

Estimating Abundance using a Density Spatial Model: The Gulf of Maine Humpback Whale Stock as a Case Study

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1 ABSTRACT

In response to the need for updated abundance estimates and trends, the Northeast Fisheries Science Center (NEFSC) and Southeast Fisheries Science Center (SEFSC) conduct aerial and shipboard line transect abundance surveys in U.S. Atlantic waters. Since 2010, year-round surveys have been carried out under the Atlantic Marine Assessment Program for Protected Species (AMAPPS) project. Historically, abundance estimates for species in Atlantic Stock Assessment Reports were derived using design-based analyses of summer coastwise line transect data. While these coastwise surveys supporting the design-based estimates encompass all U.S. Atlantic waters, in addition to some Canadian and international waters (approximately 1,193,320 km²), data from these surveys may not provide optimal estimates for all cetacean stocks, as many individuals migrate outside the study area following species-specific temporal patterns and some stakeholders require abundance estimates for only portions of the U.S. waters and for only specific short time periods. To address these limitations, spatially-explicit density surface models (DSMs) were used to provide abundance estimates and trends throughout the year and for specific spatial regions, enabling the examination of animal distribution and density across various spatiotemporal scales within the modeled area. This document provides an overview of the field data collection and analytical techniques used for line transect abundance data collected by the AMAPPS shipboard and aerial surveys from 2010 to 2023. It focuses on the application of DSMs using Generalized Additive Models (GAMs) to calculate seasonal abundance estimates and investigate trends. The Gulf of Maine humpback whale serves as a case study. This document also briefly compares these GAM DSM annual Gulf of Maine humpback abundance estimates with those derived from traditional line transect design-based methods and from capture-recapture models based on photo-identification.

2 INTRODUCTION

The [U.S. Marine Mammal Protection Act](#) mandates regular assessments of marine mammal stock status in U.S. waters. To fulfill this, the National Marine Fisheries Service (NMFS, also referred to as [NOAA Fisheries Service](#)) of the National Oceanic and Atmospheric Administration conducts research to estimate population abundance and human-caused mortalities that are summarized in the [U.S. Atlantic and Gulf of Mexico Stock Assessment Reports](#) (referred to as SARs). In response to the need for updated abundance estimates and trends, the Northeast Fisheries Science Center (NEFSC) and Southeast Fisheries Science Center (SEFSC) conducted aerial and shipboard line transect abundance surveys in U.S. Atlantic waters.

Since 2010 these year-round surveys have been carried out under the Atlantic Marine Assessment Program for Protected Species ([AMAPPS](#)) project.

AMAPPS is a collaborative program with the overarching goals of assessing the abundance, distribution, ecology, and behavior of marine mammals, sea turtles, and seabirds throughout the waters off the U.S. Atlantic states, and placing them in an ecosystem context. This information is then accessible for decision-makers and other stakeholders. Collaborating agencies include NMFS, the Bureau of Ocean Energy Management (BOEM) of the Department of the Interior; the U.S. Navy; and the U.S. Fish and Wildlife Service (USFWS) of the Department of the Interior. Comprehensive descriptions of the research results of this program are documented in three reports covering fiscal years FY10-FY14 (Palka et al. 2017), FY15-FY19 (Palka et al. 2021), and FY20-FY25 (Palka et al. in review).

Historically, abundance estimates for species in Atlantic SARs were derived using design-based analyses of line transect data. These data were collected during infrequent, coastwise summer surveys conducted by the NEFSC and SEFSC, with the most recent surveys occurring in 2021, 2016, and 2010. While these coastwise surveys encompass all U.S. Atlantic waters, in addition to some Canadian and international waters (approximately 1,193,320 km²), data from these surveys may not provide the needed estimates for all cetacean stocks. For example, ideally the SARs require an estimate of abundance of the entire stock. However, for some stocks, individuals are outside the study area during the study time period as the animals follow species-specific temporal migration patterns. For instance, some stocks have peak abundance in U.S. waters during seasons other than summer. For example, common dolphins (*Delphinus delphis*) have peak abundance in spring and fall, while fin whales (*Balaenoptera physalus*) and Atlantic white-sided dolphins (*Lagenorhynchus acutus*) peak during winter-spring. Furthermore, abundance for other species, such as the Gulf of Maine humpback whale (*Megaptera novaeangliae*) can vary significantly from summer to summer, even when summer is their peak season in U.S. waters. Additionally, NOAA Fisheries stakeholders, including the U.S. Navy and energy developers, often require abundance data for short specific times outside of summer and in limited areas within U.S. waters.

To address these limitations, spatially-explicit density surface models (DSMs) have emerged as a powerful assessment and management tool. DSMs can provide abundance estimates and trends throughout the year and for specific spatial regions, while accounting for changes in species abundance and habitat shifts over time. These models enable the examination of animal distribution and density across various spatiotemporal scales within the modeled area (for example see the [AMAPPS viewer](#)). These models also provide abundance estimates that can be used in stock assessments. For example, the 2023 U.S. Pacific SARs (Carretta et al. 2024) used abundance estimates derived from DSMs for seven cetacean stocks centralized in Hawaiian waters (Becker et al. 2021; 2022) and eleven cetacean stocks centralized in waters off the Washington to California coast (Becker et al. 2020).

This document provides an overview of the field data collection and analytical techniques used for line transect abundance data collected by the AMAPPS shipboard and aerial surveys from 2010 to 2023. Specifically, it focuses on using Generalized Additive Models (GAMs) to derive DSMs that were then used to calculate seasonal abundance estimates and investigate trends for stock assessments, with the Gulf of Maine humpback whale serving as a case study. Other AMAPPS data collected and analytical techniques to improve species-specific abundance estimates are mentioned with references. This document also briefly compares these GAM DSM Gulf of Maine humpback abundance estimates with those derived from traditional line transect design-based methods and from capture-recapture models based on photo-identification.

In addition to the above finalized summary reports (Palka et al. 2017; 2021; in review), the AMAPPS data were used in publications to generate DSMs employing GAMs and Bayesian hierarchical models. These publications are either currently available or forthcoming:

- Using data from 2010 - 2013, we identified the main environmental covariates related to the abundance of 17 cetacean species/groups in the western North Atlantic Ocean based on GAMs, to establish a current habitat suitability baseline, and to estimate abundance that incorporates habitat characteristics (Chavez-Rosales et al. 2019).
- Using data from 2010 - 2013, we developed a Bayesian hierarchical analysis approach to estimate DSMs of large whales, using fin whales as a case study (Sigourney et al. 2020)
- Using data from 2010 - 2017, we investigated shifts in the core habitats of 16 cetacean species/groups in the western North Atlantic Ocean that demonstrated an average northward shift of 178 km across the study area between 2010 and 2017 (Chavez-Rosales et al. 2022).
- Using data from 2010 - 2017 and an updated Bayesian hierarchical analysis approach, we estimated seasonal shifts in abundance of large whales as well as the probability of exceeding user-defined thresholds in a user-defined region, such as the Massachusetts and Rhode Island wind energy areas (Sigourney et al. in press).
- Using data from 2010 - 2023, and the generalized additive model analysis technique, we estimated DSMs for cetaceans (Palka et al. in review) and sea turtles (Palka et al. in review; Chavez-Rosales et al. in review).
- Other researchers who used the AMAPPS line transect data, in addition to other abundance data, in publications are listed in the summary documents (Palka et al. 2017; 2021; in review).

3 METHODS

3.1 Overview

Spatially- and temporally-explicit density models and maps were based on animal density – environmental statistical models that were fit to visual shipboard and aerial survey line-transect data, associated survey conditions, animal group characteristics, spatially- and temporally-explicit static and dynamic environmental data, and species-specific availability bias correction factors. Density models were developed for single species or species guilds.

In general, visual line transect data from ships and planes may result in incorrect density estimates when visibility biases are not accounted for. There are three types of visibility bias that we accounted for:

- Perception bias (due to animals that were available to be detected but were missed because of a variety of other reasons, such as distance from the platform or poor sighting conditions due to sun glare or sea state). Two-team visual line-transect data were used to address perception bias.
- Availability bias (due to animals that were missed because they were submerged and thus not available to be detected). Ancillary dive time data were used to address availability bias.
- Ambiguous species identification bias (due to the inability of the field observers to positively identify the species of a group of animals to a specific species, but instead only able to identify that the animals were one of several species (such as a fin or sei whale, or a beaked whale) or were one of many species (such as unidentified whale or unidentified dolphin)). Ambiguous species were separated to specific species using several different statistical methods (binomial logistic regression based on sightings of fin and sei whales (Palka et al. 2017) or genetic analyses based on pilot whales (Garrison and Rosel 2017) and bottlenose dolphins (Garrison and

Aichinger Dias 2024); discriminant analysis based on locations of passive acoustically detected beaked whales (Palka et al. in review); and hierarchical clustering and principal component analysis based on sightings of turtles (Chavez-Rosales et al. in review)).

The general work flow we used to estimate abundance of all cetacean and sea turtles is as follows. This paper focuses on the estimation methods of cetaceans using GAM techniques to estimate density-habitat models, where humpback whales were used as an example. Steps highlighted and denoted with a * are described in this paper, while all steps are detailed in Palka et al. (in review).

1. Data collection
 - a. *Conduct line transect surveys on ships and planes to collect visual and passive acoustic detections and collect data on the abiotic and biotic habitat characteristics.
 - b. *Collate concurrent environmental habitat data from satellite and ocean data assimilation derived sources.
2. Prepare data
 - a. *Conduct quality control checks on all data types.
 - b. Process passive acoustic data collected concurrently with visual data on shipboard abundance surveys.
 - c. *Define the spatiotemporal strata: 10x10 km² and 8-day intervals starting with 4 Jan 2010.
 - d. *Merge environmental habitat data with the line transect data by spatiotemporal strata with oblique Mercator grid cells using primarily bilinear interpolation (“spatially synced”).
3. Conduct supportive analyses
 - a. *Estimate a species-platform specific availability bias correction factor using information on the average surface and dive times derived from data collected from individual animals deployed with time-depth tags, group sizes, and viewing area from the platform.
 - b. Separate ambiguous species identifications of visual sightings into separate species.
 - c. Build acoustic classifiers to detect passive acoustic clicks.
4. Estimate species-specific abundance
 - a. Using only visual data
 - i. Estimate design-based bias-corrected species-specific abundance from the summer 2021 shipboard and aerial visual surveys that we reported in the Atlantic Marine Mammal Stock Assessment Report.
 - ii. *Estimate bias-corrected species-specific abundance using generalized additive models based on the 2010-2023 shipboard and aerial visual data.
 - iii. Estimate bias-corrected large whale species-specific abundance using Bayesian hierarchical models based on the 2010-2023 shipboard and aerial visual data.
 - b. Using only passive acoustic data
 - i. Estimate subsurface abundance estimate of acoustically active foraging sperm whales using passive acoustically detected events from the shipboard summer 2016 and 2021 towed hydrophone array data and design-based distance sampling analysis methods (2016 data published in Westell et al. (2022)).
 - ii. Estimate subsurface abundance of vocalizing beaked whales using passive acoustically detected events for the shipboard summer 2013, 2016, and 2021 towed hydrophone array data and design-based distance sampling analysis methods.
 - c. Integrating visual and passive acoustic data
 - i. Estimate bias-corrected abundance of beaked whales throughout the water column by combining model-based surface abundance estimates using visual

- data and design-based subsurface abundance estimates using passive acoustic data.
- ii. Estimate bias-corrected abundance of sperm whales throughout the water column by integrating visual and towed array passive acoustic data that were collected simultaneously and analyzed using a new method that combines a capture mark-recapture approach with a distance sampling analysis to estimate abundance and surface availability while accounting for transition probabilities among surfacing and diving states (Sigourney et al. 2023).

Focusing on estimating bias-corrected species-specific abundance using GAMs based on the 2010-2023 shipboard and aerial visual data the work flow was as follows:

1. Estimate species- and platform-specific ocean surface density estimates accounting for perception bias for each species (or species guild) within each spatial-temporal cell that had survey effort using Distance analysis techniques. There were four platforms (northeast (NE) ship, NE plane, southeast (SE) ship and SE plane), where NE surveys were conducted by the NEFSC and SE surveys were conducted by the SEFSC. The Distance analysis techniques that accounted for perception bias involved the estimation of a detection function, and $p(0)$ - the probability of detecting a group on the track line – using significant survey related covariates (such as, sighting conditions, group size, and animal behavior, etc.) and line transect data collected by two-independent visual teams on a ship or plane.
2. Estimate the bias-corrected density estimates that account for availability and perception bias for each spatial-temporal cell that had survey effort by applying the species-platform specific availability bias correction factor to the species-platform ocean surface density estimate that accounted for perception bias.
3. Develop an animal density-habitat GAM model using data from each spatial-temporal cell that had survey effort where several goodness-of-fit tests were used to choose the best fitting model of the relationship between the cell's bias-corrected density and associated contemporaneous static and dynamic environmental variables.
4. Predict animal density and the associated measures of uncertainty for all spatial-temporal cells using the GAM modeled animal density-habitat relationship and corresponding contemporaneous environmental values.
5. Calculate seasonal mean density and associated measures of uncertainty for areas of interest. Seasonal definitions are spring is March to May; summer is June to August; fall is September to November; and winter is December to February.
6. Calculate the core habitat of a species.
7. Present the results using maps showing spatially-explicit densities and their associated uncertainty measures, as well as trend lines for abundance and related uncertainties.

3.2 Study area

The study area extended from Halifax, Nova Scotia, Canada to the southern tip of Florida, encompassing Atlantic waters from the coastline to slightly beyond the outer boundary of the U.S. exclusive economic zone, covering approximately 1,193,320 km². (**Figure 1**).

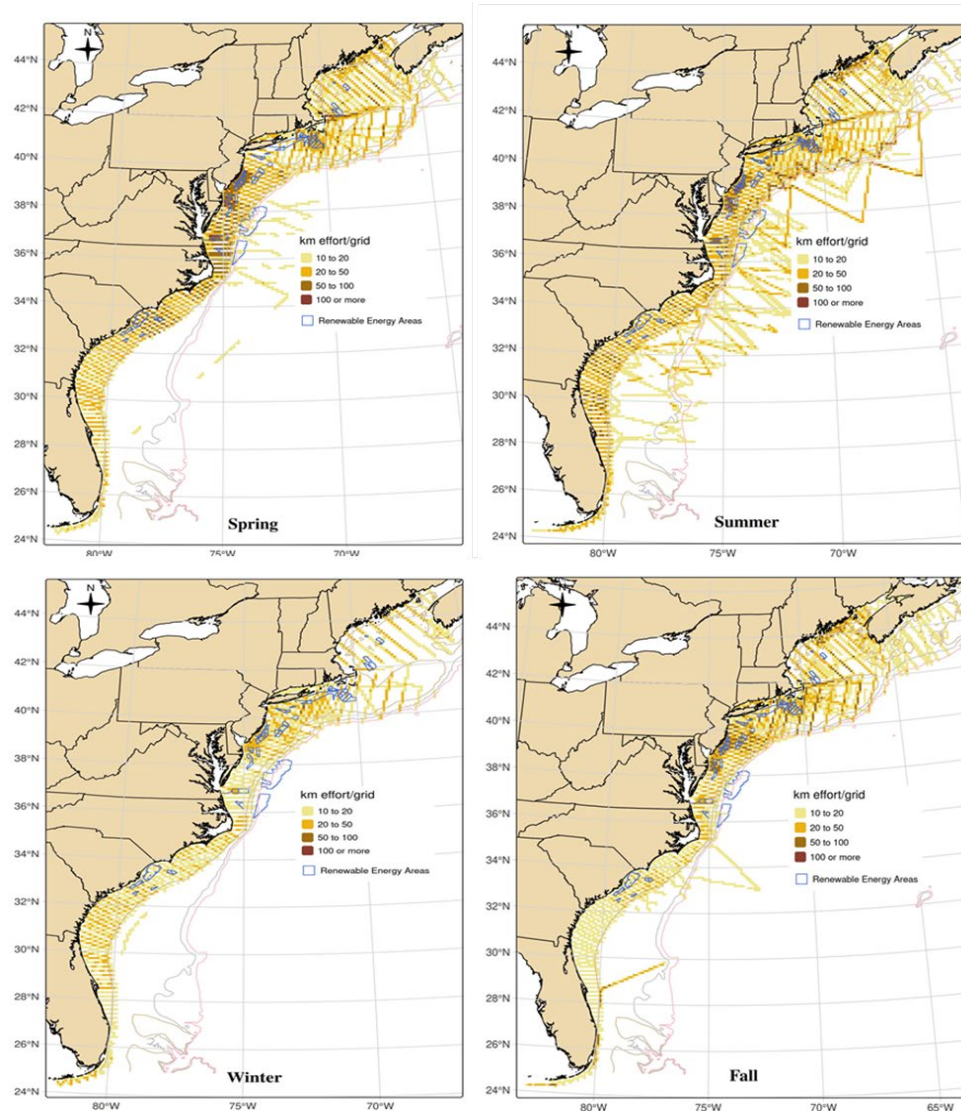


Figure 1. Visual effort by grid cell and season during 2010-2025

Spring is March to May; summer is June to August; fall is September to November; and winter is December to February. Grid cells are 10 km x 10 km.

3.3 Line transect data

Line-transect survey data were collected during 14 aerial and shipboard surveys conducted during 2010 – 2023 (**Figure 1**). Aerial surveys were generally conducted over continental shelf waters (out to the 200 to 2000 m depth contours, depending on the region) during all seasons. Shipboard surveys were generally conducted in deeper waters (farther offshore, deeper than the 100 m depth contour) and mostly in the summer. Adhering to standard line transect procedures, the track lines were strategically positioned to systematically cover the survey area, starting from a random point within each stratum. The survey track lines were covered multiple times in different seasons and years.

Aerial surveys were aboard a DeHavilland Twin Otter DHC-6 flying at 183 m (600 ft) above the water surface at about 200 kph (100 kts). In addition to two pilots on board the plane, six scientists operated as

two independent observation teams. The forward team consisted of two observers stationed in bubble windows on each side of the plane and one recorder. The back team consisted of two observers, one stationed in a rear side bubble window and one in a belly window, and one recorder. Weather and effort data were recorded at the beginning of each leg or when conditions changed. The sightings data were collected for all observed turtles, mammals, and some fish species.

Shipboard surveys were aboard NOAA research vessels, mostly the NOAA ships *Henry B. Bigelow* and *Gordon Gunter*. On each ship two teams of observers were independently visually searching for cetaceans, seals, turtles and some fish species. Each team consisted of two observers using high powered binoculars (25x150). In addition, at least one person recorded data and surveyed using the naked eye when not recording data. Weather and effort data were recorded at the beginning of each leg or when conditions changed. The sightings data were collected for all observed turtles, mammals, and some fish species.

During the two-independent team sighting surveys on either the plane or ship, there were times when only one team detected a group of animals, while at other times both teams detected the same group of animals. We determined the animal groups that both teams detected (termed a duplicate sighting) by investigating the times and locations of the sightings. This determination was done in real-time and after the survey during the data quality checking stage.

3.4 Environmental habitat data

Environmental covariate characteristics, both static and dynamic, within the study area were aggregated from various sources (**Table 1**), as described in Palka et al. (2017), Palka et al. (2021), and Palka et al. (in review). We obtained the environmental covariates from four main sources:

- The ETOPO 11 Arc-Minute Global Relief Model (Amante and Eakin 2009);
- Daily level 3 mapped (4 km resolution, sinusoidally projected) satellite ocean color data from the European Space Agency's Ocean Colour Climate Change Initiative (OC-CCI; version 6.0) (Sathyendranath et al., 2019, Sathyendranath et al, 2023) and GlobColour Project (Maritorena et al., 2010);
- Global U.S. Navy HYCOM + Navy Coupled Ocean Data Assimilation prediction system as available through the HYCOM consortium at <https://www.hycom.org/>
- The Gulf Stream location data available from [the Naval Oceanographic Office's website](#).

Environmental covariate data were partitioned into the 10x10 km grid cells and 8-day time intervals, starting with Jan 4, 2010. Furthermore, average sea state and glare conditions encountered during the line transect surveys within each spatiotemporal cell were incorporated as continuous potential predictor variables to adjust the probability of detecting a sighting along the surveyed track lines as described in Chavez-Rosales et al (2022). These data were stored in stacked rasters in annual raster bricks.

If values of an environmental variable within the AMAPPS study area were missing, a hierarchical spatial-temporal interpolation approach was used to replace missing values. This approach first filled in a missing value using the calculated mean from the nearest-neighbor cells from the same time period that contained non-missing data. Then, if that was not sufficient, the missing value was calculated from the mean value for the grid cell of interest for the 8-day time period before and after. This process provided enough information of the seasonal tendency, without compromising the overall quality of the data.

Table 1. Contemporaneous habitat covariates included in the density-habitat models

Covariate	Description	Original Resolution
SSTMUR	SST multi-scale ultra-high resolution	1 km mapped to 2 km
SSTF	Strength of SST fronts	1 km mapped to 2 km
CHLA	Chlorophyll-a concentration	1 km mapped to 2 km
CHLF	Strength of chlorophyll fronts	1 km mapped to 2 km
PIC	Particulate inorganic carbon	1 km mapped to 2 km
POC	Particulate organic carbon	1 km mapped to 2 km
PP	Primary productivity	1 km mapped to 2 km
SLA	Sea Surface Height Anomaly	1/4°
MLD	Mixed layer depth, depth	1/12°
MLP	Mixed layer thickness	1/12°
SALINITY	Surface salinity	1/12°
BTEMP	Bottom temperature	1/12°
DGSNW	Distance to the Gulf Stream north wall	meters
DGSSW	Distance to the Gulf Stream south wall	meters
Depth	Depth	3 arc-sec
Dist2shore	Distance to coastline	0.04°
Slope	Seafloor slope	3 arc-sec
Dist200	Distance to the 200 m isobath/contour	meters
Dist125	Distance to the 125 m isobath/contour	meters
Dist1000	Distance to the 1000 m isobath/contour	meters
Lat	Latitude	
LY	8-day year layer	

3.5 Summary of analysis methods to estimate abundance

We applied a two-stage DSM framework to estimate seasonal density from line-transect surveys conducted between 2010 and 2023.

In stage one, using MRDS analysis techniques, detection functions were fitted to estimate distance-based detection probabilities that were then used to estimate the at-surface density corrected for perception bias (d_s) for surveyed spatiotemporal cells. To estimate the total density (D) in a surveyed cell that includes animals both at and below the ocean's surface, the estimated at-surface density was adjusted with a corresponding availability bias correction factor (a): $D = d_s/a$.

The availability bias correction factor was defined as the average probability of an animal being at the surface and available for detection. For cetacean species, the species-specific availability bias correction factors (**Table A1**) were estimated using a two-state continuous Markov process based on Laake et al. (1997) and explained in Palka et al. (2017) and in **Appendix A**.

In stage two, the density estimates corrected for perception and availability bias within surveyed spatiotemporal cells (from stage one) were modeled as a function of contemporaneous static and dynamic environmental covariates and then used to predict density across the study area. This approach leverages habitat relationships to improve spatial prediction and can yield unbiased abundance estimates even when survey design is not fully randomized (Hammond et al. 2021).

3.6 Stage one: Mark-recapture distance sampling

The first stage estimated species (or species guild)-specific detection probabilities from surveys conducted in Beaufort sea states 0–4 (Palka 1996; Palka 2012; Barlow et al. 2001) using an independent observer configuration assuming point independence (Laake and Borchers 2004). Mark-recapture distance sampling (MRDS; Thomas et al. 2010) with a Horvitz–Thompson-type estimator (Borchers et al. 2006) was applied, eliminating the need to model group size separately.

Detection models derived for the shipboard and aerial survey data applied right- and left-truncated distances when needed (Buckland et al. 2001). Covariates were selected following Marques & Buckland (2003) and Laake & Borchers (2004). Goodness-of-fit was evaluated using χ^2 and Cramér–von Mises tests and visual diagnostics.

Data from each survey platform were analyzed independently to account for differences in observers, methods, and habitats.

3.6.1 Aerial survey

Aerial surveys followed a two-step approach (Palka 2020; 2023; Garrison 2020; Garrison & Aichinger Dias 2023) to address minor imbalances in coverage between observer teams and to estimate $p(0)$. Because of the physical limitations within the plane, the front and back teams could not search the exact same patch of water. The front team had full viewing coverage: from the horizon on the right side of the plane (90°), down to directly under the plane (on the track line; 0°), then over to the horizon on the left side of the plane (90°). The back team had limited viewing coverage: from the horizon on the right side of the plane, down under the plane through the track line, then over to about 35° from the track line on the left side of the plane.

To account for this asymmetry, the first step involved using both team's mark-recapture data (perpendicular distances and covariates) collected only from the area both teams could search to fit conditional distance sampling detection functions, based on full independence at distance zero (MRDS method = "io.fi"). This results in estimates of species (or species guild)-specific $p(0)$.

The second step used data only from the primary team in a standard single team multiple covariate distance sampling (MCDS) analysis to estimate species (or species guild)-specific densities that were then expanded by the corresponding estimate of $p(0)$ for the primary team (as estimated in the first step).

The primary team was the team that collected data resulting in the typically shaped detection function declining monotonically from the trackline. In most cases, the primary team was the front team.

3.6.2 Shipboard survey

The shipboard species (species guild)-specific density estimates accounting for perception bias were based on the independent observer approach assuming point independence (Laake and Borchers 2004) by using the mark-recapture distance sampling packages (MRDS; Laake et al. 2022) within R. This MRDS analysis method, based on the numbers of groups, size of the groups, and associated covariates, estimated the sighting probability on the trackline that implicitly includes the estimation of $p(0)$. The probability of sighting a particular group was the product of two components. The first probability component was the distance sampling (DS) component that corresponded to the standard unconditional detection function. This component was the probability of one or more observer teams detecting the group of animals, given the perpendicular distance and possibly covariate values. The probability of detection declined with increasing distance from the trackline following a known functional form (half-normal or hazard function). The second probability component was the mark-recapture (MR) component that was a conditional detection function. This component was the probability of a team detecting the animal group, given the other team detected it, and given the perpendicular distance and covariate values. The MR component resulted in a probability likelihood of detection on the trackline, which was modeled by a logistic regression approach and the "capture histories" of each sighting (i.e., seen by one or both teams). Laake and Borchers (2004) detailed the derivation, assumptions, and implementation of this estimation approach.

Detection models derived for these shipboard data applied right- and left-truncated distances when needed (Buckland et al. 2001). Covariates were selected following Marques & Buckland (2003) and Laake &

Borchers (2004). Goodness-of-fit was evaluated using χ^2 and Cramér–von Mises tests and visual diagnostics.

3.7 Stage two: Density modeling analysis

The second stage of the density surface modeling followed the same approach described in Chavez-Rosales et al (2019). Density estimates in the surveyed cells (from the first stage) were modeled as a function of contemporaneous environmental variables using GAMs in R (v4.5.1) with the mgcv package (v1.9-3).

Models were fitted using restricted maximum likelihood and assumed an overdispersed Tweedie distribution (Miller et al. 2013). Thin plate regression splines with shrinkage and null space penalization were applied, and smooth terms were limited to a maximum of six degrees of freedom to reduce overfitting and then examined to confirm appropriateness.

Since the focus was on documenting temporal trends and interannual variability in the number of animals within the study area, we prioritized dynamic variables over static ones. Additionally, to account for potential changes over time in the relationship between density and environmental covariates, we examined whether interactions between each environmental covariate and the temporal layer (defined as the combination of year and 8-day period) were significant. The spatiotemporal interaction term was assessed independently by fitting a null model and testing combinations of year and 8-day period (LY) with each dynamic environmental covariate. Candidate interaction combinations were selected based on the proportion of deviance explained. Then additional significant habitat covariates were determined by variable selection of all the covariates using automatic term selection (Marra and Wood 2011), and further supported by six diagnostic tests (**Table 2**), as described in Kinlan et al. (2012) and Barlow et al. (2009). Models were selected based on lowest prediction error and highest explained deviance.

Table 2. Diagnostic tests and criteria used to evaluate density-habitat model performance

Test	Description	Criteria	Calculated From	Formula
DE	Percentage of deviance explained from the model	Higher value	GAM model	
R ²	Coefficient of determination from the model	Higher value	GAM model	
RHO	Spearman's rank correlation	Higher value	None-zero data. 1) Initial testing and; 2) k-fold cross-validation.	
ASPE	Mean square prediction error	Lower value	All data. 1) Initial testing and; 2) k-fold cross-validation	$\sum \frac{(observed - predicted)^2}{n}$
MAPE	Mean absolute percentage error	Lower value	None-zero data. 1) Initial testing and; 2) k-fold cross-validation	$\frac{1}{n} \sum_{i=1}^n \left \frac{observed - predicted}{observed} \right * 100$
MAE	Mean absolute error	Lower value	All data. 1) Initial testing and; 2) k-fold cross-validation.	$\frac{1}{n} \sum_{i=1}^n observed - predicted $

Seasonal density maps were generated using the most parsimonious species-specific models. These models also allowed for the estimation of seasonal and annual abundance across the study area from 2010 to 2023, which facilitated the evaluation of temporal trends.

3.8 Uncertainty assessment

Several aspects contributed to the uncertainty in the point abundance estimate. Key sources of uncertainty arise from both stages of the analytical framework. In Stage One, uncertainty is introduced through the estimation of detection probabilities and resulting density estimates within surveyed areas, including corrections for both perception bias and availability bias. These corrections rely on model-based assumptions and estimated parameters, each of which carries its own variability. In Stage Two, additional uncertainty is introduced through the GAM density-habitat model, where smoothing parameters and functional relationships between covariates and density are estimated from the data and are therefore subject to sampling variability.

However, it is important to note that, at this time, the reported uncertainty estimates are incomplete, as they incorporate only the uncertainty associated with the GAM parameter estimates from Stage Two. They do not yet propagate uncertainty from Stage One detection and density estimation processes. As a result, the overall variance associated with the final point estimate is likely underestimated, and future work should aim to integrate uncertainty across both stages to provide a more comprehensive assessment of precision.

3.9 Core habitat determination

Defining the core habitat of a species is one way to visualize seasonal variability patterns. In this analysis, core habitat was defined as the area comprising grid cells with the upper 20% of predicted abundance values from the model fits in a seasonal scale.

Following the selection of the species-specific density-habitat models, the models were used to generate habitat suitability maps using QGIS. It was assumed that habitat suitability was correlated with the species' abundance in relation to the unique combination of environmental predictors included in their habitat model. That is, in times and regions with high estimated abundance it was assumed that the corresponding habitat was more suitable for the species. Thus, a species habitat suitability index for a year-season in a spatial grid cell (HS) was defined as: $HS = \sum_i^n \hat{N}_i$ where $\hat{N}_i$ was the estimated abundance from each 8-day time period (i) within the target year-season-grid cell from the species-specific model (Chavez-Rosales et al. 2019).

4 RESULTS

4.1 Survey effort

The density spatial models were constructed using data collected from approximately 417,000 km of on-effort track lines during AMAPPS shipboard and aerial surveys conducted between 2010 and 2023 (Table 3). These surveys detected 504 humpback whale groups, totaling 728 individuals (Table 4; Figure 2). Overall, the surveys detected nearly 12,400 groups of cetaceans (over 145,600 individuals) and more than 7,710 groups of sea turtles (nearly 8,840 individuals) (Tables B1 and B2).

Table 3. On-effort track line effort (km) from 2010 – 2023 by season and platform
Survey effort used in the species density-habitat models.

Platform	Spring	Summer	Fall	Winter	TOTAL
NE Shipboard	8,883	49,064	0	0	57,947
NE Aerial	38,839	52,003	87,311	24,747	202,900
SE Shipboard	2,604	18,331	2,673	302	23,910
SE Aerial	48,634	43,285	21,153	19,151	132,223
TOTAL	98,960	162,683	111,137	44,200	416,980

Table 4. Numbers of groups and individuals of humpback whales detected by season

Platform	Spring	Summer	Fall	Winter	TOTAL
Number of groups	283	123	89	9	504
Number of individuals	406	187	126	9	728

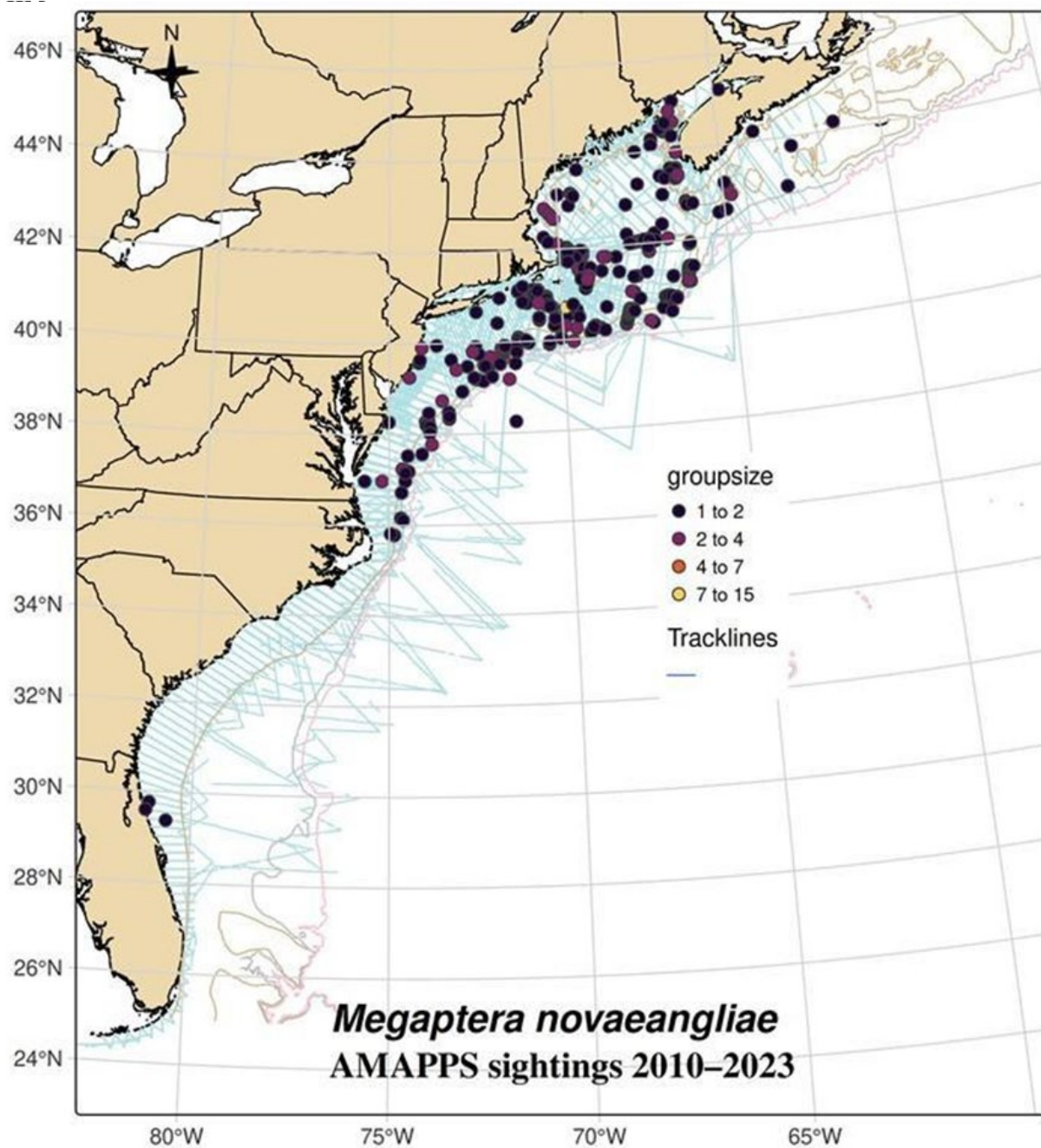


Figure 2. Distribution of track lines and humpback whale sightings 2010 to 2023

Tan, gray, and pink lines indicate the 100, 1,000 and 2,000 m depth contours.

4.2 Stage One: Mark-recapture distance sampling

The MRDS models, used to estimate perception bias-corrected densities for humpback whales and other species within surveyed spatiotemporal cells, showed a good fit to the data. This conclusion was supported by the Cramér–von Mises goodness-of-fit tests, Q-Q plots, and visual examination of the predicted versus observed detection functions (Table 6; Figure 3).

The most frequent significant covariates across all species in the distance sampling component of the detection functions were Beaufort sea state and/or glare magnitude (**Figures B1-B4**). For the mark-recapture component models, Beaufort sea state and group size were frequently significant covariates. Additionally, the observer team was a significant covariate at times in the mark-recapture component models, suggesting that team composition or observer position influenced the shape of the detection function (**Figures B1-B4**).

Table 6. Intermediate parameters in humpback whale from Stage One analysis

Derived from the mark-recapture (MR) distance sampling (DS) models. HR = hazard rate model. CvM = Cramér–von Mises goodness-of-fit test

Analysis Set	MR Model	MR Truncation (m)	DS Model	DS Truncation (m)	Key function	$p(0)$	$p(0)$ CV	CvM p-value
SE–aerial group 4	distance + observer + subjective + glare	550	distance+quality	550	HR	0.86	0.08	0.93
NE–aerial group 3	distance + seastate	900	distance + sea state + glare	900	HR	0.66	0.07	0.96
NE–ship group 8	distance * observer + time of day	10,000	distance + sea state + swell height	10,000	HR	0.39	0.17	0.99
SE–ship group 5	distance + group size	9000	distance + glare	9000	HR	0.58	0.11	0.61

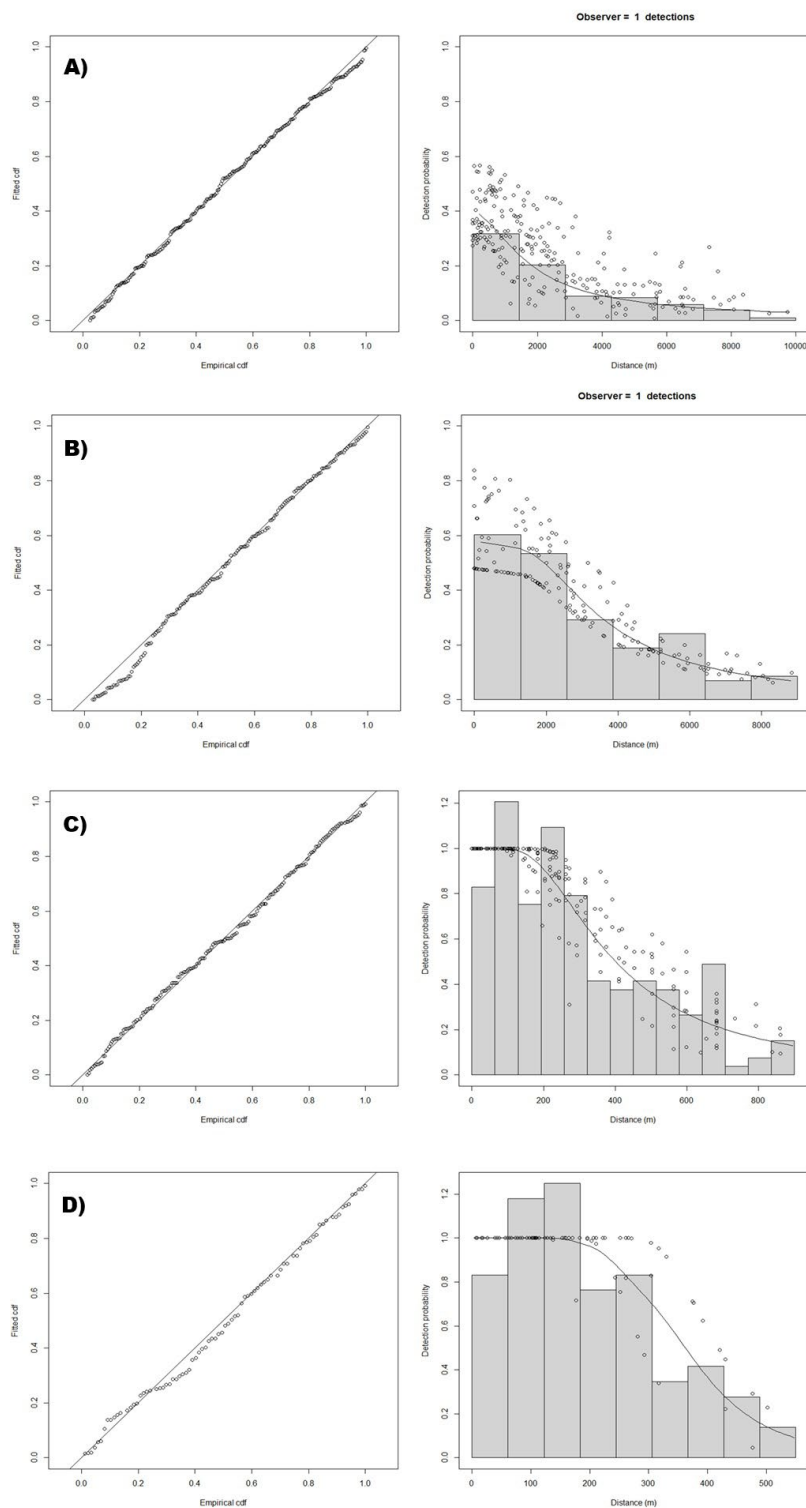


Figure 3. Q-Q plots and detection functions from the MRDS analyses

A) NE-shipboard analysis set 8; B) SE-shipboard analysis set 5; C) NE-aerial analysis set 3; D) SE-aerial analysis set 4.

4.3 Stage two: Density modeling analysis

The humpback whale GAM model successfully accounted for approximately 47% of the variation in density estimates that were corrected for both perception and availability bias. Four additional diagnostic tests further validated that the model provided a good fit to the data (**Table 7**). The term (LY, lat) in the model was the most influential factor, and represented a flexible spatiotemporal interaction, allowing the effect of time to vary across latitude and capturing changes in spatial distribution patterns over time. Other important contributors included mixed layer thickness (mlp), distance to the north wall of the Gulf Stream, and bottom temperature (**Table 8; Figure 4**).

Table 7. Results of diagnostic tests to evaluate fit of density-habitat GAM models

Diagnostic tests are the Spearman's rank correlation (RHO), mean absolute percentage error (MAPE) and mean absolute error (MAE). See **Table 2** for more details on the tests.

Species	Non-Zero RHO ¹	Non-Zero MAPE	Random RHO	Random MAE
Humpback whale	0.48	92.37	0.11	0.00166

¹ Color coding is:

RHO:	Poor= $x < 0.05$	Fair to good = $0.05 \leq x < 0.3$	Excellent= $x > 0.3$
MAPE:	Poor= $x > 150\%$	Fair to good= $150\% \geq x > 50\%$	Excellent= $x \leq 50\%$
MAE:	Poor= $x > 1$	Fair to good = $1 \geq x > 0.25$	Excellent= $x \leq 0.25$

Table 8. 2010 to 2023 density-habitat model output for humpback whales

TERM	edf	Ref.df	F	p-value	C.dev
s(sstmur)	3.72	5	7.18	<2e-16	1.75
s(btemp)	3.26	5	10.24	<2e-16	5.34
s(dist1000)	4.39	5	12.25	<2e-16	4.73
s(mlp)	3.32	5	14.76	<2e-16	5.88
s(dist2GSNw)	4.18	5	9.87	<2e-16	5.51
te(LY, latdd)	15.91	24	8.54	<2e-16	23.5

Adjusted $R^2 = 0.0204$; Deviance explained = 46.7%; REML = 976.24; Scale est. = 1.2097; n = 35,550. Includes the estimated degrees of freedom (edf), reference degrees of freedom (Ref.df), and contribution to the deviance (C.dev) explained for each habitat covariate and its associated p-value.

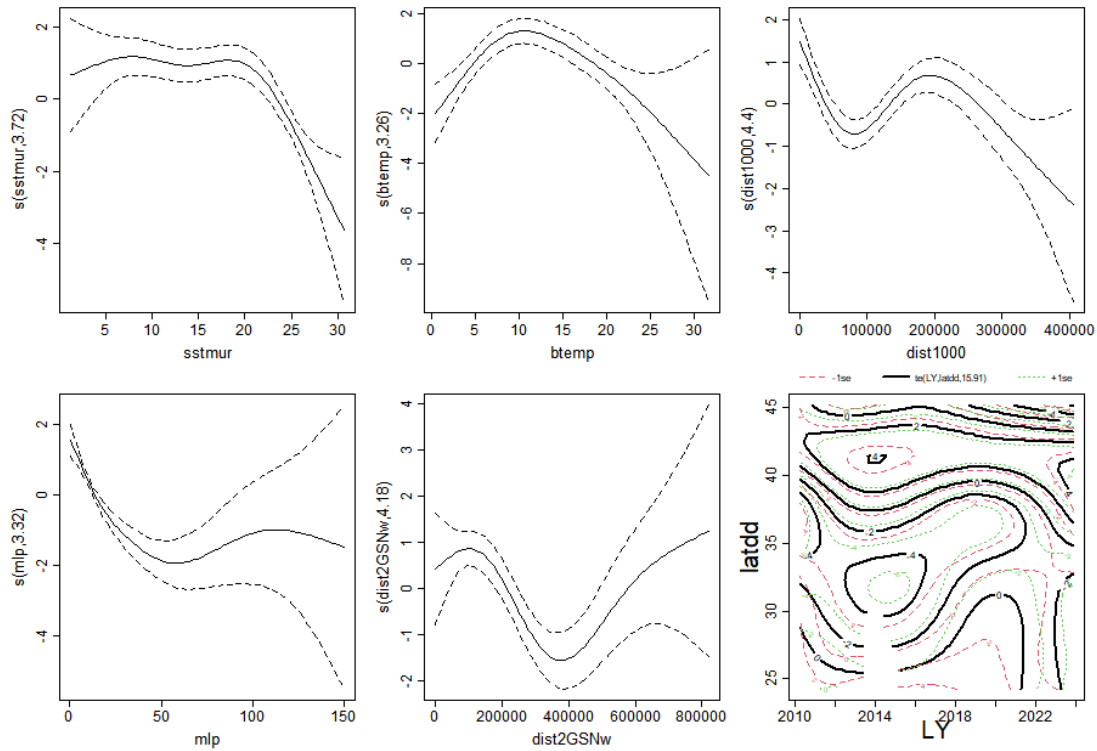


Figure 4. Humpback whale density relative to significant habitat covariates

Plots represent the partial smooths and interaction terms of the density-habitat model.

4.4 Abundance trends

Humpback whale abundance in the AMAPPS study area fluctuated across different seasons and years (Tables 9-10; Figures 5-7). Peak densities of humpbacks occur in the summer (Jun - Aug) with the least in the winter (Dec - Feb; Table 9; Figure 5).

Sightings of humpbacks in U.S. waters occurred year-round; although the humpback whale distribution varied seasonally in U.S. waters (Figures 8-11). Averaging over the 2010–2023 period, during spring (Figure 8) and fall (Figure 10), the animals were dispersed between Cape Hatteras, NC, and Cape Cod, MA, with lower densities further north and south. In an average summer (Figure 9), humpbacks were predominantly found north of Cape Hatteras, NC, with a sharp higher density located on the shelf break, extending from the southern edge of Georges Bank to the Gulf of Maine. Conversely, average winter densities (Figure 11) were low in U.S. waters, with more animals located south of North Carolina compared to the rest of the year.

Humpback whale abundance patterns in the AMAPPS study area also varied by year (Table 10; Figures 5-7). There were fewer humpbacks in U.S. waters during 2017 - 2021, with summer having the largest interannual change, where the peak abundance was about 1500 animals during 2013 – 2015 and then again in 2023 (Table 10; Figure 7).

4.5 Core habitat trends

The seasonal core habitats clearly show spatial interannual changes that occurred during 2010 to 2023 (Figures 12-15). Across all seasons, the core habitat shifted southward over this period. Specifically,

there was increased use of waters from New York to Delaware in 2023 compared to 2010. Additionally, a southern extension into waters off Virginia is apparent during the winter season.

Table 9. Humpback whale seasonal abundance estimates and confidence intervals (CI)
Averaged over 2010 – 2023.

Season	Abundance	CV	CI 2.5%	CI 97.5%
Spring (Mar-May)	447	0.49	180	1,110
Summer (Jun-Aug)	960	0.43	428	2,152
Fall (Sep-Nov)	384	0.46	163	906
Winter (Dec-Feb)	150	0.59	55	467

Table 10. Humpback whale abundance and CV by season and year
For the 2010 – 2023 period in the AMAPPS study area.

Year	Spring Abun	Spring CV	Summer Abun	Summer CV	Fall Abun	Fall CV	Winter Abun	Winter CV
2010	124	0.88	262	0.59	131	0.61	40	1.10
2011	170	0.50	554	0.42	306	0.47	77	0.56
2012	638	0.39	1208	0.40	479	0.42	188	0.49
2013	667	0.47	1596	0.44	612	0.44	239	0.50
2014	781	0.50	1689	0.42	628	0.47	260	0.57
2015	659	0.47	1619	0.40	443	0.42	236	0.61
2016	572	0.44	1385	0.37	464	0.40	165	0.55
2017	316	0.46	808	0.38	435	0.42	137	0.63
2018	219	0.43	505	0.38	189	0.41	69	0.64
2019	287	0.47	524	0.48	151	0.45	67	0.70
2020	231	0.51	433	0.44	213	0.45	79	0.60
2021	316	0.45	521	0.41	216	0.42	109	0.56
2022	430	0.46	819	0.43	396	0.47	198	0.57
2023	847	0.60	1510	0.57	713	0.64	364	0.70

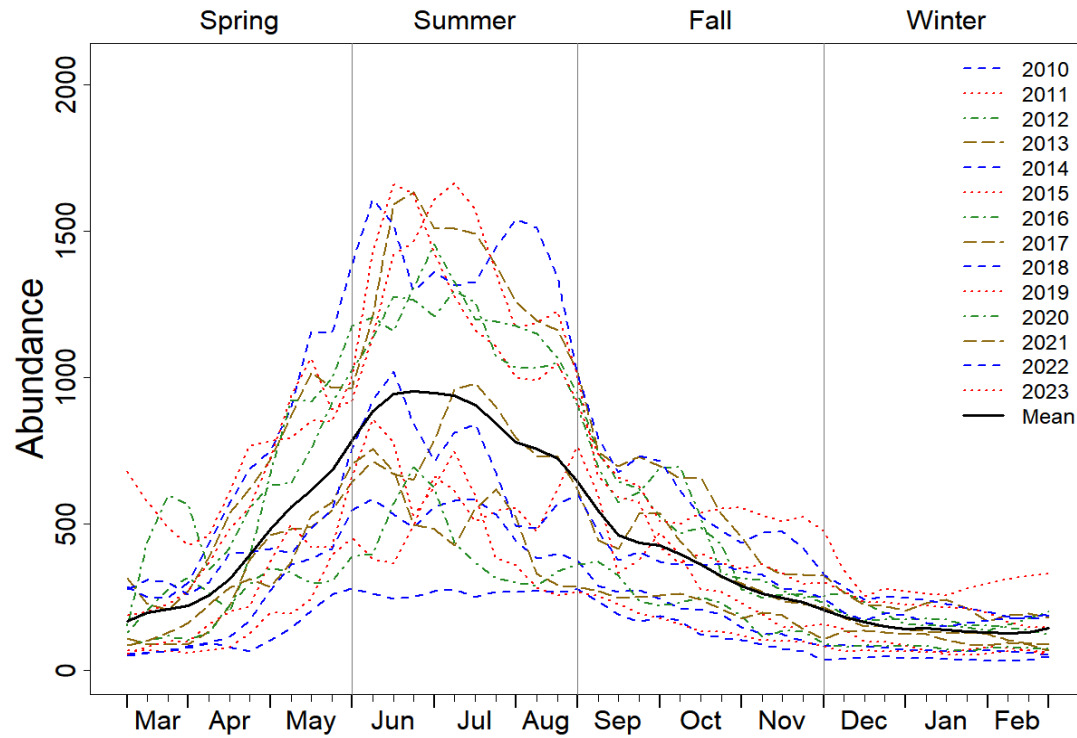


Figure 5. Annual abundance trends for humpback whales in the AMAPPS study area

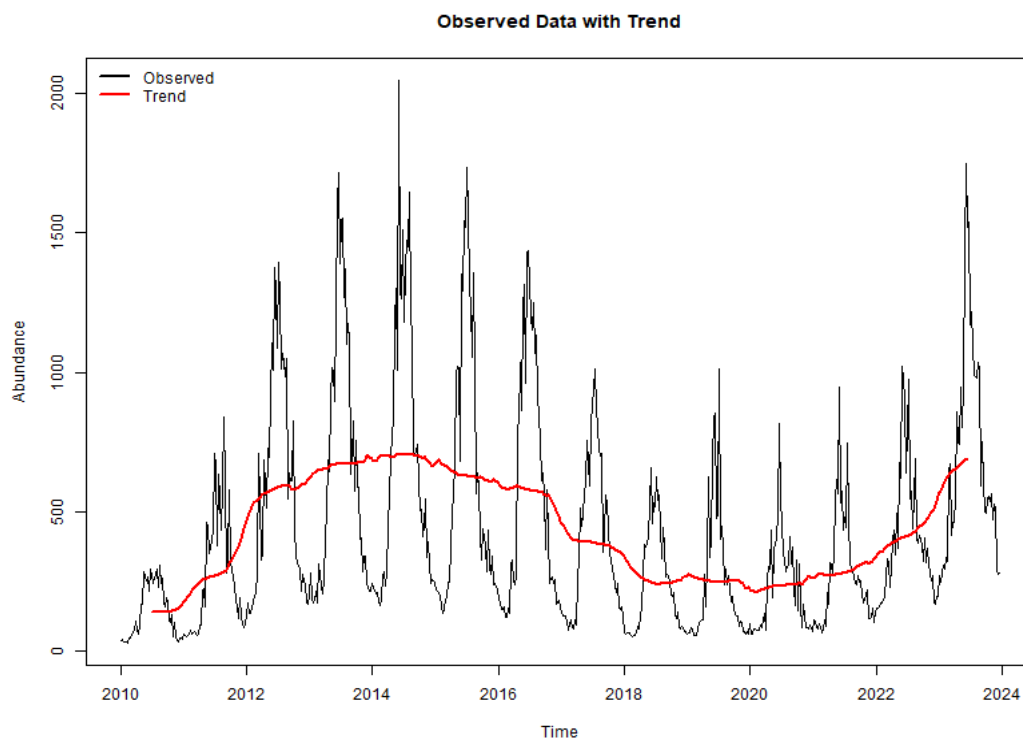


Figure 6. Humpback whale estimated trend averaged over the year in AMAPPS study area

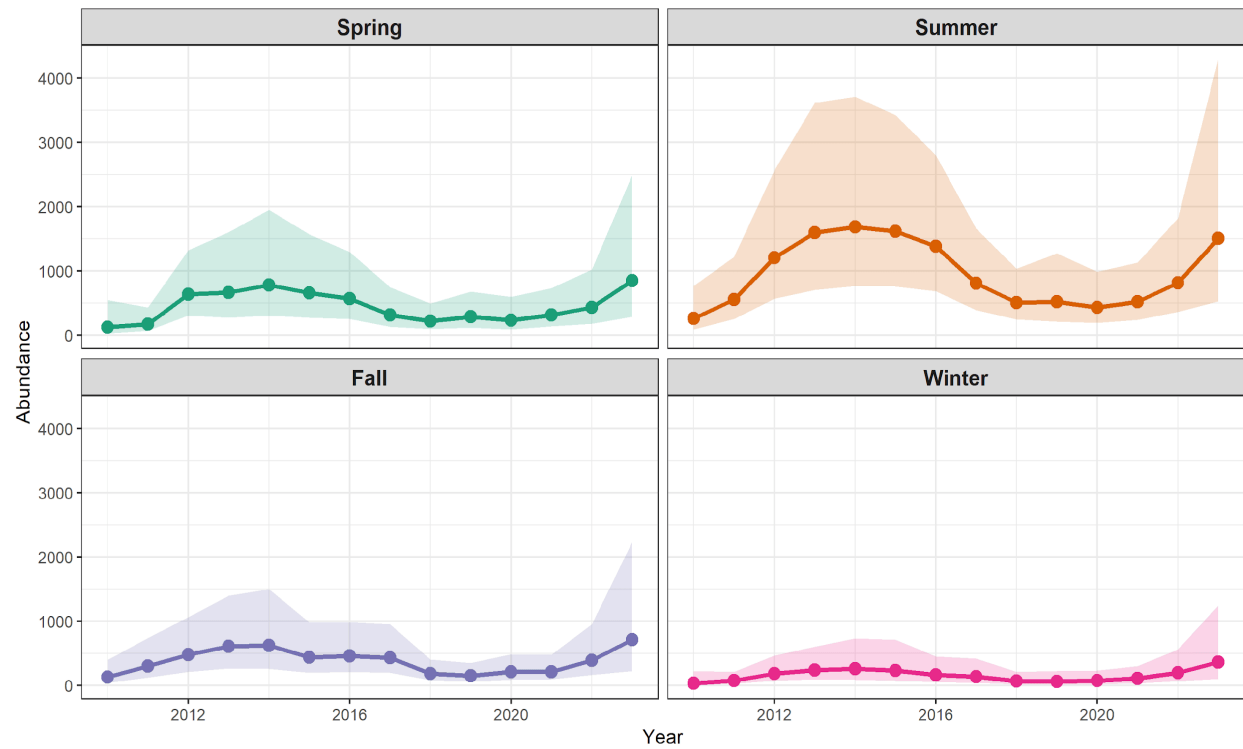


Figure 7. Humpback whale interannual abundance by season

For the 2010 – 2023 period in the AMAPPS study area. Shaded ribbon is the 95% confidence interval.

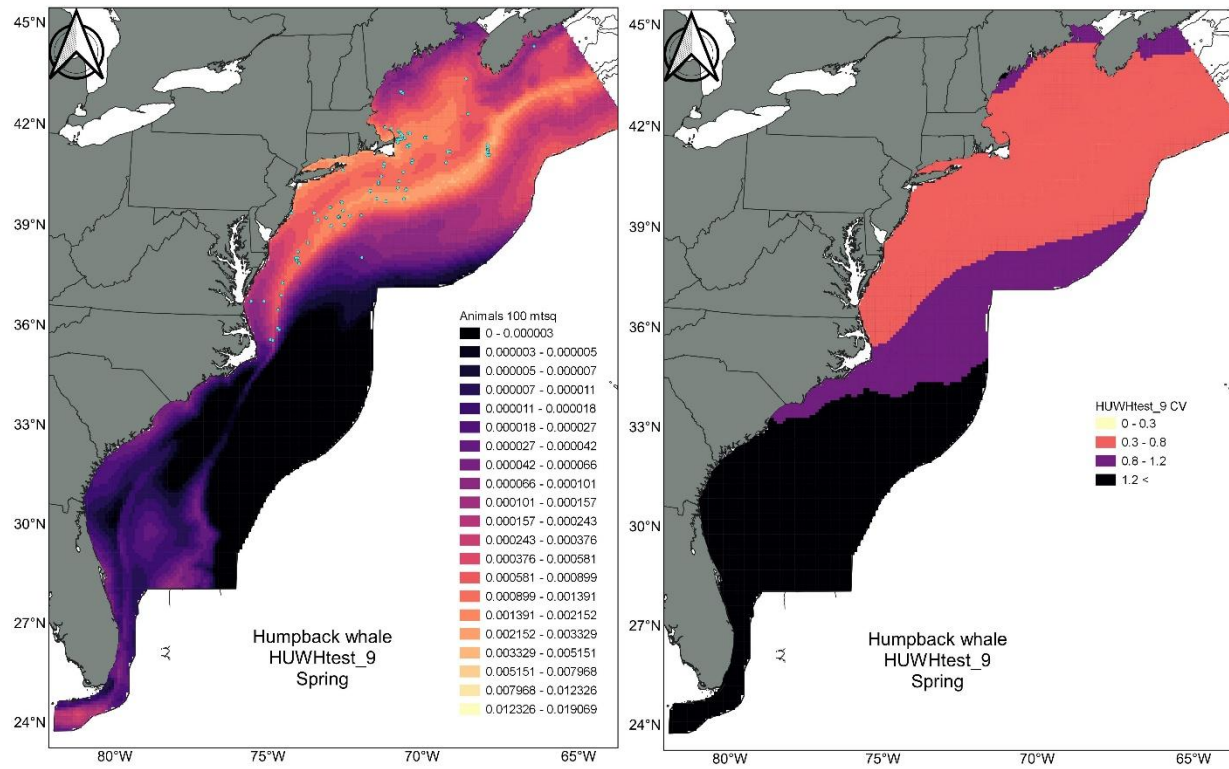


Figure 8. Humpback whale spring average density estimates and coefficient of variation
 For the 2010 – 2023 period. Densities are for grid cells of 10 km x 10 km with the exception of the coastal region. Circles indicate locations of animal sightings detected by AMAPPS.

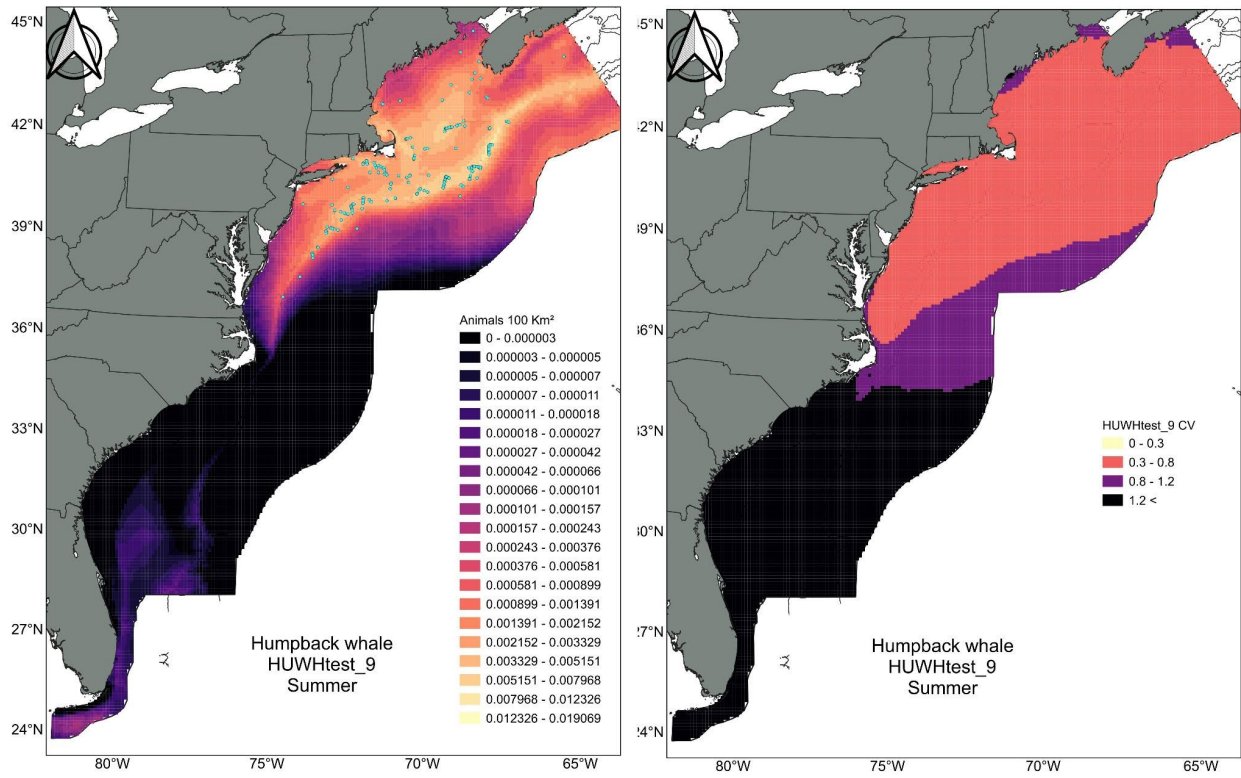


Figure 9. Humpback whale summer average density estimates and coefficient of variation
 For the 2010 – 2023 period. Densities are for grid cells of 10 km x 10 km with the exception of the coastal region. Circles indicate locations of animal sightings detected by AMAPPS.

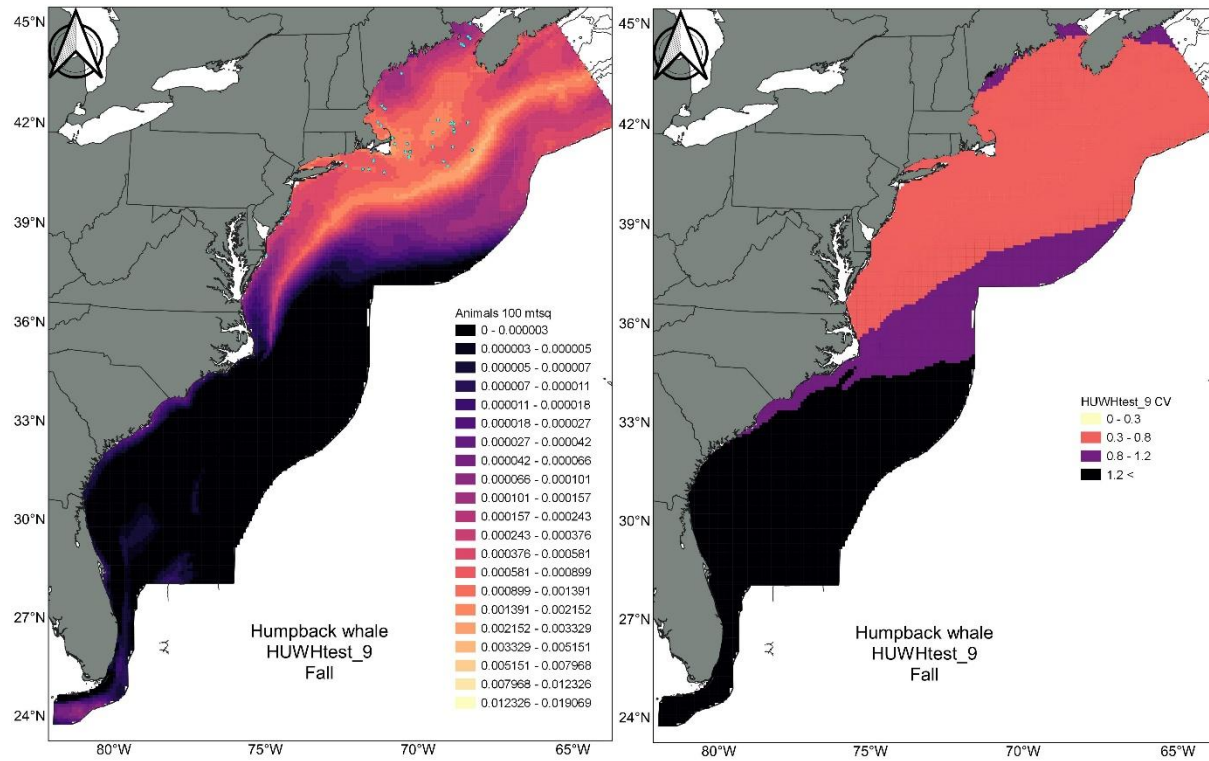


Figure 10. Humpback whale fall average density estimates and coefficient of variation

For the 2010 – 2023 period. Densities are for grid cells of 10 km x 10 km with the exception of the coastal region. Circles indicate locations of animal sightings detected by AMAPPS.

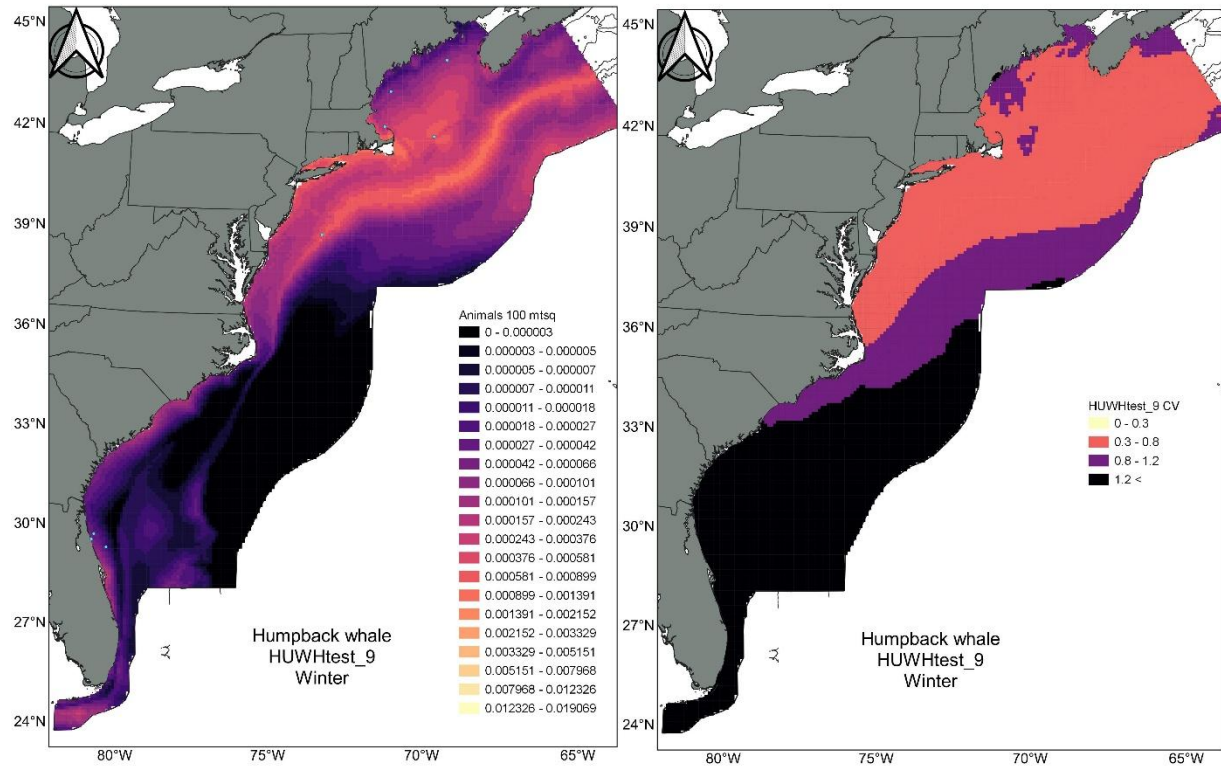


Figure 11. Humpback whale winter average density estimates and coefficient of variation
 For the 2010 – 2023 period. Densities are for grid cells of 10 km x 10 km with the exception of the coastal region.
 Circles indicate locations of animal sightings detected by AMAPPS.

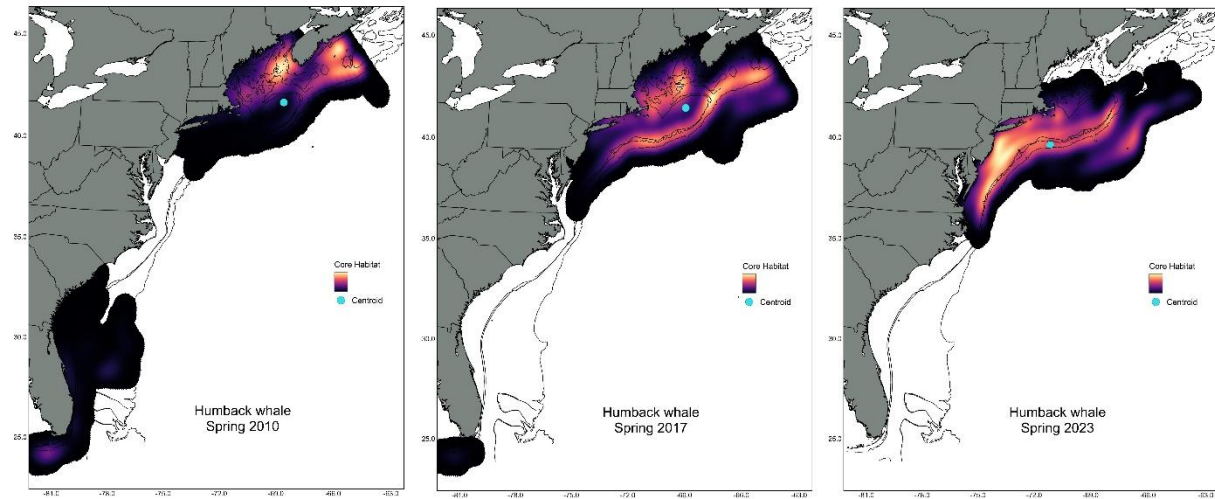


Figure 12. Spring abundance hotspots in core humpback whale habitat in 2010, 2017, and 2023
The blue dot represents the weighted centroid of the core habitat. Yellow is highest suitability area within the core habitat.

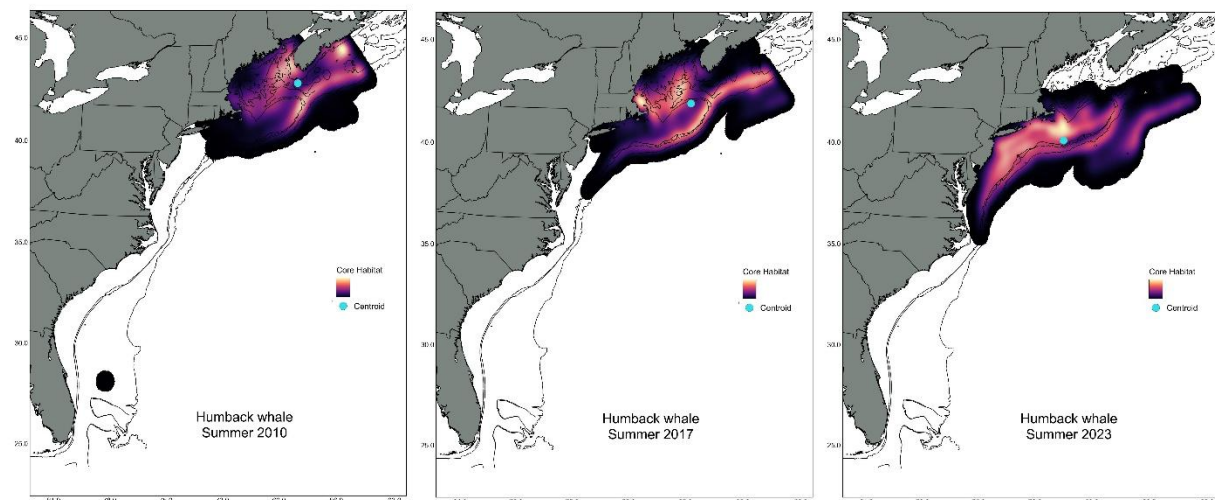


Figure 13. Summer abundance hotspots in core humpback whale habitat in 2010, 2017, and 2023
The blue dot represents the weighted centroid. Yellow is highest suitability area within the core habitat.

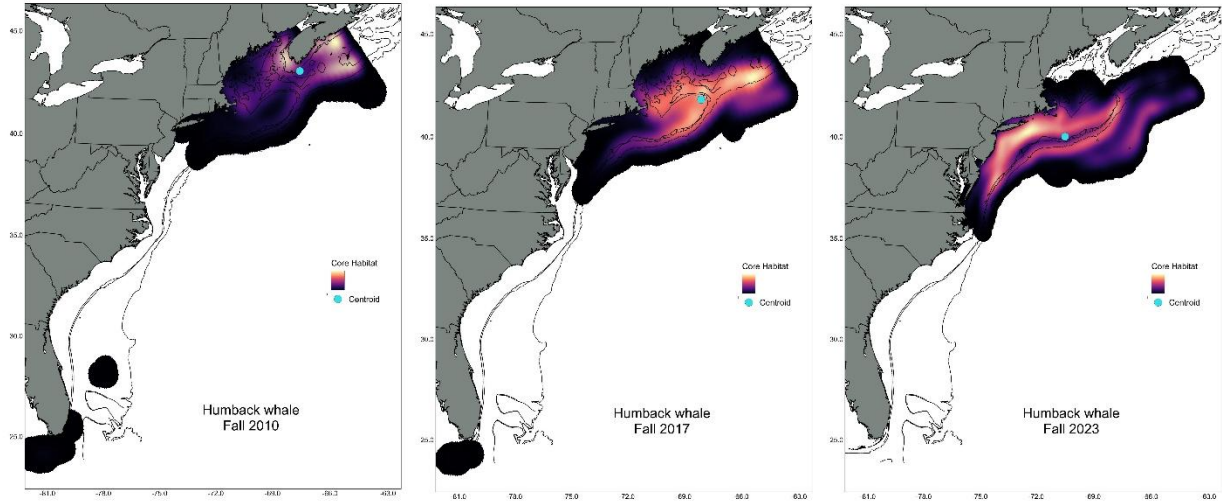


Figure 14. Fall abundance hotspots in core humpback whale habitat in 2010, 2017, and 2023
The blue dot represents the weighted centroid. Yellow is highest suitability area within the core habitat.

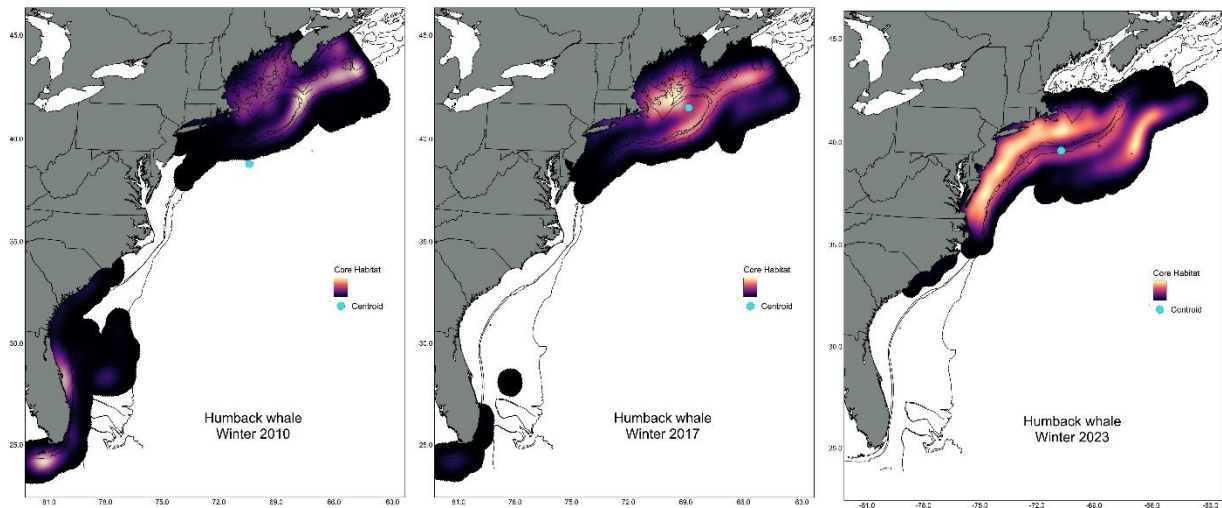


Figure 15. Winter abundance hotspots in core humpback whale habitat in 2010, 2017, and 2023
The blue dot represents the weighted centroid. Yellow is highest suitability area within the core habitat.

5 DISCUSSION: COMPARISON OF ABUNDANCE ESTIMATES

Abundance for the Gulf of Maine humpback whale stock were estimated using several techniques. This includes the GAM model-based line transect method detailed in this document, which can be directly compared with previous results from design-based line transect and photo-identification capture-recapture analyses. This comprehensive strategy allows for a direct comparison of the estimates yielded by these various approaches.

An abundance estimate of 1,706 Gulf of Maine humpback whales for 2019 was derived using a state-space capture-mark-recapture (CMR) method. This estimation relied on sightings histories constructed from the photo-identification database (Robbins et al., 2024), specifically using data available as of April

2019. The primary data source for these histories was an annual, spatially arranged survey dedicated to photo-ID data collection in the Gulf of Maine. However, the estimation process was significantly enhanced by integrating photographic captures from various other sources besides this primary survey area. These supplementary data, which were crucial in informing the known state matrix, included contributions from other cetacean research groups, cooperating whale watch vessels, and additional research efforts by the principal survey team conducted outside their dedicated effort. All sightings utilized from the primary survey were restricted to the CMR sampling strata, which is indicated by the hatched area in **Figure 16**. Applying a Bayesian hierarchical open population model to these histories produced a time series of annual abundance estimates (**Figure 17**). For the most recent year (2019), the median abundance was 1,706 individuals, accompanied by a 95% credible interval of 1,639–1,771 and an approximate estimated coefficient of variation of 0.02.

Using a design-based analysis method, the abundance of Gulf of Maine humpback whales in U.S. Atlantic waters and slightly beyond in Canadian waters was estimated at 863 (CV=0.36) based on concurrent shipboard and aerial line transect surveys conducted during the summer of 2021 (**Figure 16**; Palka 2023). This estimate incorporated corrections for perception and availability bias. The aerial survey effort (5,217 km of on-effort tracklines) covered coastal waters (from the coastline to approximately the 100 m depth contour) in the Gulf of Maine north of 38°N up to the lower Bay of Fundy. The shipboard survey (5,871 km of on-effort tracklines) covered primarily offshore waters north of 36°N, focusing on the shelf break and extending to the outer edge of the U.S. Exclusive Economic Zone (Northeast & Southeast Fisheries Science Center, 2022). Additionally, a second concurrent shipboard survey was conducted further south, covering 5,659 km of on-effort tracklines between central Florida (25°N) and approximately 38°N latitude, between the 200 m isobaths and the outer edge of the U.S. Exclusive Economic Zone, though no humpback whales were detected in this area (Northeast & Southeast Fisheries Science Center, 2022). All surveys employed an independent observer approach utilizing two visual teams to allow for the estimation of detection probability on the trackline. The multi-covariate mark-recapture distance sampling analysis method (Laake & Borchers, 2004) was applied to estimate abundance accounting for perception bias. Final estimates were then further adjusted by applying species-platform specific availability bias correction factors (**Table A1**). The results from the individual surveys were subsequently combined, and their coefficients of variation were pooled, to generate a single stock-wide abundance estimate corrected for perception and availability bias. This estimate is part of a time series of humpback abundance estimates, spanning 1989 to 2021, where each summer's data were analyzed independently using design-based multi-covariate MRDS methods (**Figure 17**). Notably, the data sets utilized for the 2010, 2016, and 2021 summer design-based estimates were also incorporated into the aforementioned GAM DSM analysis.

The abundance time series, derived from three distinct analytical methods, are compared in **Figure 17**. All of these estimates are acceptable for use in a Stock Assessment Report, each having its own advantages and disadvantages. Furthermore, the differences in the analytical approaches necessitate slightly different interpretations of the resulting abundance estimates.

As background North Atlantic humpback whales migrate between Caribbean breeding grounds in winter and northern feeding areas, such as the Gulf of Maine and Norway, in summer. This migration is neither a narrow path nor strictly scheduled. Contributing to the natural variability within any feeding ground at a given time is the fact that not all humpbacks migrate to the winter breeding grounds every year and stay in the feeding grounds, some individuals use more than one summer feeding ground, and some whales move within a feeding ground, likely tracking their prey's spatial patterns.

Interpretation of Abundance Estimates:

- Capture-Mark-Recapture (CMR): This open-population model leverages observations of individuals, which may go unobserved for one or more years before being seen again, and

provides a separate time series for age 1+ males and females. A consequence of this modeling is that the resulting time-series trend may be smoother than the actual natural variability in habitat use caused by variable migration patterns, though the general trend should remain correct. By definition, the CMR estimate represents the "super-population" of individuals present at any time during the study. A known issue with this method is the potential for unrealistically small confidence intervals, which may be the case here.

- Design-Based Line Transect: Derived from data collected during a single season in a single year, this method is at the opposite end of the spectrum. It offers a snapshot of the number of humpbacks of all ages (0+) present in the study area, and the method assumes the transects are representative of the area. Consequently, a time series of independent design-based estimates is expected to be more variable, both for a single year and between years, resulting in a less smooth time series trend compared to modeled estimates.
- Model-Based Line Transect: Similar to the CMR method, this estimate is derived from a model, in this case a density-habitat model, using multi-year and year-round data. As a result of the modeling, the time-series trend resulting from this model may also be smoother than the actual natural variability from a stock with variable migration. These estimates depend on the habitat covariate patterns in areas and times not directly surveyed. Typically, model-based line-transect estimates rely less on the assumption of representatively placed track lines relative to the target species' distribution and abundance.

Interpreting all three estimates is complicated by the uncertainty surrounding humpback whale stock structure. Specifically, it is unclear how many animals from feeding grounds north and east of the Gulf of Maine use U.S. waters as part of their migration path and thus have been included in the photo-identification and line transect data.

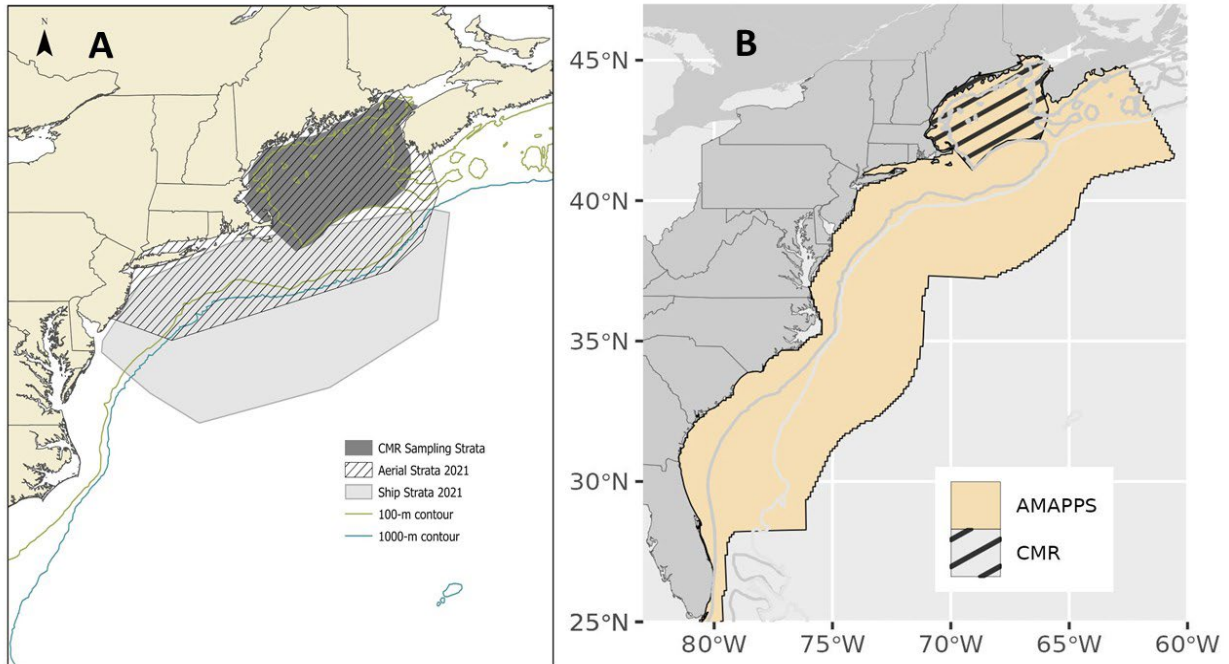


Figure 16. Sampling strata for the humpback whale abundance estimation methods

A. Capture-Mark-Recapture (CMR) sampling strata (dark gray) and shipboard (light gray) and aerial survey (striped) strata from the summer 2021 survey that had humpback whale sightings used in the design-based line transect estimate. B. The CMR sampling strata (hatched) overlapping the AMAPPS study area (beige) used in the model-based line transect analysis. Note, the entire AMAPPS strata was surveyed in summer 2021, although only the strata in (A) had humpback whale sightings for which the estimates were made.

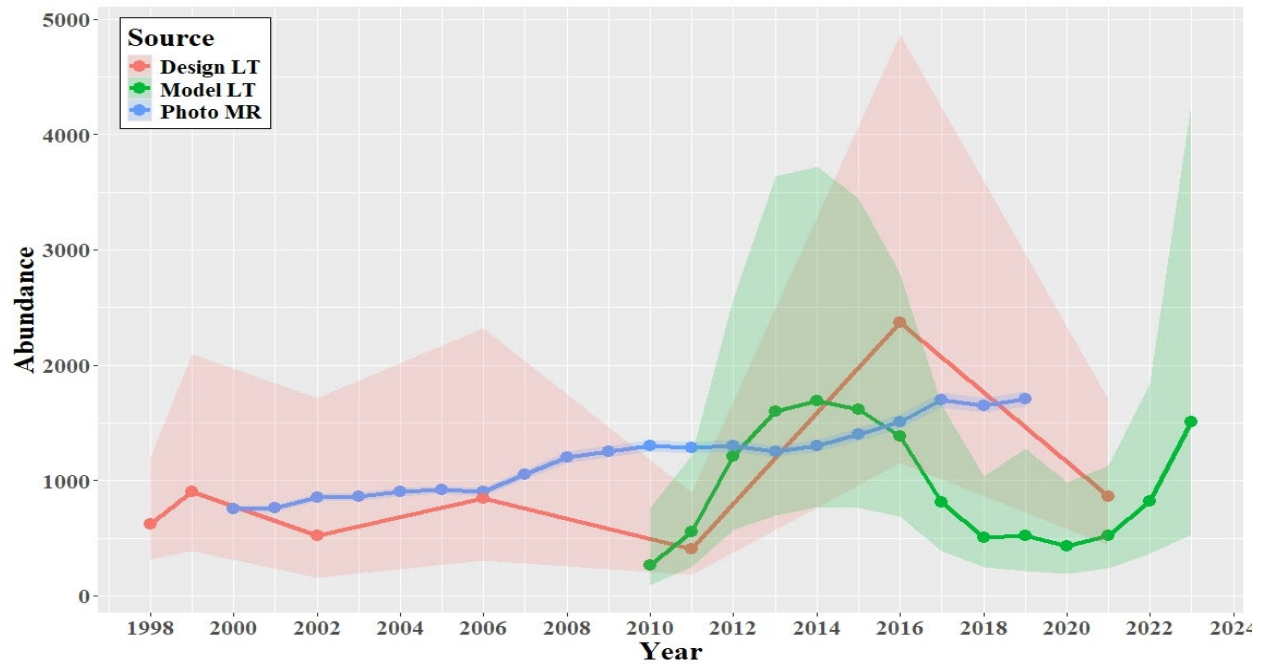


Figure 17. Time series of abundance estimates of the three analysis methods

Shaded ribbons are the 95% confidence or credible intervals.

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Appendix A: Estimation of availability bias correction factors

The availability bias correction factor, developed by Laake et al. (1997; equation 7), was defined as the probability that an animal group at a perpendicular distance (x) was at the surface and within the observer's field of view. It was modeled as a 2-state continuous-time Markov process, requiring the average time at the surface (representing time available to be seen), average time at depth (representing time unavailable to be seen), and amount of time a group at perpendicular distance x from the track line remained in view of the observers. Since the average surface and dive times were estimated from individual animals and the correction factor needs to represent a correction for groups (unit used in the surface abundance estimate), the group sizes as observed during the surveys were also accounted for.

We received processed and clean DTAG (digital acoustic recording tag) data (that is, zero-offset corrected and temperature corrected) from the principal investigators that collected the tag data. The depth readings from each tag formed a time series of dives and surface intervals. In some cases, data collected during sound experiments were deleted, just in case this stimulus resulted in un-representative dive patterns. Only daytime tag data were used to correspond with the daytime visual sighting data.

First, mean depth was calculated from the multiple depth readings per second to obtain one depth reading per second. Then these data were further smoothed by taking a running average over 21 seconds (10 s before and 10 s after each reading). Next, each mean smoothed depth reading was categorized as part of either a dive or a surface interval according to whether it was above or below a defined depth threshold. The thresholds investigated were 2 m, 3 m, 4 m and 5 m. Then, the duration of each dive and each surface interval was calculated for each tag. The next step was, for each species and time frame (day or night), a random effects model was fit where the surface or dive durations were the response variable and the tag (that is, animal) was a random variable that had normally distributed errors. From this model, the estimated mean surface and dive times (along with measures of variability) were calculated and then used to estimate the species-specific availability bias correction factor using Laake et al.'s equation (**Table A1**).

Table A1. Availability bias correction factors, specific to species and sighting platform

The – indicates not applicable.

Species	Aerial Correction Factor	CV of Aerial Correction Factor	Shipboard Correction Factor	CV of Shipboard Correction Factor
Atlantic white-sided dolphin	0.944	0.116	1	-
Common bottlenose dolphin	0.785	0.364	1	-
Cuvier's beaked whale	0.157	0.451	0.748	0.257
Fin whale	0.368	0.331	1	-
Harbor porpoise	0.628	0.299	1	-
Humpback whale	0.649	0.185	1	-
Long/short finned pilot whale	0.629	0.270	1	-
Minke whale	0.307	0.397	1	-
Risso's dolphin	0.858	0.161	1	-
Sei whale	0.410	0.536	1	-
Common dolphin	0.930	0.138	1	-
Sperm whale	0.145	0.005	0.613	0.247
Striped dolphin	1.000	-	1	-
Pygmy/dwarf sperm whale	-	-	0.539	0.307

Appendix B: Summaries from other species from the AMAPPS project

Table B1. Number of groups of species by season used in the species density models

Species	Spring (Mar-May)	Summer (Jun-Aug)	Fall (Sep – Nov)	Winter (Dec - Feb)	TOTAL
Humpback whale	283	123	89	9	504
Fin whale	104	536	94	9	743
Sei whale	43	28	5	2	78
Minke whale	77	142	59	3	281
Sperm whale	76	581	20	0	677
Goose-beaked whale	29	345	9	0	383
Sowerby's beaked whale	8	62	4	2	76
Gervais' beaked whale	1	130	4	0	135
True's beaked whale	0	66	0	0	66
Pygmy or dwarf sperm whales	14	384	2	0	400
Short-finned pilot whale	21	404	81	5	511
Long-finned pilot whale	54	44	23	0	121
Risso's dolphin	110	733	96	32	971
Atlantic white-sided dolphin	151	103	168	18	440
Common dolphin	508	871	570	126	2,075
Atlantic spotted dolphin	79	274	62	25	440
Striped dolphin	20	303	7	8	338
Common bottlenose dolphin	799	1,146	362	289	2,596
Harbor porpoise	519	421	541	66	1,547
TOTAL CETACEANS	2,896	6,696	2,196	594	12,382
Loggerhead turtle	1,761	2,635	1,206	652	6,254
Leatherback turtle	130	346	205	54	735
Green turtle	47	384	53	69	553
Kemp's ridley turtle	52	68	27	23	170
TOTAL TURTLES	1,990	3,433	1,491	798	7,712

Table B2. Number of individuals of species by season in species density models

Species	Spring (Mar-May)	Summer (Jun-Aug)	Fall (Sep - Nov)	Winter (Dec - Feb)	TOTAL
Humpback whale	406	187	126	9	728
Fin whale	143	780	124	9	1,056
Sei whale	68	38	11	5	122
Minke whale	85	147	76	3	311
Sperm whale	150	1033	50	0	1,233
Goose-beaked whale	58	930	18	0	1,006
Sowerby's beaked whale	15	195	5	2	217
Gervais' beaked whale	4	323	6	0	333
True's beaked whale	0	169	0	0	169
Pygmy or dwarf sperm whales	24	477	2	0	503
Short-finned pilot whale	332	4,980	1,197	38	6,547
Long-finned pilot whale	350	452	112	0	914
Risso's dolphin	686	5,426	793	146	7,051
Atlantic white-sided dolphin	1,099	1,213	2,856	183	5,351
Common dolphin	12,892	34,706	10,502	4,414	62,514
Atlantic spotted dolphin	1,335	7,713	1,369	548	10,965
Striped dolphin	854	13,879	325	61	15,119
Common bottlenose dolphin	7,110	14,034	4,589	2,042	27,775
Harbor porpoise	716	963	1,942	100	3,721
TOTAL CETACEANS	26,327	87,645	24,103	7,560	145,635
Loggerhead turtle	2,073	3,023	1,366	786	7,248
Leatherback turtle	141	367	213	55	776
Green turtle	48	410	55	126	639
Kemp's ridley turtle	62	70	28	26	186
TOTAL TURTLES	2,324	3,870	1,662	993	8,849

Table B3. Results of the mark-recapture distance sampling analyses for aerial survey data

Analysis Set	Truncation Distance (m) in Step 1/ Step2	Primary Team $p(0)$	CV[$p(0)$]	Cramér–von Mises p-value
NE aerial-1 (fin, sei, fin/sei whales)	500/1000	0.54	0.12	0.97
NE aerial-2 (minke, beaked whales)	380/600	0.75	0.07	0.70
NE aerial-3 (humpback, blue, right, sperm, northern bottlenose whales)	900/900	0.66	0.07	0.96
NE aerial-4 (bottlenose dolphin)	380/550	0.31	0.18	0.94
NE aerial-5 (harbor porpoise)	360/350	0.38	0.06	0.56
NE aerial-6 (Risso's dolphin)	460/600	0.49	0.12	0.91
NE aerial-7 (Pilot whales)	460/460	0.66	0.12	0.95
NE aerial-8 (white-sided and white-beaked dolphins)	400/460	0.62	0.06	0.74
NE aerial-9 (common and striped dolphins)	480/550	0.58	0.04	0.79
NE aerial-10 (loggerhead turtle)	350/450	0.60	0.05	0.95
NE aerial-11 (leatherback turtle)	350/340	0.61	0.14	0.59
SE aerial-1 (Atlantic spotted dolphin)	360/360	0.79	0.06	0.98
SE aerial-2 (Bottlenose and Clymene's dolphins)	460/460	0.86	0.02	0.78
SE aerial-3 (Common and striped dolphins)	380/380	0.85	0.04	0.89
SE aerial-4 (fin, minke, humpback, right, sperm, beaked whales)	550/550	0.86	0.07	0.89
SE aerial-5 (pilot whales, Risso's dolphin, false killer whale, rough toothed dolphin)	400/400	0.76	0.09	0.83
SE aerial-6 (loggerhead turtle)	430/300	0.60	0.01	0.61
SE aerial-7 (leatherback turtle)	350/340	0.60	0.06	0.96
SE aerial-8 (green turtle)	330/340	0.49	0.05	0.87
SE aerial-9 (Kemp's ridley turtle)	350/350	0.42	0.09	0.95

Table A4. Results of the mark-recapture distance sampling analyses for shipboard survey data

Analysis Set	Truncation (m)	Primary Team $p(0)$	CV[$p(0)$]	CvM p-value
NE ship-1 (Atlantic spotted, Pantropical spotted dolphins)	2300	0.91	0.04	0.99
NE ship-2 (Striped dolphin)	5100	0.70	0.08	0.93
NE ship-3 (Bottlenose dolphin)	4100	0.64	0.07	0.79
NE ship-4 (Risso's dolphin, rough toothed dolphin, killer whale, false killer whale, pygmy killer whale)	4500	0.51	0.10	0.55
NE ship-5 (Common, white-sided, Clymene's dolphins, harbor porpoise)	5000	0.39	0.14	0.55
NE ship-6 (Beaked whales, dwarf sperm and pygmy sperm whales)	3900	0.43	0.12	0.81
NE ship-7 (Pilot whales)	4000	0.67	0.09	0.92
NE ship-8 (Humpback whale)	10,000	0.39	0.17	0.92
NE ship-9 (Sperm whale)	6000	0.56	0.08	0.93
NE ship-10 (Fin, sei, minke, blue, right whales)	4500	0.54	0.08	0.95
SE ship-1 (Atlantic spotted, Pantropic spotted, striped, common, Clymene's, white-sided, spinner dolphins)	4000	0.59	0.10	0.52
SE ship-2 (bottlenose dolphin and harbor porpoise)	5000	0.56	0.12	0.73
SE ship-3 (Pilot whales, Risso's dolphin, rough toothed dolphin, false killer whale, killer whale)	5000	0.60	0.14	0.66
SE ship-4 (Beaked whales)	5000	0.35	0.26	0.91
SE ship-5 (Fin, humpback, right, sperm, Bryde, minke, killer whale, blue whale, sei whales)	9000	0.58	0.12	0.61
SE ship-6 (Dwarf and pygmy sperm whales)	3000	0.42	0.23	0.96

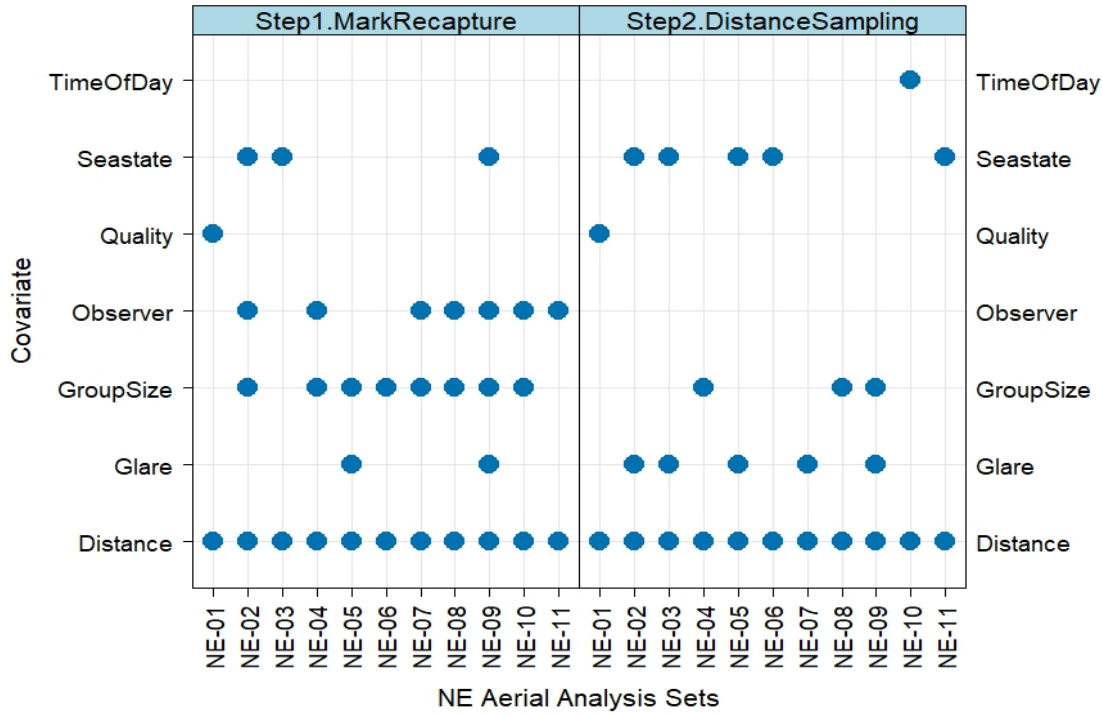


Figure B1. Significant covariates for Northeast (NE) aerial MRDS models from Stage One

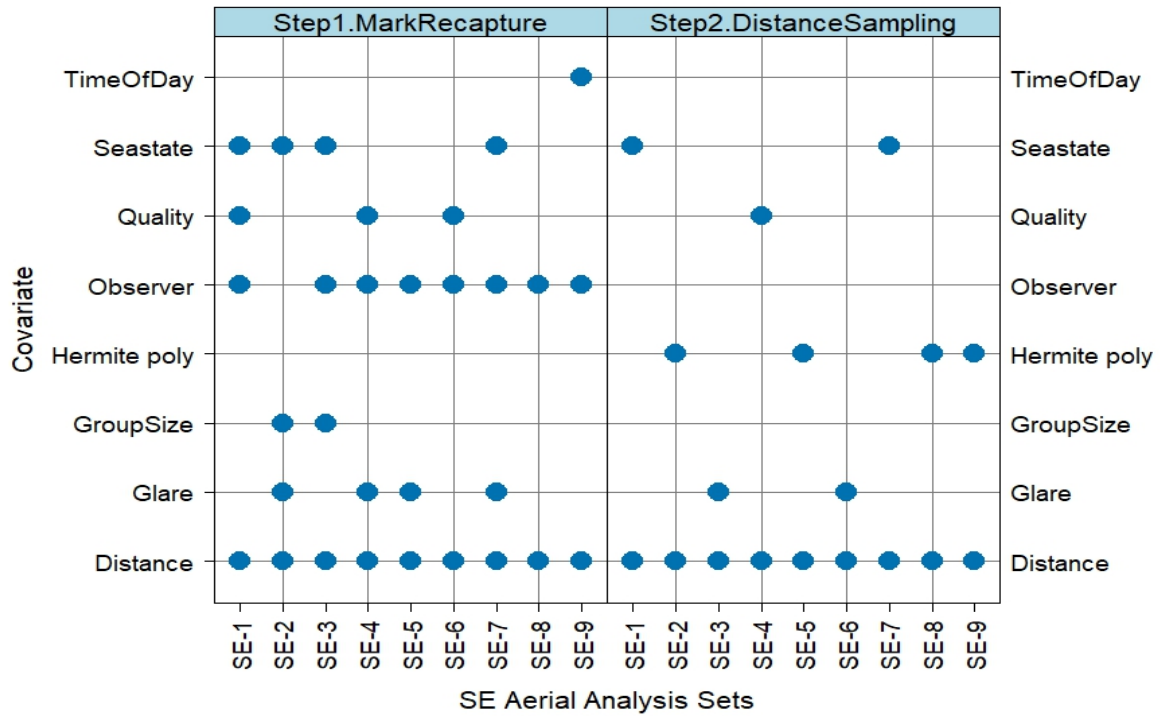


Figure B2. Significant covariates for Southeast (SE) aerial MRDS models from Stage One

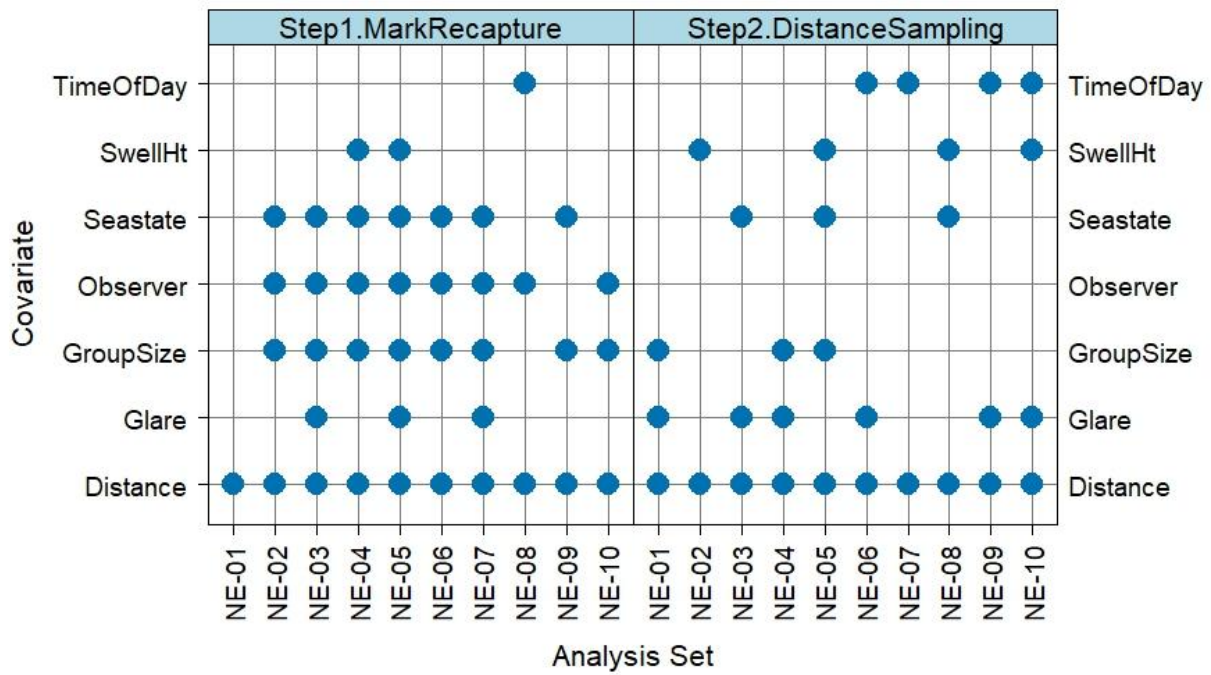


Figure B3. Significant covariates for Northeast (NE) shipboard cetacean MRDS models from Stage One

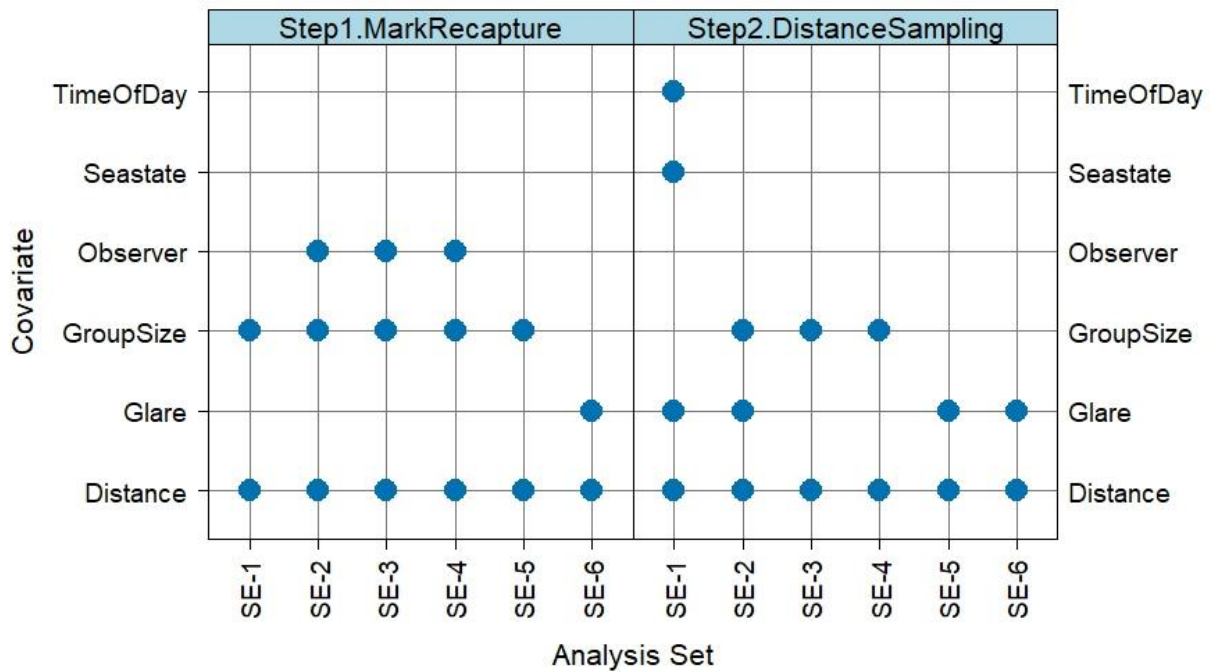


Figure B4. Significant covariates for Southeast (SE) shipboard cetacean MRDS models from Stage One