

Chapter 11: A community distance sampling model to investigate the abundance and distribution of seabirds

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Chapter 11 Highlights

Development of a multi-species modeling framework to predict seabird densities across the study area by season, incorporating environmental data and distance sampling

Context¹

A broad geographic and temporal scale of analysis is required to assess exposure to wildlife from proposed development projects. Unlike several chapters in Part IV of this report, which utilize approaches for combining boat and digital aerial survey data, this chapter focuses on using data from a single, well understood survey method (distance sampling), to develop a multi-species model that includes infrequently observed species. Distance sampling generally requires a minimum sample size of 30-60 detections in order to produce valid results. With the data collected in the shipboard surveys, it was common to have fewer than 30 observations of a single species.

In order to estimate the abundance of those species with smaller sample sizes, project collaborators developed a community distance sampling (CDS) model. The technical components of the model development are provided in this chapter, and the model is illustrated on seabird data from a single survey (April 2012). This approach accounts for imperfect detection based on distance sampling, allows incorporation of rarely observed species through a hierarchical modeling structure, and estimates habitat relationships with abundance. Chapter 12 applies the model developed here to the full two years of data collection, and presents broader ecological findings.

Study goal/objectives

Develop a model that makes efficient use of the boat survey data by allowing for estimation of abundance of all observed species, even those with a sparse number of observations.

Highlights

- Successfully developed and implemented a hierarchical community distance sampling model
- Produced estimates of abundance and covariate relationships for all 14 species considered in the analysis of the April 2012 boat survey
- Created a flexible framework for analyzing all boat survey data
- Distance to shore was a significant predictor of abundance, consistent with other findings for the boat data (see Chapter 12).

Implications

This model incorporates data from all species in to the analyses, which allows for making inferences about rare and infrequently observed species that would otherwise have to be discarded. By sharing information across species within a defined community, habitat relationships and abundance can be estimated for each species. In the context of conservation and management, rare and listed species are often of particular interest, and the ability to incorporate rare species into analyses provides important information about their abundance and distribution.

¹ For more detailed context for this chapter, please see the introduction to Part III of this report.

Abstract

Distance sampling is a common survey method in wildlife studies, because it allows accounting for imperfect detection, a known issue when trying to estimate abundance. The framework of distance sampling was employed during the shipboard surveys described in Chapters 7-8. Distance sampling generally requires a minimum sample size of 30-80 observations in order to produce valid results. With the data collected in the shipboard surveys, it was common to have fewer than 30 observations of a single species. In order to estimate the abundance of those species with smaller sample sizes, we developed a new multi-species model for distance sampling. In this chapter, we describe this model and provide an implementation example using data from the April 2012 survey. Non-technical readers may choose to skip to Chapter 12, in which all marine bird data from the boat survey were analyzed, for ecological insights provided using this model.

Specifically, in this chapter we develop a community distance sampling model that allows abundance to vary with environmental covariates. The model allows species-specific parameters, but these come from a common underlying distribution. This hierarchical model structure enables the incorporation of species with sparse data sets that would be otherwise discarded from analysis. We applied the model to marine bird data collected during the shipboard surveys in April 2012. The data set contained 14 species, out of which 10 yielded insufficient observations (< 30) for individual species models. The development of this new model allowed us to produce estimates of abundance and covariate relationships for all 14 species considered in the analysis. We found a strong negative association of community and species abundance with distance to shore. Sea surface temperature, and prey density in the top 3-5 m of the water column, both measured in situ, had weak effects on marine bird abundance. The model allowed us to make inference about ecology of the marine bird community, including rarely observed species, which is particularly important in a regulatory context.

Introduction

The mid-Atlantic region is an extremely important area for a broad range of marine wildlife species throughout the year. This is due to relatively high levels of productivity, fed in part by nutrient inputs from Chesapeake Bay and Delaware Bay, as well as the region's central location on the eastern edge of the continent and in the middle of an important migratory flyway (Chapter 1; Smith & Kemp 1995; Schofield et al. 2008). Seabirds species are globally more threatened (based on percent of bird species threatened) than comparable groups of birds, and the US ranks as a high priority area for conservation action based on species diversity, numbers of threatened species, and numbers endemic species present (Croxall et al. 2012; Sydeman et al. 2012). Current research indicates that globally monitored seabird populations have declined 70% over the last 60 years (Paleczny et al. 2015). Recently, the development of offshore wind energy facilities has raised additional concern about seabird conservation. Potential threats associated with the construction of offshore wind energy facilities include mortality through collisions, as well as displacement due to avoidance of the wind farms or the altered habitat they create (e.g., Garthe & Hüppop 2004; Petersen & Fox 2007). Minimizing the effects of future offshore wind energy development will require consideration of the distribution and abundance of seabirds across the area of interest, but studying these aspects of seabird ecology is challenging due to their large-scale movements, often clustered occurrence, and the vastness of the marine habitat in which they occur.

Evaluating potential impacts of environmental changes on this group is further complicated by the fact that seabirds comprise a diverse community of species, which are likely affected by environmental changes in different ways.

The shipboard surveys conducted in this study employed a method called distance sampling (Chapter 7). Distance sampling (Buckland 2001; Buckland et al. 2005) is a popular method to survey both terrestrial and marine wildlife species amenable to direct observation. In distance sampling, the probability of detecting an individual is assumed to decrease with increasing distance from the observer (see Figure 11A-1 for an example). This allows estimation of abundance and density while accounting for observation bias. The framework has been extended to accommodate the modeling of abundance at multiple survey sites as a function of site specific covariates (Hedley & Buckland 2004; Royle et al. 2004; Conn et al. 2012). This is also referred to as hierarchical distance sampling (HDS).

HDS provides a framework to investigate factors governing the distribution of individual species. Often, however, rare or elusive species will not yield sufficient observations to parameterize an individual model. The framework further does not allow for exploration of community-level effects of explanatory covariates. Community modeling provides a unified approach towards investigating community-level effects while maintaining the ability to model species-specific parameters (Dorazio & Royle 2005; Dorazio et al. 2006). In community models, species have individual parameters, but information is shared across species by assuming a common underlying distribution for these parameters, which in turn are governed by hyperparameters. The use of collective community data allows for inference about community and species-level patterns and processes, even for those species that are rare and elusive. This concept has been applied repeatedly in occupancy modeling (i.e., species-level detection/non-detection data, Dorazio & Royle 2005; Dorazio et al. 2006; Zipkin et al. 2009, 2010), but to our knowledge, no attempt has been made to combine community modeling with the framework of distance sampling.

Here, we develop a community distance sampling model that estimates both community-level and species-level parameters related to detection and abundance. We use the model to analyze seabird data collected from shipboard distance sampling surveys during April 2012 (analysis of all other surveys can be found in Chapter 12). Our analysis includes a community of 14 species, of which ten did not yield sufficient observations to be analyzed individually. By sharing information across species, the community distance sampling approach is able to estimate covariate effects for all 14 species of seabirds, providing important information on seabird abundance and distribution in areas actively explored for their wind energy potential. The method holds promise for many distance sampling applications to improve estimation of detection and abundance of species and communities.

Methods

This section is based on developing methods in distance sampling and thus requires a fundamental understanding of distance sampling. For a review of distance sampling and hierarchical distance sampling please see Buckland 2001, Hedley & Buckland 2004, Buckland et al. 2005, Royle et al. 2004, and Conn et al. 2012.

Development of the community distance sampling model

In distance sampling, the perpendicular distance of the object of interest to the observer is recorded along a transect or from a point. Detection on the transect line (or at the survey point) is assumed to be perfect and the detection probability of observation m is defined by a declining function f of its distance to the observer, d_m , for example, using a half-normal detection function

$$p_m = \exp\left(-\frac{d_m^2}{2\sigma^2}\right)$$

Here, σ is the scale parameter of the half-normal function. In reality, observations are frequently grouped into $k = 1, 2, \dots, K$ distance categories. Let \mathbf{b} be the $K+1$ break points of the K distance categories, and w be the width of the distance categories. Then, detection probability in k , p_k , is the integral of $f(x)$ over k :

$$p_k = \frac{\int_{b_k}^{b_{k+1}} \exp\left(-\frac{x^2}{2\sigma^2}\right) dx}{w}$$

Individuals are assumed to be uniformly distributed in space, so that the probability of an individual occurring in distance band k , ψ_k , is the proportion of the sampled area covered by k (note that in transect surveys with constant w , the area k is also constant across distance categories, but in point surveys, this area increases with increasing distance from the survey point). The vector of observations across all K distance categories, \mathbf{y} , is a multinomial random variable with size $n = \sum y$ and cell probabilities $\boldsymbol{\pi} = \mathbf{p}/\Sigma \mathbf{p}$.

We can link n to the true abundance N using the total detection probability $p.t = \sum_k p_k$:

$$n \sim \text{Binomial}(p.t, N)$$

When distance sampling surveys are carried out at $j = 1, 2, \dots, J$ survey locations, observations are indexed by location:

$$n_j \sim \text{Binomial}(p.t_j, N_j).$$

Following Royle et al. (2004), we can assume N_j to follow some probability mass function f (e.g., Poisson or negative binomial) for N , and its expected value can be modeled as a function of covariates, \mathbf{X} , e.g.,

$$N_j \sim f(\lambda_j)$$

$$\log(\lambda_j) = \alpha_0 + \boldsymbol{\alpha}'\mathbf{X}_j,$$

where α_0 is the intercept and $\boldsymbol{\alpha}$ is a vector of coefficients associated with the covariates \mathbf{X} . Analogously, detection parameters can be modeled as functions of site specific covariates (Marques & Buckland 2003; Oedekoven et al. 2013); for example, for the half-normal detection function:

$$\log(\sigma_j) = \beta_0 + \boldsymbol{\beta}'\mathbf{Y}_j,$$

Where β_0 is the intercept, and the vector $\boldsymbol{\beta}$ holds the coefficients associated with the detection covariates in \mathbf{Y} .

To expand this approach to a community model for $i = 1, 2, \dots, S$ species, the parameters are further indexed by species, and we ascribe hyperdistributions to the resulting sets of parameters. For example, each species i has an abundance intercept $\alpha_{0,i}$ such that:

$$\alpha_{0,i} \sim \text{Normal}(\mu_{\alpha 0}, \sigma_{\alpha 0}).$$

The hyperparameters of these distributions, here $\mu_{\alpha 0}$ and $\sigma_{\alpha 0}$, are estimated as part of the model and constitute the community parameters shared by all species.

Application: seabirds off the U.S. east coast

Seabird distance sampling data were collected along 656.1 km of boat transects located off the coast of Delaware and Maryland (353.2 km), and Virginia (302.9 km) (Figure 11-1), sampled over the course of four days in April 2012. At any given survey, observations were restricted to one side of the boat (but side varied among surveys) and to the quadrant defined by the line of travel and a 90-degree angle to this line of travel. If seabirds occurred in flocks or clusters, angle and distance to the center of the cluster were estimated and the cluster size was noted. Each cluster was counted as a single record, and all records were individually georeferenced using dLOG (R.G. Ford Consulting, Inc.), a seabird and marine mammal observation program that also records the ship track. Details of the boat survey protocol are described in Chapter 7.

Sea surface temperature and salinity were recorded along these transects at 30-minute intervals using a YSI Pro30 handheld conductivity meter (YSI Inc.) with water drawn through the ship's salt water pump. Sea state and visibility were also recorded at these times. In addition, hydroacoustic data were recorded using a 120 kHz split beam echo sounder (Simrad EK60) with the transducers affixed to the hull of the boat. The acoustic backscatter measured by the echo sounder can be used as an index of prey abundance (e.g., Gurshin et al. 2009). Echo sounding data were binned into 500-m intervals for analysis; due to the position of the transducers on the boat, the first two meters of the water column were not recorded. Echo sounding data were processed using Echoview 5.3 (Myriax Software Pty Ltd., Hobart, Australia). Areas of interference were removed from the data prior to integration of the signal to estimate biomass.

Data preparation

According to the observed distances, we set the maximum observation distance at 1000 m and binned observations into $K = 10$ 100-m distance categories. This binning smooths inaccuracies in distance estimation and reduces effects of movement of birds in response to observers.

Estimating abundance as a function of covariates from distance sampling requires spatial replication of surveys (Royle et al. 2004; Conn et al. 2012). To define these spatial replicates (or survey sites), we divided the 4 ship transects into 73 segments, using points at which environmental covariates were

measured in situ as cut points (Figure 11-1). The resulting segments varied in length from 1.1 to 20.5 km (mean: 8.99 km, SD: 2.51 km). This relatively coarse spatial resolution was necessary to ensure that there were in-situ measurements of the covariates of interest for all segments. We accounted for these differences by using segment length as an offset in the abundance component of the model.

The survey yielded 681 records (i.e., clusters of 1 or more individuals) of 14 seabird species (defined as species that forage at sea). We excluded records with ambiguous species identification (6 observations) and observations without angle and/or distance recordings (43 observations). This may cause some negative bias in abundance estimates, but in the present case, this bias is likely negligible, due to the low number of excluded records. Records with these missing pieces of information appeared to come from across the range of observed species and group sizes, so we expect that the removal of these observations leads to equivalent levels of bias in abundance for all species, and does not bias estimates of group size or of covariate relationships. We discuss means of addressing missing information by model extension in the discussion. The final data set contained 632 records of 14 species (Table 11A-1 in Appendix 11A). As a rule of thumb, estimating abundance from distance sampling data requires at least 60 to 80 observations (Buckland et al. 1993). We applied a more liberal criterion of 30 observations to determine whether or not a HDS model could be applied to data of an individual species; only 4 of the species in this data set had >30 observation. We plotted the number of detections per distance category for all species, both separately and combined, to investigate whether data conformed to the distance sampling assumption of decreasing detection with distance from the observer. We found no indication for violation of this assumption (Appendix 11A).

Covariates

We considered in situ collected temperature (*TEMP*, °C) and prey biomass density (*PD*) derived from echo sounding data, as well as distance to shore (*DTS*, km) as covariates on abundance. To define segment level values of *TEMP* and *DTS*, we took the mean of measurements from the start and end point of each segment. If a segment only had one associated measure (i.e., stretches leading up to the first or following the last measuring point), we used those single measurements as segment values. For *PD*, we averaged all measurements taken within a segment. Foraging depths for species in our dataset are likely to vary greatly with species, water clarity, water depth, and other factors. However, the majority of species in our dataset are visual hunters, and are likely responding to foraging cues from the top several meters of the water column. Therefore, we used prey density in the first 3 to 5 m of the water column (the first 2 m are missed by echo sounding devices). *TEMP* is considered an inverse proxy for prey availability (Hunt et al. 1981; Pinaud & Weimerskirch 2002), whereas echo sounding data gives a direct index of prey availability (e.g., Wiebe et al. 1990; Demer & Hewitt 1995).

As potential covariates on the detection parameter σ we considered sea state (Beaufort values recorded in the survey from 1 = light air/water ripples, to 4 = moderate breeze/small waves and fairly frequent white caps; *BEAU*), visibility (categories from 1 = 300-500 m to 5 = 8000 m plus; *VIS*), and bird behavior (*BEHAV*; see below). For sea state and visibility, we applied the same procedure to obtain segment level values of the observation covariates as described above. For visibility, four segments had a value of 4, and all remaining segments had values of either 1 or 5. Therefore, we transformed visibility into a binary covariate of 'poor' = 1 or 'good' = 4 or 5.

It is conceivable that detectability of birds is reduced for observers on the bridge, as compared to the upper deck. The observation platform was recorded with each observation and changed within segments. Exploratory data analysis showed, however, that close to all observations at sea state 4 were made from the bridge, and almost all observations at lower sea states were made from the deck, suggesting that by accounting for sea state we implicitly account for observation platform. To account for the confounding of sea state and observation platform, we included sea state as a categorical covariate. Finally, because observers changed within segments, it is not straightforward to include an observer effect on detection. All observers were experienced in conducting seabird surveys and used rangefinders for distance estimation. Therefore, we believe that assuming relatively homogeneous skills across observers is reasonable.

Finally, birds flying might be more easily detected than birds on the water. To account for this source of variation in detection, we categorized bird behavior for each observation into “water adjacent” (diving, feeding, loafing, sitting) and “in the air” (flying, milling, following, plunge diving).

Parameterization of the community distance sampling model for the seabird dataset

To fit the community distance sampling model to the seabird data set, we used a negative binomial distribution (with mean λ_{ij} and overdispersion parameter r) for abundance and included all abundance covariates in the predictor, because these describe the ecological process we are interested in. We included a random species-specific intercept and random species-specific coefficients for these covariates in the abundance component:

$$N_{ij} \sim \text{Negative Binomial}(\lambda_{ij}, r)$$

$$\log(\lambda_{ij}) = \alpha_{0,i} + \beta_1 \text{TEMP}_j + \beta_2 \text{PD}_j + \beta_3 \text{DTS}_j$$

To limit the number of parameters in the model due to sparseness in the data, we only included one detection covariate at a time. We assumed that the detectability of the different species is influenced in a similar way by these observation covariates and therefore estimated fixed coefficients β for all species. Differences in detectability among species were accounted for by a random species specific intercept:

$$\log(\sigma_{ij}) = \beta_{0,i} + \beta Y_j,$$

where Y is either *VIS*, *BEAU* or *BEHAV* (note that all covariates are categorical, so that a separate β is estimated for each category minus the reference category, which is absorbed by the intercept). To accommodate *BEHAV*, which is an observation-level (as opposed to environmental, segment-level) covariate, we estimated abundance for the two behavioral categories b using behavior-specific intercepts, $\alpha_{0,i,b}$, in the abundance model. This analysis also allows insight into which species are found near the water surface and which are more likely to be encountered in flight. We looked at effect strengths (Royle & Dorazio 2008) to choose among detection covariates: if the posterior distribution of a given β strongly overlapped 0, we concluded that it was not an important covariate. We based inference on seabird abundance and distribution on a final model that contains all abundance covariates and those covariates on detection deemed influential.

Accounting for clusters of birds

Seabirds are often observed in clusters. In this case, individuals are not observed independently, and clusters should be used as the unit of observation, so that N_{ij} is the estimated number of clusters of species i at site j . To get an estimate of total abundance, we augmented the above described community distance sampling model with a component describing cluster size of observation m , C_m , to be a zero-truncated negative binomial variable, with a mean and dispersion parameter shared by all species:

$$C_m \sim \text{zt Negative Binomial}(\mu_C, \rho)$$

Note that C_m is partially observed, i.e., known for observed clusters and unknown for $N_{ij} - n_{ij}$ unobserved clusters. Although it might seem biologically more appropriate to have a species-specific mean cluster size, 74% of all observations were of single individuals; 95% of all observations were of 4 or less individuals. We therefore decided against the additional complexity of a species-specific cluster size model. Because cluster size was predominantly small, we also refrained from adding it into the observation model as a covariate, but see the discussion for suggestions of how to include cluster size as a detection covariate. We calculated total abundance for a species at a site as the sum of all clusters – observed and estimated – for that species at that site, and total abundance in the survey area by summing over all (observed and estimated) clusters across all sites. The survey area is equivalent to a 1000-m strip along the combined boat transects.

Model fit

We tested model fit using Bayesian p-values (Gelman et al. 1996). These values are obtained by calculating some fit statistic (e.g., a residual) that depends on the model parameters and the observed data, determining the same fit statistic for a new set of data generated from the model under consideration, and then calculating the portion of time the residuals from the newly generated data are larger (or smaller) than those of the original data. If the model fits the data appropriately, the resulting Bayesian p-value will be close to 0.5. We used Freeman-Tukey residuals, R , of the general form

$$R(\mathbf{y}, \boldsymbol{\theta}) = \sum \left(\sqrt{y} - \sqrt{E(\mathbf{y})} \right)^2,$$

where \mathbf{y} is a collection of data, $\boldsymbol{\theta}$ are the parameters of the model describing \mathbf{y} and $E(\mathbf{y})$ is the expected value of \mathbf{y} .

Hierarchical models consist of several components, each of which can be evaluated for model fit. We calculated R and associated Bayesian p-values for the species and site-specific abundances, N_{ij} , to assess fit of the abundance component; for the observations \mathbf{y} to assess fit of the observation component; and cluster size \mathbf{C} to assess fit of the cluster size component. Note that all N_{ij} are latent and subject to the specific assumptions of the distribution they are simulated from. It may therefore be more appropriate to use number of individuals observed at each site (generated from the model as $N_{ij} * p.t_j$) to evaluate fit of the abundance model based on observed data. This, however, confounds the detection and abundance models. In the present case, using N_{ij} directly allowed us to determine that a Negative Binomial distribution provided a better fit than a Poisson distribution. Formulas for residuals and associated Bayesian p-values are listed in Appendix 11C.

Implementation

We implemented the community distance sampling model in a Bayesian framework using the software JAGS (Plummer 2003) accessed through R version 2.15.2 (R Core Team 2014). We ran three parallel Markov chains started at different initial values with a burn-in of 1,000 iterations and 50,000 post burn-in iterations. Because of the large number of parameters to be monitored, we thinned chains by 20 to reduce the size of the model output. We tested for chain convergence using the Gelman-Rubin statistic (Gelman et al. 2004). This statistic is a measure of among-chain versus between chain variance, and values < 1.1 indicate convergence. We report results as posterior means and standard deviations, as well as 2.5 and 97.5 percentiles, which represent the Bayesian equivalent to 95% Confidence Intervals (95BCI). We consider covariate effects as strong/significant if their 95% BCI do not overlap 0. Posterior distributions of total abundance estimates across all sites for the less abundant species tended to be right-skewed. Therefore, we provide the mode in addition to the mean in our summary statistic for species level abundances.

Results

The community distance sampling model provided estimates of abundance of 14 seabird species, and identified covariates influencing their detectability and distribution. Neither visibility ($\beta = 0.015 \pm 0.075$, 95BCI: -0.136, 0.161) nor behavior ($\beta = 0.089 \pm 0.068$, 95BCI: -0.043, 0.222) had a strong effect on detectability (Table 11B-1 and Table 11B-5 in Appendix 11B), but sea states 3 and 4 had a strong negative effect on detectability of seabirds, relative to sea state 1 (Figure 11-3, panel B, Table 11B-3 in Appendix 11B). Therefore, we considered the model with *TEMP*, *DTS* and *PD* as covariates on abundance, a species-specific intercept for the detection parameter σ , and sea state as detection covariate as our final model and present results from this model only. Detailed results of all models can be found in Appendix 11B. According to the Bayesian p-values, the community distance sampling model fit the seabird data appropriately (Appendix 11C).

Distance to shore had a strong negative effect on seabird abundance across the entire community, with a mean, μ_{α_1} , of -0.999 ± 0.252 (Table 11B-3 in Appendix 11B). The effect was significantly negative for all but five species; for Surf Scoters, Lesser Black-backed Gull, Laughing Gulls, Herring Gulls and Forster's Terns the effect was negative but credible intervals overlapped 0 (Figure 11-2, panel A). Although the mean effect of sea surface temperature on the seabird community was negligible at -0.001 ± 0.170 (Table 11B-3 in Appendix 11B), it had a significantly positive effect on two species (Royal Tern, Common Tern; Figure 11-2B in Appendix 11B). The community mean effect of prey density was similarly weak (-0.018 ± 0.159) and was non-significant for all species (Table 11B-3 in Appendix 11B, Figure 11-2, panel C).

The mean detection parameter across species, μ_{θ_0} , was 216.269 ± 21.104 m at sea state = 1 and declined to 159.415 ± 18.680 m at sea state = 4 (Figure 11-3, panel B). Among species, σ at sea state = 1 varied between 183.943 and 271.566 m (Figure 11-3, panel A). Mean cluster size for all species was 1.927 ± 0.107 individuals; the overdispersion parameter for the negative binomial cluster size model was 0.145 ± 0.016 . Total abundance across all survey sites was highest for Common Loons (mode = 1677) and lowest for Forster's Terns and Surf Scoters (mode = 2) (Table 11B-4 in Appendix 11B).

Discussion

The framework of community modeling so far has been applied mostly within occupancy models (Zipkin et al. 2009, 2010). We developed a community distance sampling model and used it to estimate relationships between abundance and environmental covariates for 14 species of seabirds, out of which only four species had enough observations to be modeled independently. Sharing information across ecologically similar species allows us to draw inferences about rare species, which are often of particular conservation concern.

Although information is shared by modeling covariate relationships of all species as coming from a common underlying distribution, there is still flexibility for species to have distinct covariate relationships. The community mean effect of *TEMP* on abundance, for instance, was close to 0 (Table 11B-3), yet *TEMP* had a significantly positive effect on abundance for two species (Figure 11-2, panel B). Similarly, the detection parameter σ showed some variation across species, and Northern Gannets had a significantly larger σ than the community average (Figure 11-3, panel A). This can be explained by the species' large size and predominantly bright white plumage, making it easily visible across longer distances.

Seabird abundance and distribution

Common Loon, Northern Gannet and Laughing Gull had the highest estimated abundances in the study area (here, meaning a 1000-m strip along the ship transects). Laughing Gulls are generally common in the region at this time of year (Burger 2015), as are Northern Gannets, which leave for breeding grounds in the north later in the spring (Mowbray 2002), and Common Loons, which winter in the study area and tend to leave between March and June (Evers et al. 2010). In contrast, Surf Scoters and Forster's Terns were extremely rare during the April survey. Surf Scoters winter off the east coast of the US, but by April have mostly begun migrating to breeding grounds further north (Savard et al. 1998). Forster's Terns, on the other hand, are present year round (McNicholl et al. 2001), but stay very close to the shore and are therefore rare in the offshore community surveyed in the present study.

Abundance of all species decreased with increasing distance to shore (Figure 11-2, panel A), which can be a limiting factor for foraging activities (Weimerskirch 2007; Fauchald 2009). In addition, we expect *DTS* to correlate positively with ocean depth. Bathymetry has repeatedly been shown to be an important predictor of seabird foraging activity and abundance (e.g., Freeman et al. 2010; Nur et al. 2011), and the negative effect of *DTS* may be the result of seabirds actually responding to bathymetry.

Seabirds are top predators, and we expected a positive relationship with *PD* and an inverse relationship with *TEMP* (Hunt et al. 1981; Pinaud & Weimerskirch 2002). Contrary to our expectation, we observed mostly very weak effects of *TEMP* and *PD* on the abundance of seabird species (Figure 11-2, panels B and C). Lower sea surface temperatures are generally associated with higher primary productivity. There are, however, several intermediate trophic levels between primary production and top marine predators like seabirds (Barnes & Hughes 1988), which can lead to spatio-temporal lags in the response of seabirds to changes in these covariates.

It is also conceivable that the in-situ measures of *PD* and *TEMP*, taken immediately under the boat, do not adequately represent the environmental conditions in the 1000-m strip sampled. At an average resolution of approximately 10 km (i.e., the average lengths of transect segments), our study corresponds to a coarse-scale evaluation of factors driving seabird abundance (Haury et al. 1978; Hunt & Schneider 1987). At increasing spatial scales, temporal lags in the response of seabirds to environmental characteristics become more pronounced (Wiens 1989), and in situ measures cannot accommodate such lags. This indicates a need to determine the adequate spatial and temporal scale at which explanatory covariates are measured. A comparison of model fit between remote sensed data of different spatio-temporal scales and of in situ data could provide interesting insight for optimized choice of covariates.

Modeling detection probability

Neither visibility nor whether birds were observed on the water or in the air (“behavior model”) had a significant impact on detection distances of seabirds. In order to maintain reasonable sample sizes, we felt we could not subdivide observations into more than two behavioral classes. This coarse grouping may blur detection effects associated with certain behaviors. In spite of these ambiguities, we believe that the conceptual set-up of the “behavior” model allows for some interesting ecological insight into the percentage of individuals in a population performing certain behaviors. The approach of estimating abundance separately for two behavioral categories circumvents the issue of unknown behavioral category of unobserved individuals/clusters, but likely performs poorly with an increasing number of categories (due to low sample size per category), and breaks down completely for continuous individual covariates. In these cases, a different approach is to treat individual covariates of unobserved clusters as missing data, and specify a parametric model to estimate missing covariate values (e.g., Conn et al. 2014), which is equivalent to how the present model deals with cluster size of unobserved seabirds (see Accounting for clusters of birds).

Diving behavior makes birds unavailable for detection while under water, and failure to take into account availability <1 will lead to negative bias in abundance estimates. Availability can be estimated separately, for example from intensive observation studies or telemetry studies that allow inference on animal behavior (e.g., Diefenbach et al. 2007; Conn et al. 2014), and can be incorporated into the estimator of abundance (Buckland 2001) so that Eq. 1 becomes

$$n_{ij} \sim \text{Binomial}(p \cdot t_{ij}, N \cdot a_{ij}).$$

Here, $N \cdot a_{ij}$ is the number of individuals of species i at site j that are available for detection, $p \cdot t_{ij}$ is the total detection probability, and

$$N_{ij} = \frac{N \cdot a_{ij}}{p \cdot a_{ij}},$$

where $p \cdot a_{ij}$ is the probability of being available, which can be species and site-specific.

Uncertainty about these estimates could readily be incorporated by treating availability as a parameter, rather than fixing it, and formulating an informative prior based on available information.

We did not explore differences in observer skills because the observer changed within a transect but time of change was not noted. If information was collected about where/when during the transect conditions changed, the detection parameter σ could be modeled as a weighted mean of observer-specific σ for each transect, considering which proportion of the transect was covered by each observer.

Finally, we did not include cluster size of birds as an explanatory covariate in the detection model because the present data set contained predominantly small clusters. This situation is not necessarily representative: many studies report occasional observations of large aggregations of seabirds. In these situations, the effect of cluster size on detectability (e.g., Smith et al. 1995; Pearse et al. 2008) should be considered. Observed cluster size can easily be included as a covariate on the log-linear predictor of σ . Further, different parameterizations of the cluster size model itself, for example in the form of species-specific means or distributions allowing for more variability in counts, may be required to adequately describe the observed data (Zipkin et al. 2014).

Missing individual covariate values

In the present case, we excluded observations with uncertain species identification and/or missing distance-to-transect information. Rather than excluding such incomplete observations, which can negatively bias abundance estimates, species identity and distance can be viewed as missing individual covariates, which can readily be accommodated in a Bayesian framework. The present model could be augmented with a species identification model as developed by Conn et al. (2013, 2014). Here, species identity is treated as a latent variable with a multinomial distribution. Knowledge about the species-specific identification probabilities (e.g., from double-observer surveys or experiments with known species identity) can be used to formulate informative priors on these multinomial cell probabilities (with vague priors, unidentified observations will be distributed among species according to their proportion in the identified observations). Missing distances are naturally sampled from the multinomial model (for the present case of discrete distance bins) specified for the observations \mathbf{y} (see Development of the community distance sampling model) if it is reasonable to assume that the probability of not recording a distance occurs at random across distance bins. Otherwise, additional information about this process would be necessary.

Distance sampling is employed in the study of a variety of taxa, and often, data on multiple species are collected (Jathanna et al. 2003; Somershoe et al. 2006; Williams & Thomas 2007). The present approach allows such studies to investigate community ecology and distribution of many species from within a flexible and coherent modeling framework. In the context of conservation and management, rare and listed species are often of particular interest, and the ability to incorporate rare species into analyses provides important information about their abundance and distribution.

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Figures

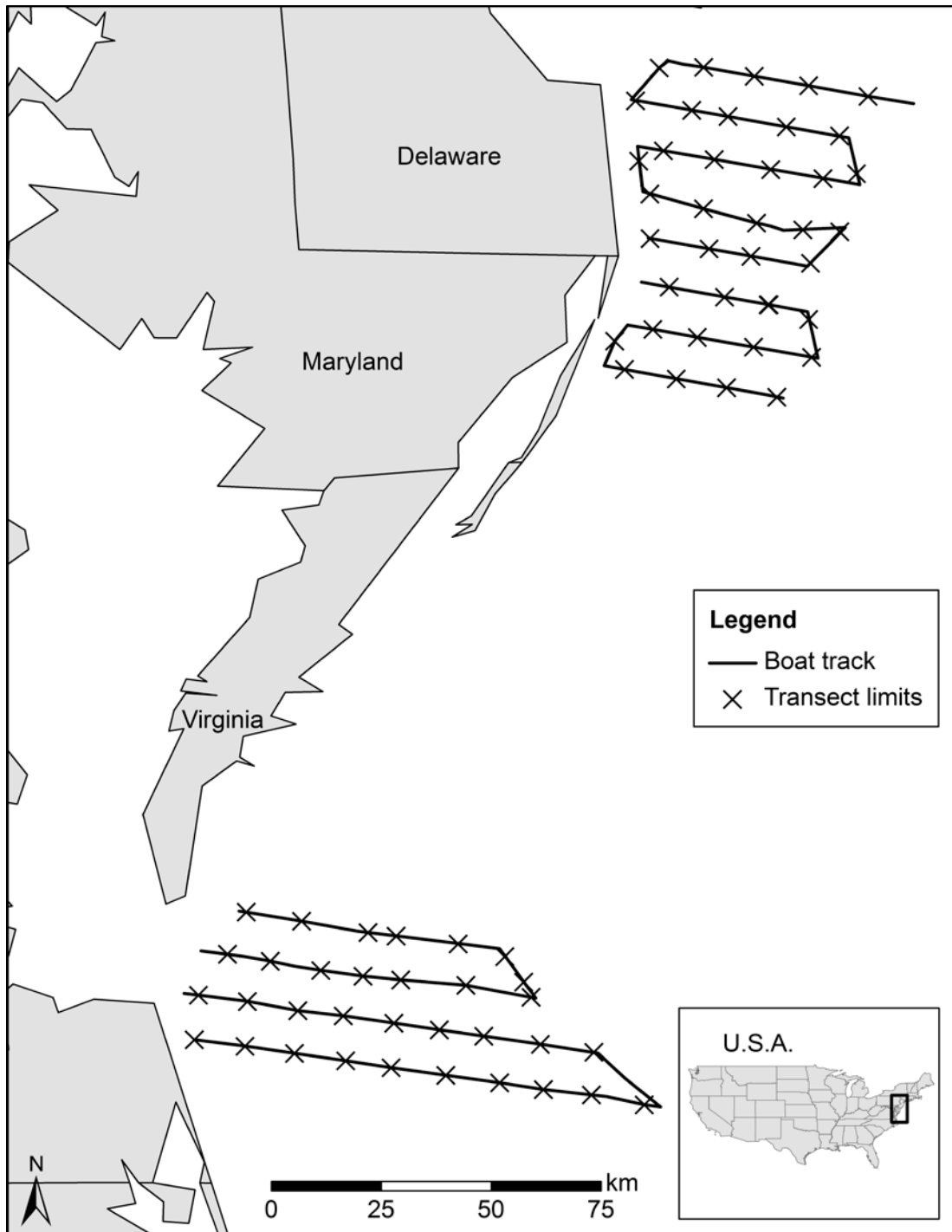


Figure 11-1. Boat distance sampling transects implemented in April 2012 to survey seabirds, subdivided into 73 segments (x); inset map shows approximate location of the study area in the U.S.A.

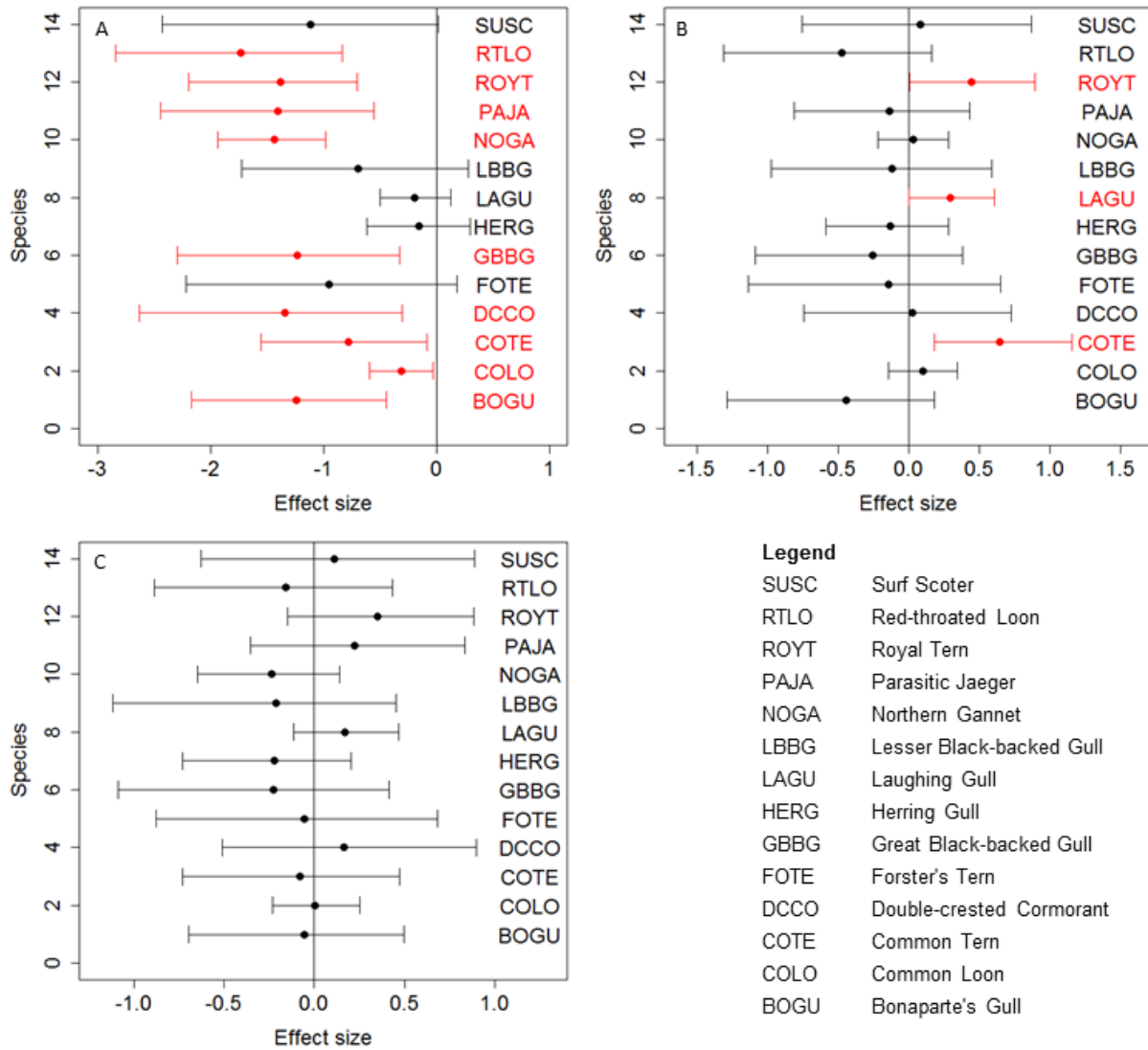


Figure 11-2. Species specific effects of distance to shore (A), sea surface temperature (B) and prey density in the first 3-5 m of the water column (C) on seabird abundance, estimated from shipboard surveys off the coast of Delaware, Maryland and Virginia, using a community distance sampling model. Red bars indicate species with effects significantly different from 0.

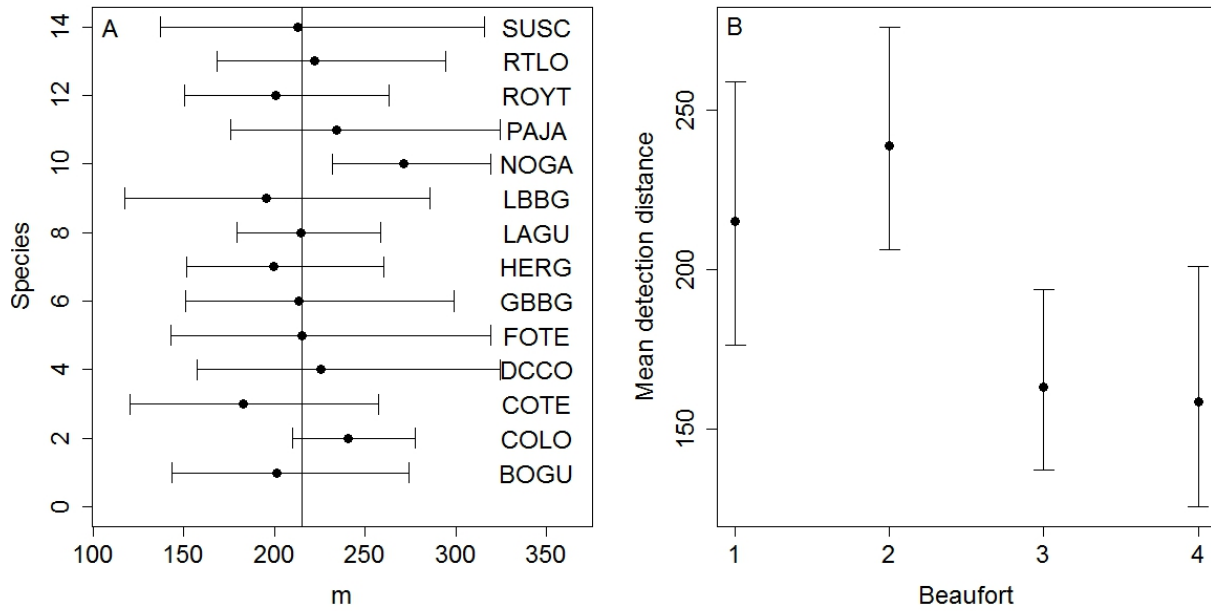


Figure 11-3. Species specific detection parameters, σ , with vertical line representing community mean (A), and community mean σ (with posterior standard deviation) as a function of sea state (B). For full species names, see Figure 2.

Supplementary material

Appendix 11A. Histograms of counts across distance classes

We plotted histograms of detection distance categories for data of all 14 seabird species (Table 11A-1), first combined (Figure 11A-1) and then for each species separately, to check for deviation from the prerequisite that detections decrease with distance (see main text for description of data set). Five species did not have the highest number of detections in the lowest distance category, but four of these species only had 1 – 3 records, so that these patterns likely arose by chance. The Red-throated Loon (Figure 11A-2) had 13 records spread across the first four distance categories without discernable pattern. This could be a spurious pattern due to low sample size, or indicate a wider shoulder in the detection function of this species. Since there was no strong indication of increasing detection with distance, evasive movements (a clear maximum at >1), or a multimodal detection function, we conclude that application of the half-normal model for detection was appropriate.

Table 11A-1. Seabird species (common name, Latin name and four-letter code used in future tables and figures) and number of records (clusters) used in the present community distance sampling model; data collected during shipboard surveys off the coast of Virginia, Delaware and Maryland in April 2012.

Common name	Latin name	Code	Number of records
Bonaparte's Gull	<i>Larus philadelphia</i>	BOGU	11
Common Loon	<i>Gavia immer</i>	COLO	282
Common Tern	<i>Sterna hirundo</i>	COTE	13
Double-crested Cormorant	<i>Phalacrocorax auritus</i>	DCCO	3
Forster's Tern	<i>Sterna forsteri</i>	FOTE	1
Great Black-backed Gull	<i>Larus marinus</i>	GBBG	6
Herring Gull	<i>Larus argentatus</i>	HERG	31
Laughing Gull	<i>Larus atricilla</i>	LAGU	91
Lesser Black-backed Gull	<i>Larus fuscus</i>	LBBG	3
Northern Gannet	<i>Morus bassanus</i>	NOGA	145
Parasitic Jaeger	<i>Stercorarius parasiticus</i>	PAJA	9
Royal Tern	<i>Sterna maxima</i>	ROYT	23
Red-throated Loon	<i>Gavia stellata</i>	RTLO	13
Surf Scoter	<i>Melanitta perspicillata</i>	SUSC	1

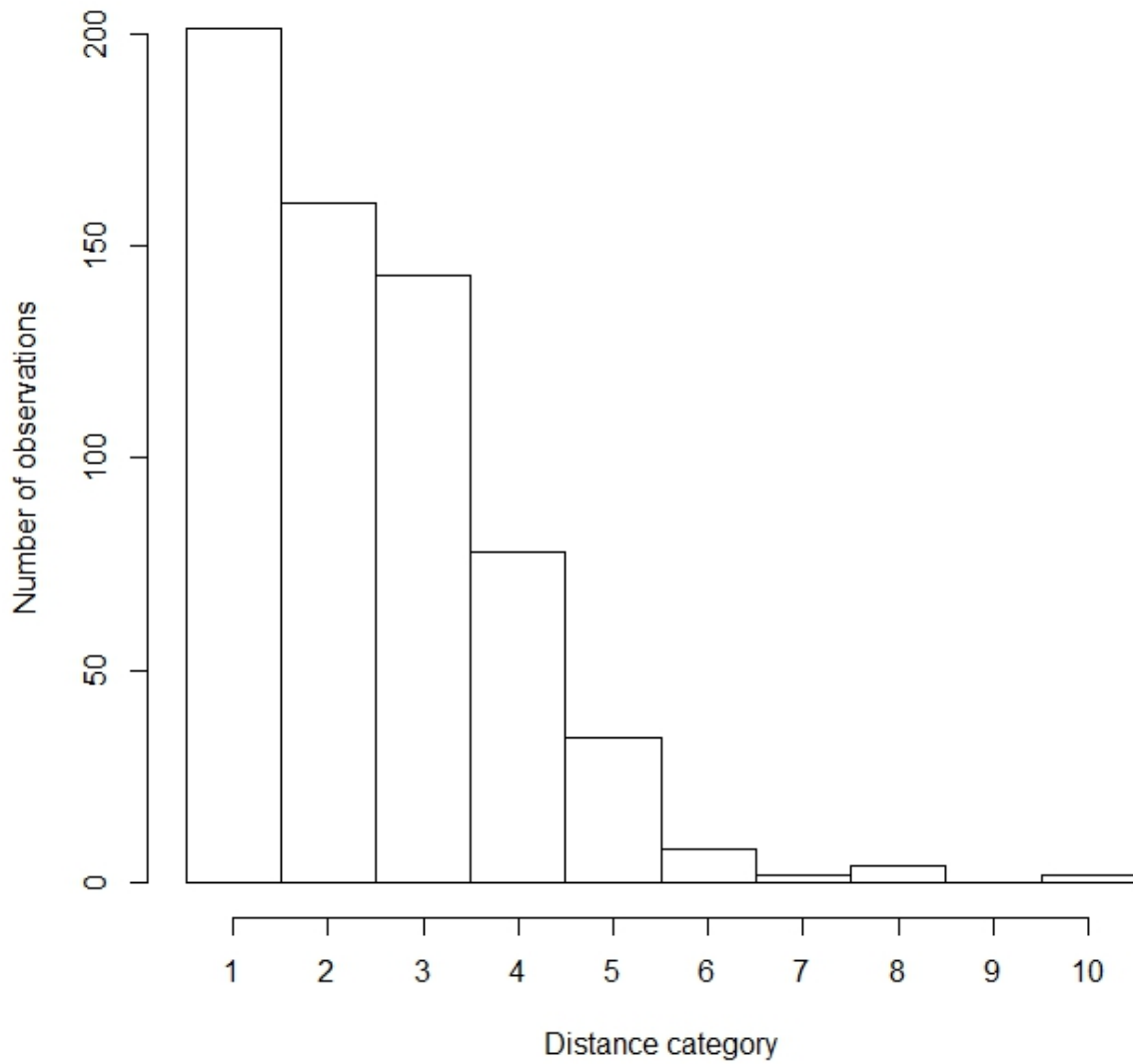


Figure 11A-1. Histogram of observations in each distance class across all species and survey sites. Each distance category is 100m in length.

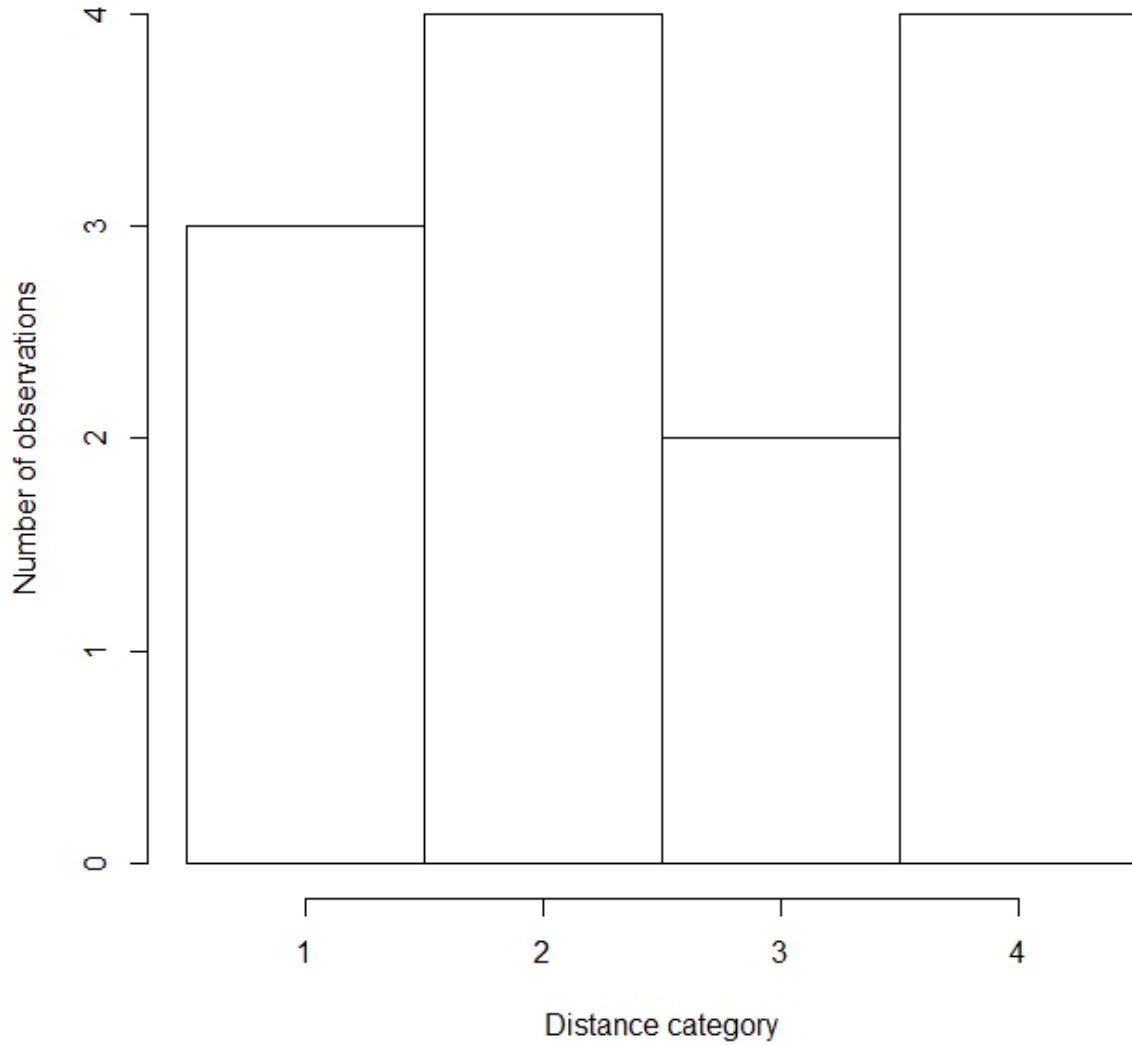


Figure 11A-2. Histogram of observations per distance class for Red-throated Loons. No observations were made in distance classes 5 – 10.

Appendix 11B. Additional model results

We ran several community distance sampling models on the seabird data set (see main text for model and data set description), all of which included distance to shore (*DS*), sea surface temperature measured in situ (*TEMP*), and prey biomass density (*PD*) as covariates on abundance. The models differed in the detection covariates: visibility (*VIS*, binary, good or poor), Beaufort (*BEAU*, categorical, 1-4) or behavior (*BEHAV*, binary, on water or flying). Main results of the model including *BEAU* are presented in the main text. Detailed results of all models are summarized here.

Visibility as a covariate

Table 11B-1. Posterior summaries for community parameters (on log scale) from a community distance sampling model with visibility (1 = poor, 2 = good) as observation covariate, fitted to seabird observations collected off the shore of Maryland, Delaware and Virginia, USA. SD is the standard deviation, 2.5% and 97.5% are the respective quantiles. DTS = Distance to shore, TEMP = sea surface temperature, PD = prey biomass density.

Component	Term	Mean	SD	2.5%	97.5%
Abundance	Intercept mean*; $\mu_{\alpha 0}$	-3.135	0.574	-4.309	-2.028
	Intercept SD*; $\sigma_{\alpha 0}$	1.978	0.469	1.279	3.099
	DTS, mean*; $\mu_{\alpha 1}$	-1.000	0.253	-1.538	-0.538
	DTS, SD*; $\sigma_{\alpha 1}$	0.694	0.210	0.379	1.196
	TEMP, mean*; $\mu_{\alpha 2}$	-0.018	0.175	-0.393	0.305
	TEMP, SD*; $\sigma_{\alpha 2}$	0.474	0.162	0.233	0.860
	PD, mean*; $\mu_{\alpha 3}$	-0.006	0.158	-0.336	0.291
	PD, SD*; $\sigma_{\alpha 3}$	0.378	0.145	0.181	0.736
	Negative binomial overdispersion; r_N	0.982	0.170	0.702	1.368
Detection	Intercept mean*; $\mu_{\beta 0}$	5.319	0.164	5.001	5.647
	Intercept SD*; $\sigma_{\beta 0}$	0.230	0.094	0.090	0.456
	Visibility 2; β_1	0.015	0.075	-0.136	0.161
Cluster size	Mean, μ_C	1.926	0.107	1.738	2.157
	Negative binomial overdispersion; ρ	0.145	0.016	0.116	0.177

* Hyperparameters for random effects across species

Table 11B-2. Posterior summaries for abundance of 14 seabird species within a 1000-m strip along 73 shipboard transect segments surveyed off the coast of Maryland, Delaware and Virginia, estimated using a community hierarchical distance sampling model with visibility as observation covariate. See Table 1 for full species names and scientific names.

Species	Mean	SD	Mode	2.5%	97.5%
BOGU	91.365	33.394	77	43	171
COLO	1669.878	149.845	1631	1400	1987
COTE	141.090	47.837	119	72	257
DCCO	26.683	13.783	15	11	62
FOTE	10.085	10.364	1	1	38
GBBG	39.993	21.047	29	12	92
HERG	244.930	62.098	224	143	384
LAGU	573.472	88.748	547	418	764
LBBG	24.783	18.044	10	4	71
NOGA	1003.751	91.133	981	842	1198
PAJA	52.309	23.169	40	19	108
ROYT	174.250	44.400	163	103	275
RTLO	79.278	29.604	67	34	149
SUSC	10.231	10.508	1	1	39

Beaufort sea state as a covariate

Table 11B-3. Posterior summaries for community parameters (on log scale) from a community distance sampling model fitted to seabird observations collected off the shore of Maryland, Delaware and Virginia, USA. SD is the standard deviation, 2.5% and 97.5% are the respective quantiles. DTS = Distance to shore, TEMP = sea surface temperature, PD = prey biomass density, BEAU = Beaufort sea state.

Component	Term	Mean	SD	2.5%	97.5%
Abundance	Intercept mean*; $\mu_{\alpha 0}$	-3.122	0.572	-4.271	-2.036
	Intercept SD*; $\sigma_{\alpha 0}$	1.980	0.474	1.286	3.119
	DTS, mean*; $\mu_{\alpha 1}$	-0.999	0.252	-1.538	-0.533
	DTS, SD*; $\sigma_{\alpha 1}$	0.698	0.210	0.383	1.185
	TEMP, mean*; $\mu_{\alpha 2}$	-0.001	0.170	-0.369	0.310
	TEMP, SD*; $\sigma_{\alpha 2}$	0.462	0.159	0.228	0.844
	PD, mean*; $\mu_{\alpha 3}$	-0.018	0.159	-0.349	0.286
	PD, SD*; $\sigma_{\alpha 3}$	0.376	0.144	0.179	0.739
	Negative binomial overdispersion; r_N	1.111	0.203	0.777	1.574
Detection	Intercept mean*; $\mu_{\beta 0}$	5.372	0.098	5.172	5.558
	Intercept SD*; $\sigma_{\beta 0}$	0.183	0.082	0.060	0.379
	BEAU = 2; β_1	0.104	0.074	-0.043	0.250
	BEAU = 3; β_2	-0.278	0.089	-0.452	-0.106
	BEAU = 4; β_3	-0.307	0.119	-0.541	-0.068
Cluster size	Mean, μ_c	1.927	0.107	1.739	2.155
	Negative binomial overdispersion; ρ	0.145	0.016	0.116	0.177

* Hyperparameters for random effects across species

Table 11B-4. Posterior summaries for abundance of 14 seabird species within a 1000-m strip along 73 shipboard transect segments surveyed off the coast of Maryland, Delaware and Virginia, estimated using a community hierarchical distance sampling model. See Table A1 for full species names and scientific names.

Species	Mean	SD	Mode	2.5%	97.5%
BOGU	89.744	31.980	74	43	166
COLO	1739.703	155.662	1677	1460	2071
COTE	132.217	42.760	118	70	235.525
DCCO	28.214	14.704	17	11	66.525
FOTE	10.307	10.550	2	1	39
GBBG	40.968	21.026	29	12	92
HERG	229.144	57.698	225	135	357
LAGU	607.911	93.989	540	443	813
LBBG	24.517	17.211	11	4	68
NOGA	1039.370	96.975	1029	867	1244.525
PAJA	55.882	24.107	44	21	114
ROYT	183.932	46.341	168	109	286.525
RTLO	83.124	30.262	71	37	155
SUSC	10.461	10.455	2	1	40

Behavior as a covariate

Table 11B-5. Posterior summaries for community parameters (on log scale) from a community distance sampling model with behavior (on the water = 1, flying = 2) as observation covariate, fitted to seabird observations collected off the shore of Maryland, Delaware and Virginia, USA. SD is the standard deviation, 2.5% and 97.5% are the respective quantiles. DTS = Distance to shore, TEMP = sea surface temperature, PD = prey biomass density.

Component	Term	Mean	SD	2.5%	97.5%
Abundance	Intercept mean, behavior = 1*; $\mu_{\alpha 0,1}$	-4.439	0.636	-5.781	-3.251
	Intercept SD, behavior = 1*; $\sigma_{\alpha 0,1}$	2.053	0.548	1.265	3.379
	Intercept mean, behavior = 2*; $\mu_{\alpha 0,2}$	-3.456	0.529	-4.544	-2.445
	Intercept SD, behavior = 2*; $\sigma_{\alpha 0,2}$	1.792	0.433	1.144	2.821
	DTS, mean*; $\mu_{\alpha 1}$	-0.925	0.233	-1.411	-0.494
	DTS, SD*; $\sigma_{\alpha 1}$	0.659	0.192	0.371	1.112
	TEMP, mean*; $\mu_{\alpha 2}$	-0.011	0.165	-0.365	0.292
	TEMP, SD*; $\sigma_{\alpha 2}$	0.456	0.152	0.227	0.816
	PD, mean*; $\mu_{\alpha 3}$	-0.020	0.156	-0.344	0.275
	PD, SD*; $\sigma_{\alpha 3}$	0.382	0.139	0.187	0.724
	Negative binomial overdispersion; r_N	0.765	0.118	0.565	1.025
Detection	Intercept mean*; $\mu_{\beta 0}$	5.265	0.111	5.033	5.471
	Intercept SD*; $\sigma_{\beta 0}$	0.255	0.097	0.108	0.487
	Behavior 2; β_1	0.089	0.068	-0.043	0.222
Cluster size	Mean, μ_C	1.925	0.107	1.738	2.154
	Negative binomial overdispersion; ρ	0.145	0.016	0.116	0.177

* Hyperparameters for random effects across species

Table 11B-6. Posterior summaries for abundance of 14 seabird species within a 1000-m strip along 73 shipboard transect segments surveyed off the coast of Maryland, Delaware and Virginia, estimated using a community hierarchical distance sampling model with behavior (on the water or flying) as observation covariate. See Table 11A-1 for full species names and scientific names.

Species	Mean	SD	Mode	2.5%	97.5%
BOGU	93.807	34.199	80	44	175
COLO	1670.765	150.078	1639	1401	1989
COTE	146.834	50.097	127	74	267
DCCO	29.537	15.110	19	12	68
FOTE	13.837	12.471	3	1	47
GBBG	42.777	22.378	32	13	98
HERG	246.100	62.362	228	144	386
LAGU	570.500	88.346	567	416	761
LBBG	28.785	19.987	15	5	80
NOGA	991.598	89.640	972	832	1183
PAJA	53.558	23.281	44	20	109
ROYT	172.406	43.738	160	102	271
RTLO	80.392	29.707	68	35	150
SUSC	14.050	12.708	3	1	48

Table 11B-7. Percent of individuals estimated to be on the water, as opposed to flying, for 14 seabird species sampled along 73 shipboard transect segments off the coast of Maryland, Delaware and Virginia, estimated using a community hierarchical distance sampling model with behavior as observation covariate. See Table 11A-1 for full species names and scientific names.

Species	Mean	SD	2.50%	97.50%
BOGU	0.295	0.137	0.078	0.597
COLO	0.773	0.044	0.679	0.850
COTE	0.164	0.102	0.027	0.414
DCCO	0.374	0.211	0.046	0.810
FOTE	0.281	0.232	0.006	0.817
GBBG	0.347	0.173	0.071	0.718
HERG	0.070	0.046	0.011	0.186
LAGU	0.092	0.036	0.037	0.176
LBBG	0.352	0.209	0.039	0.797
NOGA	0.310	0.064	0.195	0.445
PAJA	0.554	0.159	0.240	0.840
ROYT	0.322	0.111	0.133	0.559
RTLO	0.334	0.134	0.109	0.620
SUSC	0.286	0.233	0.006	0.822

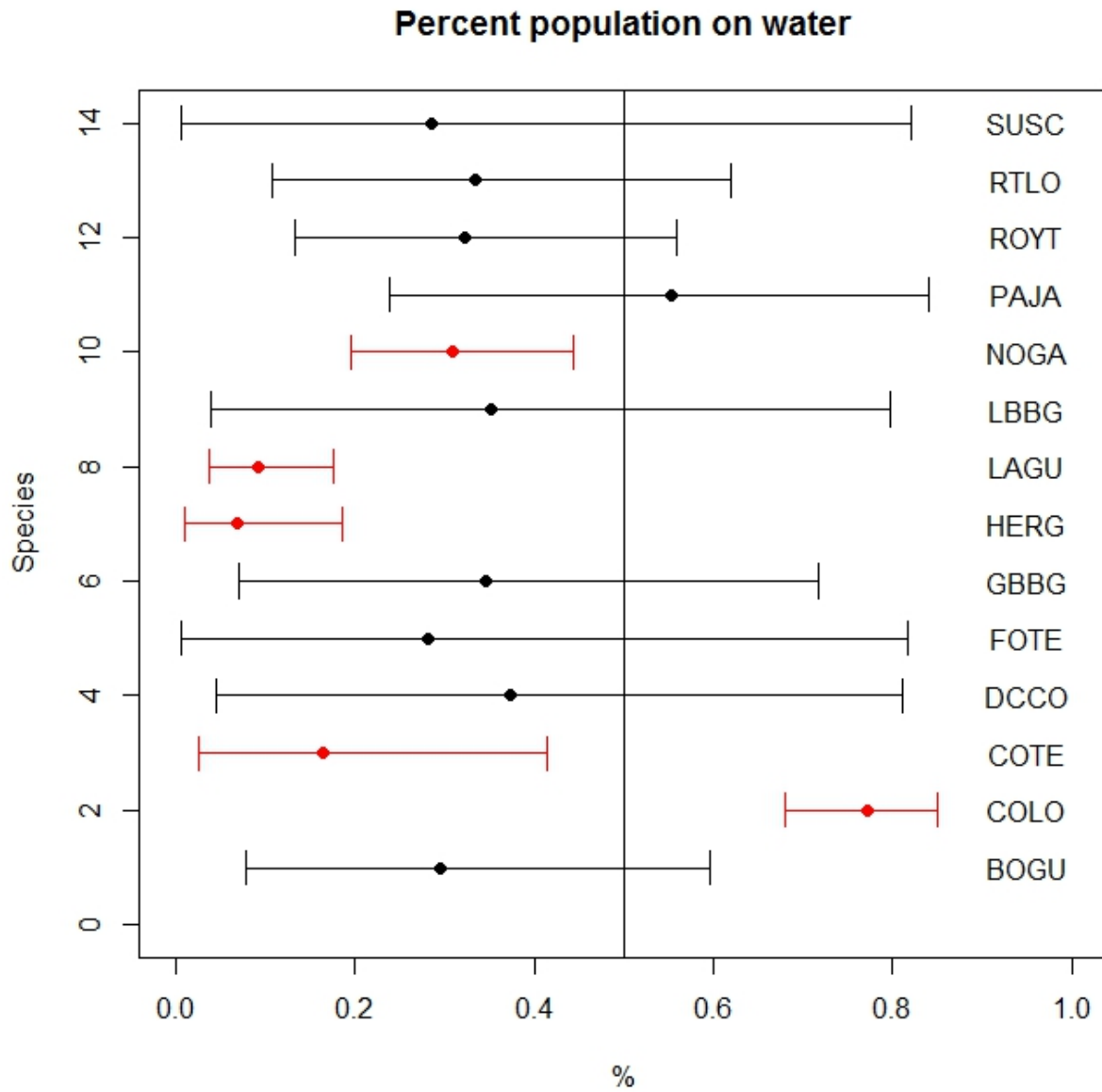


Figure 11B-1. Percent of species population on water (as opposed to in the air), from behavioral model. Red bars indicate a percentage on water significantly different than 50%.

Appendix 11C. Model residuals and Bayesian p-values for the community distance sampling model

We assessed model fit using Bayesian p-values. For the calculation of the Bayesian p-value we used Freeman-Tukey residuals, R , of the general form

$$R(\mathbf{y}, \boldsymbol{\theta}) = \sum (\sqrt{y} - \sqrt{E(y)})^2,$$

where \mathbf{y} is a collection of data, $\boldsymbol{\theta}$ are the parameters of the model describing \mathbf{y} and $E(\mathbf{y})$ is the expected value of \mathbf{y} . We calculated these residuals for the observed data and a new data set generated from the model under consideration. The Bayesian p-value is the percentage of time the residuals from the newly generated data are larger (or smaller) than those of the original data. We used this procedure to decide between a Poisson and a negative binomial distribution in the abundance component of the model (Table C1). For the community distance sampling model with the final set of covariates, we used this procedure to test fit of the three model components (see below; Table C2).

Abundance residuals

Abundance N is estimated for each species i at each site j . We generated a new set of abundances from the model under consideration:

$$N.new_{ij} \sim NegBin(\lambda_{ij}, r)$$

$$\log(\lambda_{ij}) = \alpha_{0,i} + \beta_{1,i}DS + \beta_{2,i}TEMP + \beta_{3,i}PD,$$

where DS = distance to shore, $TEMP$ = sea surface temperature measure in situ, and PD = prey biomass density derived from echo sounding.

We calculated residuals R (for N_{ij}) and $R.n$ (for $N.new_{ij}$) at each iteration t of the Markov chain as

$$R = \sum_i \sum_j (\sqrt{N_{ij}} - \sqrt{\lambda_{ij}})^2$$

$$R.n = \sum_i \sum_j (\sqrt{N.new_{ij}} - \sqrt{\lambda_{ij}})^2.$$

We calculated the Bayesian p-value as

$$p = \sum_t R.n > R.$$

Observation model residuals

In the Bayesian implementation of the model, we use a categorical distribution on the distance classes k of each individual observation m , rather than a multinomial distribution on the counts per distance class. We generated a new set of distances classes, $k.new$:

$$k.new_m \sim \text{Categorical}(\boldsymbol{\pi})$$

$$\boldsymbol{\pi} = \frac{\mathbf{p}}{\sum_k p_k},$$

where p_k is defined by the half-normal detection function as described in the main text, and the detection parameter σ is modeled as a function of species and sea state *BEAU*.

We calculated residuals R (for k_m) and $R.n$ (for $k.new_m$) at each iteration t of the Markov chain as

$$R = \sum_m (1 - \sqrt{p_k})^2$$

$$R.n = \sum_m (1 - \sqrt{p_{k.new}})^2$$

We calculated the Bayesian p-value as

$$p = \sum_t R.n > R.$$

Cluster size model residuals

Cluster size c is estimated for each observation m . We generated a new set of cluster sizes, $c.new$, as

$$c_m \sim \text{zerotruncated NegBin}(\gamma, \rho)$$

We calculated residuals R (for c_m) and $R.n$ (for $c.new_m$) at each iteration t of the Markov chain as

$$R = \sum_m (\sqrt{c_m} - \sqrt{\gamma})^2$$

$$R.n = \sum_m (\sqrt{c.new_m} - \sqrt{\gamma})^2$$

We calculated the Bayesian p-value as

$$p = \sum_t R. n > R.$$

Table 11C-1. Bayesian p-values for a community distance sampling model for seabirds without detection covariates using a Poisson and a negative binomial model to describe variation in abundance across sampling sites. Values close to 0.5 indicate good model fit.

Model component	p-value	
	Poisson	Negative binomial
Abundance	0.013	0.379
Detection	0.574	0.568
Cluster size	0.587	0.579

Table 11C-2. Bayesian p-values for the final community distance sampling model (see main text for model parameterization) for seabirds. Values close to 0.5 indicate good model fit.

Model component	p-value
Abundance	0.462
Detection	0.613
Cluster size	0.582