Evaluating annual recruitment of sea duck populations in the Atlantic Flyway using harvest and photo survey juvenile proportions

by

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A thesis submitted to the Department of Environmental Science and Ecology

of SUNY-Brockport

in partial fulfillment of the requirements for the degree

of Master of Science

August 18th, 2023

Department of Environmental Science and Ecology
Thesis Defense

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Thesis defense date 8/17/23 **Thesis seminar date** 8/17/23

Master's Degree Advisory Committee	Approved	Not Approved
Major Advisor	X	
Committee Member	X	
Committee Member	X	

Graduate Director 9-8-2023 **Date**

Chair, Environmental Science & Ecology 9-8-23 **Date**

Acknowledgments

I would like to start by thanking my advisor, Dr. Jacob Straub, for everything he's done to support my growth as a scientist over the years. From my early days working in his lab as an undergraduate student at UW – Stevens Point through this thesis project, his mentorship has been a constant source of professional guidance and expertise, for which I'm incredibly grateful. Thank you to Sea Duck Joint Venture for providing all the necessary resources to pursue my research and for all their efforts supporting sea duck conservation across North America. A huge thank you to Dr. Anthony Roberts for everything he did to get the photo survey project up and running, and for sharing his invaluable insight with me every step of the way. Thank you to Dr. Rachel Schultz and Dr. Kristen Malone for joining my committee and sharing your perspectives on my research and ecology as a whole. I would also like to thank all the biologists and technicians that participated in data collection for the photo survey: Kelsey Sullivan, Benjamin Lewis, Shawn Meyer, Joshua Stiller, Josh Homyack, Hunter Morris, Ross Wood, Douglas Howell, Ted Nichols, Jessica Carloni, Josh Loew, Jennifer Kilburn, and Kelly Hamilton. This effort was a massive undertaking that wouldn't have been possible without their hard work and commitment. Thank you to Dr. Juliet Lamb for taking the time to develop and share data and code from her previous studies, which were instrumental to my analysis. Thank you to my fellow "avian ecology lab" members; Asch McDonnell, Kayleigh Filkins, Ryan McGinty, Daria Sparks, and Hailey Mitchell, for assisting with photo classification, as well as for sharing your knowledge of avian ecology and providing

opportunities to engage with your research. Lastly, thank you to my parents, Johanna and James Hewitt, and girlfriend, Haley Burger, for their never-ending support through all the crazy adventures these past two years have brought.

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Appendix I

General Introduction: Sea Duck Ecology and Conservation

Sea ducks (tribe *mergini*) are a group of waterfowl species that occupy a circumpolar distribution in the northern hemisphere. In my study, I concentrate on eastern North American populations of four focal sea duck species: long-tailed ducks (*Clangula hyemalis*), black scoters (*Melanitta americana*), surf scoters (*M. perspicillata*), and white-winged scoters (*M. delgandi*). In North America, focal species breeding areas include boreal forest and tundra regions of Quebec, Ontario, Manitoba, Saskatchewan, Northwest Territories, Nunavut, and Alaska (Savard et al. 2015). Long-tailed ducks and black scoters favor tundra breeding habitats, whereas surf and white-winged scoters favor ponds and lakes in boreal forest regions (Mallory 2015). Sea ducks complete short to medium-distance migrations relative to other bird species (Robertson and Savard 2020). Most populations undertake annual seasonal migrations, though some individuals in Alaska and the Hudson Bay may opt not to migrate and remain residents in open waters near breeding areas year-round (Palmer 1976). Migration and wintering areas include the Hudson Bay, the Laurentian Great Lakes, and the Atlantic Coast from the Canadian Maritime provinces south to South Carolina (Lamb et al. 2021). Wintering habitats include bays and coastal shorelines of large freshwater lakes and marine waters (Zipkin et al. 2010). Sea duck food sources vary by season and region but typically include crustaceans (subphylum *Crustacea*), fish (clade *Olfactores*) and fish roe, bivalves (class *Bivalvia*), aquatic insects (class *Insecta*), and gastropods (class *gastropoda*, Goudie and Ankney 1986, Fara 2018). Sea ducks have evolved to forage by diving to great depths to reach aquatic food resources (Žydelis and Richman 2015), sometimes reaching depths of over 60 meters (Schorger 1951). Adult sea ducks are mostly preyed upon by avian predators, such as gulls and diurnal raptors, on both breeding and wintering grounds. Parasitic jaegers (*Stercorarius parasiticus*) and foxes are common nest predators (Alison 1975), with foxes frequently taking adult females on nests. Mammalian predators such as raccoons (*Procyon lotor*) and mustelids (family *Mustelidae*) also prey upon nesting females and broods of young. Hunter harvest contributes to a small proportion of sea duck annual mortality; overall hunting pressure is low but occasionally significant locally across their range (Boyd 1996). Koneff et al. (2017) estimates current average annual continental harvest of long-tailed ducks and white-winged scoters in North America is approximately 42,853 and 23,733, respectively, whereas average harvest of surf and black scoters in eastern North America is approximately 37,522 and 28,528, respectively.

Population demography of sea ducks, including the four focal species I studied, are characterized by low annual breeding productivity, delayed maturation, and great adult survival rates (Bowman et al. 2015). Sea ducks remain relatively understudied compared to other waterfowl species owing to their remote breeding distribution and low relative harvest rates, though recent research has provided more insights into various aspects of their life history (Sea Duck Joint Venture 2022). However, knowledge of reproductive ecology and population demography remain especially limited (Mallory 2015, Koneff et al. 2017) and thus constitute a significant challenge for sea duck population managers.

Recent population modeling (Koneff et al. 2017) has identified specific demographic parameters that are most sensitive to harvest, hence improving management and providing a sustainable recreational opportunity. Increased knowledge about annual productivity is thought to greatly improve estimates of harvest potential. Most biologists can identify and correctly assign sea ducks to an age class and sex based on plumage characteristics when a bird is in hand. However, capturing a representative number of birds to make this assessment is costly and difficult. A promising and cost-effective alternative is using photos of sea ducks from winter to assign birds to the correct age and sex cohorts, by species (Duncan and Marquiss 1993, Smith et. al 2001, Iverson et. al 2004, Rodway et al. 2015, Larsson 2023). Juvenile proportions (% of juveniles in the population) obtained from photos, can then be used to inform population models, identify factors that influence breeding success, and examine spatial distribution of age and sex classes.

In chapter one of this thesis, I collected and analyzed ground-based photographs of focal sea duck species with a novel photo survey methodology. The purpose of my study was to produce annual productivity estimates (juvenile proportions) for eastern North American populations of the four focal species, evaluate multiple approaches to photo survey procedures, and compare photo survey juvenile proportion estimates with existing U.S. Fish and Wildlife Service Parts Collection Survey (PCS) estimates (Raftovich et al. 2022) to calculate an estimate of juvenile harvest vulnerability.

Another consequence of scarce sea duck population information is limited knowledge on the influence of dynamic ecological factors on population vital rates, including annual recruitment (Mallory 2015). However, new research on eastern North American focal species populations has established linkages between habitats and populations across the annual cycle (Lamb et al. 2020) that provide an opportunity to examine drivers of breeding productivity using long-term datasets. In the second chapter of my thesis, I used historic (1980-2017) PCS recruitment estimates (juvenile proportions) and indicators of relevant environmental conditions at breeding, staging, and wintering areas to investigate factors influencing annual recruitment rates in eastern North American focal species populations within a Bayesian modeling framework.

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Chapter 1: Using a photo survey to estimate annual recruitment in Atlantic Flyway sea duck populations

Abstract

Sea duck (tribe *mergini*) populations in the Atlantic Flyway have experienced significant declines in recent years, though underlying causes are poorly understood. Information on population demographic parameters may provide insight for wildlife managers seeking to maintain sustainable harvest. However, population monitoring capacity for sea ducks is limited relative to other migratory bird species due to their remote breeding distribution. The U.S. Fish and Wildlife Service organizes a Parts Collection Survey (PCS) which estimates recruitment in sea duck populations using age ratios (juveniles/adult), though estimates are biased due to differential harvest vulnerability between age-cohorts. I used a direct-count photo survey to calculate improved estimates of annual recruitment for long-tailed duck, black scoter, surf scoter, and white-winged scoter (hereafter sea ducks) populations in the Atlantic Flyway. I and other surveyors collected photos of flighted sea ducks from shore and by boat in 11 states from October 15-December 15 annually in 2019-2022. We classified photographed birds according to age and sex and calculated juvenile proportions of each species using a Bayesian binomial model. To compare photo survey estimates with PCS estimates, I used a paired t-test organized by year. I found that PCS estimates of juvenile proportions were significantly greater than photo survey estimates for three sea duck species, indicating a consistent positive bias in PCS driven by harvest vulnerability. I also derived novel estimates of juvenile harvest

vulnerability using the mean difference between within-year estimates. My work demonstrated the photo survey methodology used in this study produced reliable and precise annual recruitment estimates for four poorly monitored waterfowl populations; I recommend managers continue to adopt this approach in future years with additional consideration given for spatial representation and refinement of image classification procedures for long-tailed duck estimates.

Introduction

Trends and changes in wildlife populations over time are driven by variations in demographic vital rates. Wildlife researchers and managers dedicate resources to obtain accurate estimates of vital rates and gain a robust understanding of population dynamics to inform management strategies (Flint 2015). State and federal agencies in North America monitor migratory game bird populations by conducting aerial surveys (U.S. Fish and Wildlife Service 2014), placing bands on post-breeding birds, and analyzing data from hunter's harvest (Raftovich et al. 2022). These provide the necessary data to calculate population abundance, vital rates, and harvest, which are thereafter used in population models that inform harvest regulation within an adaptive harvest management (AHM) framework (Williams and Johnson 1995). Adaptive harvest management has been considered a great success for North American migratory game bird conservation and management in recent history (Nichols et al. 2007). However, for some species, there are implicit biases and limitations to traditional migratory game bird population surveys that hinder sustainable harvest management (Koneff et al. 2017, Reed et al. 2019).

For waterfowl, AHM primarily focuses on mallard (*Anas platyrhynchos*) population dynamics given their outsized representation in total waterfowl harvest and role as a status indicator for other prairie-nesting or dabbling ducks (U.S. Fish and Wildlife Service 2022). Thus, broad-scale waterfowl surveys such as the Waterfowl Breeding Population and Habitat Survey (BPOP) were designed to monitor habitats and geographic regions important to mallards and other sympatric species (U.S. Fish and Wildlife Service 2014). But waterfowl species with spatial distributions, population dynamics, or life history characteristics that differ from mallards may be misrepresented or unreported altogether (Finger et al. 2016, Roberts et al. 2022, Schummer et al. 2015). Consequently, lack of reliable population information remains a significant challenge for migratory game bird biologists in North America seeking to effectively manage harvest across all species.

Sea ducks (tribe *mergini*) are a group of waterfowl species that occupy large inland waterbodies and coastal habitats throughout North America. Though robust population estimates remain scarce for many species, evidence suggests most sea duck populations are in a long-term decline (Bowman et al. 2015). Long-tailed ducks (*Clangula hyemalis*), black scoters (*Melanitta americana*), white-winged scoters (*M. delgandi*) and surf scoters (*M. perspicilatta*) (hereafter focal species) in particular have been identified as species of management concern by the Sea Duck Joint Venture (2022) due to great population knowledge gaps, long-term declines in abundance, and uncertainty of sustainable harvest potential. Atlantic coast populations of each focal species face greater harvest pressure and threats from coastal development relative to populations in other regions, thus meriting further prioritization of improved monitoring of these populations (Sea Duck Joint Venture 2022).

Causes of sea duck population declines are poorly understood, but populations are often most sensitive to changes in adult survival given their relative longevity and reduced annual reproductive capacity (Flint 2015). However, adult survival rates are typically stable over time, whereas annual variation in breeding productivity may be great due to environmental stochasticity (Iles et al. 2013). Thus, annual recruitment; the process by which new individuals are added to a population each year, may play an important role in influencing sea duck population changes over time.

Accurate estimates of total annual recruitment in sea ducks are often difficult to obtain at a population scale. Many breed in inaccessible boreal forest and tundra habitats at low densities (Lamb et. al 2020), which limits aerial survey and banding capabilities (Smith 1995, Reed et al. 2019). As an alternative to explicit juvenile abundance estimates, an index of annual recruitment can be calculated as the proportion of juvenile individuals post-breeding season (juvenile proportion), or as the ratio of juvenile individuals to adults (age ratios; Cowardin and Blohm 1992). A post-breeding age ratio or juvenile proportion parameter accumulates all components of breeding productivity including nesting propensity, clutch size, nest success, and fledgling survival (Ricklefs and Bloom 1997). Sea duck recruitment estimates at the population level in North America are traditionally sourced from parts collection hunter harvest survey (PCS) age ratios, which rely upon the submission of wings from birds harvested during regulated hunting seasons (Raftovich et al. 2022).

Unfortunately, PCS estimates of age ratios are biased because juvenile birds are more susceptible to harvest than adults (Stott and Olson 1972, Miller and Otis 2010, Osnas et al. 2016). To account for this bias, age-cohort-specific band recovery rates are used for species with robust post-breeding banding efforts such as mallards and northern pintails (*Anas acuta*; Zimmerman et al. 2010). No such corrections have been applied to sea duck PCS age ratios due to the lack of comparable post-breeding productivity estimates and age-cohort-specific harvest rates produced by banding data. The paucity of reliable recruitment estimates creates population model uncertainty for agencies that manage sea duck populations (Koneff et al. 2017). This also limits scientific inference of factors that influence variation of sea duck productivity over time.

Sea ducks are sexually dichromatic and do not exhibit definitive adult plumage during their first year of life (Pyle 2005). This allows trained observers to identify individual birds to sex- and age-cohort, generate cohort-specific counts, and thereafter calculate juvenile proportions or age ratios of a surveyed populations. Several studies have successfully derived sea duck juvenile proportions estimates from observational direct count surveys at wintering sites (Duncan and Marquiss 1993, Smith et. al 2001, Iverson et. al 2004, Robertson 2008, Rodway et al. 2015). If implemented with a broad-scale survey effort, careful consideration of potential sampling biases, and years of continued data collection (Rodway et al. 2015), a direct count survey of

Atlantic coast sea duck populations could present a viable alternative method of estimating focal species annual productivity.

All four focal species exhibit differential plumage between age and sex cohorts and have sympatric non-breeding ranges on the Atlantic coast (Lamb et al. 2020). Thus, a post-breeding direct-count juvenile proportion survey provides an opportunity to generate annual juvenile proportion estimates for all focal species simultaneously. In 2018, the U.S. Fish and Wildlife Service partnered with state agencies across the Atlantic Flyway and initiated a sea duck fecundity survey (hereafter photo survey) of these four focal species using the direct count survey approach (Roberts and Sullivan 2020), with the goal of producing cost-effective, reliable estimates of focal species annual breeding productivity in the region.

For this study, I used contemporaneous data collected by the Atlantic Flyway sea duck fecundity survey to examine focal species annual recruitment. My primary objectives were to calculate annual age and sex cohort proportions of each focal species, evaluate potential differences among sampling procedures, survey approaches, and regions, test differences between photo survey juvenile proportions and PCS estimates, and derive species-specific estimates of juvenile harvest vulnerability.

Methods

Photo Survey

I, with assistance from partners, including state and provincial agencies, volunteers, and the U.S. Fish and Wildlife Service from across the non-breeding ranges of sea ducks within the Atlantic coast region, conducted an autumn direct-count photo survey of the four focal sea duck species. The survey began with participation in Maine, New Hampshire, New York, New Jersey, Maryland, Virginia, and North Carolina in 2018-2020, with efforts expanding to Rhode Island, Massachusetts, and the Lake Ontario region of New York and Ontario in 2021-2022 (Figure 1). The photo collection window spanned 15 October through 15 December each year, with surveyors permitted to take photos at any time during the survey period.

I provided partners with specific guidelines (Appendix I, Supplement 1) for photo collection to ensure optimal photo quality, sample independence and randomness. Surveyors used digital cameras with telephoto zoom lenses (200 x 600mm) to capture photos of sea ducks. Breast, belly, and flank plumage characteristics differ among age and sex cohorts of sea ducks (Pyle 2005, Billerman et al. 2020). Thus, surveyors photographed only flighted birds of target species to maximize visibility of body plumage. Surveyors were encouraged to photograph all individuals, pairs, small and large flocks they encountered to represent all flock sizes. Surveyors took photos on sunny or well-lit overcast days. Surveys were either conducted from shore or boat depending upon site conditions, bird distribution, and boat availability. Surveyors focused their efforts in areas with large sea duck concentrations during winter

(Silverman et al. 2013, Lamb et al. 2020) to avoid biases from individuals or flocks that may have strayed from ordinary habitats due to injuries or navigation difficulties. Surveyors were permitted to determine their approach to conducting surveys based on access to land or water locations, camera equipment, and timing within the survey period so long as they adhered to survey guidelines.

To achieve a standard error $SE \leq 0.05$ for juvenile proportion estimation, a sample size of $n = 100$ photos is necessary (Roberts and Sullivan 2020). Thus, I requested each participating state or province collect 10 photos of each species. Surveyors compiled all photos with identifiable individuals at the end of the sampling season and reported the image name, survey method (land or over water), date taken, and location (state and county) for each photo.

Photo Processing

I processed all submitted photos with the software program GIMP (Version 2.10.30, GIMP Team 2021). First, I isolated every bird from each photo using the snip function and assigned each bird a unique image name. I used a photo identification program for species and age-sex classification through a Zooniverse online interface (created in collaboration with Zooniverse.org, available at https://www.zooniverse.org/projects/tjroberts082/sea-duck-fecundity) and uploaded the isolated images and corresponding documentation.

Through the Zooniverse project page, photo survey partners and I classified all individuals first to species, then to associated age-sex class. Age-sex classifications included (1) adult male, (2) adult female, or (3) juvenile of unknown sex. I included a fourth (4) category called “brown birds” to account for individuals that could be identified to species, were obviously not adult males, but could not be distinguished as either adult females or juveniles due to inadequate lighting or incomplete visibility of key plumage characteristics (belly, flanks, etc.). Classifications were based on plumage characteristics defined by Pyle (2005) and Billerman et al. (2020); I also used photos of known-age captive juvenile and adult white-winged and surf scoters provided by Cockrell (pers. comm., 16 March 2022) to confirm that plumage characteristics exhibited by juvenile and adult female birds matched with existing descriptions. All classifiers had access to a field guide page throughout identification that included written plumage descriptions and several reference photos and illustrations (Appendix I, Supplements 2-5) of each species and age/sex cohort. I requested surveyors classify all photos, though not all photos could be classified by every surveyor due to individual time constraints. Therefore, I randomized the order of photos such that each had an equal chance to get classified.

Individuals identified to the same species classification by at least 90% of surveyors were included in statistical analyses, whereas individuals identified to the same age/sex cohort classification by at least 75% of surveyors were included in statistical analyses (Roberts and Sullivan 2020). Additionally, all birds that did not meet the age/sex cohort classification threshold of 75% but were never classified as adult males were incorporated in the analysis as brown birds.

I assumed each individual was randomly and independently encountered with respect to differential spatial segregation and detection probability among cohorts. I considered the broad geographic scope of the project, large sample sizes, several years of continued data collection, and evidence to support sample independence among photos collected using photo survey methodology (Roberts and Sullivan 2020) to inform these assumptions.

Data Analysis

I defined annual recruitment for each focal species as the number of juveniles added to the Atlantic Flyway (eastern) portion of the population post-fall migration. Though age ratios are typically used to describe waterfowl populations (Raftovich et al. 2021), I used juvenile proportions as an index of annual recruitment. This parameterization is bounded by 0 and 1 and thereby standardized, which improves statistical modeling capabilities (Specht and Arnold 2018) and helps improve inference of trends over time.

To calculate juvenile proportion estimates, I incorporated classification data from the photo survey with hierarchical models analyzed in a Bayesian framework. I considered the observed number of individuals in a cohort to be a realization from the binomial distribution:

$$Y = \text{Binomial}(n, p) \qquad \text{Equation 1.}$$

I denoted the observed count of each cohort as Y for adult males m, adult females f, juveniles j, or brown birds b, n is the total number of photos, and p is the proportion of the cohort.

Rather than removing birds classified as brown birds from proportion estimates, I estimated the proportion of brown birds that were adult females or juveniles with a vague prior to correct for identification bias (Ketz et al. 2019, Roberts and Sullivan 2020):

$$p_b = \text{Beta}(A, B) \qquad \text{Equation 2.}$$

Where $A = \text{Normal}(2, 0.001)$, $B = \text{Normal}(3, 0.001)$.

I then split the count of brown birds (Y_b) into additional adult females (*extra f*) and juveniles (*extra j*) by using the following:

$$Y_{extra\ f} = p_b \text{ x } Y_b \qquad \text{Equation 3.}$$

$$Y_{extra\ j} = Y_b - Y_{extra\ f} \qquad \text{Equation 4.}$$

I related the true number of adult males y_m to Y_m with a Poisson distribution:

$$Y_m = \text{Poissson}(y_m) \qquad \text{Equation 5.}$$

The true number y of adult females and juveniles was related to Y_f and Y_j, respectively, assuming the observed was always less than the true number of each cohort photographed (at least one bird classified as “brown bird” was really an adult female or juvenile), using a Poisson distribution as:

$Y_f = \text{Poisson}(y_f - Y_{extra\ f})$ Equation 6.

$Y_j = \text{Poisson}(y_j - Y_{extra\ j})$ Equation 7.

I then estimated p for each cohort using the binomial model:

$y = \text{Binomial}(p, N)$ Equation 8.

where N is the total birds used in the analysis (to estimate male proportions) or total birds classified as either adult female, juvenile, or brown birds (to estimate adult female and juvenile proportions). The sum of the proportions must equal 1, so I used a Dirichlet distribution for the vague prior on p.

I calculated the photo survey recruitment estimate as the proportion of juveniles in the sum of juveniles and adult females (juvenile proportion, P) using the following equation:

$P = y_j / (y_j + y_f)$ Equation 9.

To summarize adult sex ratios, I calculated the proportion of males in the sum of adult males and females (male proportion, S):

$S = y_m / (y_m + y_f)$ Equation 10.

To evaluate any potential biases introduced by survey methodology and verify assumptions of sample independence, I derived numerous calculations of P from subsets of the photo survey data. With the addition of long-tailed duck photo samples from the Great Lakes region in 2021 and 2022, I compared Great Lakes and Atlantic coast region-specific long-tailed duck P to examine if juvenile proportions differed among regions (P_{AC} and P_{GL}). I also calculated P for each species using only one randomly-selected bird from each photo in the sample (P_{rand}), rather than all photographed birds (P_{all}), to assess if full inclusion of all individuals introduced any sample non-independence associated with flock size. Lastly, I calculated P for each species with photos captured from boat (P_{boat}) or from land (P_{land}) to evaluate if boat or land-based surveys encountered age-cohorts at differing rates. I used two-tailed t-tests ($\alpha = 0.05$) paired by year for each species to test differences between each pair of parameters. I hypothesized paired parameters; P_{AC} and P_{GL}, P_{rand} and P_{all}, and P_{boat} and P_{land}, respectively, would not differ significantly from one another.

I obtained U.S. Fish and Wildlife Service (USFWS) Parts Collection Survey (PCS) records of all four focal species in the Atlantic Flyway from 2019-2022 to compare with photo survey estimates. The survey collects wings of hunter-harvested birds from a random subset of migratory game bird hunters across the U.S. each year (Raftovich 2022). Each wing is classified to species, sex- and age-cohort by waterfowl biologists; focal species wings were aged as either “immature” (juvenile) or “adult”. Most juvenile sea duck wings in the sample were not identified to sex; I included all juveniles and assumed juvenile sex ratios were equal (Wood et al. 2021).

For each year t and species s, I calculated PCS annual recruitment P_{pcs} as the proportion of juvenile-aged wings in the summed sample of juvenile and adult female wings:

$$P_{pcs} = \text{Juvenile wings} / (\text{Juvenile wings} + \text{Adult Female wings}) \qquad \text{Equation 11.}$$

I derived the same parameter from photo survey cohort data using Equation 9 and selected the mean value from the posterior distribution (P_{photo}). I excluded adult male wings from P_{pcs} to eliminate biases associated with adult male harvest vulnerability and reporting rates, which ensured a more reliable comparison with P_{photo}. I also conducted an *a priori* proportion test power analysis to establish the minimum PCS wing sample size necessary to detect differences between P_{pcs} and P_{photo}. To establish the significance and directionality of differences between P_{pcs} and P_{photo}, I compared estimates for each species using a one-tailed t-test ($\alpha = 0.05$), with samples paired by t. I hypothesized P_{pcs} would be significantly greater than P_{photo} in all species.

I considered juvenile harvest vulnerability to be the likelihood of a juvenile bird being harvested relative to an adult female. I parameterized juvenile harvest vulnerability for each species as a probability calculated from the mean within-year difference between P_{pcs} and P_{photo} (V), with the assumption that P_{pcs} was always greater than P_{photo} due to juvenile overrepresentation in PCS:

$$V = \frac{1}{t} \sum^{t} (P_{pcs} - P_{photo}) + 1 \qquad \text{Equation 12.}$$

I derived posterior distributions of all photo survey and harvest vulnerability parameters by using Markov-chain Monte Carlo (MCMC) analysis with the rjags package (Plummer et al. 2022) in R (R Core Team 2022). I implemented juvenile proportion and differential vulnerability models for each species with three chains, 5,000 MCMC sampling iterations, and a thinning, adapt, and burn-in rate of 1, 100, and 1,000, respectively. Gelman-Rubin statistics confirmed successful convergence in all models ($R < 1.02$, Gelman and Rubin 1992). I summarized parameter posterior distributions with mean values and 95% credible intervals.

Results

We classified 2,098, 1,192, 3,263, and 2,653 individual birds from collected photos to age/sex cohort in 2019, 2020, 2021, and 2022, respectively (Figure 1). I achieved the desired sample size of 100 birds for calculating proportion estimates each species and year, except for white-winged scoters and long-tailed ducks in 2019 (Table 1). Mean number of classifications of each photo was 9.31 across all years. Mean classification agreement to species was high at 99% across all years (Table 2). Mean classification agreement to cohort among all cohorts was 95% for black and surf scoters (BLSC and SUSC hereafter, respectively), 93% for long-tailed ducks (LTDU), and 82% for white-winged scoters (WWSC). Thus, nearly all classified photos met the designated 75% agreement threshold and were included in cohort proportion calculations. Among cohorts, mean classification agreement was greatest for adult males (99%), followed by brown birds (94%), juveniles (88%), and adult females (86%). I thereafter used the classification data to model flyway-level cohort proportion estimates for each year and focal species.

I report juvenile proportions and male proportions of adult birds for each species by year of study (Table 1, Figures 5 and 6). The P_{photo} for each species varied by year but was greatest for WWSC in 2020 (0.778) and least for LTDU in 2019 (0.301). White-winged scoters consistently exhibited the greatest recruitment rates, with an average

WWSC P_{photo} = 0.709 across all years, followed by SUSC (0.540), BLSC (0.460), and LTDU (0.422).

Paired t-test comparison revealed that photo survey P did not vary significantly ($\alpha < 0.05$) in any focal species with respect to photo sampling approach (Figure 2) or photo survey methodology (Figure 3). LTDU P did not differ significantly ($\alpha < 0.05$) across survey regions, though evidence from 2021 indicates this may vary among years (Figure 4).

I obtained 1,235 focal species harvest records from the PCS in 2019-2022; I used 684 records of juveniles and adult females to calculate P_{pcs} for each year (Table 1). The power analysis indicated a minimum PCS sample size of $n > 22$ would be necessary to detect differences between P_{pcs} and P_{photo}. Sample sizes of all four focal species in 2022 and surf scoters in 2021 fell short of the minimum threshold; I excluded these P_{pcs} estimates from PCS-photo survey t-tests and V calculations.

P_{pcs} was significantly greater ($p < 0.05$) than P_{photo} in all four focal species, and greater in all years (Figure 5). I subsequently derived estimates of V for each species (Table 3).

Discussion

My examination of focal species population demography with the photo survey method delivered species-specific annual recruitment estimates for the Atlantic Flyway in 2019-2022. My comparison of juvenile proportions derived across multiple sampling and survey procedures used in the photo survey did not indicate significant evidence of bias in population-wide juvenile proportion estimates using photo survey approaches (Figures 2-4). Furthermore, I revealed compelling evidence of juvenile vulnerability bias in focal species PCS juvenile proportion estimates via comparisons with photo survey estimates (Figure 5), and thereafter used the opportunity to calculate novel estimates of juvenile harvest vulnerability.

The Atlantic Flyway sea duck fecundity survey appears to produce annual recruitment estimates that represent trends in population demography in eastern populations of the four focal species, and are likely more reflective of true population demography than PCS estimates. The broad spatial extent of the survey included large portions of each species' range and covered several key wintering sites used by concentrations of sea ducks (Silverman et al. 2013). Surveyors were able to consistently obtain large quantities of sea duck photos, which ensured substantial sample sizes for model-based age and sex cohort calculations. Photo classification agreement to species and age/sex cohort was great across all four years (Table 2), thus few photos were excluded from estimates. I did not detect influence of sample non-independence on juvenile proportion estimates: photo survey encounters were effectively random (Figure 2), and proportions derived from photos collected by boat or from shore did not differ significantly (Figure 3). These findings were consistent with those reported by Roberts and Sullivan (2020) after the initial implementation of the survey. Nonetheless, it was important to consider the potential effects of different survey approaches to limit any systematic underrepresentation of cohorts, as these biases can greatly misinform subsequent recruitment estimates (Ward et al. 2017). I also found relative recruitment rates among the four focal species were consistent with what these populations likely exhibit: white-winged scoters are most fecund, followed by surf scoters, black scoters, and long-tailed ducks, respectively (Mallory 2015). The relative recruitment rates I report also align with long-term PCS age ratio data used in Chapter 2 of this thesis, and with species-specific component reproductive rates estimated in Koneff et al. (2017).

Comparisons between PCS and photo survey juvenile proportion estimates yielded strong evidence of differential vulnerability bias in PCS. Photo survey estimates were less than PCS estimates in all species and years (Figure 4); this indicates the PCS systematically overrepresents juveniles in recruitment estimates because of greater juvenile vulnerability to harvest (Zimmerman et al. 2010). Therein, PCS may produce an inaccurate but precise recruitment estimate. Consequently, I was able to derive an estimate of juvenile harvest vulnerability for each species by pairing juvenile proportion estimates from each method (Table 3). Harvest vulnerability in sea ducks was characterized previously by Stott and Olson (1972) using direct observations; they report lower harvest vulnerability in juvenile and adult females in white-winged scoters relative to surf and black scoters, which was also indicated in my data. However, they did not provide estimates of juvenile harvest vulnerability relative to adults, so I was unable to derive any comparisons. Sea duck harvest has also likely changed dramatically over time due to changes in hunting techniques and equipment, coastal development, harvest regulations, and sea duck population trends (Rothe et al. 2015). Recent studies have relied solely on elicitation to calculate juvenile harvest vulnerability (Koneff et al. 2017); my findings provide the first contemporary empirical estimates for each species. Importantly, I found these elicited estimates from Koneff et al. (2017) were much greater ($V \sim 2.31$-2.61) than those I calculated ($V \sim 1.15 – 1.27$). Thus, my data offers an alternative to the significant discrepancies in existing estimates of this key demographic vital rate.

I found PCS estimates with sample sizes below the threshold prescribed by the power analysis ($n = 22$) deviated greatly from photo survey estimates and broke trends observed in previous years. Uncertainty and noise introduced by a small sample size likely renders these estimates unreliable. The U.S. Fish and Wildlife Service currently uses a threshold of 20 wings for calculating PCS age ratio estimates (Raftovich et al. 2022); based on my findings, this threshold appears appropriate for sea duck recruitment estimates since years with sufficient PCS sample sizes yielded proportion estimates that corresponded with photo survey estimates (Figure 5).

Spatial expansion of survey coverage in Massachusetts, New York, Ontario, and Rhode Island in 2021 and 2022 was key to the photo survey effort. Long Island Sound and the Cape Cod region support most Atlantic Flyway white-winged scoters (Silverman et al. 2013), which, prior to 2021, had smaller sample sizes and were likely underrepresented in the survey. Estimates for long-tailed ducks were also likely improved by additional samples from Lake Ontario. Long-tailed ducks wintering on the Great Lakes and the Atlantic coast constitute one contiguous eastern population (Pearce et al. 2019, Lamb et al. 2019 and 2020). However, evidence from 2021 suggests juvenile proportions on Lake Ontario may be greater than on the Atlantic coast in some years (Figure 3). Differential broad-scale spatial segregation among age-cohorts of wintering sea ducks has been observed on the Pacific coast; Iverson et al. (2004) indicated juvenile surf scoters may use wintering sites located further south than those selected by adults, and Uher-Kock et al. (2016) described differential migration between age and sex cohorts of surf scoters. If indeed long-tailed ducks distribute non-randomly with respect to age across wintering areas in eastern North America, population demography information from the Great Lakes region is crucial to appropriately characterize trends in the entire population. The Atlantic Flyway survey effort only included samples from Lake Ontario; data collection at key long-tailed duck wintering areas in the Great Lakes such as Green Bay and eastern Lake Erie would be vital in future survey efforts to ensure comprehensive coverage of the eastern population (Lamb et al. 2019 and 2020).

The broad geographic range of the survey and use of several survey locations was necessary to produce a representative population-scale recruitment estimate (Rodway et al. 2015). However, this approach limited site and region-specific insights on sea duck population demography; sample sizes from each county were often limited to 10 photos or less, which were too few to calculate reliable site-specific proportion estimates using my modeling approach. Space-use patterns between age and sex classes of sea ducks may vary temporally or by latitude, resource availability, and density dependence (Uher-Koch et al. 2016), all of which may introduce sources of bias in survey-based juvenile proportion estimates (Iverson et al. 2004, Rodway et al. 2015). Increased survey intensity across key survey sites could be used to help identify fine-scale drivers of age-cohort distribution, which may refine population-level estimates (Specht and Arnold 2018). However, this would require significant time and resource commitments that are often limiting for resource managers and was beyond the scope of this survey effort.

My approach to classifying long-tailed ducks to age and sex cohorts was informed by detailed plumage descriptions, illustrations, and reference photos of wild birds (Palmer 1976, Pyle 2005, Billerman et al. 2020). Unfortunately, I was unable to obtain known-age photos of captive juvenile long-tailed ducks to compare plumage characteristics with our identification criteria. Adult female and juvenile long-tailed ducks exhibit variable plumage throughout their annual molt cycle relative to other sea ducks and may be difficult to reliably distinguish from one another (Savard and Petersen 2015), which consequently introduces some uncertainty in cohort counts. There was notable variability in long-tailed duck photo survey adult sex proportions among the four years relative to PCS (Figure 6); this heterogeneity may be a consequence of misclassification rather than dynamic adult sex ratios (Flint 2015). Larsson (2023) postulates only males may be reliably aged using photos; they instead estimated long-tailed duck age ratios from photo surveys by calculating the ratio of adult males to all females, the ratio of juvenile males to all females, and thereafter the ratio of juvenile females to adult females with the assumption juvenile sex ratios are equal (Wood et al. 2021). Applying this approach to the Atlantic Flyway photo survey in the future may create a more robust framework for estimating long-tailed duck juvenile proportions and help reduce identification uncertainty.

Management Implications

The Atlantic Flyway sea duck fecundity survey addresses a key information gap for sea duck harvest managers in the Flyway by providing reliable population-level estimates of recruitment for four under-surveyed sea duck species (Koneff et al. 2017). Small sea duck sample sizes in the PCS in 2021 and 2022 indicates PCS is becoming a less reliable source of population data for sea ducks over time, which further underscores the importance of utilizing alternative methods to characterize sea duck population demography. Continued data collection and further refinement of survey methods would ensure the availability of reliable population information into the future (Rodway et al. 2015) and provide a useful baseline for managers to characterize trends in sea duck recruitment. I recommend that future photo survey efforts targeted at the eastern North American long-tailed duck population expand upon this effort and obtain samples from throughout the Great Lakes region to account for their entire wintering distribution (Lamb et al. 2019), and adopt the age/sex cohort classification schema proposed by Larsson (2023) to reduce uncertainty in cohort counts. The reported juvenile vulnerability estimates reported here (Table 3) also provide useful information for managers seeking to correct future sea duck harvest survey age ratio estimates or model sea duck populations. However, consideration must be given to site or region-specific harvest methods, regulations, and population status.

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Tables

Table 1: Photo and parts collection survey (PCS) sample sizes (*n*), juvenile (*P*) and male proportions (*S*)of long-tailed duck and black, surf, and white-winged scoter populations in the Atlantic Flyway in 2019-2022. Asterisks (*) indicate years where PCS sample sizes of adult females and juveniles were below $n < 22$.

				Juvenile proportion (*P*)			Male proportion of adults (*S*)		
	Species	Survey method	Sample size (*n*)	Mean/Value	2.5% CrI	97.5% CrI	Mean/Value	2.5% CrI	97.5% CrI
2019	BLSC	PCS	83	0.545			0.780		
		Photo	1133	0.472	0.314	0.608	0.691	0.630	0.750
	LTDU	PCS	196	0.500			0.719		
		Photo	43	0.301	0.150	0.500	0.569	0.407	0.720
	SUSC	PCS	147	0.822			0.843		
		Photo	309	0.603	0.409	0.810	0.658	0.559	0.799
	WWSC	PCS	41	0.800			0.870		
		Photo	41	0.688	0.429	0.917	0.814	0.619	0.955
2020	BLSC	PCS	164	0.684			0.773		
		Photo	423	0.440	0.237	0.624	0.644	0.555	0.737
	LTDU	PCS	142	0.686			0.766		
		Photo	200	0.485	0.375	0.605	0.730	0.650	0.806
	SUSC	PCS	146	0.756			0.782		
		Photo	315	0.537	0.330	0.750	0.724	0.630	0.832

				Juvenile proportion (*P*)			Male proportion of adults (*S*)		
Year	Species	Method	Sample size (*n*)	Mean/Value	2.5% CrI	97.5% CrI	Mean/Value	2.5% CrI	97.5% CrI
2020	WWSC	PCS	35	0.909			0.867		
		Photo	141	0.778	0.609	0.913	0.855	0.753	0.938
2021	BLSC	PCS	44	0.560			0.633		
		Photo	1630	0.465	0.342	0.570	0.696	0.640	0.748
	LTDU	PCS	141	0.785			0.785		
		Photo	402	0.417	0.349	0.485	0.509	0.450	0.569
	SUSC	PCS	61	0.947*			0.977		
		Photo	753	0.496	0.279	0.681	0.815	0.763	0.872
	WWSC	PCS	35	0.818			0.765		
		Photo	273	0.700	0.584	0.806	0.865	0.807	0.915
2022	BLSC	PCS	35	0.800*			0.870		
		Photo	1308	0.461	0.337	0.550	0.641	0.583	0.696
	LTDU	PCS	34	0.846*			0.909		
		Photo	461	0.484	0.416	0.552	0.584	0.527	0.643
	SUSC	PCS	31	0.833*			0.750		
		Photo	608	0.524	0.342	0.722	0.714	0.637	0.818
	WWSC	PCS	6	1.000*			1.000		
		Photo	201	0.668	0.543	0.786	0.827	0.754	0.893
All Years	BLSC	PCS		0.647			0.729		
		Photo		0.460			0.668		
	LTDU	PCS		0.704			0.757		
		Photo		0.422			0.598		

Year	Species	Method	Sample size (n)	Juvenile proportion (P) Mean/Value	Juvenile proportion (P) 2.5% CrI	Juvenile proportion (P) 97.5% CrI	Male proportion of adults (S) Mean/Value	Male proportion of adults (S) 2.5% CrI	Male proportion of adults (S) 97.5% CrI
All Years	SUSC			0.840			0.867		
				0.540			0.728		
	WWSC			0.882			0.834		
				0.709			0.840		

Table 2. Mean percent photo classification agreement among species and age/sex cohorts of long-tailed ducks (LTDU) and black (BLSC), surf (SUSC), and white-winged scoters (WWSC) in Atlantic Flyway photo survey samples from 2019-2022.

		Mean Agreement						
Year	Species	Species %	Adult Male %	Adult Female %	Juvenile %	Brown Bird %	Unknown %	All cohorts
2019	BLSC	0.992	0.984	0.890	0.924	0.960	0.412	0.943
	LTDU	0.998	1.000	0.848	0.817	0.958	0.600	0.924
	SUSC	0.988	0.993	0.842	0.923	0.936	0.205	0.927
	WWSC	0.994	0.984	0.753	0.714	0.928	0.275	0.791
2020	BLSC	0.998	0.985	0.865	0.914	0.962	0.245	0.935
	LTDU	0.999	0.995	0.813	0.724	0.979	0.278	0.939
	SUSC	0.996	0.987	0.812	0.970	0.947	0.229	0.953
	WWSC	0.998	0.988	0.882	0.825	0.883	0.091	0.769
2021	BLSC	0.999	0.989	0.905	0.886	0.960	0.454	0.947
	LTDU	1.000	0.993	0.885	0.878	0.931	0.314	0.921
	SUSC	0.997	0.997	0.886	0.925	0.940	0.251	0.959
	WWSC	0.995	0.992	0.844	0.931	0.879	0.088	0.841
2022	BLSC	1.000	1.000	0.911	0.932	0.990	0.403	0.962
	LTDU	1.000	0.995	0.866	0.851	0.981	0.237	0.935
	SUSC	1.000	1.000	0.867	0.929	0.944	0.289	0.941
	WWSC	1.000	0.994	0.832	0.916	0.914	0.088	0.874

		Mean Agreement						
Year	Species	Species %	Adult Male %	Adult Female %	Juvenile %	Brown Bird %	Unknown %	All cohorts
All Years	BLSC	0.997	0.990	0.893	0.914	0.968	0.379	0.947
	LTDU	0.999	0.996	0.853	0.818	0.962	0.357	0.930
	SUSC	0.995	0.994	0.852	0.937	0.942	0.243	0.945
	WWSC	0.997	0.990	0.828	0.846	0.901	0.136	0.819
	All	0.997	0.992	0.856	0.879	0.943	0.279	0.948

Table 3: Juvenile harvest vulnerability relative to adult females (*V*) in Atlantic Flyway long-tailed duck (LTDU) and black (BLSC), surf (SUSC), and white-winged scoter (WWSC) populations calculated from photo and parts collection survey (PCS) juvenile proportion estimates in 2019-2022. *V* represents mean of posterior distributions of parameter estimates, minimum and maximum values reported from within-year differences between PCS and photo survey

Species	Harvest Vulnerability Estimate (*V*)	Min.	Max.
BLSC	1.158	1.073	1.339
LTDU	1.271	1.199	1.368
SUSC	1.265	1.219	1.219
WWSC	1.147	1.112	1.131

Figures

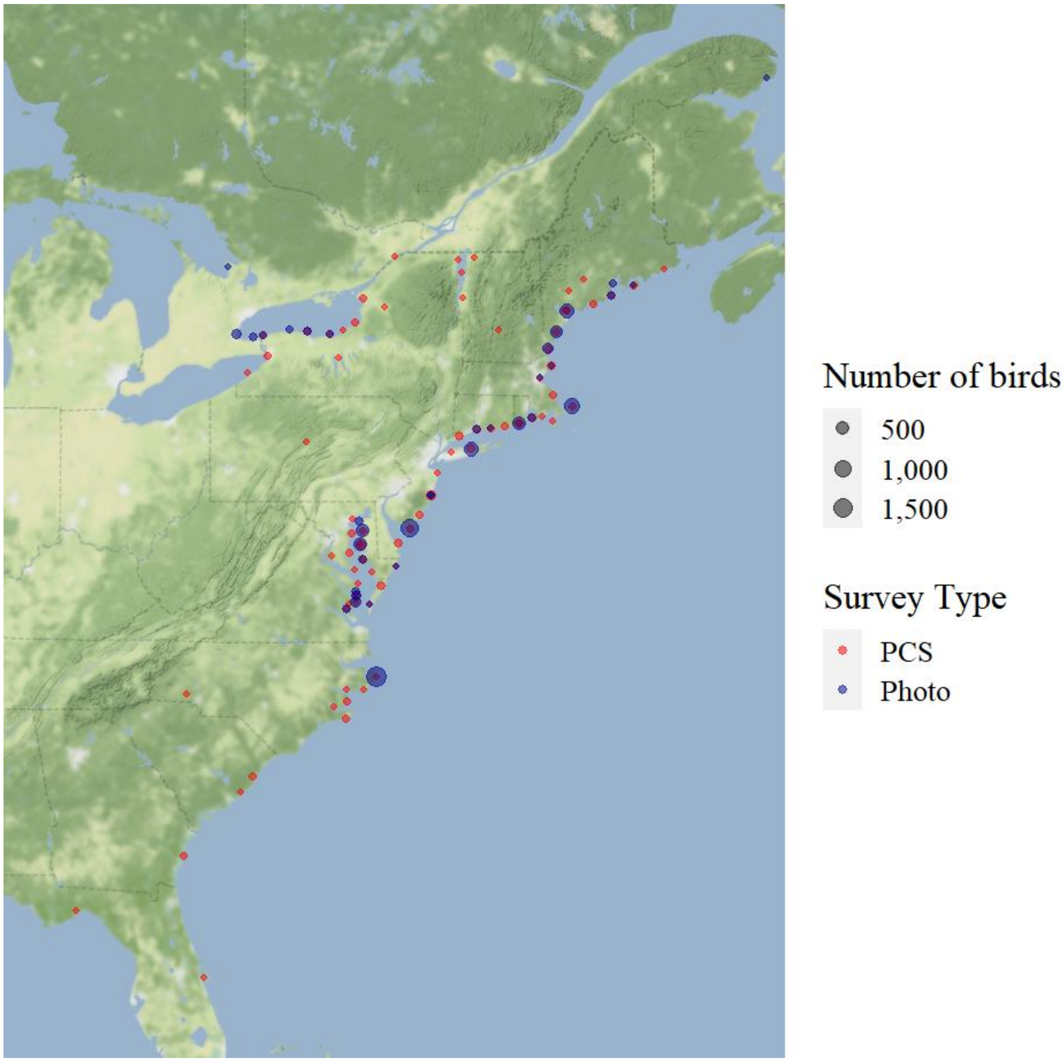


Figure 1: Locations and sample sizes of photo survey photos (blue dots) and parts collection hunter harvest survey (PCS) wings (red dots) of Atlantic Flyway sea ducks from 2019-2022. Counts at each location were aggregated at the county level.

Figure 2. Comparison of land and boat-based photo survey juvenile proportions (*P*) of Atlantic Flyway populations of long-tailed ducks (LTDU) and black (BLSC), surf (SUSC), and white-winged scoters (WWSC) in 2019-2022. Points represent mean values and lines represent 95% credible intervals.

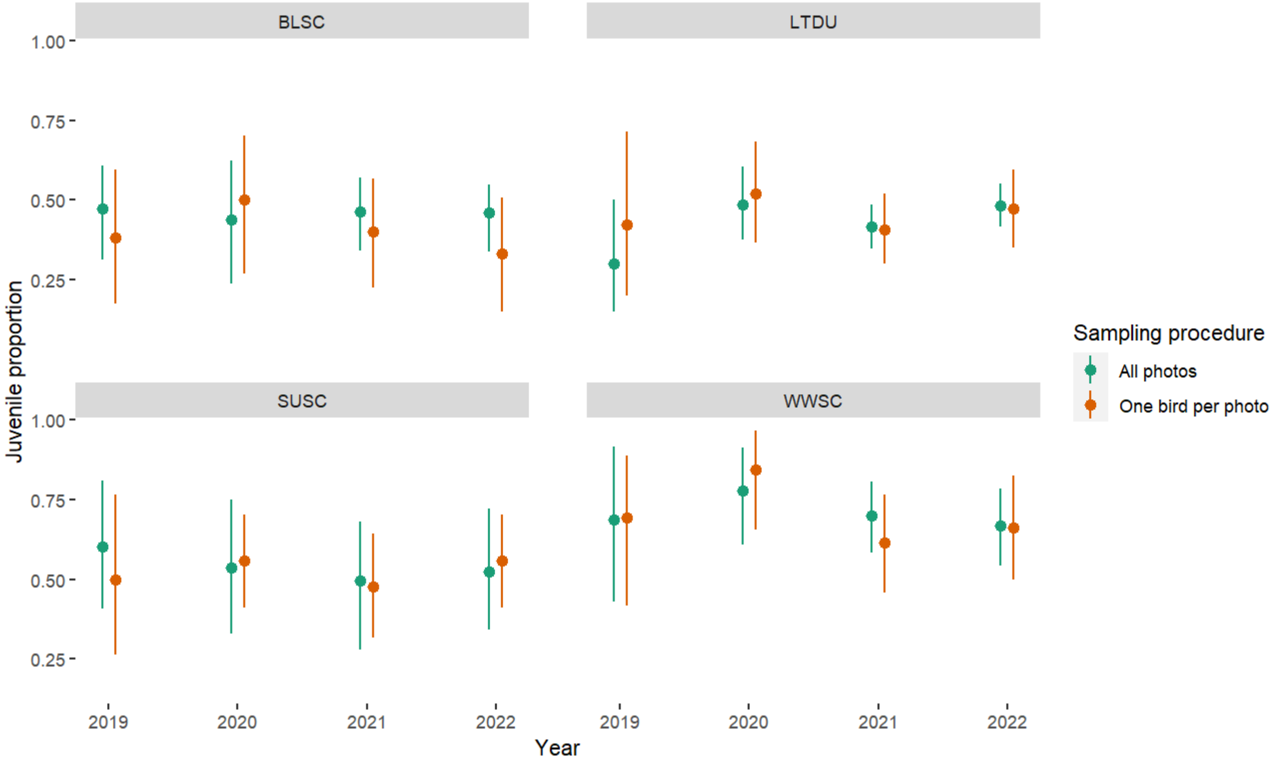


Figure 3. Comparison of photo survey juvenile proportions (*P*) of Atlantic Flyway populations of long-tailed ducks (LTDU) and black (BLSC), surf (SUSC), and white-winged scoters (WWSC) in 2019-2022 using all birds from each photo and one random bird from each photo. Points represent mean values and lines represent 95% credible intervals of posterior distributions.

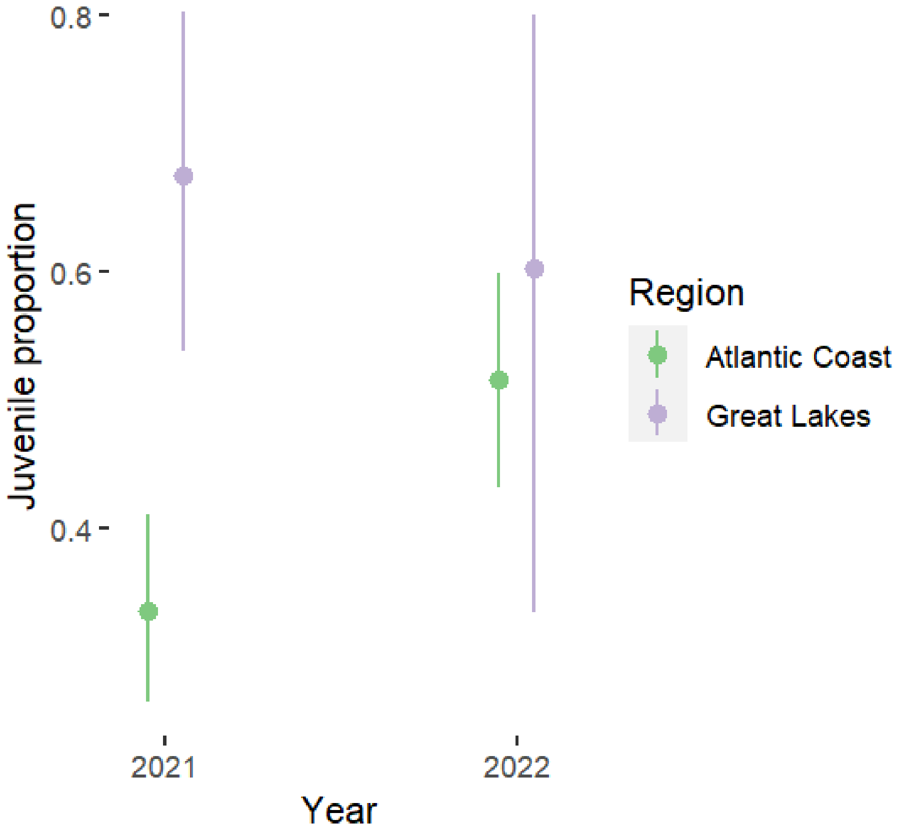


Figure 4. Comparison of Atlantic Flyway long-tailed duck photo survey juvenile proportions (*P*) in Atlantic Coast and Great Lakes regions in 2021-2022. Points represent mean values and lines represent 95% credible intervals of posterior distributions.

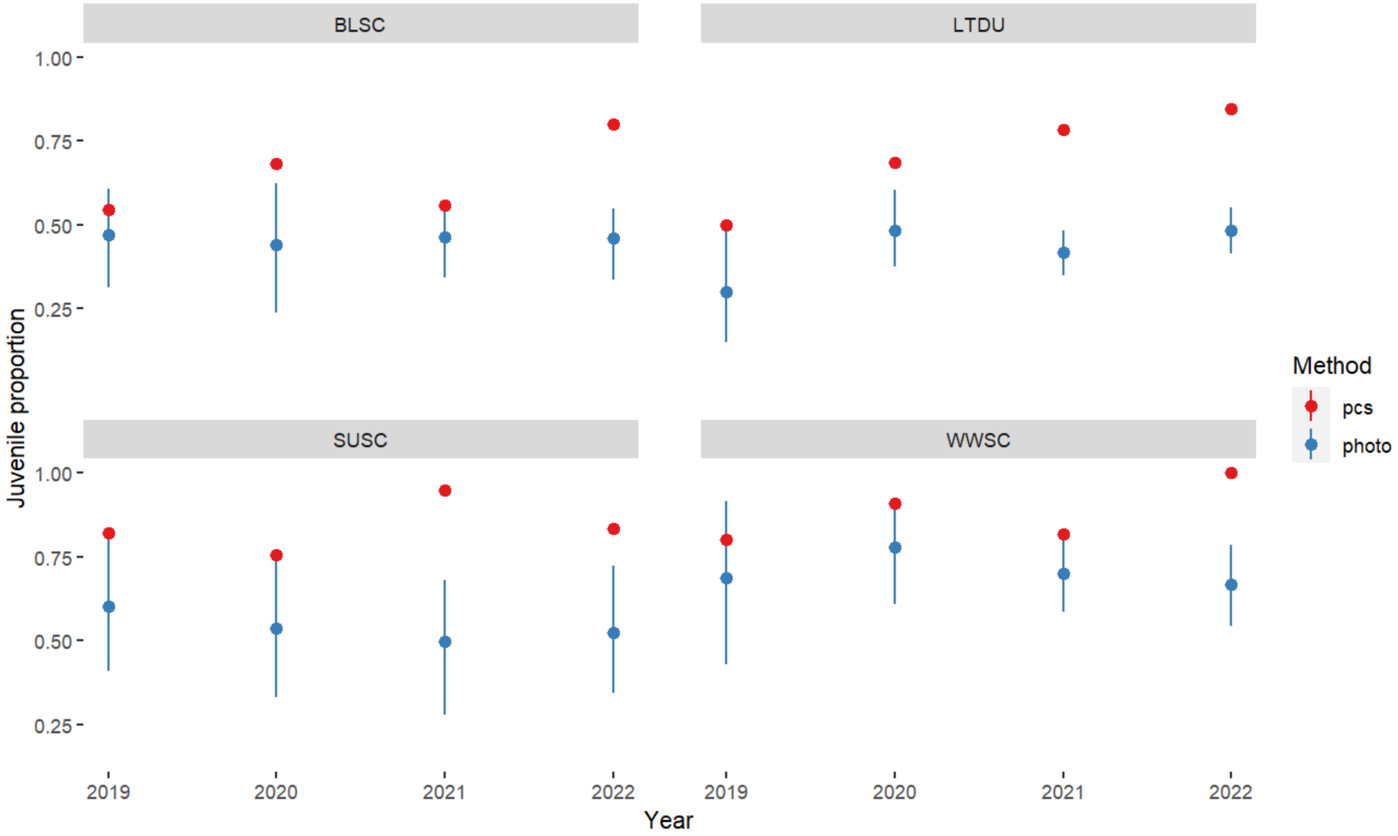


Figure 5: Estimates of photo (P_{photo}) and parts collection survey (P_{pcs}) Atlantic Flyway juvenile proportions in long-tailed ducks (LTDU) and black (BLSC), surf (SUSC), and white-winged scoter (WWSC) populations in 2019-2022 with associated 95% credible intervals (photo survey only).

Figure 6: Estimates of photo (S_{photo}) and parts collection survey (S_{pcs}) Atlantic Flyway male proportions in in long-tailed ducks (LTDU) and black (BLSC), surf (SUSC), and white-winged scoter (WWSC) populations in 2019-2022 with associated 95% credible intervals (photo survey only).

Appendix I

Supplement 1. Atlantic Flyway sea duck fecundity survey guidelines.

Photos should be collected 15 October to 15 December. Target species are black scoters, surf scoters, white-winged scoters, and long-tailed ducks. Target sample size is 10 useable photos of each species from each state during the survey window.

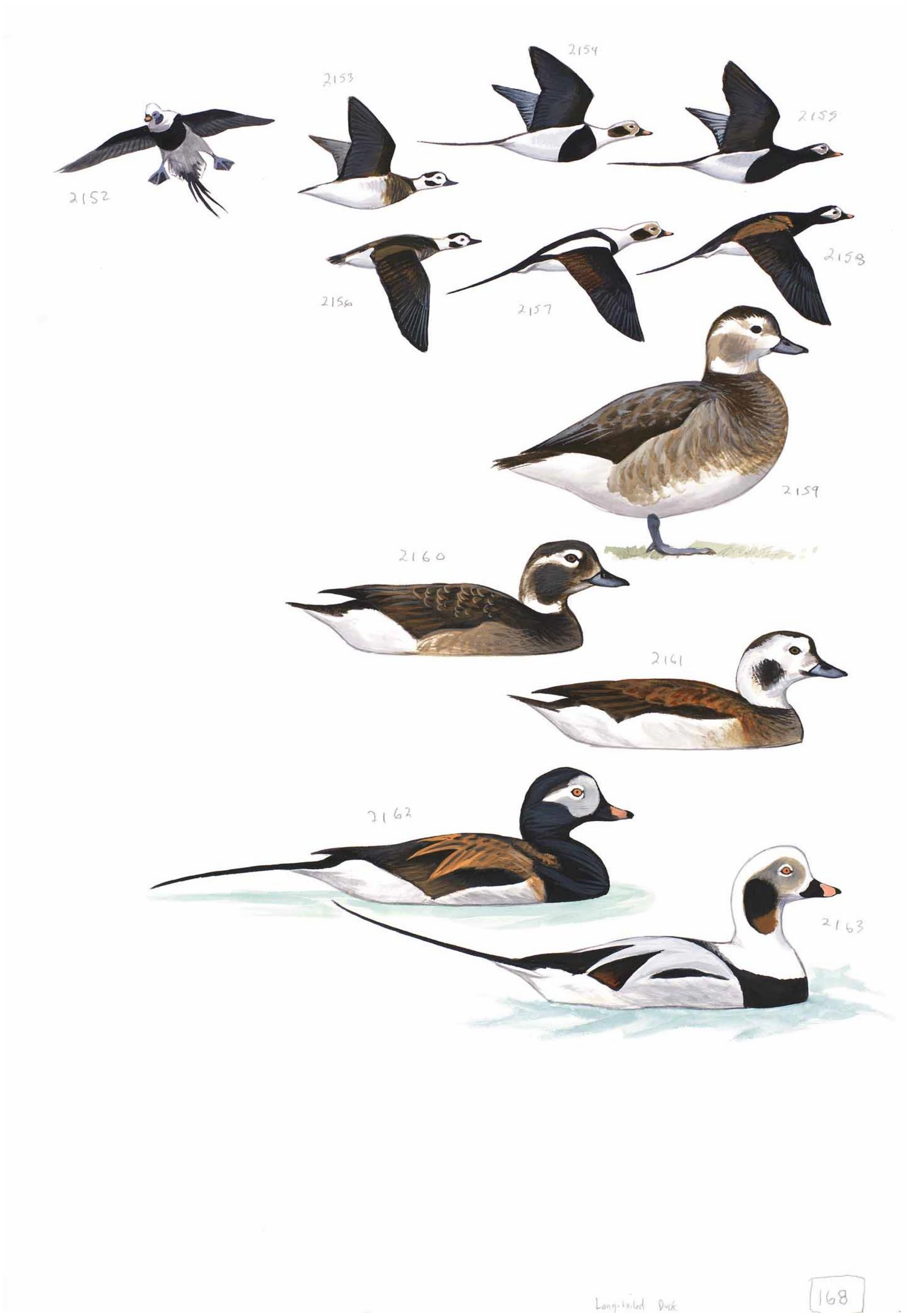
Survey guidelines:

- Choose coastal areas that have known sea duck concentrations (no photos of the rare park scoter)
- Land-based or boat-based photographs will work. Identify that in the spreadsheet (described below)
- Choose forecasted sunny days for optimal lighting.
- All attempts should be made to take photos of flying birds with the sun at the photographer’s back
- Try to frame the bird or center of the flock in the center of the picture frame.
- Photos of any number of flying birds are useful. Don’t wait for large groups as any useable photos of singles, pairs, or flocks help the effort

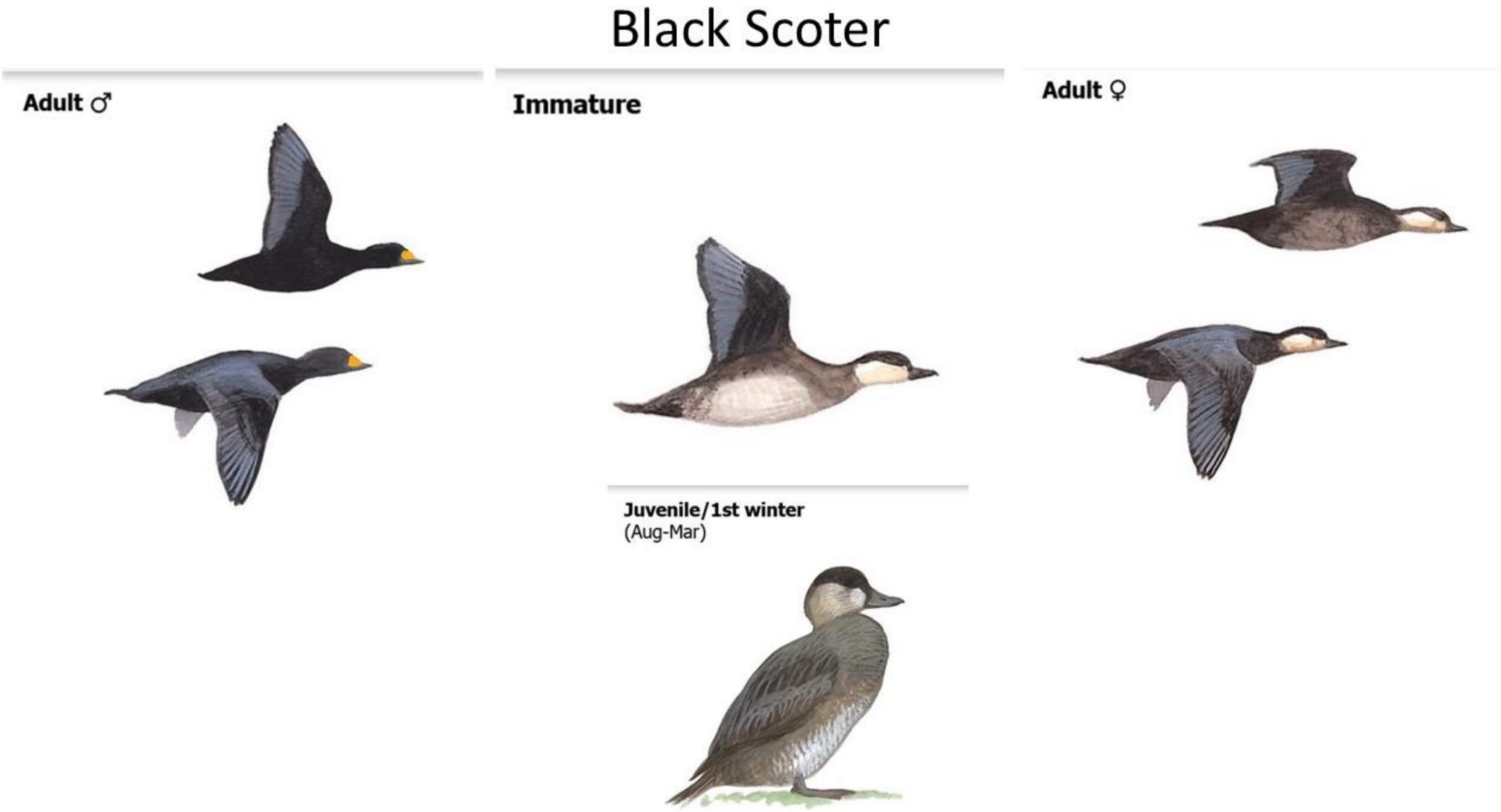
Photo management guidelines

- Remove photos where birds are blurry or otherwise unable to be identified at least to species.
- When using multi-shot function on your camera, select the photo that best represents the flock in terms of composition and resolution, at the photographer’s discretion.

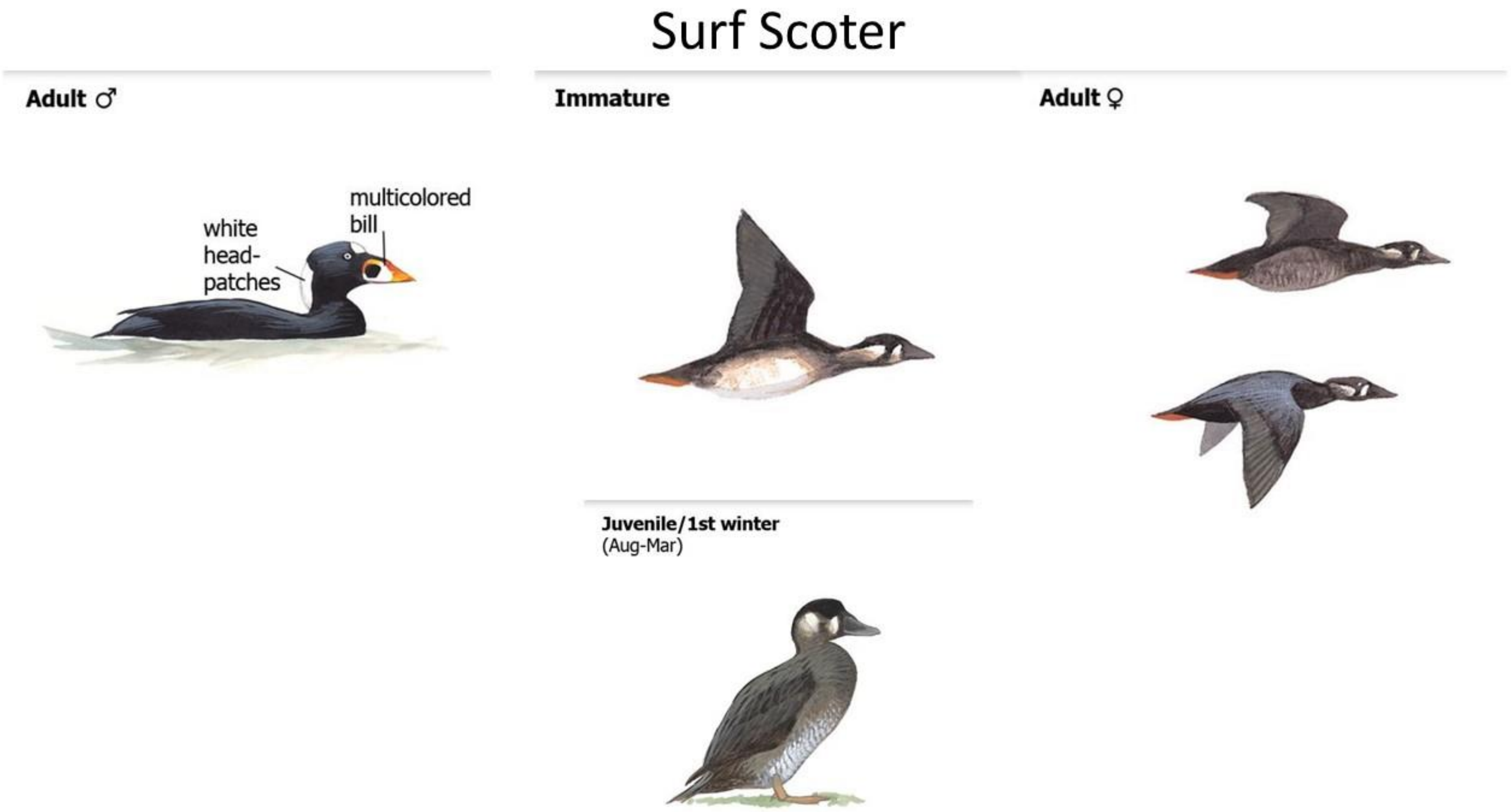
- Photo information should be entered into a spreadsheet that indicates the photo number (ex. 20181029ME001), date of the photo, location (town/county), land or boat-based photo, and Comments. (see Excel Template example).
- Upload photos and associated data sheets to the “SEA DUCK SURVEY PHOTOS” folder in the Diving Duck committee folder of the Atlantic Flyway Technical Section Sharepoint site. Create a folder for your state within the folder.



Supplement 2. Long-tailed duck age and sex cohort plumage guide for Atlantic Flyway sea duck fecundity survey image classification. From Sibley (2014).



Supplement 3. Black scoter age and sex cohort plumage guide for Atlantic Flyway sea duck fecundity survey image classification. From Sibley (2014).



Supplement 4. Surf scoter age and sex cohort plumage guide for Atlantic Flyway sea duck fecundity survey image classification. From Sibley (2014).

Supplement 5. White-winged scoter age and sex cohort plumage guide for Atlantic Flyway sea duck fecundity survey image classification. From Sibley (2014).

Chapter 2: Ecological factors drive interannual variation of sea duck recruitment rates

Abstract

Components of breeding productivity and survival rates in avian populations respond to dynamic environmental stressors across the annual cycle, which therein shape population dynamics over time. In sea ducks (tribe *mergini*), few studies have characterized the ecological factors that drive annual recruitment trends at the population level over time due to scarce scalable population information. Here, I leveraged historic harvest survey recruitment estimates (juvenile proportions) and indicators of environmental conditions at breeding, staging, and wintering areas from 1980-2017 to investigate factors influencing annual recruitment rates in eastern North American populations of long-tailed ducks (*Clangula hyemalis*), black scoters (*Melanitta americana*), white-winged scoters (*M. delgandi*) and surf scoters (*M. perspicilatta*). Recruitment rates in multiple species were positively associated with mean ambient temperatures at staging and breeding areas during spring. This supported my hypothesis that pre-nesting ice cover in key habitats limits breeding productivity by delaying breeding phenology and causing declines in female body condition. Surf scoter recruitment had a strong negative association with great gray owl irruptive migrations, suggesting surf scoters experience intensified predation pressure during low phases of vole population cycles and incur lower nest and brood survival rates. North Atlantic Oscillation patterns and staging area mean ambient temperatures in autumn showed associations with sea duck recruitment, suggesting

harsh weather conditions post-fledging may precipitate early migratory movements that reduce juvenile survival rates or elicit greater proportions of adult sea ducks in subsequent harvests. My findings highlight important relationships between sea duck annual recruitment and ecological factors that may have considerable consequences for sea duck populations as ecosystems and climatic patterns undergo significant changes in the future.

Introduction

Annual recruitment, the process by which new individuals are added to a population each year, is a fundamental component of avian population dynamics that frequently underlies changes in abundance over time (Rönkä et al. 2011, Flint 2015). Environmental variability in breeding and non-breeding habitats often dictates heterogeneity in key vital rates associated with avian productivity such as breeding propensity, clutch size, and nest survival, thereby greatly affecting overall annual recruitment (Mallory 2015). Thus, a thorough understanding of species and guild-specific relationships among key environmental factors across the annual cycle and recruitment is necessary to effectively conserve and manage avian populations (Conn et al. 2015). Furthermore, greater perturbations in habitat conditions and seasonal weather patterns associated with climate change and anthropogenic development are expected to elicit significant shifts in ecosystem composition and function (DesGranges and LeBlanc 2012, Iles et al. 2013), which underscores the importance of evaluating the effects of dynamic ecosystem processes on avian populations to inform future conservation efforts.

Inferences about the influence of complex ecological processes on population-level breeding productivity require reliable population information and effective indicators of environmental conditions (Conn et al. 2015, Specht and Arnold 2018). Population dynamics in species that exhibit cryptic behaviors, inhabit remote areas, or are otherwise difficult to monitor are therefore poorly examined in many cases (Peery et al. 2007, Koneff et al. 2017). This is especially true of sea ducks (tribe *mergini*); a group of migratory waterfowl species that occupy remote marine habitats throughout their annual cycle and breed at low densities in high-latitude boreal forest and tundra habitats, characteristics that greatly limit scalable survey efforts (Lamb et al. 2020). In North America, sea duck populations have experienced long-term declines in abundance (Bowman et al. 2015) and have elicited greater interest from migratory bird managers in recent years due to increasing uncertainty regarding harvest potential, renewable energy development in coastal environments, and climate change; populations of long-tailed ducks (*Clangula hyemalis*), black scoters (*Melanitta americana*), white-winged scoters (*M. delgandi*) and surf scoters (*M. perspicilatta*) in eastern North America (hereafter focal species) have been identified as species of high conservation priority in this regard (Sea Duck Joint Venture 2022). Though drivers of population declines are unknown, sea duck populations exhibit sensitivity to interannual variation in breeding productivity (Flint 2015), which indicates recruitment is likely a key component (Iles et al. 2013). Studies on focal species breeding ecology are especially scarce and have often been restricted to local or regional spatial scales, though dynamic ecological processes such as predation, climate, and habitat conditions have been identified as important drivers of breeding productivity in focal species and other sea duck populations (Alison 1975, Traylor et al. 2004, Kellett et al. 2005, Lehikoinen et al. 2006, Schmidt et al. 2006, Iles et al. 2013). However, ecological pressures on sea duck recruitment at the population level remain poorly understood (Mallory 2015). Consequently, there is a clear need for novel insights into relationships between focal species annual recruitment rates and dynamic ecological processes throughout the annual cycle.

Established linkages between populations and spatially explicit habitat delineations provide opportunities to investigate the effects of specific ecological factors on avian populations when sufficient population information and indicators of environmental conditions are available (Saracco et al. 2022). A viable approach to analyzing relationships among annual recruitment in avian populations and relevant ecological factors is to leverage age ratio-based recruitment estimates and datasets of remotely-sensed environmental parameters from key habitats over a long time series within a modeling approach (Boyd 1996, Alisauskas 2002, Lehikoinen et al. 2006, Specht and Arnold 2018, Saracco et al. 2021) In sea ducks, records of wing submissions from the U.S. Fish and Wildlife Service parts collection hunter harvest survey (PCS) (Raftovich et al. 2022) can be used to estimate annual recruitment by calculating the proportions of juvenile and adult female wings that are juveniles (juvenile proportions); PCS records comprise the only long-term, population-level source of annual recruitment data for the four focal species. Recent telemetry work on focal species identified discrete populations and characterized wintering, migratory staging, molt, and breeding distributions in eastern North America for the first time (Meattey et al. 2018, Lamb et al. 2019, 2020, 2021, Bowman et al. 2021); these novel delineations could be used as aggregating units for deriving estimates of key environmental indicators from historical climate observation records. Thereby, drivers of focal species annual recruitment could be identified by pairing PCS juvenile proportion estimates and new insights on focal species spatial extents throughout the annual cycle.

Annual variation in predation rates is likely a crucial force shaping trends in sea duck breeding productivity (Mallory 2015), though this dynamic remains understudied in focal species populations. Decreased primary prey abundance across landscapes frequently increases predation pressure from generalist predators such as foxes (genus *Vulpes*), pine martens (*Martes americana*), or common ravens (*Corvus corax*) on alternative prey populations (Angelstam et al. 1984) including nesting waterfowl (Bêty et al. 2001, Iles et al. 2013, Specht and Arnold 2018). In boreal forest and tundra landscapes, lemmings and voles (subfamily *Arvicolinae*) constitute the bulk of primary prey for mammalian and avian predators. Lemming and vole populations undergo multi-annual cycles that typically result in years with substantial collapses or booms in abundance during spring and summer (Fauteux et al. 2015, Poysa et al. 2016). Notably, great gray owls (*Strix nebulosa*) irruptively migrate from their typical wintering range to lower latitudes in search of prey in winters following rodent abundance collapse in the Canadian boreal forest (Cheveau et al. 2004). Conversely, boom population years for lemmings in the Canadian arctic lead to pulsed snowy owl

(*Bubo scandiacus*) breeding productivity, resulting in irruptive migrations of first-year snowy owls to lower latitudes during the following winter (Robillard et al. 2016). These irruptive migrations serve as a useful index for small mammal population cycles in northern latitudes (Cheveau et al. 2004, McCabe et al. 2022). Winter snowpack in boreal and tundra habitats may also play a critical role in mediating sea duck predation risk during the breeding season. Lemmings and voles use the subnivean environment throughout winter as thermal cover and to reduce exposure to predators; years of reduced snow cover greatly increase predation risk and can drive changes in small mammal densities (Hansson and Henttonen 1985, Fauteux et al. 2015). Consequently, the use of winter snowpack and irruptive owl migrations as indicators of small mammal abundance in sea duck breeding habitats provides an opportunity to examine how predator-prey dynamics in breeding areas may influence sea duck recruitment.

Here, I investigated potential environmental controls on focal species annual recruitment rates by testing associations between harvest survey juvenile proportions and several indicators of ecological conditions from across the annual cycle. I hypothesized broad-scale climate patterns in eastern North America would influence focal species recruitment across multiple seasons due to their influence on migratory movements (Zipkin et al. 2010) and female body condition prior to the breeding season (Lehikoinen et al. 2006). I predicted recruitment would be positively associated with temperatures at migratory staging and breeding areas because increased ice coverage constraints vital rates associated with fecundity in spring, whereas greater autumn ice coverage negatively impacts juvenile survival. I also predicted positive relationships between recruitment and seasonal precipitation in breeding areas, given each reduce predation pressure on sea ducks during nesting and brood rearing. Conversely, I predicted recruitment would be negatively associated with the frequency of precipitation events in breeding areas due to adverse effects of rain events on brood survival. Finally, I predicted associations between recruitment and owl irruptions during subsequent winters in accordance with the cyclic dynamics of small mammal populations in boreal forest and tundra habitats.

Methods

Recruitment Estimates

I obtained U.S. Fish and Wildlife Service (USFWS) Parts collection survey (PCS) records of all four focal species in the Atlantic Flyway (eastern populations) from 1980-2017. The PCS collects wings of hunter-harvested birds from a random subset of migratory game bird hunters across the U.S. each year (Raftovich 2022). Waterfowl biologists thereafter classify each wing to species, sex- and age-cohort. Most juvenile sea duck wings in the sample were not assigned a sex; I included all juveniles and assumed juvenile sex ratios to be 1:1 (Wood et al. 2021). I excluded adult male wings to eliminate biases associated with adult male harvest vulnerability and reporting rates. For each year y and species s, I calculated annual recruitment R as the proportion of juvenile-aged wings in the summed sample of juvenile and adult female wings (Figure 1):

$$R = \text{Juveniles} / (\text{Juveniles} + \text{Adult Females}) \qquad \text{Equation 1.}$$

In Chapter 1, years with small PCS sample sizes ($n < 22$) produced juvenile proportion estimates that deviated from photo survey estimates and likely misrepresent trends in sea duck population demography. The PCS also uses $n = 20$ as a sample size threshold for age ratio estimates (Raftovich et al. 2022). Thus, I excluded years where PCS sample sizes were $n < 20$ from the analysis.

Ecological Covariates

I selected biotic and abiotic factors (Table 1) based on assumptions that variability in broad-scale climate patterns, weather conditions in breeding areas during and prior to the breeding season, and predation pressure (Mallory 2015) drive focal species annual recruitment.

I used North Atlantic Oscillation index (NAO) to characterize broad-scale climatic conditions across sea duck wintering and migratory areas in the Atlantic Coast region (Hurrell 2023). To investigate relationships between NAO and R, I selected two distinct time periods of the annual cycle prior to the breeding season to derive mean NAO values from for my analysis: Winter NAO (1 November of $y – 1$ through 31 March of y) and Spring NAO (1 April through 30 June of y). I also calculated Autumn NAO (1 September through 30 November of y) to examine potential relationships between autumn climatic conditions and differential migration or survival among age-cohorts. I obtained station-based monthly NAO values (Hurrell 2023) from 1980-2017 and calculated mean values for each time period and year.

Previous research links seasonal NAO to various components of sea duck ecology, including abundance, distribution, body condition, and breeding propensity (Lehikoinen et al. 2006, Zipkin et al. 2010). Relationships between juvenile proportions and NAO are likely complex and vary among species and time of year. Therefore, I hypothesized *R* would be associated with each iteration of NAO, though I did not specify the direction of the relationship.

To assess the effect of ice cover at key migratory staging areas on *R*, I used mean spring (1 January through 31 March) and autumn (1 September through 30 November) temperature anomalies (positive or negative deviations from mean value, ºC) as indices of seasonal ice conditions (Dufour et al. 2010). James Bay and the St. Lawrence estuary serve as staging areas for all four focal species (Lamb et al. 2019); I obtained daily temperature values from weather stations at each staging area (Figure 2) from Environment and Climate Change Canada (2022, accessed 10 March 2023) and calculated mean temperature anomaly values (positive or negative) for each season and year. Though all four species use each site, for analyses I assigned seasonal values from one specific site to each species according to which sites were identified as most important to each specific population (i.e. James Bay spring values, St. Lawrence Estuary autumn values for BLSC) by Lamb et al. (2019).

Ice cover at staging areas can act as a constraint to resource availability for migratory birds, which can influence migration chronology, survival, and female body condition prior to the breeding season (Meattey et al. 2018, Lamb et al. 2021). Therefore, I hypothesized *R* would be positively associated with spring and autumn migratory staging area temperature anomalies.

I characterized habitat and climate conditions across sea duck breeding ranges using a series of climate covariates. I first defined breeding ranges for each species by using species-specific modeled suitable breeding habitat values at 100 km^2 scale calculated by Lamb et al. (2020). I selected all polygons with at least a 75% suitable breeding habitat score to represent each species' breeding range (Figure 3). Thereafter, I used delineated breeding ranges as aggregating units for gridded climate observations to calculate mean range-wide values. I obtained 10 km^2 gridded daily precipitation (mm), minimum and maximum temperature (ºC) observations from 1980-2017 from the NRCan ANUSPLIN dataset (version 2, accessed April 10 2023) to calculate all climate values for each year.

I selected a series of broad-scale breeding season climate factors that may influence sea duck annual productivity to include in my analysis based on findings from previous studies of sea ducks and other waterfowl (Mallory 2015). To represent seasonal snowpack and rainfall, I calculated mean total winter (1 October of y - 1 through 31 March of y) and spring (1 April through 31 May of y) precipitation (mm). I used mean nesting period (1 May through 30 June of y) temperature (ºC) as an indicator of ice and growing season conditions during nesting. I also calculated the mean number of days during brood-rearing (1 June through 30 July of y) where precipitation exceeded 1 mm to parameterize rain event frequency.

Snowpack and precipitation prior to the breeding season play an important role in dictating water levels in wetland habitats, which in turn shapes waterfowl breeding habitat availability (Gerber et al. 2015). Elevated water levels in wetland environments improve access to nesting and brood-rearing habitats for sea ducks, and decrease competition for breeding sites by dispersing females and broods across the broader landscape (Mallory 2015). Years with greater snowpack also improve winter survival rates of small rodent populations (Fauteux et al. 2015); greater abundance of small rodents during the breeding season may mitigate predation pressure on sea ducks, given their likely role as alternative rather than primary prey for generalist predators (Angelstam et al. 1984). However, precipitation events during nesting and brood-rearing can instigate nest failure and decreased brood survival (Schmidt et al. 2006). Consequently, I hypothesized *R* would be positively associated with both winter and spring total precipitation, and negatively associated with brood-rearing period rain event frequency.

Ice persists on the landscape during years with cooler than average temperatures in the early breeding season. Greater ice cover in breeding areas limits foraging opportunities for prospective breeding females, which in turn reduces female body condition and decreases subsequent breeding productivity (Martin et al. 2009). Ice cover may also stall spring migration and delay nest initiation, leading to reduced nesting success and brood survival. Thus, I hypothesized that *R* would be positively associated with nesting period temperature.

I calculated owl irruption indices for use as indicators of primary prey population trends in sea duck breeding habitats. I selected owl irruptions for each sea duck species in the analysis according to which habitat they most frequently occupy during the breeding season: for boreal-breeding species (black, surf, and white-winged scoters) I used great gray owl irruptions, whereas for tundra-breeding long-tailed ducks I used snowy owl irruptions. I obtained Christmas Bird Count survey data of each owl species from 1980-2017 (hereafter CBC, National Audubon Society 2020) to derive counts for my irruption index. For great gray owls, I represented the eastern Canadian boreal forest population similarly to Cheveau et al. (2004) by using observations from each Atlantic coast state from Maine to Delaware, as well as Vermont, Michigan, and Minnesota, along with the maritime provinces, Manitoba, Ontario, and Quebec. For snowy owls, I used observations from the northern prairies of North America (the Dakotas, Minnesota, Montana, Alberta, Manitoba and Saskatchewan), where irruptions are most frequent and appear to represent snowy owl populations in the long-tailed duck's arctic breeding range (Robillard et al. 2016). Given lemming and vole populations in North America typically follow four-year cycles, I defined owl irruption years as years with top 25 percentile CBC owl counts. I calculated irruption as a binary variable (1 = irruption, 0 = non-irruption). I hypothesized *R* of the three scoter species would be greater in non-irruption years, as great gray owl irruptions indicate rodent population crashes. Alternatively, I hypothesized long-tailed duck *R* would be greater in irruption years given snowy owl irruptions follow pulsed summer prey abundance.

The long-tailed duck's sympatric breeding range with snow geese (*Anser caerulescens*) provides an opportunity to assess if long-tailed duck juvenile proportions correlate with trends in snow goose breeding productivity. To examine relationships between these two species, I obtained annual juvenile proportion estimates of Atlantic Flyway greater snow geese from the Canadian Wildlife Service (Lefebvre et al. 2023), who derive estimates each year from post-breeding photographic surveys conducted on fall staging areas. I anticipated years with favorable breeding habitat conditions for snow geese in the Canadian arctic would also promote long-tailed duck breeding success; therefore I hypothesized long-tailed duck R would be positively associated with snow goose juvenile proportions.

Modeling

To evaluate relationships between sea duck annual juvenile proportions and ecological covariates, I created logit-linear regression models for each sea duck species. I used the following model structure to conduct the analyses:

$$\text{Logit}\,(R_y) = \beta_0 + \beta X_y \qquad \text{Equation 2}$$

Where Logit (R_y) is the logarithm of $R / (1 - R)$ in year y, β_0 is the model intercept, β is a vector of regression coefficients for each ecological covariate, and X_y is a matrix of values of all ecological covariates in year y.

Prior to modeling, I performed z-transformations on all covariates (excluding the binary owl irruptions) to standardize and scale values for comparison of effect sizes. I assessed collinearity among covariates for each species using pair plots and Pearson correlation coefficients (R^2, Appendix covariate pair plots) with Program R (R Core Team 2021). No paired covariates had an $R^2 > 0.7$, therefore I retained all covariates for all species (Dormann et al. 2013).

I used a Bayesian Markov-chain Monte Carlo (MCMC) approach with the rjags package (Plummer 2022) in R. I assigned vague, normally-distributed priors with mean = 0 and standard deviation = 0.25 to all regression coefficients. I implemented each model in rjags with three chains, 20,000 MCMC sampling iterations, and a thinning, adapt, and burn-in rate of 2, 100, and 2000, respectively. Gelman-Rubin statistics confirmed successful convergence in all models ($R < 1.02$, Gelman and Rubin 1992). To assess model fit, I calculated Bayesian *p*-values from Tukey-Freeman posterior predictive checks (Conn et al. 2018) and determined fit was adequate ($p \sim 0.5$). I also calculated model R^2 to summarize how much variation in the data were explained by the models. I evaluated covariate effects by summarizing posterior parameter estimates as 89% credible intervals around median values and calculating probabilities (P) of positive or negative non-zero effects; I considered effects with $P > 0.89$ to be significant (McElreath 2020). I compared the effects of covariates across all focal species by averaging non-zero effect probabilities from each model.

Results

I obtained 8,152 records of juvenile and adult female wings submitted to PCS from 1980-2017, and calculated R for each year (Figure 1). I excluded five, three, and one R_y estimates of white-winged scoters, black scoters, and long-tailed ducks respectively, from the analysis due to insufficient PCS sample sizes (chapter 1). I calculated or obtained values of ecological covariates for all species and years (Table 1).

Regression models with ecological covariates explained 12-42% of variation in focal species annual recruitment rates (Table 2). The white-winged scoter model exhibited greatest goodness-of-fit (0.42), followed by the surf scoter (0.22), long-tailed duck (0.21), and black scoter models (0.12), respectively.

Three of the four species-specific models included predictor variables with significant relationships with recruitment (Table 2, Figures 4-9): long-tailed duck recruitment was positively associated with spring temperature in James Bay (effect probability $P = 0.957$), surf scoter recruitment was negatively associated with great gray owl irruptions ($P = 0.973$), and white-winged scoter recruitment was positively associated with spring NAO ($P = 0.893$), nesting temperature ($P = 0.920$), and autumn temperature in the St. Lawrence Estuary ($P = 0.940$), and negatively associated with autumn NAO ($P = 0.929$). Mean effect probabilities of breeding range nesting temperature ($P = 0.757$) and spring migration stopover temperature ($P = 0.756$) across the four species were greatest relative to other covariates, followed by owl irruptions ($P = 0.751$) and Autumn NAO ($P = 0.748$, Table 2).

Discussion

I found evidence for notable relationships among multiple ecological processes and sea duck annual recruitment rates. Small mammal abundance in breeding habitats appears to act as a key constraint on sea duck breeding productivity; this relationship was especially apparent in surf scoters (Table 2, Figures 4, 9). Lower temperatures and greater sea ice cover during post-breeding associated with positive NAO also appear to shape trends in population demography of the three scoter populations wintering in eastern North America, as indicated by negative associations between recruitment and North Atlantic Oscillation during autumn (Table 2, Figures 4-7). Changes in white-winged scoter breeding productivity over time appear particularly responsive to variable climate patterns and habitat conditions on breeding grounds and spring staging areas relative to the other focal species, as exhibited by significant associations with breeding range temperature and spring NAO.

The strong negative response in surf scoter recruitment to great gray owl irruptions provides support for my hypothesized linkage between small mammal population cycles, surf scoter breeding success, and irruptive winter migrations of great gray owls in the eastern boreal forest of North America via the alternative prey hypothesis (Angelstam et al. 1984). A winter exodus of great gray owls from the Canadian boreal forest indicates a crash in rodent abundance during the prior summer (Cheveau et al. 2004); generalist predators across the landscape respond to this deficit in prey availability by seeking alternative food resources such as avian prey (Angelstam et al. 1984). Nesting female surf scoters and surf scoter broods likely face greatly enhanced predation pressure during depressed phases of rodent population cycles; this phenomena has been observed in common eiders and other breeding waterfowl populations (Bêty et al. 2001, Iles et al. 2013, Specht and Arnold 2018). The relationship with great gray owl irruptions may have been especially apparent in surf scoters due to their preference for taiga breeding habitats (Lamb et al. 2019), wherein they exhibit relatively strong breeding habitat sympatry with great gray owls (Bull and Duncan 2020) and thus may share linkages with consonant rodent and generalist predator populations. Alternatively, surf scoters may select nest sites or engage in brood-rearing behaviors that result in greater exposure to generalist predation relative to other scoters (Robertson 1995, Mallory 2015). Information on scoter breeding ecology remains remarkably scarce and thus limits detailed inference of factors influencing species-specific predation risk.

A negative relationship between autumn NAO and annual recruitment was detected in all three scoter species, including a significant association in white-winged scoter recruitment. Patterns in sea duck wintering distribution and breeding success have been linked to seasonal variation in NAO by previous studies (Lehikoinen et al. 2006, Zipkin et al. 2010), though a post-breeding demographic relationship with NAO is a novel finding in sea ducks. Given that autumn NAO represented climate conditions after sea duck breeding activity ceased, this pattern must be explained by an interaction between NAO and post-breeding survival rates and/or age-cohort-specific migration patterns. Positive NAO is characterized by lower temperatures and greater sea ice cover in northeastern North America, notably in key sea duck breeding, molting, and migratory staging areas but not on coastal wintering sites (Hurrell 2023). This potentially elicits a negative response in sea duck recruitment by limiting access to molt and autumn migratory stopover sites earlier in the season, forcing immature birds to undertake migratory movements with insufficient endogenous reserves and therefore experience much greater mortality rates during migration relative to adults (Hill et al. 2003). The significant positive association between white-winged scoter recruitment and autumn migratory stopover site temperature provides additional supporting evidence for this dynamic. Another potential explanation for decreased recruitment in years with greater autumn NAO may be adult birds typically opt to winter at relatively northern latitudes to remain close to breeding sites may be forced to migrate further south than usual. Great numbers of sea ducks often remain in the St. Lawrence Estuary or Hudson Bay late into autumn, whereas others still stay all winter by seeking out polynyas in sea ice (Mallory et al. 2019). An influx of adult birds to the Atlantic coast region may increase adult representation in PCS, subsequently indicating an apparent decrease in recruitment. Further investigation into factors driving sea duck migratory patterns and post-breeding survival rates is necessary to fully evaluate this demographic response to NAO. Nonetheless, these findings underscore the importance of considering the impacts of broad-scale climate processes on post-breeding sea duck populations.

White-winged scoter breeding productivity demonstrated especially strong associations with breeding range climate. Temperature during nest initiation and incubation appears to act an important constraint on white-winged scoter productivity; greater temperatures likely contributed to greater nest success by allowing earlier nest initiation and increasing foraging opportunities for incubating females (Martin et al. 2009, Mallory 2015). White-winged scoter recruitment also showed a significant positive relationship with the spring NAO index; though positive NAO phases instigate colder and more severe weather conditions in white-winged scoter breeding areas, they favor milder weather conditions along the Atlantic coast and in the Great Lakes (Hurrell 2023), and each constitute the eastern white-winged scoter's wintering range. Warmer temperatures and fewer storms during spring are favorable for prospective breeding females because females incur fewer energetic losses during migration and prior to nesting, which promotes subsequent breeding success (Lehikoinen et al. 2006, Rönkä et al. 2011). Traylor et al. (2004) postulated availability of food resources in breeding habitats was a major determinant for white-winged scoter nest survival; conclusive evidence of cross-seasonal effects on subsequent breeding productivity was further demonstrated by Gurney et al. (2014). This reliance on exogenous resources may be especially pronounced in white-winged scoters relative to other sea ducks given their long-distance spring migration (Meatty et al. 2019), which may limit their ability to store endogenous reserves for breeding and thereby decrease breeding propensity, clutch size, and nest attendance (Martin et al. 2009, Mallory 2015). Consequently, milder spring weather conditions and enhanced access to breeding habitats are likely crucial for increased white-winged scoter breeding productivity.

I detected significant positive associations in long-tailed duck recruitment with both James Bay spring temperature and greater snow goose juvenile proportions. Boyd (1996) discovered similar associations between temperature and long-tailed duck breeding productivity, wherein cold winter temperatures in the Canadian arctic resulted in fewer juveniles in the subsequent autumn harvest on the Great Lakes. Cold temperatures and greater snowpack also act as a primary limitation on snow goose breeding productivity (Alisauskas 2002, Reed et al. 2004); this indicates that habitat conditions prior to nesting in tundra habitats similarly influence both long-tailed ducks and snow geese. Interannual variation in recruitment rates was lowest in long-tailed ducks, indicating that vital rates associated with breeding productivity may remain relatively stable over time. Long-tailed duck nest success is great (Alison 1975), likely due to low densities of generalist predators in their tundra breeding habitat, whereas scoters in the boreal forest may experience greater predation pressure (Traylor et al. 2004). Female long-tailed ducks also use a unique nest strategy wherein they continually forage upon exogenous food resources throughout nest incubation to maintain body mass, whereas other sea duck species rely upon endogenous reserves (Kellett et al. 2005). Nest initiation dates are also typically much later than in sympatric species (Alison 1975). However, long-tailed duck breeding productivity still appears to be constrained by early-season habitat conditions given the strong associations I detected in my analysis.

The coarse spatial resolution of the population demography and ecological data used in this study limits detailed inference of relationships between sea duck recruitment and ecological factors. Because I was only able to derive a single population-level estimate of annual recruitment, I had to characterize environmental conditions across massive spatial extents using single parameter values. Variability in ecological processes and habitat conditions among regions and sites is potentially great, and may indeed influence patterns in breeding productivity over time at the population level (Specht and Arnold 2018). Furthermore, interactions between ecological factors may elicit variable responses in recruitment rates (Iles et al. 2013); I limited my investigation to simply the additive effects of each covariate to capture a broader suite of potential relationships. I was also unable to account for any potential effects of density-dependency on sea duck recruitment due to the paucity of sufficient sea duck population estimates. Density-dependent processes play a fundamental role in shaping wildlife population dynamics and frequently dictate trends in the reproductive output of waterfowl populations (Nichols et al. 2007, Ross et al. 2015, Specht and Arnold 2018). Sea duck populations in North America are frequently assumed to experience slight or no density-dependent mediation of breeding productivity given historic declines in abundance, persistent harvest rates, and low density in breeding areas (Flint 2015). However, few historic and contemporary estimates of abundance along with poor insight into sea duck breeding ecology continues to hinder investigation on this relationship. Approaches that generate spatially-explicit estimates of sea duck recruitment or produce population-wide abundance estimates may reveal important factors that drive variation in annual recruitment and merit further attention (Mallory 2015, Koneff et al. 2017).

Climate change is expected to instigate dramatic alterations in high-latitude ecosystems due to shifts in seasonal phenology, annual precipitation rates, and the frequency and intensity of severe weather events (DesGranges and LeBlanc 2012). Given my findings, we should expect sea duck recruitment trends to demonstrate significant responses to emerging ecosystem disturbances. Reduced snow coverage throughout the winter due to milder temperatures or decreased precipitation could create more favorable breeding conditions, especially for long-tailed ducks; however, this would likely negatively impact small mammal abundance (Hansson and Henttonen 1985) and thereby increase sea duck nest predation rates. Earlier ice breakup at breeding and staging areas associated with warmer winters or mild spring temperatures as well as later autumn ice-up (Dufour et al. 2010) may also induce greater sea duck recruitment because pre-breeding females and recently fledged juveniles would benefit from enhanced access to food resources and reduced energetic demands (Hill et al. 2003, Lehikoinen et al. 2006, Martin et al. 2009, Gurney et al. 2014). However, more extreme oscillations in weather conditions associated with climate change will likely create more disjunct seasonal phenology among years, which may incur additional costs to breeding females and immature birds and thereby influence recruitment rates. Additionally, future disturbances in oceanic regime shifts will drive rapid changes in marine ecosystem structure and likely greatly influence sea duck populations (Flint 2013). Nonetheless, predictions of responses in sea duck recruitment rates to climate change require more comprehensive insights of relationships with environmental conditions from across the annual cycle; future research efforts should explore the effects of ecological factors on specific population vital rates with fine-scale resolution to identify which environmental stressors are most limiting to sea duck populations.

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Tables

Table 1. Descriptive statistics and hypotheses of ecological covariates incorporated into regression models in long-tailed ducks (LTDU) and black (BLSC), surf (SUSC), and white-winged scoter (WWSC) annual recruitment from 1980-2017.

Covariate	Unit	Species	Mean	Min	Max	Std. Dev.	Irruption Years	Hypothesized Relationship
Winter NAO	NAO Index	All	-0.242	-1.864	0.753	0.559	N/A	Unknown
Spring NAO	NAO Index	All	-0.080	-1.573	1.563	0.603	N/A	Unknown
Autumn NAO	NAO Index	All	0.365	-1.185	1.419	0.612	N/A	Unknown
James Bay Autumn Temperature Anomaly	°C	LTDU	-0.011	-0.480	0.902	0.298	N/A	Positive
James Bay Spring Temperature Anomaly	°C	BLSC, LTDU	-0.031	-0.551	0.249	0.177	N/A	Positive
St. Lawerence Estuary Autumn Temperature Anomaly	°C	All scoters	0.016	-0.348	0.371	0.151	N/A	Positive
St. Lawerence Estuary Spring Temperature Anomaly	°C	SUSC, WWSC	-0.003	-0.557	0.547	0.272	N/A	Positive
BLSC Breeding Range Nesting Temperature	°C	BLSC	3.453	-0.270	6.270	1.562	N/A	Positive
BLSC Breeding Range Spring Precipitation	mm	BLSC	15.649	6.321	22.070	3.800	N/A	Positive

Covariate	Unit	Species	Mean	Min	Max	Std. Dev.	Irruption Years	Hypothesized Relationship
BLSC Breeding Range Wet Days	Number of Days	BLSC	8.383	5.438	10.950	1.456	N/A	Negative
BLSC Breeding Range Winter Precipitation	Millimeters	BLSC	19.969	9.445	26.692	3.844	N/A	Positive
LTDU Breeding Range Nesting Temperature	ºC	LTDU	0.007	-3.160	2.705	1.582	N/A	Positive
LTDU Breeding Range Spring Precipitation	mm	LTDU	10.212	4.158	18.084	2.900	N/A	Positive
LTDU Breeding Range Wet Days	Number of Days	LTDU	5.590	2.567	8.844	1.412	N/A	Negative
LTDU Breeding Range Winter Precipitation	mm	LTDU	12.377	5.962	18.081	2.493	N/A	Positive
SUSC Breeding Range Nesting Temperature	ºC	SUSC	6.391	3.720	9.250	1.457	N/A	Positive
SUSC Breeding Range Spring Precipitation	mm	SUSC	38.013	25.062	59.744	7.720	N/A	Positive
SUSC Breeding Range Wet Days	Number of Days	SUSC	13.659	6.543	16.743	1.985	N/A	Negative
SUSC Breeding Range Winter Precipitation	mm	SUSC	42.517	30.051	60.395	7.321	N/A	Positive
WWSC Breeding Range Nesting Temperature	ºC	WWSC	6.692	14.919	8.357	16.815	N/A	Positive
WWSC Breeding Range Spring Precipitation	mm	WWSC	2.395	6.066	5.006	10.286	N/A	Positive

Covariate	Unit	Species	Mean	Min	Max	Std. Dev.	Irruption Years	Hypothesized Relationship
WWSC Breeding Range Wet Days	Number of Days	WWSC	9.120	24.688	11.635	24.785	N/A	Negative
WWSC Breeding Range Winter Precipitation	mm	WWSC	1.483	4.889	1.607	3.661	N/A	Positive
GGOW Irruptions	Binary Index	All scoters	N/A	N/A	N/A	N/A	5	Negative
SNOW Irruptions	Binary Index	LTDU	N/A	N/A	N/A	N/A	10	Positive
SNGO Juvenile Proportions	Proportion	LTDU	0.234	0.020	0.480	0.115	N/A	Positive

Table 2: Species-specific effect probabilities (P) where estimates are >0 (for positive estimates) or <0 (for negative estimates) and model goodness-of-fit (R^2) for ecological covariates incorporated into regression models predicting long-tailed duck and black, white-winged, and surf scoter annual recruitment from 1980-2017. Bolded values indicate significant associations.

	Species				
Covariate	Black scoter	Long-tailed duck	Surf scoter	White-winged scoter	Mean P
Winter NAO	P(>0) = 0.592	P(>0) = 0.523	P(>0) = 0.793	P(>0) = 0.628	0.634
Spring NAO	P(>0) = 0.684	P(>0) = 0.637	P(>0) = 0.750	**P(>0) = 0.893**	0.741
Autumn NAO	P(<0) = 0.786	P(>0) = 0.618	P(>0) = 0.659	**P(>0) = 0.929**	0.748
St. Lawrence Estuary Spring Temperature	N/A	N/A	P(>0) = 0.563	P(>0) = 0.748	0.756
James Bay Spring Temperature	P(>0) = 0.756	**P(>0) = 0.957**	N/A	N/A	
St. Lawrence Estuary Autumn Temperature	P(<0) = 0.767	N/A	P(>0) = 0.588	**P(>0) = 0.940**	0.733
James Bay Autumn Temperature	N/A	P(>0) = 0.638	N/A	N/A	
GGOW Irruptions	P(<0) = 0.586	N/A	**P(>0) = 0.973**	P(>0) = 0.706	0.751
SNOW Irruptions	N/A	P(>0) = 0.739	N/A	N/A	
Breeding Range Winter Precipitation	P(<0) = 0.569	P(>0) = 0.851	P(>0) = 0.740	P(>0) = 0.513	0.668
Breeding Range Spring Precipitation	P(>0) = 0.624	P(>0) = 0.512	P(>0) = 0.732	P(>0) = 0.534	0.601

	Species				
Covariate	Black scoter	Long-tailed duck	Surf scoter	White-winged scoter	Mean *P*
Breeding Range Nesting Temperature	*P*(>0) = 0.532	*P*(>0) = 0.861	*P*(>0) = 0.713	***P*(>0) = 0.920**	0.757
Breeding Range Wet Days	*P*(<0) = 0.651	*P*(>0) = 0.558	*P*(<0) = 0.558	*P*(>0) = 0.790	0.639
SNGO Juvenile Proportion	N/A	***P*(>0) = 0.890**	N/A	N/A	N/A
Model R^2	0.122	0.207	0.220	0.422	

Figures

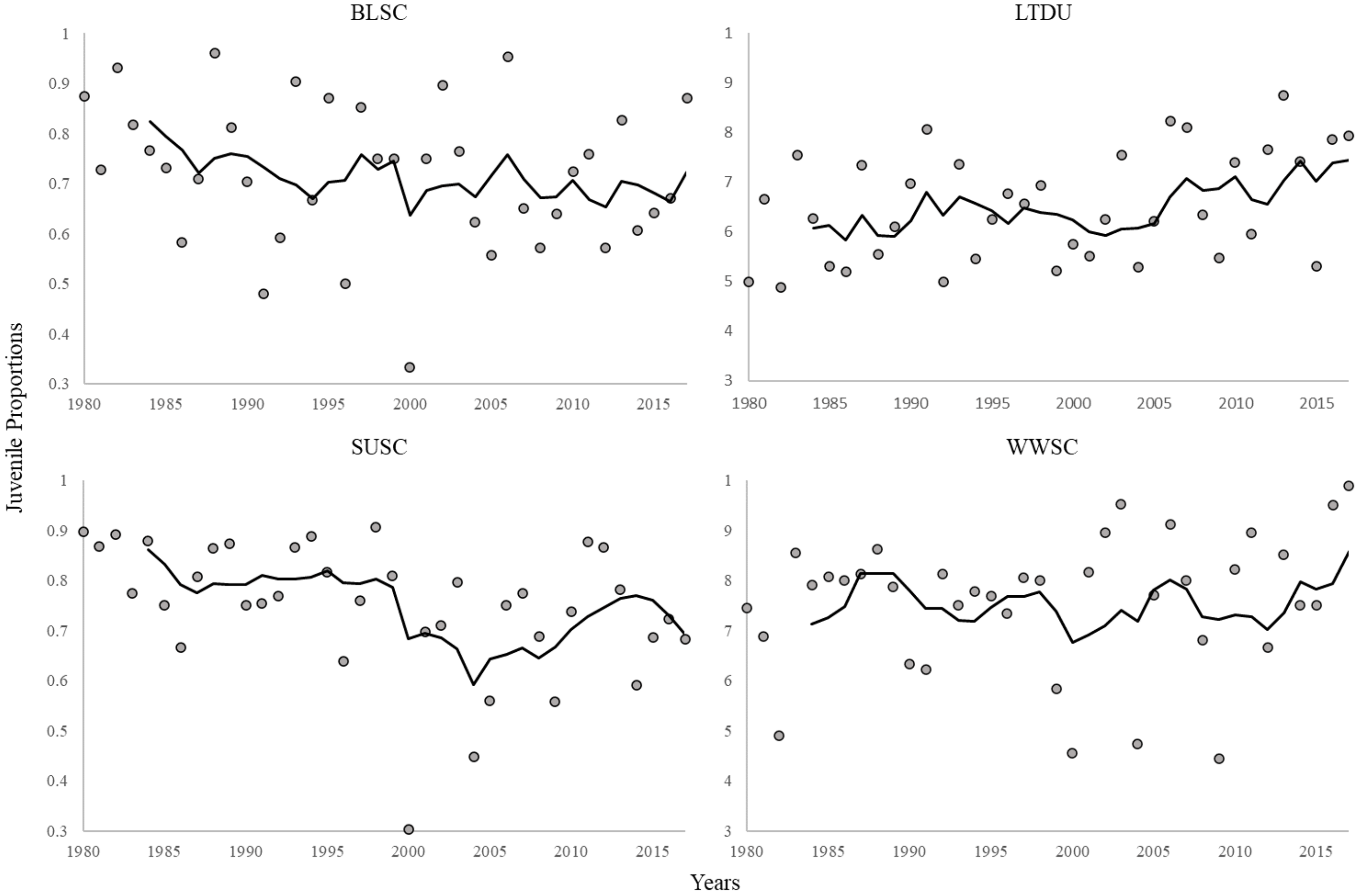

Figure 1: Parts collection survey (PCS) juvenile proportions (proportion of juvenile and adult female wings that are juveniles) of long-tailed ducks (LTDU) and black (BLSC), surf (SUSC), and white-winged scoter (WWSC) populations in the Atlantic Flyway from 1980-2017. Dots represent annual proportion estimates, black line represents five-year moving average.

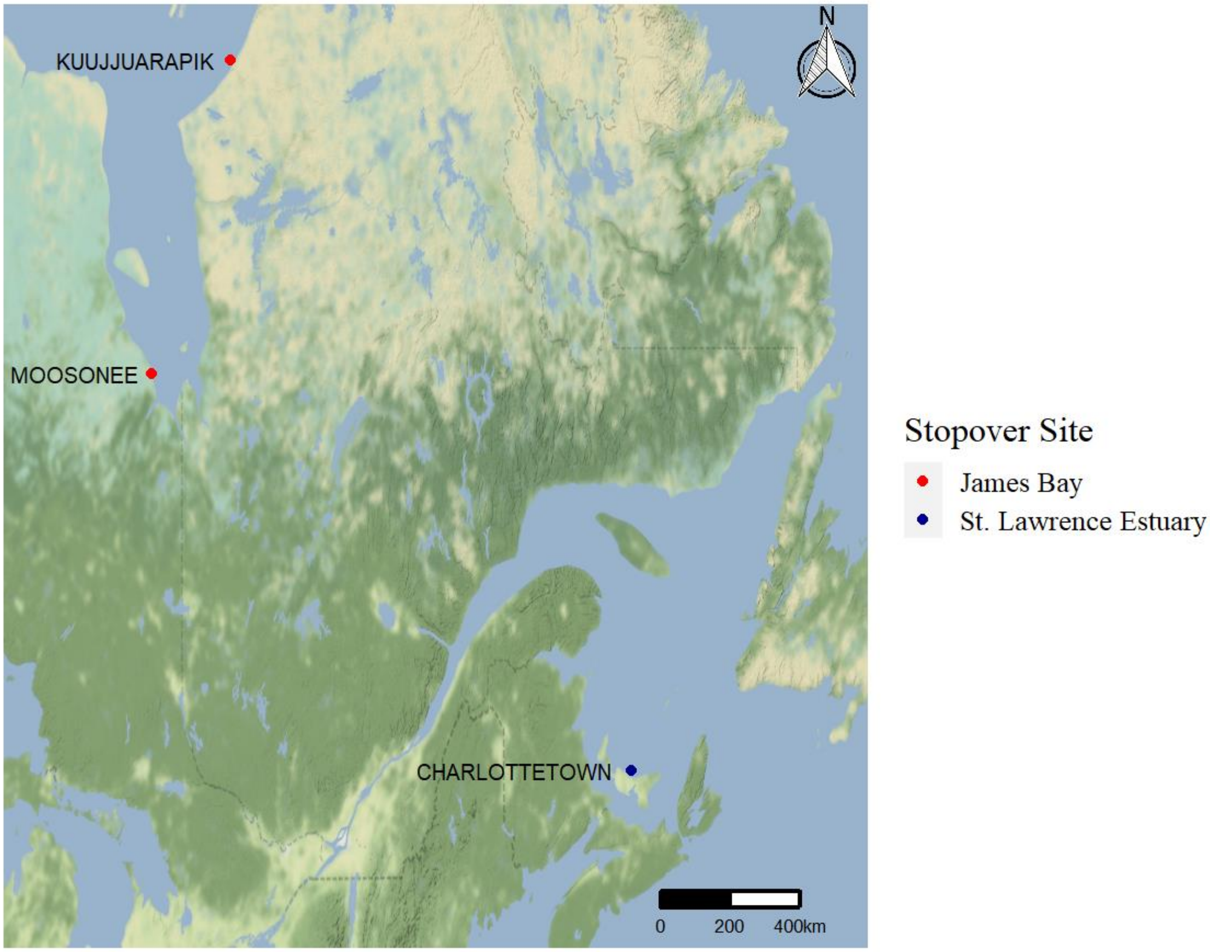

Figure 2: Names and locations of weather stations used to calculate spring and autumn temperature anomalies at sea duck migratory stopover sites.

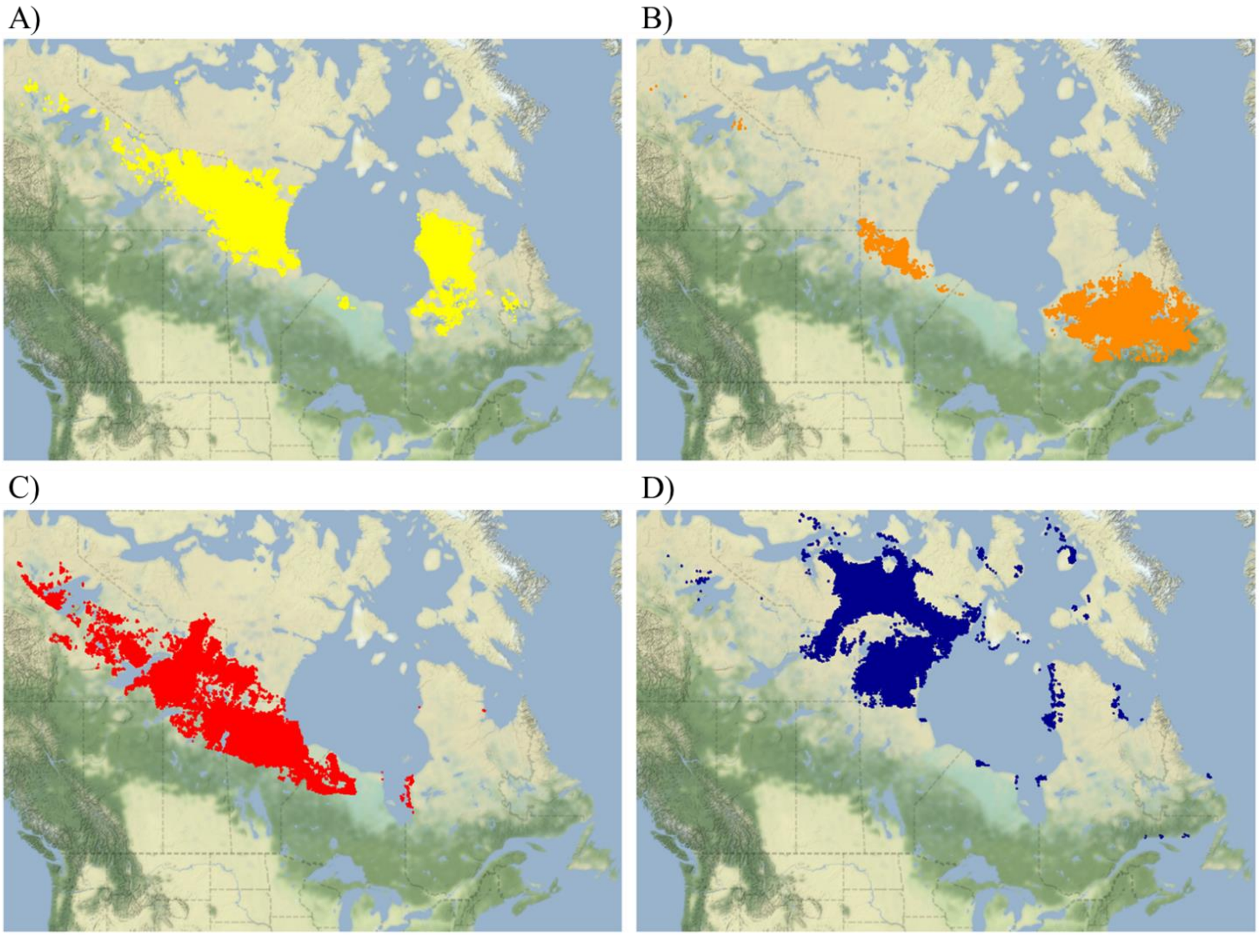

Figure 3: Breeding ranges of four sea duck species (eastern North American populations) used as aggregating units for gridded climate observations. Species-specific ranges were calculated using polygons with at least 75% suitable breeding habitat as delineated by Lamb et al. (2020). Maps show breeding ranges of (A) black scoters, (B) surf scoters, (C) white-winged scoters and (D) long-tailed ducks.

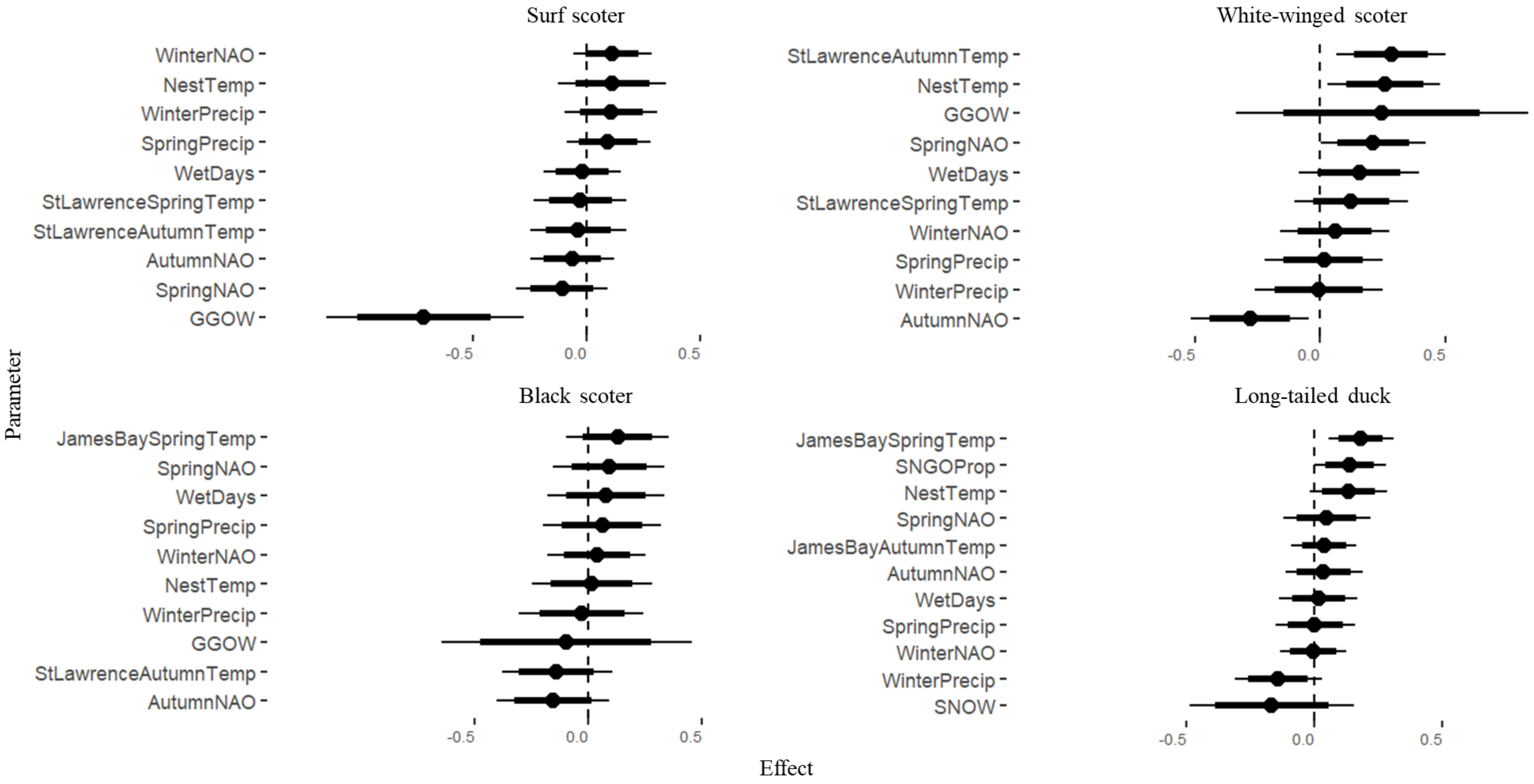

Figure 4: Posterior distributions (MCMC) of regression coefficients of environmental covariates linear regression models used to predict annual recruitment in four sea duck populations. Thick lines represent 80% credible intervals, thin lines represent 89% credible intervals, points represent mean values, and the dotted vertical lines delineate zero slope.

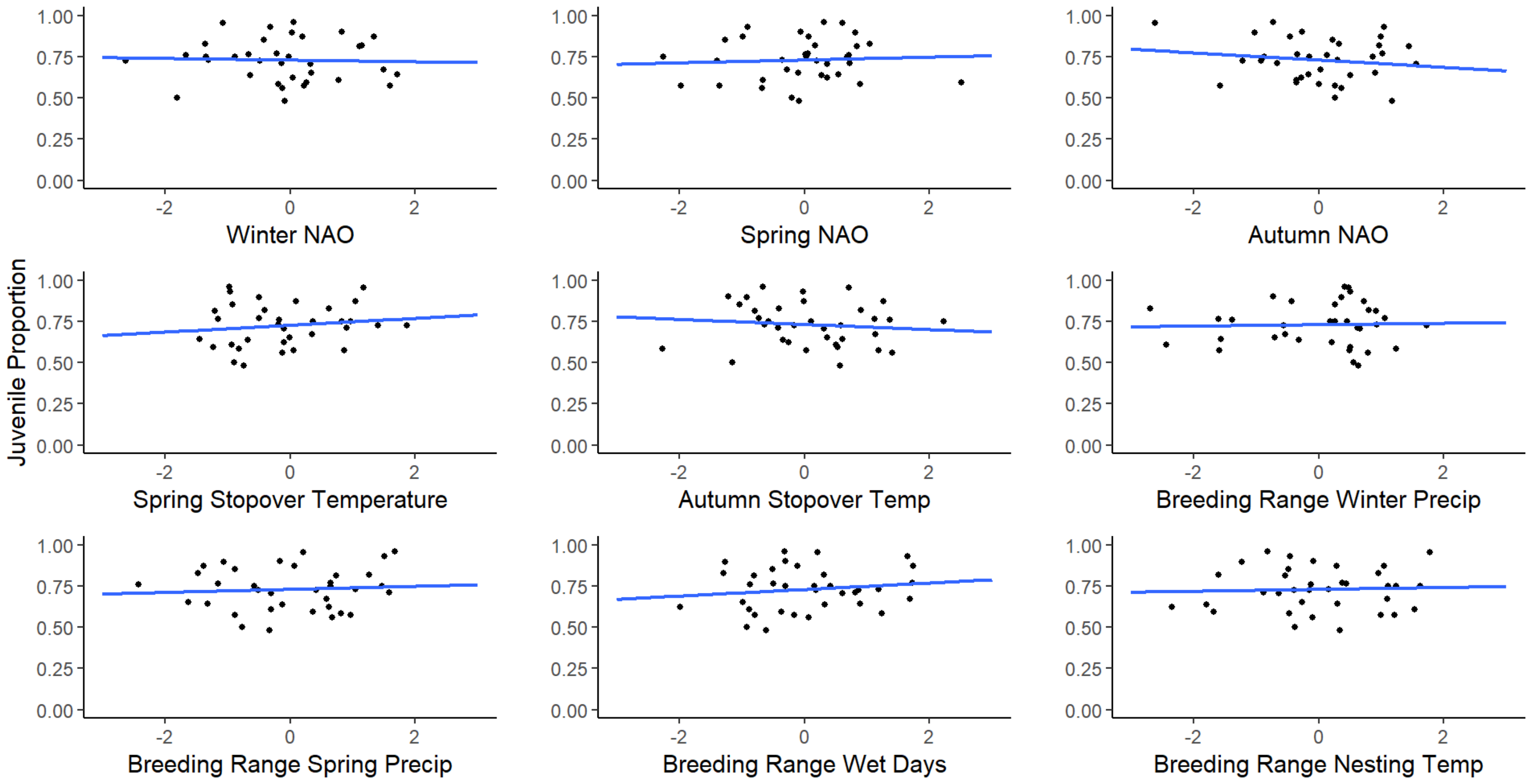

Figure 5: Associations between parts collection survey black scoter juvenile proportions from the Atlantic Flyway 1980-2017 and several environmental covariates with linear trendlines. All covariates were z-transformed to standardize for linear regression analysis.

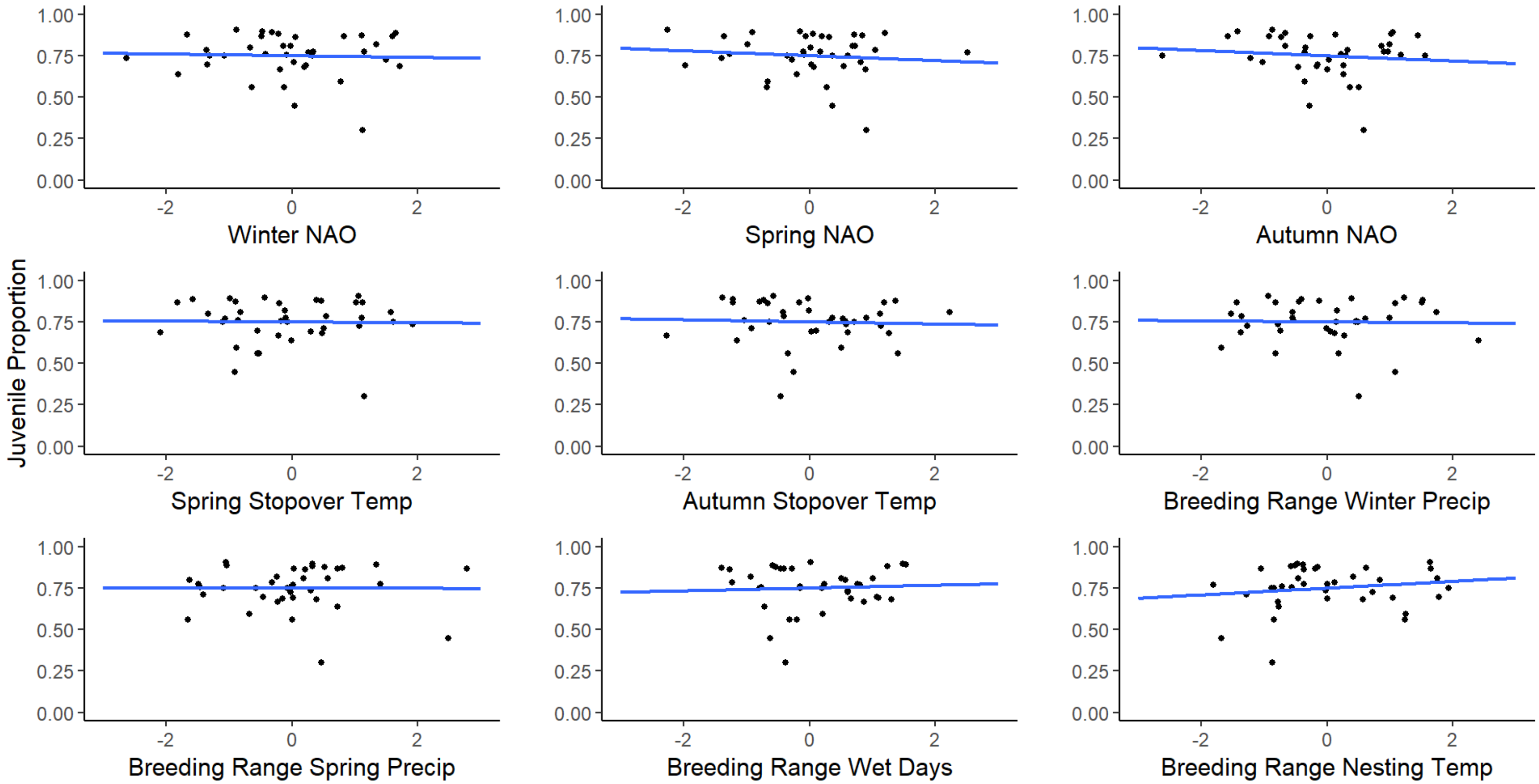

Figure 6: Associations between parts collection survey surf scoter juvenile proportions from the Atlantic Flyway 1980-2017 and several environmental covariates with linear trendlines. All covariates were z-transformed to standardize for linear regression analysis.

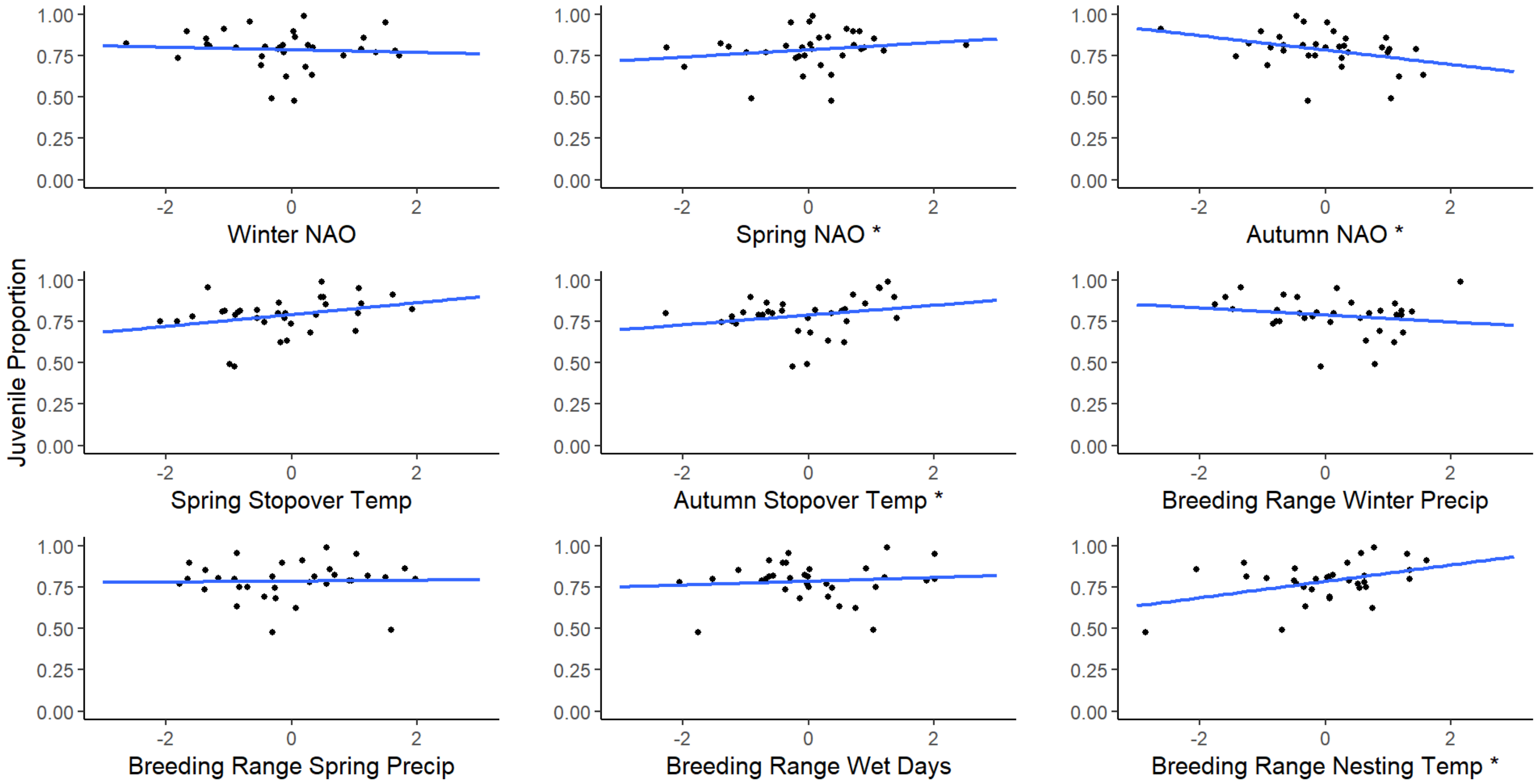

Figure 7: Associations between parts collection survey white-winged scoter juvenile proportions from the Atlantic Flyway 1980-2017 and several environmental covariates with linear trendlines. All covariates were z-transformed to standardize for linear regression analysis. Asterisks (*) denote significant associations.

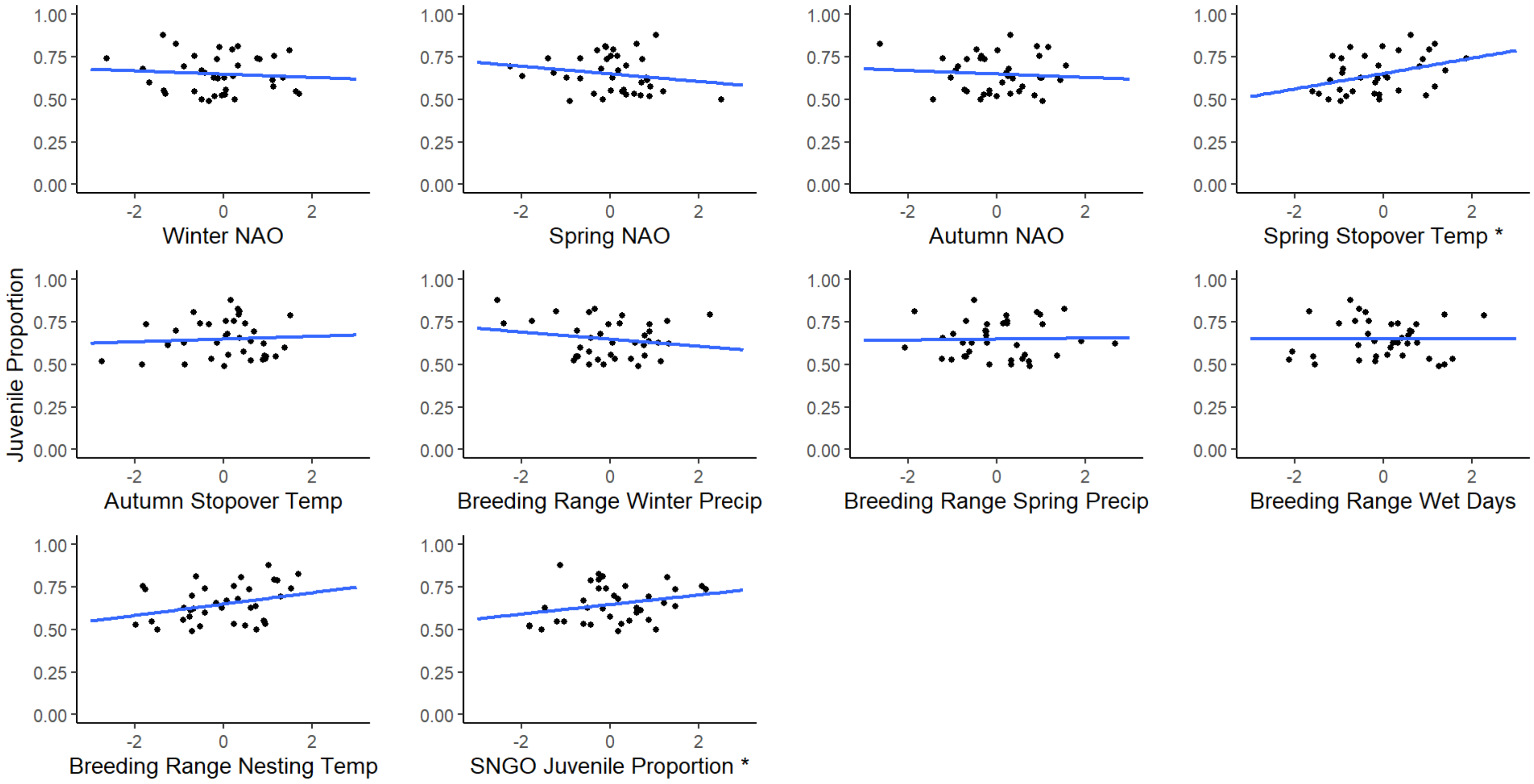

Figure 8: Associations between parts collection survey long-tailed duck juvenile proportions from the Atlantic Flyway 1980-2017 and several environmental covariates with linear trendlines. All covariates were z-transformed to standardize for linear regression analysis. Asterisks (*) denote significant associations.

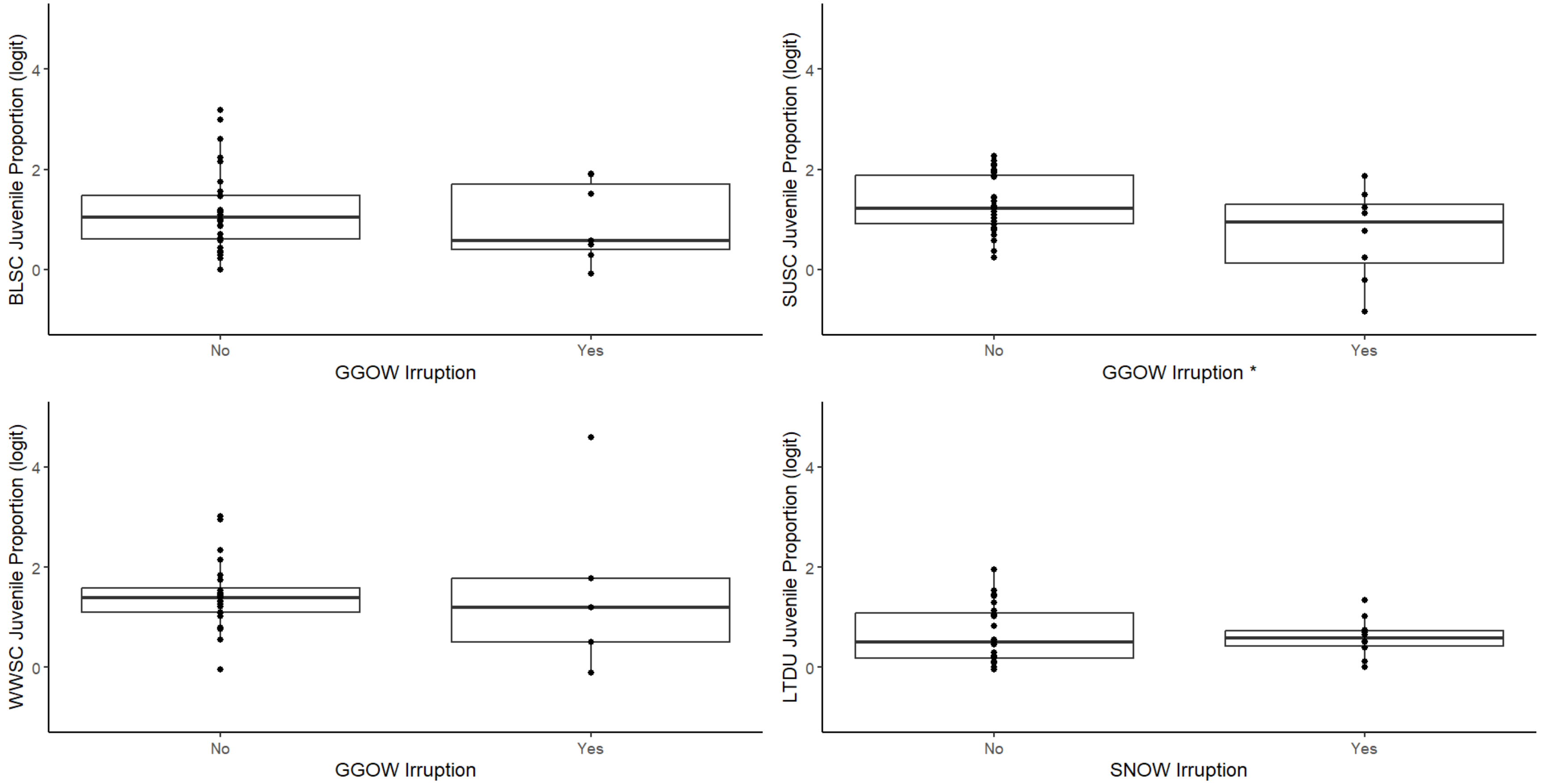

Figure 9: Associations between parts collection survey juvenile proportions of long-tailed ducks (LTDU) and black (BLSC), surf (SUSC), and white-winged scoter (WWSC) populationsin the Atlantic Flyway and winter owl irruptions (GGOW = great gray owls, SNOW = snowy owls) in eastern North America. Juvenile proportions are represented on the logit scale (logarithm of $P / (1 - P)$). Asterisks (*) denote significant associations.