimates for aircraft and shipboard platforms and, where possible, for different group sizes (to account for large groups being easier to detect than small groups) (see Roberts et al. (2016)). We then scaled the estimated abundance of each sighting with the inverse of *g(0)* appropriate for that sighting, based on the platform and group size. Details on detection function fitting and *g(0)* estimates can be found in Roberts et al. (2016).

For each taxon, we estimated the abundance in segment j, $\widehat{N}_j$, by using the Horvitz-Thompson-like estimator as follows:

$$\widehat{N}_j = \sum_{r=1}^{R_j} s_{jr}/\hat{p}(z_{jr})$$

where R_j is the number of observed groups in segment j, s_{jr} is the size of the r^{th} group in segment j and $\hat{p}(z_{jr})$ is the estimated probability of detection given observation level covariates, z_{jr} (Marques et al. 2007).

Generalized Additive Model fitting, predictions and uncertainty

We then fitted Generalized Additive Model (GAMs) with the following structure:

$$\mathrm{E}(\widehat{N}_j) = A_j \, exp \, [\beta_0 + \sum_k f_k(z_{jk})]$$

where $\widehat{N}_j$ is the response variable assumed to follow a Tweedie distribution (e.g., Foster & Bravington 2013) (and E indicates expectation); A_j, the model offset, is the area of segment j calculated as $2(w_R\text{-}w_L)l_j$ where w_R is the right-truncation distance, w_L is the left truncation distance (0 if data were not left truncated), and l_j is the segment length; f_k are the smooth functions of the environmental covariates z_k; and β_0 is the model intercept.

We considered survey segments from the U.S. east coast, Gulf of Mexico, Caribbean, mid-Atlantic ridge and European Atlantic to fit the models depending on the taxon. When contrasting density-environment relationships were expected in different seasons (*e.g.,* for baleen whales that forage in summer and breed and calve in winter), and there were sufficient sightings in each season, we fitted separate seasonal models. Otherwise, we fitted a year-round model. Modeling decisions for individual taxon are detailed in supplementary reports available at the Ocean Biogeographic

Information System Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP) repository.

Is it important to constrain model complexity based on the study objectives (Merow et al. 2014).

Consistent with our objective of extrapolating cetacean densities beyond surveyed areas, we sought to develop simple habitat models capturing dominant cetacean-environment relationships but not reproducing details present in the data (Elith et al. 2010). Simple models, *i.e.*, models characterized by few parameters and smooth species-environment relationships, have been shown to achieve higher transferability and are highly recommended for extrapolation (Wenger & Olden 2012; Merow et al. 2014). Authier et al. (2016) also found that models with a large number of covariates lead to widespread environmental extrapolation. In line with these findings, we considered models with a maximum of 4 covariates (models including 5 or more covariates led to an excessively large extent of environmental extrapolation). We fitted GAMs with all possible combinations of 4 covariates, after eliminating the pairs of covariates for which the Spearman's rank correlation coefficient (Hollander & Wolfe 1973) calculated on segments was ≥ 0.6 or ≤ -0.6. We used thin-plate regression splines with shrinkage to allow smooth term effects to be removed from the model during fitting. To model simple density-environment relationships and mitigate overfitting which is known to limit model transferability (Wenger & Olden 2012), we restricted the basis size to 4 for each smooth term. We used restricted maximum likelihood (REML) as the criterion for estimating smooth parameters because it has been shown to penalize overfitting and lead to more pronounced optima (Wood 2011). We selected the models with the lowest AIC as the 'best' models. Model selection based on AIC is effective at reducing overfitting by penalizing models with excessive complexity (Wenger & Olden 2012). . We fitted all GAMs in R using the *mgcv* package version 1.8.4 (Wood 2014).

We produced maps of mean predicted densities (individuals per 100 km^2) by averaging monthly predictions seasonally (if a seasonal model was fitted) or annually (if a year-round model was fitted) on a per-cell basis. To visualize parameter uncertainty from the spatial part of the model, we produced maps of the mean (seasonal or year-round) coefficients of variation (CVs) for each cell in the prediction grid by applying the approach described in Miller et al. (2013) (technical details explained in their Appendix S2). Model selection uncertainty is another important source of uncertainty to consider in extrapolation studies (Pearson et al. 2006). We further assessed uncertainty in the model selection process by examining mean predicted density for each of Longhurst's biogeographical provinces by the five top models (ranked by AIC) (results shown and discussed in the supplementary taxon-specific reports).

Despite our efforts to limit environmental extrapolation, we extrapolated beyond the sampled covariate ranges in some areas to provide predictions in the entire study area. Predicted densities in these areas (indicated on Fig. 2, 3 and 4 by crosshatches) are largely speculative and should be interpreted with caution.

In addition to predicted density and CV maps, we included in the supplementary reports available at the OBIS-SEAMAP repository: plots of the smooth terms in the GAMs, maps of sampled covariate ranges (*i.e.*, the so-called environmental envelopes) to visualize where the model was extrapolated, predicted density maps per Longhurst's biogeographical province, alternate models to quantify model uncertainty, residual diagnostics and discussions evaluating our relative level of confidence in predictions.

Results

We fitted habitat-based density models and extrapolated densities of 15 cetacean taxa, comprising 12 species and 3 guilds, to unsurveyed regions in the western North Atlantic. The most common predictors were depth, distance to the nearest sea surface temperature (SST) front and production of epipelagic micronekton. Explained deviances ranged from 22.9% (fin whale) to 57.2% (striped dolphin) (Table 2). The extent of extrapolation beyond the sampled covariate ranges varied from 4% (harbor porpoise) to 50% (*Globicephala spp.*) (Table 2). Environmental extrapolation mostly occurred in the westerlies biome (lower chlorophyll-a concentration, lower zooplankton production and larger distances from SST fronts in summer), and in the polar biome (lower SST in winter).

We present density modeling results for a migratory mysticete (sei whale *Balaenoptera borealis*), a deep diving odontocete (*Kogia spp.,* including *K. sima* and *K. breviceps*) and an oceanic dolphin (striped dolphin *Stenella coeruleoalba*) that represent three ecologically distinct cetacean families. Predicted density and CV maps for all taxa are freely available at the OBIS-SEAMAP repository; detailed modeling results are available in the accompanying taxon-specific reports.

Sei whale

Sei whale summer densities were predicted to increase in deep, cold waters with a reduced mesoscale activity and a high epipelagic micronekton production. In order to predict densities in the entire study area, we extrapolated to deeper waters in the North Atlantic gyre, to colder waters in the polar biome, and to a lesser extent, to waters of higher mesoscale activity in the Gulf Stream (these extrapolations comprised 40% of the cells of the study area) (Table 2, Fig. 2a). Predicted densities in these waters were largely speculative and should be interpreted with extreme caution. Sei whales were predicted to occur in temperate and sub-polar waters, primarily on the continental slope and offshore, in accordance with their described ecology (Prieto et al. 2012). They were predicted in highest densities on the continental slope north of Cape Hatteras, as well as in offshore waters of the Labrador Current. Despite being largely speculative, high predicted densities in the Labrador Sea appeared compatible with a presumed summer feeding ground revealed by satellite telemetry tracks of sei whales from the Azores (Prieto et al. 2014) . CVs were the highest in waters of high mesoscale activity in the Gulf Stream, shallow waters along the U.S. coast and warm waters in the North Atlantic gyre (Fig. 2b).

Kogia spp.

Densities of *Kogia spp.* were predicted to increase in warm waters of intermediate depth and high micronekton production. In order to predict densities in the entire study area, we extrapolated to colder waters in the polar biome (9% of the cells) (Table 2, Fig. 3a); predicted densities in these waters should be viewed with due caution. *Kogia spp.* were predicted to occur in tropical and warm offshore temperate waters, in accordance with their known ecology (McAlpine 2009). They were predicted in highest densities on the continental slope in the Gulf of Mexico and south of Cape Hatteras. CVs were the highest in shallow waters on continental shelves, and in cold waters throughout the polar biome (Fig. 3b).

Striped dolphin

Striped dolphin densities were predicted to increase in deep waters of high epipelagic micronekton production, intermediate chlorophyll concentration (CHL), and near SST fronts. In order to predict densities in the entire study area, we extrapolated to lower CHL and further from fronts in the North Atlantic gyre (these extrapolations comprised 34% of the cells) (Table 2, Fig. 4a). We urge caution regarding predicted densities in these areas. Striped dolphins were predicted to occur in offshore waters throughout most of the study area. Striped dolphins are mostly found in tropical and warm temperate waters, as well as occasionally in cold temperate waters (Archer & Perrin 1999). Highest predicted densities in the Gulf Stream appeared in line with their described affinity for the north wall of this current (Waring et al. 1992). CVs were highest in shallow waters of the continental shelves (Fig. 4b).

Discussion

Confidence in extrapolations

We developed habitat-based density models for 15 cetacean taxa and predicted their densities in a vast region of the western North Atlantic encompassing never surveyed high seas. We strived to build transferable models by incorporating over 1.1 million km of surveys that covered representative ecological biomes, limiting the extent of environmental extrapolation, and by modeling simple, ecologically sound cetacean density-environment relationships. For each taxon, we evaluated the plausibility of predictions by performing several qualitative assessments, including mapping where predictions were made outside sampled predictor ranges, examining alternate models, and comparing predicted densities to maps of cetacean sightings available in the OBIS-SEAMAP repository (Halpin et al. 2009), which catalogued sightings from a wide range of sources (*e.g.*, opportunistic sightings, telemetry data) that could not be integrated into our models.

Overall, we have a reasonable confidence in predictions for tropical and warm temperate taxa for which survey data were available within most of the distributional range (Atlantic spotted dolphin, *Kogia spp.* and bottlenose dolphin), and a comparatively lower confidence in predictions for cold temperate and sub-polar waters taxa for which survey data only covered the southern part of their range (Atlantic white-sided dolphin, harbor porpoise and all species of mysticetes). Although the models correctly predicted the occurrence of these taxa in northern waters, predicted densities were largely speculative and should be interpreted cautiously. The incorporation of line transect surveys from Canada (Lawson & Gosselin 2009) and Greenland (Heide-Jørgensen et al. 2007) would increase the reliability of these models. Unfortunately, we were unable to obtain permission to incorporate these surveys in the current models but remain hopeful that they can be incorporated in future iterations. We call for increased collaboration and data sharing in order to better model cetaceans in international waters.

Caveats of the approach

The geographical distribution of line transect surveys available for this study was heterogeneous with the highest concentration of effort in the U.S. EEZ. Despite our efforts to incorporate surveys external to the study area to increase the coverage of the westerlies and polar biomes poorly covered by U.S. surveys, these ecological biomes remained largely underrepresented. To examine the sensitivity of density modeling results to heterogeneity in survey coverage, we implemented a cross-validation approach by splitting the available survey data into 11 geographical regions, excluding each region and examining predictions of the resulting models (Appendix S2). The results indicate that models remained generally capable of reproducing overall inter-regional patterns in taxa distributions when data from one region were withheld. This suggests that predictions in underrepresented regions are overall plausible, but we urge caution regarding the absolute accuracy of density values in certain situations.

Furthermore, it is important to note that some unsurveyed regions (*e.g.*, the Labrador Sea, the North Atlantic gyre) have oceanographic conditions that are very different from conditions in surveyed regions despite showing some overlap with sampled covariate ranges. Inter-covariate correlations may also be expected to differ between unsurveyed and surveyed regions. Changing correlations between the sample and prediction datasets can lead to unreliable predictions in areas where they differ the most (Elith et al. 2010). In Appendix S3, we compared covariate correlations in the sample and prediction data, and found that covariates that were moderately correlated in one direction in the sample data were always correlated in this same direction in the prediction data.

By design, our models were simple and not tightly fitted to the data. Complex models do not transfer well to new regions because species-environment relationships apply specifically to the sample data but do not generalize well (Elith et al. 2010; Wenger & Olden 2012; Merow et al. 2014). In contrast, in a related study limited to U.S waters, we were less concerned with model transferability and developed more complex models to accurately map cetacean densities within extensively surveyed areas (Roberts et al. 2016). In the present study, limiting the basis size of smooth terms prevented overfitting and helped model general relationships that likely transfer better to unsurveyed regions. Of course, underfitting also limits model transferability as it can lead to misunderstandings of the drivers of species distributions, and potentially biased predictions (Merow et al. 2014). To ensure that our models did not result in severe bias in extrapolation, we always assessed predictions against ecological knowledge. However, bias in predicted densities beyond predictor ranges cannot be ruled out, and we once again urge caution for their interpretation.

It is important to monitor the shapes of fitted relationships at the edges of sampled covariate ranges to prevent spurious extrapolation (Elith et al. 2010; Merow et al. 2014). For smooth functions that use the thin plate regression spline basis (Wood 2003), fitted relationships outside the observed data tend to extreme values as the distance from observed values increases. Steeply increasing relationships may be particularly problematic as they result in unrealistically high density predictions when extrapolated beyond the sampled covariate ranges. Such situations did not occur in our study and the shapes of relationships at the edges of sampled covariate ranges appeared ecologically plausible. However, for some cold water taxa (*e.g.,* sei whale and fin whale), the relatively steep decrease of densities at the lower edge of the sampled SST range may have resulted in an underestimation in northern waters.

Along with predicted density maps, we produced maps of CVs to quantify the relative uncertainty from the spatial part of the model over the study area. We advise caution when interpreting these maps as they document a single source of uncertainty (the spatial model), and do not reflect the uncertainty associated with predicted densities beyond covariate ranges, the detection functions, *g(0)* estimates or model covariates. Covariate uncertainty may be highest for biological covariates derived from the SEAPODYM model. Thanks to the assimilation of *in situ* acoustic data for parameter optimization (Lehodey et al. 2014), SEAPODYM outputs are becoming increasingly accurate, making their use as covariates in cetacean extrapolation models promising. The development of statistical methods propagating these various sources of uncertainty to final densities estimates constitutes an area of active research (*e.g.*, Foster et al. 2012).

Our inference was based on a single best supported model; however, different models can lead to widely different predictions beyond predictor ranges (Pearson et al. 2006). To account for model uncertainty, we examined the sensitivity of mean predicted density for each biogeographical province by the five top models (see the supplementary reports). Overall, mean predicted densities by models with statistical support *sensu* Burnham & Anderson (2002), *i.e.*, with a delta AIC lower than 2, were not widely different. Notable exceptions were mean predicted densities of sperm whale in the Atlantic Arctic and boreal polar provinces (differing by a factor of 5), and mean predicted densities of striped dolphin in the Atlantic Arctic province (differing by a factor of 4.5).

Applications

This study provides baseline density predictions for 15 cetacean taxa in a very large portion of the western North Atlantic. Our confidence in the predictions depends on the taxon and region; users of these predictions are strongly advised to review taxon-specific supplementary reports and proceed with caution where indicated. In the future, the predictions may be improved by incorporating new LTS data in underrepresented regions. To facilitate this, we call for expanded collaboration that would allow us to incorporate extant data not able to be incorporated into the present study (*e.g.*, Heide-Jørgensen et al. 2007; Lawson & Gosselin 2009), and urge increased surveying in underrepresented regions.

Beyond the example application of facilitating a quantitative assessment of military training impacts on cetacean populations, our density estimates can inform a variety of management needs in the high seas. Management applications include quantifying the impacts of industrial activities that generate underwater noise, including deep-sea mining and seismic surveying, quantifying cetacean interactions with offshore fisheries and trans-oceanic shipping, and informing the delineation of areas of special biological significance in international waters (*e.g.*, the Sargasso Sea, recently proposed as a potential UNESCO World Heritage site). Finally, the approach presented here is generally applicable to other geographic regions, marine taxa and management needs in areas of sparse data.

Acknowledgments

We thank the numerous researchers who collected and shared line transect data with us. D. Palka, T. Cole and colleagues contributed the NEFSC surveys; L. Garrison and colleagues contributed the

SEFSC surveys; A. Whitt, S. Bates, and G. Buchanan contributed the NJDEP surveys; G. Lockhart contributed the VAMSC surveys; B. McLellan and colleagues contributed the UNCW surveys; V. Ridoux and colleagues contributed the French REMMOA surveys; P. Hammond, C. Lacey and colleagues contributed the SCANS-II and CODA surveys; O. A. Bergstad, T. de Lange Wenneck, L. Nøttestad, and G. Waring contributed the MAR-ECO survey under the Norwegian License for Open Government data (**NLOD**). We are grateful to P. Lehodey and colleagues who provided the micronekton and zooplankton outputs from SEAPODYM, and S. Maritorena and E. Fields who provided chlorophyll data from the Ocean Color MEaSUREs project. We thank many colleagues for providing advice and reviewing results, especially E. Becker, D. Cholewiak, P. Corkeron, A. DiMatteo, K. Forney, J. Harrison, L. Hatch, D. Johnston, B. Josephson, D. Nowacek, J. Ortega-Ortiz, A. Read, D. Risch, J. Robbins, M. Soldevilla, J. Stanistreet, L. Thomas, S. Van Parijs, D. Waples, and S. Wood. We are grateful to J. Cleary for his help with map automation in Python and E. Fujioka for his help extracting sightings from OBIS-SEAMAP. This study benefited from discussion during meetings of the PELAGIC project funded by the *Fondation pour la Recherche sur la Biodiversité* and *Fondation Total*, and hosted by the Centre for the Synthesis and Analysis of Biodiversity. Funding for this study came from the U.S. Fleet Forces Command (Cooperative Agreement N62470-13-2-8008), NASA (NNX08AK73G) and NOAA/NMFS (EE-133F-14-SE-3558).

Literature cited

Archer FI, Perrin WF. 1999. Stenella coeruleoalba. Mammalian Species **603**:1–9.

Authier M, Saraux C, Péron C. 2016. Variable Selection and Accurate Predictions in Habitat Modelling: a Shrinkage Approach. Ecography:n/a-n/a.

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L. 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, UK.

Burnham KP, Anderson DR. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Science & Business Media.

Ciminello CA et al. 2013. Determination of Acoustic Effects on Marine Mammals and Sea Turtles for the Atlantic Fleet Training and Testing Environmental Impact Statement/Overseas Environmental Impact Statement (Technical report). Naval Undersea Warfare Center Division Newport, Rhode Island.

Conn PB, Johnson DS, Boveng PL. 2015. On Extrapolating Past the Range of Observed Data When Making Statistical Predictions in Ecology. PloS one **10**:e0141416.

DeRuiter SL et al. 2013. First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. Biology Letters **9**:20130223.

Doniol-Valcroze T, Berteaux D, Larouche P, Sears R. 2007. Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. Marine Ecology Progress Series **335**:207–216.

Elith J, Kearney M, Phillips S. 2010. The art of modelling range-shifting species. Methods in ecology and evolution **1**:330–342.

Ferguson MC, Barlow J, Fiedler P, Reilly SB, Gerrodette T. 2006. Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. Ecological Modelling **193**:645–662.

Foster SD, Bravington MV. 2013. A Poisson–Gamma model for analysis of ecological non-negative continuous data. Environmental and ecological statistics **20**:533–552.

Foster SD, Shimadzu H, Darnell R. 2012. Uncertainty in spatially predicted covariates: is it ignorable? Journal of the Royal Statistical Society: Series C (Applied Statistics) **61**:637–652.

Goldbogen JA et al. 2013. Blue whales respond to simulated mid-frequency military sonar. Proceedings of the Royal Society B: Biological Sciences **280**:20130657–20130657.

Halpin P et al. 2009. OBIS-SEAMAP: The World Data Center for Marine Mammal, Sea Bird, and Sea Turtle Distributions. Oceanography **22**:104–115.

Hammond PS et al. 2009. Cetacean Offshore Distribution and Abundance in the European Atlantic (CODA). Final Report. Saint Andrews.

Hammond PS et al. 2013. Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. Biological Conservation **164**:107–122.

Hedley SL, Buckland ST. 2004. Spatial models for line transect sampling. Journal of Agricultural, Biological, and Environmental Statistics **9**:181–199.

Heide-Jørgensen MP, Borchers DL, Witting L, Simon MJ, Laidre KL, Rosing-Asvid A, Pike D. 2007. Final estimates of large whale abundance in West Greenland waters from an aerial survey in 2005. IWC/SC/59/AWMP7. Available from the International Whaling Commission (http://www. iwcoffice. org/).

Henderson EE, Smith MH, Gassmann M, Wiggins SM, Douglas AB, Hildebrand JA. 2014. Delphinid behavioral responses to incidental mid-frequency active sonar. The Journal of the Acoustical Society of America **136**:2003–2014.

Hollander M, Wolfe D. 1973. Non parametric statistical methods. Wiley. New York.

Jepson PD et al. 2003. Gas-bubble lesions in stranded cetaceans. Nature **425**:575–576.

Kaschner K, Quick NJ, Jewell R, Williams R, Harris CM. 2012. Global coverage of cetacean line-transect surveys: status quo, data gaps and future challenges. PloS one **7**:e44075.

Laake JL, Borchers DL, Thomas L, Miller D, Bishop JR. 2014. Mark-Recapture Distance Sampling (mrds) package Version 2.1.10.

Lambert C, Mannocci L, Lehodey P, Ridoux V. 2014. Predicting cetacean habitats from their energetic needs and the distribution of their prey in two contrasted tropical regions. PLoS One **9**:e105958.

Lawson JW, Gosselin J-F. 2009. Distribution and preliminary abundance estimates for cetaceans seen during Canada's Marine Megafauna Survey-A component of the 2007 TNASS. Canadian Science Advisory Secretariat. Available from http://biblio.uqar.qc.ca/archives/30125408.pdf (accessed March 25, 2014).

Lehodey P, Conchon A, Senina I, Domokos R, Calmettes B, Jouanno J, Hernandez O, Kloser R. 2014. Optimization of a micronekton model with acoustic data. ICES Journal of Marine Science: Journal du Conseil:fsu233.

Lehodey P, Murtugudde R, Senina I. 2010. Bridging the gap from ocean models to population dynamics of large marine predators: A model of mid-trophic functional groups. Progress in Oceanography **84**:69–84.

Longhurst AR. 2007. Ecological geography of the sea. Academic Press, Oxford.

Mannocci L, Monestiez P, Bolaños-Jiménez J, Dorémus G, Jeremie S, Laran S, Rinaldi R, Van Canneyt O, Ridoux V. 2013. Megavertebrate communities from two contrasting ecosystems in the western tropical Atlantic. Journal of Marine Systems **111**:208–222.

Mannocci L, Monestiez P, Spitz J, Ridoux V. 2015. Extrapolating cetacean densities beyond surveyed regions: habitat-based predictions in the circumtropical belt. Journal of Biogeography **42**:1267–1280.

Marques FFC, Buckland ST. 2004. Covariate models for the detection function. Pages 31–47 Advanced Distance Sampling. Oxford, New York.

Marques TA, Thomas L, Fancy SG, Buckland ST. 2007. Improving estimates of bird density using multiple- covariate distance sampling. The Auk **124**:1229–1243.

McAlpine DF. 2009. Pygmy and dwarf sperm whales. Pages 936–938 Encyclopedia of marine mammals 2nd Edition. Academic Press.

Merow C, Smith MJ, Edwards TC, Guisan A, McMahon SM, Normand S, Thuiller W, Wüest RO, Zimmermann NE, Elith J. 2014. What do we gain from simplicity versus complexity in species distribution models? Ecography **37**:1267–1281.

Miller DL, Burt ML, Rexstad EA, Thomas L. 2013. Spatial models for distance sampling data: recent developments and future directions. Methods in Ecology and Evolution **4**:1001–1010.

Pauly D, Christensen V, Trites AW. 1998. Diet composition and trophic levels of marine mammals. ICES Journal of Marine Science **55**:467–481.

Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, Miles L, Segurado P, Dawson TP, Lees DC. 2006. Model-based uncertainty in species range prediction. Journal of Biogeography **33**:1704–1711.

Pollock KH, Marsh HD, Lawler IR, Allderdge M. 2006. Estimating Animal Abundance in Heterogeneous Environments: An Application to Aerial Surveys for Dugongs. Journal of Wildlife Management **70**:255–262.

Prieto R, Janiger D, Silva MA, Waring GT, GonçAlves JM. 2012. The forgotten whale: a bibliometric analysis and literature review of the North Atlantic sei whale Balaenoptera borealis: North Atlantic sei whale review. Mammal Review **42**:235–272.

Prieto R, Silva MA, Waring G, Gonçalves JM. 2014. Sei whale movements and behaviour in the North Atlantic inferred from satellite telemetry. Endangered species Research. Available from http://www.int-res.com/abstracts/esr/v26/n2/p103-113/ (accessed January 5, 2015).

Ramirez-Llodra E et al. 2011. Man and the Last Great Wilderness: Human Impact on the Deep Sea. PLoS ONE **6**:e22588.

Roberts JJ et al. 2016. Habitat-based cetacean density models for the U.S. Atlantic and Gulf of Mexico. Scientific Reports **6**:22615.

Roberts JJ, Best BD, Dunn DC, Treml EA, Halpin PN. 2010. Marine Geospatial Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. Environmental Modelling & Software **25**:1197–1207.

Swartz SL, Martinez A, Stamates J, Burks C, Mignucci-Giannoni AA. 2002. Acoustic and Visual Survey of Cetaceans in the Waters of Puerto Rico and the Virgin Islands, February-March 2001. NOAA Technical Memorandum NMFS-SEFSC- 463. US Department of Commerce, National Oceanic and Atmospheric Administration, NOAA Fisheries, Southeast Fisheries Science Center. Available from http://manatipr.org/wp-content/uploads/2010/01/Swartz2001NOAA.pdf (accessed October 23, 2014).

Waring GT, Fairfield CP, Ruhsam CM, Sano M. 1992. Cetaceans associated with Gulf Stream features off the northeastern USA shelf. ICES Marine Mammals Comm. CM:29.

Waring GT, Nøttestad L, Olsen E, Skov H, Vikingsson G. 2008. Distribution and density estimates of cetaceans along the mid-Atlantic Ridge during summer 2004. Journal of Cetacean Research and Management **10**:137–146.

Wenger SJ, Olden JD. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. Methods in Ecology and Evolution **3**:260–267.

Wood S. 2014. Mixed GAM Computation Vehicle with GCV/AIC/REML smoothness estimation (mgcv) package Version 1.8-4.

Wood SN. 2003. Thin plate regression splines. Journal of the Royal Statistical Society: Series B (Statistical Methodology) **65**:95–114.

Wood SN. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society: Series B (Statistical Methodology) **73**:3–36.

Table 1: Line transect survey data incorporated in habitat-based density models.

Region	Platform	Surveyor	Effort (km)	Number of segments	Survey years	Reference
East coast (EC)	Shipboard and aerial	NEFSC, NJDEP, SEFSC, UNCW, VAMSC	887,963	89,426	1992–2014	Complete list of references available in Roberts et al. (2016)
Gulf of Mexico (GOM)	Shipboard and aerial	SEFSC	194,715	19,988	1992–2009	Complete list of references available in Roberts et al. (2016)
Caribbean (CAR)	Shipboard	SEFSC	8,975	914	2000, 1995	Swartz et al. (2002)
	Aerial	University of La Rochelle	15,289	1,528	2008	Mannocci et al. (2013)
European Atlantic (EU)	Shipboard	Partners of the CODA Program	9,584	957	2007	Hammond et al. (2009)
Mid Atlantic Ridge (MAR)	Shipboard	Partners of the SCANS-II Program	17,942	1,805	2005	Hammond et al. (2013)
	Shipboard	Partners of the MAR-ECO Program	2,424	243	2004	Waring et al. (2008)
TOTAL			1,136,892	114,861		

Surveyors: NEFSC = NMFS Northeast Fisheries Science Center, NJDEP = New Jersey Department of Environmental Protection, SEFSC = NMFS Southeast Fisheries Science Center, UNCW = University of North Carolina at Wilmington, VAMSC = Virginia Aquarium & Marine Science Center, SCANS-II = Small Cetacean Abundance in the North Sea and adjacent waters-II, CODA = Cetacean Offshore Distribution and Abundance in the European Atlantic, MAR-ECO = Mid-Atlantic Ridge Ecology Program.

Table 2: Overview of density modeling results. Detailed results are presented in the supplementary taxon-specific reports.

Taxon	Season	Number of sightings	Predictors (listed in decreasing order of importance according to F-scores)	Explained deviance (%)	Extent of environmental extrapolation (%)	Described range
Mysticetes						
Fin whale (*Balaenoptera physalus*)	Year-round	1785	EpiMnkPB, Slope, SST, DistToFront	22.9	29	Cosmopolitan
Humpback whale (*Megaptera novaeangliae*)	Summer	2578	Depth, CHL, SLAStDev, DistToFront	36.6	44	Cold temperate and sub-polar waters (summer)
Minke whale (*Balaenoptera acutorostrata*)	Year-round	1109	PkPB, Depth, DistToFront	23.6	20	Cosmopolitan
Sei whale (*Balaenoptera borealis*)	Summer	852	Depth, SLAStDev, SST, EpiMnkPP	38.5	40	Cold temperate and sub-polar waters (summer)
Odontocetes						
Atlantic spotted dolphin (*Stenella*	Year-round	1150	SST, Depth, PkPP, EKE	41.8	50	Tropical and war

frontalis)						m temperate waters
Atlantic white-sided dolphin (*Lagenorhynchus acutus*)	Year-round	2329	SST, Depth, EpiMnkPP, DistToFront	35.2	28	Cold temperate and sub-polar waters
Beaked whales[a]	Year-round	395	Depth, DistToCanyonOrSeamount, CHL, CurrentSpeed	42.8	34	Cosmopolitan
Bottlenose dolphin (*Tursiops truncatus*)	Year-round	6524	PkPB, Depth, EpiMnkPP, DistToFront	25.7	20	Tropical and warm temperate waters
Globicephala spp.[b]	Year-round	1058	Depth, PkPP, SLAStDev, EpiMnkPP	23.3	50	Cosmopolitan
Harbor porpoise (*Phocoena phocoena*)[c]	Year-round	2018	PkPB, Depth, EpiMnkPP, SLAStDev	46.5	4	Cold temperate and sub-polar waters
Kogia spp.[c]	Year-round	256	SST, Depth,	41.8	9	Tropi

			EpiMnkPP			cal and warm temperate waters
Risso's dolphin (*Grampus griseus*)	Year-round	1002	Depth, PkPB, EpiMnkPP, DistToFront	38.4	20	Tropical and temperate waters
Short-beaked common dolphin (*Delphinus delphis*)	Year-round	1428	Slope, SLAStDev, CHL, DistToFront	36.6	34	Temperate waters
Sperm whale (*Physeter macrocephalus*)	Year-round	941	Depth, DistToCanyonOrSeamount, CHL	42.0	33	Cosmopolitan
Striped dolphin (*Stenella coeruleoalba*)	Year-round	336	Depth, EpiMnkPP, CHL, DistToFront	57.2	34	Tropical and temperate waters

[a] includes Blainville's beaked whale (*Mesoplodon densirostris*), Cuvier's beaked whale (*Ziphius cavirostris*), Gervais' beaked whale (*Mesoplodon europaeus*), Sowerby's beaked whale (*Mesoplodon bidens*), True's beaked whale (*Mesoplodon mirus*) and unidentified *Mesoplodon.*

[b] includes long-finned pilot whale (*Globicephala melas*) and short-fined pilot whale (*Globicephala macrorhynchus*).

[c] includes dwarf sperm whale (*Kogia sima*) and pygmy sperm whale (*Kogia breviceps*).

Predictors: DistToCanyonOrSeamount = distance to the nearest submarine canyon or seamount, SST = sea surface temperature, DistToFront = distance to the nearest sea surface temperature front, CurrentSpeed = absolute current speed, SLAStDev = standard deviation of sea level anomaly, EKE = eddy kinetic energy, CHL = chlorophyll-a concentration, EpiMnkPB = biomass of epipelagic micronekton, EpiMnkPP = production of epipelagic micronekton, PkPB = biomass of zooplankton, PkPP = production of zooplankton. For dynamic predictors, climatological monthly means were used

Figure legends

Figure 1. (a): Map of the North Atlantic basin showing the AFTT study area, line transect surveys included in the analysis and color-coded biomes from Longhurst's classification (2007) (available at http://www.marineregions.org). Longhurst's biogeographical provinces are shown within the study area. 1: Caribbean; 2: North Atlantic tropical gyre; 3: North Atlantic subtropical gyre; 4: Gulf Stream; 5: northwest Atlantic shelves; 6: Atlantic Arctic; 7: boreal polar. Note that the AFTT area excludes territorial waters (<12 nmi from shore) outside of the United States. (b): Map of the North Atlantic basin showing major surface currents.

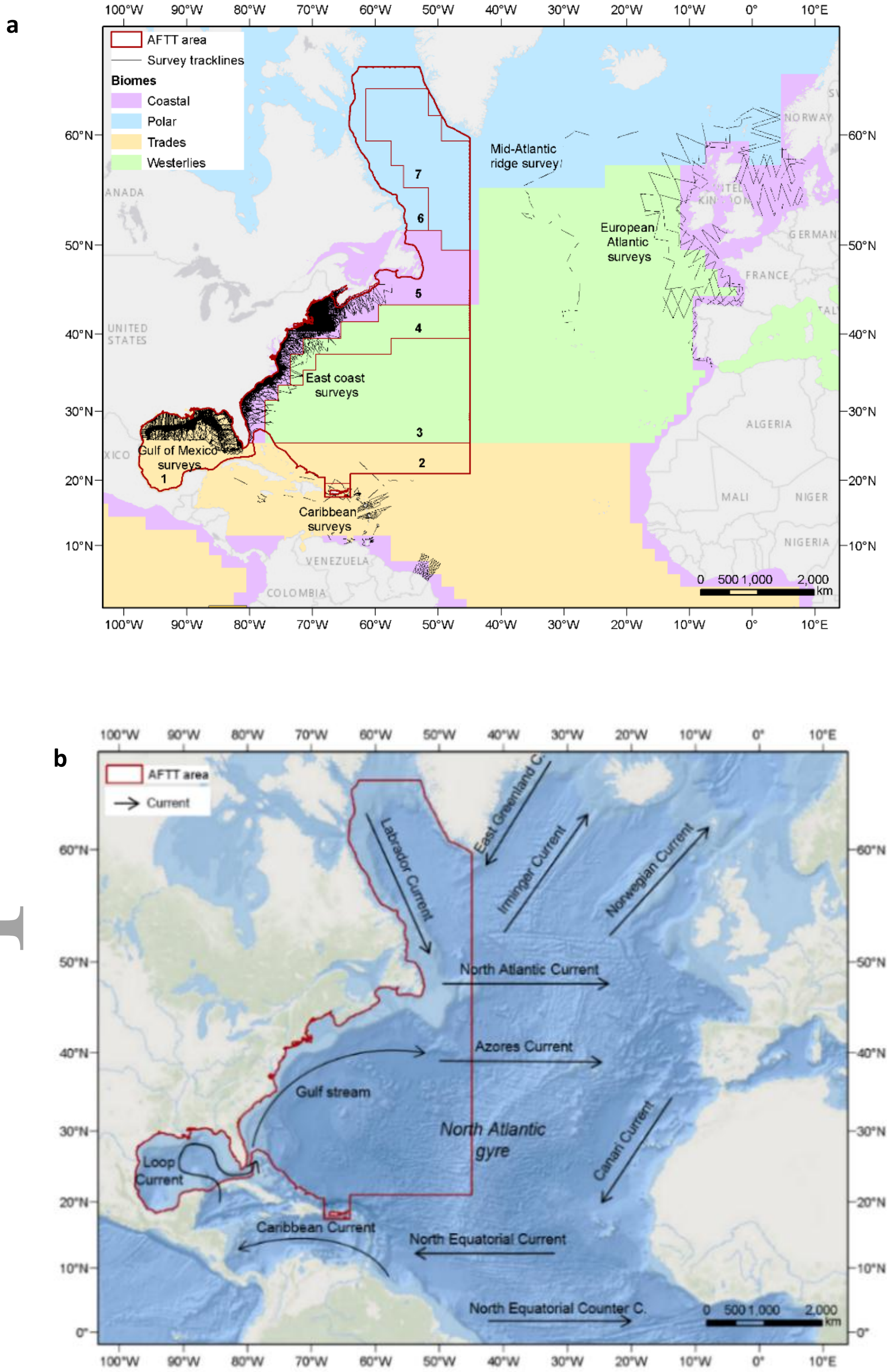
a
AFTT area
Survey tracklines
Biomes
Coastal
Polar
Trades
Westerlies
100°W
90°W
80°W
70°W
60°W
50°W
40°W
30°W
20°W
10°W
0°
10°E
60°N
50°N
40°N
30°N
20°N
10°N
Mid-Atlantic ridge survey
European Atlantic surveys
East coast surveys
Gulf of Mexico surveys
Caribbean surveys
1
2
3
4
5
6
7
NORWAY
UNITED KINGDOM
GERMANY
FRANCE
ALGERIA
MALI
NIGER
NIGERIA
VENEZUELA
COLOMBIA
UNITED STATES
CANADA
MEXICO
0 500 1,000 2,000 km
b
AFTT area
Current
East Greenland C.
Labrador Current
Irminger Current
Norwegian Current
North Atlantic Current
Azores Current
Gulf stream
North Atlantic gyre
Canari Current
Loop Current
Caribbean Current
North Equatorial Current
North Equatorial Counter C.
0°
0 500 1,000 2,000 km

Figure 2. Maps of (a) mean predicted densities (individuals per 100 km^{-2}) and (b) mean CVs from the spatial part of the model for sei whale in summer. The areas where we extrapolated beyond the sampled covariate ranges and predicted densities should be viewed with extreme caution are indicated with black crosshatches. An Albers equal area projection is used.

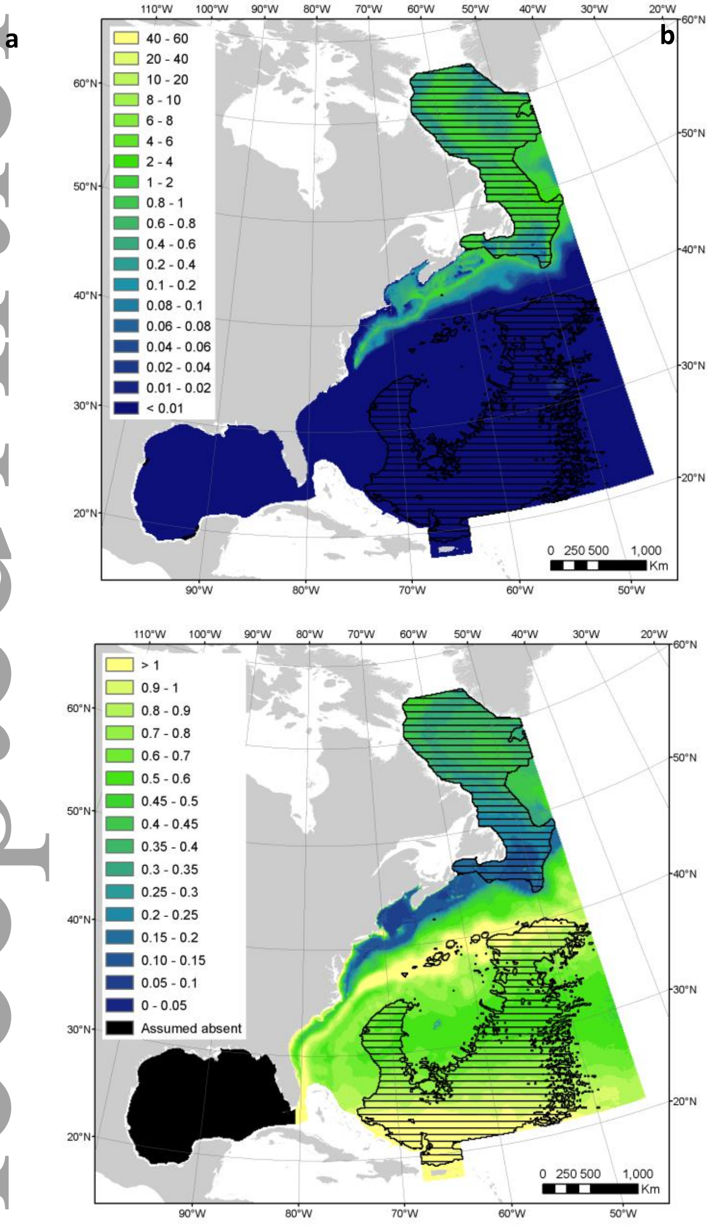

Figure 3. Maps of (a) mean predicted densities (individuals per 100 km^{-2}) and (b) mean CVs from the spatial part of the model for *Kogia spp.* year-round. The areas where we extrapolated beyond the predictor ranges and predicted densities should be viewed with extreme caution are indicated with black crosshatches. An Albers equal area projection is used.

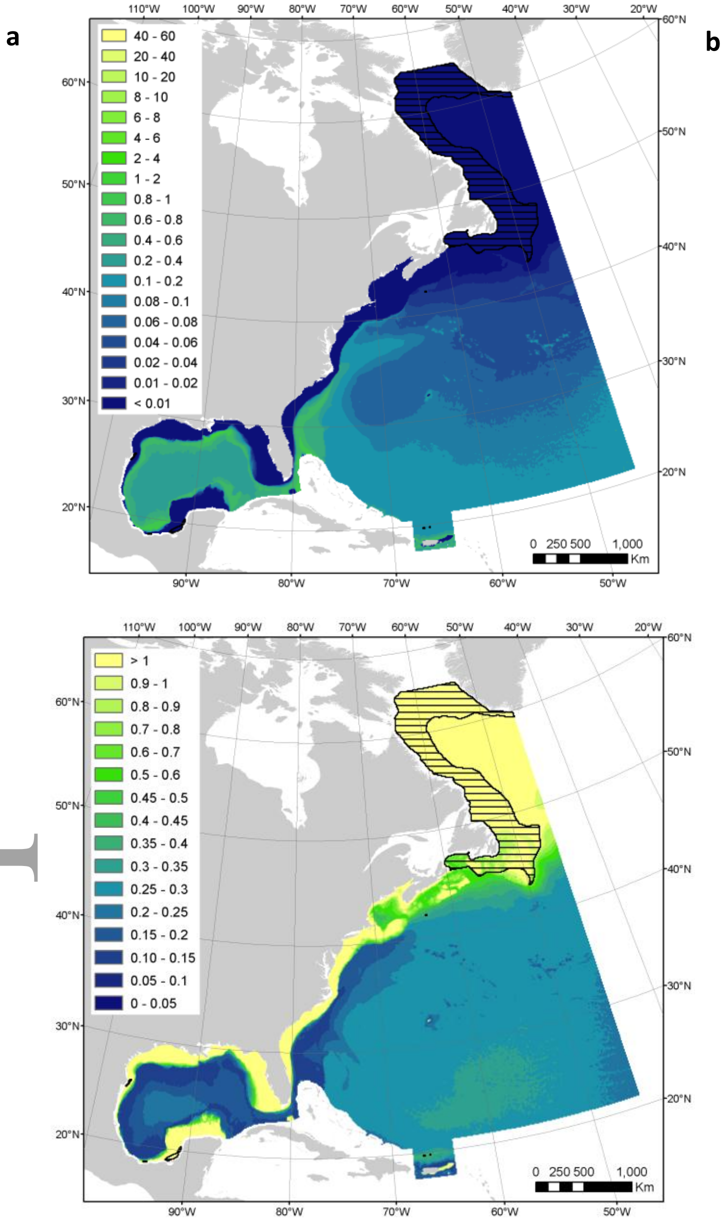

Figure 4. Maps of (a) mean predicted densities (individuals per 100 km^{-2}) and (b) mean CVs from the spatial part of the model for striped dolphin year-round. The areas where we extrapolated beyond the predictor ranges and predicted densities should be viewed with extreme caution are indicated with black crosshatches. An Albers equal area projection is used.