

**SPRING MIGRATION OF SCOTER AND LOON SPECIES IN THE BAY OF
FUNDY: QUANTIFYING ENVIRONMENTAL INFLUENCES, ESTIMATING
AFTERNOON MIGRATION, AND ANALYZING TRENDS BETWEEN 2000
AND 2017**

by

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ABSTRACT

Waterfowl migration has been monitored at the Point Lepreau Bird Observatory in the Bay of Fundy every spring since 1996. Derived scoter and loon population estimates from previous studies have suggested declines but there is uncertainty in the estimates due to unequal sampling during mornings and afternoons. This study examines: 1) if afternoon migration rates can be accurately modelled using morning rates and environmental conditions; 2) scoter and loon migration rates through the Bay of Fundy; 3) changes in migration rates between 2000 – 2017. I found: 1) morning migration and environmental data were insufficient to accurately model afternoon migration; 2) greater numbers of Black and Surf Scoter migrate through the Bay of Fundy; 3) migration rates of scoter species have declined, and loons increased between 2000 and 2017. Afternoon migration monitoring is important in maintaining effectiveness of this and similar migration monitoring projects to evaluate changes in populations over time.

DEDICATION

A reminder to myself

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List of Abbreviations

Abbreviation	Meaning
ACS	Afternoon Counting Sessions
AR	Afternoon Rate
BLSC	Black Scoter
BNA	Birds of North America
CI	Confidence Interval
COLO	Common Loon
DOY	Day of Year
DWSC	Dark-winged Scoter
EWS	Eastern Waterfowl Survey
GM	Grand Manan
IUCN	International Union for Conservation of Nature
LOsp	Loon Species
MR	Morning Migration Rate
PACS	Predicted Afternoon Counting Sessions
PLBO	Point Lepreau Bird Observatory
RTLO	Red-throated Loon
SJNC	Saint John Naturalists' Club
SUSC	Surf Scoter
TH	Tidal Height
WBPHS	Waterfowl Breeding Population and Habitat Survey
WD	Wind Direction
WS	Wind Speed
WWSC	White-winged Scoter

Introduction

Migration is the cyclical, large-scale movement of populations between specific areas for purposes such as breeding and feeding (Dingle and Drake, 2007). Migration is particularly well represented among birds, as approximately half of all recorded species undertake migratory movements (Hickman *et al.*, 2008). Across taxa, migration can serve many functions (Dingle and Drake, 2007), but in birds it typically involves breeding, as outlined in the “two worlds” (Greenberg and Marra, 2005) description of seasonally linked movements of populations between breeding grounds and wintering areas (Dingle, 1996). Migration is accepted as having evolved primarily as a response to alternating cyclical patterns of seasonal shortage and abundance in resource availability (e.g., food, water, etc.; Dingle and Drake, 2007). However, avian species in North America benefit from migration in several important ways that influence their survival and reproductive success (Hickman *et al.*, 2008). For example, migration allows for greater breeding ranges throughout the remote Northern Territories in Canada, regions only accessible a few months of the year that have significantly reduced predator densities as a result of limited productivity. This promotes greater reproductive success and limits territorial conflict. Additionally, migration can function to reduce overall energetic expenditures in maintaining homeostasis for species in seasonally dynamic environments, as migrating reduces the variability in environmental conditions experienced by individuals (Hickman *et al.*, 2008).

Avian migration in temperate regions, such as most of North America, is typically north-south in orientation, with most species breeding in northern regions in

the summer months and overwintering in the warmer south, including South America for many species. They travel between areas using common migration routes known as flyways, often pausing periodically at predetermined stopover sites along the route to rest, refuel, and molt (Petersen and Savard, 2015). These migration routes can be used in a “to-and-fro” (Dingle and Drake, 2007) strategy, where migrants travel the same route both to and from breeding sites, or a “loop” (Dingle and Drake, 2007), where migrants use different routes to and from breeding sites. Interestingly, there is significant inter- and intra-specific variation in which strategy is used as well as hybrid strategies (Petersen and Savard, 2015).

North America is part of well documented bird migrations (e.g., Arctic tern [*Sterna paradisaea*]), however some populations of non-colonial waterfowl, such as scoters (*Melanitta spp.*) and loons (*Gavia spp.*), are among the least understood and most challenging to study because of their wide geographic distribution and low densities during both the wintering and breeding seasons (Brown and Fredrickson, 1997; Savard *et al.*, 1998; Barr *et al.*, 2000; Bordage and Savard, 2011). Recently, telemetry studies tracking Eastern North American waterfowl migration, including the three North American scoter species (Black [*M. Americana*], Surf [*M. perspicillata*] and White-winged [*M. deglandi*]), and Red-throated Loons (*G. Stellata*), have been conducted by the Sea Duck Joint Venture (Sea Duck Joint Venture, 2015) and Biodiversity Research Institute (Williams, 2013), respectively. The main findings of these studies highlight the broad extent of wintering, stopover, and breeding grounds used by these species, many of which were previously unknown or misunderstood. Eastern populations of scoters were found to winter all along the Western Atlantic, with individuals found in coastal

waters from Maine to Florida (Sea Duck Joint Venture, 2015), and breed throughout the Canadian North from Labrador into the Yukon. Red-throated Loons showed a similar wide geographic range in breeding dispersal, wintering in the Atlantic and breeding throughout Nunavut and into Greenland (Gray and Gilbert, 2015). Their winter range is more restricted and extends south from Maine to North Carolina, with many periodically travelling inland from the coast in the Chesapeake and Delaware Bay systems (Gray and Gilbert, 2015).

The wide geographical distributions and low population densities of scoters and loons means population surveys are logistically complicated. Furthermore, most waterfowl population surveys are aerial and this greatly limits the ability to distinguish between morphologically similar species (Bowman *et al.*, 2015). Current cumulative North American population estimates indicate there are several hundred thousand scoters (Bowman *et al.*, 2015), and tens of thousands of Red-throated Loons (Barr *et al.*, 2000), but data used to generate these estimates have uncertainty (Bowman *et al.*, 2015). On the other hand, populations of Common Loons (*G. immer*) are well documented and more numerous along both the Atlantic and Pacific coasts with combined estimates of over 700,000 individuals throughout North America (Evers *et al.*, 2010).

Many of the waterfowl surveys in North America, such as the Waterfowl Breeding Population and Habitat Survey (WBPHS) and Eastern Waterfowl Survey (EWS), originated to study prairie dabbling ducks (e.g., American Black Ducks [*Anas rubripes*]) and not scoters or loons, which are recorded when observed but not specifically targeted (Bowman *et al.*, 2015). As a result, surveys are often ill-timed to capture peak activity of scoters and loons and cover only fractions of their respective

breeding ranges. Using these data to accurately estimate populations and evaluate trends is challenging, especially on the East Coast where total surveyed area is limited (Bowman *et al.*, 2015). Highly dispersed species such as scoters and loons tend to aggregate in significant numbers only during migration, where large proportions of the populations travel the same routes along well-defined flyways (Newton, 2008). Therefore, sampling these species during migration is a practical and cost-effective approach to monitoring population trends along the North American Atlantic coast, provided locations where migration can be consistently monitored during spring and/or fall can be identified and are easily accessible.

In Avalon, New Jersey, a sea watch project has been documenting fall migration since 1993 and is believed to count the majority of Black Scoters, Surf Scoters, and Red-throated Loons wintering south of Delaware, but counts a smaller proportion of the White-winged Scoter and Common Loon populations in the Atlantic (Sea Duck Joint Venture, 2007). Using their maximum annual counts, it is estimated that there are at least 250,000 Black Scoters, 210,000 Surf Scoters, 6,100 White-winged Scoters, and 90,000 Red-throated Loons in the Atlantic populations (New Jersey Audubon Society). Evers *et al.* (2010) estimates that nearly 500,000 Common Loon winter on the Atlantic and Gulf Coasts in Birds of North America (BNA). Analyses of population trends are difficult, given a lack of comparable data, but the general consensus is that North American populations of all three scoter species and Red-throated Loons have declined substantially since the 1970s (Bowman *et al.*, 2015; Groves *et al.*, 1996). Black Scoter in particular have been listed as near threatened globally on the International Union for Conservation of Nature (IUCN) red list (BirdLife International, 2018) Furthermore,

overall declines in spring Black Scoter and Surf Scoter migration rates have been found over the past 15 years in the Bay of Fundy (Bond *et al.*, 2007; Button, 2015; Cameron, 2014).

Thousands of marine birds can be seen migrating through the Bay of Fundy every spring and fall on route to or from major staging areas in the Saint Lawrence Estuary and Chaleur Bay in the Gulf of Saint Lawrence (Gray and Gilbert, 2015; Sea Duck Joint Venture, 2015). Since 1996, the Saint John Naturalists' Club (SJNC) has maintained a dedicated migration-monitoring project at the Point Lepreau Bird Observatory (PLBO) at Point Lepreau, New Brunswick. Point Lepreau, itself, is a peninsula that extends approximately three kilometers southward into the Bay of Fundy. This topographic feature, and the tendency of oceanic waterfowl to migrate close to coastlines (Newton, 2008), means most migrants are believed to pass by the observatory at observable distances. The data collected at the Point Lepreau Bird Observatory over the past 21 years, using consistent protocols is ideal to study population trends of migrating waterfowl; though, only three studies using the Point Lepreau Bird Observatory's data have been completed (Bond *et al.*, 2007; Cameron, 2014; Button, 2015).

Due to limited funding and because daily peak migration rates are believed to occur during morning hours (i.e., 0600h – 1100h AST), morning observation sessions are favoured in the Point Lepreau Bird Observatory dataset. Preliminary afternoon data suggested migration rates decreased over the course of the day; though, distinct morning and afternoon peaks were noted (Bond *et al.*, 2007). Methods previously used to estimate migrating population size from this database assumed a constant hourly

migration rate over the course of a day (Bond *et al.*, 2009; Button, 2015) or described the change in mean migration rate over the course of the day (daylight hours only) with a simple linear relationship (Cameron, 2014; Button, 2015). However, there are probable issues with both methods; the former knowingly leading to overestimates of the number of birds each day, and the latter is a poor fit given the observed bimodal trend (Bond *et al.*, 2007; Button, 2015).

Absolute population estimates require an assumption that all individual migrants are counted. This assumption is almost certainly untrue, but the Point Lepreau data can be used to effectively estimate relative abundances and trends over time. However, these estimates of relative abundance will be improved if we can model the diurnal patterns in waterfowl migration in the Bay of Fundy. An effective approach to modelling afternoon migration may be using morning migration data in combination with local, short-term weather conditions. Weather conditions, such as wind speed and direction, precipitation, cloud cover, and temperature, have been shown to influence migratory movements in a variety of avian species (Lack, 1960b; Richardson, 1990). Wind conditions in particular are of great importance as migration tends to favour following winds that limit energetic cost of travel (Liechti and Bruderer, 1998), a cornerstone of the energy-minimalised strategy of Optimal Migration Theory (Alerstam and Lindstrom, 1990). By flying during favourable wind conditions, a bird could, theoretically, increase its distance traveled proportional to the speed of the wind using the same energy resources (e.g., 20 km/h direct tailwind allows individuals to travel 20 km further each hour than no wind; Newton, 2008). This has the further potential of reducing the frequency or time needed to refuel during stopovers by making more efficient use of available energy. Conversely,

a headwind would have the opposite effect by increasing energetic expense to travel the same distance and may require more frequent or longer stopovers (Newton, 2008).

Another component of Optimal Migration Theory suggests birds seek to maximize the efficiency of fat deposition during stopovers, preferring prey and locations that offer the highest yield per effort expended (Liechti and Bruderer, 1998; Petersen and Savard, 2015). This fits well with general descriptions of avian foraging through Optimal Foraging Theory (MacArthur and Pianka, 1966), and suggests depth-restricted, benthic foragers like scoters, would prefer foraging at times when conditions, such as tide status, will maximize energy return for investment during migration. Incorporating wind and tidal data in modelling the Point Lepreau Bird Observatory migration rates could provide more accurate predictions of afternoon migration rates.

Objectives and Hypotheses

The overall objectives of my project are to understand daily variability in waterfowl migration timing and to accurately estimate afternoon spring migration rates of five focal species (Black Scoter, Surf Scoter, White-winged Scoter, Common Loon, and Red-throated Loon) in the Bay of Fundy between 2000 and 2017.

Objective A:

- i. Estimate the effect of morning migration rates for the five focal species and afternoon environmental conditions (median afternoon wind speed (WS), direction (WD) and tidal height (TH)) on afternoon migration rates during spring migration between 2000 and 2016 in the Bay of Fundy.
- ii. Evaluate how well the models predict spring 2017 afternoon migration rate data.

Hypothesis A: If daily scoter and loon migration rates vary in response to foraging behaviour, flight energetics, and overall daily rate then afternoon scoter and loon migration rates will change with tidal height, wind speed and direction, and morning migration rate.

Prediction A: Daily scoter and loon afternoon migration rates at the Point Lepreau Bird Observatory are lower during low tide, as the waterfowl feed during this period to conserve energy by diving shorter distances towards the benthos. Migration rates are lower during strong headwinds, as it is more energetically expensive to fly, and are high during strong tailwinds, as it conserves energy. Afternoon migration rates increase with morning migration rate, as higher morning migration represents an increase in migratory activity.

Objective B:

- i. Estimate afternoon migration rates for 484 days with morning only data collection between 2000 and 2017 using the best performing prediction method.
- ii. Evaluate trends in migration rates between 2000 – 2017.

Study Design and Methods

Since 1996, SJNC has been collecting waterfowl migration data (i.e., counts of migrating waterfowl) at the Point Lepreau Bird Observatory (45.069°N, 66.455°W) located at Point Lepreau, in the southeastern terminus of New Brunswick, Canada (Figure 1). My analysis of the Point Lepreau Bird Observatory's dataset for scoter and loon species uses count data collected between March 30th and May 9th, 2000 – 2017, as current collection protocols were not in place prior to 2000. I collected afternoon migration count data in the springs of 2016 and 2017 to use with morning migration data to describe the relationship between morning and afternoon migration rates for three scoter species (Black, Surf, and White-winged) and two species of loon (Common and Red-throated). I also included afternoon Bay of Fundy weather variables (wind speed [WS], wind direction [WD], and tidal height [TH]) in model building to better account for variability in migration rates between days. I estimated afternoon migration rates in 2017 using the top performing or averaged environmental models, morning/afternoon equivalent models, and morning/afternoon proportional models. I compared these estimates to observed afternoon migration rates collected in 2017 to evaluate predictive ability. I used the best performing predictive method to estimate afternoon migration rates for 484 days with only morning data between 2000 and 2017. I evaluated if morning migration rates have changed over this period in the Bay of Fundy.

Observational Procedures

Observers at the Point Lepreau Bird Observatory follow protocols adapted from Hussell and Ralph (1998). Migrating waterfowl are identified and counted during a four-

hour session typically between 0600-1100h Atlantic Standard Time (AST) each spring (March 15th – May 9th). Counting sessions are conducted in alternating 15-minute intervals of observations and rest so that, during each four-hour session, a total of two hours of observations are completed. Observations are completed by a dedicated observer and volunteers at least five days a week, regardless of weather conditions affecting visibility (i.e., fog) except in the event of a severe weather system. Passing flocks of marine birds are counted and identified to species, whenever possible, using binoculars and spotting scopes. Flight direction is recorded as either east or west. Marine birds observed sitting on the water surface are noted as probable known stopovers and added to a directional count only if they later move off in one of the two flight directions. Local non-migratory species, such as Herring Gulls (*Larus argentatus*), are not recorded.

Dark-winged Scoter and Loon Species Counts

White-Winged Scoters are easily identified by their flight feathers, but Black and Surf Scoters are nearly impossible to distinguish from a distance, especially when travelling in large and dynamic flocks and/or during poor visibility. As a result, observers at the Point Lepreau Bird Observatory have grouped the two as a working taxon called Dark-Winged Scoters for use when identification to species is not possible. This category represents over 25% of the total scoter counts since its implementation. Additionally, distinguishing between Red-throated Loons and non-breeding or juvenile Common Loons at distance can be challenging. In instances where loon identification to species is not possible, observers simply record those observed as loon species. As has been done in similar cases (Button, 2015; Cameron, 2014; Aerts *et al.*, 2013), I divided

the Dark-winged Scoter and Loon species daily counts between Black Scoter and Surf Scoter, and Red-throated Loon and Common Loon, according to their proportions in grand total counts from 2000 – 2016 (Table 1).

Calculating Migration Rates

Point Lepreau Bird Observatory data are recorded in eight 15-minute migration counts for each observed species throughout the four-hour counting session on every observation date; dates with both morning and afternoon data collection have two sessions (i.e., 16 migration counts). For each observation day, I calculated migration rates (number of migrating birds per hour ($\bar{\beta}$)) for each session independently (i.e., morning rate and afternoon rate). The morning session consisted of all data collected between 0600 and 1000h AST and the afternoon session 1000 and 1400h AST. These rates were calculated as:

$$\bar{\beta} = \frac{m}{h}$$

where m and h represent the total number of migrants and observation hours within the session. Between 2000 and 2017 (March 30th and May 9th), I calculated morning migration rates for 645 days and afternoon migration rates for 161 days. Data prior to March 30th each year were not used to limit observer bias from the absence of a dedicated observer. A previous study using this dataset found this window of interest still captures the vast majority of scoter migration activity and observer effort (Button, 2015). Only the easterly migrants were used in this study as that is the spring migratory direction; westerly movements and probable known stopover counts were not included in the analyses as they represent a negligible proportion of the data.

Table 1. Total counts of Black and Surf Scoters (BLSC, SUSC) and Red-throated and Common Loons (RTLO, COLO) between 2000 and 2016 at the Point Lepreau Bird Observatory. Also shown are the resultant proportional divisions for Dark-winged Scoter (DWSC) and Loon species (LOsp) counts.

Species	Total Count	DWSC and LOsp Division
BLSC	424,367	0.6817
SUSC	198,186	0.3183
RTLO	13,858	0.7816
COLO	3,873	0.2184

Environmental Data Acquisition and Organization

I downloaded wind data (speed and direction) for the Bay of Fundy from the Environment and Climate Change Canada historical weather database (http://climate.weather.gc.ca/historical_data/search_historic_data_e.html). I used the Grand Manan Island Station (44.712 N, 66.802 W; Figure 1) as it is the only recording weather station within the Bay of Fundy itself and best represents the conditions in the area. It is also relatively close to the Point Lepreau Bird Observatory, being approximately 37 km away. I extracted hourly data (1000-1400h AST) for March 30th to May 9th from 2000 – 2017. Direct observational tide data through tide gauges within the Bay of Fundy had inconsistent coverage throughout migration season in some years; thus, hourly tidal data were provided by the Canadian Hydrographic Service from their predictive tidal model for the same time period described above. As there were four hours of data per session and afternoon migration was modelled on a daily scale, I used the median values of weather variables to represent the afternoon period in model building. The median values were used over maximum or minimum values because one could not be justifiably chosen over the other.

Wind directional data in this database are collected on a circular 360° scale in 10-degree intervals and are difficult to include as a continuous variable in linear modelling techniques unadjusted. I combined wind direction and speed components into wind vectors using methodology analogous to fetch estimation by Cattaneo (1990). Specifically, I first defined a migration corridor along the general direction migrants are flying through the Bay of Fundy (i.e., southwest to northeast). This migration corridor runs in a straight line between Portland, ME, USA (43.659°N, 70.257°W) and a point

approximating the end of the Bay of Fundy, which I call the terminus (45.598°N, 64.847°W) (see Figure 1). These points were selected as the coastline maintains a reasonably consistent angle between them, in comparison to locations more south than Portland. I transformed the 360° direction scale into two equivalent and linear 180° scales around the migration corridor. The angle of this migration corridor was measured to be approximately 30° north of due east (i.e., 60° on a 360° directional chart); therefore, the migration corridor runs from 240° to 60°. For each of the 132 days between 2000 and 2016 with morning and afternoon data collection, I calculated the angles at which the wind directions met this migration corridor (e.g., wind from 265° or 215° creates an angle of 25°, wind from 25° or 85° creates an angle of 155°). This gives angular values between 0° and 180°. By taking the cosine of these angles, I created wind directional scores between 1 (0°) and -1 (180°). Lastly, I multiplied these scores by their respective wind speed to give a wind vector where higher positive values indicate strong tailwind conditions and higher negative values indicate strong headwind conditions.

I assumed migrants would not be affected differently by wind drift inland or seaward and so differences between whether the wind direction met the migration corridor from its northern or southern side were ignored as it would result in a net beneficial, neutral, or detrimental effect regardless. The formula for wind vector calculation is:

$$Wvec = \cos(yi) * WS$$

where $Wvec$ is the wind vector, yi is the angle the wind direction meets the migration corridor, and WS is wind speed.

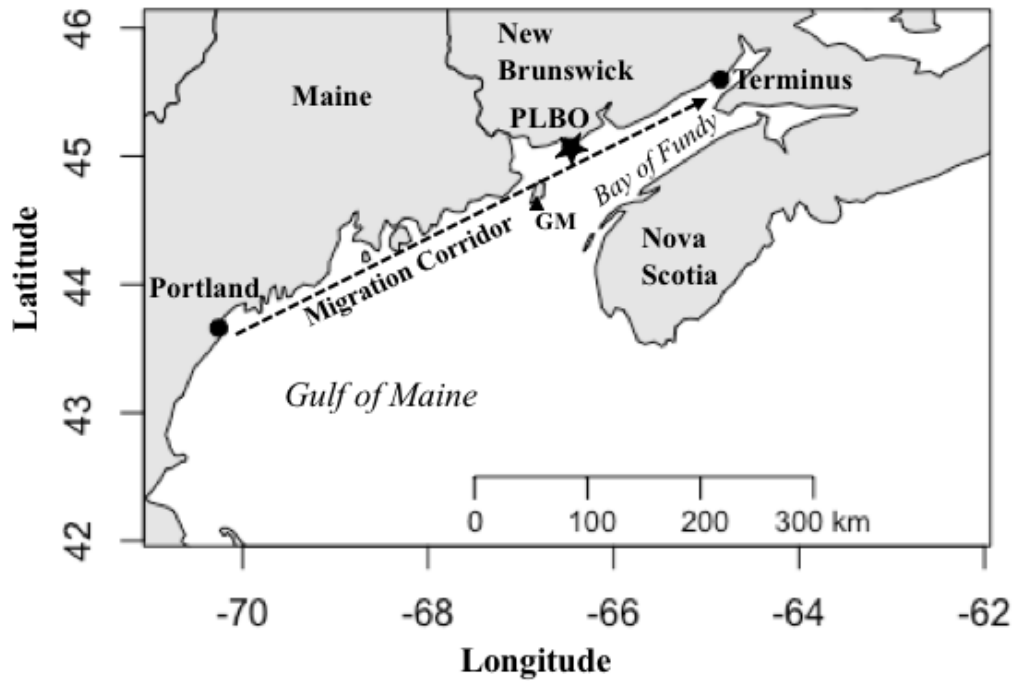


Figure 1. Regional map of the linear migration corridor (dashed arrow line) between Portland ME, USA, and the terminus of the Bay of Fundy (black dot). Also shown are the relative positions of the Point Lepreau Bird Observatory (PLBO, black star), and the Grand Manan weather station (GM, black triangle) in the Bay of Fundy. Latitude displayed on -90 (South) to 90 (North) scale and longitude on -180 (West) to 180 (East) scale.

Modelling Afternoon Migration Rates

All modelling and statistical analyses were done using R statistical software version 3.3.3 (R Core Team, 2017). For each of the five species, I modelled the effects of daily morning migration rates and afternoon environmental conditions on afternoon migration rates with generalized linear mixed models (GLMM) using the glmmADMB package (Skaug *et al.*, 2016). To account for over-dispersion in the count data, I used a negative binomial distribution with a log-link function. I built a candidate model set of eight models (Table 2), including an intercept only null model, using all combinations except interactions of my predictor variables (morning migration rate, median tidal height, and median wind vector) except interactions over 132 days between 2000 and 2016 where both morning and afternoon data had been collected. I included Year as a random term in every model to account for inter-annual variability in the dataset. Model likelihood was assessed using Akaike's Information Criterion for small sample sizes (AICc), ranked for greatest influence according to AICc weights (Burnham and Anderson, 2002). If there was no clear dominant model (i.e., AICc $wt > 0.9$), model averaging was used with the MuMIn package (Bartoń, 2016) on all models with model weight.

Estimating Afternoon Migration Rates

For each of the five species, I used three methods (termed A, B, and C) to estimate daily afternoon migration rates for 23 days where both morning and afternoon data were collected in 2017. Data were collected over 29 days, but estimates could only be generated for 23 of the 29 days because of wind anemometer error over the first six

days of collection. Method A used the top ranked or averaged model with morning migration data and environmental data over the 132 days between 2000 and 2016 (from Modelling Afternoon Migration Rates above). Method B estimated afternoon migration rates assuming that afternoon and morning migration rates were equivalent. Method C generated afternoon migration rate estimates assuming that afternoon migration rate was a consistent proportion of the morning migration rate based on the ratio of mean afternoon and morning migration rates over 132 days between 2000 and 2016 (Table 3). A sample calculation for each method can be found in Table 4.

Table 2. Eight candidate models for combinations of three parameters (morning migration rate [MR], wind vector [Wvec], and tidal height [TH]) for modelling afternoon migration rates of Black Scoter, Surf Scoter, White-winged Scoter, Red-throated Loons, and Common Loons over 132 spring days between March 30 and May 9, 2000 – 2016 at the Point Lepreau Bird Observatory in the Bay of Fundy.

Model	Parameters Included
1	Null (intercept only)
2	MR+Intercept
3	Wvec+Intercept
4	TH+Intercept
5	MR+ Wvec +Intercept
6	MR+TH+Intercept
7	Wvec +TH+Intercept
8	MR+ Wvec +TH+Intercept

Table 3. Mean morning and afternoon migration rates (birds/h) and the ratio of mean afternoon to morning migration rates for Black Scoter (BLSC), Surf Scoter (SUSC), White-winged Scoter (WWSC), Red-throated Loon (RTLO), and Common Loon (COLO) over 132 spring days between 2000 and 2016 at Point Lepreau Bird Observatory in the Bay of Fundy.

Session	BLSC	SUSC	WWSC	RTLO	COLO
Morning	414.44	160.08	8.14	6.57	1.88
Afternoon	270.48	75.61	6.63	5.36	1.55
Ratio (A/M)	0.65	0.47	0.82	0.82	0.82

Table 4. Sample calculations showing the estimated afternoon migration rate (AR) for a morning migration rate of 100 Black Scoter using three methods: A) model that included morning migration rates (MR) and environmental parameters (tidal height [TH] and wind vector [Wvec]), B) afternoon rates equal morning rates, and C) afternoon rates are a fixed proportion of morning rates based on the ratios presented in Table 3.

Estimation Method	Morning Migration Rate	Estimated Afternoon Migration Rate
A	100	Function of MR, TH, and Wvec
B	100	AR = MR; 100 = 100
C	100	AR = MR×0.65; 65 = 100×0.65

Evaluating Model Predictions

For each of my five focal species, I compared the predicted daily afternoon migration rates generated using the three methods outlined above (Estimating Afternoon Migration Rates) to the actual observed afternoon migrations collected over 23 days in 2017. I calculated the mean relative prediction error for each of the three predictive methods as:

$$\frac{|(\text{Mean 2017 Observed Rate} - \text{Mean 2017 Predicted Rate})|}{\text{Mean 2017 Observed Rate}}$$

Means were used to circumvent the high frequency of zeros present in the observed migration rates for White-winged Scoters, Red-throated Loons, and Common Loons. Additionally, predictions were evaluated using a cumulative running count of the net difference between predictions and observations over the 23 days to get a sense of the total number of birds per hour predictions differed by over the entire migration season. The mean relative prediction errors and cumulative running differences of three predictive methods were compared intra-specifically (i.e., which was lowest) to determine if inclusion of environmental data (Method A) improved predictions over more simplistic techniques (Methods B and C). The predictive method resulting in the best predictions for the most species was used to estimate afternoon migration rates over a total of 484 days between 2000 and 2016, where only morning migration data were recorded, and then used to generate mean annual afternoon migration rates from 2000 to 2017.

Trends in Migration Rates

As collected afternoon migration data are limited prior to 2016 and the prediction of afternoon rates relies on using morning data, only migration rates from the morning sessions themselves were used in these analyses. For each species, I used GLMM with a negative binomial distribution and log-link function to examine the effect of year (continuous) on morning migration rates over 645 days between 2000 and 2017. Day of the Year (DOY; e.g., January 1 is DOY 1 and December 31 is DOY 365/366) was included as a random term in all models to account for intra-annual variability in the dataset. I compared these models to intercept only null models (representing no change over time) for each of the five species using the same AICc approach as described above (see Modelling Afternoon Migration Rates) to assess whether migration rates have changed between 2000 and 2017.

Results

Modelling Afternoon Migration Rates

Afternoon migration rates increased with higher morning migration rates and tidal heights for all species (Figures 2 and 3). The effect of tidal height was strongest for Surf Scoter, White-winged Scoter, and Red-throated Loon migration rates (Figures 3.2 – 3.4). For Surf Scoters in particular, all but one afternoon with migration rates higher than 200 occurred near or above a tidal height of five meters (Figure 3.2). Afternoon migration rates increased with rising wind vectors for all species but Common Loons (Figures 4.1 – 4.4), which had a weakly negative relationship (Figure 4.5).

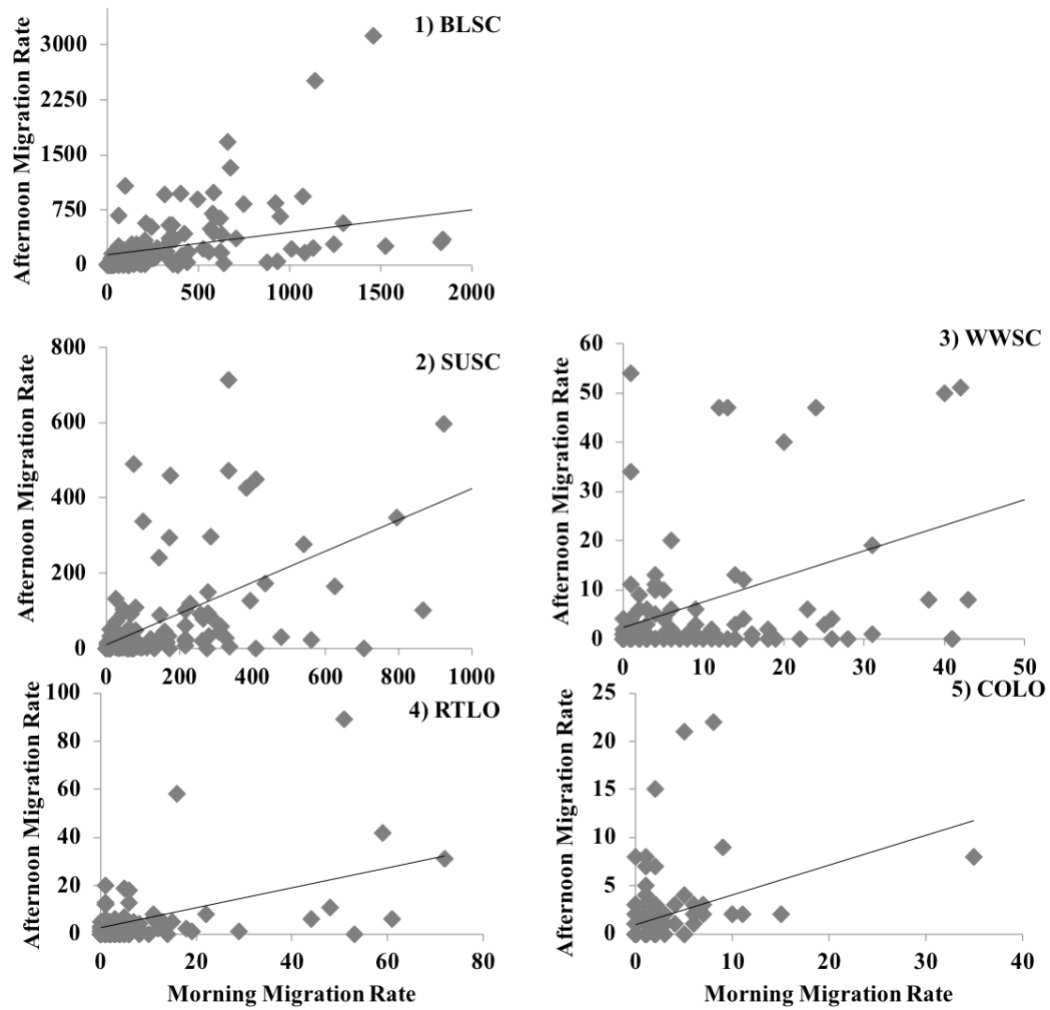


Figure 2. Relation of morning migration rates (birds/h) and afternoon migration rates (birds/h) for: 1) Black Scoter (BLSC), 2) Surf Scoter (SUSC), 3) White-winged Scoter (WWSC), 4) Red-throated Loon (RTLO), and 5) Common Loon (COLO) over 132 spring days between March and May 2000 – 2016, at the Point Lepreau Bird Observatory in the Bay of Fundy.

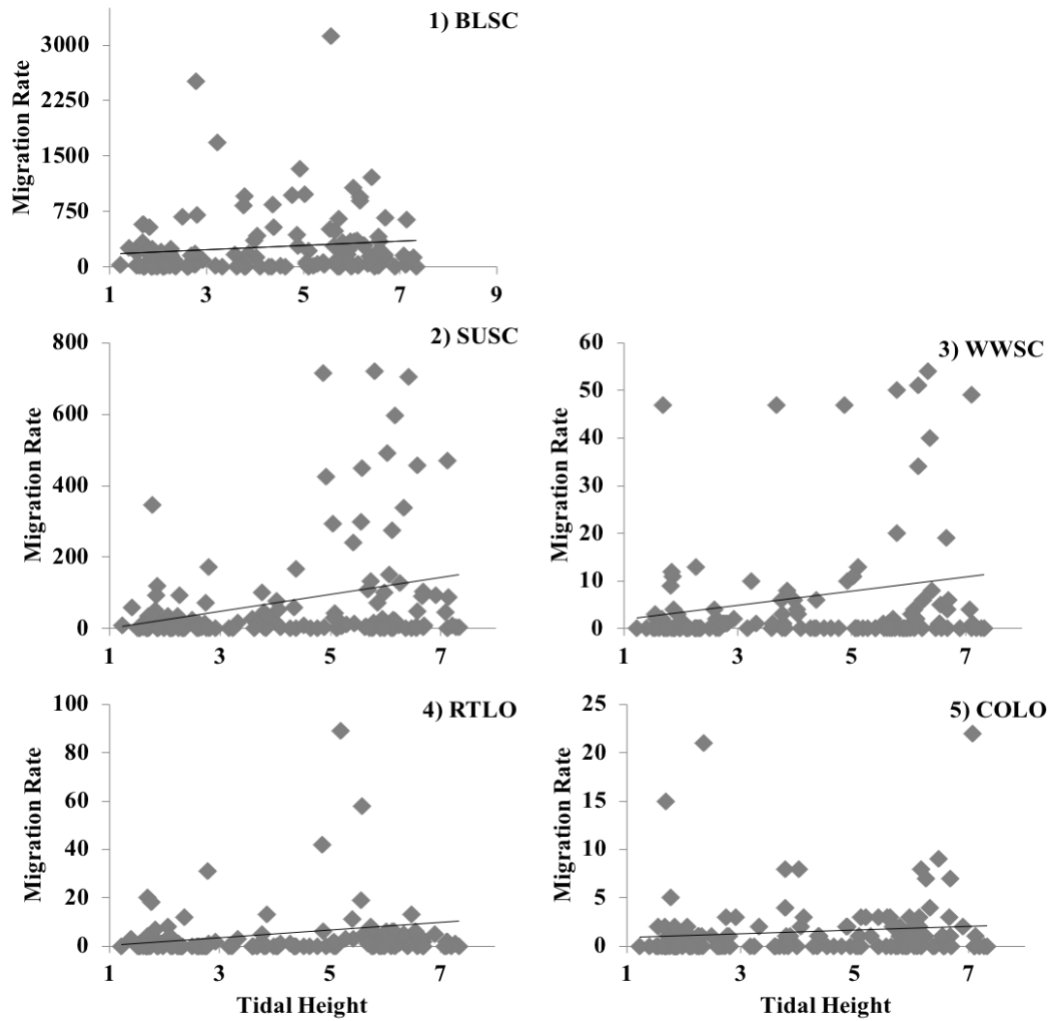


Figure 3. Relation of tidal height (m) and afternoon migration rates (birds/h) for: 1) Black Scoter (BLSC), 2) Surf Scoter (SUSC), 3) White-winged Scoter (WWSC), 4) Red-throated Loon (RTLO), and 5) Common Loon (COLO) over 132 spring days between March and May 2000 – 2016, at the Point Lepreau Bird Observatory in the Bay of Fundy.

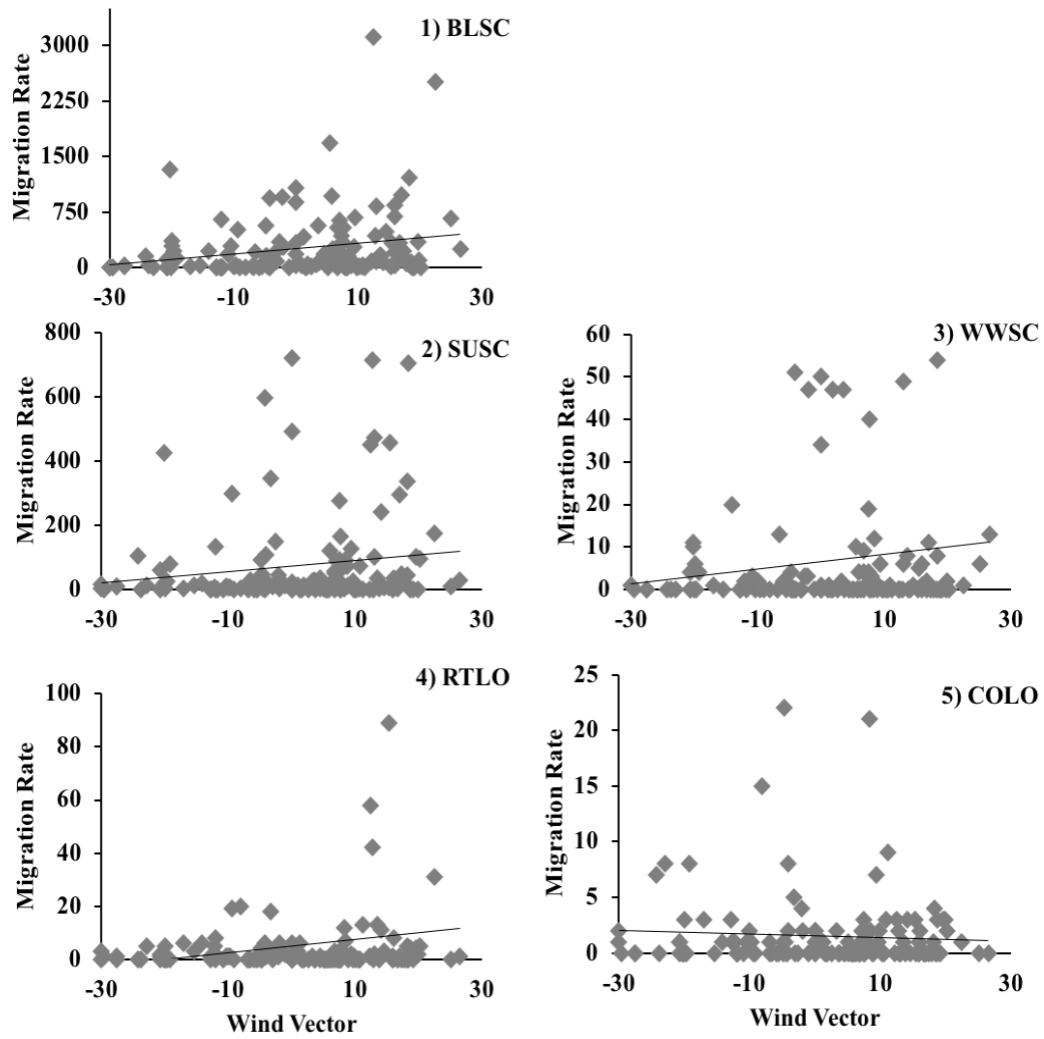


Figure 4. Relation of wind vector and afternoon migration rates (birds/h) for: 1) Black Scoter (BLSC), 2) Surf Scoter (SUSC), 3) White-winged Scoter (WWSC), 4) Red-throated Loon (RTLO), and 5) Common Loon (COLO) over 132 spring days between March and May 2000 – 2016, at the Point Lepreau Bird Observatory in the Bay of Fundy.

For all species, the top four candidate models comprised > 99% of all model weight and included the terms morning migration rate alone, and morning migration rate with tidal height and/or wind vector (Tables 5 – 9). Model averaging was required for all species, but the global model (i.e., the model containing all parameters) had the most model weight for all except Common Loons and White-winged Scoters, for whom the weight distribution was comparatively more even amongst the four models (Tables 5 – 9). For all species, parameter estimates show afternoon migration rates increased with morning migration rates and tidal height (Table 10). However, tidal height parameter estimates for Black Scoters, White-winged Scoters, and Common Loons bound zero with standard error suggesting the effect is weak for these species (Table 10). Also, parameters estimates show afternoon migration rates increased positively with wind vector for all species except Common Loons, where it decreased (Table 10). However, these parameter estimates bound zero with standard error for all species but Black Scoter (Table 10). This suggests the effect of wind on afternoon migration is weak. Individual parameter likelihoods show morning migration rate was the most important variable for modelling afternoon migration in all species except Surf Scoter where tidal height was equally important (Table 10). Wind vector was the least important variable for every species but Black Scoter (Table 10).

Table 5. Number of parameters (k), log-likelihood, ΔAICc , and AICc weights (wt) for eight models of Black Scoter afternoon migration rates during 132 spring days between March and May 2000 – 2016, in the Bay of Fundy.

Model	k	logLik	ΔAICc	wt
MR+TH+Wvec	6	-810.736	0.000	0.460
MR+Wvec	5	-812.660	1.650	0.201
MR	4	-813.885	1.940	0.174
MR+TH	5	-812.860	2.050	0.165
Wvec+TH	5	-820.764	17.86	0.000
Wvec	4	-823.306	20.78	0.000
TH	4	-826.279	26.73	0.000
Null	3	-827.754	27.55	0.000

Table 6. Number of parameters (k), log-likelihood, ΔAICc , and AICc weights (wt) for eight models of Surf Scoter afternoon migration rates during 132 spring days between March and May 2000 – 2016, in the Bay of Fundy.

Model	k	logLik	ΔAICc	wt
MR+TH+Wvec	6	-583.590	0.000	0.573
MR+TH	5	-584.989	0.600	0.424
MR+Wvec	5	-590.823	12.27	0.001
MR	4	-592.243	12.95	0.001
Wvec+TH	5	-599.948	30.52	0.000
TH	4	-601.552	31.57	0.000
Wvec	4	-607.843	44.15	0.000
Null	3	-609.899	46.13	0.000

Table 7. Number of parameters (*k*), log-likelihood, ΔAICc , and AICc weights (*wt*) for eight models of White-winged Scoter afternoon migration rates during 132 spring days between March and May 2000 – 2016 in the Bay of Fundy.

Model	k	logLik	ΔAICc	<i>wt</i>
MR+TH	5	-284.169	0.000	0.321
MR	4	-285.413	0.330	0.272
MR+TH+Wvec	6	-283.538	0.930	0.201
MR+Wvec	5	-284.663	0.990	0.196
Wvec+TH	5	-288.405	8.470	0.005
TH	4	-289.845	9.190	0.003
Wvec	4	-290.671	10.84	0.001
Null	3	-292.270	11.91	0.001

Table 8. Number of parameters (*k*), log-likelihood, ΔAICc , and AICc weights (*wt*) for eight models of Red-throated Loon afternoon migration rates during 132 spring days between March and May 2000 – 2016 in the Bay of Fundy.

Model	k	logLik	ΔAICc	<i>wt</i>
MR+TH+Wvec	6	-273.099	0.000	0.500
MR+TH	5	-274.589	0.780	0.338
MR+ Wvec	5	-275.716	3.040	0.109
MR	4	-277.594	4.630	0.049
Wvec+TH	5	-279.446	10.50	0.003
Wvec	4	-282.321	14.09	0.000
TH	4	-283.313	16.07	0.000
Null	3	-286.161	19.64	0.000

Table 9. Number of parameters (*k*), log-likelihood, ΔAICc , and AICc weights (*wt*) for eight models of Common Loon afternoon migration rates during 132 spring days between March and May 2000 – 2016 in the Bay of Fundy.

Model	k	logLik	ΔAICc	<i>wt</i>
MR	4	-202.939	0.000	0.321
MR+TH	5	-202.071	0.43	0.260
MR+Wvec	5	-202.152	0.59	0.239
MR+TH+Wvec	6	201.359	1.200	0.176
TH	4	-208.145	10.41	0.002
Wvec+TH	5	-207.794	11.87	0.001
Null	3	-210.309	12.61	0.001
Wvec	4	-209.913	13.95	0.000

Table 10. Parameter estimates (Estimate), unconditional standard errors (SE), and Parameter likelihoods (Likelihood) from averaged models for: 1) Black Scoter (BLSC), 2) Surf Scoter (SUSC), 3) White-winged Scoter (WWSC), 4) Red-throated Loon (RTLO), and 5) Common Loon (COLO) describing the relationship between afternoon migration rate, and morning migration rate (MR), tidal height (TH), and wind vector (Wvec) over 132 spring days between March and May 2000 – 2016, at the Point Lepreau Bird Observatory in the Bay of Fundy.

Species	Parameter	Likelihood	Estimate	SE
BLSC	Intercept	1.0000	4.34657	0.41709
	MR	1.0000	0.00149	0.00037
	TH	0.6200	0.08576	0.09023
	Wvec	0.6600	0.01351	0.01303
SUSC	Intercept	1.0000	1.78256	0.36707
	MR	1.0000	0.00406	0.00093
	TH	1.0000	0.30497	0.07776
	Wvec	0.5700	0.01056	0.01217
WWSC	Intercept	1.0000	0.47922	0.62026
	MR	0.9900	0.06781	0.02497
	TH	0.5300	0.09877	0.12683
	Wvec	0.4000	0.00791	0.01426
RTLO	Intercept	1.0000	-0.30354	0.61108
	MR	1.0000	0.05218	0.01751
	TH	0.8400	0.19263	0.12272
	Wvec	0.6400	0.01612	0.01712
COLO	Intercept	1.0000	-0.44215	0.39868
	MR	0.1000	0.16706	0.05954
	TH	0.4400	0.04580	0.07442
	Wvec	0.4200	-0.00562	0.00973

Evaluating Model Predictions

Mean differences between predicted and observed afternoon migration rates for 23 days during 2017 (Figure 5) and mean relative prediction errors (Table 11) were lowest for method C for all species but Red-throated Loons, where method A was the lowest. These trends are also shown in the daily net differences (Figure 6) and running cumulative differences (Figures 7) between predicted and observed afternoon migrations where method C deviates less from zero, on the daily and whole-season scale, respectively, than other methods for all species except Red-throated Loons (Figures 6.4 and 7.4). Across the majority of species, method C predicts afternoon migration rates consistently closer to observed values than the other methods. Additionally, trends in Figures 6.2, 6.4, and 6.5 showed several anomalous days where predictions generated from method A were many-fold greater than those of the two other methods for Surf Scoter (Day 13, Figure 6.2), Red-throated Loon (Day 29, Figure 6.4), and Common loon (Days 10 and 29, Figure 6.5).

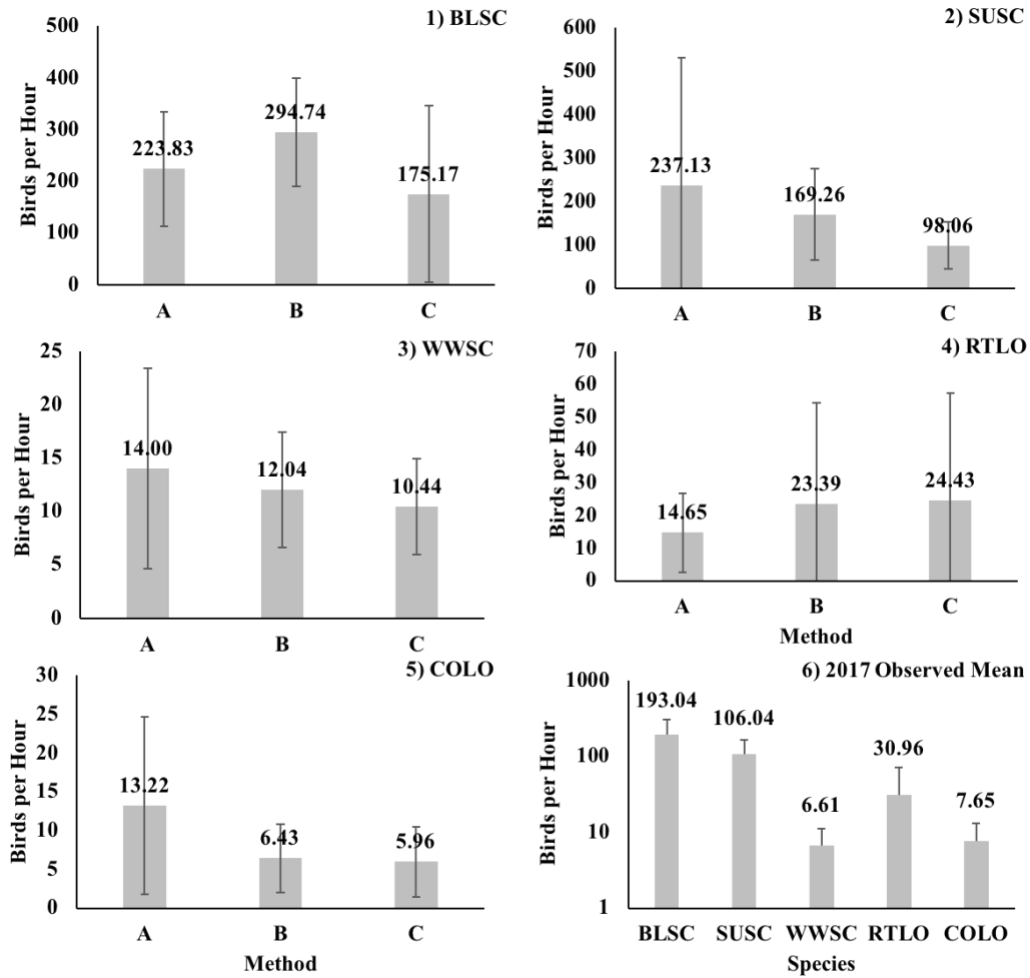


Figure 5. Mean differences (birds/h; +/- 95% CI) between observed and predicted afternoon migration rates for: 1) Black Scoter (BLSC), 2) Surf Scoter (SUSC), 3) White-winged Scoter (WWSC), 4) Red-throated Loons (RTLO), and 5) Common Loons (COLO) from three methods: A) averaged model that included morning migration rates and environmental parameters, B) afternoon rates equal morning rates, and C) afternoon rates are a fixed proportion of morning rates. 6) 2017 mean observed afternoon migration rates (birds/h; +95% CI) for the five focal species on logarithmic scale. Data were collected over 23 days during March and May 2017, at the Point Lepreau Bird Observatory in the Bay of Fundy.

Table 11. Mean relative prediction errors for Black Scoter (BLSC), Surf Scoter (SUSC), White-winged Scoter (WWSC), Red-throated Loon (RTLO), and Common Loon (COLO) over 23 spring days in 2017 at the Point Lepreau Bird Observatory in the Bay of Fundy. Predictions used three methods: A) averaged model that included morning migration rates and environmental parameters, B) afternoon rates equal morning rates, and C) afternoon rates are a proportion of morning rates.

Species	Method A	Method B	Method C
BLSC	115.9	152.7	90.74
SUSC	223.6	159.6	92.47
WWSC	211.8	182.2	157.9
RTLO	47.33	75.56	78.91
COLO	172.7	84.09	77.84

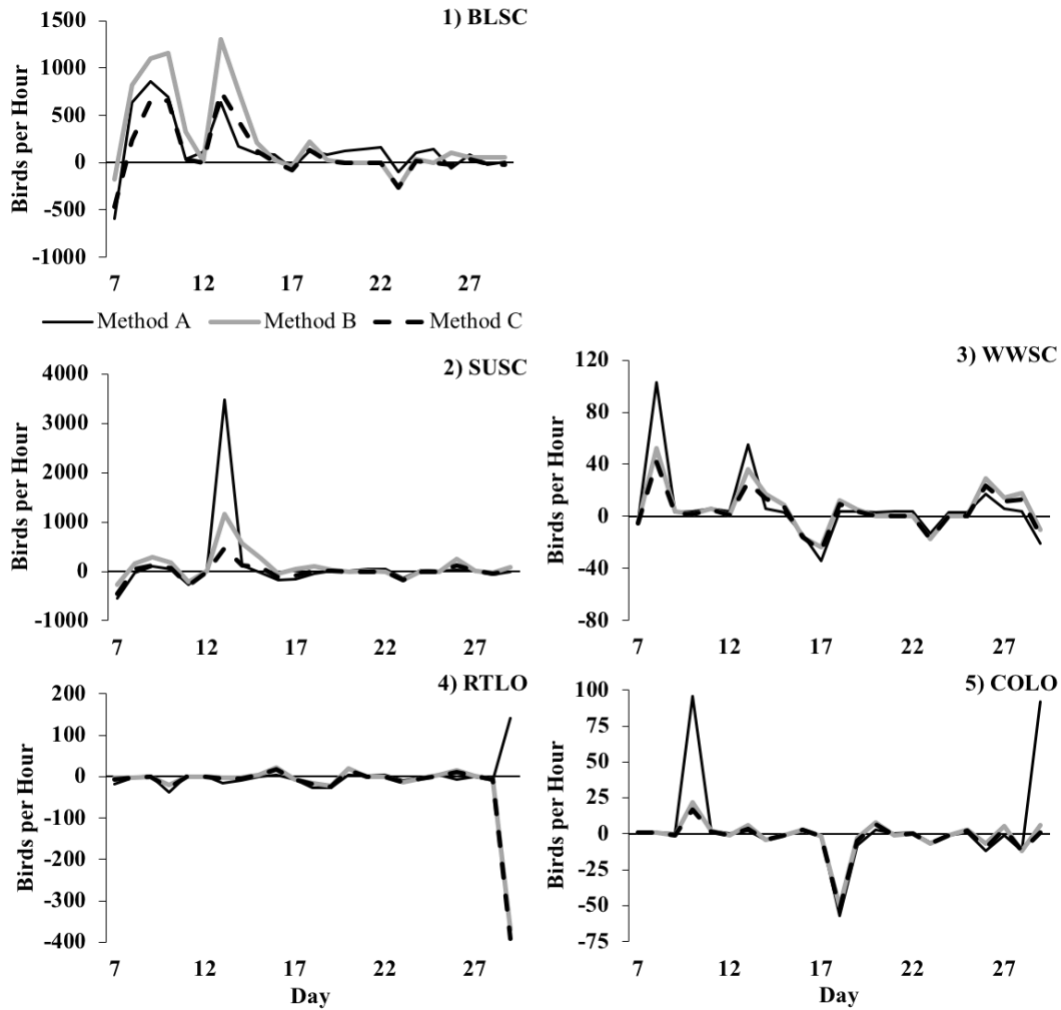


Figure 6. Daily net differences (birds/h) between observed and predicted afternoon migration rates for: 1) Black Scoter (BLSC), 2) Surf Scoter (SUSC), 3) White-winged Scoter (WWSC), 4) Red-throated Loons (RTLO), and 5) Common Loons (COLO) from three methods: A) averaged model that included morning migration rates and environmental parameters, B) afternoon rates equal morning rates, and C) afternoon rates are a fixed proportion of morning rates. Data were collected over 23 days during March – May 2017, at the Point Lepreau Bird Observatory in the Bay of Fundy.

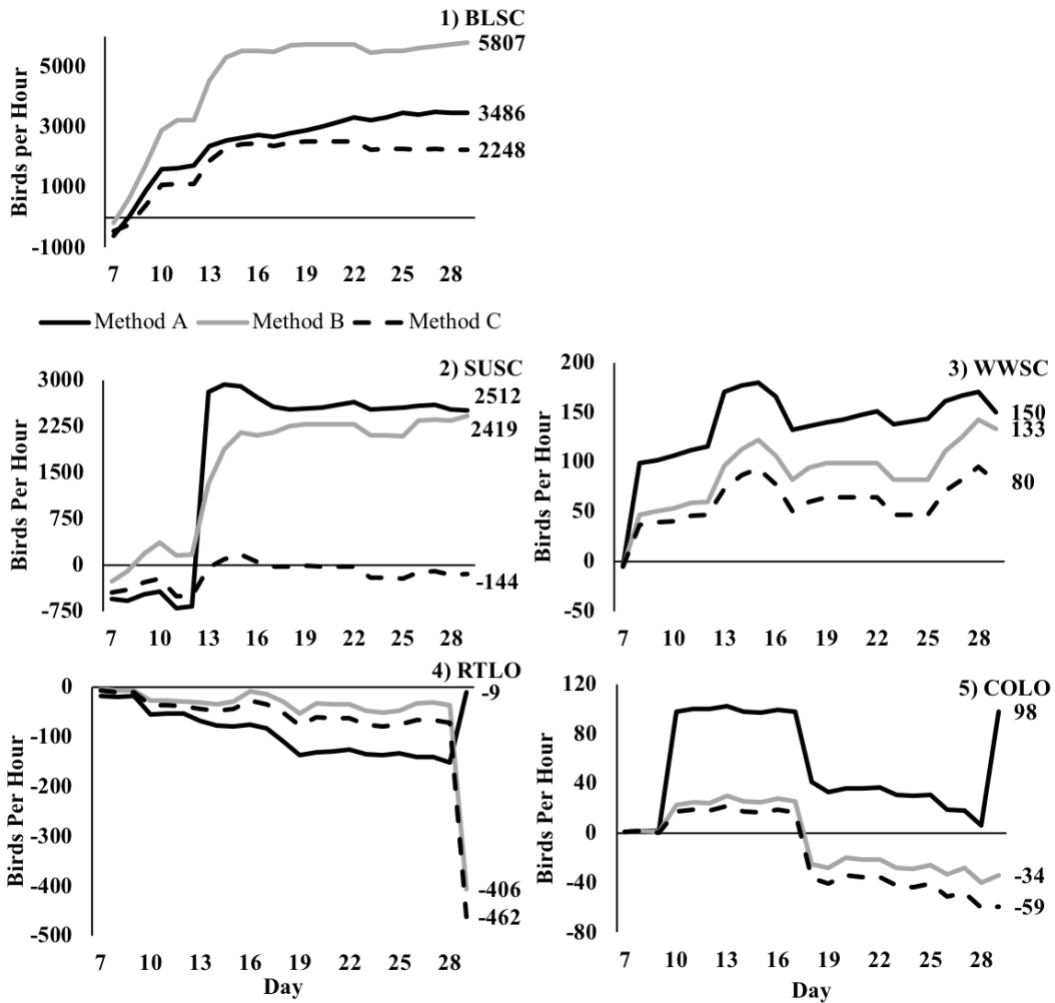


Figure 7. Running cumulative net differences (birds/h) between observed and predicted afternoon migration rates for: 1) Black Scoter (BLSC), 2) Surf Scoter (SUSC), 3) White-winged Scoter (WWSC), 4) Red-throated Loons (RTLO), and 5) Common Loons (COLO) from three methods: A) averaged model that included morning migration rates and environmental parameters, B) afternoon rates equal morning rates, and C) afternoon rates are a fixed proportion of morning rates. Data were collected over 23 days during March – May 2017, at the Point Lepreau Bird Observatory in the Bay of Fundy.

Estimating Afternoon Migration Rates

Estimates of afternoon migration rates were highest for Black and Surf Scoters throughout all years, with the Black Scoter notably higher on average (Table 12). White-winged Scoters and Red-throated Loons migration estimates were much lower than Black and Surf Scoters but still several times greater than those of Common Loon. There were a greater number of days with estimated afternoon migration rates than observed rates in all years but 2016 and 2017.

Trends in Migration Rates

Trends in mean annual morning migration rates for Black Scoter, Surf Scoter, and White-winged Scoter declined over the 18 years used in my study (Figures 8.1 – 8.3). Red-throated Loons and Common Loons showed an increasing trend (Figures 8.4 and 8.5). Additionally, for all species, daily morning migration rates were highly variable, and years with highest mean migration rates tended to have higher variability (Figure 8). For all species, the model including the parameter Year received more model weight than the null (Table 13), indicating changes in mean morning migration over 18 years. Similar to the overall trend data, parameter estimates and standard errors for the three scoter species suggest a decline in migrating populations, whereas parameter estimates and stand errors for the two species of loon suggest increasing migrating populations (Table 13).

Table 12. Annual mean afternoon migration rates (birds/h) for Black Scoter (BLSC), Surf Scoter (SUSC), White-winged Scoter (WWSC), Red-throated Loon (RTLO), and Common Loon (COLO) in the Bay of Fundy between March and May 2000 – 2017, with 18-year grand means, 95% CIs, numbers of afternoon counting sessions (ACS), and numbers of predicted afternoon counting sessions (PACS) each year.

Year	ACS	PACS	BLSC	SUSC	WWSC	RTLO	COLO
2000	3	31	343	223	11	13	2
2001	12	23	269	117	11	5	3
2002	12	26	330	70	10	8	2
2003	12	29	278	88	7	4	2
2004	14	23	193	94	11	6	2
2005	8	28	258	68	5	4	2
2006	9	29	240	90	10	12	2
2007	4	36	213	77	9	9	3
2008	8	29	235	120	9	2	4
2009	6	29	167	78	4	12	4
2010	3	36	207	72	9	13	4
2011	7	23	146	43	6	4	2
2012	5	29	191	69	10	20	6
2013	1	29	304	61	6	17	3
2014	4	31	235	87	8	6	2
2015	4	30	309	62	5	8	2
2016	23	13	244	61	4	8	4
2017	29	7	237	67	8	9	4
18-year Mean	-	-	244	86	8	9	3
95% CI	-	-	29.1	13.9	1.19	1.82	0.58

Table 13. Year parameter estimate, unconditional standard errors (SE), number of parameters (k), log likelihood, ΔAICc , and AICc weights (wt) for models evaluating change in annual Black Scoter (BLSC), Surf Scoter (SUSC), White-winged Scoter (WWSC), Red-throated Loon (RTLO), and Common Loon (COLO) morning migration rates over 645 days between March and May 2000 – 2017, at the Point Lepreau Bird Observatory in the Bay of Fundy.

Species	Model	Estimate	SE	k	LogLik	ΔAICc	wt
BLSC	Year	-0.0214	0.0100	4	-4366.3	0.00	0.780
	Null			3	-4368.6	2.53	0.220
SUSC	Year	-0.0223	0.0120	4	-3701.2	0.00	0.694
	Null			3	-3703	1.63	0.306
WWSC	Year	-0.0219	0.0114	4	-1978.2	0.00	0.694
	Null			3	-1980.2	1.65	0.306
RTLO	Year	0.0235	0.0109	4	-2028.6	0.00	0.780
	Null			3	-2030.9	2.53	0.220
COLO	Year	0.0288	0.0111	4	-1301.7	0.00	0.913
	Null			3	-1305	4.69	0.087

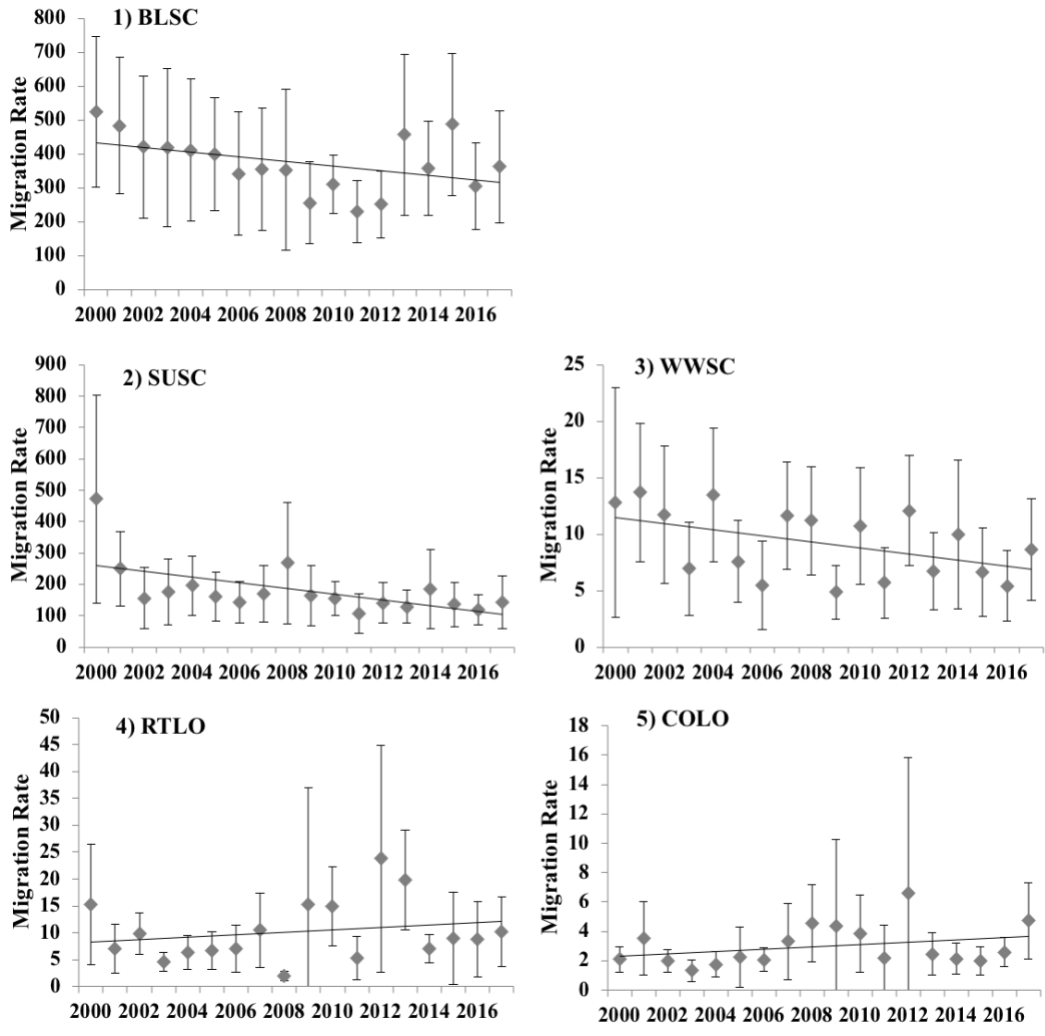


Figure 8. Mean annual morning migration rates (birds/h; +/- 95% CI) for: 1) Black Scoter (BLSC), 2) Surf Scoter (SUSC), 3) White-winged Scoter (WWSC), 4) Red-throated Loon (RTLO), and 5) Common Loon (COLO) over 645 spring days between March and May 2000 – 2017, at the Point Lepreau Bird Observatory in the Bay of Fundy.

Discussion

The Point Lepreau Bird Observatory migration monitoring project has successfully recorded spring marine bird migration in the Bay of Fundy for over 20 years. Increased interest has been raised recently in the use of coastal, fixed location count sampling, like that employed at Point Lepreau, for species inadequately sampled using common aerial survey techniques (e.g., scoter species and Red-throated Loons). To date, three studies have attempted to estimate numbers of Bay of Fundy scoter migrants using the Point Lepreau database (Bond *et al.*, 2007; Cameron, 2014; Button, 2015). However, uncertainty regarding the accuracy of estimates from this database have been raised because of the comparative imbalance of morning and afternoon data collection (Button, 2015). In this study, I examined if afternoon migration rates could be accurately modelled using available data (i.e., morning migration rates and environmental data) for five species: Black Scoter, Surf Scoter, White-winged Scoter, Red-throated Loon, and Common Loon. This was done with the objectives of understanding the role of environmental factors (tide height, and wind speed and direction) in migration rates and retroactively estimating afternoon migration rates during spring days between 2000 and 2017. I predicted afternoon migration rates would be greater on days with higher morning migration, during higher tidal heights, and stronger tailwind wind conditions. I found afternoon migration was most strongly associated with higher morning migration, tidal heights, and strong tailwinds in competing models for the majority of species. However, predictions from the simpler proportional models based off morning migration rate alone performed better (i.e., were better predictors) than the models containing these environmental parameters for all

species except Red-throated Loons. This method (i.e., afternoon migration rates are a fixed proportion of morning migration rates) was used to estimate afternoon migration rates on 484 dates between 2000 and 2017 where only morning migration sampling occurred. I found morning migration rates between 2000 and 2017 decreased for scoter species and increased for loons.

Modelling Afternoon Migration Rates

I found spring afternoon migration generally increased as morning migration, tidal heights, and wind vector did for Black Scoter, Surf Scoter, White-winged Scoter, Red-throated Loon, in the Bay of Fundy. Afternoon migration rates for Common Loons varied positively with morning migration rates and tidal height but negatively with wind vector. I predicted migration rates would be higher during stronger winds from a tailwind direction, represented in the analysis as more positive wind vector values. This hypothesis was supported for all species but Common Loons; however, I found wind vector to have a very weak influence individually on all species but Black Scoter, where the effect of wind was still much weaker than morning migration rate. This was unexpected given it is more energy efficient to fly downwind, especially during migration when energy budgeting is critical to individual survival and reproductive success (Newton, 2008). However, wind tends to blow stronger and more consistently over oceans, given the reduced friction experienced over water compared to land (Spear and Ainley, 1997). This means birds in a marine environment are near constantly exposed to wind and have evolved adaptations to deal with frequently adverse conditions.

Scoters and loons, for example, have comparatively small wing area for their size when compared to other marine birds like Procellariiformes (Spear and Ainley, 1997). As a result, they have high wing loading (body mass/wing area) and rely on flight by continuous wing beats (Zydelis and Richman, 2015), as opposed to the more energy efficient soaring or gliding found in species with low wing loading like albatross (family *Diomedidae*). The continuous beating of their wings results in high speed of flight for these species; for example, Bergman and Donner (1964) found Common Scoters (*M. nigra*) travelled at an average of 84 km/h during spring migration in Southern Finland. Given the limited morphometric differences among scoter species with respect to wing and body ratios, it is likely Black, Surf, and White-winged can migrate at a similar speed. Through their high mass and by flying at greater speeds, they are less affected by wind drift through inertial force than, for example, smaller, lighter species such as passerines (*Passeriformes* spp.). Desholm (2003) found geese (*Anser* and *Branta* spp.) and Common Eiders (*Somateria mollissima*) migrating in Denmark deviated minimally from straight-line flight over water between areas, regardless of wind conditions encountered. Black Scoter may be more influenced by wind than other scoter species as they are slightly smaller in overall body size and weight (Brown and Fredrickson, 1997; Savard *et al.*, 1998; Bordage and Savard, 2011).

Afternoon migration was higher during periods of greater tidal heights in all five species; however, the individual influence of tides was found to be weak for all but Surf Scoters and Red-throated Loons. This result was unexpected as foraging in shallower water, especially in a hyper-tidal, high energy region like the Bay of Fundy, where differences in daily high and low tides are several meters, could conserve substantial

energy. Though, how often these species feed during migration remains unknown and, despite common sightings of scoters and loons foraging during counting sessions at the Point Lepreau Bird Observatory, they may not always be feeding within the Bay of Fundy. Major stopover sites for refueling, like the Saint Lawrence Estuary for scoters, are consistently used each year by large numbers of migrants (Petersen and Savard, 2015). The frequency of stopovers during the whole of migration is dependent on a bird's overall migratory condition and would vary greatly both between and among individuals in a population year to year (Newton, 2008; Petersen and Savard, 2015).

Scoters are known to be opportunistic predators and tend to aggregate in high prey density areas to feed (Zydalis and Richman, 2015). Therefore, the availability of resources is likely to be a more important factor in efficient foraging than depth of water, as foraging where appropriate prey are most plentiful would yield a greater energetic return than diving in shallower water with more scarce food resources. Additionally, scoters are unlikely to feed daily as they often display gorge-feeding behaviours at stopover sites (e.g., Saint Lawrence Estuary) during migration, where they remain in an area feeding for an extended period of time (Zydalis and Richman, 2015). Therefore, tidal height may only factor into migration decisions on days when and in locations where feeding occurs. This being said, Bay of Fundy tides can vary by meters over the course of a four-hour counting session; therefore, much variability in the data could have been lost by using a median tidal value in modelling. I found Surf Scoters were the only species where tidal height was as important a variable as morning migration rate. They may be more influenced by tides than other scoter species as their maximum dive depth (10 – 12 m) is comparatively shallow, only half that of Black

Scoter and less than half of White-winged Scoter (Zydelsis and Richman, 2015). They may be more restricted in when they can forage in these high prey density locations as a result and may have to take advantage of lower water levels more often at low tide than other scoter species. Additionally, Surf Scoter are known to increase foraging frequency as they travel further north during migration, even increasing in overall mass over the migration period (Anderson *et al.* 2009). The Bay of Fundy lies at the northern terminus of the Atlantic Flyway and Surf Scoters may begin foraging more frequently than other scoter species by the time they arrive there.

Inclusion of environmental variables in modelling afternoon migration resulted in worse predictions than either the morning rate alone or the proportional morning migration rates for all species but Red-throated Loons. This could be because migration timing is complex and depends more on a combination of individual conditions and their unique migratory states (Newton, 2008); in other words, their fitness to undertake migration and the urgency of the physiologic drive to do so. Therefore, variation in when individual birds and flocks can be expected relative to their condition and the date in the season (Alerstam and Hedenstrom, 1998). Scoters are very gregarious during migration, forming flocks more often than flying as individuals or pairs, and these flocks tend to aggregate together forming very large rafts on the water to roost (Brown and Fredrickson, 1997; Savard *et al.*, 1998; Barr *et al.*, 2000; Bordage and Savard, 2011). However, individuals and/or groups of scoter are routinely observed leaving larger floating rafts at different times throughout the day at the Point Lepreau Bird Observatory, likely because of differences in individual condition (e.g., fat reserves, fatigue, etc.). When morning migrations rates were elevated in the Bay of Fundy, it is

reasonable to expect more birds later in the day that did not migrate with the earlier groups, assuming most individuals will not roost for multiple days outside stop-over areas. Therefore, same day morning migration rate was likely the variable related most strongly to afternoon migration of those examined because it best relates to the migratory state of individuals and may include effects of other influences not explicitly included in my analysis.

Simplistic models explaining afternoon migration as a proportion of morning migration in the Bay of Fundy performed poorly but were comparatively superior in predicting afternoon migration than models including environmental variables. Inclusion of other untested environmental variables, or parameters that better describe individual variation in condition, may improve predictions from estimation models. The lack of accurate afternoon predictions from the three employed methodologies in this study emphasizes the usefulness of continuing afternoon migration sampling in the Bay of Fundy as sustained, balanced sampling will eliminate the need to estimate absent data and generate more accurate migration rates and confidence in derived trends over time. Accuracy is critical if this database is to be used effectively to monitor trends in migrating scoter and loon populations or evaluate effects of future developments in the Bay of Fundy on them.

Examining the trends of daily net differences between predicted and observed afternoon migration rates over 23 days in 2017 revealed several days with abnormally large differences between prediction methodologies. Specifically, predictions generated using environmental models (method A) were considerably larger than those from the other two methods for three species on days 10, 13, or 29. While this appears visually

suspect, it can be attributed to the modelling technique I used in this study. Count data requires the use of specific probability distributions, such as Poisson and Negative Binomial, that account for inherent over-dispersion within these kinds of data (Puig and Valero, 2006). These distributions are in the exponential family and describe the response variable as an exponential function of the predictor variable and its parameter estimate. Therefore, the exponential model will predict abnormally large estimates in the event the value of the predictor variable is itself sufficiently greater than the majority of data used to generate the model. With respect to this study, my analysis used morning migration as a predictive indicator of afternoon migration and the morning migration data on these three days in 2017 for Surf Scoter, Red-throated Loon, or Common Loon were eight, 16, and 15 times greater, respectively, than their mean morning migration rates between 2000 and 2017. Additionally, Red-throated Loon estimates from methods B and C drastically underpredicted afternoon migration on day 29 in 2017. This particular date had one of the highest Red-throated Loon migrations ever recorded at the Point Lepreau Observatory and was more heavily concentrated in the afternoon. As methods B and C predict afternoon migration as either exactly equal to or a fixed proportion of morning migration, substantial underpredictions were found on days where there were many more afternoon migrants than morning.

Estimating Afternoon Migration Rates

For the coastal migration monitoring sampling technique used at the Point Lepreau Bird Observatory, the pursuit of absolute abundance estimates to use in evaluating trends over time using is problematic in three main ways. First, afternoon migration data were collected on 161 of 645 possible days (i.e., ~25% of the time) from

2000 to 2017 and, while modelling afternoon rates as a proportion of the morning rates yielded the best comparative estimated rates, they predicted poorly overall. Second, this study limited data usage on two temporal scales, as I only included data from days between March 30th and May 9th and hours between 0600 and 1400 h AST. The migration season begins two weeks earlier in mid-March and, while this period is typically dominated by Common Eider migration, some movement of scoter and loons does take place (Point Lepreau Bird Observatory, unpublished data). In addition, migration occurs past 1400 h, again at a reduced rate, but later afternoon and evening sampling is very limited (Bond *et al.* 2007). Third, the Point Lepreau Bird Observatory uses observers to collect count data and some migrants flying outside of visual range are missed, including individuals or flocks too far into the Bay of Fundy for visual detection and those passing behind the observatory cutting overland across the peninsula. This behaviour is often noted with Common Loons flying at a greater altitude during rest periods. Furthermore, weather (e.g., fog) can directly influence detection probability of migrants by limiting range of visibility. Such variables were not included in these analyses but may impact results. Cumulatively, these three issues highlight how unlikely it is derived population estimates would be a correct or even close approximation of the true number of birds migrating through the Bay of Fundy. The use of relative abundance estimates, such as migration rates, are required with the Point Lepreau Bird Observatory dataset because sampling only occurs for half of each hour. As population estimates derived from this database would rely on using migration rates, and they have less associated estimation, it is more appropriate to use rates themselves in analyzing trends over time.

I found migration rates of Black and Surf Scoter were substantially higher than those of White-winged Scoter, Red-throated Loons and Commons during both the morning and afternoons between 2000 and 2017. These migration rates suggest the Bay of Fundy is an important migration corridor for North American Black and Surf Scoters wintering in the Atlantic. The Bay of Fundy does not appear to be an important migration corridor for either loon species, as their migration rates are low relative to their estimated Atlantic wintering populations of 90,000 Red-throated Loons (New Jersey Audubon Society) and 500,000 Common Loons (Evers *et al.*, 2010). No complete population estimates exist for White-winged Scoter for either coast of North America (Bowman *et al.* 2015). However, Bellrose (1980) estimated they may be the most populous of the three scoter species on both coasts and Johnsgard (2010) describes a pre-1950s report where more than 100,000 White-winged scoter were counted off the Massachusetts coast in a single day. Though, this information is dated and its applicability to present day is limited. The maximal fall count for White-winged Scoters at the Avalon Sea Watch was only 6,100 as of 2011 (New Jersey Audubon Society) and, although accounts by Bellrose (1980) and Johnsgard (2010) are extremely dated, it is doubtful the Atlantic wintering White-winged Scoter population has decreased so substantially. Therefore, the Avalon Sea Watch likely captures a very small proportion of the whole Atlantic population of White-winged Scoter and using their maximum fall count to estimate the entire Atlantic population may be inappropriate for this species. Given the morning and afternoon Bay of Fundy migration rates are so low, it is unlikely to be a major migration corridor for White-winged Scoter. Most of their population must

take one of the two overland routes identified in the Atlantic and Great Lakes Sea Duck Migration Study (Sea Duck Joint Venture, 2015).

Trends in Migration Rates

Morning migrations for Black Scoter, Surf Scoter, and White-winged Scoter were found to have a weak decrease between 2000 and 2017 in the Bay of Fundy. The trend for Black Scoters is particularly interesting as there is a clear and consistent decrease between 2000 and 2012, which was found to be strongly significant relative to a null model ($\Delta AICc$: 10.95, $AICc$ *wt*: 0.995; analysis not shown), but subsequent migration rates in 2013-2017 increased and were more variable. While the analysis across all years suggests a weak decrease in Black Scoter population within the Bay of Fundy, and the strong negative trend between 2000 and 2012 is concerning, the increase over subsequent years may be indicative of a rebound in the population. Continued close monitoring is required to determine whether the increasing trend continues or if it is part of a long-term, natural cycle for this Black Scoter population.

Little comparable data exist for scoters in other regions of North America to accurately evaluate long-term trends in their populations. The Waterfowl Breeding Population and Habitat Survey (WBPHS) suggests the Pacific Black Scoter population breeding in Alaska decreased over thirty years between 1974 and 2004 and has been increasing since (Bowman *et al.* 2015). Alaskan breeding populations have been decreasing for Surf Scoter (Bowman *et al.* 2015), similar to the trends found in this study, and increasing for White-winged Scoter since 1993 (Bowman *et al.* 2015), opposite of my results. However, Atlantic and Pacific populations are known to be distinct for Black Scoter and suspected for Surf Scoter (Sea Duck Joint Venture, 2015);

therefore, trends cannot be extrapolated between the two populations. Nevertheless, the strong and sustained decreasing Black Scoter trend prior to their recent resurgence in the Bay of Fundy suggests they be a species of concern, especially as Black Scoter are listed as near threatened on the IUCN red list (BirdLife International, 2018). The impact of any future changes in the Bay of Fundy (i.e., coastal development) should be carefully monitored as the results of this study suggest the Bay of Fundy is an important migration corridor for North American Black Scoter wintering in the Atlantic. Surf Scoter were found to have a weak decrease over the 18 years included in my study and the Bay of Fundy was found to be an important migration corridor for them as well; therefore, the impacts of developments on their abundance should be monitored. It is unlikely that a significant proportion of the North American Atlantic White-winged Scoter population migrates through the Bay of Fundy and any changes in the Bay of Fundy would have little effect on their population as a whole.

I found spring Common Loon morning migration rates increased between 2000 and 2017 in the Bay of Fundy, while Red-throated Loons were more stable overall with a slight increasing trend. Comparative long-term data sources are limited for Red-throated Loons, but Common Loons are well documented within northwestern United States, the Great Lakes, and central Canada (Evers *et al.* 2004). Groves *et al.* (1996) reported the Red-throated Loon breeding population in Alaska declined by more than 50% between 1977 and 1993. Little is known about the status of the Atlantic wintering population and the trend detected in this study suggests the Atlantic population is increasing. However, the Bay of Fundy is used as a migration corridor for only a fraction of their total population and any changes in Bay of Fundy would have limited effects on

their population as a whole. The status of Common Loons in North America is region specific but believed to be stable overall (Evers *et al.* 2004). The population within the Canadian Maritimes appears unchanged as of the mid 1990s (Evers *et al.* 2004), though current data are limited. It is unknown to which breeding population Bay of Fundy Common Loon migrants belong as there are breeders located in New Brunswick, Nova Scotia, Newfoundland, and even farther north along the East Coast (Evers *et al.* 2004). Only small proportion of the total Atlantic population of Common Loon migrate through the Bay of Fundy each year. However, it could service a larger proportion of the New Brunswick breeding population (Evers *et al.* 2004), if only New Brunswick breeders use this corridor. Therefore, a greater understanding of the demographics of the migrating population of Common Loons in the Bay of Fundy is needed to ascertain the potential effect of future changes to the Bay of Fundy as the localized effect on the New Brunswick population could be significant.

Conclusions

- (1) I found afternoon spring migration rates for Black Scoter, Surf Scoter, White-winged Scoter, and Red-throated Loons varied positively with morning migration rates, tidal heights, and wind vector. Afternoon migration rates for Common Loons varied positively with morning migration and tidal height, but negatively with wind vector. However, the individual effects of tides and wind were weaker in comparison to morning rate for most species.
- (2) Averaged environmental models explaining afternoon migration predicted poorly on new data for most species. Models including environmental variables consistently predicted worse than more simplistic proportional relationships between morning and afternoon migration rates. Modelling may be improved with inclusion of variables better reflective of individual condition. Given difficulties in estimating absent data, afternoon migration monitoring is essential in maximizing utility of the Point Lepreau Bird Observatory database and should be continued in the future.
- (3) I found Bay of Fundy migration rates of Black and Surf Scoter were much higher than those of White-winged Scoter, Red-throated Loons, and Common Loons. Therefore, the Bay of Fundy is a more important migration corridor for these species.
- (4) In the Bay of Fundy between 2000 and 2017, I found: Black Scoter migration rates strongly decreased between 2000 and 2012 and then increased between 2013 – 2017, Surf Scoter and White-winged Scoter migration rates had a weak

decrease, Red-throated Loon migration rates had a weak increase and Common Loon migration rates a strong increase.

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