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Climate change and coastal wetland salinization: Physiological and ecological consequences for Arctic waterfowl

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Abstract

1. Coastal wetland salinization related to warming climate has the potential to impact ecological systems globally. In Alaska, the Yukon-Kuskokwim Delta (YKD) supports large concentrations of breeding water birds and is an ecologically important area for conservation of migratory bird biodiversity. On the YKD, the majority of waterfowl nest in low elevation coastal tundra where storm surges drive saline water into terrestrial wetland habitats. Because newly hatched water birds lack functional salt glands to process saline water, salinization may negatively impact their growth and survival.
2. We investigated potential demographic impacts of wetland salinization by conducting controlled physiological experiments to determine consequences of saline water exposure to spectacled (*Somateria fischeri*) and Steller's eider (*Polysticta stelleri*) ducklings, and analyzed habitat

suitability based on experimentally defined tolerance thresholds and sampled wetland salinity levels.

3. We found physiological and behavioral pathologies in < 1 week old ducklings at exposure levels of 6 parts per thousand (ppt), and found some evidence of reduced growth in ducklings first exposed after 1 week of age. We conclude that the acute toxicity threshold for ducklings < 1 week of age is ≤ 6 ppt.
4. We found that the area of coastal tundra where wetland salinity exceeded 6 ppt varied considerably among years, suggesting that some portion of the breeding range is unsuitable for rearing ducklings in some years. However, we also found that most eiders in most years nested in areas with salinity at or exceeding the tolerance threshold for ducklings, suggesting that nesting eiders do not appear to avoid saline habitats. We suggest that localized fresh water refugia currently may allow resilience to salinization during the critical period.
5. Understanding how species and habitats respond to climate driven changes is essential for predicting future patterns of distribution and abundance, and is necessary for making informed decisions about conservation priorities. Our study provides insights into the extent of wetland salinization in Alaska, mechanism of impact, and current ecological consequences on avian communities depending on these habitats. With ongoing climate change, the probability of species crossing physiological tolerance thresholds of wetland salinity may change in the future.

Keywords: climate change, coastal wetlands, salinity, water birds, duckling survival, spectacled eider, Steller's eider, Alaska

1. Introduction

In the Arctic, the climate is warming at a rate at least twice the global average, with most of the warming documented since 1976 (IPCC 2013, 2021). The warming climate is exerting broad scale

impacts on coastal ecosystems including rise in water temperature and levels, and changes in circulation patterns, storminess, precipitation, winds, and in sea ice (Doney et al. 2012, Vermaire et al. 2013, Terenzi et al. 2014, McCrystall et al. 2021, Irrgang et al. 2022). Salinization of coastal wetlands, due to related climate-mediated factors such as alterations to freshwater input, sea level rise, and storm surges, is occurring at an unprecedented rate and broad geographic scale (Vermaire et al. 2013, Herbert et al. 2015). In the future, these impacts on hydrologic cycles are expected to further increase the extent and severity of wetland salinization, physiological stress in wetland biota, and potential cascading food web effects to higher trophic levels resulting in displacement of species and changes in community composition (Kingsford et al. 2011, Lorenz 2013, Herbert et al. 2015, Haig et al. 2019). Consequences of living in saline environments have been studied in various taxa including birds and amphibians, but relatively little is known about impacts of salinization on water birds relying on wetland ecosystems for breeding (Gomez-Mestre and Tejedo 2003, Gutierrez 2014).

In western Alaska, the Yukon-Kuskokwim Delta (YKD) supports one of the largest concentrations of water birds in the world and is an ecologically important area for conservation of migratory bird biodiversity (Saalfeld et al. 2017). Millions of waterfowl and shorebirds breed on the YKD annually, and the area provides critical breeding habitat for two species of waterfowl threatened with extinction: the spectacled eider (*Somateria fischeri*) and the Steller's eider (*Polysticta stelleri*) (U.S. Fish and Wildlife Service 1993, 1997). Spectacled and Steller's eiders spend most of their annual cycle in marine habitats and move to coastal wetlands in May or June to breed (Petersen et al. 2000, Fredrickson 2001). On the breeding grounds, eiders feed on invertebrates in tundra ponds, and females rear their broods from late June to August on coastal wetlands until ducklings fledge and move to marine habitats. High degree of breeding site fidelity has been found in spectacled eiders nesting on the YKD (Grand and Flint 1998). Because Steller's eider breeding is rare on the YKD, no comparable information is available although Flint and Herzog (1999) did document a single female that returned to breed in multiple years. Further,

analyses by Safine et al. (2020) suggest breeding site fidelity and moderate to high degree of natal philopatry for Steller's eiders near Utqiagvik, Alaska. In the U.S., the spectacled eider was listed as threatened by the U.S. Fish and Wildlife Service (USFWS) due to a greater than 95% decline in the breeding population on the YKD between the 1970s and 1990s, and the area is of critical importance to the recovery of the species. The Steller's eider was listed as threatened by the USFWS due to declines and reduction in nesting range, and the species has now nearly disappeared from the YKD (Flint and Herzog 1999). Spectacled eiders are classified as near threatened and Steller's eiders as vulnerable in the IUCN Red List of Threatened Species (BirdLife International 2022). Understanding habitat conditions and potential factors limiting breeding success is important for conservation of both species.

On the YKD, the majority of water birds nest in low elevation tundra within 20 km of the of Bering Sea coast (Saalfeld et al. 2017). In these low elevation coastal areas, storm surges have been shown to drive saline water into terrestrial wetland habitats, resulting in salinization of coastal ponds (Jorgenson and Ely 2001, Terenzi et al. 2014, Jorgenson et al. 2018). Newly hatched waterfowl do not have functional salt glands and exposure to saline water through drinking or ingestion of water while feeding can have negative consequences for growth and survival (Schmidt-Nielsen and Kim 1964, Schacter et al. 2021). Captive Canada goose (*Branta canadensis*) goslings showed negative effects of salinity on both survival and growth (Stolley et al. 1999), and similar effects on survival and growth have been shown for mallards (*Anas platyrhynchos*), mottled ducks (*A. fulvigula*), American black ducks (*A. rubripes*) and common eiders (*S. mollissima*) (Mitcham and Wobeser 1988, Barnes and Nudds 1991, Moorman et al. 1991, DeVink et al. 2005). Though wetland salinity has been linked to negative consequences for juvenile survival and growth for multiple species, the actual magnitude of the effects, and critical salinity levels, appear to vary among species (Schmidt-Nielsen and Kim 1964, Barnes and Nudds 1991, Stolley et al. 1999, DeVink et al. 2005).

Duckling mortality is an evident demographic consequence of exposure to high levels of salinity, while low growth rates can also lead to demographic consequences. Small waterfowl fledglings had lower first-winter survival and tend to breed less frequently, resulting in potential long-term impacts on population growth (Sedinger et al. 1995). Flint et al. (2006) showed regional variation in survival and growth of spectacled eider ducklings on the YKD and speculated that salinity may have been one proximate cause. In recent years, declines have been observed in the average body weight of 30-day old spectacled eiders on Kigigak Island, one of the primary coastal nesting sites on the YKD (Yukon Delta National Wildlife Refuge, unpublished data), and exposure to increasingly saline water has been suggested as a contributing factor. Thus, under the current conditions, we hypothesized that saline wetlands on brood rearing areas may be having negative consequences at the population level for eiders and other species of water birds on the YKD. However, the threshold and magnitude of such effects have not been quantified for most of the species on the YKD.

Information about tolerance thresholds and demonstrable effects of exposure to salinity in ducklings are needed to understand suitability of brood rearing habitats and demographic consequences of wetland salinity to breeding bird populations. This study focused on understanding consequences of saline water exposure to two species of conservation concern, the spectacled and Steller's eider, in their critical breeding habitat in western Alaska. Prior to this study, no information was available about salinity tolerance and effects of exposure in these two species. Furthermore, eiders can serve as a model for understanding consequences in other waterfowl species. Our overall goal was to apply information about physiological tolerance to salinity as determined in controlled experimental studies to habitat data collected on the coastal breeding areas, thus combining experimentally derived physiological threshold data and ecological data.

Our first objective was to experimentally determine tolerance thresholds for salinity exposure in newly hatched spectacled and Steller's eider ducklings, and characterize effects of salinity exposure on growth and behavior. Thus, we were interested in characterizing the potential direct impact of salinity on ducklings. In a pilot experiment conducted in 2014, we had found preliminary evidence of physiological effects from 6 parts per thousand (ppt, approximating g/kg) salinity water treatment in four Steller's eider ducklings exposed at hatch for a 36 hr period. DeVink et al. (2005) found effects on growth and survival of common eider ducklings exposed to an 11 ppt salinity level, with 17% mortality in the group by 6.5 days post exposure. Based on these findings and observations in 2012-2014 with mean salinity levels of 2.60-10.2 ppt in ponds at four breeding sites on the YKD, we chose exposure concentrations of 3 ppt and 6 ppt to represent conservative yet realistic levels of wetland salinity. Overall, we predicted that the tolerance level in both spectacled and Steller's eider ducklings would be ≤ 6 ppt salinity, and that sub-lethal salinity exposure would lead to reduced growth of ducklings.

Our second objective was to determine the developmental age of salt gland functionality in spectacled and Steller's eider ducklings. In several other waterfowl species, including Canada goose and mountain duck (*Tadorna tadornoides*), salt glands were not found to be fully functional before 6 days of age (Ellis et al. 1963, Riggert 1977, Stolley et al. 1998). Given physiological similarities between these species and eiders, we predicted that eider ducklings would have functional salt glands by 1 week of age.

Our third objective was to determine patterns of wetland salinity in the eider breeding areas on the YKD, and examine temporal and spatial variability in wetland salinity using pond salinity data collected over 15 years from nesting areas on the YKD. Our fourth objective was to assess effects of variation in wetland salinity conditions on eider populations. Due to their rarity on the YKD, we did not include Steller's eiders in the nesting distribution analysis. For spectacled eiders, we identified years and areas where wetland salinity exceeded the experimentally determined physiological tolerance limits of

ducklings, determined what proportion of the eider population nested in areas above the tolerance threshold of ducklings, and examined the relationship between eider density and predicted wetland salinity. Our ultimate goal was to characterize variability in conditions and identify areas of potentially unsuitable brood rearing habitat to help managers understand how current and future habitat conditions based on observed and predicted wetland salinity patterns on the coastal breeding areas impact eider populations.

2. Materials and Methods

2.1 Data collection

2.1.1 Salinity exposure experiments

We conducted exposure experiments at the Alaska SeaLife Center (ASLC) in Seward, Alaska, in 2015-2017 under an Institutional Animal Care and Use Committee permit R15-06-03 and a Federal Fish and Wildlife permit 65912. We labeled and hatched eggs in an incubator and hatcher (Rcom Pro 20 and Rcom Pro 50, Auto Elex Co., Gimhae-si, Korea; Marsh Automatic Incubator Model RX1, Lyon Electric Company, Inc., Chula Vista, CA), and identified individual ducklings with unique color-coded leg bands. We hatched 25 Steller's eider and 27 spectacled eider ducklings, with a successful hatch rate of 96% for both species. Steller's eiders were randomly assigned to Control (n=10), Treatment 1 (3 ppt; n=7), Treatment 2 (6 ppt; n=5), and Treatment 3 (6 ppt delayed; n=3) groups. Spectacled eiders were assigned to Control (n=13), Treatment 2 (6 ppt; n=9), and Treatment 3 (6 ppt delayed; n=5). We did not expose spectacled eider ducklings to 3 ppt salinity to allow for larger sample size in other treatment groups. During 0-14 days of age, we housed ducklings in groups of 2-4 in fiberglass rearing tanks (0.97 x 1.3m) indoors. Each tank was equipped with a dedicated water supply, drain system and heat lamp. One-half of each tank was swimming water adjustable to 0.20m deep, and the other half was haul out space. After 14 days of age, ducklings were moved to outdoor enclosures of 3.0 x 3.7m with a 0.61m deep

swimming pool. We fed all ducklings *ad libitum* with Mazuri© Starter Diet (Purina Mills, Inc., St. Louis, MO) during early rearing, and gradually transitioned them to Mazuri© Sea Duck Diet (Purina Mills, Inc., St. Louis, MO) from approximately 3 weeks of age. Three times a day during the early rearing, we also offered ducklings an equal mass ratio mixture of three invertebrate types; bloodworms (*Chironomus plumosus*), glassworms (*Charborus crystallinus*) and mysis shrimp (*Mysis relicta*) (San Francisco Bay Brand, Inc., Newark, CA). The invertebrate diet mass did not exceed 25% of daily total food offered.

We created and maintained salinity levels in circulating water by mixing freshwater and saltwater sources in a manifold prior to entering the experimental treatment totes, and adjusted flows to maintain the control and treatment levels of 0-1 ppt, 3 ppt, and 6 ppt in both swimming and drinking water. We used an open-water system with water flow rates of up to 15.1 L/min and water recirculation turnover occurring approximately every 31 minutes. We monitored salinity levels at least every 3 to 12 hours using an YSI Pro1030 device (YSI Incorporated, Yellow Springs, OH) to maintain desired concentrations. Measured salinity concentrations for control, 3 ppt treatment, and 6 ppt treatment groups were 0.1 ppt, 2.2-3.4 ppt, and 5.3-6.8 ppt, respectively.

At hatch, we weighed individually marked ducklings and assigned each randomly into treatment groups: Control (0-1 ppt salinity), Treatment 1 (3 ppt salinity from day 0), Treatment 2 (6 ppt salinity from Day 0) and Treatment 3 (6 ppt delayed salinity from Day 8). We weighed ducklings twice daily (09:00 and 21:00) during days 0-14, daily (09:00) during days 15-30, and every 3 days during days 31-45 (Steller's eiders) and 31-60 (spectacled eiders) (Hollmen and Ulman 2020). The monitoring period was longer for spectacled eiders due to their later fledging age (Petersen et al. 2000). We examined bills for nasal salt secretions at each handling event (Fringes and Fringes 1959).

The same experienced observers monitored ducklings for behavioral abnormalities and clinical signs of illness throughout each day of the experiments. We established a set of criteria for decision-making

about removing individuals from saltwater exposure if their body condition or behavior signaled an effect threshold of “non-survivable” without intervention. Based on previous reference data from our pilot experiment and other healthy and compromised ducklings previously raised at the ASLC, we considered a 15% negative deviation from average body weight to represent a threshold when the individual would be assumed not to survive without intervention. If an individual exhibited abnormal behaviors or other signs of illness (including lethargy, abnormal posture, lack of appetite, absence or abnormal fecal droppings, labored breathing, abnormal discharges, and poor waterproofing), we made the removal decision in consultation with attending veterinarian.

Any ducklings removed from the exposure treatments due to behavioral or clinical abnormalities were placed in freshwater and monitored until behaviors returned to normal and body weight recovered to the pre-established baseline. Ducklings were assessed twice a day (9:00 and 21:00 hrs), and considered recovered when behavioral and clinical abnormalities were not observed and body weight was stable or increasing in two consecutive assessments. After recovery, ducklings were returned to their original treatment group and continued to be exposed.

2.1.2 Wetland salinity measurements

We obtained water samples from ponds on the YKD in western Alaska (Fig. 1) during the U.S. Fish and Wildlife Service (USFWS) YKD Nest Plot Surveys (late May – early June; Fischer et al. 2017) from 2006-2011 and 2013-2019, from random and fixed sampling locations (Wilson and Osnas 2023). The random locations (n=95 to 138 per year; USFWSrandom, Table 1) were associated with annually randomized nest plots surveyed each year by ground crews. On each random plot, water samples were collected from 1-4 individual ponds each year during the approximate mid-incubation period of waterfowl nesting on the YKD. In addition to the random samples, we annually sampled a series of fixed locations (n=39; USFWSfixed, Table 1), distributed throughout the YKD, with the exception of years where logistical

constraints prevented access to individual sites. Fixed ponds were chosen based primarily on accessibility and associated likelihood of collecting replicate samples over consecutive years. During early breeding season, crews collected water samples from the edge of 1-2 ponds that were >5 m across and > 30 cm deep, and typically selected ponds nearest random plot corners. For each sample, crews collected approximately 110 ml of water in a plastic specimen jar, by scooping just below the water-surface, sealing the jar, and transporting it to the USFWS laboratory in Anchorage, Alaska. Each collection jar was marked with plot number, GPS coordinates (or nearest plot corner if no GPS was available), observer initials, and date of collection. Sample processing occurred in late June-early July of each year (typically, within 3 weeks of collection), at a USFWS laboratory. Salinity readings for each sample were collected using a handheld YSI 30 (2006-2016) and later YSI 63 (2017-2019) salinity meter (YSI Incorporated, Yellow Springs, OH), after calibration and ensuring a cell constant (k) of 5 ± 0.5 .

In addition to the samples associated with the random nest plot project (detailed above), an additional, small series of fixed pond sites were established in the primary eider nesting areas, including Kigigak Island (n=38; Table 1)), and along a gradient on the Kashunuk River (Hock Slough n=15, River Camp n=18 and Old Chevak n=12; Table 1) in 2014. In this series, ponds were initially randomly selected, and then resampled annually thereafter. Sampling occurred in mid-June from 2014–2019 at Kigigak Island and 2014–2015 on the Kashunuk River sites. Additional sampling occurred during late-July in 2014 and late-June and late-July in 2015 at Kashunuk sites, as well as late-June and late-July on Kigigak Island from 2014–2016. At each of these sites, we sampled three locations in a linear arrangement across the pond, including two locations along the shore and one in the middle of pond reaching out to collect sample from an undisturbed area. If a pond was too deep (≥ 1 m) to sample in the middle, we added a third location along the shore. We averaged measurements across sampling locations. A handheld YSI Pro 1030 salinity meter (YSI Incorporated, Yellow Springs, OH) was used to collect the salinity readings (ppt).

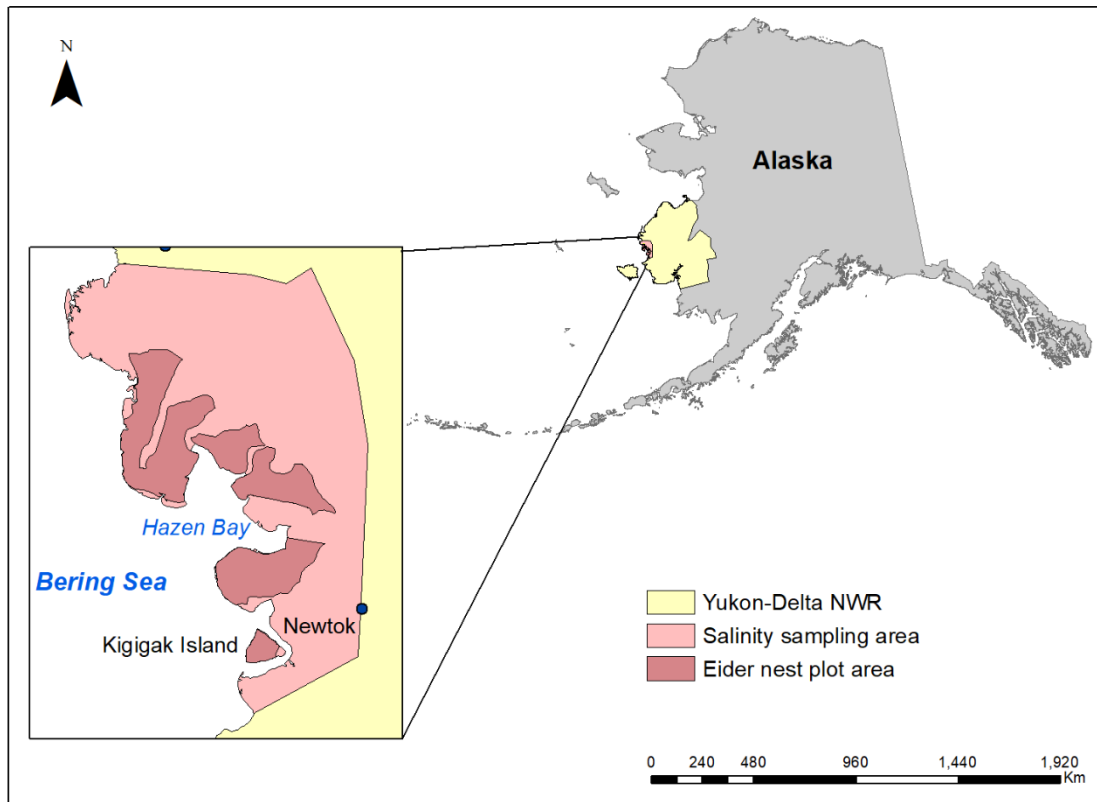


Figure 1. Eider breeding and wetland salinity sampling areas on the Yukon Kuskokwim Delta within the Yukon Delta National Wildlife Refuge (NWR), Alaska.

Dataset	n	Years	Day of year (DOY) range	Salinity (ppt) range
USFWSfixed	209	2006-2019	149-191	0-39
USFWSrandom	1414	2006-2019	129-179	0-46.5
Kashunuk River	226	2014-2015	165-211	0-23.6

Kigigak Island 421 2014-2019 166-208 0-32.6

Table 1. List of sample sizes, years, day of year (DOY) ranges, and range of salinity values (ppt) for variables included in wetland salinity analysis.

2.1.3 Nest plot survey methods

Randomly selected plots were searched for all waterfowl, loon, gull, and crane nests from 1995 to 2019 in late May to early June (Fischer et al. 2017, Fischer et al. 2023). The study area was a 716 km² core nesting area of the spectacled eider in the central coastal area of the YKD (Fig. 1). Plots were 45.0 ha in 1995, 36.0 ha in 1996, and 32.4 ha (402 x 805 m) in size after 1996. Plots were selected by random sampling of point locations and excluding any plot that overlapped a plot from the current or previous 5 years. Approximately 85 plots were selected each year, but the actual number of plots searched varied by year from 50 to 87 due to logistical constraints or unforeseen field contingencies. Plots were usually searched by teams of two field staff (range from 1 to 4 staff), and species, nest status, nest site habitat, GPS location, and clutch size recorded for each nest (Fischer et al. 2017). We summarized the total number of spectacled eider nests (both active and inactive or destroyed) for each plot and assigned the plot center as the location for spatial analysis, described below, to estimate density.

2.2 Data analysis

2.2.1 Salinity exposure

We divided ducklings into groups by species and treatment (control, 3 ppt, 6 ppt, and 6 ppt delayed). We compared the pattern of weights between control birds and those exposed to salinity treatments using a randomization procedure and PopTools program (Manly 2006, Hood 2011). To calculate the initial test statistic, we calculated the average weight at each time step for the treatment and control groups (1/2 day for the first 14 days, then daily). In cases where an individual duckling weight was not

recorded at a given time step, these missed observations were not used in calculation of the average for that specific day and group. We then estimated the difference between treatment and controls at each time step as $(\text{average treatments weight} - \text{average control weight})^2 / \text{overall average weight}$. This functional standardized deviance accounts for the fact that ducklings changed greatly in mass during the course of the study. As such, differences in mass between treatment and controls at each time step are scaled relative to duckling size. We then summed these individual time step standardized deviances for 0 to 60 days. This summed deviance was designed to describe the total area between the two growth curves (control and treatment). We then used a randomization procedure to determine the probability that these summed deviances (i.e., differences) between treatment and controls occurred by chance (Manly 2006) (See Appendix S1 in Supporting information). The randomization procedure randomly assigned each individual duckling's time series of measurements to either treatment or control groups (without replacement) such that each group retained its original sample size. We calculated the total summed deviance for each repetition of the random assignment. We repeated the randomization procedure 1000 times and report the number of trials where the random assignment of individuals resulted in a deviance that was greater than or equal to the deviance observed between the treatment categories. We conducted this overall procedure separately for each species (spectacled and Steller's eiders) and each salinity treatment. This approach of resampling individuals, as opposed to individual daily weight measurements, assumes independence in measurements among individuals but not within. The randomization procedure makes no assumptions regarding the distribution of these data and directly assesses the probability that the treatment effect occurred purely by chance given the sample size and these study subjects.

2.2.2 Wetland salinity

We used four datasets from the YKD for points that included spatial location information (Table 1). Spatial coverage of samples varied by year. We examined spatio-temporal variation in salinity using a general additive model (GAM, Wood 2017) with a Tweedie distribution (Tweedie 1984), including spatial (sample location) and seasonal smooths that varied across years. We evaluated seven model structures that treated year effects as either continuous or categorical and allowed spatial and seasonal effects to vary or be static across years. We restricted the number of knots (k) to 70 for spatial smooths and 10 for the interaction between space and year after exploratory analyses suggested these were the minimum necessary to produce robust results. We also evaluated an intercept-only model to ensure terms improved predictive ability (See Appendix S2). We evaluated relative model fit using AIC model selection (Burnham and Anderson 2002), modified for use in GAMs (Wood et al. 2016), and selected the model with the lowest AIC value to make predictions. We conducted analyses using the `mgcv` package (version 1.8-41) in R version 4.0.1 (Wood 2011, R Core Team 2020) (See Appendix S3). We predicted salinity within 1-km² cells across eider nesting area and at the center of each nest survey plots to compare with eider density.

2.2.3 Eider nesting patterns and wetland salinity

We first fit a series of GAMs to predict the spatial-temporal variation in eider nesting density independent of any salinity covariate. Initial model exploration suggested that a negative binomial distribution was the best likelihood for the number of nests found on a plot. We then explored the effect of the number of knots (k) on the spatial smooth and found that after 200 in each spatial dimension, there was little difference in the smooth. We fit models with a continuous space-time interaction smooth, allowing the knots to vary from 10 to 200 for the spatial dimensions and fixing the knots for the time dimension to 10. We found 10 knots for time smooths to be sufficient for all models, as there was little difference in resulting smooths with increased number of knots. We also fit a model

with time as a random effect, and a model with year as a random effect and a categorical year-specific spatial smooth. Finally, we fit an intercept-only model. All models included an offset of log plot area (km^2) because plot size varied through time, and this allows the model to predict number of nests per unit area. Models were compared using AIC (See Appendix S2, Table S2.1., and Appendix S3), and the model with lowest AIC was used for prediction at 1- km^2 cells across the eider nesting area.

We first compared predicted mean eider density and salinity on approximate mean hatch date in each 1- km^2 cell to explore general spatial relationships between the two parameters (See Appendix S2, Table S2.2.). We then used the space- and year-specific predictions (2006-2011, 2013-2019) at each grid cell to estimate the expected proportion of the eider population initiating nests in a low salinity location (model expectation < 6 ppt). We estimated this proportion by sampling from two different multivariate normal distributions of the parameter estimates for the salinity and eider models 1000 times. For each sample, we calculated the value of the linear predictor for each model at each grid cell for each year, backtransformed values to the response scale for each model (ppt salinity or number of eiders per 1 km^2), summed the expected number of eiders for all cells where salinity < 6 ppt for each year, and then divided by the total expected eider population over all cells for each year. We then calculated the mean and standard deviation of the proportion of the population in low or high salinity areas for each year.

Additionally, we used a GAM with a salinity covariate to directly assess the effect of salinity on eider density, including interactive effect with space and time. We used the most supported salinity model to predict expected salinity at each nest plot for the years we had both salinity and nest plot data (2006-2011, 2013-2019), and then used this prediction as a covariate in a series of models similar to those described above for predicting eider density. We examined competing models with no salinity covariate, but a year random effect and spatial smooth effect, a year random effect, spatial smooth, and year-space interaction smooth. All other models included salinity covariates either as a main effect smooth or

as an interactive smooth between space and salinity, or as an interactive smooth between space, year, and salinity (See Appendix S2, Table S2.3.). We then compared results using AIC and made inference on the most supported model (i.e., lowest AIC value).

3. Results

3.1 Salinity exposure experiments

We did not observe any abnormal behaviors in Steller's eiders in the control group or those exposed to 3 ppt salinity. However, all Steller's eider ducklings in the 6 ppt exposure group developed abnormal behaviors and clinical signs of illness 21–24 hours after salinity exposure including imbalance, lethargy, agitation, dehydration, and poor waterproofing. We observed imbalance during standing, walking, and preening. Symptoms of lethargy included head droop, unresponsiveness, and lack of self-maintenance activities. Agitation included bouts of hyperactivity, restlessness, and overpreening. Behaviors categorized as signs of dehydration included inability to pass fecal matter combined with excessive preening of vent area and hunched tail, and sunken, squinty eyes (See Appendix S4). At 36–48 hours post-exposure, the ducklings were removed from exposure due to progressive severity of symptoms. Recovery time to normal behaviors ranged from 6 days and 15 hours to 8 days and 17 hours. After ducklings had recovered from initial exposure, they were re-exposed to 6 ppt salinity and remained at that exposure until fledging age. We did not observe any further behavioral or clinical abnormalities after re-exposure. We did not observe any behavioral or clinical abnormalities in the group that was exposed to 6 ppt salinity after 1 week of age.

We did not observe any abnormalities in the control group of spectacled eiders. We observed abnormal behaviors in all ducklings in 6 ppt exposure group 18-36 hours after saltwater exposure. Observed behaviors included the same five categories as in Steller's eiders: imbalance, lethargy, agitation and hyperactivity, dehydration, and poor waterproofing. We removed ducklings from exposure at 36–72

hours post-exposure and monitored ducklings using the same protocol as for Steller's eiders. The recovery time to normal behaviors ranged from 5 days and 5 hours to 6 days and 19 hours. When ducklings were considered recovered from the initial exposure, we re-exposed them to 6 ppt salinity. After re-exposure, seven of the nine ducklings remained at 6 ppt exposure until fledging age with no further abnormal behaviors or signs observed. We removed two ducklings after 34 hours of re-exposure due to poor waterproofing. Waterproofing improved after 72 hours in fresh water, and we re-exposed ducklings again to 6 ppt salinity. They remained at 6 ppt exposure with no abnormal observations until fledging age. We did not observe any abnormal behaviors or clinical signs of illness in spectacled eider ducklings exposed to 6 ppt salinity after 1 week of age.

Steller's eider ducklings in the salinity exposure groups were consistently lighter than control ducklings after 13 days of age, but there was no significant difference between overall growth functions up to age 60-days (3 ppt: Fig. 2a, $P=0.366$; 6 ppt: Fig. 2b, $P=0.225$; 6 ppt delayed: Figure 2c, $P=0.164$). For all levels of exposure treatment, there was very little difference from control ducklings in final weight at 60 days of age. The proportion of missed body mass data was 0.6% of all measurement times.

Spectacled eider ducklings in the 6 ppt exposure group had no significant differences in growth pattern up to 60 days of age compared to control ducklings (Fig. 2d, $P=0.546$). Spectacled eider ducklings in the delayed exposure group were significantly lighter than control ducklings, particularly from 10 to 25 days of age (Fig. 2e, $P=0.004$). The proportion of missed body mass data was 3% of all measurement times.

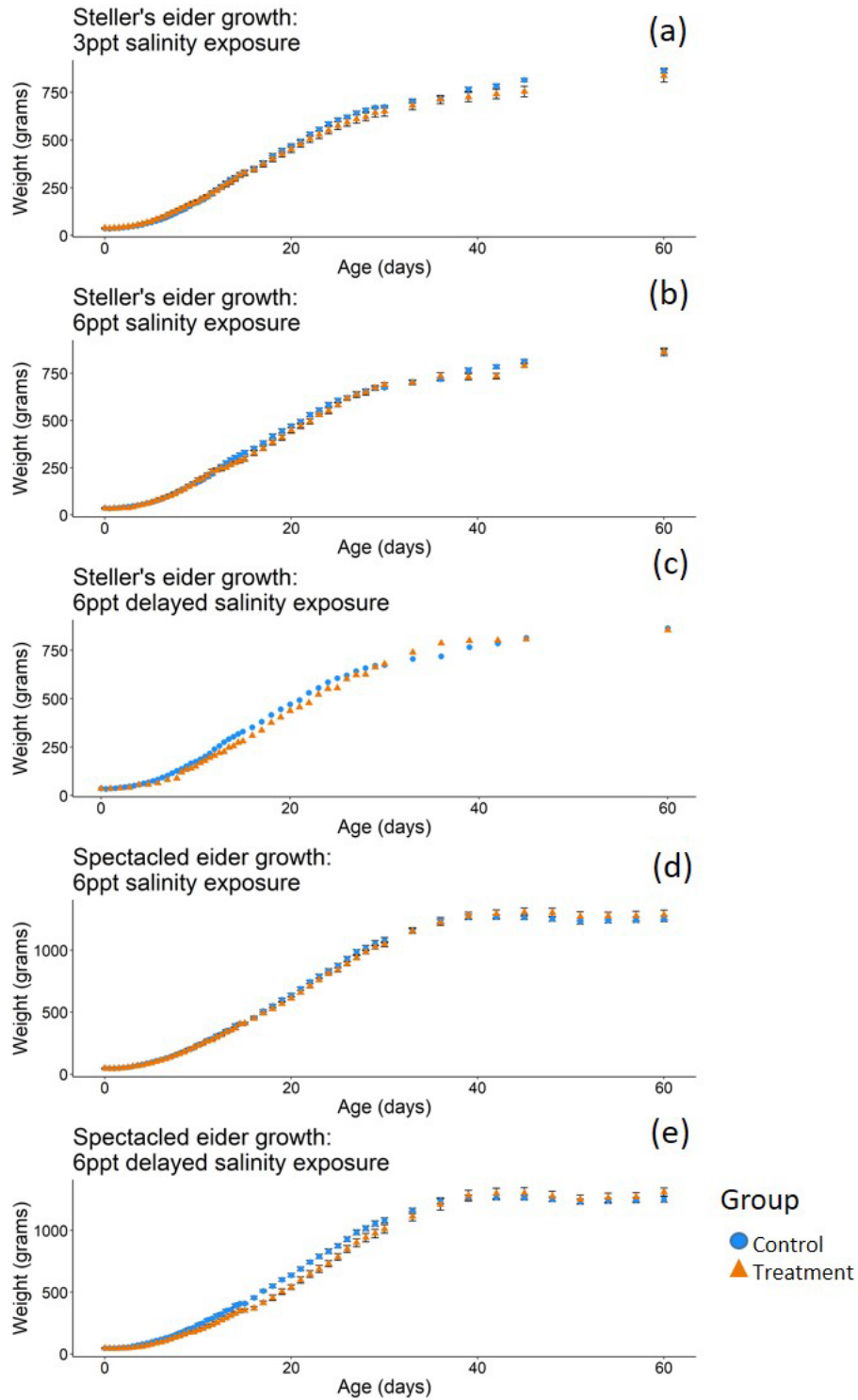


Figure 2. (a) Body weight (mean±SE) growth curves from hatch to 60 days of age for Steller’s eider ducklings reared on fresh water (blue circles) and ducklings exposed to 3 ppt salinity water (orange

triangles), (b) body weight (mean±SE) growth curves from hatch to 60 days of age for Steller's eider ducklings reared on fresh water (blue circles) and ducklings exposed to 6 ppt salinity water (orange triangles), (c) body weight (mean±SE) growth curves from hatch to 60 days of age for Steller's eider ducklings reared on fresh water (blue circles) and ducklings exposed to 6 ppt salinity water at 8 days of age (orange triangles), (d) body weight (mean±SE) growth curves from hatch to 60 days of age for spectacled eider ducklings reared on fresh water (blue circles) and ducklings exposed to 6 ppt salinity water (orange triangles), and (e) body weight (mean±SE) growth curves from hatch to 60 days of age for spectacled eider ducklings reared on fresh water (blue circles) and ducklings exposed to 6 ppt salinity water at 8 days of age (orange triangles).

We observed evidence of nasal secretions at 37 and 40 hours of age in two of the Steller's eiders in Treatment 1 (exposed to 3 ppt salinity). We observed nasal secretions in each of the five Treatment 2 (6 ppt) ducklings at 29 – 54 hours of age. We observed nasal secretions in each of the three Treatment 3 (6 ppt delayed exposure) Steller's eider ducklings at 9.6–10 days of age. We observed nasal secretions in all spectacled eiders ducklings in Treatment 2 (6 ppt salinity) at 18 – 45 hours of age and in all ducklings in Treatment 3 (6 ppt delayed exposure) at 8.7– 9 days of age.

3.2 Wetland salinity patterns

We obtained 2270 salinity samples from 946 unique locations surveyed 1 – 11 years (mean = 1.43 years) from 2006–2011, 2013-2019 (Table 1). Salinity measurements averaged 7.70 ppt (range: 0-46.5 ppt). Model selection results suggested salinity was best described by spatial and seasonal variation that varied by categorical year (See Appendix S2, Table S2.1.-S2.3.). Overall salinity was similar among years (See Appendix S2, Table S2.4.), but spatial patterns in salinity varied by year (See Appendix S2, Fig. S2).

Within-season patterns in salinity varied by year, but when averaged across sampling sites, salinity was higher on the last day of the season than the first during 10 of 13 years of our study.

Over the study period, most areas were high salinity, but areas of reliably low salinity did occur (Fig. 3a).

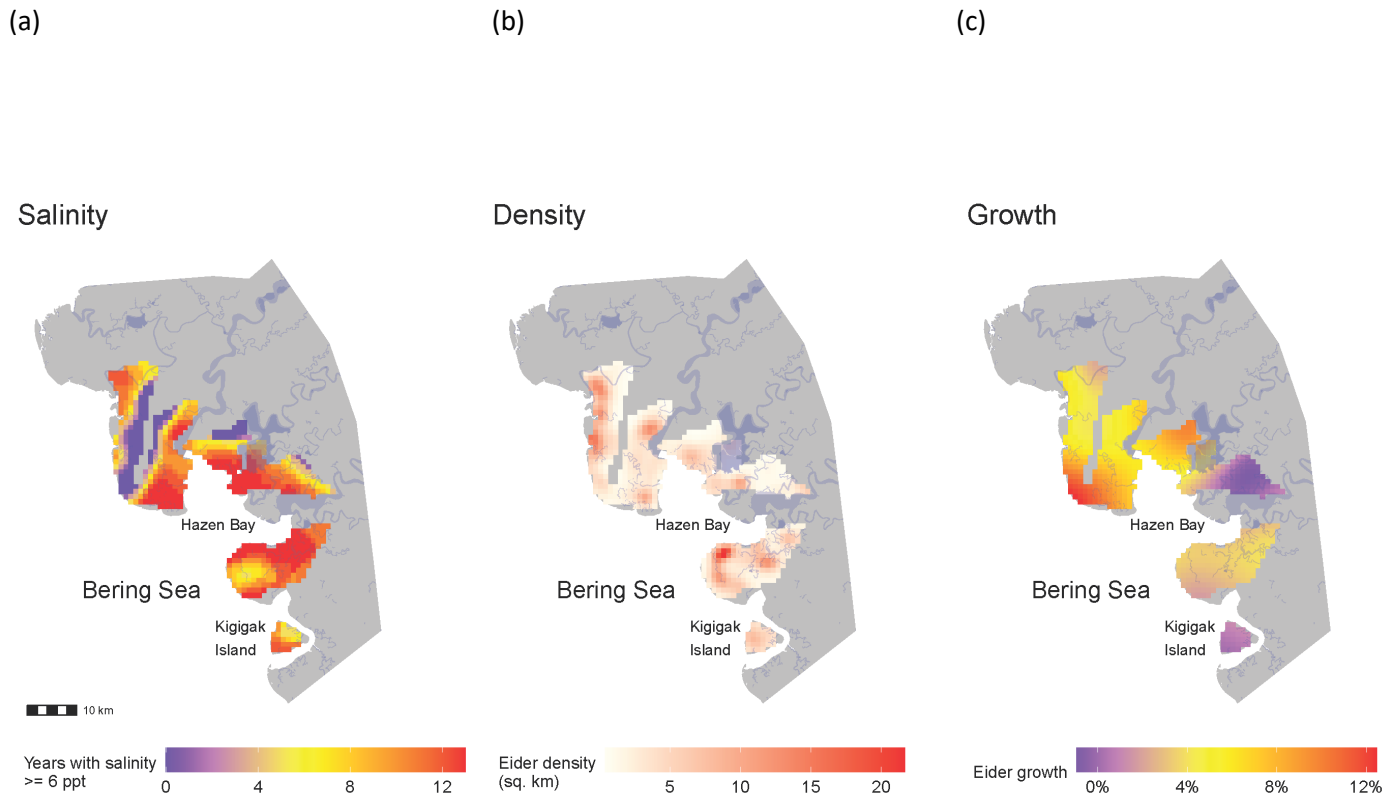


Figure 3. (a) Predicted salinity (ppt) at locations (1 km²) within the spectacled eider nest plot area on the Yukon Delta National Wildlife Refuge (NWR), 2006- 2011 and 2013-2019, (b) eider nest density across the Yukon Delta NWR study area predicted after removing year effects from the best fit model (See Appendix S2, Table S2.2.), and (c) spatial variation in growth rate of eider nest density presented as the geometric mean change from 2000 to 2018 as predicted from the best fit model.

3.3 Eider nesting patterns and wetland salinity

Model selection results for eider nesting density (See Appendix S2, Table S2.2.) suggested that density varied across space (Fig. 3b), increased after a low around year 2000 (Fig. 4), and that the increase depended on location (Fig. 3c). When averaged across years, there was no clear pattern between eider density and salinity. Year-specific predictions of the proportion of eiders nesting in low salinity areas (< 6

ppt) showed that few eiders (< 50%) nested in low salinity locations in most years (Fig. 5). In a few notable years (2011, 2014, 2015, 2017), however, the proportion of eiders nesting in low salinity areas was much greater (Fig. 5). When year- and location-specific predictions of salinity were added as a covariate to a model of eider nest density, none of the models using salinity improved model fit when compared to models without a salinity covariate (See Appendix S2, Table S2.3.), and the best model that included salinity received only a small proportion of model weight ($w = 0.06$) (See Appendix S2, Table S2.3.), suggesting that salinity was a poor predictor of eider density or the change in density through time.

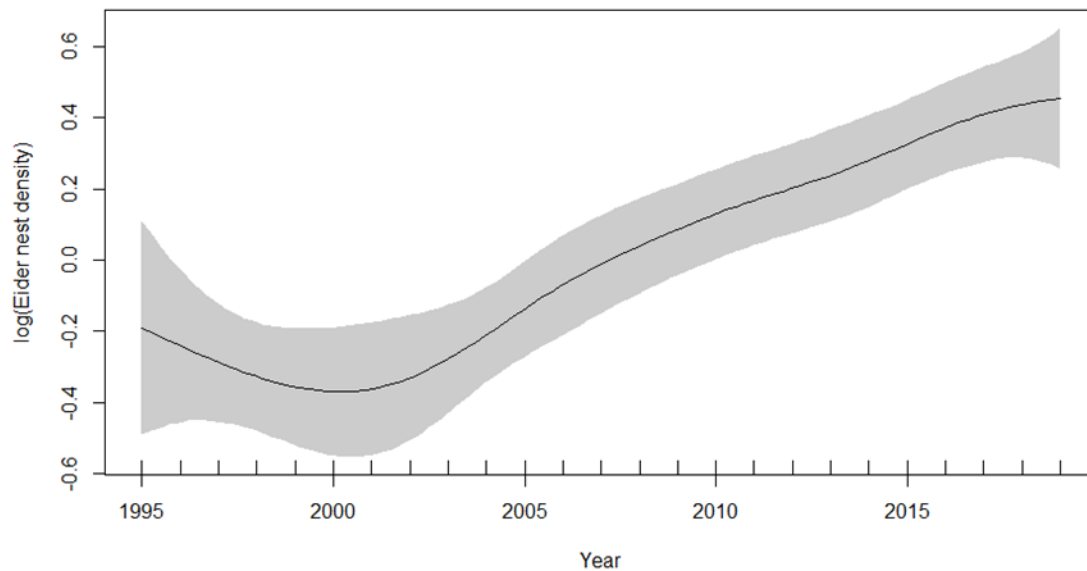


Figure 4. Average change (± 2 SE) in eider nest density across the study area estimated from a smooth function of year from the best fit model (See Appendix S2, Table S2.2.).

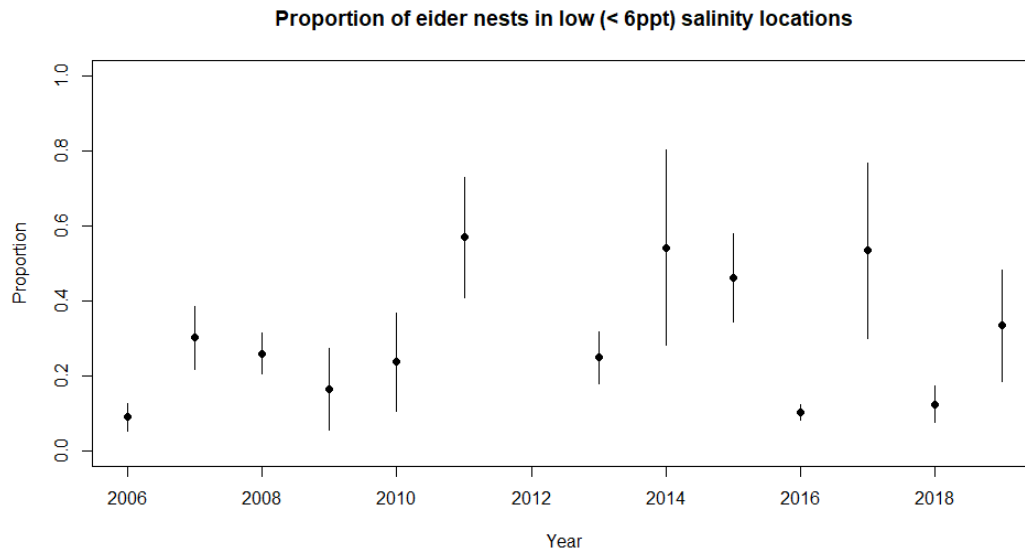


Figure 5. Predicted proportion of eiders nesting in low salinity (< 6 ppt) locations for each year. Predictions were based on sampling from parameter multivariate normal distributions (posterior distributions) of the best-fitting eider and salinity models (See Appendix S2, Table S2.3.). Points are the posterior mean proportion and error bars represent 1 SD.

4. Discussion

Salinity toxicity thresholds and manifestation in ducklings. We found adverse behavioral and physiological effects of exposure at 6 ppt salinity exposure level in young ducklings of both species. The behavioral and clinical signs observed were consistent with a salt toxicosis syndrome previously described in other species of water birds, including common eiders and mountain ducks, with the onset of symptoms discovered within 24 hours from exposure followed by a rapid progression of symptoms (Riggert 1977, Wobeser 1981, Stolley and Meteyer 2004, DeVink et al. 2005). These findings illustrate the impacts of acute exposure to salinity in eider ducklings. We did not allow ducklings to die before intervening, but our observations suggest that young Steller's and spectacled eider ducklings cannot survive when they only have access to water with salinity levels at or exceeding 6 ppt. All ducklings

recovered when moved to fresh water supporting our conclusion of salt toxicosis and we found no adverse effects of 3 ppt salinity level exposure in newly hatched Steller's eider ducklings. Thus, we conclude that the acute toxicity threshold for young Steller's eiders occurs between 3 and 6 ppt and for spectacled eiders in ≤ 6 ppt. This threshold appears to relax as salt glands mature and become effective, and the critical period when eiders need access to relatively fresh water is during the first week of life.

De Vink et al. (2005) found a 17% mortality rate in common eider ducklings exposed to 11 ppt salinity. Our findings suggest a lower tolerance threshold of 6 ppt to saline exposure in Steller's and spectacled eider ducklings as compared to common eider ducklings. Finding of lower tolerance threshold for Steller's and spectacled eiders as compared to common eiders was anticipated, considering differences in sizes and life histories among the species. In general, common eiders move broods to salt water environments at a relative young age whereas Steller's and spectacled eiders raise brood in freshwater habitats during the first weeks (Swanson et al. 1984, Grand et al. 1997, Quakenbush et al. 2004). We suspect that salt glands mature faster in common eiders allowing them to withstand exposure to higher salinity at young ages.

Exposure to saline water had minor effects on eider duckling growth (Fig. 2). Exposure to 3 ppt water did not appear to cause potential mortality (i.e., ducklings in our study did not require intervention) and effects on growth rates were minor. Exposure to 6 ppt water always had potential for mortality (intervention required) and had somewhat stronger effects on duckling growth. Spectacled eider ducklings exposed to salinity after 1 week of age were significantly lighter than controls, particularly during 10-25 days of age. In all cases, the effects of salinity exposure on duckling weight occurred from 10–30 days of age and there appeared to be little remaining effect at the end of the study (i.e., 60 days). As such, saltwater exposure may slow initial growth but does not appear to have a major effect on asymptotic body size. We did not conduct detailed analyses to assess factors related to variation in

growth, but potential causes include individual variation in physiological ability to process salt, variation in energetic demands during growth, or behavioral responses. We caution that these results were found under laboratory conditions with *ad libitum* access to food, and actual growth rates may differ under field conditions where exposure to weather, predators, and foraging conditions may exacerbate the effects of salt toxicosis syndrome or link to increased energetic consequences. Although we found some evidence for reduction in the growth rate of ducklings exposed to salinity, potential long-term effects of exposure on fitness remain unknown.

Recovery from exposure. When exposed and affected Steller's and spectacled eider ducklings were moved to freshwater, they recovered from clinical signs of salt toxicosis in 5–9 days. Thus, the symptoms in the observed illness syndrome were reversible. However, recovery to normal behaviors and maintenance activities took several days, and sub-lethal salinity exposure could thus render ducklings susceptible to other mortality factors for an extended time period even after exposure is removed. During this time period, multiple factors could indirectly impact survival of affected ducklings: lethargy could predispose ducklings to predation (Swennen 1989), inability to preen could lead to hypothermia, and inability to move normally could impact foraging in the wild or moving to wetlands with lower salinity levels.

Nasal gland secretions were observed in all ducklings exposed to 6 ppt salinity at 8 days of age. Steller's and spectacled eider ducklings showed excretions in 26–31 hours and 12 hours post-exposure, respectively. This finding indicates that Steller's and spectacled eider ducklings possess functional salt glands by 1 week of age, similar to the timing found in other waterfowl (Ellis et al. 1963, Riggert 1977, Stolley et al. 1998). Furthermore, we found evidence of secretions at an earlier age in some Steller's eider ducklings exposed to 3 ppt salinity, and all eider ducklings exposed to 6 ppt salinity, suggesting that salt glands can develop at least some degree of physiological functionality earlier than 1 week of

age. The timing of the earliest observed salt gland function is similar to observations in common eiders (De Vink et al. 2005). However, Steller's and spectacled eider ducklings exposed to 6 ppt salinity levels at hatch concurrently developed symptoms of salt toxicosis, despite salt gland secretions, suggesting that the ducklings were not able to fully process and compensate for salinity at the 6 ppt level at the early age. This finding further supports the conclusions that Steller's and spectacled eider ducklings require access to water at less than 6 ppt salinity during early rearing.

Coastal wetland salinization patterns. Patterns of salinity varied among years at the YKD (Fig. 3). In coastal areas, wetland salinity is a function of storm surge extent, storm surge frequency, and precipitation patterns. If storm surges increase in frequency, average pond salinities will increase, and if storm surges increase in scale, then the proportion of ponds in the coastal zone with saline input will increase (Jorgenson and Ely 2001, Terenzi et al. 2014). Most storm surges are associated with fall storms that occur before shelf ice forms along the coast (Terenzi et al. 2014). Thus, wetland salinity in a given year is directly dependent on the storm surge occurrence in the previous fall. Early season wetland salinity is also influenced by overwinter snowpack and the degree of dilution and flushing that occurs during spring runoff. Finally, seasonal variation in salinity is directly related to summer precipitation. In dry years, evaporation leads to pond draw-down and can concentrate salinity to very high levels in some locations. However, these late season increases in salinity typically occur after the ducklings are >7 days old and as such likely have little influence on eiders, although potentially increased energy expenditure may influence the daily energy budgets of ducklings.

Eider nesting patterns and response to salinization. We discovered that in nine of 13 years of our study, over 50% of eiders nested in areas with salinity at or above the tolerance threshold value for ducklings, suggesting that eiders do not appear to actively avoid saline habitats (Fig. 5). This may be because salinity of wetlands during brood rearing is unknown (or unpredictable) at the time of nest

initiation and thus, eiders appear to engage in sub-optimal habitat selection because of imperfect information. Alternatively, the overlap may represent a trade-off between direct salinity effects and overall wetland productivity. Previous work has shown that moderately saline wetlands may have higher primary productivity. Grand et al. (1997) showed a positive relationship between salinity and primary productivity, as measured by chlorophyll concentration, for wetlands on the YKD. Thus, brackish conditions may represent a cost in early brood rearing before salt glands are mature, but these same habitats may offer an advantage in terms of forage availability later in brood rearing. Other potential advantages of saline habitats could relate to reduced pathogen loads (Gutierrez 2014). Overall, our findings relating to nesting patterns may indicate that current salinity conditions do not have major effects on eider fitness.

Local scale heterogeneity in wetland salinity may facilitate optimal brood rearing because eiders have precocial young and broods are highly mobile. As an example of this at a large scale, Grand et al. (1997) showed that northern pintails (*Anas acuta*) nested in highly saline habitats but then quickly moved broods several km into less saline areas after hatch. On a more localized scale, Swanson et al. (1984) showed that ducklings on saline lakes utilized freshwater inflows, nearby less saline wetlands, or areas with chemical stratification to access fresher water and, in addition, summer precipitation events may offer fresh water sources for ducklings. Fine scale salinity measurements in our study area suggest that within broad salinity strata, there may be specific ponds with adequately fresh water for ducklings to survive prior to salt gland functionality within 1 km of high salinity wetlands. Examination of a high-intensity sampling site suggested, conservatively, that a high salinity wetland was on average 962 m from the nearest low salinity wetland (median = 653 m; range = 4– 4479 m) (See Appendix S5, Grand and Flint 2022). These data suggested there is a 35.5% and 60.5% chance of encountering a low salinity water body within 500 m and 1 km of a high salinity water body, respectively. Thus, even within broader areas classified as above the 6 ppt threshold, ducklings may be able to access areas at the micro

scale with suitable water to avoid salt toxicosis. Importantly, the ability of broods to identify and locate these ponds in a timely fashion would offer an important adaptive capacity to maximize offspring survival in a dynamic, changing wetland habitat. Casazza et al. (2020) concluded that female dabbling ducks prospected brood rearing sites during nest initiation breaks for birds breeding in a brackish location. Spectacled eider females take regular incubation breaks during which they leave the nest site (O'Connell 2001). Females may be using information gained during these breaks to inform post hatch movement patterns in relation to salinity.

In a previous study, Flint et al. (2006) showed regional variation in survival and growth of spectacled eider ducklings on the YKD. Both Steller's and spectacled eiders nest at low elevation habitat on the coastal fringe of the YKD, and spectacled eider broods have been observed to move from nesting habitats to fresher water habitats within a few days of hatch (Swanson et al. 1984, Grand et al. 1997). Flint and Grand (1997) studied timing of duckling mortality at one breeding area on the YKD and found that most of spectacled eider duckling mortality occurred during the first 10 days of age. Based on these findings, Flint et al. (2006) speculated that salinity may have been the proximate cause of spectacled eider duckling mortality. Based on findings in this study, ability of broods to move to adequately fresh water habitats or locate fresh water during the early rearing period is critical for duckling health and survival.

Eider population growth and salinization. Our data demonstrate that eiders are not specifically avoiding saline habitats for nesting. We found little effect of salinity on nesting density or change in density. Further, the overall spectacled eider population has been increasing for the last two decades despite the majority of the population nesting in habitats above the salinity threshold we measured (Fischer et al. 2017, Fig. 4). However, the two general regions of highest eider population growth rate occurred in transition areas where salinity changed from consistently high to low across years (Fig. 3.).

We suspect these transition zones represent high heterogeneity in salinity within localized areas. However, not all areas that showed similar patterns of salinity experienced an increase in eider density. One noteworthy consideration with our analyses is that we attempted to link eider nesting to broad salinity patterns, as we lacked sufficient sampling intensity to explore fine scale patterns of salinity. It is clear from the high density sampling that did occur in one area that there may be substantial heterogeneity in salinity within areas we assigned to a specific salinity class. It may be that eiders are selecting habitats that have heterogenous patterns of salinity allowing them to access both highly productive, but relatively saline, wetlands and still have access to relatively fresh water in nearby wetlands. The scale of our sampling for both eiders and salinity preclude direct examination of heterogeneity in salinity and its relationship to breeding eiders. It may be worth considering how increases in storm surge frequency and magnitude influence local scale heterogeneity in salinity.

Conclusions. Understanding how species and their habitats will respond to climate driven changes is essential for predicting future patterns of distribution and abundance, and is necessary for management agencies to make informed decisions about conservation priorities. Due to current rates of rapid change in the Arctic, information about habitat relationships and ecological impacts of change are urgently needed for conservation of Arctic species. The coastal YKD in western Alaska supports large concentrations of breeding water birds, including sea ducks, geese, swans, and shorebirds, and is a globally important area for conservation of migratory bird biodiversity. Furthermore, local communities in the area rely on migratory birds for subsistence foods, and understanding climate-derived changes in populations is necessary to predict impacts on food security. Results from this study contributed new knowledge about impacts of wetland salinization on two waterfowl species of international conservation concern, the spectacled and Steller's eider. We describe a behavioral and physiological syndrome that provides mechanistic understanding of impacts of salinization on eiders that may be broadly applicable to other waterfowl and water birds in general. The tolerance thresholds determined in the experiments

were directly applicable to analysis of habitat suitability using existing maps of wetland salinity and known eider nesting distribution, and the data suggest that some portion of the breeding range may be unsuitable for rearing eider ducklings in some years due to wetland salinization. In species showing a high degree of natal philopatry or breeding site fidelity, such as eiders, behavioral adaptation to changing conditions in nesting areas may be influenced by this trait. In conclusion, our study provided essential information to predict consequences of wetland salinity patterns with data on measured effects of salinity exposure on ducklings and effects of variation in wetland salinity conditions on the landscape on eider populations. The YKD supports one of the largest aggregations of water birds in the world, and our findings have implications to eiders and other species relying on the area for breeding. Our findings also have broader ecological relevance and conservation implications for other coastal water bird breeding areas subject to increases in wetland salinization.

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Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1: Randomization procedure outcomes

Appendix S2: Model structures and annual salinity predictions

Appendix S3: R code for nesting patterns and wetland salinity analyses

Appendix S4: Duckling images

Appendix S5: Small-scale variation in salinity

Climate change and coastal wetland salinization: Physiological and ecological consequences for Arctic waterfowl

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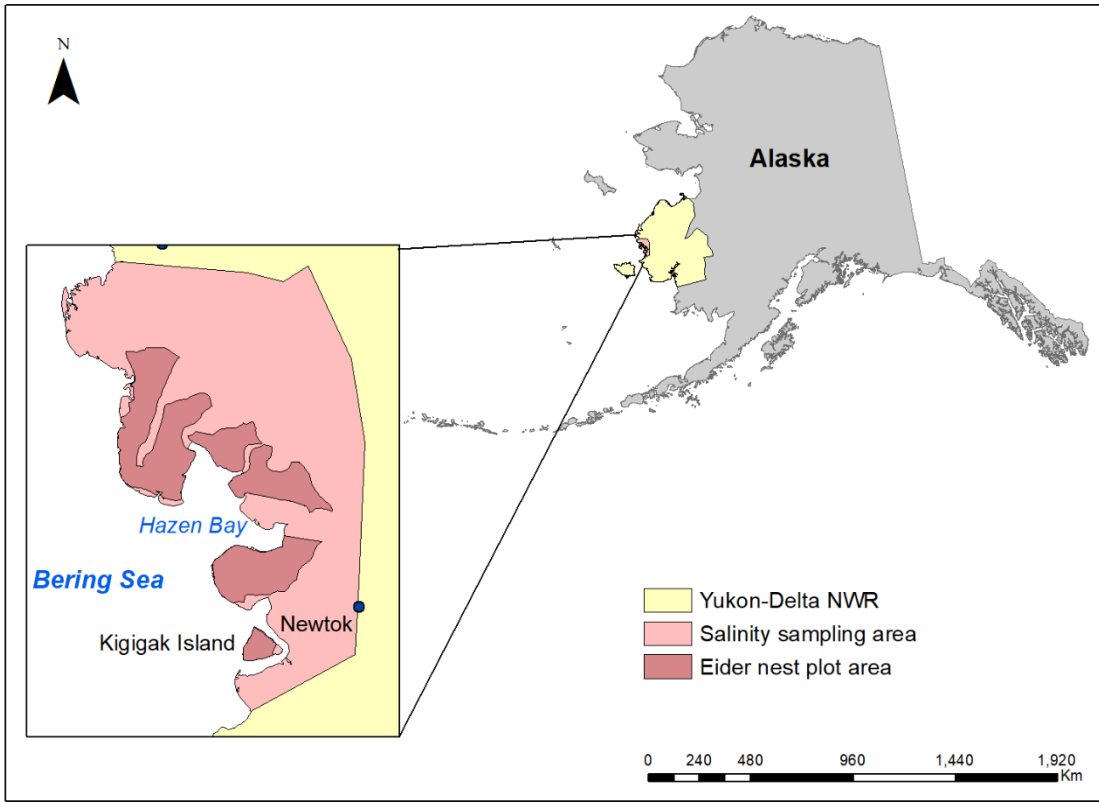
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Author's contributions: TEH and PLF conceived the idea; TEH, PLF, SEGU, and HMW collected the data; TEH, PLF, CLA, and EEO analysed the data; TEH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement: Data are available from DataONE <https://doi.org/10.24431/rw1k46t> (Hollmen and Ulman 2020), USGS data release <https://doi.org/10.5066/P9HWRN22> (Grand and Flint 2022), USFWS Data Repository <https://doi.org/10.7944/P9FFYJXD> (Fischer et al. 2023), and USFWS Data Repository <https://doi.org/10.7944/P9Z6RC5L> (Wilson and Osnas 2023).



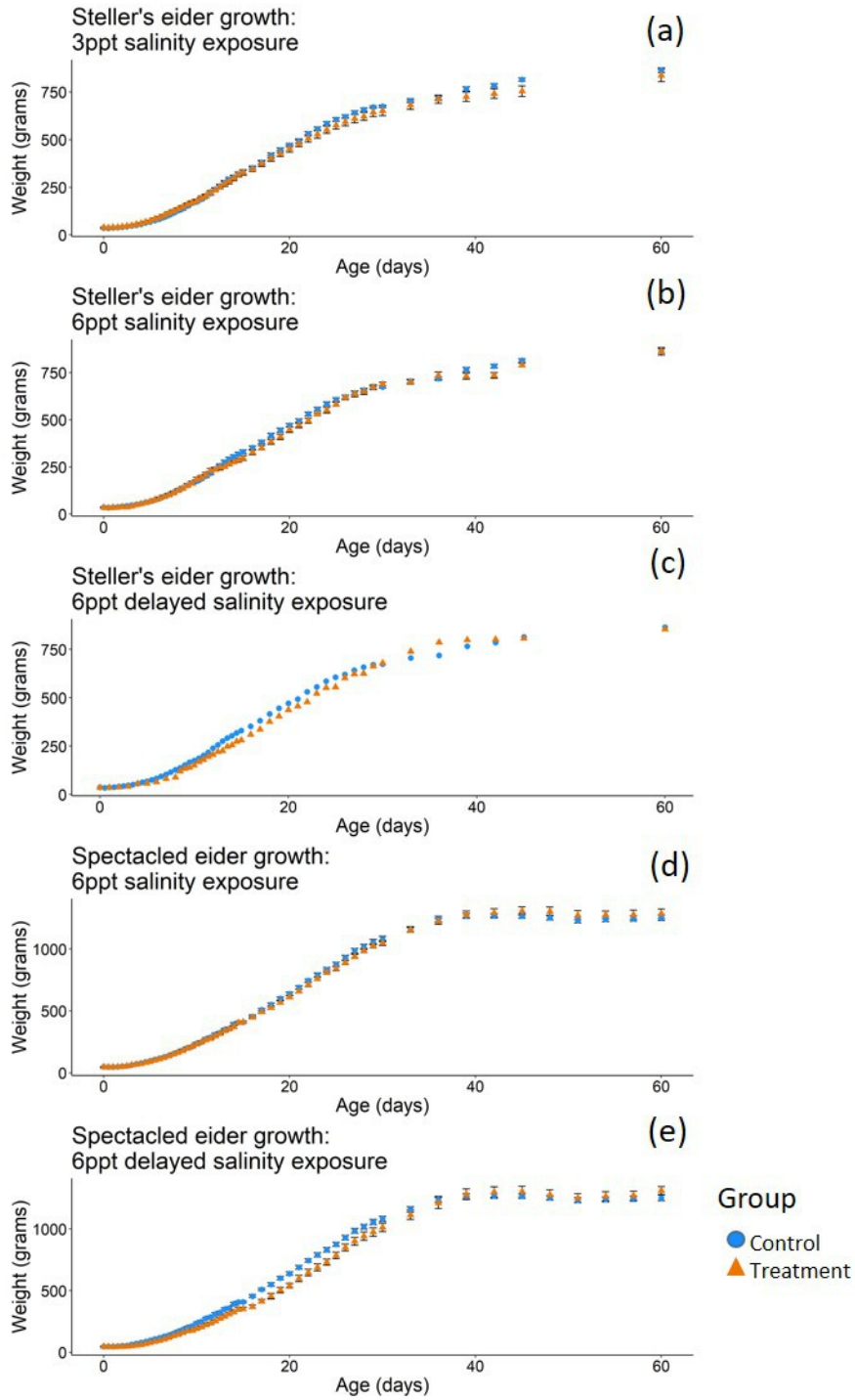
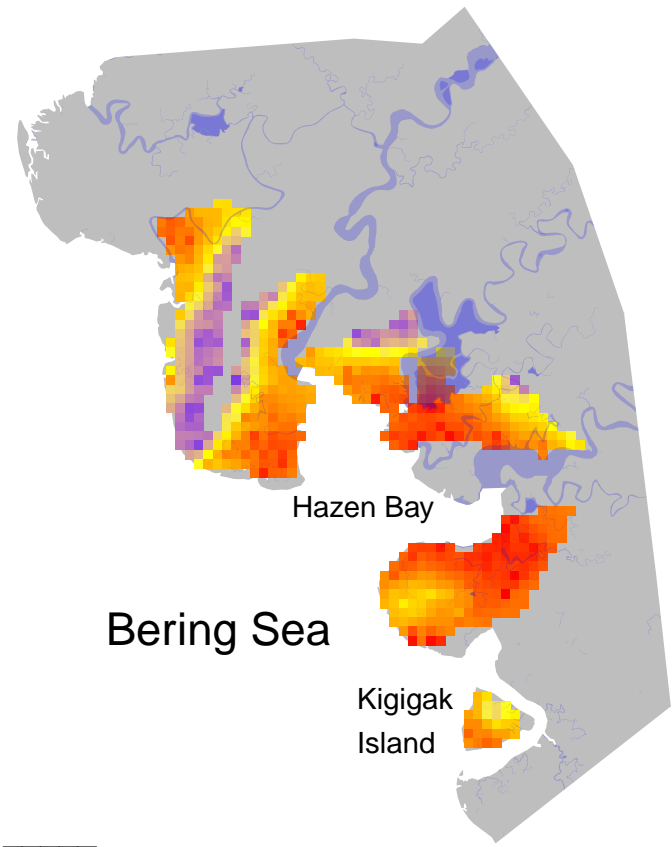
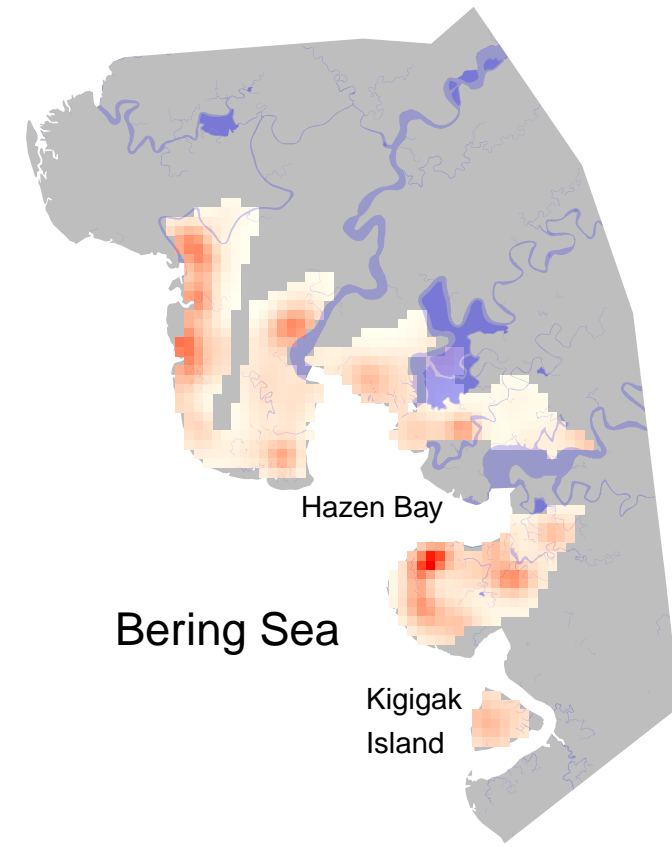


Figure 2.jpg

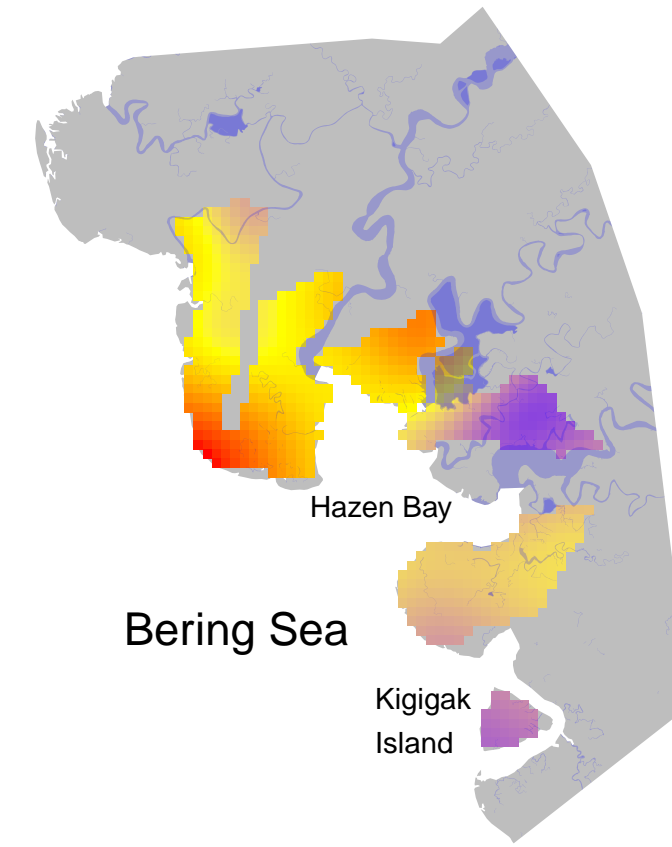
Salinity



Density



Growth



10 km

Years with salinity ≥ 6 ppt

4 8 12

Eider density (sq. km)

5 10 15 20

Eider growth

0% 4% 8% 12%

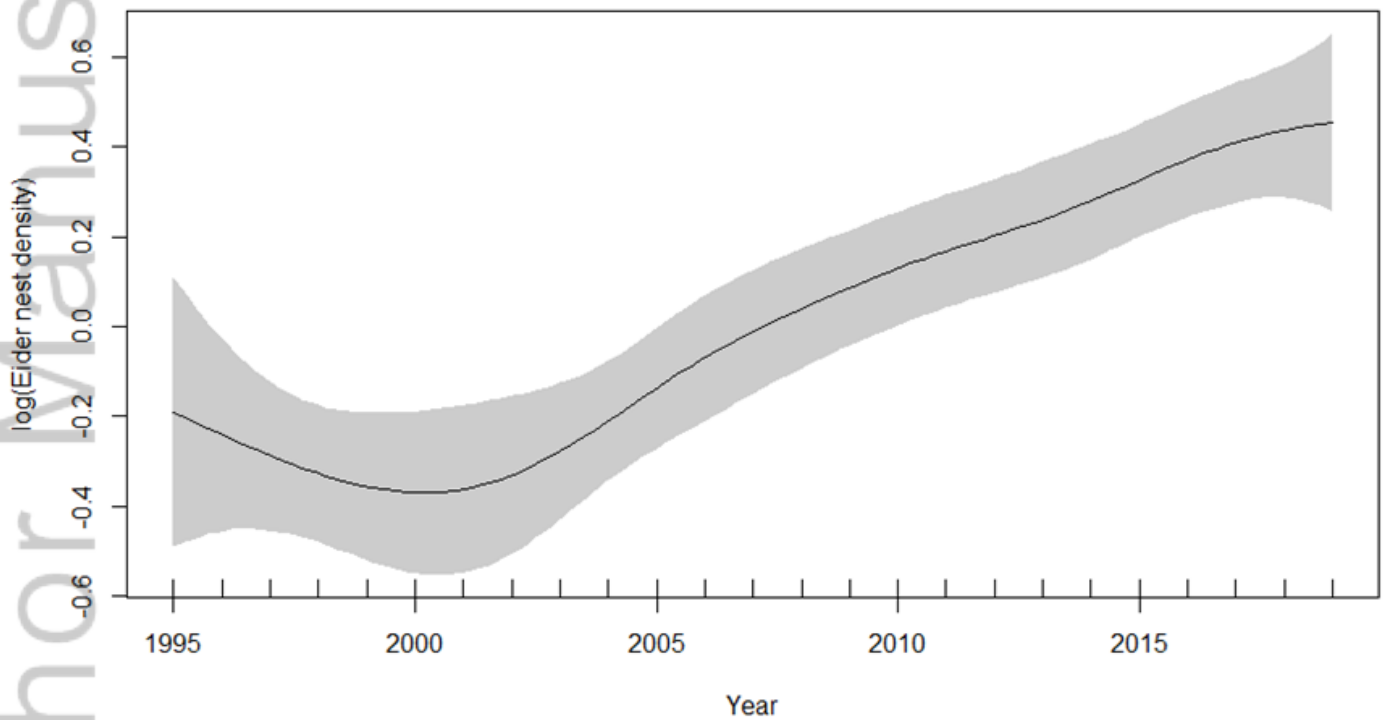


Figure 4.png

Proportion of eider nests in low (< 6ppt) salinity locations

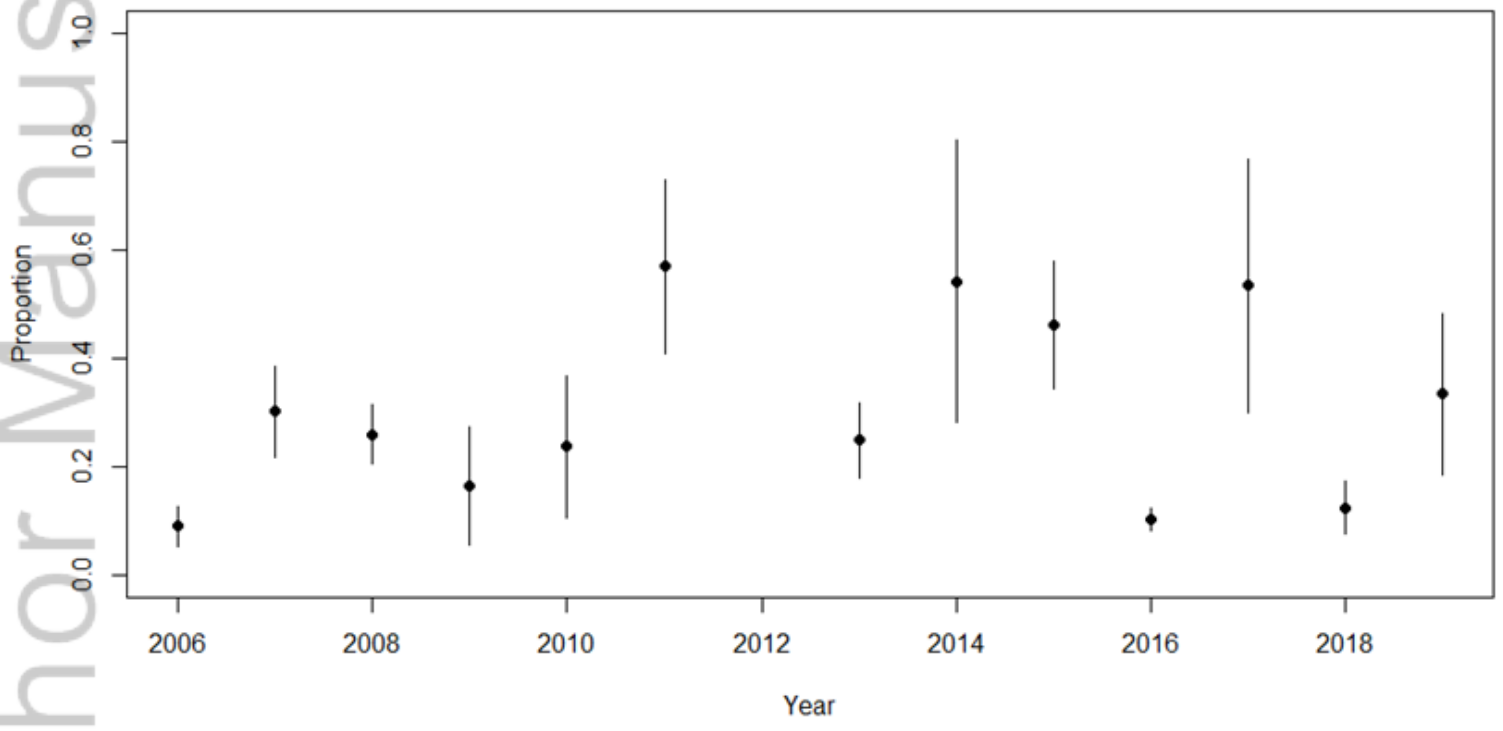


Figure 5.png



spectacled eider duckling.jpg