

# Distribution patterns of wintering sea ducks in relation to the North Atlantic Oscillation and local environmental characteristics

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**Abstract** Twelve species of North American sea ducks (Tribe Mergini) winter off the eastern coast of the United States and Canada. Yet, despite their seasonal proximity to urbanized areas in this region, there is limited information on patterns of wintering sea duck habitat use. It is difficult to gather information on sea ducks because of the relative inaccessibility of their offshore locations, their high degree of mobility, and their aggregated distributions. To characterize environmental conditions that affect wintering distributions, as well as their geographic ranges, we analyzed count data on five species of sea ducks (black scoters *Melanitta nigra americana*, surf scoters *M. perspicillata*, white-winged scoters *M. fusca*, common eiders *Somateria mollissima*, and long-tailed ducks *Clangula hyemalis*) that were collected during the Atlantic Flyway Sea Duck Survey

for ten years starting in the early 1990s. We modeled count data for each species within ten-nautical-mile linear survey segments using a zero-inflated negative binomial model that included four local-scale habitat covariates (sea surface temperature, mean bottom depth, maximum bottom slope, and a variable to indicate if the segment was in a bay or not), one broad-scale covariate (the North Atlantic Oscillation), and a temporal correlation component. Our results indicate that species distributions have strong latitudinal gradients and consistency in local habitat use. The North Atlantic Oscillation was the only environmental covariate that had a significant (but variable) effect on the expected count for all five species, suggesting that broad-scale climatic conditions may be directly or indirectly important to the distributions of wintering sea ducks. Our results provide critical information on species–habitat associations, elucidate the complicated relationship between the North Atlantic Oscillation, sea surface temperature, and local sea duck abundances, and should be useful in assessing the impacts of climate change on seabirds.

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## Introduction

Current evidence suggests that ten of the 15 North American sea duck species may be in decline, including eight out of 12 species that winter off the Atlantic coast (Sea Duck Joint Venture 2003). Yet there is much uncertainty on the status of sea ducks because population data are limited. The causes of sea duck declines are not well understood, as relatively little is known about the distributions and habitat preferences of each species. The Atlantic coast of the

United States (US) and Canada is a major wintering area for a number of migratory species, including sea ducks, which face a variety of pressures associated with human populations and potential climate changes. For example, increased harvest pressure on sea ducks in the 1980s, resulting from more restrictive hunting regulations on other waterfowl (e.g., Canada goose *Branta canadensis*), led to concern about the condition of sea duck populations along the Atlantic flyway (Perry and Deller 1995; Caithamer et al. 2000). More recently, wind turbines, proposed in locations along the Atlantic coast (e.g., Kempton et al. 2007), are raising questions about potential adverse impacts on survival and habitat use (e.g., Larsen and Guillemette 2007). Before we can assess the influence of factors such as harvest, offshore energy development, contaminants, and climate change on sea duck populations, it is necessary to accurately characterize the spatial distribution, annual variability, and habitat associations of these species.

North American sea ducks breed at high northern latitudes throughout the US and Canada; these ducks migrate south to winter in coastal waters, reaching as far as Florida on the Atlantic coast. Yet, despite the potential impacts resulting from their seasonal proximity to large, urbanized areas, we have comparatively limited information on winter habitat preference and use. It is difficult to gather information on sea ducks during the winter, not only because of the inaccessibility of their offshore locations, but also due to the tendency of some species to aggregate in large, mobile flocks. Outside of a few areas (e.g., Chesapeake Bay—Perry et al. 2007), the status and trends of sea ducks along the eastern US and Canadian coasts have not been well established (Caithamer et al. 2000; Sea Duck Joint Venture 2003).

The spatial distribution of wintering sea ducks along the Atlantic coast is determined by both broad-scale and local processes. General winter conditions and habitat gradients are likely to influence the northern and southern boundaries of their wintering ranges, while distributions within those ranges may be based on a variety of site-specific factors, including food availability, local environmental conditions, and habitat suitability (Lewis et al. 2008). Thus, it is necessary to examine how both large-scale processes (such as annual climatic conditions) and local factors (such as ocean bottom depth, ocean floor topography, and sea surface temperature) affect the distributions and abundance of sea ducks.

The North Atlantic Oscillation (NAO) is a driver of climate variability that has been shown to affect the marine environment (Hurrell et al. 2003) and ecosystems (Ottersen et al. 2001; Stenseth et al. 2002) along the eastern coast of the US and Canada. The NAO is the fluctuation in sea surface pressure across the northern Atlantic Ocean between areas of high (Azores High) and low (Icelandic

Low) pressure; it exerts strong control over the climate in the Atlantic Ocean region, particularly in the winter (Hurrell 1995; Hurrell et al. 2003). A positive NAO index indicates an increase in winter storms with greater intensity in the northern Atlantic Ocean, leading to cold, dry winters in northern Canada and mild, wet winters in the eastern US. A negative NAO index indicates fewer and weaker winter storms in the Atlantic Ocean, leading to cold and snowy conditions along the east coast of the US and Canada (Bell and Visbeck 2009). The NAO is a composite measure of winter conditions and has been linked to ecological processes in plants (Post and Stenseth 1999), terrestrial invertebrates (Halkka et al. 2006), ungulates (Post and Stenseth 1999; Post and Forchhammer 2002), fish (Suski and Ridgway 2007), and amphibians (Forchhammer et al. 1998). In birds, the NAO has been linked to breeding phenology (Forchhammer et al. 1998; Moller 2002; Weatherhead 2005) and migration patterns (Hüppop and Hüppop 2003), and has been correlated specifically with adult survival (Sandvik et al. 2005; Sandvik and Erikstad 2008), breeding success (Lehikoinen et al. 2006; Sandvik and Erikstad 2008) and general population dynamics (Thompson and Grosbois 2002) in seabirds. Given these correlations, it is possible that climatic conditions, including the NAO, may also be influencing distributions of wintering sea ducks.

Studies from other regions provide evidence that distributions of sea ducks may be linked to local environmental characteristics, such as ocean depth and water temperatures. Common eiders (*Somateria mollissima*) in Greenland (Merkel et al. 2006) and surf scoters (*Melanitta perspicillata*) in British Columbia (Kirk et al. 2008) were found to have strong site fidelity within the wintering season, but Kirk et al. (2008) noted that prey availability influenced small-scale movement. Wintering common eiders foraged most frequently in depths of between 0 and 6 m, although they are capable of diving much deeper (Guillemette et al. 1993). Surf scoters, white-winged scoters (*Melanitta fusca*), and common eiders also appear to prefer coastal areas with relatively shallow depths (Guillemette et al. 1993; Lewis et al. 2008).

In the early 1990s, the US Fish and Wildlife Service (FWS) initiated the Atlantic Flyway Sea Duck Survey (AFSDS) to assess distributions of sea ducks along the nearshore of the eastern US and Canada (Migratory Bird Data Center 2009). Because the timing and scale of movements by wintering sea ducks are not well characterized, the survey offers limited information about the overall abundance of each species. This ten-year dataset can, however, provide critical information on how distributions of sea duck populations vary both spatially and temporally along the nearshore Atlantic coast. Using survey data from the AFSDS, we characterize the winter

distributions of five sea duck species along the eastern US and Canada and relate observed counts to pertinent broad- and local-scale environmental characteristics. Defining the relationships among sea duck distributions, latitude, and habitat will provide a quantitative basis for understanding wintering ecology and movements, help with the design of future monitoring programs, and inform targeted conservation and management actions.

## Methods

### Sea duck aerial surveys

The AFSDS was flown between mid-January and mid-February along the eastern coast of the US and Canada in 1991, 1992, 1994, 1995, and 1997–2002 from southern Georgia (30.8°N, 81.4°W) to Nova Scotia (48.1°N, 64.8°W) (Fig. 1). A single aerial transect was flown parallel to the coast, a quarter mile from the shore, and data were reported within approximately ten-nautical-mile segments. The segments were defined by drawing the survey transect on an aeronautical chart and marking increments of ten nautical miles. Since the survey was initiated and conducted primarily in years when geographic positioning technology was unavailable to the crew (i.e., pre-GPS), ten nautical miles represented the smallest practical spatial unit for collecting and recording data. All sea ducks identified to species were counted within 500 m (250 m on each side of the route) of the transect line, which defined the boundaries for each segment (10 nautical miles by 500 m). Roughly 451 segments were flown once yearly, 335 of which were in the US, with the remaining segments in Canada. Two-person crews conducted the surveys, flying at an altitude of 250 feet. The pilot and an observer recorded the species and number in each segment (Caithamer et al. 2000).

Eleven sea duck species were observed at least once during the ten years of the AFSDS survey. We focused our analyses on five species for which there were adequate data and whose wintering ranges sufficiently overlap with the study area: black scoters (*Melanitta nigra americana*; 85,000 observed over all years of the survey), surf scoters (100,000 observed), white-winged scoters (25,000 observed), common eiders (414,000 observed), and long-tailed ducks (*Clangula hyemalis*; 95,000 observed). We did not include counts in which sea ducks were not identified to species (e.g., birds identified only as scoters).

### Habitat and climate covariate data

We used hand drawn maps of the survey route (the only maps available) to digitally recreate the survey path and identify start and stop points for each segment in ArcGIS 9.3 (Environmental Systems Research Institute Inc., Redlands, CA, USA). The digital survey path was buffered by 250 m on each side in ArcGIS to recreate the segments, which averaged 11.4 (SD 2.6) nautical miles long and 500 m wide. We validated the recreated digital route using GPS tracking data from flights in 2001 and 2002, the only years with a GPS record of the route, to ensure that our recreated transect segments included the areas in which sea ducks had been observed during the two years with known flight paths.

To characterize the yearly winter climatic conditions along the Atlantic coast, we obtained monthly values for NAO, based on the difference between the normalized sea level pressure over Gibraltar and the normalized sea level pressure over Southwest Iceland (Jones et al. 1997) from the Climatic Research Unit, University of East Anglia, Norwich, UK (<http://www.cru.uea.ac.uk/cru/data/nao.htm>). We hypothesized that overall conditions (as characterized by NAO) during migration would have a large effect on sea duck winter distributions, since previous research suggests that sea ducks may

**Fig. 1** Map of the Atlantic Flyway Sea Duck Survey route flown ten years between 1991 and 2002. Segments shown in green were included as bays; all others are shown in blue

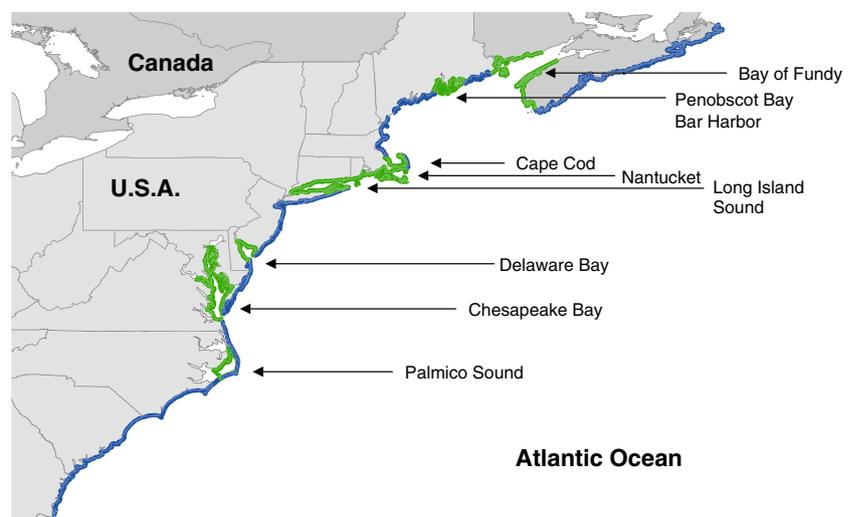


exhibit within-season site fidelity after migration, at least on local scales (Kirk et al. 2008). Thus, we averaged the NAO values for the three months prior to the survey (October–December) to characterize the climatic conditions around migration. Average NAO values may differ from winter averages calculated using other measures of NAO (e.g., Cook et al. 2002), but data from the Climatic Research Unit provided a sufficiently long period of record for our study.

To assess local factors affecting sea duck distributions, we summarized relevant environmental data to characterize the habitat of individual segments. We included three static, segment-level variables: (1) whether or not the segment occurred in a bay (binary variable with 1 indicating that the segment was in a bay and 0 otherwise; Fig. 1), (2) bottom depth, and (3) ocean floor topography. Coarse-resolution bathymetry data are available for the global oceans, but no fine-scale data are available for both US and Canadian Atlantic waters, so we acquired data separately from each country. We downloaded the coastal relief model for the US Atlantic, available from the National Geophysical Data Center (Divins and Metzger 2008). US bathymetry data were available in a 3 arc-second (approximately 90 m) grid, with depths resolved to 0.1 m. We obtained a similar bathymetry dataset from the Canadian Hydrographic Service (CHS), Fisheries and Oceans Canada, a new product produced for the Canadian Atlantic. Bathymetry data were received from the CHS as point data with 500 m or closer spacing, from which a 500 m raster was created using routines developed in ArcGIS 9.3. Depths were again resolved to 0.1 m. For bottom depth, we averaged depth values for all pixels within a segment to achieve a single estimate for each segment. The segment-level depth values were measured in negative values (i.e., the surface is zero) and ranged from  $-80.16$  to  $0$  m (95% range  $-31.29$ ,  $-0.35$ ;  $\bar{x}_{\text{bays}} = -9.1$ ;  $\bar{x}_{\text{non-bays}} = -6.2$ ). To characterize the ocean floor topography, we used the slope routine in ArcGIS 9.3 to calculate the bottom slope or the maximum rate of change for each depth cell (i.e., pixel) from its adjacent eight cells. We used the maximum slope for all cells within each segment, rather than the average, which provided a realistic measure of the topography range for each segment. The segment-level slope values ranged from  $0$  to  $21.39$  (95% range  $0.20$ ,  $10.55$ ;  $\bar{x}_{\text{bays}} = 3.0$ ,  $\bar{x}_{\text{non-bays}} = 2.3$ ).

We also gathered monthly averages for sea surface temperature (SST) as measured through satellite data from the NOAA/NASA AVHRR Pathfinder Program (<http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/>). Data were downloaded from the NASA Physical Oceanography Distributed Active Archive Center ([ftp://podaac.jpl.nasa.gov/pub/sea\\_surface\\_temperature/avhrr/pathfinder/data\\_v5/monthly/](ftp://podaac.jpl.nasa.gov/pub/sea_surface_temperature/avhrr/pathfinder/data_v5/monthly/)). We used the best estimate (BSST) from the 4.1 km resolution (version 5) SST data. These data were derived using the Reynolds Optimally Interpolated SST,

version 2, methodology (Reynolds et al. 2002), which provides complete areal coverage even where clouds are masking the ocean by filling in missing data with optimally interpolated SST data. We hypothesized that segment-level SST would likely affect movement within the winter season and calculated winter averages from monthly BSST data that coincided with the end of migration and the dates of the survey (December–February). Since the resolution of each SST pixel was larger (4,100 m) than the buffered segment (500 m), we reduced the cell size of each seasonal SST pixel to one-twentieth the original resolution and calculated the weighted average SST for each segment for every year of the survey. The segment-level SST values across all years ranged from  $0.65$  to  $22.65^{\circ}\text{C}$  (95% range  $1.32$ ,  $21.45$ ).

## Model

The sea duck survey produced spatially and temporally indexed counts for which a modeling framework based on generalized linear models (GLMs) is appropriate (Clarke et al. 2003). Poisson GLMs are frequently used in analyses of count data for other avian monitoring programs, including trend analysis, models of abundance and distribution, and for modeling landscape and habitat effects (e.g., the North American Breeding Bird Survey, Link and Sauer 2007). In most avian surveys, and in the case of the AFSDS, the assumption of equality of mean and variance for Poisson models is not realistic, as there is high variation in the observed number of individuals. For the AFSDS, a high variance to mean ratio likely results because some sea duck species tend to be highly aggregated in the winter. Because of the extreme overdispersion of the data in our survey, we modeled the counts using a zero-inflated negative binomial distribution (Hall 2000, Martin et al. 2005), which allows for a higher variance compared to the mean and has provided a better fit to data in previous analyses of other duck species (Wenger and Freeman 2008). To do so, we define  $y_{i,j,t}$  as the count of species  $i$  at survey segment  $j$  in year  $t$ . The mean of  $y_{i,j,t}$  is  $\mu_{i,j,t} = \lambda_{i,j,t} \cdot z_{i,j}$ , where  $z_{i,j} \sim \text{Bernoulli}(\psi_{i,j})$  is a random variable that indicates whether or not a segment should be included in the model (variable for each species but constant over the ten years of the survey). When  $z_{i,j} = 1$ , the count for species  $i$  in segment  $j$  at time  $t$  has a negative binomial distribution,  $(y_{i,j,t} | z_{i,j} = 1) \sim \text{NegBinom}(r_i, p_{i,j,t})$ , with mean  $\lambda_{i,j,t} = \frac{r_i(1-p_{i,j,t})}{p_{i,j,t}}$  and variance  $\sigma_{i,j,t}^2 = \frac{\lambda_{i,j,t}}{p_{i,j,t}}$ . Thus, the parameter  $\lambda$  is the estimated mean count when  $z_{i,j} = 1$ , otherwise the expected count is zero. Since the AFSDS was not designed to accommodate the specific geographic range of each species, we hypothesized that  $z$  would vary by latitude and modeled the inclusion probability ( $\psi_{i,j}$ ) for each segment

as a function of latitude such that  $\text{logit}(\psi_{i,j}) = \beta_0 + \beta_1 \cdot \text{lat}_j$ , where  $\beta_0$  is the intercept and  $\beta_1$  is the coefficient on latitude. Although a segment's inclusion probability could depend on a number of factors, we chose to include only latitude in order to (1) investigate the north–south range distributions for each species and (2) explore the effects of habitat covariates on the abundance of birds within the north–south boundaries of their range, because the available data limit further complexity (i.e., inclusion of habitat covariates in both the Bernoulli and negative binomial components of the model).

We modeled sources of variation in  $\lambda$  using a log-linear function:

$$\begin{aligned} \log(\lambda_{i,j,t}) = & \alpha_0 + \alpha_1 \cdot \text{NAO}_t + \alpha_2 \cdot \text{SST}_{j,t} + \alpha_3 \cdot \text{depth}_j \\ & + \alpha_4 \cdot \text{slope}_j + \alpha_5 \cdot \text{bays}_j + \alpha_6 \cdot \text{NAO}_t \cdot \text{SST}_{j,t} \\ & + \alpha_7 \cdot \log(y_{i,j,t-1} + 1) + \log(\text{offset}_j) \end{aligned}$$

where  $\alpha_0$  is the intercept and  $\alpha_1$  through  $\alpha_6$  are the effects of each of the covariates for species  $i$  on the estimated count: NAO for each year ( $\text{NAO}_t$ ); sea surface temperature at each segment in each year ( $\text{SST}_{j,t}$ ); mean bottom depth at each segment ( $\text{depth}_j$ ); maximum slope at each segment ( $\text{slope}_j$ ); a binary vector indicating whether a segment was in a bay ( $\text{bays}_j$ ); and an interaction effect between segment-level sea surface temperature and NAO ( $\text{NAO}_t \cdot \text{SST}_{j,t}$ ). The latitude, SST, depth, and slope data were each standardized to have a mean of zero and a standard deviation of one. We incorporated temporal correlation into the model at the segment level by estimating an effect ( $\alpha_7$ ) of the observed count in the previous year. The temporal effect was only estimated when data were available in the previous year (e.g., years 1991, 1994, and 1997 were excluded). An offset term was included to account for differences in counts due to variation in segment length. During the development of the model, we included an explicit spatial effect using a conditional autoregressive (CAR) model. The results from the CAR model were uninformative when habitat covariates were not incorporated (likely due to the high variation in the data), and parameter estimates were unstable with the inclusion of both explicit spatial correlation and covariates. The purpose of including spatial correlation in a model is based on the notion that counts are likely to be similar within some neighborhood (a predefined region). Often, the reason for such correlations is similarities in landscape features within a neighborhood. If sea ducks are responding to habitat factors, inclusion of relevant landscape covariates should account for variation in observed counts and render the inclusion of an explicit spatial correlation unnecessary. We determined that habitat covariates explained more of the variation in the data, and we thus removed the CAR component.

We analyzed the model separately for each species and estimated the parameter values using a Bayesian framework with the programs R and WinBUGS. Since our model includes a temporal correlation component ( $\alpha_7$ ), analysis using standard canned statistical software would be difficult. As such, we specified code in R to estimate the parameters by Markov chain Monte Carlo (MCMC) using the software program WinBUGS (see “Electronic Supplementary Material” for the complete model code). The idea behind MCMC is to generate a Monte Carlo sample of the model parameters from their posterior distributions (Gelman and Hill 2007). An additional benefit of the Bayesian approach is that interpretation of parameter values is straightforward and intuitive. For example, if 95% of a parameter's posterior distribution does not overlap with zero, we can directly interpret that as a 95% probability that the parameter is nonzero. To run our model, we used uninformative priors for all of the covariates. We ran three chains for 10,000 iterations after a burn in period of 10,000 iterations and estimated the posterior distributions after thinning the chains by 10. We checked that the model and all parameters had converged by examining the R-hat scores (Gelman and Hill 2007, p. 358).

## Results

The model estimated significant temporal correlation in the mean count and a latitude effect in the inclusion parameter for all five species of sea ducks (see Table 1 for parameter estimates). There was a positive relationship at the segment level between expected count in year  $t$  and observed count in the previous year ( $\alpha_7$ ) for all species, with white-winged scoters having the highest consistency in local habitat use. As expected, there was also a consistent and positive relationship to latitude ( $\beta_1$ ) in the inclusion parameter, indicating that the probability of observing each species increased from south to north, with common eiders followed by long-tailed ducks showing the strongest relationship (Fig. 2).

The NAO ( $\alpha_1$ ) was the only environmental covariate that had a significant effect on all five sea duck species: negative for the three scoter species and positive for the common eiders and long-tailed ducks. This suggests that climatic conditions along the Atlantic coast during migration and settlement may have strong influences, either directly or indirectly (e.g., by affecting distributions of prey), on sea duck distributions, with the scoter species observed in higher abundances in the nearshore during cold, snowy winters, and common eiders and long-tailed ducks observed in higher abundance in the nearshore during wet, mild winters. SST ( $\alpha_2$ ) had a significant negative effect on long-tailed duck and white-winged scoter counts

**Table 1** Posterior summary of species-specific parameter estimates

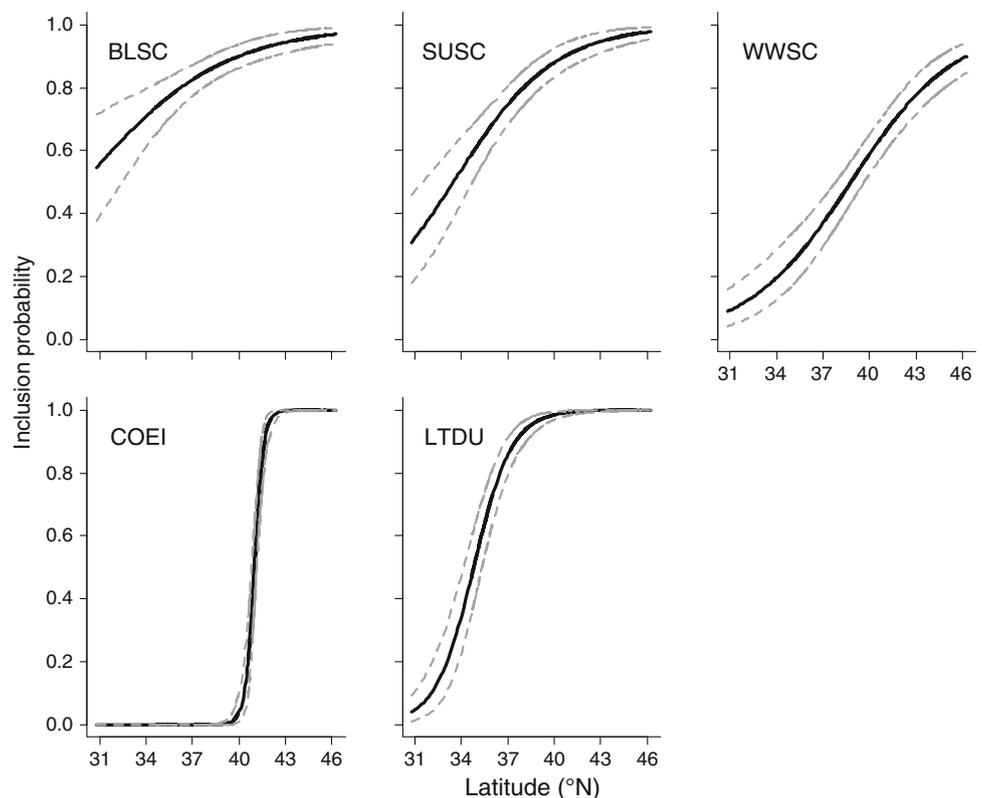
Parameter		Black scoters	Surf scoters	White-winged scoters	Common eiders	Long-tailed ducks
Intercept: count	$\alpha_0$	3.10 (0.11)	3.31 (0.12)	1.38 (0.19)	5.96 (0.20)	2.20 (0.06)
NAO	$\alpha_1$	<b>-0.42 (0.09)</b>	<b>-0.36 (0.10)</b>	<b>-0.71 (0.18)</b>	<b>0.70 (0.14)</b>	<b>0.38 (0.05)</b>
SST	$\alpha_2$	-0.07 (0.10)	0.28 (0.15)	<b>-0.55 (0.20)</b>	<b>1.27 (0.25)</b>	<b>-1.04 (0.07)</b>
Depth	$\alpha_3$	<b>0.26 (0.08)</b>	<b>0.32 (0.07)</b>	0.21 (0.10)	<b>0.26 (0.06)</b>	<b>0.25 (0.03)</b>
Slope	$\alpha_4$	-0.12 (0.09)	<b>-0.41 (0.08)</b>	-0.08 (0.11)	<b>0.16 (0.06)</b>	0.06 (0.04)
Bay	$\alpha_5$	<b>-0.36 (0.16)</b>	-0.27 (0.15)	<b>0.63 (0.20)</b>	-0.17 (0.13)	0.09 (0.07)
SST*NAO	$\alpha_6$	-0.01 (0.11)	-0.11 (0.17)	<b>0.52 (0.24)</b>	<b>1.18 (0.24)</b>	<b>0.39 (0.08)</b>
Year	$\alpha_7$	<b>0.22 (0.05)</b>	<b>0.17 (0.05)</b>	<b>0.38 (0.07)</b>	<b>0.18 (0.02)</b>	<b>0.18 (0.02)</b>
Intercept: inclusion	$\beta_0$	2.35 (0.25)	2.19 (0.26)	0.53 (0.14)	-1.58 (0.42)	4.76 (0.54)
Latitude	$\beta_1$	<b>0.88 (0.20)</b>	<b>1.23 (0.20)</b>	<b>1.19 (0.16)</b>	<b>13.99 (2.40)</b>	<b>3.30 (0.41)</b>

The mean and the standard error of the mean estimate (SD) are shown for each parameter

Environmentally relevant parameters that are statistically different from zero (95% posterior intervals that do not overlap with zero) are highlighted in *bold*

Note that the intercepts for both count and inclusion terms were also statistically different from zero for all species

**Fig. 2** Probability of inclusion by latitude for each sea duck species. The mean estimate is shown in *black* and the 95% posterior interval is shown with *gray dashed lines*. *BLSC*, black scoters; *SUSC*, surf scoters; *WWSC*, white-winged scoters; *COEI*, common eiders; *LTDU*, long-tailed ducks

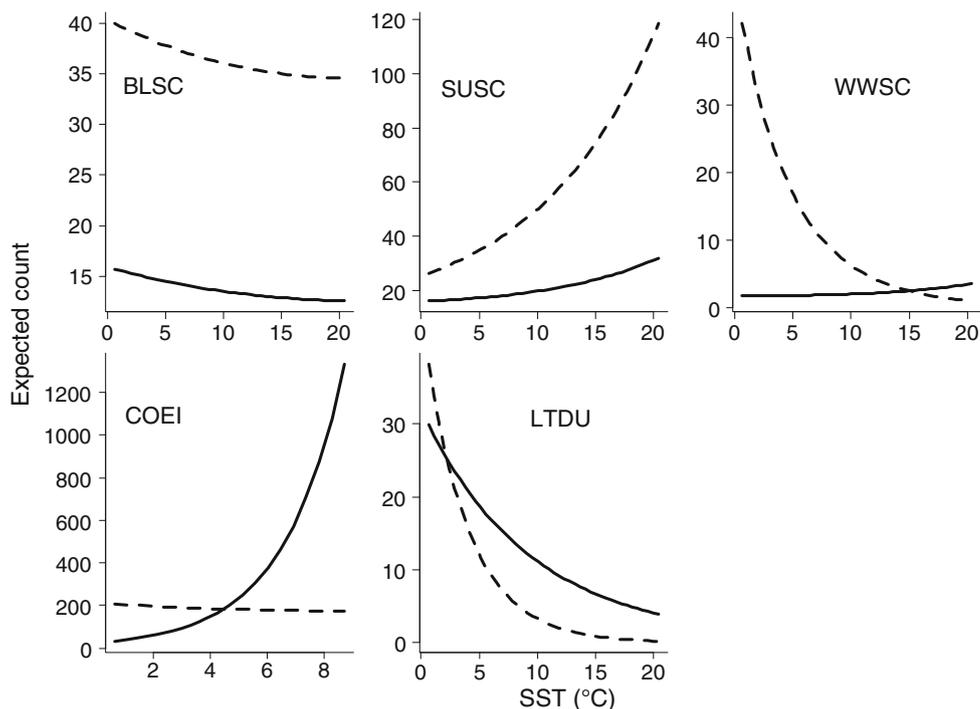


and a positive effect on common eider counts (but see below for details on the interaction between NAO and SST). A negative relationship with temperature suggests that the expected count increases with colder SST values for long-tailed ducks and white-winged scoters. Because the model incorporates a latitude-dependent inclusion parameter (Fig. 2), the positive relationship between SST and the expected count for common eiders can be

interpreted to mean that, within the northern latitudes where common eiders are present (greater than 40°N latitude), the ducks are found in higher abundance in segments with moderate temperatures (note that the *x*-axis temperature range in Fig. 3 for common eiders is smaller than those for the other four species).

The relationship among NAO, SST, and the expected count was highly variable by species (Fig. 3). The expected

**Fig. 3** Expected count for each sea duck species (given inclusion, i.e.,  $z_{i,j} = 1$ ) by sea surface temperature (SST) in years with the highest positive (1994; *solid line*) and lowest negative (1998; *dashed line*) NAO values. *BLSC*, black scoters; *SUSC*, surf scoters; *WWSC*, white-winged scoters; *COEI*, common eiders; *LTDU*, long-tailed ducks



count in the nearshore for all three scoter species was generally higher in years with a negative NAO index compared to years with a positive index for nearly all ranges of SST. Yet the difference in expected count was consistent across SST for black scoters, highest at warmer SST values for surf scoters, and highest at colder SST values for white-winged scoters (even reversing the relationship at very warm values of SST). In contrast, the expected counts for common eiders and long-tailed ducks in the nearshore, although very different from each other, were generally higher in positive years, compared to negative NAO years, in warmer SST ranges (Fig. 3). The expected count of common eiders, within the temperature range where they were observed, was fairly constant across SST in negative years, but had a strong positive relationship with SST in positive NAO years. Conversely, the expected count of long-tailed ducks tended to decrease with SST in both NAO scenarios.

All species, except for white-winged scoters (which had a similar although not significant response), had positive relationships with ocean bottom depth ( $\alpha 3$ ), measured in negative values where zero is sea level, indicating that sea duck abundance is greater in shallower sections of the shoreline. Maximum slope ( $\alpha 4$ ) had a negative effect on all three scoter species (but was significant only for surf scoters) and positive effects on the other two species (but again, significant only for common eiders), suggesting that the scoters may occur in areas with flat topography, while eiders and long-tailed ducks may prefer areas with steeper, more rugged bottoms. Black scoters were significantly less

abundant in bays ( $\alpha 5$ ), while white-winged scoters were significantly more abundant.

**Discussion**

Our results provide critical information on the spatial and temporal distributions of wintering sea ducks in the nearshore habitat of the US and southern Canadian Atlantic coast. Sea duck distributions appear to be responding to a combination of local habitat conditions and broad-scale weather patterns. All species had strong consistency in local habitat use among years and exhibited significant responses to latitude. Yet, the effects of environmental conditions were largely species-specific, with similarities among the scoter species and different responses by common eiders and long-tailed ducks. Common eiders and long-tailed ducks had sharp southern range boundaries compared to the scoters (Fig. 2), which had more gradual range boundaries and were sometimes found in southern waters. Research within the last decade has demonstrated northerly extensions in some bird species ranges (Thomas and Lennon 1999), and if climate-induced winter range shifts do occur in sea ducks, they may be comparatively easier to detect in common eiders and long-tailed ducks.

The North Atlantic Oscillation was the only environmental covariate that had a significant effect on all five sea duck species (Table 1), suggesting that site-specific abundance may be influenced by large-scale weather conditions. This result is consistent with recent studies on the NAO,

which suggest that broad-scale climatic indices, rather than measurements of local weather, can have stronger correlations with ecological processes (Hallett et al. 2004; Stenseth and Mysterud 2005). However, our results show that the response to NAO varied by species and was dependent on segment-level SST values (Fig. 3). SST has been correlated with the NAO at interannual timescales, and evidence suggests that the NAO itself may be altered by SST in the Atlantic Ocean on the order of six decades (Higuchi et al. 1999). Although we did not find a significant correlation between the NAO and mean annual SST values in our data, the relationship between the NAO and SST may be influencing sea duck distributions at differing scales (hence the inclusion of the interaction term of NAO and SST in our model) and may possibly have greater effects at longer time scales. Seabirds, in general, have shown variable and complex responses to the NAO (e.g., Thompson and Ollason 2001; Thompson and Grosbois 2002; Lehikoinen et al. 2006; Sandvik and Erikstad 2008), and climate change may affect the NAO in unpredictable ways (e.g., Hoerling et al. 2001). The response of sea duck distributions in the nearshore to fluctuations in the NAO and climate change is likely to be species specific, due to differences in the influence of weather conditions, physiological constraints, and other habitat factors such as food availability. Lehikoinen et al. (2006), for example, found that in the Baltic Sea, the body condition of female common eiders during egg hatching was positively correlated with the NAO. Together with our results, their work suggests that sea ducks may demonstrate intricate and indirect responses to fluctuations in the NAO during the wintering and subsequent breeding seasons. To protect sea ducks from decline, it may be useful to make annual predictions about abundance in relation to NAO in areas along the Atlantic coast and mitigate or limit human interference where the abundances of several species are predicted to be high.

We found ecologically relevant relationships between sea duck abundances and climatic conditions. However, survey data from the AFSDS were limited to one north-south transect a quarter mile off the Atlantic coast; future research should investigate whether our results are relevant over the entire winter range. Because the available data represent nearshore observations, we cannot make inferences on overall sea duck abundances or determine whether the differences in mean counts reflect changes in wintering locations or more general shifts further offshore (Braeger et al. 1995). The results from our model can help determine optimal sampling strategies based on the estimated relationships among abundance, latitude, and the environmental covariates. For example, our results on the effect of latitude (Fig. 2) suggest that it may be possible to exclude or limit effort in southerly portions of the coast in

future surveys. Recent offshore survey efforts, conducted by the FWS and including transects extending offshore as well as parallel to the coast, should help to further characterize sea duck distributions, their range limits, and the potential tradeoffs between nearshore and offshore abundance.

The relationships between the local habitat covariates and sea duck abundance were similarly variable across species. While all species were associated with shallow depths, there was greater variation in responses to bottom slope. As a group, the scoters were more abundant in flatter areas along the coast (Table 1), which is consistent with previous research showing that black, surf, and white-winged scoters prefer sandy sections along the Atlantic shoreline (Stott and Olson 1973). Observational data from other studies have demonstrated that common eiders may prefer rugged substrate, but long-tailed ducks have not been clearly linked to bottom substrate (Perry et al. 2007). These results, as well as bay associations, may be related to the resolution of the count and covariate data. The sea duck data in the AFSDS were recorded at a 10 nautical mile by 500 m resolution. Because we did not know the location of each observation more precisely (pre-GPS era), we used environmental covariate data at similar spatial and temporal resolutions. However, it is possible that sea ducks are responding to habitat factors that occur on much finer scales, such as areas with upwellings or high local productivity. Future surveys with GPS coordinates of sea duck locations should be analyzed with finer-scale covariate data to assess the strength of our results. Additionally, because the US and Canada provide bathymetry data at different resolutions, slope values were smaller than expected for the Canadian segments, which might indicate that the 500 m resolution of this dataset was effectively “smoothing” the bottom surface, limiting our ability to detect the true ruggedness.

Knowledge of wintering sea ducks is limited and data from the AFSDS provide the only distributional information in the nearshore Atlantic across a large temporal and spatial scale. The results from our analyses clarify how both local and broad landscape factors can influence distributions of bird species. Specifically, we demonstrated the importance of climate and weather processes to distributions of sea ducks in North America. Given that NAO had a significant effect on all species in our study, it is reasonable to believe that NAO, as well as other climatic factors, can exert powerful and complicated forces on distributions of bird species in North America, and worldwide. Our analysis improves understanding of inter-annual variation in sea duck distributions, interspecific differences in response to environmental conditions, and provides a basis for understanding how wintering sea ducks may respond to climate change—information that is critical

for effective conservation planning and the design of future monitoring programs.

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