Development of a species distribution model for fin whales (*Balaenoptera physalus*) within a Bayesian hierarchical framework: Implications for uncertainty

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informed management decisions. Our results highlight the additional sampling uncertainty that is propagated in a hierarchical framework. Future applications of SDMs should consider techniques that allow all sources of error to be fully represented in final density predictions.

Development of a species distribution model for fin whales (*Balaenoptera physalus*) within a Bayesian hierarchical framework: Implications for uncertainty

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Development of a Species Distribution Model for Fin Whales (*Balaenoptera physalus*)

within a Bayesian Hierarchical Framework: Implications for Uncertainty

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Abstract

22   Species distribution models (SDMs) have proven to be an integral tool in the

23 conservation and management of cetaceans. Many applications have adopted a two-step

24 approach where a detection function is estimated using conventional distance sampling in the

25 first step and subsequently used as an offset to a density-habitat model in the second step. A

26 drawback to this approach, hereafter referred to as the conventional species distribution model

27 (CSDM), is the difficulty in propagating the uncertainty from the first step to the final density

28 estimates. We describe a Bayesian hierarchical species distribution model (BHSDM) which has

29 the advantage of simultaneously propagating multiple sources of uncertainty. Our framework

30 includes 1) a mark-recapture distance sampling observation model that can accommodate two

31 team line transect data, 2) an informed prior for surface availability 3) spatial smoothers using

32 spline-like bases and 4) a compound Poisson-gamma likelihood which is a special case of the

33 Tweedie distribution. We compare our approach to the CSDM method using a simulation study

34 and a case study of fin whales (*Balaenoptera physalus*) off the East Coast of the USA.

35 Simulations showed that the BHSDM method produced estimates with lower precision but with

36 confidence interval coverage closer to the nominal 95% rate (94% for the BSHDM vs 85% for

37 the CSDM). Results from the fin whale analysis showed that density estimates and predicted

38 distribution patterns were largely similar among methods. Abundance estimates were also

39 similar though modestly higher for the CSDM (4700, CV=0.13) than the BHSDM (4526,

40 CV=0.26). Estimated sampling error differed substantially among the two methods where the

41 average CV for density estimates from BHSDM method was approximately 3.5 times greater

42 than estimates from the CSDM method. Successful wildlife management hinges on the ability to

43 properly quantify uncertainty. Underestimates of uncertainty can result in ill-informed

44 management decisions. Our results highlight the additional sampling uncertainty that is

45 propagated in a hierarchical framework. Future applications of SDMs should consider

46 techniques that allow all sources of error to be fully represented in final density predictions.

47

Introduction

49   Species distribution models (SDMs) have become valuable tools to help characterize the

50 spatial distribution and abundance of many species (Elith & Leathwick, 2009) and have provided

51 critical information to help guide management decisions of cetacean populations (Forney et al.,

52 2012; Roberts et al., 2016). The rapid development of techniques for fitting SDMs to data has

53 provided multiple options and the need to evaluate their advantages and limitations. Some

54 attempts have been made to compare methods with a focus on prediction accuracy (Elith &

55 Graham, 2009; Oppell et al., 2012). Uncertainty, however, is rarely addressed when evaluating

56 SDMs (Robinson et al., 2017). Because proper assessment of uncertainty is critical to effective

57 management of cetacean populations (Taylor et al., 2000) attempts to model their distribution

58 and abundance should carefully consider the ability of the chosen method to quantify

59 uncertainty.

60   For cetaceans, line transect data are often used to fit SDMs. Fitting SDMs to these data

61 can be challenging because relationships between habitat variables and density are often

62 nonlinear and subject to unexplained variance. In addition, not all animals are detected on the

63 trackline and therefore probability of detection needs to be taken into account. Diving animals

64 such as cetaceans offer particular challenges because detection can be influenced by two

65   independent factors. Surface detectability refers to the probability observers detect animals that

66   are at the surface. This probability can be estimated using conventional distance sampling

67   techniques (Buckland et al., 2001). Surface availability refers to the probability that animals are

68   at the surface and therefore available for detection. Surface availability is not as easily estimated

69   from line transect data alone and requires additional information on diving behavior (Langrock et

70   al., 2013).

71   One common approach is to use a two-step method where the detection function is

72   estimated using conventional distance sampling techniques in the first step and used as an offset

73   when relating observed animal counts to habitat covariates in the second step (Miller at al.,

74   2013). Generalized additive models (GAMs) are commonly used in the second step due to their

75   flexibility to capture non-linear density-habitat relationships and flexible distributions such as the

76   negative binomial or Tweedie distribution can be adopted to model overdispersion. This

77   method, hereafter referred to as the conventional species distribution model (CSDM) method,

78   has proven quite robust (Forney et al., 2012; Roberts et al., 2016). However, it is difficult to

79   propagate uncertainty from the detection function that is estimated in the first step to the final

80   density predictions that are made in the second step. Bootstrap techniques can be used to

81   estimate uncertainty (Hedley & Buckland, 2004), but this method requires resampling the data

82   multiple times and coverage can be poor (Miller et al., 2013). Williams et al. (2011) used a

83   random effects approach to propagate error from the detection function but their method is

84   limited to cases where there is only a single team of observers. As an alternative, a number of

85   studies have adopted a Bayesian hierarchical framework.

86   Hierarchical analysis of distance sampling data has also been developed in the literature

87   (Royle, Dawson & Bates 2004; Royle & Dorazio, 2008). This approach integrates over the

88   uncertainty in the detection function, effectively propagating the uncertainty into final density

89   estimates (Miller et al., 2013). When estimated in a Bayesian framework, prior information

90   about other sources of error (e.g. surface availability) can also be included. Although there are a

91   number of examples of applying a Bayesian hierarchical approach to line transect data (Eguchi &

92   Gerrodoette, 2009; Moore & Barlow, 2011; Conn, Johnson & Laake, 2012) this framework is

93   still ripe for further development. For example, applications to line transect data of cetaceans

94   have generally used single team shipboard data where detectability on the trackline (i.e. *g(0)*)

95   cannot be estimated directly (Moore & Barlow, 2011; Pardo et al., 2015; Pavanato et al., 2017).

96   There have been fewer attempts to develop a framework that can accommodate two team survey

97   data (but see Conn, Laake & Johnson, 2012 for an example). In addition, recent examples of

98   estimating SDMs in a Bayesian framework have used generalized linear models (GLMs) to

99   parameterize the habitat function (Conn, Laake & Johnson, 2012; Pardo et al., 2015; Goyert et

100   al., 2016). Thus, they lack the flexibility that GAMs provide in the two-step method.

101   In this paper we present a Bayesian hierarchical species distribution model (BHSDM).

102   Our main goal was to develop a comprehensive framework that incorporates the multiple

103   components that influence detection, flexibility in the habitat function and flexible distributions

104   that can accommodate overdispersion and excessive zeros. A secondary goal was to verify that

105   an appropriate level of uncertainty is propagated into final density estimates. We compare the

106   BHSDM with a CSDM analysis using a simulation study and a case study with line transect data

107   of fin whales (*Balaenoptera physalus*) off the east coast of the U.S.

108

109   **Materials & Methods**

110   *Data Collection*

111

112   Line transect data were collected as part of the Atlantic Marine Assessment Program for

113   Protected Species (AMAPPS) conducted by the Northeast Fisheries Science Center (NEFSC)

114   and the Southeast Fisheries Science Center (SEFSC). The study area ranged from Halifax, Nova

115   Scotia, Canada to the southern tip of Florida and from the coastline to slightly beyond the US

116   exclusive economic zone covering approximately 1,193,320 km² (Fig. 1). A total of 16

117   AMAPPS surveys were conducted using both shipboard and aerial platforms from July 2010 to

118   August 2013 covering approximately 104,000 km of line transect survey effort (Table 1).

119   Shipboard surveys were primarily conducted during summer months in offshore waters and

120   aerial surveys were conducted throughout the year primarily in coastal waters. Each platform

121   included two independent observer teams.

122   We divided the study site into 10 x10 km oblique Mercator grid cells and into 8-day

123   temporal time periods. For each spatial-temporal cell we calculated the amount of on-effort

124   trackline, number of sightings and obtained the corresponding values of a suite of static

125   physiographic variables and dynamic environmental variables (Table S1). More details on the

126   methods to collect and process the line transect and environmental data are found in Palka et al.

127   (2017).

128

129   *Model Overview*

130   A general form of the SDM model for a given unit of a study area can be written as

131

$$E(n_i) = \hat{p}_i A_i \exp(f(x)), \qquad \text{eqn 1}$$

133   where $E(n_i)$ is the expected number of sightings in unit i, $\hat{p}_i$ is a distance integrated probability

134   of detection within the search area of unit i, A_i is an offset term for the amount of search effort

135   and $f(x)$ is a user-defined habitat function that relates habitat covariates to the true density of

136   animals in unit i. This model can be fit within a frequentist framework using a two step process

137   (Miller et al., 2013).

138   We take a hierarchical approach to modeling the spatial density of animals. Our

139   modeling framework consists of a number of subcomponent models that include 1) a detection

140   function model based on distance sampling, 2) a group size model to model the average group

141   size (i.e. number of individuals within a group), 3) an informed prior for surface availability

142   based on information on the diving behavior of tagged fin whales and 4) an underlying habitat

143   model. Below we outline the development of each subcomponent and its implementation in a

144   Bayesian framework.

145

146   *Detection Function*

147   To estimate surface detectability we used information from the double platform survey

148   method. Information collected from this survey design allowed us to apply mark-recapture

149   distance sampling (MRDS) methods (Laake & Borchers, 2004). To model the sightings data

150   from the dual observers we adopt the formulation for point independence outlined by Laake and

151   Borchers (2004). This estimator combines a mark-recapture analysis with conventional distance

152   sampling to estimate detection probability such that detection on the trackline (i.e. *g(0)*) can be

153   estimated directly, and therefore, is not assumed to be 1.   The estimator is

154
$$\hat{p}_{it} = g(0, \boldsymbol{Z_{it}}) * \frac{\int_0^W g(y, \boldsymbol{Z_{it}}) dy}{W} \quad , \qquad \text{eqn 2}$$

155   where $\hat{g}(0, \boldsymbol{Z_{it}})$ represents the estimate of detection probability on the trackline and is estimated

156   from the mark-recapture data; $\hat{g}(y, \boldsymbol{Z_{it}})$ represents the detection function at distance *y* and is

157   estimated from the distance data; $\boldsymbol{Z_{it}}$ is a matrix of detection covariates that influence surface

158   detectability in grid cell *i* at time *t* and *W* is the truncation distance. To model the likelihood for

159   the distance data, we considered half-normal and hazard rate detection functions. For the mark-

160   recapture component of the data we adopted the approach outlined by Laake and Borchers

161   (2004). Specifically, we modeled the binary outcome of whether or not an observer successfully

162   detected an animal group that was present at distance *y* as the outcome of a Bernoulli trial.

163   Further details of analyzing the double platform line transect data using the MRDS method are

164   provided in Appendix S1.

165   For the aerial surveys, the secondary team was situated toward the back of the plane but

166   had an obstructed view of the trackline complicating a direct implementation of the MRDS

167   approach. Therefore, we estimated an average *g(0)* for both the NEFSC and SEFSC aerial

168   surveys independently where we treated the front team as a single platform and estimated *g(0)*

169   using a trial configuration (i.e., using detections by the rear observers as "trials" for the front

170   observers). The estimated *g(0)* was 0.50 (CV=0.17) and 0.90 (CV=0.09) for NEFSC and

171   SEFSC, respectively. We used these estimates to develop informative priors in the BHSDM.

172   Information on estimating *g(0)* and applying it to the aerial data is provided in Appendix S1.

173   For each platform and survey, the best detection function was determined through a

174   stand-alone MRDS analysis using the program Distance and fitting both half-normal and hazard

175   rate likelihoods (see Palka et al., 2017). Because sample sizes were low for fin whales, we

176   pooled data from several other large whale species to estimate survey specific detection

177   functions. Models were compared using AIC and the top model for each survey was included in

178   the Bayesian framework. A description of top model used for each platform and survey

179   combination is provided in Appendix S2.

180

181   *Surface Availability*

182   Because most marine animals spend some amount of time below the surface there is a

183   need to also correct for surface availability ($\hat{a}$) (Laake et al. 1997; Forcada et al. 2004). Species-

184   specific surface availability and the corresponding standard error by platform, was taken from

185   Palka et al. (2017) who adopted the method of Laake et al. (1997). This method was based on

186   the probability of an animal being detectable at the surface during a survey, and took into

187   consideration the species diving and aggregation behaviors, in addition to the amount of time the

188   observer had to analyze any spot of water from each of the survey platforms. This correction

189   tended to be larger for aerial surveys than for shipboard surveys, and larger for long diving

190   species than for short diving species. The estimate for fin whales for aerial surveys was 0.37

191   (CV=0.34). This information was then used to develop an informative prior. Combining surface

192   detectability and surface availability, our final correction for detection probability in each grid

193   cell *i* at time *t* can be written as:

194

195
$$\hat{P}_{it} = \hat{p}_{it} * \hat{a},$$
eqn 3

196

197 *Habitat Function*

198   We take a generalized additive modeling (GAM) approach to parameterize the habitat

199 function. Because the smooth terms of a GAM have a common multivariate Gaussian (MVN)

200 form they can be estimated relatively easily with standard Markov Chain Monte Carlo (MCMC)

201 techniques (Hastie & Tibshirani, 1990; Wood, 2016). The basic GAM formula can be written as

202
$$f(x) = \sum_{j=1}^{K} \beta_j b_j(x),$$
eqn 4

203 where $b_j(x)$ are spline like basis functions and β_j are parameters to be estimated. The scalar K is

204 usually chosen by the user to be large enough to allow appropriate amount of flexibility in $f(x)$.

205 To avoid overfitting quadratic penalty terms are included which take the form

206
$$\sum_j \gamma_j \beta^T S_j \beta,$$

207 where S_j are matrices of known coefficients and γ_j are smoothing parameters to be estimated.

208 The precision matrix of these distributions can be derived such that

209

210
$$\beta \sim \text{MVN}(0, \sum_j \gamma_j S_j),$$

211 where the penalty terms are given a vague, gamma prior such as

212
$$\gamma_j \sim \text{Gamma}(0.05, 0.005),$$

213   The terms can be estimated efficiently using Gibbs sampling with conjugate priors.

214   To calculate the precision matrices we used the jagam function in the R package mgcv

215   (Wood, 2016). This function allows the user to specify a number of different smooths (cubic

216   splines, tensor products, etc.) and provides the basic code and input of a JAGS model. In

217   addition, it centers the smooths to facilitate faster convergence.

218   We can now combine the habitat function with detection probability and an offset from

219   the amount of search effort in each grid cell to estimate the total number of animal groups per

220   grid cell using eqn (1). The offset term was calculated by dividing the area searched within grid

221   cell I by the total area of the grid cell i ($Area_i$) such that $A_i = 2*W*L_i/Area_i$, where L_i is the

222   length of on-effort line transect.

223   *Likelihood*

224   Line transect data tend to be noisy so it is common when constructing SDMs to use a

225   likelihood model that can accommodate outliers. We implemented a Tweedie distribution which

226   has been shown to provide a good fit to cetacean data (Miller at al. 2013; Roberts et al., 2016).

227   The Tweedie distribution is a three parameter family of distributions that can take the form of

228   more commonly used distributions such as the normal, Poisson and gamma. If the power

229   parameter is in the range $1<p<2$ than the distribution can also be referred to as the compound

230   Poisson-gamma (CPG). Because the Tweedie random variables are a sum of G gamma variables

231   where G is Poisson distributed (Jørgensen, 1987), it can be expressed in terms of a Poisson and a

232   gamma distribution such that

233

234                         $$G \sim Poisson(\lambda_p)$$

235

236 $$M\sim\text{Gamma}(\alpha, \beta)$$

237

238 where

239 $$\lambda_g = \frac{\alpha}{\beta}$$ eqn 5

240 and

241

242 $$x = \begin{cases} \sum_{i=1}^{G} M, & G > 0 \\ 0 & G = 0 \end{cases}$$ eqn 6

243

244 the expectation is then $E(x)=\lambda_p\lambda_g$. Lauderdale (2012) shows that under a specific

245 parameterization, the coefficients of the regression model can be estimated by estimating both

246 the Poisson and gamma components separately. Specifically, this parameterization can be

247 written as

248

249

250 $$\lambda_P = e^{\frac{X(\beta - \phi)}{2}}$$ eqn 7

251

252 $$\lambda_g = e^{\frac{X(\beta + \phi)}{2}}$$ eqn 8

253

254   where $\mathbf{X}$ is a matrix of covariate values, β is a vector of regression coefficients and ϕ is a vector

255   of coefficients that control the extent to which the regression coefficients vary between the

256   Poisson component and gamma component of the compound distribution (Lauderdale, 2012).

257

258

259   *Group Size*

260

261   To model group size we use a zero truncated Poisson such that the group size of each

262   sighting is modeled as

263                            $$(s_k\text{-}1)\sim\text{Pois}(\lambda_s),$$

264   where s_k is the k_{th} observation of group size and λ_s+1 represents the average group size. This

265   approach assumes that group size is unrelated to detection probability. This assumption is

266   supported by our analysis of fin whale sightings data which did not indicate a strong influence of

267   group size on detection probability.

268   *Density and abundance estimation*

269   To estimate the density within a grid cell we multiply the estimate of group size with the

270   estimate of group density such that

271                    $$N_{it} = D_{it} * (\lambda_s + 1), \qquad \text{eqn 9}$$

272   where D_{it} is the predicted number of groups in grid cell i at time t estimated from the GAM

273   model, $\lambda_s + 1$ represent the average group size and N_{it} is the predicted number of individuals in

274   grid cell i at time t. To estimate total abundance of individuals within the study area we sum N_{it}

275   over all grid cells within the study area.

Model Fitting

277   We fit the BHSDM outlined above using MCMC sampling implemented with the JAGS

278   software (Plummer 2003). Vague prior distributions were used for all parameters with the

279   exception of $g(0)$ for the aerial surveys and $\hat{a}$ where we used estimates and associated CVs to

280   develop informative beta prior distributions using the approach of Pardo et al. (2015). We

281   included a burnin of 20000 samples and two chains of 50000 with a thinning rate of 50.

282   Convergence was assessed by examining traceplots and calculating Gelman-Rubin diagnostics.

Simulation study

284   To quantify differences in precision and statistical coverage probability between the

285   BHSDM and CSDM method we used a simulation study. We simulated spatial variation in

286   abundance over 300 hypothetical grid cells that were all 100 km^2 in area. Each grid cell was

287   assigned a covariate value and the associated density of animals was generated as a quadratic

288   function of its covariate value. We simulated variation in search effort and detection including

289   both surface detectability and surface availability. We applied both the CSDM method and the

290   BHSDM method to each of 1000 independently simulated datasets. For each simulation, we

291   estimated population size by summing up the estimated number of animals in each grid cell. We

292   estimated statistical interval coverage by determining whether or not the true population size fell

293   within the 95% confidence intervals of the CSDM method or the 95% credible region of the

294   posterior estimate of the BHSDM method. In addition, we calculated percent relative bias for

295   each simulation and method as $(\hat{N}_{ij} - N_i)/ N_i * 100$ where N_i is true abundance for simulation i and

296    $\hat{N}_{ij}$ is the estimate of population size for simulation i and method j. A more detailed explanation

297   of the simulations is provided in Appendix S2.

298

299   *Case Study with Fin Whales*

300   We tested our model on a four year dataset of fin whale sightings collected during the

301   AMAPPS surveys. Similar to our simulation study we also compared model predictions to

302   predictions from a CSDM using a version of the two-step method. Details for fitting the CSDM

303   to the fin whale dataset are explained elsewhere (see Palka et al., 2017) but we briefly review the

304   process here. In the first step, we calculated densities of fin whales from the stand-alone MRDS

305   analysis in program Distance. We adjusted estimates from the aerial surveys by dividing by an

306   estimate of surface availability. In the second step, we fit GAMs to these effort-corrected

307   estimates of density using the mgcv software (Wood, 2011) using thin plate regression splines

308   and restricted error maximum likelihood (REML) to estimate parameters. To account for

309   overdispersion, a Tweedie distribution was assumed. A multi-stage process was used to

310   determine the best set of covariates and the best structure of the smooth terms (see Palka et al.

311   2017 Appendix I, chapter 3 for results). We then fit the same model using the BHSDM. Our

312   interest was in keeping as many components of the model structure consistent so we could focus

313   on comparing output across modeling frameworks.

314

315   **Results**

316   *Simulation Study*

317   Simulations demonstrated higher uncertainty and higher statistical interval coverage

318   using the BHSDM method as compared to the CSDM method. We found approximately 94%

319   coverage probability for the BHSDM compared to 84% coverage probability for the CSDM (Fig.

320   2). The average CV of $\hat{N}$ calculated from the BHSDM method was approximately 20% higher

321   than the average CV calculated from the CSDM method demonstrating the additional uncertainty

322   that is propagated in a BHSDM framework. Overall bias was low and positive for both methods

323   but slightly more positive for the CSDM method (Fig. 2).

324   *Case Study*

325   A comparison of the resulting detection functions between the stand alone MRDS and the

326   BHSDM showed detection probabilities were similar (Table 2). Estimates from the distance

327   sampling component were similar among all framework although estimates from the BHSDM

328   were consistently higher. Similarly, estimates of *g(0)* for the shipboard surveys were also similar

329   but consistently higher in the BHSDM framework. The posterior estimate of mean group size

330   was 1.4 (CV=0.14) indicating relatively small group sizes. Most observed group sizes were less

331   than 2 animals with 4 % greater than 3 animals.

332   The top model for the habitat function included latitude, chlorophyll, sea surface

333   temperature and distance to 125 m isobath as covariates (see Palka et al,. 2017 Appendix I,

334   chapter 3**)** and were subsequently used in the BHSDM. Results from fitting the BHSDM to the

335   observed sightings data showed good agreement between predicted and observed number of

336   groups per grid cell although there was some tendency of the model to under predict as the

337   number of sightings increased (Fig. S1). In comparison to the CSDM, density estimates for the

338   grid cells during the summer time period were similar between the two frameworks (Fig. 3).

339   Overall abundance estimate for the entire study area was 4 % lower with lower precision for the

340   BHSDM (4526,CV=0.26) compared to the CSDM (4718,CV=0.13) .

341   In contrast to density estimates, sampling uncertainty of the grid cell density estimates

342   varied substantially between the two frameworks (Fig. 4). The median CV's were 0.28 and 0.98

343   for the CSDM and the BHSDM, respectively. The distribution of CV's from the BHSDM were

344   highly skewed. However, the highest CV's from BHSDM were associated with low density

345   estimates (Fig. 4). Ignoring grid cells with low density estimates (density <0.0001 animals/km^2),

346   the median CV's were 0.45 and 0.15 for the BHSDM and CSDM, respectively.

347   The predicted spatial average seasonal density distribution patterns were largely similar

348   for the two frameworks (Fig. 5a and Fig. 5b). Both modeling frameworks indicated that the Gulf

349   of Maine and the shelf break where areas of relatively high density. There were some minor

350   differences south of the Gulf of Maine where the CSDM indicated slightly higher densities than

351   the BHSDM. The overall pattern of uncertainty was similar for the two frameworks where

352   uncertainty was lowest in areas with the highest density and vice versa for the areas of highest

353   uncertainty (Fig. 5c and Fig. 5d).

354

Discussion

356   The use of SDMs to predict the abundance and distribution of animals in time and space

357   is increasingly becoming a cornerstone in the conservation and management of cetacean

358   populations (Gregr et al., 2012). Techniques for fitting SDMs have grown rapidly and although

359   there have been a number of attempts to compare methods in terms of model fit and prediction

360   (Elith & Graham, 2009; Oppel et al., 2012), few studies have focused specifically on uncertainty.

361   Yet, properly accounting for uncertainty is crucial to informing good management decisions

362   (Ludwig, Hilborn, & Walters 1993). Our focus was on further developing the one-step BHSDM

363   and comparing its performance to the more standard CSDM with the explicit goal of highlighting

364   differences in uncertainty between the two methods.

365   Two-step approaches to SDMs have the advantage of being able to use all the built-in

366   options available in different software packages such as Distance to model detection and mgcv to

367   model habitat relationships (Miller et al. 2013). In contrast, Bayesian methods have been more

368   limited in these options. We have taken steps to expand the BHSDM framework such that it is

369   more compatible with the two-step approach and similar models can be compared. For example,

370   we adopted the MRDS approach available in Distance to model two team data while also

371   including a hazard rate option. Previous Bayesian applications to line transect data of cetaceans

372   have generally been applied to single shipboard team data using a half-normal detection function

373   (Moore & Barlow, 2011; Pavanato et al., 2017). We have also included nonparametric GAMs

374   which allow for flexible, data-driven relationships between habitat and density. Other

375   approaches to BHSDM have included quadratic terms in a GLM framework (Pardo et al., 2015;

376   Goyert et al., 2016) to capture nonlinear relationships, but this approach is still parametric in

377   form and limited in flexibility. Finally, we implemented a Tweedie distribution within this

378   framework. Because the Tweedie is not a built in distribution in most Bayesian software

379   packages, we adopted the CPG approach of Lecomte et al. (2013). This approach is a limited

380   version of the Tweedie where the power parameter is constrained between 1 and 2; however, it is

381   not uncommon in studies using the two-step approach with a Tweedie distribution to restrict the

382   power parameter to be within this range (Williams et al., 2011; Cañadasa et al., 2018). Together

383   these features provide more options for users when applying a BHSDM to line transect data.

384   In a review of marine SDMs, Robinson et al. (2017) notes that uncertainty is rarely

385   assessed rigorously. We explicitly addressed this issue with simulations. We found the BHSDM

386   method not only results in higher uncertainty but greater statistical coverage than the CSDM

387   method. When interpreting the magnitude of the difference between the two methods it is

388   important to take into account the simplicity of the simulations. For instance, we assumed a low

389   amount of scientific uncertainty around the estimate of surface availability (as represented by a

390   relatively narrow distribution). In addition, our estimates of surface detectability were relatively

391   precise as we used simulated data with no detection covariates. Finally, we did not include

392   uncertainty in group size. Whether using the two-step method or one-step method it is important

393   to consider all the sources of uncertainty and their influence on final predictions. For example,

394   estimates of surface availability from tag data are generally limited to a few individuals and may

395   include high uncertainty. As a corollary, these results also point to the value of trying to derive

396   more precise estimates of detectability. Recent advances in sampling technology such as passive

397   acoustic technology (Marques et al., 2012) and aerial drones (Brack et al., 2018) may be greatly

398   beneficial in estimating both more accurate and more precise measurements of surface

399   availability and in turn could greatly reduce uncertainty in final estimates.

400   Our simulations also demonstrated that overall bias of the BHSDM method is relatively

401   small and slightly positive. When using Bayesian methods, bias will partly be a function of how

402   one calculates point estimates using posterior samples. For our simulations we used the posterior

403   mean, but the posterior median or mode could also be used. In a study of harbor seals, Ver Hoef

404   and Jansen (2007) showed that in cases where the posterior distributions are skewed, the

405   posterior median estimate can be biased low and the posterior mean estimate can be biased high.

406   They suggest use of the linex loss function to achieve more accurate estimates (Varian, 1975).

407 We did not take that approach here, but it is worth considering if small amounts of bias are a

408 concern.

409   When applied to field data, the BHSDM produced density estimates and distribution

410 patterns that were similar to the CSDM albeit not exact. Although we attempted to keep the two

411 frameworks as similar as possible, there were some structural differences that may have

412 influenced density estimates. For example, the CSDM used a Horvitz-Thompson like estimator

413 to estimate observed densities whereas the BHSDM models used the observed sighting of groups

414 in each grid cell directly and used a mean estimate of group size to calculate total density of

415 animals. In addition, the estimates of detection from the BHSDM tended to be higher than

416 estimates from a stand-alone MRDS analysis which might have translated into slightly lower

417 density estimates. Overall, the spatial distribution and abundance from both methods were

418 comparable to a previous study by Roberts et al. (2016) for the same general area.

419   Estimates of precision differed substantially between the two methods. This result was

420 anticipated as the hierarchical structure of the BHSDM framework propagates more uncertainty

421 from the other components of the model. Several factors contributed to uncertainty including

422 uncertainty in average group size, surface detectability and surface availability. Estimates of

423 precision from most of these components were relatively high with CVs ranging from 0.06 to

424 0.26. Our estimate of surface availability had the lowest precision with a CV of 0.34 and likely

425 contributed the most to differences in CVs among density estimates.

426   Proper consideration of uncertainty is crucial to effective management of natural

427 resources (Ludwig, Hilborn & Walters, 1993). A number of studies have shown how failure to

428 consider uncertainty can result in poor management decisions (Regan et al., 2005; Artelle et al.,

429 2013). For example, in population viability analysis, ignoring error in initial population size may

430   result in misleading estimates of population persistence (McLoughlin & Messier, 2004). In the

431   management of cetacean populations, overly precise estimates of abundance can have direct

432   consequences on the determination of potential biological removal and may result in a lack of

433   management action when action should be taken (Taylor et al., 2000). Using a BHSDM,

434   Gerrodette & Eguchi (2012) demonstrated how a more complete consideration of uncertainty of

435   spatial distribution can result in a more cautionary approach to the design of a marine reserve

436   that may ultimately be more effective for conservation. Taken together, these studies suggest

437   that modeling tools used to inform management decisions must prioritize a full assessment of

438   uncertainty to avoid undesirable outcomes.

439

Conclusions

441   Rigorously quantifying uncertainty is a challenging but important goal. Recently,

442   Bravington, Miller & Hedley (2018) developed alternative methods for propagating uncertainty

443   from estimation of detectability into final density estimates within two-stage line transect SDMs.

444   Their approach appears promising, and we expect it will likely become common practice for

445   those conducting two-stage SDM modeling with line transect data. Nevertheless, one stage

446   hierarchical models may be the only way to resolve certain detection processes – for instance, in

447   cases where detectability is a function of individual covariates such as group size, or when

448   species misclassification occurs (e.g. Conn et al. 2012, Conn et al. 2013). Thus, we expect to see

449   continued, parallel development of hierarchical models for line transect data together with two-

450   stage SDMs.

451

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452

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Table 1(on next page)

Summary of effort by season and platform

1   **Table 1: Summary of effort by season and platform.**

Platform	Effort (km)			
	Spring	**Summer**	**Fall**	**Winter**
NE Shipboard	0	8,146	0	0
NE Aerial	7,502	10,468	11,038	3,573
SE Shipboard	0	8,537	2,093	0
SE Aerial	17,978	16,835	11,818	6,007

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3

Table 2(on next page)

Comparison of posterior estimates for detection functions

Comparison of posterior estimates for the detection function estimated from the Bayesian hierarchical species distribution model (BHSDM) to estimates of the detection function from the mark-recapture distance sampling (MRDS) analysis using program Distance. Results are shown for each survey along with the truncation distance (W) used in each analysis. Estimates of detection from the distance sampling component (P_D) and g(0) from the mark-recapture component are shown with coefficients of variation in parentheses.

1 **Table 2: Comparison of posterior estimates for detection functions**

2

3 Comparison of posterior estimates for the detection function estimated from the Bayesian

4 hierarchical species distribution model (BHSDM) to estimates of the detection function from the

5 mark-recapture distance sampling (MRDS) analysis using program Distance. Results are shown

6 for each survey along with the truncation distance (W) used in each analysis. Estimates of

7 detection from the distance sampling component (P_D) and g(0) from the mark-recapture

8 component are shown with coefficients of variation in parentheses.

Model	Survey	W (km)	P_D	g(0)
BHSDM	NE Ship	4	0.31 (0.26)	0.79 (0.06)
MRDS	NE Ship	4	0.28 (0.26)	0.78 (0.08)
BHSDM	SE Ship	8.84	0.53 (0.11)	0.82 (0.08)
MRDS	SE Ship	8.84	0.51 (0.10)	0.77 (0.13)
BHSDM	NE Air	5.24	0.13(0.11)	0.50 (0.17)*
MRDS	NE Air	5.24	0.11 (0.10)	0.50 (0.17)*
BHSDM	SE Air	0.56	0.59 (0.14)	0.90 (0.10)*
MRDS	SE Air	0.56	0.56 (0.12)	0.90 (0.10)*

9 *Estimates of g(0) for aerial surveys were taken from Palka et al. (2017)*

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Figure 1(on next page)

AMAPPS study area

Map of the AMAPPS study area with the shipboard survey track lines in blue and aerial survey track lines in orange for surveys conducted from 2010-2013.
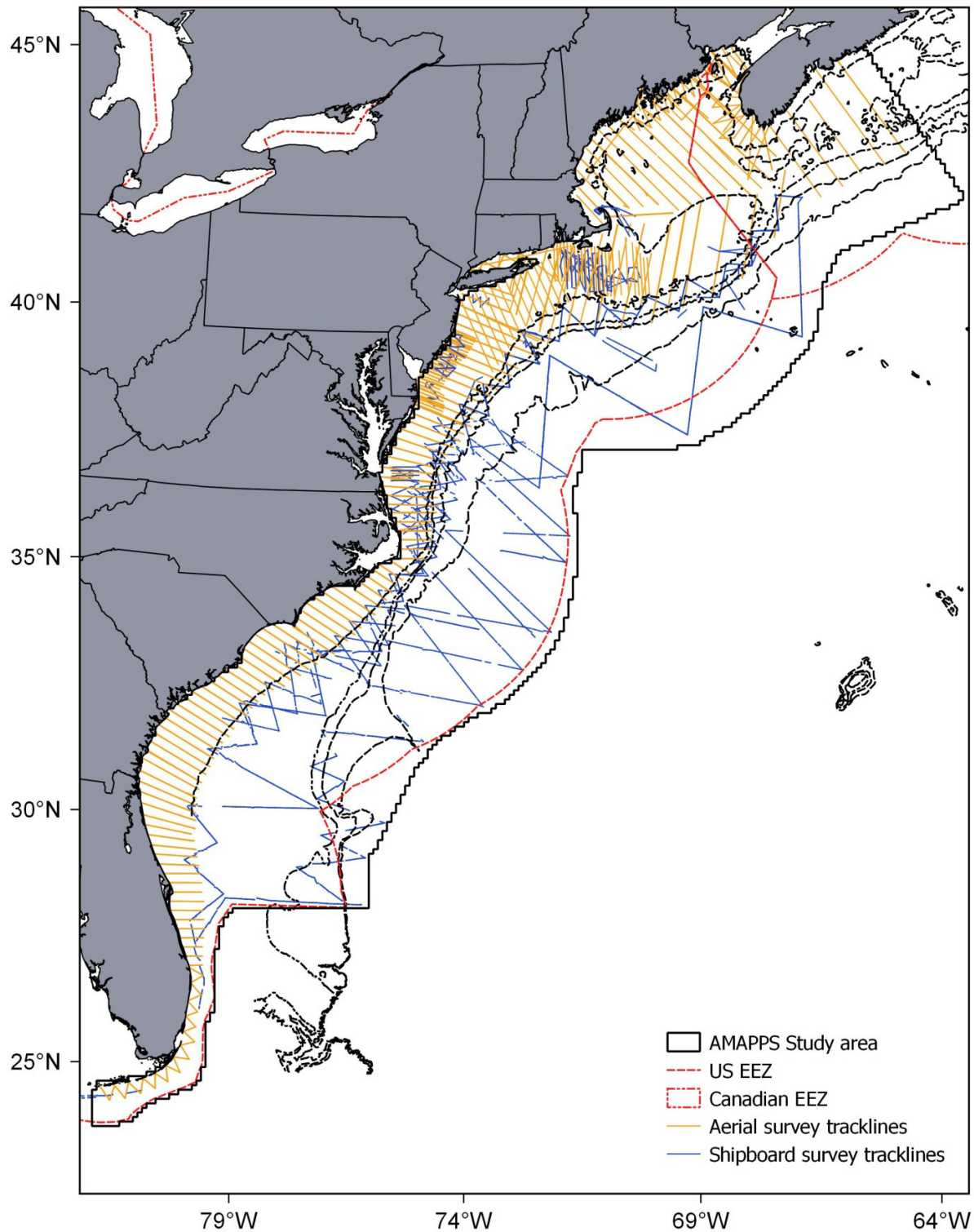
Figure 1: AMAPPS study area

Map of the AMAPPS study area with the shipboard survey track lines in blue and aerial survey

track lines in orange for surveys conducted from 2010-2013.

Figure 2(on next page)

Summary of simulations

Summary results comparing coverage probability after applying the BHSDM and CSDM methods to 1000 simulated datasets. Black lines indicate estimates that covered the true value and red lines indicate estimates that did not cover the true value (a & b). Histograms of coefficients of variation (CV) (c & d) and bias in estimates of population size (e & f) are also shown.
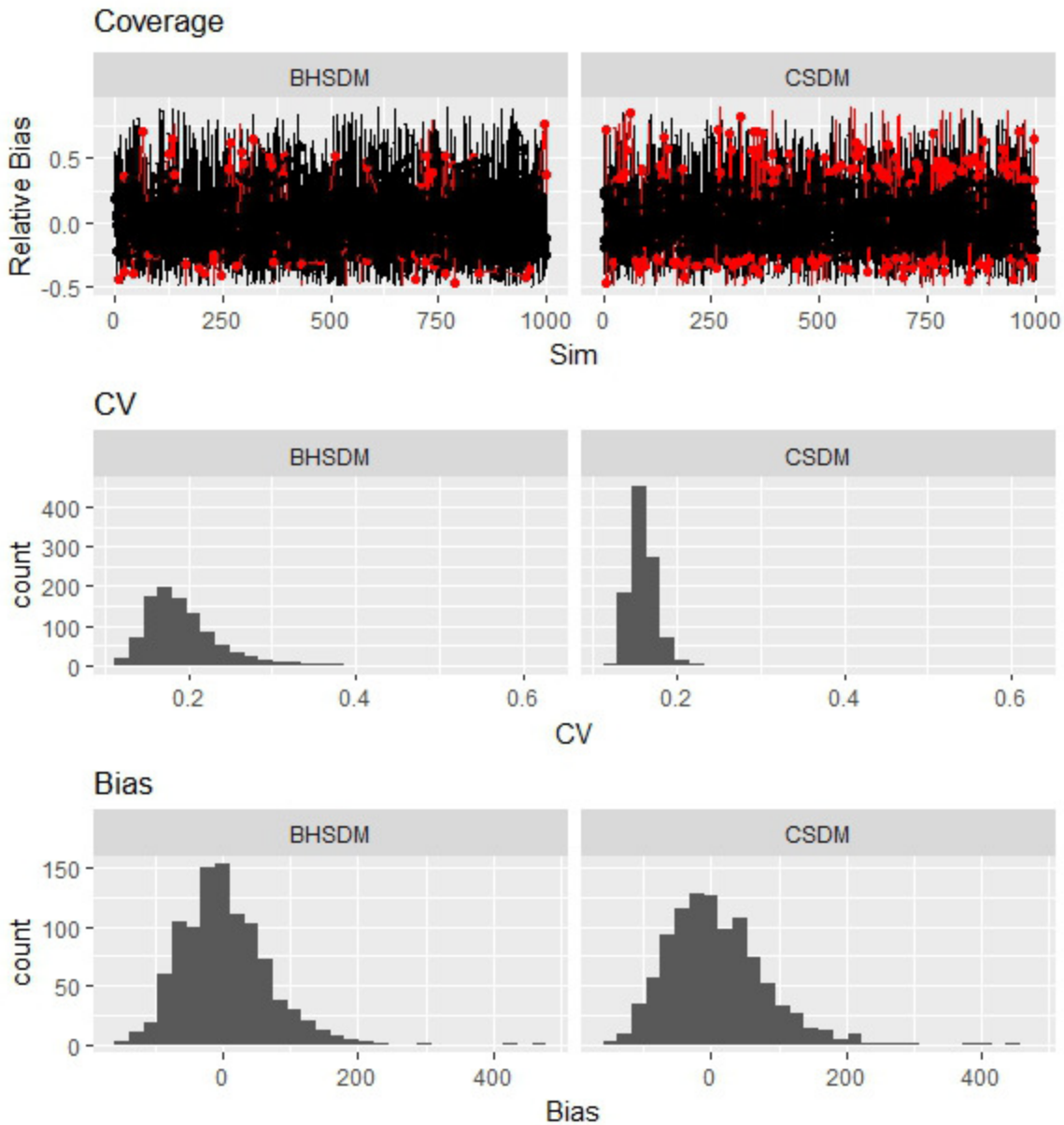
Figure 2: Summary of simulations

Summary results comparing coverage probability after applying the BHSDM and CSDM methods to 1000 simulated datasets. Black lines indicate estimates that covered the true value and red lines indicate estimates that did not cover the true value (a & b). Histograms of coefficients of variation (CV) (c & d) and bias in estimates of population size (e & f) are also shown.

Figure 3 (on next page)

Comparison of density estimates.

Comparison of density estimates from the Bayesian hierarchical species distribution model (BHSDM) vs density estimates from the Conventional species distribution model (CSDM) framework.
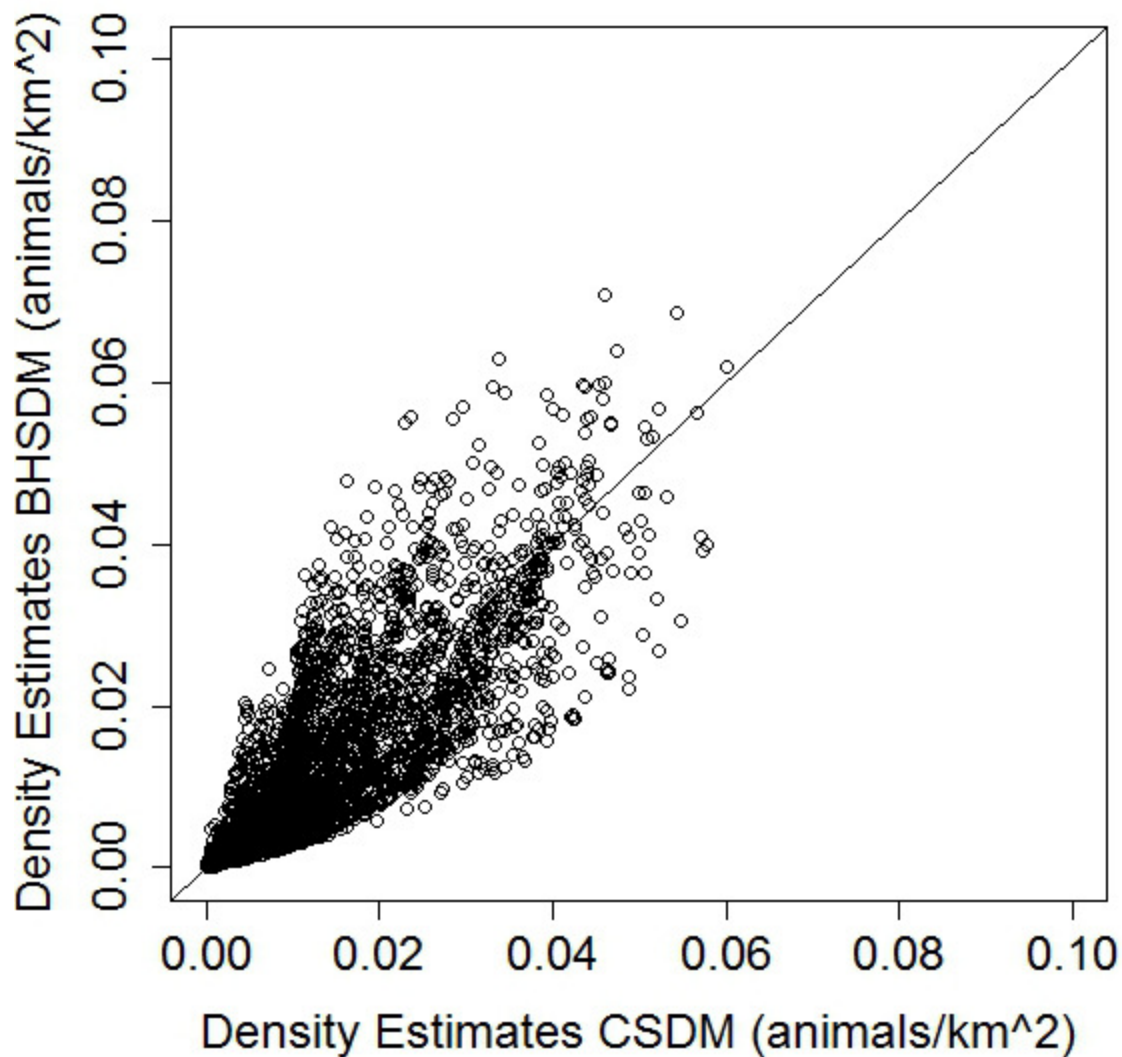
Figure 3: Comparison of density estimates.

Comparison of density estimates from the Bayesian hierarchical species distribution model

(BHSDM) vs density estimates from the Conventional species distribution model (CSDM)

framework.

Figure 4(on next page)

Comparison of coefficients of variation (CVs) for density estimates

Comparison of coefficients of variation (CVs) for density estimates from the Bayesian hierarchical species distribution model (BHSDM) and conventional species distribution model (CSDM). Inner panel shows a histogram of CVs for all density estimates for both the BHSDM and CSDM with median CVs represented by dashed lines. Outer panel shows a plot of CVs vs density estimates for both the BHSDM and CSDM. Only density estimates greater than 0.00001 animal/km^2 are shown.

Figure 4: Comparison of coefficients of variation (CVs) for density estimates

Comparison of coefficients of variation (CVs) for density estimates from the Bayesian hierarchical species distribution model (BHSDM) and conventional species distribution model (CSDM). Inner panel shows a histogram of CVs for all density estimates for both the BHSDM and CSDM with median CVs represented by dashed lines. Outer panel shows a plot of CVs vs density estimates for both the BHSDM and CSDM. Only density estimates greater than 0.00001 animal/km^2 are shown.

Figure 5(on next page)

Predicted densities of fin whales in summer.

Predicted densities and abundance estimates with corresponding coefficients of variation (CV) of fin whales in summer from a species distribution model using a) the CSDM framework and b) the BHSDM framework. Coefficients of variation for the density estimates from c) the CSDM framework and d) BHSDM framework are also provided.
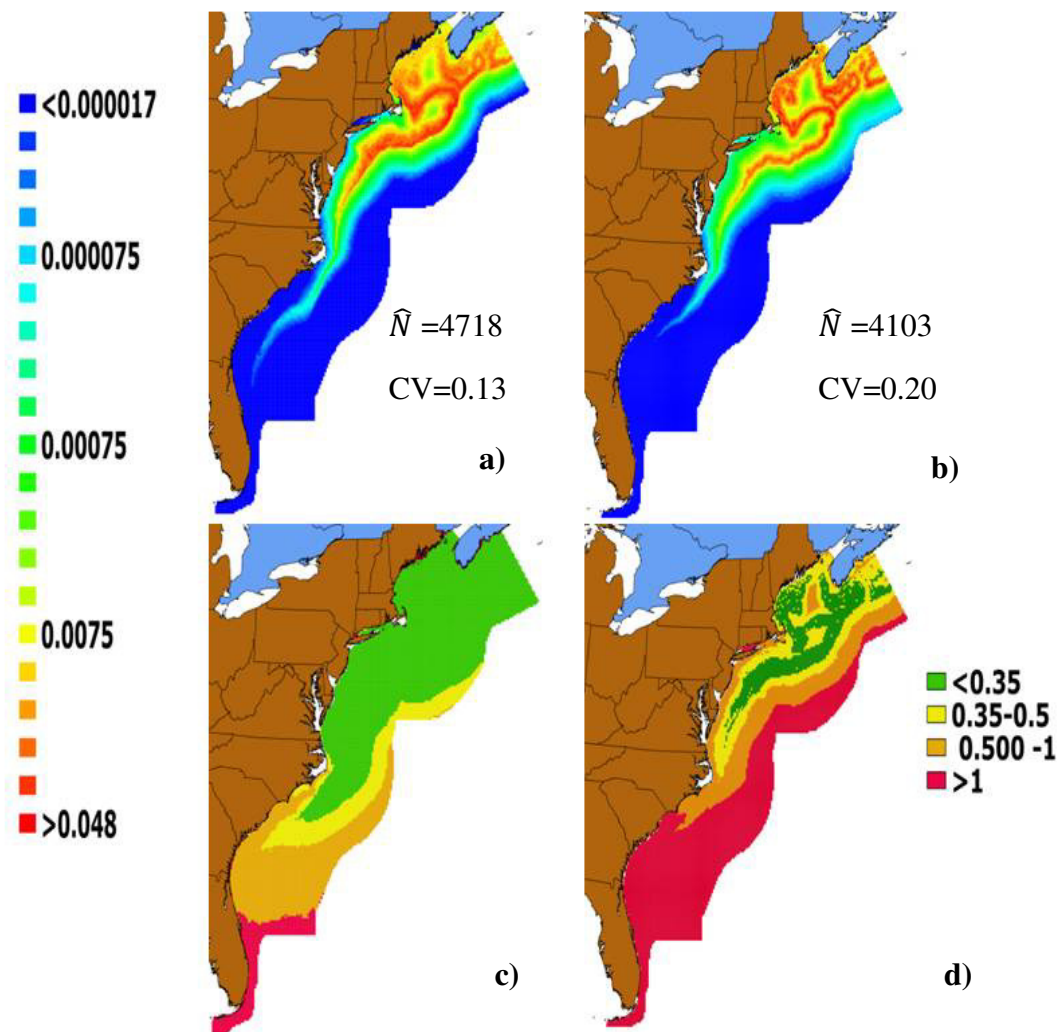
Figure 5: Predicted densities of fin whales in summer.

Predicted densities and abundance estimates ($\hat{N}$) with corresponding coefficients of variation (CV) of fin whales in summer from a species distribution model using a) the CSDM framework and b) the BHSDM framework. Coefficients of variation for the density estimates from c) the CSDM framework and d) BHSDM framework are also provided.