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Characterizing residence patterns of North Atlantic right whales in the southeastern USA with a multistate open robust design model

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ABSTRACT: Effective conservation of endangered North Atlantic right whales *Eubalaena glacialis* requires information about their spatio-temporal distribution. Understanding temporal distribution is particularly important, because a portion of the population migrates between high-latitude summer feeding grounds off the northeastern US and Canadian Maritimes coasts and lower-latitude calving and wintering grounds off the southeastern US coast (SEUS). Here, we modeled SEUS residence patterns using photo-identification data from coastal South Carolina, Georgia, and Florida from 7 winter seasons (2004/2005–2010/2011). We used multistate open robust design models to evaluate effects of reproductive status, demographic group, and environmental conditions on SEUS residence. Model estimates accounted for temporal variation and imperfect detection and provided probabilities of entering the SEUS, staying in the SEUS, and being sighted in the SEUS. We also derived estimates for residence time and seasonal abundance. We observed staggered arrival and departure patterns and demographic differences in residence patterns that are characteristic of a differential migration strategy. Calving females arrived earliest and, in most seasons, had mean residence periods more than twice as long as other demographic groups. Conversely, adult males arrived the latest and had the shortest residence times. Within-season detection was positively influenced by survey effort, and overall seasonal mean (±SE) detection rate estimates ranged from 0.83 ± 0.08 for non-calving adult females to 0.98 ± 0.02 for calving females. Results provide insights into right whale behavior, biology, and temporal distribution in the SEUS and can be used to evaluate spatially and temporally dynamic management measures.

KEY WORDS: Mark-recapture · Open robust design · Phenology · Residence · *Eubalaena glacialis* · North Atlantic right whale

INTRODUCTION

Despite protection since 1935, endangered North Atlantic right whales *Eubalaena glacialis* remain vulnerable to human-related threats along the industrialized Atlantic coast of North America (NMFS 2005). Primary causes of serious injury and mortality are ship strikes and fishing gear entanglements (Knowlton & Kraus 2001). Reducing deaths and serious injuries from these threats is the focus of conservation efforts and regulatory measures to support population recovery (NMFS 2005). Conservation

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efforts include aerial surveys to mitigate ship strikes by notifying mariners about whale locations as well as monitoring programs that provide right whale sighting information to monitor population status, habitat use, and the effectiveness of regulatory measures (Brown et al. 2007). Regulatory measures to reduce encounters between right whales and ships or fishing gear include fishery time-area closures (Farmer et al. 2016), vessel routing schemes (Vanderlaan & Taggart 2009), and time-area vessel speed restrictions (Conn & Silber 2013).

These measures are implemented seasonally in high-latitude summer feeding grounds along the northeastern United States and Canadian Maritimes coasts and lower-latitude calving and wintering grounds in the southeastern United States (SEUS), which have been identified as critical habitat areas based on their ecological importance and the current understanding of right whale distribution and movement patterns (Winn et al. 1986, NMFS 2014). However, an incomplete understanding of variation in right whale distribution among aggregation areas complicates the development of effective management and conservation strategies (Schick et al. 2013). In fact, limited knowledge of right whale migration timing and residence duration in critical habitat areas has contributed to a lack of comparable protective measures and monitoring efforts along the mid-Atlantic coast (Firestone et al. 2008), which is the presumed migratory corridor for the annually variable portion of the right whale population that migrates seasonally between high-latitude feeding grounds and the SEUS (Kraus et al. 1986, Winn et al. 1986). An improved understanding of when and where right whales aggregate is necessary to design conservation and management actions that support population recovery (Vanderlaan & Taggart 2009, Farmer et al. 2016).

Although descriptions of right whale distribution and movement patterns are available, there are few quantitative studies of North Atlantic right whale residence timing within high-use or critical habitat areas. Since direct estimates of residence time from tagging are limited, most estimates of arrival and departure times and total residence time within a given habitat are based on the first and last sighting dates of individual whales identified from photographed sighting events (e.g. Burnell & Bryden 1997, Mayo et al. 2004, Fortune et al. 2013). Other approaches have quantified SEUS residence and departure timing by modeling frequency distributions of individual resighting histories (Hiby & Leaper 2005) or with linear regression modeling of aggregated sighting data (Firestone et al. 2008). Hiby & Leaper (2005) estimated a modal departure date from Jacksonville, FL, of the third week in February and predicted later departure in years with more calves present, while Firestone et al. (2008) predicted a later modal departure date of 2–11 March from Jacksonville, FL, and that almost all whales departed the calving grounds by the end of March. These estimates are consistent with the generally accepted migration model where right whales arrive in the SEUS in the fall and leave the SEUS in the spring (Winn et al. 1986), but do not account for imperfect detection, survey effort influences, or demographic differences beyond calf presence or absence. Not accounting for imperfect detection can lead to incorrect inferences or ineffective management decisions due to biased estimates (Gu & Swihart 2004). These issues can be addressed with capture-recapture models, which use encounter histories of identifiable individuals from multiple sampling periods to estimate population parameters while accounting for imperfect detection and have been used to estimate residence timing for southern right whales (Fewster & Patenaude 2009).

Here, we apply a multistate open robust design capture-recapture model (Kendall & Bjorkland 2001, Kendall et al. in press) to 7 seasons (2004/2005 to 2010/2011) of right whale photo-identification data for the SEUS wintering area. Our objectives were to describe the phenology and duration of right whale residence in the SEUS while accounting for imperfect detection and to assess variability in residence patterns across winter seasons; among life history states defined based on age, sex, and reproductive class; and in relation to environmental covariates. Specifically, we hypothesized that the duration of residency would vary across demographic groups due to differences in life history and energy requirements, with calving females having the longest SEUS residency to support calf development. Additionally, we hypothesized that right whales would reside in the SEUS for more time during cold winters, but for less time following years of low prey availability, to meet energetic demands. We also provide the first estimates of winter right whale abundance in the SEUS that account for differences in detection across demographic groups. Quantifying phenology, residency, and abundance for ecologically important areas like the SEUS provides insight into the biology of this highly mobile species, while also informing monitoring and management actions to mitigate impacts from ship strikes and entanglements. In particular, knowledge of the phenology and duration of residence can increase the effectiveness of management

actions by identifying the appropriate timing and extent of monitoring surveys and protective measures (Bowlin et al. 2010, Bunnefeld et al. 2011); inform risk assessments by identifying when whales may be exposed to threats outside of existing protected areas (NMFS 2005); and inform marine spatial planning to manage impacts to whales while minimizing economic and social costs (Petruny et al. 2014).

MATERIALS AND METHODS

Right whale data

Within the SEUS wintering grounds, systematic aerial surveys have been conducted from approximately December to March since 1994 through the multi-agency Early Warning System (EWS) aerial survey and communication network (Brown et al. 2007). Although the objectives, level of effort, spatial extent, and configuration of these surveys have varied, all surveys consisted of daily (weather-permitting) visual survey flights of up to 4 fixed-wing aircraft. Survey teams documented right whale *Eubalaena glacialis* sightings and collected high-quality photographs of whales and their callosity patterns, scars, and other distinguishing characteristics or markings, which uniquely identify individual whales (Payne et al. 1983, Kraus et al. 1986). Photographed sightings from aerial surveys, along with sightings from opportunistic and other research platforms, were integrated within the North Atlantic Right Whale Consortium (NARWC) Identification database (Hamilton et al. 2007), which is curated by the New England Aquarium. The Identification database also contains genetic information for individual identification from skin biopsies collected during vessel surveys, which are paired with photos of the sampled individuals (Frasier et al. 2007, 2009).

For this study, we obtained photo-identification records from the Identification database (accessed 14 February 2014; NARWC 2014) and analyzed sighting records from south of the North Carolina/South Carolina border for 7 winter seasons: 2004/2005 to 2010/2011. This study area (SEUS region, Fig. 1) is part of the South Atlantic Bight, which is characterized by a broad continental shelf ranging from ~10 to ~120 km wide (Blanton et al. 2003) and a gently sloping topography interspersed with areas of hard bottom habitat (Good 2008). We defined a winter season from November to April, since aerial surveys were expanded to these months in some years. This study area and range of years had relatively consistent aerial survey coverage of nearshore waters from the central east coast of Florida to approximately North Myrtle Beach, South Carolina (Good 2008, Gowan & Ortega-Ortiz 2014), thus reducing heterogeneity in detection probability.

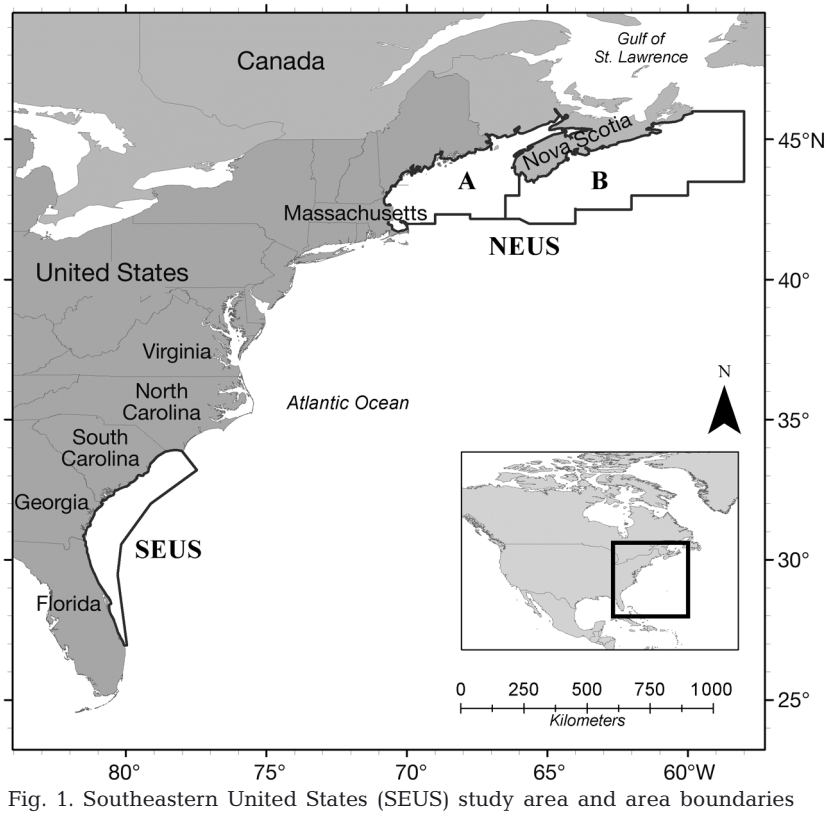


Fig. 1. Southeastern United States (SEUS) study area and area boundaries used to summarize environmental covariates in the northern right whale habitats (NEUS). The NEUS-A area contains right whale habitats in the Bay of Fundy, Gulf of Maine, Grand Manan Banks, Jeffrey's Ledge, Cape Cod Bay, and Massachusetts Bay, and the NEUS-B area includes habitats on the East Scotian Shelf and Roseway Basin

Individual photo-identification records included sighting date and location, descriptions of observed associations, a unique identification, and age class and gender information. This information was used to assign whales into 5 demographic groups for each winter season: calving or non-calving adult females, adult males, juveniles, or unknown age/sex. Sex was determined based on observation of the genital area, close association

with a calf, or genetic information (Brown et al. 1994). Whales were considered adults when they had a known age or sighting history of at least 9 yr or, for females, after having their first calf (Hamilton et al. 1995). Individuals of any sex class (male, female, or unknown) were classified as juveniles if they were first identified as calves and had a known age <9 yr. Individuals were classified as calving females based on close association with a calf (Knowlton et al. 1994) at any point during the winter season. Since demographic group classifications were constant within seasons, the calving female group included both females that were seen with a calf at their first sighting in the SEUS and females that were first seen without a calf and then later with a calf in the same season. We assumed whales were classified as calving females without error because the intensive survey effort and nearshore tendency of whales in the SEUS allows observers to reliably identify the presence of a calf (Browning et al. 2010). Calves or yearlings still associated with their mothers were excluded from the analyses to prevent pseudoreplication.

Data analysis

Multistate open robust design model

We modeled the phenology and duration of right whale winter residence in SEUS coastal waters using multistate open robust design capture-recapture models (MSORD; Kendall 2004, Kendall et al. in press). The MSORD model structure includes parameters for arrival, detection, and persistence probabilities across secondary sampling periods (e.g. weeks) within a series of primary sampling periods (e.g. years), in addition to survival probabilities and probabilities of transition among states between each successive primary period. However, in this application, we ignore survival and state transitions and use only the within-season part of the model structure to characterize right whale residence.

For this study, primary periods were the 7 winter seasons (hereafter seasons) from 2004/2005 to 2010/2011, and secondary periods consisted of eleven 14 d time periods (henceforth referred to as biweeks) from 15 November to 17 April (or 16 April in 2007/2008). We chose a biweekly secondary period to balance the number of parameters estimated relative to the amount of available data. Sighting histories were compiled for these time periods from photo-identification records by determining if an individual was identified at least once during each biweek in each season.

For each season and life history state (calving females, non-calving adult females, adult males, juveniles, and unknown age/sex), we estimated parameters $pent_j$, the probability an individual arrives in the SEUS in biweek j; p_j, the probability an individual present in the SEUS in biweek j is detected; and $\varphi_j^{(v)}$, the probability an individual in the SEUS in biweek j, which has been in the study area for the previous v biweeks, is still in the study area in biweek $j + 1$. The probabilities of entry and detection probabilities can be modeled as a function of state, covariates, or time. Persistence can be modeled as a function of these factors and as a function of the number of biweeks since first arrival in the study area (i.e. the time since arrival). Moreover, $pent_j$ is conditional on those that use the study area for at least 1 time period and, therefore, must sum to 1.0 across all l_t biweekly sampling periods each season (l_t):

$$\sum_{j=1}^{l_t} pent_j = 1.0 \quad (1)$$

An example model structure for a study that includes 3 time periods and has a detection history of 011 (1 for detection and 0 for non-detection in each period) is:

$$pent_1(1-p_1)\varphi_1^{(0)}p_2\varphi_1^{(1)}p_3 + pent_2 p_2 \varphi_2^{(0)} p_3 \quad (2)$$

where the individual is first detected in sampling Period 2 and continues to be detected in Period 3, but could have entered in Period 1 and was not initially detected.

From the MSORD model structure, we also used 2 derived parameters for each life history state and season t: abundance and residence time. The total abundance of whales in each life history state that utilized the SEUS in season t, $N_t^\star$, was estimated as $\hat{N}_t^\star = n_t^\star / \hat{p}_t^\star$, where $n_t^\star$ is the number of individuals of a given state sighted at least once within the season (Kendall 2006, Kendall et al. in press). Effective capture probability $p_t^\star$ is the probability that an individual in the SEUS in season t is sighted at least once during the season, which is, in turn, a function of the various model parameters $pent_j$, p_j, and $\varphi_j^{(v)}$. The total expected residence time in the study area for each state and season t, R_t, was estimated as a weighted average of biweekly periods, weighted by the probability that an individual is in residence for exactly that duration. For example, for a season of 3 sampling periods, the expression would be:

$$\begin{aligned} R_t = {} & 1\times[pent_1(1-\varphi_1) + pent_2(1-\varphi_2) + pent_3] \\ & +2\times[pent_1\varphi_1(1-\varphi_2) + pent_2\varphi_2] \\ & +3\times[pent_1\varphi_1\varphi_2] \end{aligned} \quad (3)$$

(Kendall 2006, Kendall et al. in press). The delta method was used to estimate variances for N_t^*, R_t, and p_t^*.

The model assumes closure (i.e. no changes in occupancy due to births, deaths, immigration, or emigration) of the population among biweeks and that members of the population enter and exit the study area just once each season. Given that right whales are long-lived, large mammals (Brown et al. 2009) and that calf sighting data were not modeled, closure assumptions related to births and deaths are reasonably met. However, movement into or out of the study area more than once within a season is possible because surveys do not cover the entire area potentially available to right whales in the SEUS (e.g. offshore waters) and long-distance travel has been observed for right whales within periods as short as 2 wk (Mate et al. 1997). Nevertheless, completely random movement in and out of the study area within the season would not bias estimates of arrival or persistence probabilities and would simply reduce the effective sighting probability (Kendall 1999). Another assumption is that whales do not arrive before or depart after the duration of sighting effort; violation of this assumption would require interpretation of residence time estimates as minimum estimates.

We developed a candidate model set (see Table S2 in the Supplement at www.int-res.com/articles/suppl/n036p279_supp.pdf) to assess variation in residence patterns across time and to evaluate hypotheses for factors that may influence SEUS residence time by combining different models for each parameter type ($pent_j$, $\varphi_j^{(v)}$, and p_j). We estimated parameters using maximum likelihood with Program MARK (v. 8.1; White & Burnham 1999) via the RMark package (v. 2.1.13; Laake 2013) in R (R Core Team 2015). Model selection was based on Akaike's Information Criterion corrected for small sample sizes (AICc), and parameter estimates were averaged based on AICc weights (w_i) to account for model selection uncertainty (Burnham & Anderson 2002). AICc was calculated based on unadjusted parameter counts rather than the numerically derived number of estimable parameters (Laake 2013). Currently, there is no general goodness-of-fit (GOF) test for the MSORD model so we evaluated fit for fully time-dependent Cormack Jolly Seber models run individually for each season (Lebreton et al. 1992). We did not consider demographic group differences here due to limited data. Cumulative χ^2 statistics and degrees of freedom for Test 2 + Test 3 were obtained from Program RELEASE GOF implemented in Program MARK (v. 8.1; White & Burnham 1999). These tests assess violation of model assumptions due to heterogeneity in capture probability (Test 2) and survival (Test 3) where, for our study, survival is interpreted as remaining in the study area.

Covariates for within-season parameters

The phenology of migration is likely influenced by factors that are either group-specific, environmental, or interactions between these factors (Knudsen et al. 2007). For right whales, we evaluated differences in arrival ($pent_j$), persistence ($\varphi_j^{(v)}$), and sighting probabilities (p_j) as a function of seasons, biweeks within each season, and demographic groups, and we modeled relationships of parameters with environmental covariates representing sea surface temperature (SST), primary production, and climatic conditions. Seasonal variation was evaluated using a factor variable (SEASON) to group capture histories of individuals that were observed in each season. To quantify time dependence in arrival and persistence parameters, we evaluated models with time effects that either varied across all biweeks (~Time) or that had linear or quadratic relationships (on the logit scale) for biweeks with either a multiplicative (~SEASON × QUAD) or additive (~SEASON + QUAD) seasonal effect. The linear and quadratic models were used to characterize temporal trends in arrival and persistence within a season while requiring fewer parameters than a fully time-dependent model. We also considered an effect of survey effort (Caswell et al. 1999, Fujiwara & Caswell 2001) on p_j. We summarized EFFORT as kilometers flown in the SEUS study area within each biweek standardized relative to the mean biweekly effort across the study period. We ignored the small contribution of non-aerial sightings to effort, due to the absence of comparable effort data.

Demographic factors

We expected differences in arrival and persistence probabilities among age, sex, and reproductive classes due to different life history and energy requirements (Clapham 2001, Craig et al. 2003, Fortune et al. 2013) and expected different sighting probabilities across demographic groups due to differences in surface-to-dive time ratios or calf presence (Hain et al. 1999, Fewster & Patenaude 2009). We therefore evaluated differences across the 5 demographic groups for all parameters by comparing models with and without a demographic group factor variable

(DG). Additionally, we tested the hypothesis that calving female persistence is a function of the time since arrival in the SEUS (i.e. the number of biweeks since arrival; ~Cow:TSA), which may relate to a minimum amount of time needed for a calf to develop prior to migrating north (e.g. developing sufficient swimming skills; NMFS 2014). Differences across demographic groups were also evaluated for interactions with environmental covariates.

Environmental factors

Environmental covariates were summarized within a subset of 4 regions among the SEUS and northeast US and Canadian Maritimes (NEUS) coasts. Environmental conditions in the SEUS (prior to northward migration) were only considered relative to persistence probabilities, and conditions in the NEUS (prior to southward migration) were only considered relative to arrival probabilities. Regions in the NEUS were defined based on historically high-use right whale habitats that were simplified by aggregating adjacent areas into either the NEUS-A (Bay of Fundy, Gulf of Maine, Grand Manan Banks, Jeffrey's Ledge, Cape Cod Bay, and Massachusetts's Bay) or NEUS-B (East Scotian Shelf and Roseway Basin) regions (Schick et al. 2013; Fig. 1). Aggregation was based on similarities in observed SST during the study period. We also considered the entire NEUS region by combining the NEUS-A and NEUS-B regions. The SEUS region was defined as the North Carolina/South Carolina border south to Jupiter, FL, with an offshore extent out to the approximate location of the mid-continental shelf (Fig. 1). This extent encompasses historical right whale sightings in the SEUS region since 1991 (Gowan & Ortega-Ortiz 2014).

Sea surface temperature. Variation in right whale distribution has been linked to SST (Keller et al. 2006, Pendleton et al. 2012), and right whales may have an upper thermal limit (Kenney 2007, Good 2008), while cow-calf pairs may avoid particularly cold water (Keller et al. 2006). Since SEUS shelf waters typically cool rapidly between September and October (Blanton et al. 2003), we quantified the timing of seasonal cooling for the corresponding period in the NEUS using SST anomalies calculated as the difference between October SST in the NEUS-A or NEUS-B regions and mean October SST across the study period in each region (Covariates 1 and 2; Table 1). We expected earlier arrival in years with below-average October SST. We also expected earlier arrival when NEUS winter SST was colder than average (Covariate 3; Table 1). Conversely, we pre-

Table 1. Definitions of environmental covariates (SST: sea surface temperature; CHL: chlorophyll *a*; NAO: the North Atlantic Oscillation index) evaluated for the arrival and persistence parameters of the multistate open robust design model. See Fig. 1 for region locations in the northeastern United States and Canadian Maritimes coasts (NEUS) and the southeastern United States (SEUS)

Parameter	Covariate	Description
Arrival		
1	$SSTAnom_{Oct,NEUS\text{-}A}$	Anomaly of mean NEUS-A October SST relative to mean October NEUS-A SST across all seasons
2	$SSTAnom_{Oct,NEUS\text{-}B}$	Anomaly of mean NEUS-B October SST relative to mean October NEUS-B SST across all seasons
3	$SSTAnom_{Winter,NEUS}$	Anomaly of mean December–February NEUS SST relative to mean winter NEUS SST across all seasons
4	$CHLAnom_{Spring,NEUS}$	Anomaly of mean March–April NEUS CHL relative to mean spring NEUS CHL across all seasons
5	$CHLAnom_{Summer,NEUS}$	Anomaly of mean May–July NEUS CHL relative to mean summer NEUS CHL across all seasons
6	$CHLAnom_{Fall,NEUS}$	Anomaly of mean August–November NEUS CHL relative to mean fall NEUS CHL across all seasons
7	NAO	Mean North Atlantic Oscillation index values for October to April of each season
Persistence		
8	SST_{SEUS}	Mean SEUS SST in degrees Celsius for each biweek
9	$SSTSlope_{SEUS}$	Rate of change in SEUS biweekly mean SST from the previous biweek
10	$SST_{Winter,SEUS}$	Mean SEUS SST in degrees Celsius from December to February for each season
11	$SSTAnom_{Winter,SEUS}$	Anomaly of mean December–February SEUS SST relative to mean winter SEUS SST across all seasons
12	NAO	Mean North Atlantic Oscillation index values for October to April of each season

dicted departure timing to be influenced by warming SEUS SST and expected persistence probabilities to decrease (1) with increasing biweekly mean SEUS SST; (2) after the rate of change in biweekly SEUS SST values became positive; or (3) earlier in the season (i.e. earlier departure) when SEUS winter mean SST values for each season and SEUS winter SST anomalies were above the study period mean winter SEUS SST (Covariates 8 to 11, respectively; Table 1).

SST covariates were derived from global daily mean SST (°C) data for October 2004 to April 2011 obtained from the NOAA OI SST V2 high resolution blended data set (Reynolds et al. 2007) provided online by the NOAA Earth System Research Laboratory Physical Sciences Division (www.esrl.noaa.gov/psd/). Daily mean SST data were used as a bulk measure of regional temperature and were summarized into biweekly, October, and seasonal means and anomalies across the study period (Table 1).

Primary production. Given the energetic demands of long-distance migration and fasting within SEUS wintering grounds (Kenney et al. 1986, Fortune et al. 2013), we expected arrival timing to be related to the quality, abundance, and phenology of food resources available to right whales prior to migration. Abundance and phenology of *Calanus finmarchicus*, the primary prey for right whales (Baumgartner et al. 2003), are influenced by oceanographic processes and large-scale climatic fluctuations, such as the North Atlantic Oscillation (Drinkwater et al. 2003, Greene & Pershing 2003) as well as the magnitude, timing, and duration of phytoplankton blooms (Durbin et al. 2003, MERCINA 2004, Johnson et al. 2008).

We evaluated effects of phytoplankton bloom magnitude and timing prior to the winter season on arrival probabilities across seasons using satellite-derived surface chlorophyll *a* concentrations in mg m^{-3} (CHL) as an indicator of primary production (Song et al. 2010). Seasonal NEUS CHL anomalies were calculated relative to study period seasonal means (Covariates 4–6 in Table 1) from 2004 to 2010, with seasons defined according to climatological seasonal cycles observed for *C. finmarchicus* (Spring: March–April, Summer: May–July, Fall: August–November; MERCINA 2004). Seasonal mean values were derived from monthly mean CHL data from SeaWiFS level-3, 1/12 degree resolution data for 2004–2010 obtained from the NASA Ocean Biology Processing Group (NASA 2014) using Marine Geospatial Ecology Tools v. 0.8a43 (Roberts et al. 2010) and summarized within the NEUS region with the Spatial Analyst Zonal Statistics tool in ArcGIS (ESRI 2014).

North Atlantic Oscillation Index. The North Atlantic Oscillation (NAO) is a coupled ocean-atmospheric system quantified using NAO index values that indicate the difference of pressure anomalies between the Azores and Iceland (Hurrell 1995). Most prominent during boreal winter, the NAO influences northern hemisphere climate, weather, and ecosystems, including plankton communities (Hurrell 1995, Drinkwater et al. 2003, Greene & Pershing 2003). Negative winter NAO indices indicate a decreased pressure gradient and are generally associated with increased transport of cool, fresh Labrador Current water to south of the Grand Banks and lower *C. finmarchicus* abundance in the northwest Atlantic (Greene & Pershing 2000, Conversi et al. 2001, Greene et al. 2013). Changes in oceanic conditions associated with NAO variability have been linked to ecological dynamics at multiple trophic levels (Ottersen et al. 2001), including *C. finmarchicus* abundance in the Gulf of Maine (Greene & Pershing 2000) and right whale body condition (Miller et al. 2012) and calf production (Meyer-Gutbrod et al. 2015).

We calculated the winter NAO index from monthly mean NAO index values normalized to 1981–2010 monthly means obtained from the NOAA Climatic Prediction Center (www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml). Monthly mean NAO index values were averaged from October to April for each winter season (Covariates 7 and 12 in Table 1). We expected later arrival (i.e. peak arrival probabilities later in the season) during seasons with a negative NAO index, since whales may arrive later if more time is needed to accumulate sufficient energy stores before migrating or if whales disperse to alternative feeding grounds and then must travel farther to reach the SEUS (Meyer-Gutbrod et al. 2015). Alternatively, we expected higher persistence probabilities to extend later into the season (i.e. later departure) during negative NAO seasons because coastal waters within the SEUS would be expected to stay cooler longer than during a positive phase NAO season.

RESULTS

Right whale sightings

Of the records obtained from the Identification database, we analyzed 7601 photo-identified sighting records for 408 individual whales *Eubalaena glacialis*. Most records (86%) were from EWS aerial surveys, with other sighting sources consisting of

vessels (10.3%), land-based sightings (2.5%), and unspecified platforms (1.1%). The 2009/2010 season had the most unique individuals (220), while 2008/2009 had the highest number of sightings (1560; see Fig. S1 in the Supplement). Except for 2004/2005 when adult males were most common, most identified individuals in each season were juveniles, and the proportion of juveniles increased across the study period (Table S1). Across all demographic groups, the average number of days between sightings was 5.3 d (SD = 6.6), but 7% of sighting gaps were longer than the biweekly secondary period. Where SEUS sighting gaps were >14 d, the Identification database (NARWC 2014) was further examined for movement out of the study area, but we found no photo-identified sightings of these whales in other locations to confirm the whales had left the SEUS during these gaps (P. Hamilton pers. comm.).

Model results

Of the models evaluated (Table S2), 6 models had some support ($w_i > 0.001$), and Model 1 had 90.7% of the AICc weight (Table 2). Cumulative goodness-of-fit results did not indicate a lack of fit ($\chi^2 = 134.34$, df = 125, p = 0.268; $\hat{c} = 1.07$). The models best supported by the data indicated differences among DGs for all parameters; differences in arrival (*pent*) and persistence (φ) parameters across biweeks that were modeled with a quadratic time trend (QUAD); and biweekly sighting probabilities (*p*) that were modeled with an interaction between demographic group and survey effort (DG × Effort). Four of the 6 supported models included 1 of 3 environmental anomaly covariates for arrival timing: NEUS-A October SST, NEUS-B October SST, or NEUS fall CHL (Fig. S2). In contrast, top persistence models did not indicate support for the environmental covariates evaluated or for the time-since-arrival hypothesis for calving females. All top models included either additive or multiplicative seasonal effects on persistence, and models with an additive effect received the most support (cumulative w_i = 0.950; Table 2). We used model averaging to account for model selection uncertainty and present averaged results for each parameter, noting that Model 1 had the most support.

Arrival probabilities indicated staggered arrival that varied across demographic groups and time (Fig. 2a–e). For each season, each biweekly arrival probability was >0 for at least 1 demographic group, indicating that right whales arrived throughout the winter. However, arrival patterns were distinct among demographic groups, with calving and non-calving adult females tending to arrive earliest, followed by juveniles, unknown age/sex individuals, and then adult males (Fig. 2a–e). Across seasons, some calving females and non-calving adult females arrived or were already present in the study area during the first biweek from 15 November to 28 November (first occasion *pent* values; Fig. 2a,b). In contrast, few juveniles were present in the first biweek (Fig. 2d), unknown age/sex individuals did not arrive until the second biweek except in 2006/2007 (Fig. 2e), and most adult males did not arrive until after late January (Fig. 2c). Juvenile whale arrival patterns were very consistent across seasons (Fig. 2d).

Similar to arrival probabilities, departure times were staggered, with variation across seasons and demographic groups. In all seasons, calving females stayed in the SEUS until at least mid-January, while other groups had lower persistence probabilities

Table 2. Top 6 multistate open robust design models of arrival (*pent*), persistence (φ), and sighting probabilities (*p*), with >0.001 AIC_c weight (w_i) where AIC_c is Akaike's information criterion corrected for small sample sizes, *K* is the total number of parameters in each model, and ΔAIC_c is the difference in AIC_c values from model [1]. Variation in linear and quadratic relationships for secondary periods across seasons is indicated by the QUAD term. Factor variables were demographic group (DG) and the primary period winter seasons (SEASON), while covariate values were October sea surface temperature anomalies for the NEUS-A ($SSTAnom_{Oct,NEUS-A}$) and NEUS-B ($SSTAnom_{Oct,NEUS-B}$) regions; surface chlorophyll *a* anomalies for August to November in the NEUS region ($CHLAnom_{Fall,NEUS}$); and standardized biweekly aerial survey effort (EFFORT). See Table S2 in the Supplement at www.int-res.com/articles/suppl/n036p279_supp.pdf for full AIC_c table

	Model	*K*	ΔAIC_c	w_i	Deviance
1	*pent* (DG × QUAD × $SSTAnom_{Oct,NEUS-A}$), φ (QUAD × DG + SEASON), *p* (DG × EFFORT)	61	0.000	0.907	8039.49
2	*pent* (DG × QUAD × $SSTAnom_{Oct,NEUS-A}$), φ (QUAD × DG × SEASON), *p* (DG × EFFORT)	145	5.863	0.048	7864.27
3	*pent* (DG × QUAD), φ (QUAD × DG + SEASON), *p* (DG × EFFORT)	46	6.814	0.030	8077.49
4	*pent* (DG × QUAD × $SSTAnom_{Oct,NEUS-B}$), φ (QUAD + SEASON × DG), *p* (DG × EFFORT)	61	8.971	0.010	8048.46
5	*pent* (DG × QUAD × $CHLAnom_{Fall,NEUS}$), φ (QUAD × DG + SEASON), *p* (DG × EFFORT)	61	11.549	0.003	8051.04
6	*pent* (DG × QUAD), φ (QUAD × DG × SEASON), *p* (DG × EFFORT)	130	14.035	0.001	7905.61

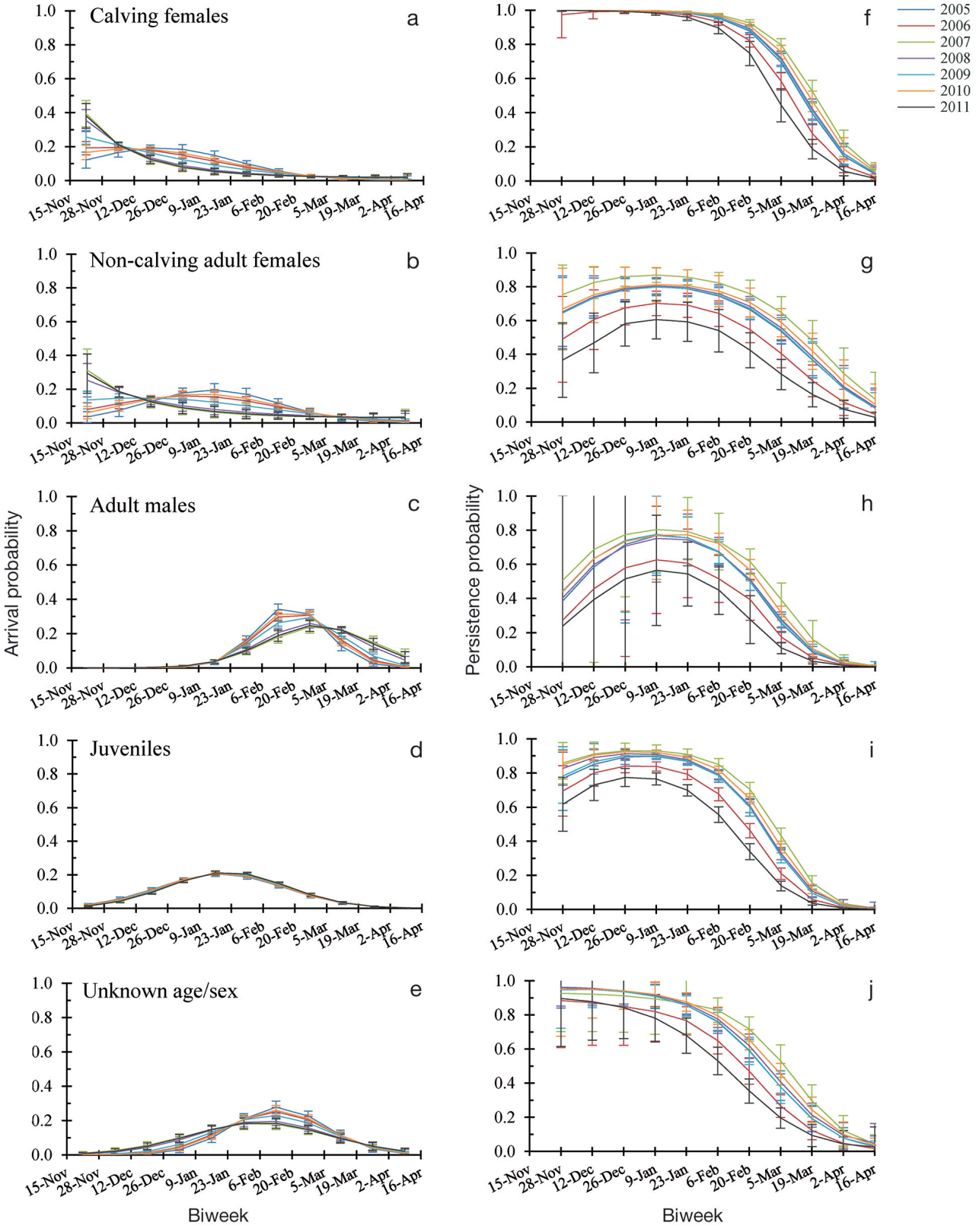


Fig. 2. Model-averaged parameter estimates for biweekly probabilities of (a–e) arrival (*pent*) and (f–j) persistence (φ) for each season for (a,f) calving females, (b,g) non-calving adult females, (c,h) adult males, (d,i) juveniles, and (e,j) unknown age/sex individuals. Error bars indicate SE

overall (Fig. 2). In fact, calving female persistence probabilities were >0.50 through at least Biweek 7 (7–20 February) for all seasons, indicating that these individuals were more likely to stay in the study area than to leave (Fig. 2f). Similar patterns were observed for non-calving adult females, except in 2005/2006, 2006/2007, and 2010/2011. For juveniles and unknown age/sex individuals, 7 of 11 biweeks had persistence probabilities > 0.50 in most seasons; persistence probabilities were lower for these groups in 2005/2006 and 2010/2011 and higher in 2006/2007 (Fig. 2i,j). In contrast, adult males were more likely to leave than to stay during the majority of biweeks in each season except for 2006/2007, 2007/2008, and 2009/2010 (Fig. 2h). We note the large uncertainty associated with persistence estimates for adult males for the first 3 biweeks; this is because persistence is conditional on prior arrival, and male arrival probabilities were near zero for these biweeks. Adult males were the only demographic group for which persistence probabilities decreased to zero in all seasons, with this occurring during Biweek 11 (3–16 April). Across demographic groups, 2005/2006 and 2010/2011 had the lowest overall persistence probabilities, and persistence probabilities were highest during 2006/2007 (Fig. 2f–j).

Table 3. Expected mean residence times for each season (±1 SE) and the entire study period (±1 average SE) in days for each demographic group

Primary period	Calving females	Non-calving adult females	Adult males	Juveniles	Unknown age/sex
2004/2005	80.8 ± 5.0	41.3 ± 4.6	21.7 ± 1.1	41.5 ± 2.2	27.5 ± 2.4
2005/2006	78.9 ± 5.2	33.1 ± 4.5	18.9 ± 0.9	34.9 ± 2.0	24.6 ± 2.0
2006/2007	99.6 ± 5.9	55.5 ± 9.7	21.5 ± 1.5	45.3 ± 3.0	38.4 ± 5.4
2007/2008	93.8 ± 4.7	44.3 ± 6.9	20.1 ± 1.1	41.1 ± 1.9	33.3 ± 3.8
2008/2009	89.3 ± 3.5	42.7 ± 5.3	20.9 ± 0.9	40.8 ± 1.6	29.8 ± 2.5
2009/2010	87.4 ± 4.1	45.0 ± 6.8	22.8 ± 1.1	44.1 ± 1.8	30.4 ± 2.6
2010/2011	82.3 ± 5.3	26.1 ± 4.3	16.8 ± 1.0	29.2 ± 1.6	25.3 ± 3.6
Mean	87.5 ± 4.9	41.1 ± 6.3	20.4 ± 1.1	39.6 ± 2.1	29.9 ± 3.4

Table 4. Seasonal and overall mean probabilities (±1 SE) that an animal in the study area is observed at least once during the primary period t ($p_t^\star$)

Primary period	Calving females	Non-calving adult females	Adult males	Juveniles	Unknown age/sex
2004/2005	0.99 ± 0.00	0.90 ± 0.04	0.95 ± 0.02	0.96 ± 0.10	0.91 ± 0.03
2005/2006	0.99 ± 0.02	0.87 ± 0.06	0.95 ± 0.03	0.96 ± 0.01	0.89 ± 0.04
2006/2007	0.99 ± 0.01	0.89 ± 0.04	0.92 ± 0.07	0.96 ± 0.01	0.86 ± 0.04
2007/2008	0.98 ± 0.01	0.85 ± 0.06	0.91 ± 0.08	0.95 ± 0.01	0.89 ± 0.04
2008/2009	0.99 ± 0.01	0.86 ± 0.05	0.90 ± 0.05	0.95 ± 0.01	0.84 ± 0.05
2009/2010	0.99 ± 0.01	0.84 ± 0.07	0.92 ± 0.03	0.95 ± 0.01	0.87 ± 0.04
2010/2011	0.94 ± 0.04	0.58 ± 0.17	0.66 ± 0.11	0.89 ± 0.02	0.74 ± 0.07
Mean	0.98 ± 0.02	0.83 ± 0.08	0.89 ± 0.06	0.95 ± 0.01	0.86 ± 0.05

Differences in arrival and persistence probabilities across seasons and groups were reflected in variation in residence patterns. In most seasons, calving females stayed in the SEUS more than twice as long as individuals in other groups, with an overall mean residence time (±1 average SE) of 87.5 ± 4.9 d (range: 78.9 – 99.6 d; Table 3). Adult males consistently had the shortest residence times with an overall mean of 20.4 ± 1.1 d (range: 16.8 – 22.8 d; Table 3). Mean residence times for non-calving adult females and juveniles were similar in all seasons (Table 3). Within demographic groups, estimated mean residence times were shortest in 2010/2011 (except for calving females and unknown age/sex individuals, which were shortest in 2005/2006) and longest in 2006/2007 (except for adult males, which were longest in 2009/2010).

Demographic and seasonal differences were also indicated in estimates of p_j (i.e. biweekly sighting probabilities); however, overall patterns generally followed patterns in biweekly aerial survey effort (Fig. S3). Survey effort and detection probabilities were lower during the first and last biweeks, due in part to variable timing in survey start and end dates across seasons. In all seasons, calving females had the highest seasonal detection rates ($p^\star$), followed by juveniles, adult males, unknown age/sex individuals, and non-calving adult females (Table 4). However, $p^\star$ values decreased for all demographic groups during the 2010/2011 season, which had 21% less effort than the study period average (Fig. S3 in the Supplement). Seasonal abundance estimates indicated that there were more juveniles, adult males, and unknown age/sex individuals in the SEUS than observed (Fig. 2).

DISCUSSION

Although right whale *Eubalaena glacialis* distribution and movement patterns have been described (Winn et al. 1986, Schick et al. 2013), temporal components of right whale distribution, including residence time in high-use areas, are less well understood. The generally accepted North Atlantic right whale seasonal migration model consists of south-

ward movement during fall or early winter and northward movement during late winter or spring (Kraus et al. 1986, Winn et al. 1986, Firestone et al. 2008). However, we observed staggered arrival and departure patterns that are not consistent with this model. Instead of a distinct peak in arrival probabilities early in the season, our models indicated arrivals for at least one demographic group in all biweeks of the winter. Furthermore, instead of a sharp decline in persistence probabilities at the end of the season, we observed persistence probabilities below 0.50 as early as Biweek 6 (24 January to 6 February), which indicates that some right whales likely leave the SEUS in the middle of the winter season. Our capture-recapture modeling framework results described variation in SEUS wintering ground residence patterns among demographic groups, identified potential influences for variation across time, and provided estimates of winter abundance in the SEUS study area, which can inform monitoring and management actions to support right whale recovery.

Demographic factors

We observed distinct residence patterns among demographic groups, which supports our hypothesis that life history and behavioral differences influence right whale residence timing in the SEUS. Demographic differences were more apparent in arrival patterns than in persistence, with calving and non-calving adult females arriving earlier than other groups (Fig. 2a–e). Our estimates of right whale arrival patterns for the SEUS area are consistent with arrival patterns for males and females described by Schick et al. (2013), although that work did not consider differences due to age class or calving status. Earlier arrival by calving females contributed to calving females having the longest mean (± 1 average SE) residence time of any demographic group (87.5 ± 4.9 d; Table 3). Fortune et al. (2013) also described longer SEUS residence periods for calving females (46.32 ± 14.60 d) than for non-lactating females (23.75 ± 18.6 d), juveniles (16.33 ± 8.50 d), or adult males (3.11 ± 3.33 d) using first and last sighting dates in the SEUS from 1991 to 2009 (estimates from Fortune et al. 2013 are means ±SD). Longer mean residence periods have also been documented for Southern right whale *Eubalaena australis* calving females relative to other demographic groups at wintering grounds in Península Valdés, Argentina (calving females mean = 77 d; other groups mean = 52 d; Rowntree et al. 2001) and southern Australia (calving females mean = 70.9 d; whales without calf mean = 20.4 d; Burnell & Bryden 1997). Our mean residence time estimates are longer than estimates for these Southern right whale wintering grounds and much longer than previous estimates by Fortune et al. (2013). This disparity may reflect real differences across time, populations, or habitats; however, direct comparison may not be appropriate since these other studies did not account for imperfect detection, which could result in underestimates of residence duration. Furthermore, our calving female residence time estimates should be considered a minimum residence period since calving females have occasionally been sighted in the SEUS before aerial surveys begin (NARWC 2014) and may stay after aerial surveys end (last occasion φ values > 0; Fig. 2f). This interpretation may not apply to adult males if they only enter and exit the SEUS once, since adult male arrival and departure was fully encompassed by the timing of dedicated aerial surveys. Underestimating residence time by not accounting for imperfect detection or survey effort influences can lead to incorrect inferences. For example, our longer residence duration estimates suggest the physiological implications of fasting in the SEUS wintering grounds predicted by Fortune et al. (2013) may be underestimated.

The SEUS residence patterns described by our study are more typical of differential migration than the generally accepted North Atlantic right whale migration model. Differential migration is characterized by variable migration timing among individuals in different age, sex, and reproductive classes and has been observed in other baleen whale species, including Antarctic blue whales (Thomisch et al. 2016) and humpback whales (Craig et al. 2003, Stevick et al. 2003). Possible reasons for a differential migration strategy for right whales include the influence of feeding ground location on migration timing and the impacts of migration timing on body condition and fitness. For example, adult females may require different prey types at different times of their reproductive cycle and exhibit flexibility in their use of spring, summer, and fall feeding habitats (Brown et al. 2001). In turn, flexibility in feeding ground location may result in variable arrival and departure timing due to the difference in time required to migrate to and from the SEUS from different locations (Stevick et al. 2003). Additionally, early arrival and longer residence times by calving females may increase calf fitness by allowing calves more time to develop in the supportive conditions of the SEUS habitat prior to migration to higher-latitude habitats (Clapham 2001). Although a time-since-arrival co-

variate was not supported in our top models for calving female persistence (Table 2), this was not surprising since arrival does not necessarily coincide with calf birth (Kraus et al. 1986) and cow-calf associations can last longer than one winter season (Hamilton & Cooper 2010). Estimates of calf survival will be required to compare the fitness of calves of early-arriving females to calves of later-arriving females, while also accounting for calf age. Furthermore, departure timing patterns across demographic groups were more similar than arrival timing patterns across demographic groups, which may be due to whales leaving the SEUS to take advantage of NEUS food resources that occur at a predictable time in late winter or early spring. In particular, the end date of *Calanus finmarchicus* seasonal dormancy (approximately late January through late February) is more consistent than when it begins (Melle et al. 2014). Potential impacts of climate change, including warmer deep-water temperatures in the Gulf of Maine, could shift food resource phenology, causing *C. finmarchicus* to end dormancy earlier and resulting in shorter residence of right whales in the SEUS (Melle et al. 2014, Thomisch et al. 2016).

For demographic groups other than calving females, whose motivation for migration is unclear (Corkeron & Connor 1999), observed arrival timing patterns are likely influenced by social factors, life-history related differences in energetic needs, and distributions prior to migration (Corkeron & Connor 1999, Clapham 2001). For example, Murison & Gaskin (1989) proposed that migrating to fast in warmer, low-latitude waters may be more beneficial than competing for potentially limited food resources in colder, high-latitude waters throughout the year. Our observations of peak adult male arrival during February corresponding with the coldest SST in our NEUS summary area during February and March are consistent with this theory. Social considerations may be important for juveniles, who lack historical knowledge about temporally or spatially variable aspects of the seasonal migration (Hamilton & Cooper 2010). Shaw & Couzin (2013) also theorized that individuals without knowledge of resource conditions would rely on social sources to inform migration, including pooling individual knowledge of conditions through social interactions. Consistent with this theory, we observed juvenile arrival patterns that were similar over all seasons and overlapped with those of other demographic groups (Fig. 2a–e), which may reflect reliance on social interactions for migrating juvenile whales.

For unknown age/sex individuals, arrival patterns were similar to those of juveniles and adult males (Fig. 2c–e). This is not unexpected since juveniles and adult males may be harder to age or sex due to lack of calving identifiers. Interestingly, calving and non-calving females had similar arrival patterns, which may reflect some uncertainty in the assignment of calving status. Although we expected low uncertainty for the calving female state assignment due to the intensive survey effort and survey conditions in the SEUS, some calving females may have been misclassified as non-calving females due to terminated pregnancies, undetected calf mortality, or departure from the SEUS before a calf was detected (Browning et al. 2010). If present, this misclassification would result in non-calving female residence time estimates being biased towards that of calving females while abundance estimates of non-calving females and calving females would be overestimated and underestimated, respectively. In future work, model frameworks that account for state uncertainty (Kendall 2004, Pradel 2005) could potentially use observed patterns in residence or other behaviors to inform the assignment of age, sex, or reproductive state for some unknown age/sex individuals or to account for potential misclassification of calving status.

Environmental factors

Demographic group influences on arrival time varied with changes in environmental factors across seasons. For instance, arrival patterns among seasons differed with NEUS October SST anomalies, although this relationship was different between adult males and all other demographic groups. Calving females, non-calving adult females, and unknown age/sex individuals arrived later, while adult males tended to arrive earlier, during seasons with below-average October NEUS-A SST (2004/2005, 2005/2006, and 2009/2010; see Fig. S2 in the Supplement). In seasons where October NEUS-A SST was above average (2006/2007, 2007/2008, 2010/2011; Fig. S2), arrival timing for these groups was earlier and later, respectively. This may indicate differences in thermal tolerance or energetic budgets across demographic groups or that whales respond to another, unknown environmental cue that is correlated with NEUS October SST.

In contrast to arrival, none of the environmental covariates evaluated for persistence had support in our top models; however, support for the seasonal effect suggests that temporal variability in some unidentified environmental condition influences departure timing from the SEUS. The lack of support

for models with persistence SEUS SST covariates was unexpected given the importance of SST in SEUS habitat models (Gowan & Ortega-Ortiz 2014). Within-season weather variability that influences SEUS SST may have masked the relationship between the SST covariates considered and variation in persistence among seasons. For example, 2010/2011 had the lowest persistence probabilities overall and the warmest SEUS biweekly temperatures for the last biweek, which agrees with our prediction that warmer SEUS biweekly SST at the end of the season would be associated with earlier departure. However, 2010/2011 also had the coldest SEUS December SST of the seasons considered and this variability likely contributed to the relative lack of support for SST covariates for persistence in the top models. Future work should account for such within-season variability when evaluating relationships with environmental covariates.

The NAO index was not a useful predictor of arrival or persistence in our models. The duration of our study may have been insufficient to detect effects of the NAO, which operates at a decadal scale (Greene & Pershing 2000). In fact, 2007/2008 was the only winter in our study that had a positive winter index. We also did not consider lagged or cumulative effects that might be more relevant to right whale condition and behavior (Meyer-Gutbrod et al. 2015). Furthermore, the spatial or temporal scale used to summarize environmental data may not match the scale relevant to right whales. In addition to considering other environmental or biological variables such as right whale health (Rolland et al. 2016), future work should evaluate summarizing the variables we considered at different scales and incorporate information from large-scale oceanographic and physical-biological models (Pendleton et al. 2012).

Management implications

Beyond insights into right whale life history, our results can inform temporal components of monitoring, management, and conservation actions along the Atlantic coast. Current protection measures for right whales are determined based on the generally accepted migration model. However, our results show that this model is incomplete and that inferences should not be determined based on residence patterns averaged across demographic groups. For instance, Hiby & Leaper (2005) predicted later modal departure dates in years with more calves present. This suggests that the presence of calves influences the residence time of all whales, whereas our results indicate that the later departure timing in seasons with more calves was due to the presence of more calving females, which had much longer residence periods than other groups. Also, variable residence patterns and phenology may result in different risk exposure among demographic groups if current protections do not provide spatial or temporal coverage for all individuals. For example, with the longest residence times and potential to arrive in the SEUS prior to the start of dedicated surveys, calving females that are critical to population growth (Fujiwara & Caswell 2001) may have increased exposure to threats in the SEUS or while in transit along the mid-Atlantic coast if regulations do not account for the different residence patterns among demographic groups.

In addition to clarifying residence timing and duration in the SEUS, our results support the potential for right whale occurrence outside of known, high-use areas. Specifically, staggered arrival and persistence patterns suggest that whales may occur along the mid-Atlantic coast throughout the winter. This is consistent with observations from acoustic monitoring efforts that have documented winter acoustic presence of right whales along North Carolina and Georgia during all seasons without the bi-modal occurrence pattern that would be expected if southward and northward migrations occurred collectively (Hodge et al. 2015). Another acoustic study detected right whale presence off Virginia with peaks in detections during October to December and February to March (Salisbury et al. 2016). Although these peaks align with the expected southward and northward migration periods, the spring peak was larger than the fall peak. Our results suggest that the smaller fall peak could be explained by the higher variability in arrival dates across demographic groups compared to departure in the spring, or that the larger spring peak might include southward movement of late-arriving migrating individuals such as adult males. However, these explanations cannot be fully evaluated since Salisbury et al. (2016) did not identify individual animals. Our results, together with observations from other work, provide additional evidence that SEUS winter residence and migratory corridor use are more dynamic than previously thought. The residence timing estimates provided by our study could provide preliminary information to plan more detailed surveys of the presumed migratory corridor.

Aerial surveys are an important tool for monitoring right whale population status, habitat use, and the effectiveness of management actions. Our models highlighted the close relationship between aerial sur-

vey effort and right whale detection probabilities in the SEUS. Survey effort should therefore be allocated to meet desired conservation and management objectives. For example, if identifying calving females to estimate their survival and reproductive rates (Fujiwara & Caswell 2001) or mitigating their ship strike risk (e.g. Keller et al. 2006, Martin et al. 2016) are primary goals, survey effort levels observed across the study period were very effective (mean $p^\star$ = 0.98 ± 0.02 SE) at sighting these individuals even when reduced effort in 2010/2011 decreased $p^\star$ to 0.94 ± 0.04 SE. This effectiveness is likely due to the typically long residence periods of calving females in the area, which make calving females more available to be sighted at least once in a given season. In contrast, $p^\star$ values for individuals in other groups were more negatively impacted by the decrease in survey effort in the last season of our study period, possibly due to their shorter residence times. Detection rates could be further reduced if the timing of residency coincides with poor survey conditions. For instance, survey effort decreased in Biweeks 5 or 6 in most seasons during the short window when adult males were present, and this decrease may be related to poor weather conditions that can impact the ability to fly surveys in the SEUS during late January and early February.

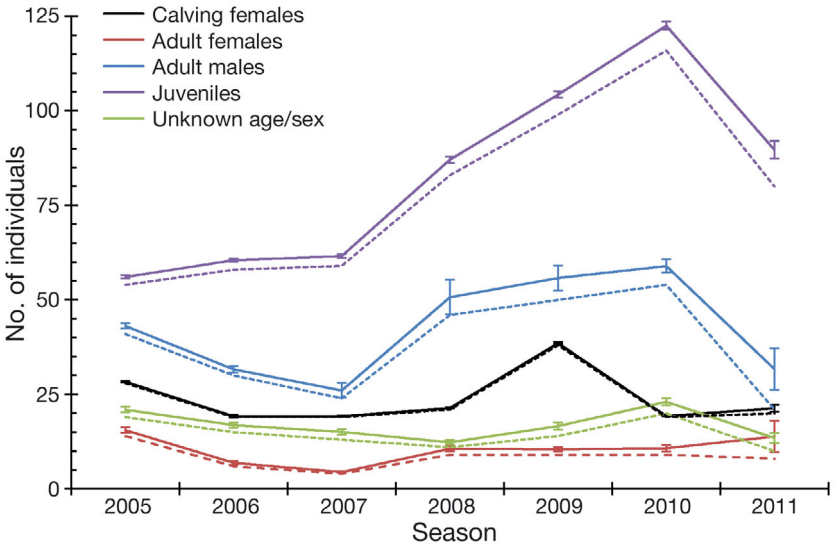


Fig. 3. Estimated abundances (solid lines with error bars indicating SE) and observed counts (dashed lines) of identified whales in the SEUS study period for each demographic group and season

In addition to informing monitoring efforts, detection probabilities can also be used to adjust abundance estimates from observed counts. Here, we provided the first estimates that account for imperfect detection of the number of whales in each demographic group that used the study area each winter (Fig. 3). These abundance estimates could be used to make better predictions about risk of mortalities associated with major threats (e.g. ship strikes, see Martin et al. 2016), for example. We recommend that future population assessments consider the effects of survey effort and variable residency on right whale detection probabilities.

The modeling approach presented in this study provides information about the temporal distribution and phenology of mobile or migratory species where mark-recapture-type data are available and could be applied to other species or other right whale aggregation areas. For right whales, our within-season models can also be used to inform a more comprehensive capture-recapture modeling analysis using the full MSORD model to estimate survival, state transitions, and temporary emigration dynamics. Our work contributes to a more complete understanding of right whale phenology and duration in the SEUS. Understanding where and when whales occur is critical for planning spatially and temporally dynamic conservation, research, and monitoring efforts; evaluating habitat use; and completing risk assessment analyses to reduce deaths and serious injuries from ship strikes and fishing gear entanglements, which impede the recovery of this highly endangered species.

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