Spatiotemporal modelling of sea duck abundance: implications for marine spatial planning

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RUNNING HEAD: Model-based distribution and abundance

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1. Effective marine spatial plans require information on the distribution and abundance of biological resources that are potentially vulnerable to anthropogenic change. In North America, spatially-explicit abundance estimates of marine birds are necessary to assess potential impacts from planned offshore wind energy developments (OWED). Sea ducks are particularly relevant in this context as populations of most North American species are below historic levels and European studies suggest OWEDs.

2. We modelled species occupancy using a generalized additive model and conditional abundance with generalized additive models for location, scale, and shape; the models were subsequently combined to estimate unconditional abundance. We demonstrate this flexible, model-based approach using sea ducks (Common Eider \textit{Somateria mollissima}, Black Scoter \textit{Melanitta americana}, Surf Scoter \textit{M. perspicillata}, White-winged Scoter \textit{M. deglandi}, and Long-tailed Duck \textit{Clangula hyemalis}) in Nantucket Sound, Massachusetts, USA, which supports some of the largest concentrations of wintering sea ducks in eastern North America and where a 454-MW OWED is proposed.

3. Spatiotemporal effects were the dominant explanatory features in sea duck occupancy and conditional abundance models. Biophysical covariates also influenced occupancy (i.e., highest at intermediate sea surface temperatures and in areas with coarser sea floor sediments), but their effects on conditional abundance were less consistent among species. Spatially-explicit abundance estimates suggested that while the planned OWED in Nantucket Sound may displace some sea ducks from potential foraging habitat, most occurred in areas away from the proposed OWED.

4. \textit{Synthesis and application}. Our approach to species distribution and abundance modelling offers several useful features including (1) the ability to model all conditional
distribution parameters as a function of covariates, (2) integrated variable reduc-
tion and selection among many covariates, (3) integrated model selection, and (4) 
the efficient incorporation of smooth effects to capture spatiotemporal trends poorly 
explained by other covariates. This modelling approach should prove useful for ma-
rine spatial planners in siting OWEDs while considering key habitats and areas po-
tentially vulnerable to anthropogenic stressors. Moreover, the approach is equally 
suitable for terrestrial or aquatic systems.

Key words. abundance, distribution, generalized additive models, gradient boosting, Nan-
tucket Sound, stability selection, wind energy
Introduction

Marine spatial plans (MSP) can provide a rigorous framework to protect marine ecosystems from a variety of anthropogenic stressors (Polasky et al. 2008; Foley et al. 2010). A key element of MSPs is accurate spatially-explicit estimates of the abundance and distribution of biological resources (Douvere 2008; Punt et al. 2009; Bradbury et al. 2014). Along the northwest Atlantic Coast, numerous offshore wind energy developments (OWED; Breton & Moe 2009; Musial & Ram 2010) are proposed, including a 30-MW facility in Rhode Island Sound to be the first U.S. operational OWED by fall 2016. Therefore there is a pressing need to develop spatially-explicit models of key biological resources that can assist marine spatial planners in siting OWEDs while considering marine ecosystem integrity.

Understanding the distribution and abundance of marine birds represents a particular challenge for MSPs because the environmental factors associated with their distribution and abundance remain notably understudied (Zipkin et al. 2010; Bowman et al. 2015; Flanders et al. 2015). Sea ducks (Tribe: Mergini) are particularly important to consider in the context of marine spatial planning because populations of most North American species are below historic levels and there is considerable uncertainty in population trajectories (Bowman et al. 2015). Moreover, evidence from Europe suggests that OWEDs may negatively impact sea duck populations (Larsen & Guillemette 2007; Langston 2013; Bradbury et al. 2014).

Model-based approaches are a useful framework to generate spatially-explicit estimates of animal abundance and changes in animal distribution independent of abundance (Borchers et al. 2002; Certain & Bretagnolle 2008; Nur et al. 2011; Kinlan et al. 2012; Winiarski et al. 2014). However, modelling the spatial ecology of marine organisms such as sea ducks presents a variety of analytical challenges. First, the spatiotemporal distribution of marine organisms can be highly irregular and surveys often produce zero-inflated (Martin et al. 2005; Cunningham & Lindenmayer 2005), overdispersed (Richards 2008) count data that
may vary with biophysical features in complex, non-linear ways (Austin 2007). Second, an adequate modelling approach usually must identify a small suite of important covariates among many potentially correlated covariates while avoiding overfitting, a process that often is complicated by data from repeated surveys that regularly exhibit spatial and temporal autocorrelation (Hoeting 2009).

We demonstrate a flexible model-based approach to predict animal distribution and abundance using aerial transect surveys of sea ducks in Nantucket Sound, Massachusetts, USA. We implemented generalized additive models (GAMs; Hastie & Tibshirani 1990; Wood 2006) and their recent extension (GAMLSS - GAMs for location, scale, and shape; Rigby & Stasinopoulos 2005) in a gradient descent boosting framework (Friedman 2001). GAMLSS methods extend GAMs to allow all parameters of the conditional response distribution to be modelled as a function of relevant covariates (Rigby & Stasinopoulos 2005). This approach provides spatially-explicit insights into the covariates associated with sea duck abundance and its variability. The boosting algorithm accommodates the inclusion of various effect types (e.g., linear, smooth, spatial, spatiotemporal, and random effects; Hofner et al. 2014) and correlated covariates (i.e., parameter estimates are regularized), identifies the most relevant subset among potentially many covariates (i.e., variable selection), and evaluates competing representations of continuous covariates (e.g., linear vs. nonlinear effects; Kneib et al. 2009; Maloney et al. 2012). Our specific objectives were to demonstrate a flexible, model-based approach that (1) provides spatially- and temporally-explicit estimates of sea duck abundance and distribution while accommodating many of the challenges inherent in animal survey data; and (2) describes the associations between biophysical features and sea duck distribution and abundance in one of the most important migrating and wintering areas for sea ducks in the western Atlantic.
Materials and methods

Study area and species.—We conducted fieldwork throughout Nantucket Sound in Massachusetts, USA (Figure 1). Our study area encompassed ca. 1,500 km$^2$, was relatively shallow (generally < 20 m deep), and included some of the most important sea duck wintering habitat in the western Atlantic (Silverman et al. 2013). The primary species of sea ducks found in Nantucket Sound were Common Eider (Somateria mollissima; hereafter eider), Black Scoter (M. americana), Surf Scoter (M. perspicillata), and White-winged Scoter (Melanitta deglandi), and Long-tailed Duck (Clangula hyemalis). Additionally, approximately 62 km$^2$ of Horseshoe Shoal in northwestern Nantucket Sound is fully permitted for OWED (Figure 1; Santora et al. 2004), which may affect sea duck use of this important wintering area (Flanders et al. 2015).

Aerial strip transect surveys.—During the winters (late October to mid-April) of 2003-2005, we conducted 30 (2003/2004: 13, 2004/2005: 10, 2005/2006: 7) standardized aerial strip-transect surveys (Flanders et al. 2015) throughout an 1,100 km$^2$ study area in Nantucket Sound (Figure 1). Surveys occurred primarily from November - March ($n = 27$), with occasional October ($n = 1$) or April ($n = 2$) surveys. During each survey, we flew along 15 parallel north-south transects, separated by ca. 2.5 km (Figure 1), using a high-wing, twin-engine aircraft at an altitude of 152 m and speed of 167 km/h (90 kts). This altitude allowed us to identify most birds on the sea surface and reduced disturbance (i.e., flushing birds to another part of the study area and, thus, potential double counting). Surveys occurred only on days with wind speeds $\leq$ 15 kts and good visibility (>15 km). Surveys, typically 2.5 h in duration, occurred between 0900 to 1600 to avoid post-dawn and pre-sunset movements by ducks (e.g., Davis 1997) and to reduce glare due to low sun angles.

Observers monitored the sea surface within a ca. 90-m wide transect on both sides of the plane; we thus sampled approximately 6% (median; 68.4 km$^2$) of the study area during
a survey. Observers geographically referenced the number and species of ducks using the plane’s onboard GPS. We subsequently consolidated counts for each species (eider and Long-tailed Duck) or species group (scoter) into 2.25km² segments (Figure 1); this resolution (1.5 km x 1.5 km) corresponded approximately to the coarsest level of resolution of biophysical covariates (see below).

**Modelling approach.—** We related spatiotemporal variation in sea duck occupancy and abundance to potentially relevant biophysical and spatiotemporal covariates. We applied a negative binomial hurdle model that first modelled (1) the probability of occurrence of at least one individual (hereafter, the occupancy model) observed on the combined 180 m wide transect within a given segment using a logistic regression model and then (2) the abundance of sea ducks observed on the transect in that segment conditional on their presence (hereafter, the count model) using a truncated negative binomial model. The prevalence of zero counts (e.g., 75% of eider segment observations) prompted the use of a hurdle model, which we fit separately for each sea duck species group (Zipkin *et al.* 2010). GAMs and GAMLSS accommodated potential nonlinear effects of covariates on sea duck occupancy and the conditional mean and overdispersion of sea duck abundance, respectively.

We implemented GAMs and GAMLSS in a component-wise functional gradient descent boosting framework. We first computed the negative gradient of a user-specified loss function, which can be viewed as working residuals. We used as the loss functions the (negative) binomial log-likelihood for occupancy models and the (negative) truncated negative binomial log-likelihood for count models.

Next step, we fit user-specified functional forms of the covariates relative to the response, called base-learners (Hofner *et al.* 2014), separately to the negative gradient and a fraction of the single best fitting base-learner was added to the current model fit. The negative gradient was then reevaluated at the current model fit and the procedure iterated for a
user-specified number of iterations, \( m_{\text{stop}} \) (see Bühlmann & Hothorn 2007 for details). We fit boosted GAMLSS models similarly, although in each iteration the negative gradient was computed separately with respect to each GAMLSS parameter (i.e., mean and overdispersion) while holding the other parameter constant. We then fit base-learners to the resulting parameter-specific negative gradient vector and model updates were computed separately for each GAMLSS parameter as for boosted GAMs (see Mayr et al. 2012 for details).

As only the single best-fitting base-learner was selected in each iteration, the algorithm integrated intrinsic selection of the most relevant covariates and their functional form (i.e., some base-learners were never selected). Variable selection was further fostered by stopping the algorithm prior to convergence to maximum likelihood estimates to maximize predictive accuracy while avoiding model overfitting (early stopping; Mayr et al. 2012; Maloney et al. 2012). We used 25-fold subsampling to determine the optimal stopping iteration for each model by randomly drawing (without replacement) 25 samples of size \( n/2 \) from the original data. We used the selected sample to estimate the model and the balance of the data in each sample to determine the out-of-bag prediction accuracy (empirical risk) measured by the negative log-likelihood of each model; the optimal stopping iteration (\( \hat{m}_{\text{stop}} \)) was the iteration with the lowest average empirical risk. In boosted GAMLSS models, we used multi-dimensional subsampling to determine the stopping iteration for each GAMLSS parameter while allowing for potentially different model complexities in the parameters (see Hofner et al. 2015b).

Despite these agreeable features, boosting methods typically produce “rich” models relying to some extent on many base-learners (Hofner et al. 2015a). Thus, we applied stability selection (Meinshausen & Bühlmann 2010; Shah & Samworth 2013) to identify the most commonly selected base-learners, and thus covariates, in each model while preserving an upper bound of \( \alpha \approx 0.06 \) for the per-comparison error rate (see Appendix S1 and Hofner.
et al. 2015a for details).

Covariates.—We evaluated biophysical covariates expected to influence the distribution and abundance of sea ducks and their benthic prey (see Appendix S2), as we were unaware of data related directly to the distribution of preferred prey (e.g., mollusks and crustaceans). Additionally, we included interactions that allowed the effects of two covariates to vary over time within a given winter (see Appendix S2). We standardized (i.e., mean centered and scaled) all continuous covariates and developed a custom function to visualize the spatial and temporal distribution of covariates in Nantucket Sound (Appendix S3).

For each continuous covariate, we specified two base-learners: a linear base-learner and a base-learner for the smooth deviation from the linear effect via penalized splines (i.e., P-splines; Eilers & Marx 1996; Fahrmeir et al. 2004; Schmid & Hothorn 2008). This allowed the algorithm to select between no effect, a linear effect, or a smooth effect for each covariate. For categorical covariates, we included $K - 1$ (dummy-coded) linear base-learners for a $K$-level covariate. To address potential spatial autocorrelation, we included a smooth surface function of the spatial coordinates of segment centers (Kneib et al. 2008); this surface comprised linear base-learners for the easting and northing, their linear interaction, and a penalized nonlinear tensor product P-spline (Kneib et al. 2008, 2009; Maloney et al. 2012). We also allowed this surface to vary over time within a winter.

The decomposition of continuous covariates into centered linear and penalized orthogonal nonlinear base-learners allowed us to weight base-learners equally and thus allowed unbiased model choice (i.e., prevented the preferential selection of smooth base-learners; Kneib et al. 2009; Hofner et al. 2011). We restricted each base-learner to a single degree of freedom and omitted the intercept term from each base-learner.

The occupancy and count models had the following structure (see Appendix S2 for descriptions of abbreviated covariates):
$g(\cdot) = \text{int} + \text{time} + f(\text{time}) + \text{SST}_w + f(\text{SST}_w) + \text{SST}_m + f(\text{SST}_m) + \text{SST}_r + f(\text{SST}_r) + \text{SST}_r \cdot \text{time} + f(\text{SST}_r, \text{time}) + \text{SBT} + f(\text{SBT}) + \text{NAO}_w + \text{depth} + f(\text{depth}) + \text{depth} \cdot \text{time} + f(\text{depth}, \text{time}) + \text{d2land} + f(\text{d2land}) + \text{chla} + f(\text{chla}) + \text{cdom} + f(\text{cdom}) + f(\text{cdom}, \text{chla}) + \text{meanphi} + f(\text{meanphi}) + \text{SAR} + f(\text{SAR}) + \text{tidebmean} + f(\text{tidebmean}) + \text{tidesd} + f(\text{tidesd}) + \text{strat} + f(\text{strat}) + \text{ferry} + y2004 + y2005 + xkm + ykm + xkm \cdot ykm + f(xkm, ykm) + xkm \cdot \text{time} + ykm \cdot \text{time} + xkm \cdot ykm \cdot \text{time} + f(xkm, ykm) \cdot \text{time} + \text{obs\_window} + f(\text{obs\_window})$.

In our occupancy models, $g(\cdot)$ is $g(\pi_{\text{sea ducks}})$, the occupancy probability of a given duck species and $g$ is the logit link. In our count models, $g(\cdot)$ took two forms within the GAMLSS framework – the (conditional) mean count of sea ducks, $g(\mu_{\text{sea ducks}})$, and the (conditional) overdispersion in sea duck counts, $g(\sigma_{\text{sea ducks}})$; $g$ is the log link in both cases. Base-learners denoted as $f(\cdot)$ indicate the penalized nonlinear deviations from the corresponding linear base-learner. The explicit intercept ($\text{int}$) was a necessary byproduct of our decomposition of base-learners (see Kneib et al. 2009; Hofner et al. 2011). We included $\text{obs\_window}$, our measure of survey effort (see Appendix S2), as a covariate because small values in some segments impaired model estimability when treating $\text{obs\_window}$ as an offset.

Subsequent to their independent fitting, we consolidated occupancy and conditional count models (see Equation 6 in Zeileis et al. 2008) to generate spatially-explicit estimates of unconditional sea duck abundance. These estimates were used to evaluate the approximate explanatory power of our final models using a pseudo $R^2$ measure of the explained variation (Nagelkerke 1991; Maloney et al. 2012).
All analyses were conducted in R (Version 3.1.3; R Core Team 2014) with the add-on packages gamboostLSS (Hofner et al. 2015c,b), mboost (Hothorn et al. 2010, 2015), and stabs (Hofner & Hothorn 2015). The data and code for reproducing this manuscript and analyses are given as an online electronic supplement at http://github.com/adamdsmit/NanSound_JAppEcol.

Results

We modelled occupancy and conditional count independently for each species. Bootstrapped empirical risk suggested that occupancy models for all species converged to the maximum likelihood estimates (see Appendix S4). Conversely, bootstrapped empirical risks prescribed early stopping for both the conditional mean and overdispersion parameter in all count models (see Appendix S4). Final occupancy models and conditional count models included only a subset (12% to 38%) of the 48 base-learners initially specified for selection (see equation 1). Occupancy models generally contained more covariates and their interactions (8-10 of 23) than did count models (3-6 of 23), particularly among stably selected covariates and their interactions (Figure 2, see also Appendices S5 - S7).

Sea duck occupancy.—The covariates associated with occupancy were relatively consistent among species (Figure 2). The influence of univariate effects on the response is reflected in the range of the effect over the Y-axis and, due to standardization, can be compared among species and covariates within a model. For example, monthly sea surface temperature ($SSTm$) associated more strongly with eider occupancy than did distance to land ($d2land$) because it spanned a larger range of the Y-axis (Figure 2). In contrast, monthly sea surface temperature ($SSTm$) associated much more strongly with occupancy of Long-tailed Duck than eider and scoter for the same reason (Figure 2). Covariate interactions, illustrated with bivariate plots, are similarly comparable within a model. Only the general association (i.e., positive or negative) with the additive predictor is given for factor
variables. Comparing univariate, bivariate, and categorical effects is accomplished using the detailed covariate plots for eider, scoters, and Long-tailed Duck (Appendices S5 - S7, respectively).

Spatiotemporal effects (i.e., the $xkm$-$ykm$ location of segments and the change over time within winter [$time$]) were the dominant explanatory features in occupancy models, although these patterns varied considerably among species (Figure 2; see Day of season, Northing x Easting). Occupancy increased, but at a decreasing rate, with survey effort ($obs\_window$) in a given segment, as well as at intermediate monthly sea surface temperature ($SSTm$), greater distances from land ($d2land$), and in areas with coarser sediments (i.e., smaller $meanphi$; Figure 2). Eider occupancy associated negatively with chromomorphic dissolved organic material ($cdom$) and positively with sea floor surface area relative to planimetric area ($SAR$; our measure of the topographic variability of the sea floor; Figure 2), whereas scoter occupancy likewise related to $SAR$ and $cdom$, but in the opposite direction in both cases (Figure 2). Scoter occupancy was modestly greater in deeper waters ($depth$), whereas Long-tailed Duck occupancy was greatest in shallow waters during early winter and in deeper waters during later winter (Figure 2; $depth$ x $time$ covariate). Other effects were relatively minor and inconsistent among species.

The strong spatial effects ($xkm$-$ykm$) on occupancy resulted in distinct spatial patterns of occupancy among species (Figure 3, top row) despite the relative similarity of occupancy associations with biophysical covariates. Occupancy was typically highest for eider in northwest and southwest Nantucket Sound, in interior Nantucket Sound for scoter, and in northeast and south Nantucket Sound for Long-tailed Duck (Figure 3, top row). All species tended to avoid the western edge of the Sound northeast of Martha’s Vineyard. Generally, the areas of highest occupancy exhibited the lowest relative variability (Figure 3, bottom row), defined as the median absolute deviation (MAD) of occupancy relative to median occupancy within a segment (a measure analogous to the coefficient of variation).
Sea duck conditional abundance and overdispersion.—Spatial effects (xkm-ykm) were the dominant explanatory feature of conditional abundance estimates for scoters and Long-tailed Duck, but not for eider (Figure 2). In contrast to their occupancy model, scoter conditional abundance decreased with increasing sediment grain size (meanphi). Additionally, the relationships between eider conditional abundance and dissolved organic material (cdom) and sea floor topography (SAR; Figure 2) were more complex than with eider occupancy. The conditional abundance of eider and scoter was also associated with relatively warm or cool sea surface temperatures (SSTrel; Figure 2). Biophysical covariates associated with Long-tailed Duck conditional abundance exhibited general agreement with their corresponding occupancy model.

Spatially-explicit patterns of median conditional abundance (Figure 4, top row) did not necessarily reflect occupancy patterns (cf. Figure 3, top row). Some areas of Nantucket Sound exhibited mutually high conditional abundance and occupancy for a given species (e.g., eider in the southwest, scoter in the interior, and Long-tailed Duck in parts of the northeast). However, conditional abundance was low despite relatively high occupancy in some areas (e.g., eider in the northeast and Horseshoe Shoal, scoter in the northeast and southeast, and Long-tailed Duck along the northern margin). Conversely, other areas of Nantucket Sound exhibited lower occupancy but sea ducks, when present, were more abundant (e.g., eider along the eastern margin, and scoter and Long-tailed Duck in the southwest). As in occupancy models, sea ducks were relatively absent from the middle-western margin of Nantucket Sound (i.e., northeast of Martha’s Vineyard; see Figure 1). In contrast to sea duck occupancy, however, areas of highest conditional sea duck abundance typically exhibited the highest relative variability over time (Figure 4, bottom row). Overdispersion in conditional sea duck abundance also varied with biophysical covariates, although there was less consistency in the associated covariates among species (Figure 2; see also Appendices S5 - S7). Variability (i.e., overdispersion) in sea duck counts was het-
erogeneous in space (Appendix S8; Figure S8.1, top row) and time (Appendix S8; Figure S8.1, bottom row), particularly for eider and scoter (as indicated by the magnitude of the overdispersion parameter values).

**Expected sea duck abundance.**—Consolidated occupancy and conditional count models provided estimates of unconditional sea duck abundance in the study area over the survey period (Figure 5, top row). Final models of expected sea duck abundance explained moderate amounts of variation in observed counts of eider, scoter, and Long-tailed Duck (pseudo $R^2 = 0.31, 0.48, \text{ and } 0.32,$ respectively). Sea duck species exhibited relatively distinct patterns of abundance in Nantucket Sound. Eider were consistently most abundant in southwestern Nantucket Sound and relatively abundant in the northeastern part of the study area but less consistently so as evidenced by the relatively high MAD/median abundance over time (Figure 5). Scoter were also most abundant, with occasional extremely large flocks, in southwestern Nantucket Sound, although this also represented the area of highest relative variation in scoter abundance; relatively high abundances of scoter also occurred in central Nantucket Sound (Figure 5). Long-tailed Ducks were consistently most abundant in northeastern Nantucket Sound, as well as along its southern margin (Figure 5). No species’ highest abundances occurred in the OWED permitted Nantucket Shoal area, although expected eider and scoter abundances were consistently elevated in some parts of the Shoal (west and southeast, respectively; Figure 5).

We compared the total count of each sea duck species observed in aerial strip transects with the corresponding estimated total abundance in surveyed segments for each of the 30 aerial surveys (Figure 6). Our models tended to overestimate sea duck abundance when actual numbers were relatively low, although overestimation was typically less than an order of magnitude. Additionally, scoter abundance was occasionally extreme relative to typical counts and somewhat prone to underestimation during these extreme counts. Nonetheless, the general adherence of observed and predicted abundance to a line of unit
slope indicated that it may be reasonable to estimate sea duck abundance for the entire study area based on observed sea duck densities in transects (Figure 6).

**Temporal dynamics in wintering sea ducks.**—The MAD/median estimates (bottom rows of Figures 3-5, Figure S8.1 in Appendix S8) show that our spatially-explicit estimates of occupancy, abundance, and overdispersion invariably change over time, either explicitly via the selection of a within- or among-winter temporal effect (\textit{time} and \(y_{2004}/y_{2005}\), respectively) or implicitly via the selection of biophysical covariates that change within or among winters. The temporal dynamics of the wintering sea duck system in Nantucket Sound was one of its most striking attributes (see an animation for scoter occupancy and abundance in Appendix S9).

**Discussion**

**Utility of a boosted GAMLSS modelling framework.**—We demonstrated a flexible model-based approach to evaluate the environmental associations of species distribution and abundance based on multiyear replicated surveys. This approach proved particularly useful for sea ducks that exhibited considerable within and between year variation in their spatial distribution and abundance (Zipkin \textit{et al.} 2010; Winiarski \textit{et al.} 2014; Flanders \textit{et al.} 2015). The boosted GAMLSS framework offered several useful features including (1) the ability to model all conditional distribution parameters (e.g., conditional mean and overdispersion) as a function of covariates, (2) integrated variable reduction and selection among many covariates, and (3) integrated model selection via the simultaneous consideration of competing functional covariate forms (e.g., linear vs. non-linear). Additionally, this framework allowed us to incorporate smooth effects to efficiently account for spatiotemporal trends in the data that were poorly explained by other covariates and to identify those covariates and their functional forms most consistently associated with animal distribution and abundance (via stability selection). Moreover, the approach is equally suitable for
terrestrial or aquatic systems.

The importance of spatial scale.—The distribution and abundance of species is often spatially and temporally dynamic because it is often driven by biophysical covariates that may furthermore differ in importance depending on spatial scale (Johnson 1980; Johnson et al. 2004, 2006). Considering our sea duck example, a larger-scale occupancy model developed by Flanders et al. (2015) suggested that eiders were relatively uniformly distributed across Nantucket Sound, whereas our higher resolution abundance models found that eiders were concentrated in southwestern and central, eastern areas within Nantucket Sound. Indeed, the spatiotemporal patterns of unconditional sea duck abundance in Nantucket Sound largely reflect patterns in their conditional abundance and less the patterns of occupancy. This suggests that occupancy models alone may be inadequate for assessing risk from anthropogenic disturbances and for describing the fine-scale distribution of marine species (e.g., Winiarski et al. 2014; Flanders et al. 2015). We suggest that while large-scale models are useful to identify general geographic areas of import to sea ducks (Silverman et al. 2013; Flanders et al. 2015), our localized models provide more detailed estimates of sea duck distribution and abundance within Nantucket Sound. In the context of MSPs, large-scale models can help identify the areas to zone for OWED while localized models may better inform the placement of the OWED within the zoned area.

Environmental covariates that best explain sea duck distribution and abundance.—The biophysical associations with occupancy derived from our models were relatively consistent among species, whereas their associations with conditional abundance were more species-specific. Distance to land, which often is positively associated with bathymetry, often has a strong influence on sea duck occupancy estimates (Guillemette et al. 1993; Lewis et al. 2008; Winiarski et al. 2014; Flanders et al. 2015). Sediment grain size can also have a strong influence on prey availability for foraging sea ducks (Goudie & Ankney 1988; Lovvorn et al. 2009; Loring et al. 2013) and affected occupancy and conditional
abundance in this study. In addition, sea floor topographic variability also influenced occupancy and conditional abundance, although the influence of topography on prey availability is less understood. Sea surface temperature and chlorophyll $a$ can have a strong influence on occupancy estimates for sea ducks (Zipkin et al. 2010; Flanders et al. 2015), although we found no effect of chlorophyll $a$ during this study. Similarly, Zipkin et al. (2010) found the North Atlantic Oscillation (NAO) was important in all these species of sea ducks at a continental scale, whereas we found no support that the NAO affected the distribution of sea ducks at the scale of this study. Certain covariates may associate with marine bird abundance or behavior at specific scales and not at others (Logerwell & Hargreaves 1996) and this may explain the apparent discrepancy between studies in the effect of chlorophyll $a$ and NAO.

The unexplained variation in our models and the predominance of marginal spatiotemporal effects suggest that we probably omitted important variable(s) relevant to the distribution of sea ducks in Nantucket Sound. Moreover, we likely need better biophysical proxies for the distribution of prey eaten by sea ducks or concurrent prey distribution information (e.g., Vaitkus & Bubinas 2001; Kaiser et al. 2006; Žydelis et al. 2009; Cervencl & Fernandez 2012; Cervencl et al. 2014), although this is typically considerably more difficult to characterize at appropriate scales and does not guarantee improved predictive accuracy (Grémillet et al. 2008; Torres et al. 2008; Benoit-Bird et al. 2013).

Marine Spatial Planning: where to place a wind farm in Nantucket Sound given these estimates of the distribution and abundance of sea ducks?—In the past decade, ecosystem-based MSPs have become a reality because comprehensive land use planning is a central component of development plans in North America and Europe (Douvere 2008). One of the biggest challenges facing marine spatial planners is the paucity of relevant information on the spatial distribution and abundance of biological resources including marine birds (Bradbury et al. 2014; Flanders et al. 2015). We developed fine-scale, spatially- and
temporally-explicit maps of the estimated distribution and abundance of sea ducks in Nantucket Sound that could assist marine spatial planners during the zoning process. At a continental scale, Nantucket Sound regularly supports one of the largest concentrations of wintering sea ducks in eastern North America (White et al. 2009; Zipkin et al. 2010; Silverman et al. 2013). Therefore if any OWEDs are constructed in Nantucket Sound steps should be taken to minimize impacts to this key wintering habitat. Bradbury et al. (2014) developed a sensitivity index that suggested that sea ducks were particularly vulnerable to habitat displacement from foraging sites, while they are less vulnerable to collision risk from OWEDs. Our models suggest that the permitted OWED zone on Horseshoe Shoal is not located in prime foraging habitat for most species of sea ducks, although large numbers of eiders can use this area (see also Flanders et al. 2015). Potential vulnerability to OWED has been incorporated into some recent spatially-explicit planning efforts for seabirds (Garthe & Hüppop 2004; Winiarski et al. 2014; Bradbury et al. 2014) though to our knowledge not yet for sea ducks.

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Figure Legends

Figure 1. Actual aerial strip transect tracks (gray lines) during winter (October - April, 2003 - 2005) sea duck surveys (n = 30) in Nantucket Sound, Massachusetts, US. The grid indicates the extent of the 1100 km$^2$ study area and its division into 504 2.25km$^2$ segments. The polygon in northwest Nantucket Sound indicates the 62 km$^2$ area of permitted wind energy development on Horseshoe Shoal.

Figure 2. Marginal functional plots for stably selected covariates in the occupancy (probability of presence) and conditional abundance (mean and overdispersion of count models) of Common Eider (COEI), scoter (SCOT), and Long-tailed Duck (LTDU) in Nantucket Sound during three winters, 2003 - 2005. Plots illustrate the partial contribution to the additive predictor (Y-axis) of a covariate holding all other covariates at their mean. Within a model, univariate plots (i.e., lines) share a Y-axis scale, enabling direct comparisons of effect sizes among covariates and species. For bivariate plots, the Y-axis and X-axis reflect the first and second variables listed in the interaction, respectively; colors indicate the direction and magnitude of the partial contribution (blacks = negative, reds = positive; darker colors = larger effect) and are likewise comparable within a model. Northing by easting effects are given only at 31 December. For factor variables, only the general association (i.e., positive or negative) with the additive predictor is given. Covariate abbreviations correspond to Equation 1.

Figure 3. Occupancy probability for Common Eider (COEI), scoter (SCOT), and Long-tailed Duck (LTDU) in Nantucket Sound during three winters, 2003 - 2005. Occupancy probabilities (top row) represent the median expected probability of sea duck presence in a 1.5 km x ca. 180 m transect through a given segment predicted on 10 evenly-spaced dates from 15 November through 1 April in each winter. Spatiotemporal variation in occupancy (%; bottom row) is indicated by the median absolute deviation, MAD, of occupancy probability relative to the median. Predicted values are categorized based on their quartiles;
segments with the highest occupancy or variability (values ≥ 98th percentile) are outlined in black.

**Figure 4.** Conditional abundance of Common Eider (COEI), scoter (SCOT), and Long-tailed Duck (LTDU) in Nantucket Sound during three winters, 2003 - 2005. Conditional abundances (top row) represent the median expected number of sea ducks, assuming their presence, in a 1.5 km x ca. 180 m transect in each segment predicted on 10 evenly-spaced dates from 15 November through 1 April in each winter. Spatiotemporal variation in conditional abundance (%) (bottom row) is indicated by the median absolute deviation, MAD, relative to the median. Predicted values are categorized based on their quartiles; segments with the highest conditional abundance or variability (values ≥ 98th percentile) are outlined in black.

**Figure 5.** Unconditional abundance of Common Eider (COEI), scoter (SCOT), and Long-tailed Duck (LTDU) in Nantucket Sound during three winters, 2003 - 2005. Median abundances (top row) represent the expected number of sea ducks along a 1.5 km x ca. 180 m transect within each segment predicted on 10 evenly-spaced dates from 15 November through 1 April in each winter. Spatiotemporal variation in abundance (%) (bottom row) is estimated from the median absolute deviation, MAD, relative to the median. Predicted values are categorized based on their quartiles; segments with the highest abundance or variability (values ≥ 98th percentile) are outlined in black.

**Figure 6.** Relationship between observed and predicted total abundance of Common Eider (COEI), scoter (SCOT), and Long-tailed Duck (LTDU) during 30 aerial surveys of Nantucket Sound over three winters, 2003 - 2005. The dashed line indicates a 1:1 relationship between predicted and observed abundances in surveyed segments; points below and above this line indicate underestimates and overestimates of predicted abundances, respectively.
| Occupancy | Abundance (mean) | Abundance (overdispersion) |
|-----------|----------------|---------------------------|
| Cpei      | SCOT           | LTDU                      |
| Bathymetry (depth) |                  |                           |
| depth x time                     |                  |                           |
| Sediment grain size (meanphi)    |                  |                           |
| Sea floor surface area : planimetric area (SAR) |                  |                           |
| Epibenthic tidal velocity (mean; tidebmean) |                  |                           |
| Epibenthic tidal velocity (standard deviation; tidesd) |                  |                           |
| Water column stratification potential (strat) |                  |                           |
| Chlorophyll – a (chla)           |                  |                           |
| Chromomorphic dissolved organic matter (cdom) |                  |                           |
| chla x cdom                        |                  |                           |
| Sea bottom temperature (May – Oct; SBT) |                  |                           |
| Sea surface temperature (monthly; SSTm) |                  |                           |
| Sea surface temperature (Nov – Mar; SSTn) |                  |                           |
| Sea surface temperature (relative; SSTrel) |                  |                           |
| SSTrel x time                      |                  |                           |
| North Atlantic Oscillation (Dec – Mar; NAOw) |                  |                           |
| Distance to land (d2land)           |                  |                           |
| Ferry route (within 1 km; ferry)    |                  |                           |
| Winter 2004 (y2004)                |                  |                           |
| Winter 2005 (y2005)                 |                  |                           |
| Northing (ykm) x Easting (xkm)      |                  |                           |
| Survey effort (obs_window)          |                  |                           |

Figure 2
Figure 3
Figure 4
Figure 5
Figure 6