

Nantucket Sound Sea Ducks

*Adam D. Smith, Benjamin Hofner, Jason E. Osenkowski, Taber Allison,
Scott R. McWilliams, and Peter W. C. Paton*

06 May, 2015

Third, my spatiotemporal plots remain more “complicated” than those you created in our recent proceedings paper, as you can see in Figure 2. I have yet to recreate the plot with a clean session, but I’ll do so in short order.

Biophysical features at multiple spatial and temporal scales affect the distribution and abundance of vertebrates and their prey (*general citations*). Nonetheless, these key environmental factors have not been revealed for many species that inhabit marine ecosystems despite increasing anthropogenic impacts on these systems (*citations*). The distribution and abundance of top consumers in marine ecosystems, such as sea ducks (Tribe Mergini), are notably understudied. Moreover, current evidence suggests that populations of most species of North American sea ducks are below historic levels with negative or unknown population trends (Merkel 2004, Cameron 2014, Sea Duck Joint Venture 2014, Bowman et al. 2015). Thus there exists considerable interest in identifying the biophysical characteristics of the marine environment that influence the distribution and abundance of sea ducks.

At broad spatial scales, the North Atlantic Oscillation can have a major influence on the distribution of sea ducks (Zipkin et al. 2010), and regime shifts in oceanic conditions can also affect sea duck population trends (Flint 2013). At more localized spatial scales, food availability and quality (Stott and Olson 1973; Guillemette et al. 1993, 1996; Zydelis and Ruskyte 2005, Kirk et al. 2008), preferred food types and foraging strategies (from next paragraph?), substrate characteristics (Zydelis et al. 2006, Loring et al. 2013), ocean depth (Guillemette et al. 1993; Winiarski et al. In press), and anthropogenic disturbances (ferry; shipping activity; Kaiser et al. 2006, SF Bay) can dictate sea duck distribution and abundance. Maybe bring up the offshore wind energy stuff...?

To AS: rework this Although there are many single-species or single-season studies of sea duck distribution and abundance, some of which identify important key env factors (e.g., *citations*), we know of no published studies that apply a consistent quantitative approach applied to aerial survey data to generate predictive models of the distribution and abundance of sea ducks, based on key env factors, at multiple spatial and temporal scales...

If we’re aiming for Ecological Applications, we should frame the manuscript as equal parts ecology and methodology. However, I think making the case that it’s the best approach is unnecessary (and sounds like much more work:)). I’ve incorporated some of your comments. Please edit as desired. I need to think more about the material leading up to this point. Our details in the methods may now have some redundancy that can be deleted.

I need to form these notes into a better topic sentence Marine birds (sea ducks)

distribution is patchy (*citations*); abundance can be extremely variable; often interested in evaluating the relevance of many potential covariates with possibly complex (i.e., nonlinear) associations with animal presence and abundance (*citations*). To address these challenges, we implemented generalized additive models (GAMs; Hastie and Tibshirani 1990, Wood 2006) and their recent extension (GAM for location, scale, and shape; GAMLSS; Rigby and Stasinopoulos 2005) in a gradient descent boosting framework (Mayr et al. 2012, Hofner et al. 2015b) to evaluate the distribution and abundance of sea ducks in Nantucket Sound, Massachusetts, USA. GAMLSS methods extend GAMs to allow all parameters of the conditional response distribution to be modeled as a function of relevant covariates (Rigby and Stasinopoulos 2005); this approach thus grants insight not only into the covariates associated with sea duck distribution and abundance but also their variability. Moreover, the model-based 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 of covariates (i.e., variable selection), and evaluates competing representations of continuous covariates (e.g., linear vs. nonlinear effects of covariates; Maloney et al. 2012).

To AS: we ignore imperfect detection (justification included in next section) and potential temporal autocorrelation. Address?

Methods

Aerial strip transect surveys.—We conducted aerial surveys throughout an 1,100 km² study area in Nantucket Sound, Massachusetts, USA (Figure 1). Nantucket Sound is an important wintering area for sea ducks in southern New England (White et al. 2009, Silverman et al. 2013, Loring et al. 2014). Wind energy development has been fully permitted on 62 km² of Horseshoe Shoal in the northwest portion of the study area (Figure 1). During the winters (late October to mid-April) of 2003-2005, we conducted 30 (2003/2004: 13, 2004/2005: 10, 2005/2006: 7) aerial strip-transect surveys (e.g., Pollock et al. 2006, Certain and Bretagnolle 2008) to evaluate sea duck distribution and relative abundance; surveys occurred primarily from mid-November - late March (n = 27), with an occasional October (n = 1) or April (n = 2) survey. During each survey, we flew along 15 parallel (ca. 2.3 km apart), roughly north-south transects (Figure 1) using a high-wing, twin-engine aircraft (Cessna Skymaster 337) at an average altitude of 152 m and speed of 167 kmh⁻¹ (90 kts). This altitude allowed us to identify most birds at the sea surface and reduced the possibility of flushing birds to another part of the study area (i.e., double counting). The airspeed was the slowest at which the aircraft could safely fly. Surveys occurred only on days with wind speeds ≤ 15 kts and good visibility (>15 km). All surveys occurred from 0900 to 1600 h (average duration of ~ 2.5 h) to ensure that birds had completed their post-dawn movements but had yet to initiate pre-sunset movements from feeding to roosting areas; this time window also reduced glares due to low sun angles.

On each survey flight, two observers used their unaided eyes to continuously detect individuals or flocks, identifying sea ducks to species with the aid of binoculars as needed. Observers monitored the sea surface on their side of the plane in a ~ 90 m wide transect between ~ 56 -

147 m from the plane; observers could not see beneath the plane out to 56 m on each side of the plane. The narrow strip width ensured birds were detectable and identifiable with the naked eye and allowed us to avoid situations in which ducks were too abundant or spread over too wide an area to count accurately. This last point was especially relevant because sea ducks occasionally congregated in extremely large aggregations. **To AS: mention photographs and subsequent estimation of large rafts?** Moreover, our flight altitude and narrow transect width increased the likelihood that we met that the assumption of homogeneous detection (at least with regards to survey parameters; e.g., Certain and Bretagnolle 2008) within the strip transect (Buckland et al. 2012). **To AS: mention that we did not, therefore, adjust for imperfect detection?**

Observers verbally communicated duck sightings to a recorder, who entered the number of ducks, species, behavior (i.e., on the water or flying), and geographic location into a laptop computer linked to the plane's onboard GPS; we report results only from ducks observed sitting on the water. Sea duck species of interest included Common Eider (*Somateria mollissima*; hereafter eider), White-winged Scoter (*Melanitta deglandi*), Surf Scoter (*M. perspicillata*), Black Scoter (*M. americana*), and Long-tailed Duck (*Clangula hyemalis*). However, we considered all scoter species collectively (hereafter, scoters), as it was regularly difficult to identify scoters to species. We subsequently consolidated counts for each species (eider and Long-tailed Ducks) or species group (scoters) 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).

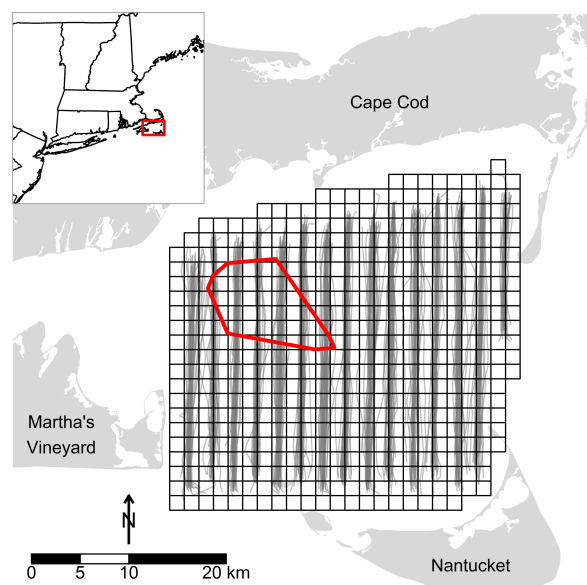


Figure 1. Nantucket Sound, Massachusetts, US study area. The grid indicates the extent of the study area and its division into 504 2.25km² segments. Gray lines indicate all aerial transects flown over the 30 surveys comprising the study. The red polygon in the northwest corner of Nantucket Sound indicates the location of permitted wind energy development on Horseshoe Shoal.

Modeling approach.—We related spatiotemporal variation in sea duck occupancy (i.e., probability of presence) and abundance to potentially relevant biophysical and spatiotemporal

covariates. We used component-wise functional gradient descent boosting to fit the models (see Bühlmann and Hothorn 2007 for a detailed introduction). We applied a negative binomial hurdle model that separately modeled (1) the probability of occurrence of at least one individual (hereafter referred to as the occupancy model) in a given segment using a logistic regression model and (2) the abundance of sea ducks in that segment conditional on their presence (hereafter count model) using a truncated negative binomial model. The prevalence of zero counts (e.g., 75% of eider segment observations) prompted our use of a hurdle model. We generated separate hurdle models for each sea duck group (i.e., eider, scoters, and Long-tailed Duck; Zipkin et al. 2010).

Perhaps we should start with the simple GAM model for occupancy (both in the next paragraph and in the boosting paragraph below) and then move towards the more complex GAMLSS model?

Sounds worthwhile to me; I've taken a first crack at it but please edit as you see fit. Some of this might be unnecessary given the paragraph in the introduction.

To model sea duck occupancy, we used a logistic generalized additive model (GAM; Hastie and Tibshirani 1990, Wood 2006) that flexibly accommodated potential nonlinearities between covariates and sea duck occupancy. We used GAMs for location, scale, and shape (GAMLSS) methods (Rigby and Stasinopoulos 2005) to model the zero-truncated negative binomial count models. The GAMLSS count models flexibly accommodated potential nonlinearities between covariates and the conditional mean and overdispersion of sea duck abundance.

We implemented GAMs and GAMLSS in a gradient descent boosting framework (Mayr et al. 2012, Hofner et al. 2015b) that automatically implemented variable and model selection. *You mean the general concept of base-learners? I mean to introduce how base-learners relate to, but are distinct from, covariates..* Component-wise gradient boosting selects only the single best-fitting base-learner (i.e., functional representation of the covariate-response relationship?; Hofner et al. (2014); *maybe just define it briefly parenthetically here?*) in each iteration, which thus integrates into the algorithm intrinsic selection of the most relevant covariates and their functional form (i.e., some base-learners may never be selected). Moreover, variable selection and prediction accuracy are maximized in gradient boosting frameworks, and model overfitting avoided, by stopping the iterative algorithm prior to convergence to maximum likelihood estimates (i.e., early stopping; **BH: check if these are best citations** Mayr et al. 2012, Maloney et al. 2012). We used 25-fold subsampling to determine the optimal stopping iteration for each model. Specifically, we randomly drew (without replacement) 25 samples of size $n/2$ from the original data set. 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 loglikelihood of each model; the optimal stopping iteration (m_{stop}) is the iteration with the lowest average empirical risk. *We should add that we need bivariate cross-validation for gamboostLSS models as we need to find the optimum stopping iteration for the mean and overdispersion together.* I'll leave this to you. A detailed explanation of the cross-validation scheme is given in Hofner et al. (2015b).

Despite these agreeable features, boosting methods typically produce “rich” models with many selected base-learners (Hofner et al. 2015a). Thus, we additionally applied stability selection (Meinshausen and Bühlmann 2010, Shah and Samworth 2013) to identify those base-learners, and thus covariates, most commonly selected in each model (i.e., selected on the majority of 100 random subsamples of the data); see Appendix 1 and Hofner et al. (2015b) for more details.

Covariates.—We evaluated biophysical covariates expected to influence the distribution and availability of benthic prey or the distribution, abundance, and movements of sea ducks (see Appendix 1). Biophysical covariates could be characterized as strictly spatial or temporal effects (i.e., varying only among segments or within or among winters, respectively) or as spatiotemporal effects (i.e., varying among segments and within or among winters; see Appendix 2 *a not yet completed table defining covariates and their abbreviations as used in the model specification*). Additionally, we included interactions that allowed the effects of two covariates to vary over time within a given winter (see Appendix 2). We standardized (i.e., mean centered and scaled) all continuous covariates.

For each continuous covariate, we specified two base-learners: a linear base-learner and a penalized nonlinear base-learner (i.e., P-splines; Eilers and Marx 1996, Schmid and Hothorn 2008). We dummy-coded categorical covariates, resulting in $K - 1$ linear base-learners for a K -level covariate. To address potential spatial autocorrelation (**is this true? or is “unmeasured heterogeneity” better?**), we included a smooth surface function of the spatial coordinates of segment centers (Kneib et al. 2008); this surface comprised four base-learners – linear base-learners for the easting x and northing y and their 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. See Hofner et al. (2014) for a detailed description of base-learners.

The decomposition of continuous covariates into centered linear and penalized orthogonal nonlinear base-learners allowed us to weight base-learners equally allow unbiased model choice, i.e., to prevent the preferential selection of smooth base-learners (Kneib et al. 2009, Hofner et al. 2011). Specifically, we restricted each base-learner to a single degree of freedom and omitted the intercept term from each base-learner (Kneib et al. 2009, Hofner et al. 2011). Consequently, we added an explicit linear base-learner for the model intercept. The occupancy and count models had the following structure (see Appendix 2 for descriptions of abbreviated covariates):

$$\begin{aligned}
g(\cdot) = & int + time + f(time) + SSTw + f(SSTw) + SSTm + f(SSTm) + SSTrel + \\
& f(SSTrel) + SSTrel \cdot time + f(SSTrel, time) + SBT + f(SBT) + NAOw + \\
& depth + f(depth) + depth \cdot time + f(depth, time) + d2land + f(d2land) + \\
& chla + f(chla) + cdom + f(cdom) + f(cdom, chla) + meanphi + f(meanphi) + \\
& SAR + f(SAR) + tidebmean + f(tidebmean) + tidesd + f(tidesd) + strat + \\
& f(strat) + ferry + y2004 + y2005 + xkm + ykm + xkm \cdot ykm + \\
& f(xkm, ykm) + xkm \cdot time + ykm \cdot time + xkm \cdot ykm \cdot time + \\
& f(xkm, ykm) \cdot time + obs_window + f(obs_window).
\end{aligned} \tag{1}$$

In our occupancy models, $g(\cdot)$ is $g(\pi_{\text{sea ducks}})$, the (conditional) occupancy probability of a given duck species or group in a segment 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 $f(\cdot)$, e.g., $f(time)$, indicate the penalized nonlinear deviations from the corresponding linear base-learner. The explicit intercept (int) was a necessary byproduct of our decomposition of base-learners (see above; Kneib et al. 2009, Hofner et al. 2011). We note that small values in some segments for the obs_window variable, our measure of survey effort (see Appendix 2), impaired the estimability of models including obs_window as an offset; we thus included it as a covariate.

Recent extensions of traditional measures of model fit (e.g., coefficient of determination) to generalized linear mixed models (e.g., Nakagawa and Schielzeth 2013, Johnson 2014) do not apply within our boosting framework. To evaluate the explanatory power of our models for each species group, we calculated the square of the correlation coefficient between the predicted counts and the observed counts in analogy to the coefficient of determination in Gaussian regression models. This gives us an approximation of the amount of variation in sea ducks counts accounted for by our models (**is there a citation**). **Placeholder: what about the pseudo-R² calculations using bootstrap (e.g., Maloney et al. 2012)?**

All analyses were conducted in R (Version 3.1.2; R Core Team 2014) with the add-on packages gamboostLSS (Hofner et al. 2015b), mboost (Hothorn et al. 2015), and stabs (Hofner and Hothorn 2015). The data and code for reproducing this manuscript and analyses are given as an online electronic supplement at *TBD*.

Results

I'm not sure what is the best way to open the results section. I welcome any ideas or suggestions

Bootstrapped empirical risk suggested that occupancy models for all species converged on the maximum likelihood estimates (i.e., occupancy models failed to stop early; see Appendix 3). **brief statement of the implications of convergence/not stopping early. We**

won't mention this beyond here. Conversely, bootstrapped empirical risks prescribed early stopping for both parameters (i.e., conditional mean and overdispersion) in all count models (see Appendix 3). Consequently (**is this the consequence?**), final occupancy models generally contained more covariates than did count models, particularly among stably selected covariates. Nonetheless, we obtained sparse models that included only a subset of the initially specified base-learners. Specifically, occupancy and count (conditional mean) models contained only 12% (Long-tailed duck conditional abundance) to 38% (scoter occupancy) of the 48 base-learners available for selection, translating to 3 and 10 of 23 covariates of interest, respectively (Figure 2). **If this is a reasonable opening, should we mention difference between # of “selected” base-learners vs. number of base-learners in the final model? I think I'd vote against doing so.**

This may be the best place to mention model appropriateness/approximate explanatory power: The eider, scoters, and Long-tailed Duck models explained approximately 12%, 24%, and 16% of the variation in observed (log) sea duck counts, respectively. **The r^2 s increase slightly from the previous models except for COEI, which dropped from 15% to 12%. Any concern it decreased given that we only added base-learners?**

Sea duck occupancy.—More covariates were consistently selected as stable in occupancy models relative to conditional count models (Figure 2; see below). However, the suite of stably-selected covariates associated with occupancy was relatively consistent among sea duck species, with modest variation in the form of those associations (Figure 2). **I think it's worth noting, if I'm correct, that the strong spatiotemporal effect in all three groups suggests we're somewhat deficient in our ability to model the ecology of sea ducks or, more likely, their prey. How much do we want to go on here describing variables and what forms their associations with occupancy take?** Spatiotemporal effects (i.e., x - y location of segments and within-winter time effects), distance to land, and the survey effort in a given segment were important non-biophysical predictors of occupancy. Among biophysical variables, monthly sea surface temperature (SST), sea floor surface:planimetric area (SAR), sediment grain size, chromomorphic dissolved organic material (CDOM), and water depth were selected in at least two species groups. Other effects were less consistent among species. **Worth noting that the strength of the effects can be gleaned from the figure due to standardization?** Detailed relationships between covariates and occupancy are provided for eider, scoters, and Long-tailed Duck in *not finished* Appendices 4 - 6, respectively.

This text is not finished yet, but next I'll discuss some of the similarities and differences in the species occupancy maps; see Figure 3: Eider were ...

Sea duck conditional abundance.—In contrast to occupancy, fewer covariates associated consistently with the abundance of sea ducks, conditional on their presence, and the suite of stably-selected effects varied more markedly among sea duck species (Figure 2). However, selected variables tended to fall within the suite of covariates selected in occupancy models. The primary exception to this pattern is the apparent increase in eider and scoter abundance, given presence, in segments with relatively warm or cool SSTs (Figure 2). **Again, I don't want to dwell too long on describing variables and what forms their associations**

with conditional abundance take, but the spatiotemporal effect in scoter and Long-tailed Duck again seems to dominate the patterns and suggests our available covariates are incomplete.

Overdispersion in conditional sea duck abundance also varied with biophysical covariates (Figure 2). Don't need to belabor this other than to point out that sea duck count variability (i.e., overdispersion) varied over the study area. **What is the ultimate take-home message here? That the assumption typically made – overdispersion is fixed – doesn't always hold in practice and that it can be useful to consider that variability (overdispersion), not simply the conditional mean, also depends (on some occasions) on covariates?** Detailed relationships between covariates and conditional abundance and overdispersion are provided for eider, scoters, and Long-tailed Duck in *not finished* Appendices 4 - 6, respectively.

This text is not finished yet, but do you think it's worth talking about the similarities/differences in conditional abundance maps? I was only going to do it for μ (see Figure 4) and reserve σ for an appendix, but now I'm thinking that talking about abundance conditional on occupancy is somewhat pointless; what seems most relevant to discuss is the combined occupancy/count model (see next section). Or, perhaps, it's interesting to compare the patterns of conditional abundance with those of occupancy? Sometimes they match up, whereas in other areas median occupancy may be lower but, when they ducks are present, they are more abundant (e.g., COEI in the eastern portion of Nantucket Sound) or vice versa (e.g., COEI in the Horseshoe Shoals area). Your thoughts?

Expected overall sea duck abundance.—Consolidating the occupancy and conditional count models (according to Equation 6 in Zeileis et al. 2008) provided an estimate of overall sea duck abundance in the study area over the survey period (Figure 5). **Again, text not finished but there is plenty to mention with regards to overall abundance and the variation in this abundance over time.**



Figure 2. Please check this wording Partial effects (i.e., covariate effect with all others at their mean) for stably selected covariates in the occupancy (probability of presence) and conditional abundance (mean and overdispersion parameters) of Common Eider (COEI),

scoters (SCOT), and Long-tailed Duck (LTDU) in Nantucket Sound during winters 2003 - 2005. Within a model, the magnitude of univariate effects (i.e., lines) is comparable 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 linear predictor (blacks = negative, reds = positive; darker colors = larger effect) and are comparable within a model. Northing by easting effects are given only at the mean survey time although these spatial effects regularly changed over time. For factor variables, only the general association (i.e., positive or negative) with the additive predictor is given.

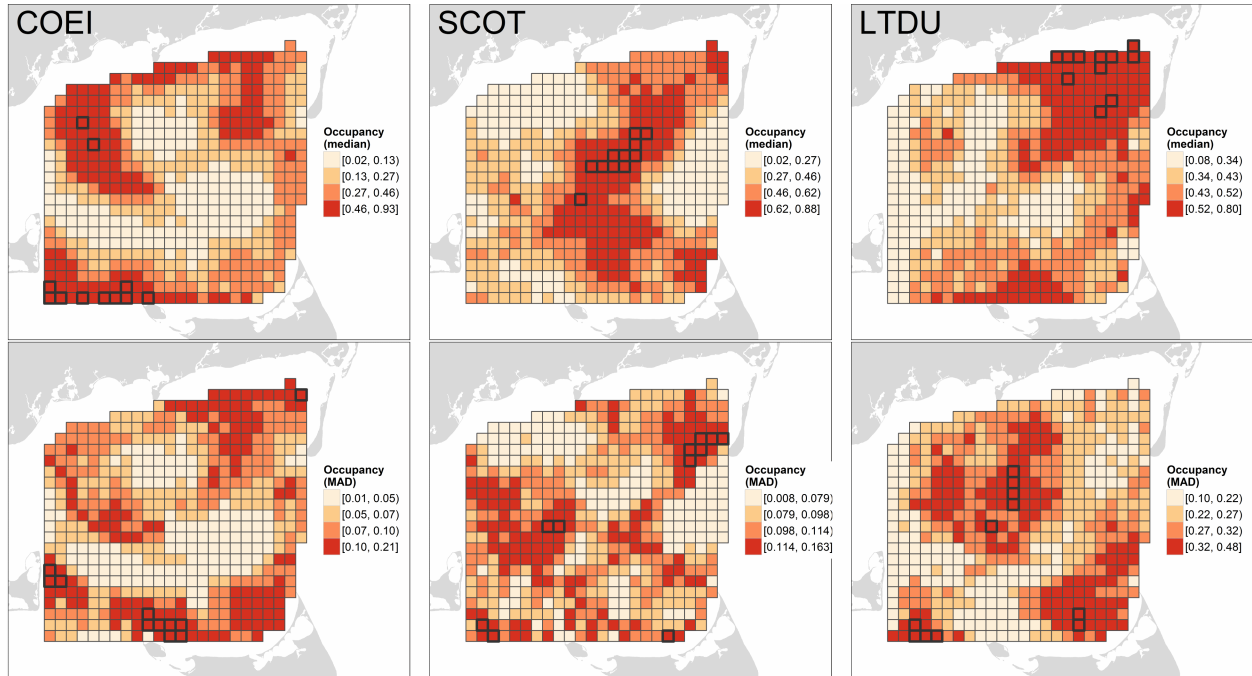


Figure 3. Median (first row) and median absolute deviation (MAD; second row) of Common Eider (COEI), scoter (SCOT), and Long-tailed Duck (LTDU) occupancy predicted at 10 dates evenly-spaced from 15 November through 1 April in three winters (2003 - 2005) of aerial surveys in Nantucket Sound. Predicted values are categorized based on their quartiles; segments with predictions ≥ 98 th percentile are outlined. Occupancy values represent the predicted probability of sea duck presence in a 1.5 km x ca. 180 m transect through the segment.

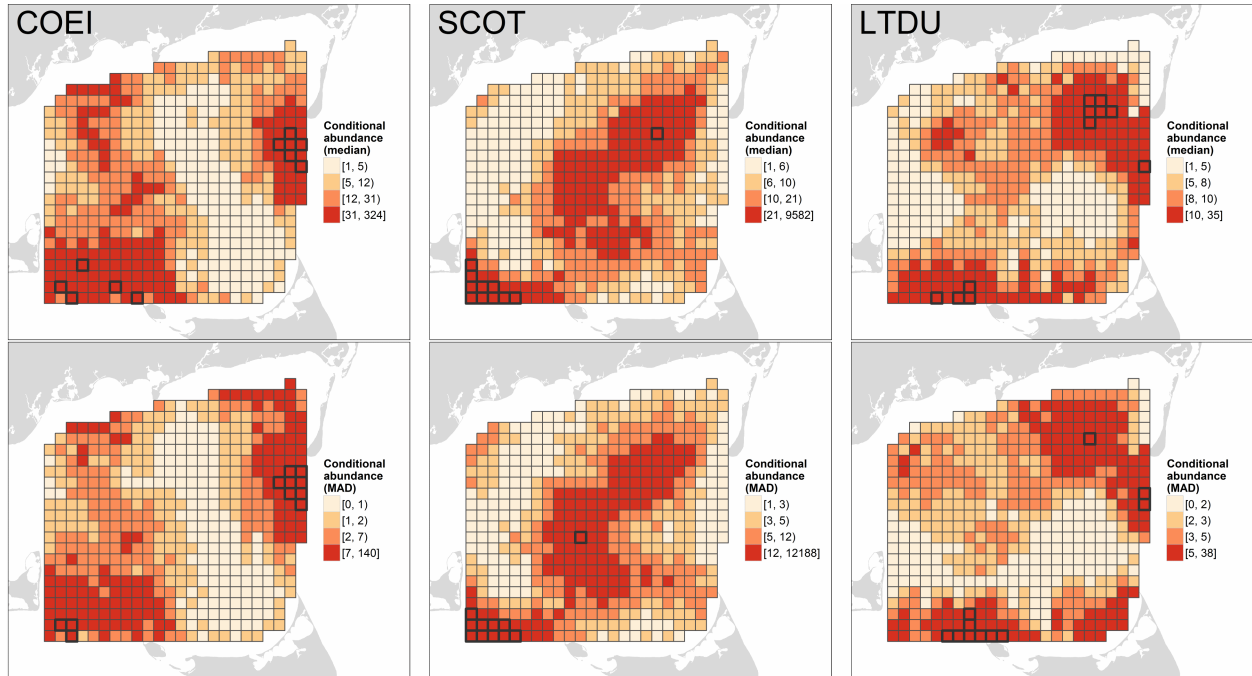


Figure 4. Median (first row) and median absolute deviation (MAD; second row) of Common Eider (COEI), scoter (SCOT), and Long-tailed Duck (LTDU) conditional abundance (i.e., given sea duck presence) predicted at 10 dates evenly-spaced from 15 November and 1 April in three winters (2003 - 2005) of aerial surveys in Nantucket Sound. Predicted values are categorized based on their quartiles; segments with predictions ≥ 98 th percentile are outlined. Conditional abundance values represent the expected number of sea ducks, conditional on their presence, in a 1.5 km x ca. 180 m transect through the segment.

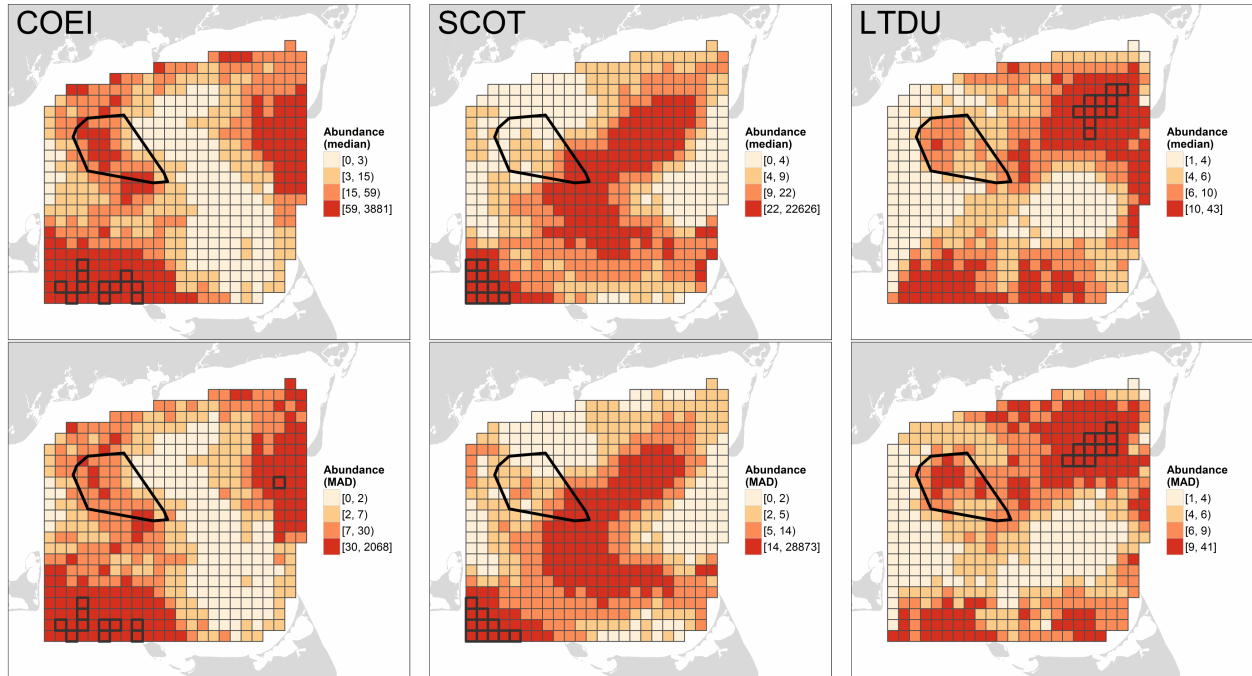


Figure 5. Median (first row) and median absolute deviation (MAD; second row) of Common Eider (COEI), scoter (SCOT), and Long-tailed Duck (LTDU) overall abundance (i.e., a function of expected sea duck occupancy and conditional abundance) predicted at 10 dates evenly-spaced from 15 November and 1 April in three winters (2003 - 2005) of aerial surveys in Nantucket Sound. Predicted values are categorized based on their quartiles; segments with predictions \geq 98th percentile are outlined. Conditional abundance values represent the expected number of sea ducks in a 1.5 km x ca. 180 m transect through the segment. The polygon in the northwest corner of Nantucket Sound indicates the location of permitted wind energy development on Horseshoe Shoal.

Literature cited

- Bowman, T. D., E. D. Silverman, S. G. Gilliland, and J. B. Leirness. 2015. Status and trends of north american sea ducks: Reinforcing the need for better monitoring. Pages 1–27 *in* J.-P. L. Savard, D. V. Derksen, D. Esler, and J. M. Eadie, editors. Ecology and conservation of north american sea ducks. studies in avian biology. CRC Press, New York, NY, USA.
- Buckland, S. T., M. L. Burt, E. A. Rexstad, M. Mellor, A. E. Williams, and R. Woodward. 2012. Aerial surveys of seabirds: The advent of digital methods. *Journal of Applied Ecology* 49:960–967.
- Bühlmann, P., and T. Hothorn. 2007. Boosting algorithms: Regularization, prediction and model fitting. *Statistical Science* 22:477–505.
- Cameron, I. R. 2014. An analysis of spring migration rates of scoter species and common eider recorded at the point lepreau bird observatory on the bay of fundy over the period 2000 to 2012. *New Brunswick Naturalist* 41:94–99.
- Certain, G., and V. Bretagnolle. 2008. Monitoring seabirds population in marine ecosystem: The use of strip-transect aerial surveys. *Remote Sensing of Environment* 112:3314–3322.
- Eilers, P. H. C., and B. D. Marx. 1996. Flexible smoothing with B-splines and penalties (with discussion). *Statistical Science* 11:89–121.
- Flint, P. L. 2013. Changes in size and trends of north american sea duck populations associated with north pacific oceanic regime shifts. *Marine Biology* 160:59–65.
- Hastie, T. J., and R. J. Tibshirani. 1990. Generalized additive models. CRC Press, Boca Raton, FL, USA.
- Hofner, B., and T. Hothorn. 2015. Stabs: Stability selection with error control, r package version 0.5-1.
- Hofner, B., L. Boccuto, and M. Göker. 2015a. Controlling false discoveries in high-dimensional situations: Boosting with stability selection. *BMC Bioinformatics* in press.
- Hofner, B., T. Hothorn, T. Kneib, and M. Schmid. 2011. A framework for unbiased model selection based on boosting. *Journal of Computational and Graphical Statistics* 20:956–971.
- Hofner, B., A. Mayr, N. Fenske, and M. Schmid. 2015b. gamboostLSS: Boosting methods for GAMLSS models, r package version 1.1-3.
- Hofner, B., A. Mayr, N. Robinsonov, and M. Schmid. 2014. Model-based boosting in r: A hands-on tutorial using the r package mboost. *Computational Statistics* 29:3–35.
- Hothorn, T., P. Buehlmann, T. Kneib, M. Schmid, and B. Hofner. 2015. Mboost: Model-based boosting, r package version 2.4-2.
- Johnson, P. C. 2014. Extension of nakagawa & schielzeth’s r^2_{GLMM} to random slopes models. *Methods in Ecology and Evolution* 5:944–946.

- Kneib, T., T. Hothorn, and G. Tutz. 2009. Variable selection and model choice in geosadditive regression models. *Biometrics* 65:626–634.
- Kneib, T., J. Müller, and T. Hothorn. 2008. Spatial smoothing techniques for the assessment of habitat suitability. *Environmental and Ecological Statistics* 15:343–364.
- Loring, P. H., P. W. Paton, J. E. Osenkowski, S. G. Gilliland, J.-P. L. Savard, and S. R. McWilliams. 2014. Habitat use and selection of black scoters in southern new england and siting of offshore wind energy facilities. *Journal of Wildlife Management* 78:645–656.
- Maloney, K. O., M. Schmid, and D. E. Weller. 2012. Applying additive modelling and gradient boosting to assess the effects of watershed and reach characteristics on riverine assemblages. *Methods in Ecology and Evolution* 3:116–128.
- Mayr, A., N. Fenske, B. Hofner, T. Kneib, and M. Schmid. 2012. Generalized additive models for location, scale and shape for high-dimensional data - a flexible approach based on boosting. *Journal of the Royal Statistical Society: Series C (Applied Statistics)* 61:403–427.
- Meinshausen, N., and P. Bühlmann. 2010. Stability selection (with discussion). *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 72:417–473.
- Merkel, F. R. 2004. Evidence of population decline in common eiders breeding in western greenland. *Arctic* 57:27–36.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining r^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Pollock, K. H., H. D. Marsh, I. R. Lawler, and M. W. Alldredge. 2006. Estimating animal abundance in heterogeneous environments: An application to aerial surveys for dugongs. *Journal of Wildlife Management* 70:255–262.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rigby, R. A., and D. M. Stasinopoulos. 2005. Generalized additive models for location, scale and shape (with discussion). *Journal of the Royal Statistical Society: Series C (Applied Statistics)* 54:507–554.
- Schmid, M., and T. Hothorn. 2008. Boosting additive models using component-wise P-splines. *Computational Statistics & Data Analysis* 53:298–311.
- Sea Duck Joint Venture. 2014. Atlantic and great lakes sea duck migration study: Progress report february 2014. http://seaduckjv.org/atlantic_migration_study.html, accessed 2 december 2014.
- Shah, R. D., and R. J. Samworth. 2013. Variable selection with error control: Another look at stability selection. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 75:55–80.
- Silverman, E. D., D. T. Saalfeld, J. B. Leirness, and M. D. Koneff. 2013. Wintering sea duck distribution along the atlantic coast of the united states. *Journal of Fish and Wildlife Management* 4:178–198.

- White, T. P., R. R. Veit, and M. C. Perry. 2009. Feeding ecology of long-tailed ducks *clangula hyemalis* wintering on the nantucket shoals. *Waterbirds* 32:293–299.
- Wood, S. N. 2006. Generalized additive models: An introduction with r. Chapman; Hall/CRC, Boca Raton, FL, USA.
- Zeileis, A., C. Kleiber, and S. Jackman. 2008. Regression models for count data in r. *Journal of Statistical Software* 27:1–25.
- Zipkin, E. F., B. Gardner, A. T. Gilbert, A. F. O. Jr, J. A. Royle, and E. D. Silverman. 2010. Distribution patterns of wintering sea ducks in relation to the north atlantic oscillation and local environmental characteristics. *Oecologia* 163:893–902.