RESEARCH ARTICLE

Integrating aerial and ship surveys of marine birds into a combined density surface model: A case study of wintering Common Loons

Kristopher J. Winiarski,[1,3]* M. Louise Burt,[2] Eric Rexstad,[2] David L. Miller,[1] Carol L. Trocki,[1] Peter W. C. Paton,[1] and Scott R. McWilliams[1]

[1] Department of Natural Resources Science, University of Rhode Island, Kingston, Rhode Island, USA
[2] Centre for Research into Ecological and Environmental Modelling, University of St Andrews, The Observatory, Buchanan Gardens, St Andrews, Fife, United Kingdom
[3] Current address: Department of Environmental Conservation, University of Massachusetts, Amherst, Massachusetts, USA
* Corresponding author: withakri@gmail.com

ABSTRACT

Biologists now use a variety of survey platforms to assess the spatial distribution and abundance of marine birds, yet few attempts have been made to integrate data from multiple survey platforms to improve model accuracy or precision. We used density surface models (DSMs) to incorporate data from two survey platforms to predict the distribution and abundance of a diving marine bird, the Common Loon (*Gavia immer*). We conducted strip transect surveys from a multiengine, fixed-wing aircraft and line surveys from a 28 m ship during winter 2009–2010 in a 3,800 km^2 study area off the coast of Rhode Island, USA. We accounted for imperfect detection and availability bias due to Common Loon diving behavior. We incorporated spatially explicit environmental covariates (water depth and latitude) to provide predictions of the spatial distribution and abundance of wintering Common Loons. The combined-platform DSM estimated the highest Common Loon densities (>20 individuals km^{-2}) in nearshore waters <35 m deep, with an average daily abundance of 5,538 (95% CI = 4,726–6,489) individuals in the study area. The combined-platform model offered substantial improvement in the precision of abundance estimates from the ship-platform model, and modest improvement in the precision of the aerial-platform model. The combined model had relatively low predictive power, which previous research indicates is primarily a consequence of the dynamic marine environment. We show that the DSM approach presents a flexible framework for developing spatially explicit models of a marine bird from different survey protocols.

Keywords: abundance estimation, Common Loon, density surface model, distance sampling, *Gavia immer*, spatial modeling, spatially explicit abundance models

Integrando monitoreos en barco y aéreos de aves marinas en un modelo combinado de densidad de superficie: Un estudio de caso con *Gavia immer* durante el invierno

RESUMEN

Los biólogos utilizan actualmente una variedad de plataformas de muestreo para evaluar la distribución espacial y abundancia de aves marinas, sin embargo, existen pocos intentos para integrar datos de múltiples plataformas de muestreo para mejorar la exactitud o precisión del modelo. Utilizamos modelos de densidad de superficie (DSM) para incorporar los datos de two plataformas de muestreo para predecir la distribución y abundancia de un ave marina buceadora, *Gavia immer*. Monitoreamos en transectos sectoriales con una aeronave de ala fija multimotor y muestreos lineales en un barco de 28 m, durante el invierno de 2009–2010, en un área de estudio de 3.800 km2, a las afueras de la costa de Rhode Island. Consideramos la detección imperfecta, el sesgo de disponibilidad debido al comportamiento de buceo de *Gavia immer,* e incorporamos covariables ambientales espacialmente explícitas (profundidad del agua y latitud) para proveer predicciones de distribución espacial y abundancia de invernación de *Gavia immer*. La plataforma combinada de DSM estimó las densidades más altas de *Gavia immer* (>20 individuos km^{-2}) en las aguas cercanas a la costa <35 m de profundidad, con una abundancia promedio diaria de 5,538 (95 % IC = 4,726–6,489) individuos en el área de estudio. El modelo combinado de plataformas ofreció una mejora sustancial en la precisión de las estimaciones de abundancia que el modelo de plataforma desde el barco, y una modesta mejora en la precisión del modelo de plataforma aérea. El modelo combinado produjo relativamente bajo poder predictivo; investigaciones anteriores indican que esto es consecuencia, principalmente del ambiente marino dinámico. Demostramos que la propuesta DSM presenta un marco flexible para desarrollar modelos espacialmente explícitos de un ave marina con diferentes protocolos de monitoreo.

Palabras clave: estimaciones de abundancia, *Gavia immer*, modelo combinado de densidad de superficie, modelos espacialmente, modelos de abundancia espacialmente explícitos

INTRODUCTION

Ornithologists are interested in developing spatially explicit estimates of avian abundance because they have broad applications to avian ecology and conservation. Robust distribution and abundance estimates of birds have become more relevant with increasing conservation concerns due to anthropogenic activities associated with large-scale energy development. Currently, spatially explicit abundance estimates of marine birds are needed to address the increasing interest in renewable energy development in nearshore and offshore waters. This need is especially relevant on the North American Atlantic continental shelf, which has an estimated 4,000 GW of potential wind energy (U.S. Department of Energy 2011). The lack of information on the distribution and abundance of marine birds, particularly at fine spatial scales, is due in part to the paucity of systematic long-term marine bird surveys in the region; however, spatially explicit abundance estimates identify critical areas of high marine bird densities and could be used to protect these areas from development and reduce potential negative impacts (Fox et al. 2006, Langston 2013).

Spatially explicit predictive abundance models have recently been used to estimate the distribution and abundance of marine birds (Clarke et al. 2003, Ainley et al. 2009, Oppel et al. 2012, Winiarski et al. 2013). In contrast to simply calculating density in areas directly surveyed and multiplying that value by the total survey area to obtain an estimate of overall abundance, a spatially explicit abundance model can incorporate relevant environmental covariates (both biotic and abiotic) that may be driving the distribution and abundance of a given marine bird species. Such higher-resolution, spatially explicit models allow more accurate predictions and identification of areas important to the focal species or taxa (Clarke et al. 2003, Certain et al. 2007, Oppel et al. 2012).

For decades, systematic surveys from ships or aircraft have been the primary platforms to determine the distribution and abundance of marine birds (Ainley et al. 2012). Choice of platform often depends on target species (i.e. some species cannot adequately be surveyed with ship or aerial platforms), size of surveyed area, distance from shore of surveyed area, budgetary constraints, safety considerations, logistics, and specific research goals (Camphuysen et al. 2004). Survey protocols with both platforms have evolved to improve overall accuracy (Tasker et al. 1984, Camphuysen et al. 2004, Ainley et al. 2012). Historically, strip transects were used with both survey platforms, but line transects are now more common because this protocol accounts for imperfect observer detection probabilities (Buckland et al. 2001, Camphuysen et al. 2004, Ronconi and Burger 2009). Over time, many different governmental and nongovernmental organiza-tions have collected data at different times using different field methodologies. Recent interest in investigating longer-term trends in abundance (e.g., to assess the impact of climate change) means that combining these datasets is essential to building a representative picture of distribution. Hence, combining marine bird survey data from multiple platforms or protocols to increase overall temporal or spatial coverage could improve overall model performance and accuracy.

We integrated an aerial strip transect dataset with a ship-based line transect dataset to develop a predictive spatial model of a diving marine bird, the Common Loon (*Gavia immer*), in southern New England, USA. We selected Common Loons for this case study because they are classified as a species of special concern in Massachusetts, New York, and Connecticut; threatened in New Hampshire; and endangered in Vermont where they breed (Evers et al. 2007, Kenow et al. 2009). Their sensitivity to displacement from offshore wind energy development (Petersen et al. 2006, Furness et al. 2013) makes the Common Loon a marine bird of interest to biologists, regulators, and developers in southern New England.

We first assessed data compatibility of Common Loon abundance estimates between the 2 survey datasets and then combined the datasets to model the distribution and abundance of Common Loons wintering off the coast of Rhode Island, USA, using a density surface model (DSM; Hedley and Buckland 2004). DSM is a 2-stage approach: (1) abundances are estimated over sections of each transect (segments) using distance sampling methods for line transect data; (2) estimated per-segment abundances are then modeled as a function of environmental covariates using generalized additive modeling (GAM; e.g., Wood 2006). Due to the diving behavior of foraging Common Loons, we also incorporated a correction for this availability bias. Recently, the DSM approach has been successfully used to predict the distribution and abundance of sea ducks (Buckland et al. 2012), pinnipeds (Herr et al. 2009), and mollusks (Katsanevakis 2007). Here we present a DSM approach integrating ship- and aerial-based survey platforms that used line and strip transect survey protocols, respectively.

METHODS

Study Area

We conducted marine bird surveys off the coast of Rhode Island, USA, in a 3,800 km^2 study area in Rhode Island Sound, Block Island Sound, and portions of the Inner Continental Shelf (Figure 1). In early 2009, we initiated ship-based line transect surveys to determine the distribution and abundance of marine birds in the nearshore and offshore waters as part of the Rhode Island Ocean Special Area Management Plan (OSAMP). By midsummer
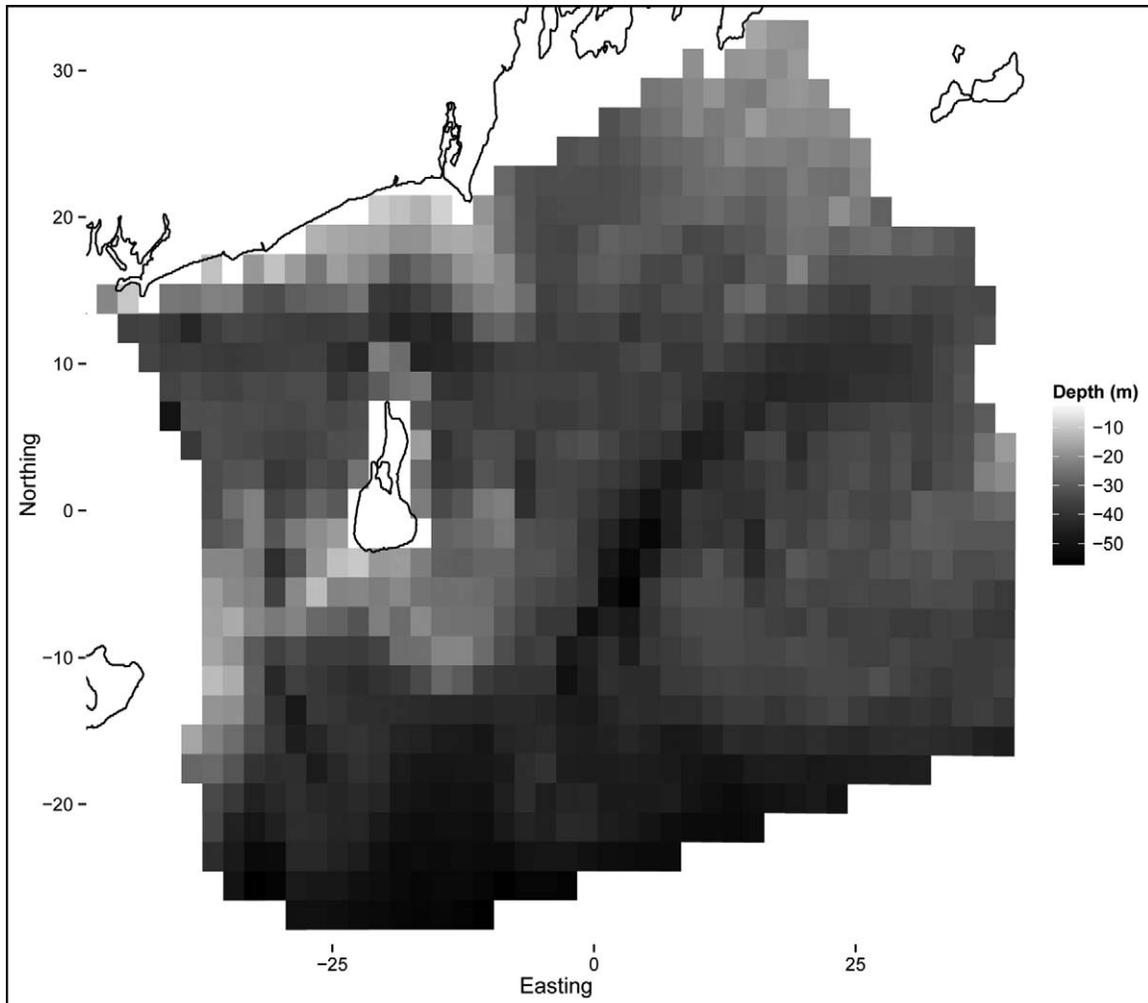
FIGURE 1. Bathymetry of the Rhode Island Special Area Management Plan (OSAMP) study area. Darker shading indicates deeper water. Block Island is located in the middle of the study area.

2009, additional sites for offshore wind facilities were proposed in the OSAMP area, so we initiated aerial-based strip transect surveys to increase overall spatial survey coverage while continuing the ship-based line transect surveys.

Systematic Surveys

Ship-based surveys. We conducted ship-based surveys on 8 grids randomly located across the study area (Figure 2) over 10 days between December 2, 2009, and February 13, 2010 (Supplemental Material Appendix A1). Each 69.8 km^2 grid, 7.5 × 9.3 km, contained a 46 km sawtooth transect that allowed observers to constantly stay on survey, increasing overall effort (Figure 2). We were able to survey 2 grids per day, given the speed constraints of the ship. We surveyed 4 grids twice and the other 4 grids 3 times during the survey period (Supplemental Material Appendix A1). The survey design tool in Distance 6.1 was

used to randomly place transect grids across the study area (Thomas et al. 2010). Length of the transect grids was determined by the transect distance we could sample between dawn and 1400 hr including transportation time to and from the sampling grids. Surveys were conducted from the flying bridge (12 m ASL) of a 27.5 m long ship traveling at 18.5 km hr^{-1} only when the Beaufort sea state was <4 and visibility was >1 km.

Using the ship-based line transect survey protocol outlined in Camphuysen et al. (2004), we recorded the distance and angle to each flock or nonflying Common Loon that occurred within a "moving box" that extended 300 m in front of the bow of the ship and 300 m perpendicular to the flying bridge. Sun glare determined which side of the ship (port or starboard) was surveyed. All surveys were conducted by one observer, and one observer/recorder used unaided vision to initially detect individual birds or flocks and then 10 × 42 power
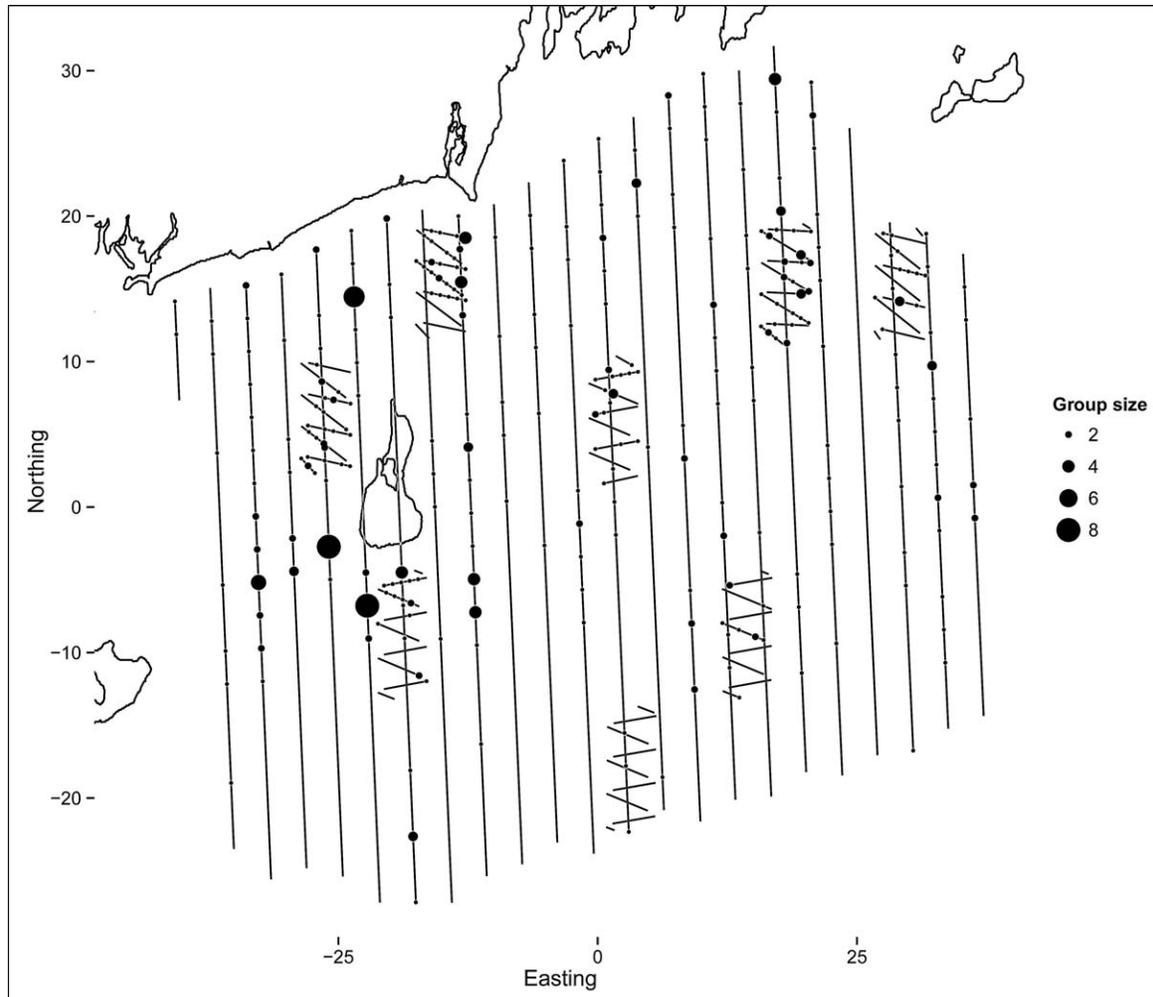
FIGURE 2. Common Loons (black circles) observed sitting on the water along aerial strip transects and ship line transects off southern Rhode Island during winter 2009–2010. Sawtooth lines represent 8 grids surveyed during ship-based surveys; the 24 parallel vertical lines represent the aerial-based survey transects.

binoculars to identify birds to species. Perpendicular distance to each detection (an individual or flock) was calculated from the estimated distance and bearing (estimated using a large protractor mounted on the flying bridge). We used a handheld global positioning system (GPS)-enabled personal digital assistant (PDA; Trimble Juno) using Cybertracker data collection software (Cape Town, South Africa) to collect observation locations and a handheld GPS (Garmin Marine GPS 76) to log the coordinates of the ship every 15 s.

Aerial-based surveys. We conducted aerial surveys along 24 fixed transects (Figure 2) on 9 days from December 2, 2009, to February 22, 2010 (Supplemental Material Appendix A1). We determined the location of the 24 transects using the survey design tool in Distance 6.1, which placed a grid of transect lines at equally spaced intervals across the study area at a random offset (Thomas

et al. 2010). In a 3.5 hr flight, we were able to survey 8 transect lines; thus, every third transect was visited on a given flight, and all transect lines were sampled by conducting ~3 flights per month. Each transect was sampled 1–3 times during the survey period (Supplemental Material Appendix A1). Surveys were conducted from a twin-engine Cessna 337 Skymaster flying at 185 km hr^{-1} at 152 m above the water surface. Following protocols used by Perkins et al. (2005), 2 observers used unaided vision to search 107-m-wide strip transects on either side of the plane (0–44 m was not visible to observers). The boundaries of the observation strip were denoted by markings taped to the wing struts. Observers stopped surveying when the sea state exceeded Beaufort state of 4, or sometimes an observer on one side of the plane stopped surveying when sun glare was intense. Detections were recorded to the nearest second on a digital voice recorder

with a stopwatch synchronized with a GPS (Garmin Map 496) recording the plane's position every 2 s.

Environmental Covariates

The explanatory environmental variables available for inclusion in our Common Loon DSM included latitude and longitude (lat and lon; both transformed into kilometers from the center of the region of interest, 41.17°N and 71.34°W: Northing and Easting), closest distance to coast (cdist), and water depth in meters (depth; Figure 1) from the National Oceanic and Atmospheric Administration (NOAA) Coastal Relief Model (http://www.ngdc.noaa.gov/mgg/coastal/crm.html).

Statistical Analyses

Data processing. We first aggregated Common Loon observations to rectangular, contiguous sections of the transects, hereafter referred to as segments. Length of each aerial-based segment was 2,270 m; the length of each ship-based segment was 830 m. Segment length was determined by the spatial scale of the modeled environmental covariates. For this analysis, we ignored flying loons and used only observations of Common Loons "sitting" on the water, so predictions from the spatial model reflected foraging Common Loons in southern New England.

Calculating loon abundance per segment. The first stage of DSM consisted of estimating the per-segment abundances of loons for the aerial and ship datasets, which form the response variable in our spatial model. Although we surveyed transects more than once during our survey period, we assumed the segments were independent because surveys were at least 1 month apart on a given transect, so Common Loons likely moved between surveys, albeit relatively short distances given their relatively small wintering home ranges (Kenow et al. 2009).

We assumed that all Common Loons within the aerial strip transects were detected with certainty (Certain and Bretagnolle 2008), a reasonable assumption because Common Loons are relatively large birds (66–91 cm long), the plane was flying at a low altitude above the surface of the ocean, and observers were looking directly beneath the plane in a relatively narrow strip width (107 m). A proportion of Common Loons were likely undetectable because they were foraging below the surface of the water and did not surface until after the plane passed. We corrected for this availability bias by dividing the counts of Common Loons per segment by the proportion of time the Common Loons were available, thereby appropriately inflating the counts. We assumed that Common Loons were available for detection 70% of the time, based on observations of the percentage of time Common Loons spent underwater, drifting, and preening in a past behavioral study in Rhode Island waters (Ford and Gieg 1995). For aerial surveys, we estimated the number of

Common Loons in segment j, $\hat{n}_j$, as:

$$\hat{n}_j = \left(\sum_{r=1}^{R_j} s_{jr} \right) / 0.7,$$

where s_{jr} was the recorded size for flock r, and R_j was the number of flocks in segment j.

We used conventional distance sampling (CDS; Buckland et al. 2001) to estimate the abundance of Common Loons in each segment from the ship surveys. CDS assumes that the detection on the track line is certain and decreases with increasing perpendicular distance from the line. We fitted a detection function characterizing this relationship to the perpendicular distances, and the probability of detection, $\hat{p}$, was then estimated from the detection function (Buckland et al. 2001). Here, we fitted both half-normal and hazard-rate detection functions, via maximum likelihood with R package mark-recapture distance sampling (mrds; Laake et al. 2011) and selected between the 2 using Akaike's Information Criterion (AIC; Akaike 1973). Two covariates (size and wave height) were considered for inclusion but were not selected in the final model (see Supplemental Material Appendix A3); therefore, given the constant probability of detection for all detections, we estimated the number of Common Loons in ship-based segments by dividing Common Loon flock size by $\hat{p}$ and then summed overall flocks in segment j to estimate the number of Common Loons in segment j as:

$$\hat{n}_j = \sum_{r=1}^{R_j} \frac{s_{jr}}{\hat{p}}.$$

We assumed that availability bias was not an issue for ship surveys because the ship speed was relatively slow, and diving Common Loons tend to be detected prior to diving or detected when they surface before the ship passes (Lukacs et al. 2010).

Survey platform compatibility. Before combining the 2 sets of survey data, we performed checks to ensure that the data from the 2 platforms were compatible. We assessed compatibility in the areas where the 2 surveys overlapped (i.e. within a bounding box created by a convex hull around each ship-based zigzag grid), and within these areas we looked at per-segment densities (to remove the effect of differing segment size between aerial and ship surveys). Because we could not match segment for segment between aerial and ship surveys, we instead used diagnostics that assessed the quantiles of the distributions of densities: a quantile–quantile (Q–Q) plot and a 2-sample Kolmogorov–Smirnov test.

Density surface modeling. Having obtained estimates of the number of Common Loons in each segment and finding segment abundances were compatible (see Re-

sults), we combined the Common Loon segment abundance estimates from aerial and ship surveys. The per-segment abundances, $\hat{n}_j$, were modeled as a function of the spatially referenced covariates using a GAM of the following form (assuming a log link function):

$$E[\hat{n}_j] = exp\Big(\log(a_j) + \beta_0 + \beta_{survey}z_{survey} + \sum_{k=1}^{K} f_k(z_{kj})\Big),$$

Where β_0 is an intercept; f_k are smooth functions of the K spatially referenced explanatory variables (see below), z_{kj}; the covariate z_{survey} is a factor indicating the survey type (ship or aerial) and has corresponding coefficient β_{survey}. The term log (α_j) is an offset that corresponds to the area of the segment, calculated as:

$$\alpha_j = w_j m_j l_j,$$

where w_j is the width and l_j is the length of segment j; and the variable m_j gives the number of sides of the platform surveyed (only one side of the ship was surveyed at all times).

We limited the maximum basis size for the smooth terms to 7 for the univariate terms and 20 for the bivariate terms. The maximum basis size controls the complexity of the smooth terms; because the smooth terms were penalized, only the maximum basis size needed to be set, and the penalty reduced the complexity of the smooth terms to an appropriate level while maintaining a good fit (section 4.1.7 in Wood 2006; if necessary, the maximum basis size can be increased). Survey platform was included as a potential factor variable. We tested several response distributions including negative binomial, quasi-Poisson, Gamma, and Tweedie, and selected the appropriate distribution by inspection of residual plots. We performed model selection by building a model with all covariates included and then removed terms if they were nonsignificant (Supplemental Material Appendix A2). An additional penalty was included for each smooth term, allowing their degrees of freedom to be decreased below 1 (i.e. terms were allowed to be completely removed from the model; Wood 2006, section 4.1.6). We performed smoothness selection by REstricted Maximum Likelihood (REML; Wood 2011).

Once the model was selected, we calculated the predicted abundance of Common Loons during winter over the study area using spatially referenced data over 920 square grid cells. Each grid cell had a 2 km^2 area that served as the offset (α_j, previous equation). Summing over the predicted values yielded an estimate of abundance in the study area. We calculated uncertainty in the abundance estimates for each prediction grid cell and the overall abundance using the variance propagation method of Williams et al. (2011). This method incorporates uncer-

tainty from the estimation of the detection function parameters (as well as from the GAM) by fitting a second model (used only for variance calculations), which includes an extra term (the derivative of $\hat{p}$, with respect to the detection function parameters) that accounts for the extra variability incurred by the 2-step estimation procedure. Uncertainty in the availability bias used to adjust counts from the aerial survey could not be quantified and was not included in variance estimates for abundance. Variance propagation is not prone to the instabilities of simulation-based variance estimation methods (e.g., moving block bootstrap; Efron and Tibshirani 1994). To visualize the uncertainty in the Common Loon abundance predictions over the survey area, we calculated the coefficient of variation for each prediction grid cell and plotted these as a map of the region.

To ensure that the model was robust to several decisions made as part of the modeling process, we analyzed the sensitivity of our results. To check that the model was not sensitive to varying the values of the availability correction, we varied the availability correction value and looked at the resulting Common Loon predicted abundance (Supplemental Material Appendix A3). To investigate whether correlations in Common Loon abundance estimates between adjacent segments would affect the overall Common Loon abundance estimate, we subsampled the data to create 2 datasets in which every second segment was selected, 3 datasets in which every third segment was selected, and 4 in which every fourth segment was chosen. From these resulting 9 datasets, Common Loon abundance was then calculated using the methods outlined earlier (Supplemental Material Appendix A3).

Using the models fitted to the subsets of the data, predictions were made for those segments not included in the model fitting process and compared with the corresponding observed counts for each subset to indicate the predictive power of the model. To quantify performance, we fitted a linear model to the predicted counts for the missing segments and used the observed (but excluded) counts as an explanatory variable; the slope coefficient of the resulting model can then be used for comparison (a slope of 1 indicates perfect agreement between excluded and observed counts and model predictions). We used R version 2.15.1 (R Development Core Team 2012) for all statistical analyses and models.

RESULTS

Aerial-based Surveys

Aerial surveys yielded 337 detections of Common Loons (2,758 km of transects; Table 1), detected in 235 of 1,215 (19%) segments. The majority of Common Loon aerial-based detections were 1 or 2 birds, with flocks up to 8 individuals recorded (Table 1), in nearshore waters, with

TABLE 1. Frequency of recorded flock sizes of Common Loons detected during aerial-based and ship-based surveys off the coast of Rhode Island during winter 2009–2010.

Flock size	Aerial surveys	Ship surveys
1	280	139
2	38	16
3	7	5
4	7	1
5–8	5	0
Total	337	161

highest detections in waters southwest of Block Island (Figure 2).

Ship-based Surveys

Ship surveys yielded 161 detections of Common Loons (808 km of transects; Table 1) in 125 of 974 (13%) segments. Similar to aerial surveys, the majority of Common Loon ship-based detections were 1 or 2 birds, with flocks of up to 4 individuals recorded (Table 1), in nearshore waters, with highest detections in those waters adjacent to southern Rhode Island's coast and Block Island (Figure 2).

Ship-based Detection Function

To avoid numerical issues in estimating a detection function with a long tail and potential induced bias, perpendicular distances of sightings from ship-based surveys were truncated at 180 m, which excluded 5% of observations resulting in 154 Common Loon ship-based detections (of 161 observed; Figure 3). A hazard rate detection function (Figure 3) was selected (AIC = 1549.64) over a half-normal detection function (AIC = 1550.58). The abundance estimate was not found to be sensitive to choice of detection function (Supplemental Material Appendix A3). The expected flock size from the size bias regression (1.187 birds; CV = 0.02) was slightly larger than the mean flock size (1.175; CV = 0.03), a 0.8% difference (Table 1). Fitting a detection function with flock size as a covariate did not improve the AIC of the resulting detection function significantly (<3 point difference), so flock size was not used in the final detection function model. The abundance estimate was not found to be sensitive to the choice of detection function form (Supplemental Material Appendix A3).
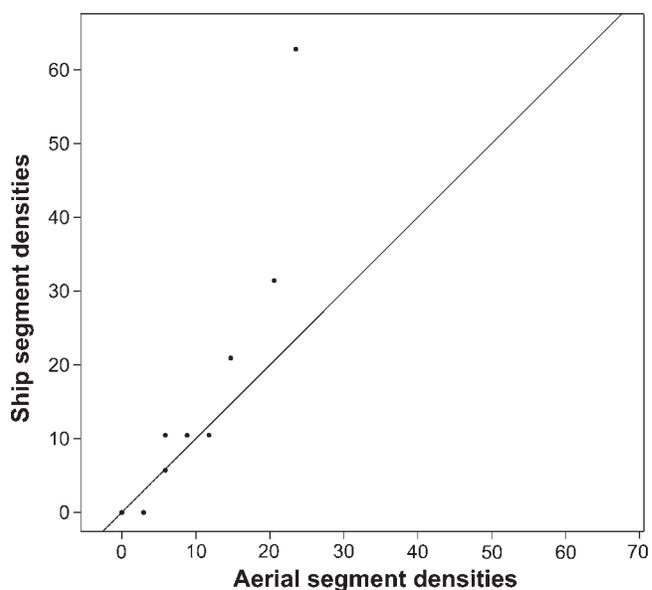
Survey Compatibility

Common Loon segment densities were compatible by platform, although at least 1 ship-based segment with much higher loon abundance was estimated than found with the aerial surveys (Figure 4); however, a Kolmogorov-Smirnov 2-sample test indicated that the 2 sets of densities could have come from the same distribution ($P = 0.259$).
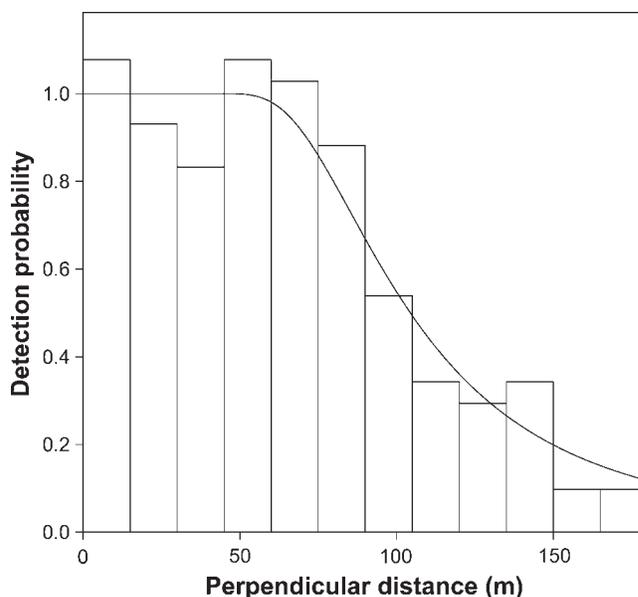
FIGURE 3. Distribution of perpendicular detection distances of Common Loons during ship-based line transect surveys, with the fitted (hazard-rate) detection function overlaid onto the scaled perpendicular distance distribution, truncated at 180 m.

Density Surface Model

A negative binomial distribution for the response provided the best fit to the data based on evaluation of residual plots that consisted of 2 univariate smooths of lat and depth (other terms, including the factor term for survey type, were nonsignificant; Supplemental Material Appendix A2).

FIGURE 4. Quantile–quantile plot of observed aerial and ship per-segment densities (note: ship- and aerial-based segment densities were corrected by segment area). The black line indicates perfect compatibility.

The dispersion parameter of the negative binomial was estimated as 0.185. The DSM predicted the highest densities of loons closest to the coast in waters <35 m deep (Figure 5), evidenced by the smooth of depth (Figure 6B); the smooth is roughly constant for depths >40 m and then increases as depth decreases. The confidence intervals are wider for the deepest and shallowest waters due to the reduced coverage for these depths. The peak in the smooth of lat (Figure 6A) corresponds to the high abundances of Common Loons around Block Island.

The estimated abundance over the whole study area was 5,538 Common Loons (CV = 0.081; 95% CI = 4,726–6,489). The model using only ship-based line survey data estimated 6,367 loons (95% CI = 4,268–9,499), and the model using only aerial strip transect data estimated 4,949 loons (95% CI = 4,094–5,983; Supplemental Material Appendix A3). Thus, the confidence interval for the pooled data model was ~7% smaller than that of the aerial model and 66% smaller than the ship survey model. These abundance estimates can be regarded as a daily average number of birds foraging in the waters off Rhode Island in winter. A plot of the CVs for each prediction cell shows that the highest uncertainty was along the southern edge of the region and in the northwest corner, where some of these grid cells occurred beyond the range of the survey effort (Figure 6B). The diagonal stripe of high uncertainty in the center of the study area corresponded to habitats of greater depths (Figure 1), which were not sampled as much as other depth ranges. This depth profile, combined with the high abundance estimated elsewhere in that horizontal band (due to the high estimates around Block Island), led to higher uncertainty in that area.

To test the effect of changing the availability bias, we varied the value of the correction factor over the 0.5–1 range, refitting the model each time (smooth terms were kept the same so the model was the same form, but parameters were estimated each time). This led to a series of abundance estimates within the confidence interval reported earlier for availabilities between 0.55 and 0.9. When plotted against the correction factor, these estimates followed an approximately exponential curve, decreasing as the correction factor increased (Supplemental Material Appendix A3). This pattern suggests that (1) the availability affects the model in an entirely deterministic way, which is evident from the mathematical form of the model, and (2) we can be relatively certain that our confidence interval is robust to reasonable changes in the correction factor. We assessed autocorrelation using the subsampling strategy detailed above, and resulting abundances showed little sensitivity to changes in subsampling (Supplemental Material Appendix A3).

The final DSM was validated by fitting a model (again keeping the same form) to subsets of the data and predicting for segments excluded from the subset. Simple linear regression models were then fitted to the observed (as the explanatory variable) and predicted values (as the response) for segments excluded from the subset. Nine subsets were generated (see Supplemental Material Appendix A3), and the mean and median of the regression model intercepts were 0.394 and 0.408, respectively (range 0.381–0.476). The mean and median of the slope parameters were 0.138 and 0.124, respectively (range 0.087–0.200). An intercept of 0 and a slope of 1 would indicate perfect agreement between model predictions and observations.

DISCUSSION

Our DSM approach allowed us to combine multiple datasets collected using different survey platforms and provide a predictive model of Common Loon distribution and abundance in the nearshore and offshore waters of southern New England. Our DSM accounted for 3 factors that could affect Common Loon abundance estimates: (1) we used a detection function to account for imperfect detection probabilities in the ship-based line transect survey data; (2) we used an availability bias correction to account for loon diving behavior when surveyed with aerial-based strip transects; and (3) we used a spatially explicit model with environmental covariates to account for nonuniform distribution of loons across our 3,800 km^2 study area. Results from this case study highlight both the utility and flexibility of the DSM approach for predicting the distribution and abundance of a marine diving bird when combining survey data from multiple platforms using strip and line transect survey protocols.

Common Loon Winter Distribution and Abundance in Southern New England
Based on the combined DSM, Common Loons in our study area were present in relatively shallower waters, typically <35 m, and most abundant in waters <20 m surrounding Block Island. Higher densities of Common Loons in relatively shallow waters (<35 m) is consistent with previous research (Haney 1990). Kenow et al. (2009) found that satellite-tagged Common Loons were most likely found in waters 3–20 m deep. Further research is needed to determine why the shallow waters in the central portion of our study area (those surrounding Block Island) have higher densities of Common Loons than shallow waters at the northern boundary of our study area.

The area west of Block Island is highly influenced by Long Island Sound, which inputs low salinity water from several major rivers, including the Connecticut River, and has the highest tidal circulation velocities in the study area (Mau et al. 2007, Codiga and Ullman 2010). Chlorophyll *a* surface concentrations are also higher in this area, indicating higher primary productivity (Winiarski et al.
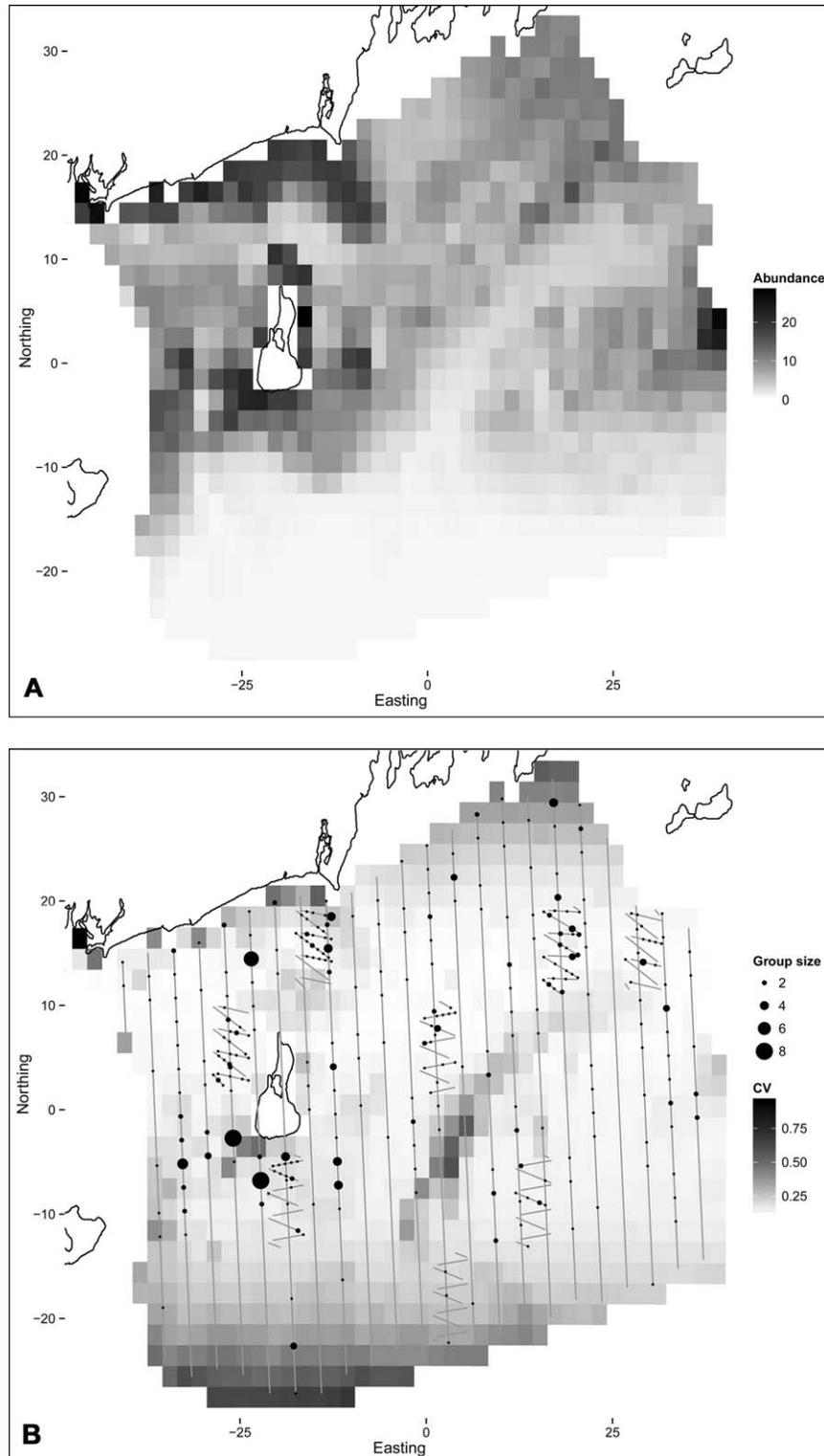
FIGURE 5. Predicted abundances of Common Loons (individuals km^{-2}) across the 3,800 km^2 Rhode Island OSAMP study area. Dark colors indicate higher abundances (**A**). Plot of the coefficient of variation of Common Loon abundances for each prediction grid cell with aerial- and ship-based survey efforts and Common Loon detections also given (**B**). Note the increase in model uncertainty at the northern and southern extremes and the diagonal ridge in the center of the study area. The northern and southern extremes correspond to areas with lower survey effort; the diagonal ridge corresponds to larger depth values (relatively unsampled) combined with high predicted abundances for similar values of latitude (e.g., around Block Island).
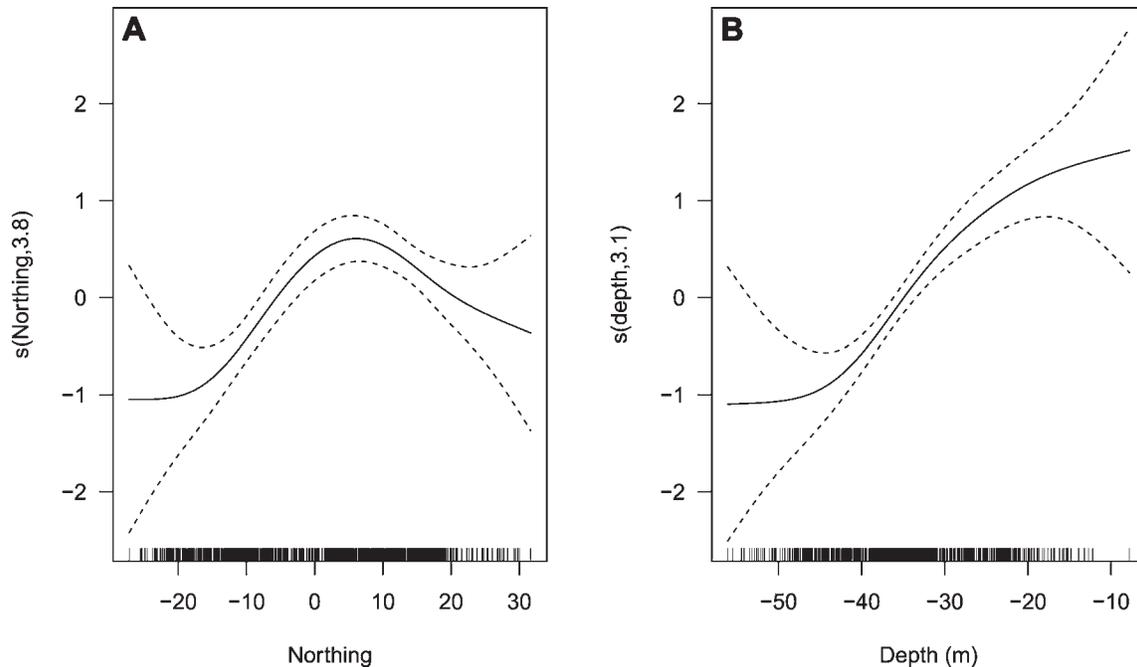
FIGURE 6. Plots of the smooth functions for latitude (transformed to Northing; **A**) and depth (**B**) that were used in the final Common Loon density surface model. Dotted lines show ~95% CI for the smooth terms. Numbers in brackets indicate the effective degrees of freedom of the smooth term; note that the y-axes are on a log scale.

2013) and supplying conditions that could support higher densities of Common Loon forage prey, including small demersal fish, crabs, lobsters, and flounder (Evers et al. 2007). Our abundance estimate for Common Loons in our study area during winter is similar to the overall adult population of Common Loons breeding in New York and New England (~5,500 individuals; Evers 2007) and consistent with other research highlighting the importance of our study area to wintering Common Loons (Kenow et al. 2009).

Conservation Implications for Common Loons

Post-construction avian monitoring of offshore wind energy development (OWED) in European waters has found less than expected densities of loons within an OWED impact area and at distances of 2–4 km from installed turbines (Petersen et al. 2006, Langston 2013). Avoidance by loons was also found in areas with high shipping intensities (Schwemmer et al. 2011), suggesting that development of those areas with high Common Loon densities in our study area could potentially lead to displacement and a loss of important foraging habitat, although it is currently unknown how much habitat would need to be developed to negatively impact Common Loon populations in southern New England. At the present, we can only recommend that construction of these facilities avoid areas of high Common Loon (and other marine bird)

densities until the effects of such development on Common Loon populations are better understood.

Survey Platform Compatibility

Before developing our DSM by combining data from 2 survey platform datasets with different survey protocols, we first needed to provide evidence of compatibility between the 2 datasets. Our analysis revealed the segment abundances were compatible for Common Loons and were similar to results found with another survey platform comparison of loon density (Henkel et al. 2007). The compatibility we found between survey platforms and protocols for Common Loons may not be true for all marine bird taxa, however, and must be carefully assessed prior to combining datasets to develop a single spatial model (Briggs et al. 1985, Henkel et al. 2007).

Advantages of Combining Multiple Datasets

The ability to combine data from multiple surveys enables investigators to use multiple, potentially historical survey datasets and to make inferences about marine bird distribution and abundance over broader areas and longer time periods. Combining data in this way and using a single spatial model also allows uncertainty to be calculated in a unified way rather than relying on per-model variance estimates or bootstrap procedures. By fitting DSMs separately to our ship-based dataset and aerial-based dataset we found that were both within the

confidence interval of the combined model, but the confidence interval for the combined-platform model was ~7% smaller than the aerial-platform model and 66% smaller than the ship-platform model. Given that ship-based surveys covered only ~15% of the our study area, the improvement in the precision of the ship-based model by integrating aerial surveys, which had much broader coverage of our study area, was not unexpected. Previous studies have shown that density estimates can vary for some species between aerial and ship surveys (Briggs et al. 1985), and the ability to identify individuals to species can vary between survey platforms (Briggs et al. 1985), so care must be taken before combining datasets. Investigators wishing to incorporate many surveys into a single DSM should consider the compatibility checks described in this study before attempting to fit a DSM.

Advantages of a Density Surface Modeling Approach

Using a DSM has several advantages over other modeling techniques. Compared to approaches developed by Royle et al. (2004) and Fiske and Chandler (2011), the choice of response distribution is much greater. Although we did not model detection jointly with the spatial distribution, this omission is not particularly problematic because transects are long compared to their width and spacing, so variation "along" a transect is much more important than "across" it. The 2-stage approach also is not an issue for variance estimation because we can propagate uncertainty from the detection function through to the spatial model using the method of Williams et al. (2011).

A GAM spatial model allows simple extensions (compared with other spatial modeling techniques) to include a temporal component as well as random effects and correlation structures, in addition to smooth terms to improve our understanding of the distribution of Common Loons off the coast of New England in both space and time. GAMs also offer the advantage that their interpretation follows from generalized linear model theory, so interpretation and model checking procedures are well-developed and relatively straightforward for nonexperts.

Improving Future Marine Bird Predictive Models

Our DSM had relatively low predictive power according to our cross-validation procedure, which unfortunately is typical of marine bird predictive models (Oppel et al. 2012, Winiarski et al. 2013). The highly dynamic marine environment and the brief time window in which systematic marine bird surveys are usually conducted inevitably reduces the predictive power of such models. For example, these conditions may increase the number of falsely zero-inflated counts (Oppel et al. 2012) or make it difficult to accurately assess flock size for large flocks. Although digital methods (Buckland et al. 2012) improve some elements of data collection (specifically, detection is

certain in the recorded strip), they do not change the dynamic nature of the marine environment, so it is unclear how well these digital methods will improve model fit and predictive power.

Our DSM seemed relatively insensitive to the availability bias correction factor, but it would be useful to improve these estimates with further studies. Availability bias is likely not constant and depends on environmental factors (e.g., water depth or day length) or important periods in marine bird annual life history, such as molt, which may require increased forage consumption and hence more time underwater unavailable to the observer. Improved availability bias measures and variability of this metric could be included in future spatial marine bird predictive models (Buckland et al. 2012). Recent work by Borchers et al. (2013) describes possible adaptations of current survey methodology that could be used for this purpose to validate our results, although they may potentially be difficult to implement for marine birds. Chandler et al. (2011) provides an approach that could provide stronger estimates of availability bias in the future with repeated surveys and these types of spatial models. Also, marine bird distribution and abundance is likely strongly tied to the distribution, abundance, and availability of prey items. Without spatial data available for many lower tropic level organisms, we can only use environmental covariates to serve as proxies for prey distribution and density. Improved input data will lead to predictive models with higher confidence in their estimates, which is important when using these models to guide future industrial marine development to reduce risk to marine birds.

ACKNOWLEDGMENTS

LITERATURE CITED

Ainley, D. G., K. D. Dugger, R. G. Ford, S. D. Pierce, D. C. Reese, R. D. Brodeur, C. T. Tynan, and J. A. Barth (2009). Association of predators and prey at frontal features in the California Current: Competition, facilitation, and co-occurrence. Marine Ecology Progress Series 389:271–294.

Ainley, D. G., C. A. Ribic, and E. J. Woehler (2012). Adding the ocean to the study of seabirds: A brief history of at-sea

seabird research. Marine Ecology Progress Series 451:231–243.

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In Second International Symposium on Information Theory (B.N. Petrov and F. Csa'aki, Editors.). Akademiai Kiado, Budapest, Hungary. pp. 267–281.

Borchers, D. L., W. Zucchini, M. P. Heide-Jørgensen, and A. Cañadas (2013). Using hidden Markov models to deal with availability bias on line transect surveys. Biometrics 69:703–713.

Briggs, K. T., W. B. Tyler, and D. B. Lewis (1985). Comparison of ship and aerial surveys of birds at sea. Journal of Wildlife Management 49:405–411.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas (2001). Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, London, UK.

Buckland, S. T., M. L. Burt, E. A. Rexstad, M. Mellor, A. E. Williams, and R. Woodward (2012). Aerial surveys of seabirds: The advent of digital methods. Journal of Applied Ecology 49:960–967.

Camphuysen, C. J., A. D. Fox, M. Leopold, and I. K. Petersen (2004). Towards standardized seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms. U.K. COWRIE 1 Report. Royal Netherlands Institute for Sea Research, Texel, Netherlands.

Certain, G., E. Bellier, B. Planque, and V. Bretagnolle (2007). Characterising the temporal variability of the spatial distribution of animals: An application to seabirds at sea. Ecography 30:695–708.

Certain, G., and V. Bretagnolle (2008). Monitoring seabirds population in marine ecosystem: The use of strip transect aerial surveys. Remote Sensing of Environment 112:3314–3322.

Chandler, R. B., J. A. Royle, and D. I. King (2011). Inference about density and temporary emigration in unmarked populations. Ecology 92:1429–1435.

Clarke, E. D., L. B. Spear, M. L. Mccracken, F. F. C. Marques, D. L. Borchers, S. T. Buckland, and D. G. Ainley (2003). Validating the use of generalized additive models and at-sea surveys to estimate size and temporal trends of seabird populations. Journal of Applied Ecology 40:278–292.

Codiga, D. L., and D. S. Ullman (2010). Characterizing the physical oceanography of coastal waters off Rhode Island, Part 1: Literature review, available observations, and a representative model simulation. Rhode Island Ocean Special Area Management Plan, Coastal Resources Center, Narragansett, RI, USA.

Efron, B., and R. J. Tibshirani (1994). An Introduction to the Bootstrap. Chapman and Hall, New York, NY, USA.

Evers, D. C. (2007). Status assessment and conservation plan for the Common Loon (Gavia immer) in North America. BRI Report 2007-20. U.S. Fish and Wildlife Service, Hadley, MA, USA.

Fiske, I., and R. Chandler (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Ford, T. B., and J. A. Gieg (1995). Winter behavior of the Common Loon. Journal of Field Ornithology 66:22–29.

Fox, A. D., M. Desholm, J. Kahlert, T. K. Christensen, and I. K. Petersen (2006). Information needs to support environmental impact assessment of the effects of European marine offshore wind farms on birds. Ibis 148:129–144.

Furness, R. W., H. M. Wade, and E. A. Masden (2013). Assessing vulnerability of marine bird populations to offshore wind farms. Journal of Environmental Management 119:56–66.

Haney, J. C. 1990. Winter habitat of Common Loons on the continental shelf of the southeastern United States. Wilson Bulletin 102:253–263.

Hedley, S. L., and S. T. Buckland (2004). Spatial models for line transect sampling. Journal of Agricultural, Biological and Environmental Statistics 9:181–199.

Henkel, L. A., R. G. Ford, W. B. Tyler, and J. N. Davis (2007). Comparison of aerial and boat-based survey methods for Marbled Murrelets Brachyramphus marmoratus and other marine birds. Marine Ornithology 35:145–151.

Herr, H., M. Scheidat, K. Lehnert, and U. Siebert (2009). Seals at sea: Modeling seal distribution in the German bight based on aerial survey data. Marine Biology 156:811–820.

Katsanevakis, S. (2007). Density surface modeling with line transect sampling as a tool for abundance estimation of marine benthic species: The Pinna nobilis example in a marine lake. Marine Biology 152:77–85.

Kenow, K. P., D. Adams, N. Schoch, D. C. Evers, W. Hanson, D. Yates, L. Savoy, T. H. Fox, A. Major, R. Kratt, and J. Ozard (2009). Migration patterns and wintering range of Common Loons breeding in the Northeastern United States. Waterbirds 32:234–247.

Laake, J. L., D. L. Borchers, L. Thomas, D. L. Miller, and J. Bishop (2011). mrds: Mark-Recapture Distance Sampling. http://cran.r-project.org/web/packages/mrds/index.html

Langston, R. H. W. (2013). Birds and wind projects across the pond: A UK perspective. Wildlife Society Bulletin 37:5–18.

Lukacs, P. M., M. L. Kissling, M. Reid, S. M. Gender, and S. B. Lewis (2010). Testing assumptions of distance sampling of a pelagic seabird. The Condor 112:455–459.

Mau, J. C., D. P. Wang , D. S. Ullman, and D. L. Codiga (2007). Comparison of observed (HF radar, ADCP) and model barotropic tidal currents in the New York Bight and Block Island Sound. Estuarine, Coastal and Shelf Science 72:129–137.

Oppel, S., A. Meirinho, I. Ramírez, B. Gardner, A. F. O'Connell, P. I. Miller, and M. Louzao (2012). Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. Biological Conservation 156:94–104.

Perkins, S., G. Sadoti, T. Allison, E. Jedrey, and A. Jones (2005). Relative waterfowl abundance within Nantucket Sound, Massachusetts during the 2004–2005 winter season. Massachusetts Audubon Society Technical Report, Lincoln, MA, USA.

Petersen, I. K., T. K. Christensen, J. Kahlert, M. Desholm, and A. D. Fox (2006). Final results of bird studies at the offshore wind farms at Nysted and Horns Rev, Denmark. National Research Institute Report, Ronde, Denmark.

R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org

Ronconi, R. A., and A. E. Burger (2009). Estimating seabird densities from vessel transects: Distance sampling and implications for strip transects. Aquatic Biology 4:297–309.

Royle, J. A., D. K. Dawson, and S. Bates (2004). Modeling abundance effects in distance sampling. Ecology 85:1591–1597.

Schwemmer P., B. Mendel, N. Sonntag, V. Dierschke, and S. Garthe (2011). Effects of ship traffic on seabirds in offshore waters: Implications for marine conservation and spatial planning. Ecological Applications 21:1851–1860.

Tasker, M. L., P. Hope-Jones, T. Dixon, and B. F. Blake (1984). Counting seabirds at sea from ships: A review of methods employed and a suggestion for a standardized approach. The Auk 101:567–577.

Thomas, L., S. T. Buckland, E. A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. B. Bishop, T. A. Marques, and K. P. Burnham (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

U.S. Department of Energy (2011). Offshore energy workshop. A joint workshop by the Energy Department's office of Energy Efficiency and Renewable Energy and the Department of the Interior's Bureau of Ocean Energy Management. Washington, DC, USA.

Williams, R., S. L. Hedley, T. A. Branch, M. V. Bravington, A. N. Zerbini, and K. P. Findlay (2011). Chilean blue whales as a case study to illustrate methods to estimate abundance and evaluate conservation status of rare species. Conservation Biology 25:526–535.

Winiarski, K. J., D. L. Miller, P. W. C. Paton, and S. R. McWilliams (2013). A spatially explicit model of wintering common loons: Conservation implications. Marine Ecology Progress Series 492:273–278.

Wood, S. N. (2006). Generalized Additive Models: An Introduction with R. Chapman & Hall/CRC, New York, NY, USA.

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