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Complete List of Authors:	Winiarski, Kristopher; University of Rhode Island, Natural Resources Science Burt, M. Louise; University of St Andrews, Centre for Research into Ecological and Environmental Modelling Rexstad, Eric; University of St Andrews, Centre for Research into Ecological and Environmental Modelling Miller, David; University of Rhode Island, Natural Resources Science Trocki, Carol; University of Rhode Island, Natural Resources Science Paton, Peter W. C.; University of Rhode Island, Department of Natural Resources Science McWilliams, Scott; University of Rhode Island, Natural Resources Science
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LRH: WINIARSKI ET AL.

RRH: DENSITY SURFACE MODEL OF COMMON LOONS

A DENSITY SURFACE MODEL OF WINTERING COMMON LOONS INCORPORATING SURVEY DATA
FROM AERIAL AND SHIP-BASED PLATFORMS

KRISTOPHER J. WINIARSKI^{1, 3}, M. LOUISE BURT², ERIC REXSTAD², DAVID L. MILLER¹, CAROL L. TROCKI¹, PETER W.
C. PATON¹AND SCOTT R. MCWILLIAMS¹

¹Department of Natural Resources Science, 1 Greenhouse Road, University of Rhode Island,
Kingston, RI 02881 USA

²Centre for Research into Ecological and Environmental Modelling, University of St Andrews,
The Observatory, Buchanan Gardens, St Andrews, Fife, KY16 9LZ, UK

³E-mail: withakri@gmail.com

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ABSTRACT.-We develop a density surface model (DSM) for predicting the distribution and abundance of a diving marine bird, the Common Loon (*Gavia immer*). We surveyed birds during the winter of 2009-2010 (12 December 2009 to 22 February 2010) in a 3,800 km² study area off the coast of Rhode Island. Our spatially-explicit abundance model incorporated compatible data from two survey platforms, ship line transect and aerial strip transect survey protocols. We accounted for imperfect detection, availability bias due to Common Loon diving, and incorporated spatially-explicit environmental covariates (water depth and latitude) to provide accurate predictions of the spatial distribution and abundance of wintering Common Loons. Common Loon densities were greatest (>20 individuals/km²) in nearshore waters <40m deep in western Rhode Island and off Block Island. The DSM predicted an average daily abundance of 5,538 (95% CI = 4,726-6,489) Common Loons in our study area during the winter of 2009-2010. Our results highlight the applicability of the DSM approach for predicting marine bird distribution and abundance using data collected from multiple survey platforms using different survey protocols.

Key words: abundance estimation, density surface model, distance sampling, *Gavia immer*, spatial modeling, spatially-explicit abundance models.

ALTHOUGH THERE ARE no current offshore wind energy developments (OWEDs) in North America, there is an estimated 4,000 GW of potential wind energy off the coasts of the USA (DOE 2011) that has fueled interest in renewable energy in the marine environment. Evaluating potential impacts of OWEDs requires accurate information on the distribution and abundance of marine animals, particularly marine birds. Such information is particularly important because the primary impact of OWEDs on marine birds in western Europe was displacement from the developed site and thus loss of suitable foraging habitat (Petersen et al. 2006, Langston 2013). Identifying important areas used by marine birds prior to development of offshore wind facilities could reduce potential impacts (Fox et al. 2006, Langston 2013).

Systematic surveys from ships or aircraft have been the primary approaches used to determine marine bird distribution and abundance, although survey protocols with both platforms have evolved over time to improve overall accuracy (Tasker et al. 1984, Camphuysen et al. 2004, Ainley et al. 2012). Line transects are gradually replacing strip transects for ship and aerial platforms as line transects allow investigators to account for imperfect detection (Buckland et al. 2001, Camphuysen et al. 2004). Line transect protocols require the recording of distances from the observer to each detection (e.g., flock of birds). A *detection function* is then fitted to this distance data following the assumption that probability of detection is perfect at zero distance and decreases with distance from the observer. The detection function controls for this imperfect detection, whereas when strip transects are used perfect detection is assumed within the surveyed strip. This assumption of perfect detection is often false unless a relatively narrow strip width is surveyed, which leads to lower totals of overall detections (Buckland et al. 2001).

Spatially-explicit abundance models can provide accurate predictions of marine bird distribution and abundance. In contrast to simply calculating marine bird density in those areas directly surveyed and then multiplying that value by the total survey area to obtain overall abundance, a spatially-explicit model can incorporate relevant environmental (biotic and abiotic) covariates driving the distribution and abundance of marine birds. This allows for more accurate predictions and better identifies areas of importance to the taxa in question (Clarke et al. 2003, Certain et al. 2007, Oppel et al. 2012). These spatial models typically involve the modeling of a single marine bird dataset with observations collected from one survey platform (e.g., aerial or ship-based surveys). However, depending on available or collected survey data, it may be desirable for those developing spatial models to integrate marine bird survey data from multiple platforms to increase overall spatial and temporal coverage.

Here we integrate an aerial-based, strip transect and a ship-based, line transect dataset to develop a predictive spatial model. We first assess data compatibility between the two datasets and then integrate the datasets to model the distribution and abundance of Common Loons (*Gavia immer*) wintering off the coast of Rhode Island using a density surface model (DSM; Hedley and Buckland 2004). Density surface modeling is a two-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 a 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 used to predict the distribution and abundance of seabirds (Buckland et al. 2012), pinnipeds (Herr et al. 2009) and

mollusks (Katsanevakis 2007). Here for the first time we present a DSM approach integrating ship and aerial-based survey platforms that used line transect and strip transect survey protocols, respectively.

METHODS

We conducted marine bird surveys in a 3,800 km² study area in Rhode Island Sound, Block Island Sound, and portions of the Inner Continental Shelf (Fig. 1). Due to funding constraints and a limited number of areas of interest where offshore wind facilities might be located in our study area, we initially used ship-based line transect surveys to survey marine birds in the nearshore and offshore waters of the Rhode Island Ocean Special Area Management Plan (OSAMP) starting in early 2009. By mid-summer 2009, a number of potential 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.

Aerial-based surveys.-We conducted aerial surveys along 24 fixed transects (Fig. 2) on 5 days from 2 December 2009 to 22 February 2010. Location of the 24 transects was determined 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 eight transect lines, thus every third transect was visited on a given flight and all transect lines were sampled by conducting approximately three flights per month. Each transect was sampled up to four times during the survey period (See online Supplementary Material). Surveys were conducted from a twin-engine Cessna 337 Skymaster

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3 flying at 185 km per hr at 152 m above the water surface. Following protocols used by Perkins
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5 et al. (2005), two observers used their unaided eyes to search 107 m wide strip transects on
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7 either side of the plane (we could not see directly below the plane from 0-44m). The
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9 boundaries of the observation strip were denoted by markings taped to the wing struts.
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11 Observers stopped surveying when the sea state exceeded Beaufort state of four and when sun
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13 glare was intense, which sometimes affected an observer on one side of the plane. Detections
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15 were recorded to the nearest second on a digital voice recorder with a stopwatch that was
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17 synchronized with a GPS (Garmin Map 496) recording the plane's position every 2 s.
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23 *Ship-based surveys.*-We conducted ship-based surveys on eight grids randomly located across
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25 the study area (Fig. 2) over 10 days between 2 December 2009 and 13 February 2010. Each grid
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27 was a 46 km saw tooth transect that allowed observers to stay on survey, increasing overall
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29 effort (Fig. 2). Two grids were surveyed per day, with four grids surveyed twice and the other
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31 four grids surveyed three times during the survey period (See online Supplementary Material).
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33 Location of transect grids was determined using the survey design tool in Distance 6.1, which
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35 randomly placed transect grids across the study area (Thomas et al. 2010). Length of the
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37 transect grids was determined by how much transect length we could sample between dawn
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39 and 1400 including transportation time to and from the sampling grids. Surveys were
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41 conducted from the flying bridge (12 m above sea level) of a 27.5 m long ship traveling at 18.5
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43 km per hr only when the Beaufort sea state was < 4 and visibility was > 1 km.
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52 Using the ship-based, line transect survey protocol outlined in Camphuysen et al. (2004),
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54 we recorded the distance and angle to each flock or non-flying Common Loon that occurred
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3 within a “moving box” that extended 300 m in front of the bow of the ship and 300 m
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5 perpendicular to the flying bridge. Sun glare determined which side of the ship was surveyed
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7 (port or starboard). All surveys were conducted by one observer and one observer/recorder
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9 using their unaided eyes to initially detect individual birds or flocks and then 10 x 42 power
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11 binoculars to identify birds to species. Perpendicular distance to each detection (an individual
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13 or flock) was calculated from the estimated distance and bearing (estimated using a large
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15 protractor mounted on the flying bridge). A handheld GPS-enabled PDA (Trimble Juno) using
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17 Cybertracker data collection software (Cybertracker, Cape Town, South Africa) was used to
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19 collect observation locations and a handheld-GPS (Garmin Marine GPS 76) was used to record
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21 the coordinates of observers every 15 s.
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28 *Data processing.*-We first aggregated the observations to rectangular, contiguous sections of
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30 the transects (*segments*). Length of the aerial-based segments was 2,270 m, while the length of
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32 the ship-based segments was 830 m. Within each segment, Common Loon density and the
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34 values of geographically referenced covariates did not vary substantially, which is important to
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36 the overall modeling process (Hedley and Buckland 2004).
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41 *Calculating segment abundance.*- The first stage of density surface modeling consisted of
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43 estimating the per-segment abundances for the aerial and ship datasets, which form the
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45 response variable in our spatial model. Although transects were surveyed more than once
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47 during our survey period, we assumed the segments were independent because surveys were
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49 at least one month apart on a given transect and so Common Loons likely moved between
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51 surveys (Kenow et al. 2009). For this analysis, we ignored flying loons and used only
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observations of Common Loons sitting on the water to quantify the distribution and abundance of foraging Common Loons.

Aerial-based survey data.-As previously mentioned, a strip transect survey protocol was used with the aerial platform and detection was assumed to be perfect within the survey strip. We believe that this assumption is reasonable as 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 strip of a relatively narrow width (107 m). A proportion of Common Loons were likely not available for detection because they were foraging below the surface and did not surface until after the plane passed flying at high speed. 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, 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 the aerial surveys we estimated the number of Common Loons in segment j as

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

where s_{jr} is the size of the r^{th} flock (of R_j) in segment j .

Ship-based survey data.-Conventional distance sampling (CDS; Buckland et al. 2001) was used 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. A detection function characterizing this relationship was fitted to the perpendicular distances. The probability of detection, \hat{p} , was then calculated from the detection function following Buckland et al. (2001). Here we fitted both half-normal and hazard-rate detection functions via maximum likelihood with the R package mrds (Laake et al. 2011). No covariates were modeled in the detection function and we chose between the two models using AIC (Akaike 1973). We divided 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:

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

where s_{jr} was the recorded size for flock r , and R_j was the number of groups in segment j . 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 (see Lukacs et al. 2010).

Survey data compatibility.- In order to ensure that it was appropriate to combine aerial strip and ship-based line transect data, we compared the observed per-segment densities for the two platforms (densities were used rather than counts to take into account the size of the segments). We compared densities via a quotient-quotient plot in all segments and those segments where the two platforms overlapped spatially. This analysis found that the datasets were compatible (see online Supplementary Materials for details).

Density surface modeling.-Having obtained estimates of the number of Common Loons in each segment and showed that the datasets were compatible, we combined the Common Loon

segment 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 generalized additive model (GAM) of the following form (assuming a log link function):

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

Here β_0 is an intercept and 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 $\log(a_j)$ is an offset that corresponds to the area of the segment, calculated as:

$$a_j = w_j m_j l_j$$

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

The explanatory variables available for inclusion in the models were univariate smooth functions of 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), closest distance to coast (*cdist*) and water depth (*depth*; Fig. 1). A bivariate smooth of *lat* and *lon* was also included. To avoid fitting overly complex models, the maximum basis size for the smooth terms was limited to 7 for the univariate terms and 20 for the bivariate terms. Survey platform was included as a potential factor variable. Several response distributions were tested including: negative binomial, quasi-Poisson, Gamma, and Tweedie and selected by inspection of residual plots. We performed model selection by building a model with all of the covariates included, and then

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removing terms if they were non-significant. 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). Smoothness selection was performed by REstricted Maximum Likelihood (REML; Wood 2011).

Having selected a model, 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 an area 2 km² which served as the offset (a_j , above). Summing over the predicted values gave an estimate of abundance in the study area. Uncertainty in the abundance estimates for each prediction grid cell and the overall abundance were obtained by the *variance propagation* method of Williams et al. (2011). The method incorporates uncertainty 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), which accounted for the extra variability incurred by the two-step estimation procedure. Uncertainty in the availability bias could not be quantified and as such was not included in variance estimates for the 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.

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3 *Sensitivity analysis.* - Several decisions were made as part of the modeling process; in order to
4 ensure that the model was robust to these choices we analyzed the sensitivity of our results.
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6 To check that the model was not sensitive to varying the values of the availability correction,
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8 we varied the availability correction value and looked at the resulting Common Loon predicted
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10 abundance.
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16 To investigate whether correlations in Common Loon abundance estimates between
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18 adjacent segments would affect the overall Common Loon abundance estimate, we
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20 subsampled the data, creating two data sets where every second segment was selected, three
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22 data sets where every third segment was selected, and four where every fourth segment was
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24 chosen. From these resulting nine data sets, Common Loon abundance was then calculated
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26 using the methods outlined above.
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31 *Model validation.*- Using the models fitted to the subsets of the data described above,
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33 predictions were made for those segments not included in the model fitting process and
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35 compared to the corresponding observed counts. This gives an indication of the predictive
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37 power of the model. To quantify performance, we fitted a linear model to the predicted counts
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39 for the missing segments and used the observed (but excluded) counts as an explanatory
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41 variable, the slope coefficient of the resulting model can then be used for comparison (a slope
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43 of 1 indicates perfect agreement between excluded, observed counts and model predictions).
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46 We used R, version 2.15.1 (R Development Core Team 2012) for all statistical analyses and
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49 models.
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RESULTS

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

Ship-based surveys.- There were 161 detections of Common Loons during the ship surveys (808 km of transects) (Fig 2). Common Loons were detected in 125 of 974 (13%) segments. As for the aerial surveys, the majority of Common Loon ship-based detections were of 1 or 2 birds, with flocks of up to 4 individuals recorded (Table 1).

Ship-based detection function.- A hazard rate detection function (Fig. 3) was selected (AIC=1549.64) over a half-normal detection function (AIC=1550.58). To avoid a long tail in the Common Loon detection function, perpendicular distances of sightings from ship-based surveys were truncated at 180 m, which excluded 5% of observations resulting in a total of 154 Common Loon ship-based detections used in the analysis versus the total 161 observed (Fig. 3). Using a half-normal detection function gave similar overall results (see online Supplementary Materials) and an analysis where the distances were binned into 30-m intervals gave a similar detection function, so exact distances were used. The expected group size from the size bias regression (1.187 birds; CV=0.02) was slightly larger than the mean group size (1.175; CV=0.03); a 0.8% difference (Table 1). Fitting a detection function with size as a covariate did not improve the AIC of the resulting detection function significantly (<3 point difference), so size was not used in the final detection function model.

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3 *Survey compatibility.*- Aerial and ship-based survey platforms appeared to be compatible, and
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5 this compatibility was stronger in those areas where coverage of the two survey platforms
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7 overlapped (Fig. 4). See online Supplementary Materials for details.
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11 *Density surface model.*- A negative binomial response distribution provided the best fit to the
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13 data based on evaluation of residual plots. The best fitting model consisted of two univariate
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15 smooths of *lat* and *depth*, with a negative binomial response and a scale parameter of 0.185
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17 (other terms, including the linear survey type term, were non-significant). The DSM predicted
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19 the highest densities of loons closest to the coast in waters < 40m deep (Fig. 5). This can be
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21 seen in the smooth of depth (Fig. 6, right panel); the smooth is constant for depths greater than
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23 approximately 40 m and then increases as depth decreases. The confidence intervals are wide
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25 for the deepest and shallowest waters as there was less coverage for these depths. The peak in
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27 the smooth of *lat* (Fig. 6, left panel) corresponds to the high abundances of Common Loons
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29 around Block Island.
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38 The estimated abundance over the whole study area was 5,538 Common Loons
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40 (CV=0.081; 95% CI = 4,726-6,489), and had a smaller confidence interval than DSMs of the
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42 survey platforms modeled independently; models using ship-based line-transect survey data
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44 estimated 6,367 (95% CI 4,268-9,499) and aerial strip-transect data estimated 4,949 (95% CI
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46 4,094-5,983) (See online Supplementary Materials). This abundance estimate can be thought of
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48 as a daily average number of birds foraging in the waters off Rhode Island in winter. A plot of
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50 the CVs for each prediction cell shows that the highest uncertainty is along the southern edge
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52 of the region and in the northwest corner, where some of these grid cells lie beyond the range
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3 of the survey effort (Fig. 6; right panel). The diagonal stripe of high uncertainty in the center of
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5 the study area corresponds to habitats of greater depths (Fig. 1), which were not sampled as
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7 much as other depth ranges. This depth profile combined with the high abundance estimated
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9 elsewhere in that horizontal band (due to the high estimates around Block Island) lead to high
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11 uncertainty in that area.
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15 *Sensitivity analysis.*- To test the effect of changing the availability bias, we varied the value of
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17 the correction factor over the range 0.5-1, refitting the model each time (smooth terms were
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19 kept the same so the model was of the same form, but parameters were estimated). This lead
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21 to a series of abundance estimates that lay within the confidence interval reported above for
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23 availabilities between 0.55 and 0.9. When plotted against the correction factor, these
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25 estimates follow an approximately exponential curve, decreasing as the correction factor
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27 increased (see online Supplementary Materials). This suggests that (1) the availability affects
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29 the model in an entirely deterministic way, which is evident from the mathematical form of the
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31 model, and (2) we can be relatively certain that our confidence interval is robust to reasonable
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33 changes in the correction factor. Further details of model selection are given in the online
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35 Supplementary Materials. Autocorrelation was assessed using the subsampling strategy
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37 detailed above and resulting abundances showed little sensitivity to changes in subsampling
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39 (see online Supplementary Materials).
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43 *Model validation.*- The final DSM was validated by fitting a model to subsets of the data (again
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45 keeping the form of the models the same) and predicting those segments excluded from the
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47 model. Extracting the slope coefficients from linear models fitted to the excluded and
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49 predicted segments, we calculated the mean and median, which were 0.138 and 0.124,
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3 respectively (range = 0.087 – 0.2). A coefficient close to 1 would indicate very good agreement
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6 between model and data.
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16 Our DSM approach accurately estimated the distribution and abundance of a wintering
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18 population of Common Loons across a large study area (3,800 km²) in nearshore and offshore
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20 waters of Rhode Island. Our model accounts for three factors that could affect abundance
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22 estimates: (1) imperfect detection of Common Loons in the ship-based line transect survey data
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24 using a detection function, (2) diving behavior of Common Loons surveyed with aerial-based
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26 strip transects using an availability bias correction, and (3) non-uniform distribution of Common
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28 Loons using a spatially-explicit model for their distribution to calculate their abundance across
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30 our study area. Our results highlight both the utility and flexibility of the DSM approach for
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32 predicting the distribution and abundance of a marine diving bird integrating survey data from
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34 multiple platforms using strip and line transect survey protocols.
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41 *Compatibility of survey datasets.*— Integration data from two survey platforms for our DSM first
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43 required evidence of compatibility between the two datasets. Our analysis revealed the
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45 segment densities were compatible for Common Loons, which was supported by other survey
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47 platform comparisons of loon density (Henkel et al. 2007). It is important to note that this
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49 compatibility we found between survey platforms and protocols for Common Loons may not be
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51 true for all marine bird taxa (Briggs et al. 1985, Henkel et al. 2007). We did find that fitting a
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DSM to the ship data only and aerial data only were within the confidence interval of the "full" analysis, which was smaller than the confidence intervals for the two analyses individually. This result was expected for the ship-based survey since the spatial coverage was so much smaller. A naïve estimator of abundance found by adding the two single platform models weighted by effort estimated 5,281 Common Loons in our study area (see online Supplementary Materials). We also note that in both single platform models latitude and depth were selected as important covariates.

Common Loon distribution and abundance in the maritime waters of Southern New England.-To our knowledge this study represents the first attempt to model the fine-scale spatial distribution and abundance of Common Loons wintering at a North American coastal site. Our abundance estimate for winter in our study area is as large as the overall adult population of Common Loons breeding in New York and New England (ca. 5,500 individuals; Evers 2007), consistent with other research highlighting the importance of our study area to wintering Common Loons (Kenow et al. 2009).

Common Loon distribution and abundance in relation to habitat parameters.- Common Loons in our study area were present in relatively shallower waters, typically less than 40m, and most abundant in those waters <20m surrounding Block Island. Higher densities of Common Loons in relatively shallow waters (<40m) is consistent with previous research (Haney 1990). Kenow et al. (2009) found that satellite-tagged Common Loons were most likely found in waters 3 to 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

those shallow waters at the northern boundary of our study area. This 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), conditions which could provide higher densities of Common Loon forage prey to support greater densities of Common Loons.

Proposed OWED in Common Loon wintering habitat.-Post-construction avian monitoring of OWED in European waters have found less than expected densities of loons within a OWED impact area and at distances of 2 to 4 km from installed turbines (Petersen et al. 2006, Langston 2013) and avoidance by loons of areas with high shipping intensities (Schwemmer et al. 2011). Our model predictions and previous post-construction studies of OWED suggest that this type of large-scale marine development could potentially lead to displacement and a significant loss of important foraging habitat for wintering Common Loons in southern New England. Therefore gathering spatially-explicit information on the distribution of Common Loons and other marine birds prior to the construction of OWED is important to help biologists and policy makers gain a clearer understanding of important areas for marine birds that should be protected from overdevelopment.

Density surface modeling.-Our results highlight the utility of the DSM approach for predicting marine bird distribution and abundance integrating ship and aerial platform data collected using different survey protocols. The ability to integrate data from multiple surveys enables investigators to use many, potentially historical survey datasets and perform inference over a longer time period that could revealing temporal patterns.

Using a DSM has several advantages over other modeling techniques. In comparison to approaches developed in Royle et al. (2004) and Fiske and Chandler (2011), the choice of response distribution is much greater. Although we do not model detection jointly with the spatial distribution, we note that this is not particularly problematic since transects are long in comparison to their width and spacing, so variation “along” the transect is much more important than “across” it. The two-stage approach also does not present an issue for variance estimation as we can propagate uncertainty from the detection function through to the spatial model using the method of Williams et al. (2011).

Model validation.— The DSM had relatively low predictive power according to our cross-validation procedure. Oppel et al. 2012 highlighted a number of reasons why predictive power of marine bird spatial models is relatively low including: extremely dynamic conditions in the marine environment, environmental covariates potentially not being suitable proxies of high productivity (e.g., forage) and survey data which provides very brief temporal windows that could lead to falsely zero-inflated counts.

Future work.— Although our DSM appeared relatively insensitive to the availability bias correction factor, it would be useful to verify this by further experimentation. 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.

Using a GAM for the spatial model allows for simple extensions 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.

ACKNOWLEDGEMENTS

We wish to thank the following people for their assistance with various aspects of the project. For help collecting survey data, we thank observers Brian Harris, Alex Patterson and John Veale. We thank George Breen for piloting the Cessna Skymaster. We thank Frances Fleet and their many captains for navigating the survey ship. We thank Chris Damon and Aimee Mandeville (URI EDC) for assistance with GIS analysis. J.F. Piatt, S. Oppel and an anonymous reviewer provided helpful comments that greatly improved this manuscript. This research was supported grant support from the State of Rhode Island for the Ocean Special Area Management Plan.

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

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

FIGURE CAPTIONS

FIG. 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.

FIG. 2. Common Loon detections (black circles) observed sitting on the water along aerial strip transects and ship line transects during the winter of 2009-2010 off of southern Rhode Island. Saw tooth lines represent eight grids that were surveyed during ship-based surveys, whereas the 24 parallel vertical lines represent the aerial-based survey transects.

FIG. 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 180m.

FIG. 4. Quotient-quotient plot of observed aerial and ship per-segment densities (note: ship and aerial segment densities were corrected by segment area). The left panel shows a Q-Q plot for all segments of both data sets, the right shows observed counts in overlapping segments. The black line indicates perfect compatibility. Darker circles indicate overlapping segments.

FIG. 5. Predicted abundances of Common Loons (individuals per km²) over the 3,800 km² Rhode Island OSAMP study area. Dark colors indicate higher abundances (left panel). 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 (right panel). Note the increase in model uncertainty at the north and south extremes of the study region and the diagonal ridge in the center of the study area. The former two correspond to where there was

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3 lower survey effort, the latter to large depth values (relatively unsampled) combined with high
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6 predicted abundances for similar values of latitude (e.g., around Block Island).
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10 FIG. 6. Plots of the smooth functions for latitude (left panel) and depth (right panel) that were
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12 used in the final Common Loon density surface model. Dotted lines show approximate 95%
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14 confidence intervals for the smooth terms. Numbers in brackets indicate the effective degrees
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16 of freedom of the smooth term; note that the y-axes are on a log scale.
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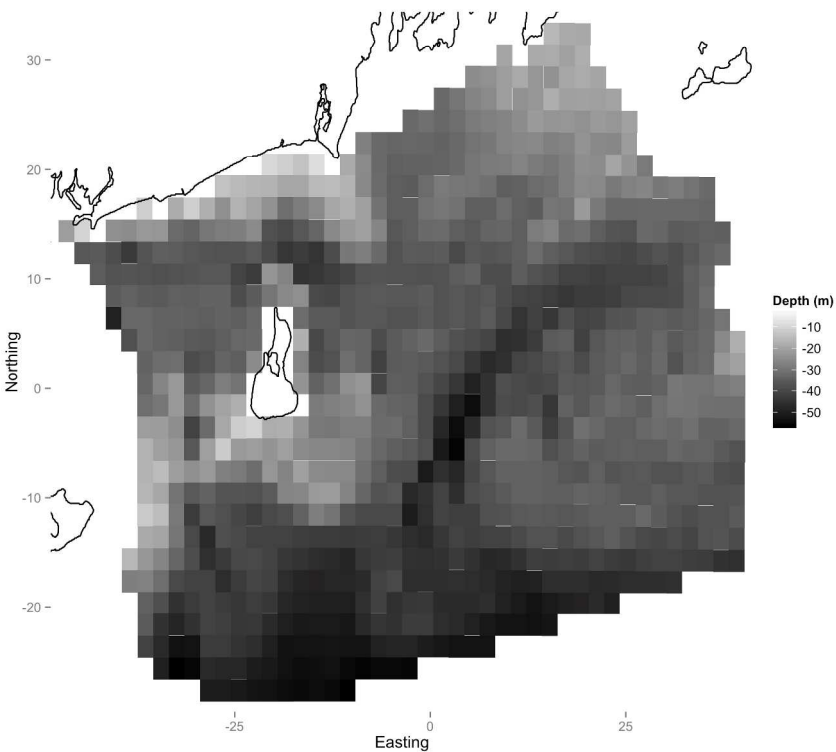


FIG. 1.

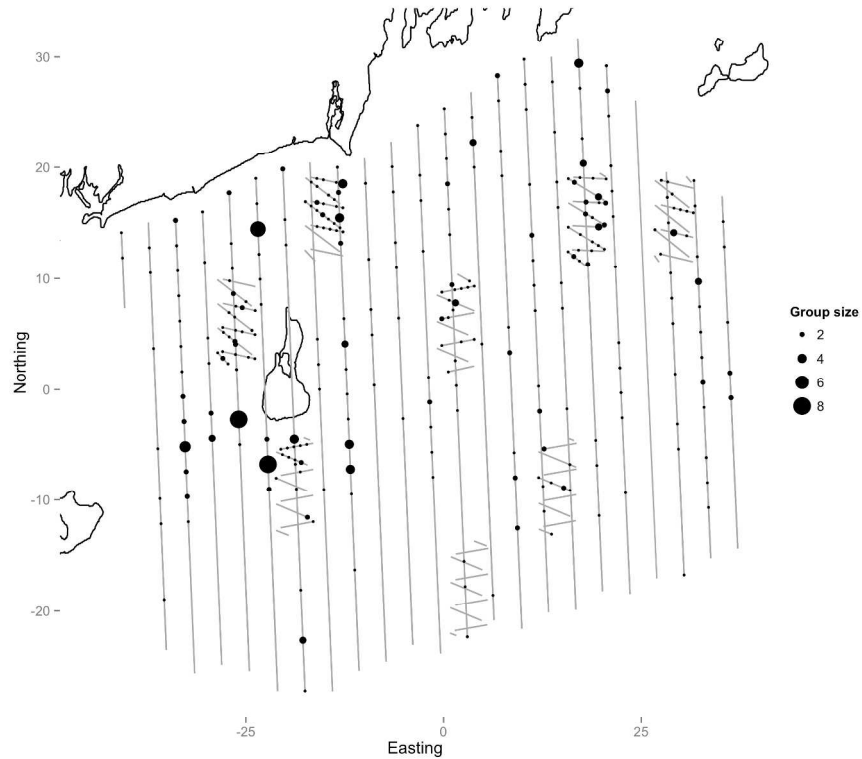


FIG. 2.

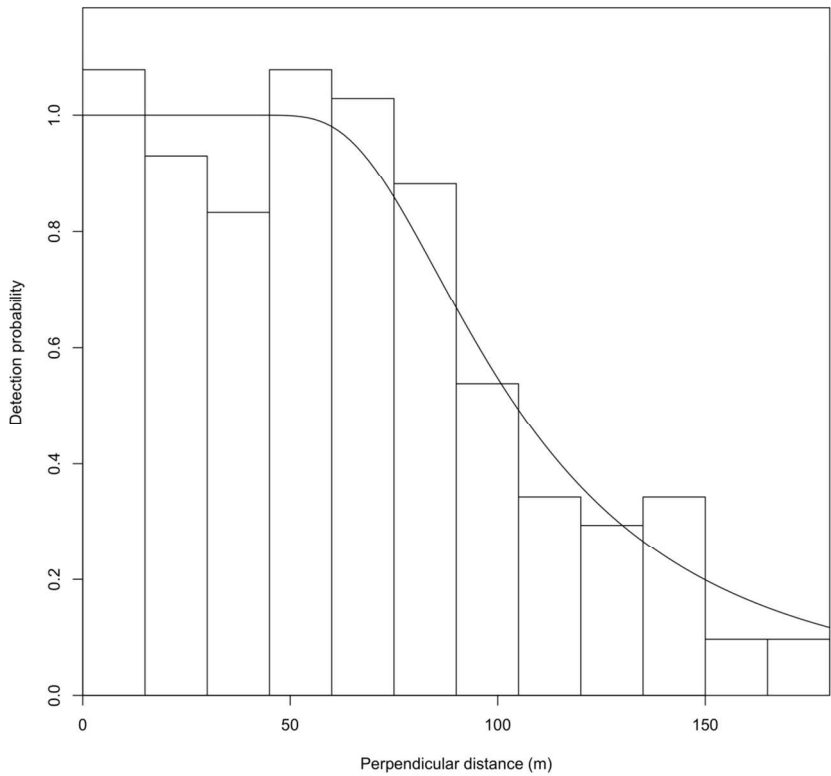


FIG. 3.

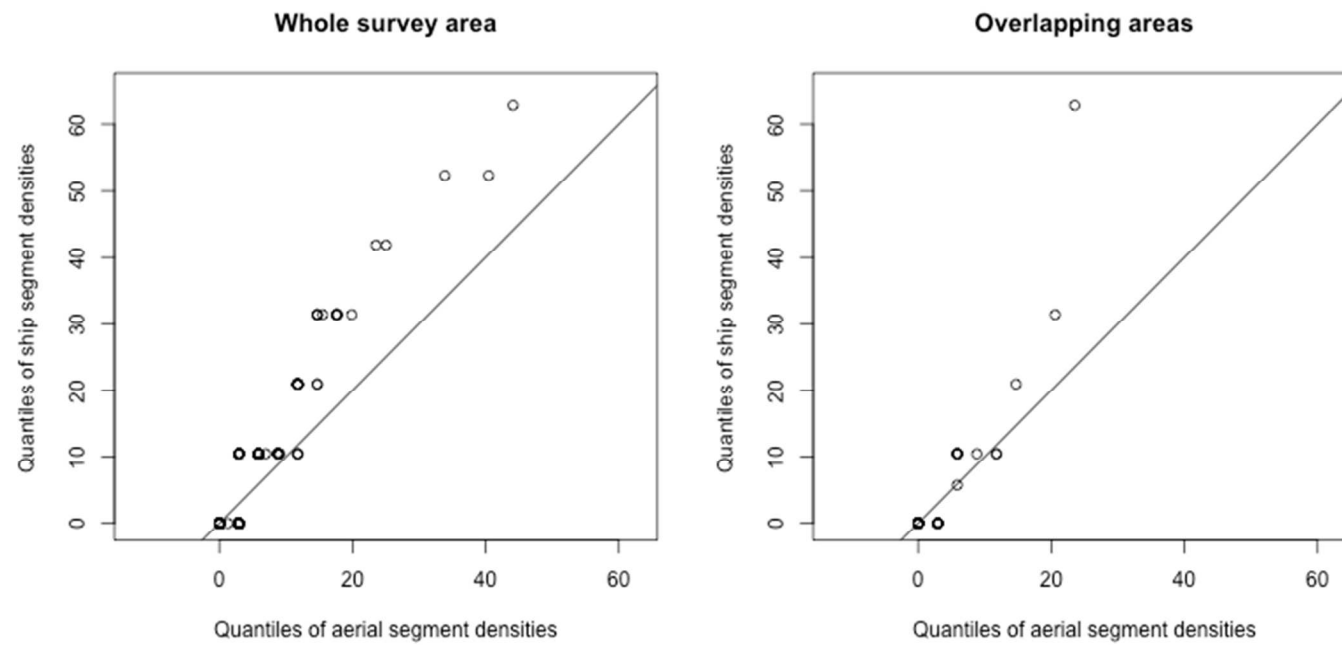


FIG. 4.

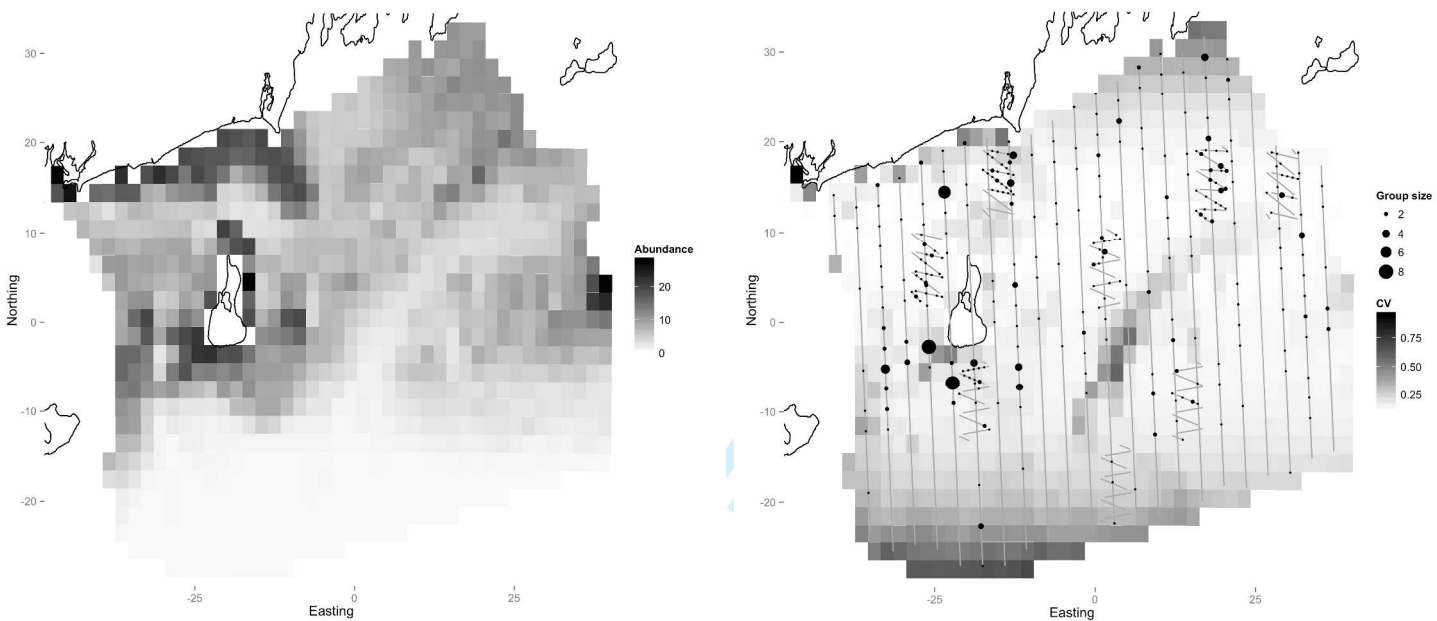


FIG. 5.

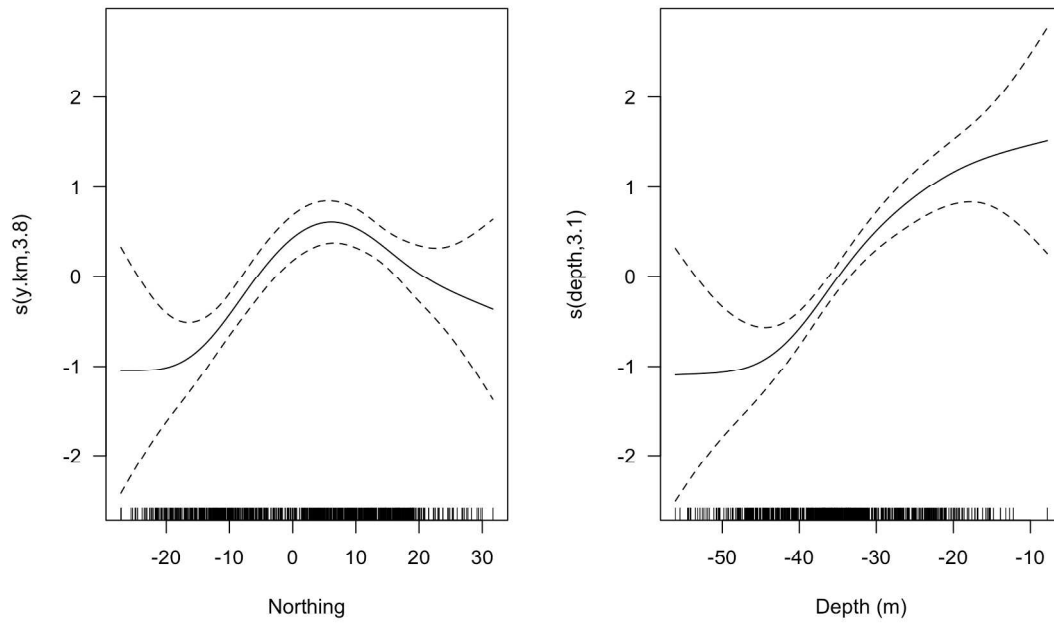


FIG. 6.

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LRH: WINIARSKI ET AL.

RRH: DENSITY SURFACE MODEL OF COMMON LOONS

ONLINE SUPPLEMENTARY MATERIAL FOR A DENSITY SURFACE MODEL OF WINTERING
COMMON LOONS INCORPORATING SURVEY DATA FROM AERIAL AND SHIP-BASED PLATFORMS

KRISTOPHER J. WINIARSKI^{1, 3}, M. LOUISE BURT², ERIC REXSTAD², DAVID L. MILLER¹, CAROL L. TROCKI¹, PETER W.
C. PATON¹ AND SCOTT R. MCWILLIAMS¹

¹Department of Natural Resources Science, 1 Greenhouse Road, University of Rhode Island,
Kingston, RI 02881 USA

²Centre for Research into Ecological and Environmental Modelling, University of St Andrews,
The Observatory, Buchanan Gardens, St Andrews, Fife, KY16 9LZ, UK

³E-mail: withakri@gmail.com

Appendix A1 - Sensitivity analysis and model evaluation.

Several parts of the final DSM rely on modeling decisions made by the authors. In order to ensure that the model was robust to these choices we checked model assumptions and analyzed the sensitivity of our results.

Suitability of data combination— In order to ensure that it was appropriate to combine aerial and ship-based survey data, we compared the observed per-segment counts for the two platforms (Fig. 4). We compared densities rather than counts so as to take into account the differing areas of the segments. In each plot, the solid black line shows the line $x=y$; if there was perfect agreement, the points would all lie on that line. The left plot shows the quantiles of all the data from both platforms, the plot shows that there is relatively good agreement between the platforms in terms of segment density, although the aerial segments appear to be slightly higher. The right plot shows quantiles of segments that overlapped between both aerial and ship-based platforms. These overlaps were calculated by building a convex hull around each sawtooth and finding those aerial segments which had midpoints lying within the hull. Segment densities are more similar with this comparison, although there is a single aerial segment with a very high Common Loon density value.

We also checked that modeling each platform individually gave comparable results to the combined analysis. Fitting the DSM using only the ship-based line-transect survey data resulted in a predicted abundance of 6,367 (95% CI 4,268-9,499) Common Loons (Fig. A1). Using only the aerial strip-transect data resulted in a predicted abundance of 4,949 (95% CI 4,094-5,983) (Fig. A2). Both estimates are within the confidence interval of the "full" analysis,

which is smaller than the confidence intervals for the two analyses individually, though this is unsurprising for the ship-based survey since the spatial coverage was so much smaller. A naïve estimator of abundance found by adding the two single platform models weighted by effort gives an estimated abundance of 5,281 Common Loons.

Availability bias correction— As described in the main article, we varied the value of the correction factor over the range 0.5-1, refitting the model each time to test the effect of the availability bias. Fig. A3 shows a plot of availability against the predicted abundance over the OSAMP area. Estimates follow an approximately exponential curve, decreasing as the correction factor increased.

Ship-based detection function— We re-ran the analysis using the half-normal detection function fitted to our ship-based observations, this gave an abundance estimate in our combined platform model of 5,931 with a corresponding 95% CI of 5,062-6,948. This is not a large difference (5,538 loons with the hazard-rate detection function) and the coefficient of variation was 0.0809, close to that when the hazard-rate detection function was used. We therefore conclude that our final combined platform model was not sensitive to the form of the detection function. We also included two covariate models in our set of candidate detection functions. These consisted of including group size and wave height. Neither of these provided a significant (>3 point) improvement in AIC, so were not considered further.

Autocorrelation— Although there did not appear to be substantial correlation in the estimated number of birds per segment along transect lines, nine subsets of the data were created (created by removing every 2nd segment, 2 data sets; every 3rd segment, 3 data sets; and 4th

segment, 4 data sets). Abundance estimates were then calculated using the resulting models (models had the same form as our final model). The results from these subsamples were of the same order as that produced using the all the data. Abundance estimates from these models ranged from 4,638-6,344 loons, with a median abundance of 5,966. This leads us to believe that our model is stable. Results are summarized in Fig. A4 and Table A1.

Predictive power– To assess the predictive power of the model we used the subsamples created above and predicted the values of the segments excluded in each model. Comparing the predicted values to the observed per-segment counts will then allow us to evaluate the predictive power of the model. To quantify this process, rather than plot the results, we fitted a linear regression model to the predicted values using the observed values as an explanatory variable. Extracting the slope coefficients from these models (which were 0.193, 0.101, 0.117, 0.135, 0.116, 0.167, 0.124, 0.2, 0.087) we calculated the mean and median, which were 0.138 and 0.124 respectively. A coefficient close to 1 would indicate very good agreement between predicted and observed counts and although our results are some way from this, we expect that the values would not be particularly high due to the nature of the observational study.

Appendix A2 - Model selection.

As described in the main article, we performed “model selection” by including all terms in the model and then using a combination of p-values and an extra shrinkage smoother (as in Wood, 2006, Section 4.1.6). To decide which response distribution was most appropriate, we selected response distributions via inspection of residual plots to assess model fit. In our final model, the negative binomial had the best residual plots. The parameter of the negative binomial distribution was estimated jointly with model coefficients and smoothing parameters using the “outer iteration” method (see Wood, 2006, Section 4.7). We used REstricted Maximum Likelihood (REML) to estimate the smoothing parameters (over GCV/UBRE), as it is less prone to oversmoothing (Wood 2011).

Appendix A3 - Survey effort

The number of surveys conducted for each segment varied from one to four (Fig. A5).

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TABLE A1. Summary of results from modeling subsets of the data. In each case, a systematic set of segments was removed to assess the impact of between-segment correlation.

Subset	Set	Number of segments	%Dev. Exp.	Estimated abundance
Every 2 nd point	1	1118	18.86	6149
	2	1069	14.07	5279
Every 3 rd point				5403
	1	761	13.57	
	2	724	15.95	5966
	3	702	20.32	5221
Every 4 th point	1	508	18.97	6344
	2	558	10.40	6144
	3	538	18.28	5975
	4	508	17.45	4638

FIGURE CAPTIONS

FIG. A1. Predicted abundance of Common Loons (individuals per km²) in the OSAMP study area using a model which included only observations from the ship-based surveys (left panel). Plot of the coefficient of variation of Common Loon densities for each predicted grid cell when only the ship-based data was used to build the model (right panel). Ship transect centerlines and observations are overlaid.

FIG. A2. Predicted abundance of Common Loons (individuals per km²) in the OSAMP study area using a model which included only observations from the aerial-based surveys (left panel). Plot of the coefficient of variation of Common Loon densities for each predicted grid cell when only the aerial data was used to build the model. Aerial survey transect centerlines and observations are overlaid (right panel).

Fig. A3. Plot of availability bias correction factor versus predicted Common Loon abundance estimates for the OSAMP area. Each point gives an abundance estimate for the corresponding availability correction bias factor, line indicate a 95% confidence interval. The semi-transparent band gives the confidence interval for our final model (when the availability bias correction factor is 0.7), most of the abundance estimates lie within this band.

FIG. A4. Plot of the Common Loon abundance estimates obtained when subsamples of the data were used to fit the DSM. The semi-transparent band gives the confidence interval for our final model (with full data). The exact values of abundance and their associated confidence intervals are given in Table A1.

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FIG. A5. Plot of number of surveys per segment in the study area for ship-based and aerial based-surveys from 12 December 2009 to 22 February 2010.

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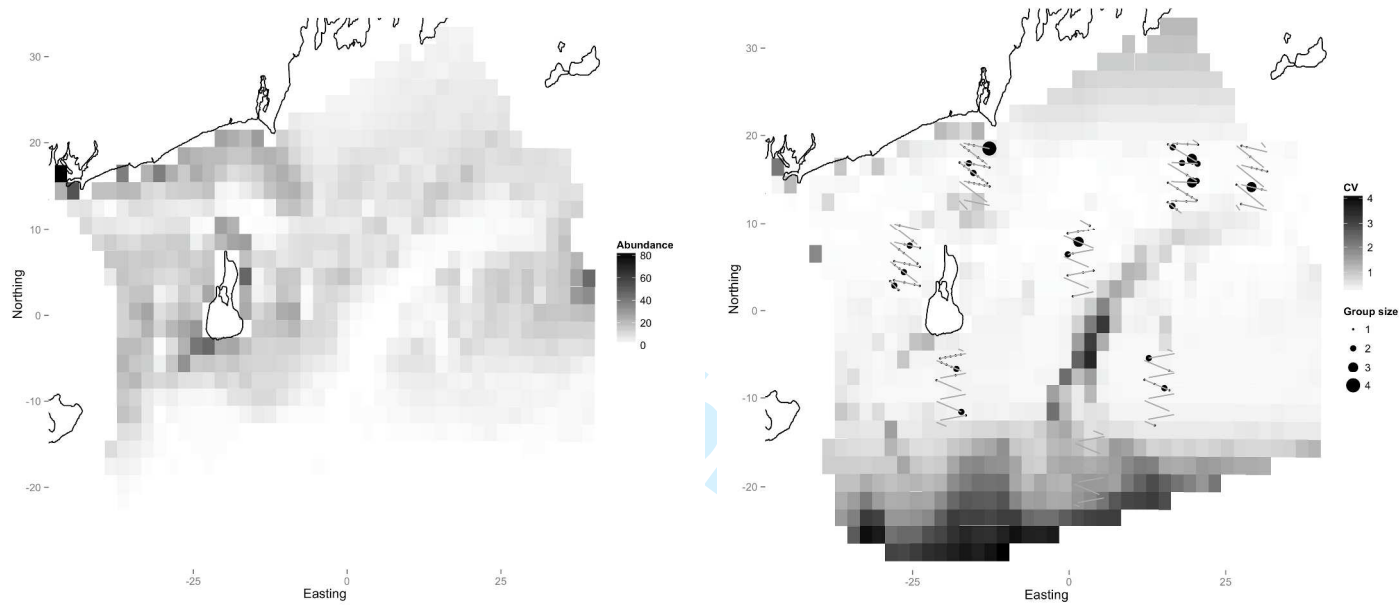


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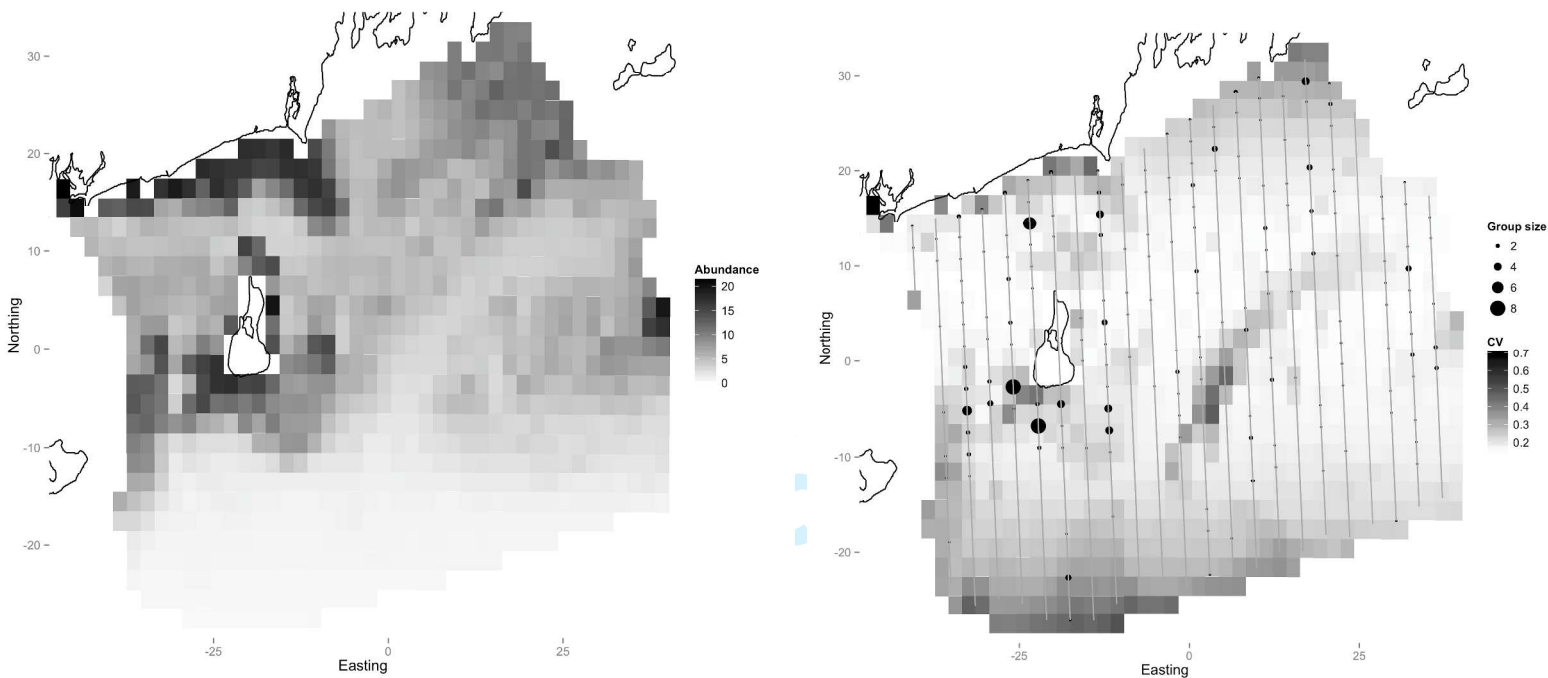


Fig. A2.

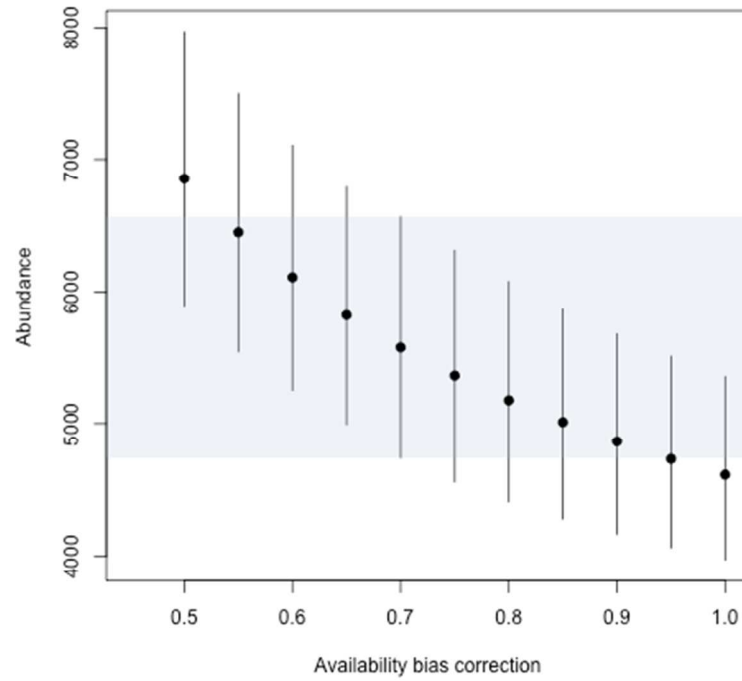


Fig. A3.

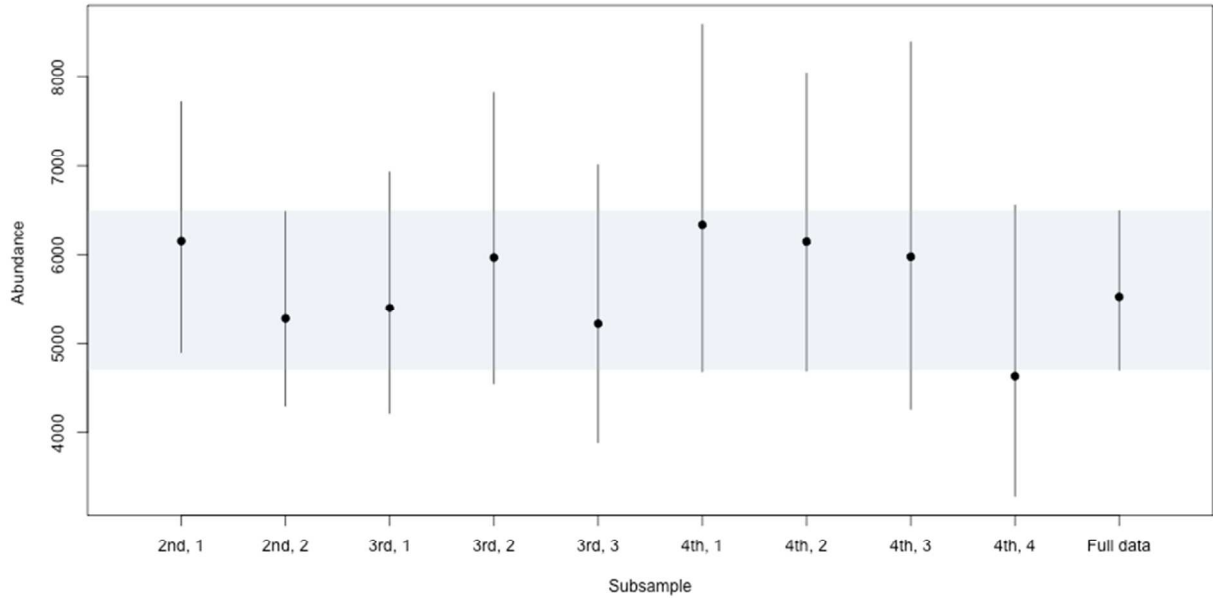


Fig. A4.

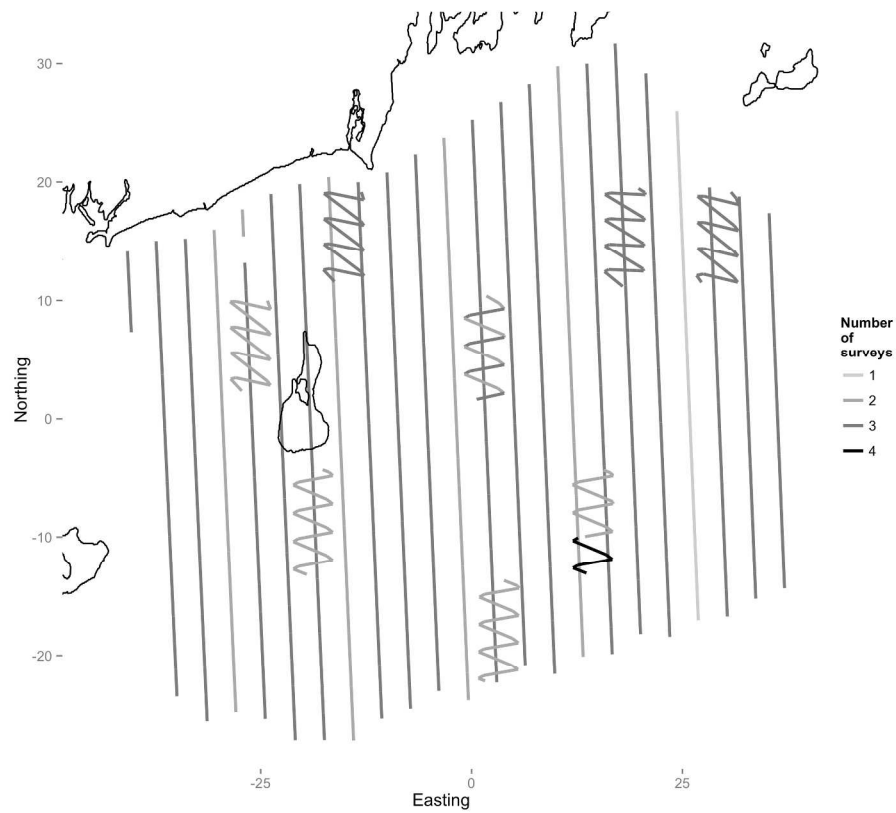


Fig. A5.