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What we see is not what there is: estimating North Atlantic right whale *Eubalaena glacialis* local abundance

Laura C. Ganley[1,2,*], Solange Brault[1], Charles A. Mayo[2]

[1]Biology Department, University of Massachusetts, Boston, MA 02125, USA
[2]Right Whale Ecology Program, Center for Coastal Studies, Provincetown, MA 02657, USA

ABSTRACT: Aerial surveys can be used to estimate animal abundance, but animals unavailable for detection for portions of the survey can cause biased abundance estimates. Moreover, these biases may be variable owing to changes in behavior. We conducted focal follows to obtain surface and dive times of North Atlantic right whales *Eubalaena glacialis* in Cape Cod Bay (CCB) and measured the aircraft field of view; these metrics were combined to estimate availability and correct monthly abundance estimates from 1998 to 2017 generated via distance sampling methodology. We used a general least squares model to test for trends in abundance. Availability varied with month (0.27–0.85), likely linked to changes in the depth of copepod food resources. Detection probability varied across the years (0.43–0.87). Sightings per unit effort and counts of whales were significant, but downward-biased indicators of abundance and availability caused changes in bias over the season. Estimated abundance in CCB increased during the study period (4.9 whales yr^{-1}), and estimated abundance in peak months increased at a faster rate (10% yr^{-1} for 1998–2017) than for the overall population (2.8% yr^{-1} for 1990–2010). Accurate abundance estimates are necessary to monitor long-term changes in abundance of right whales in CCB, to understand the importance of CCB relative to other areas, and improve management strategies to protect this endangered species from entanglements in fishing gear and ship-strikes. Failing to correct for seasonal variation in availability results in substantial and variable underestimation of abundance.

KEY WORDS: Abundance estimation · Availability bias · Bayesian · Distance sampling · $g(0)$ · Right whales · Transect sampling · Diving

1. INTRODUCTION

North Atlantic right whales *Eubalaena glacialis* (hereafter right whales) were documented in Cape Cod Bay (CCB) as early as 1620 and were the target of intense whaling off the New England coast (Allen 1916). By the mid-1700s, the right whale population had declined dramatically and whaling for the species ended in this area (Allen 1916), but in the 1950s Watkins & Schevill (1982) observed right whales utilizing CCB. Right whales are classified as Endangered under the US Endangered Species Act and by the International Union for the Conservation of Nature (Reilly et al. 2012). Every year, from January through May (hereafter the season), right whales return to CCB, an important feeding ground for this species (Mayo & Marx 1990, Clark et al. 2010, Mayo et al. 2018), which has been designated as critical habitat for right whales (NOAA 1994). The main copepod taxa on which right whales feed are abundant in these waters and whale diving behavior is influenced by the copepods' vertical distribution, which varies seasonally (Mayo & Marx 1990, Baumgartner & Mate 2003, Parks et al. 2012).

*Corresponding author: laura.ganley@gmail.com

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Since 1997, the Center for Coastal Studies has conducted systematic aerial line-transect surveys to monitor right whale habitat use in CCB (Mayo et al. 2018). During the surveys, photographs of individual whales are collected and used for health assessments (Pettis et al. 2004, Rolland et al. 2016), reporting and monitoring entanglements in fishing gear (Knowlton et al. 2012, Robbins et al. 2015), and population studies (Pace et al. 2017). Pace et al. (2017) used photo-identification data from these and similar surveys in other areas for a population-wide mark–recapture analysis to estimate mortality rates and abundance trends of right whales. However, in CCB, abundance estimates corrected for observer biases have not been calculated and long-term temporal trends have not been analyzed.

Aerial surveys can be used to estimate abundance using distance sampling methodology (Marsh & Sinclair 1989, Buckland et al. 2001). Distance sampling involves the estimation of detection probability within a nominal strip by modeling the decline in observations as a function of perpendicular distance from the transect line. The method assumes that the probability of detection is certain on the transect line while variation in detection probability away from the transect line is accounted for in the fitted detection function. However, indices of abundance such as simple counts or sightings per unit of effort (SPUE) that do not include correction for detectability may be susceptible to bias if detectability varies. One way this may occur is if the availability of animals is variable, which can occur in species that are out of view and thus unobservable some of the time, such as burrowing animals, those hidden by vegetation, and diving marine species (Samuel et al. 1987, Laake et al. 1997, Hain et al. 1999). Availability has been shown to vary with season and physical conditions (e.g. depth and temperature) for some marine species, such as sperm whales *Physeter macrocephalus*, loggerhead turtles *Caretta caretta*, and green sea turtles *Chelonia mydas* (Jaquet et al. 2000, Thomson et al. 2012). Roberts et al. (2016) used previously collected data (CeTAP 1982) to estimate right whale availability as 0.334 on feeding grounds, and between 0.434 and 0.861 on the calving grounds, depending on group size (Hain et al. 1999). However, data on right whale dive cycles are limited and indicate considerable variation among geographic areas, and possibly between sexes and age classes (CeTAP 1982, Winn et al. 1995, Hain et al. 1999, Baumgartner & Mate 2003, Roberts et al. 2016, Baumgartner et al. 2017). Furthermore, feeding right whales follow the vertical distribution of their prey (Baumgartner & Mate 2003, Parks et al. 2012, Baumgartner et al. 2017), which varies seasonally. The resulting variation in dive times likely causes seasonal changes in the whales' availability to observers. 'Time in view', a component of availability bias, measures the length of time an animal at the surface is visible to observers, and is dependent on the observer's physical view forward and aft of the airplane (field of view), airplane altitude, and speed (Caughley 1974).

Availability bias results in an underestimation of abundance (Laake et al. 1997, Buckland et al. 2001). In this study, we focused on quantifying monthly availability biases and estimating long-term abundance trends in CCB. In addition, we compared our abundance estimates with other measures of relative abundance: counts of whales and SPUE. Although SPUE data are routinely used as indicators of abundance for right whales (Nichols et al. 2008, Pendleton et al. 2009, Mayo et al. 2018) and other cetaceans (MacLeod et al. 2004, Weir et al. 2007), the relationship between right whale SPUE or counts of whales and abundance has not been measured. Clarifying those relationships is crucial because inaccurate indicators may be detrimental to the effectiveness of management strategies for this species. Accurate estimates allow us to monitor long-term changes in abundance in CCB, understand the importance of CCB to the population relative to other areas, and finally, to improve management strategies to protect this endangered species from entanglements in fishing gear and ship-strikes.

2. MATERIALS AND METHODS

2.1. Aerial surveys

Cessna 336 or 337 Skymaster airplanes were used to conduct annual surveys for right whales in CCB. Between January and May from 1998 to 2017, 542 partial or complete surveys were conducted, resulting in 4913 right whale sightings. The timing of the season was determined based on previous research on the occurrence of right whales in CCB (Hamilton & Mayo 1990). Complete surveys consisted of 15 east–west tracklines spaced 2.8 km apart, and one north–south trackline, approximately 5.5 km east of Cape Cod (Mayo et al. 2018). Surveys were flown at 185 km h^{-1} and either 228 or 304 m altitude. One observer on each side of the aircraft scanned for marine mammals and updated environmental conditions throughout the survey. Altitude, speed, and position were recorded from the aircraft's GPS either by hand, Logger 2000, or Mysticetus software. When a right whale was sighted, the aircraft broke from the trackline to obtain sighting location, photographs, group size, and behavioral data, before resuming at the location where the trackline was broken.

2.2. Distance sampling analysis

Distance sampling methodology estimates a detection function, the probability an animal is observed given its distance from the trackline, using the perpendicular distance between the trackline and the animal (Buckland et al. 2001). We used ArcGIS (ESRI 2011) to calculate perpendicular distances using the angle and flight distance from the trackline break location to the sighting. Distance sampling assumes all of the whales directly on the trackline are observed; i.e. $g(0) = 1$. In this study, this assumption was violated because whales that were on the trackline but on a dive were unobserved, and thus required an availability correction. Using the methods outlined by Buckland et al. (2001), abundance ($\hat{N}$) was estimated as:

$$\hat{N} = \frac{nA}{2wL\hat{P}_a} \tag{1}$$

where n is the number of animals counted, A is the area of the study, w the width of the observer viewing swath, L is the total length of trackline flown, and $\hat{P}_a$ is the proportion of animals detected within the covered area.

Analyses were carried out using the R package 'Distance' (R Core Team 2009, Miller 2015). Truncation can be used to remove sightings from the analysis that are between the trackline and a specified distance. The aircraft used for the survey have a blind spot beneath them, resulting in a field of view that does not begin directly on the trackline; in the analysis this is dealt with by left-truncating the detection function (Gowan & Ortega-Ortiz 2014). We left-truncated the data to 100 m except for surveys in 2016, for which a 250 m left-truncation distance was necessary to achieve adequate goodness-of-fit (Buckland et al. 2001). Sightings at large distances from the trackline (outliers) often cause ill-fitting detection functions; in these instances, right-truncation can be used to remove these sightings (Buckland et al. 2001). We right-truncated the data to 3000 m except in 2002 and 2003, which were right-truncated at 4000 m.

A preliminary multi-covariate distance sampling (MCDS) analysis was conducted using the 2016 data in which Beaufort sea-state, group size, time of year, and behavior were considered covariates that could have influenced detection probability. The 2016 conventional distance sampling model, which was without covariates, had a lower Akaike's information criterion score than the MCDS models; therefore, we used the conventional model from each year to generate monthly abundance estimates. We obtained a separate detection function for each year using a hazard-rate key function without covariates. We calculated survey abundance estimates and their standard error for each month of the season of each year and evaluated model fit using the Kolmogorov-Smirnov and Cramer-von Mises goodness-of-fit tests (Burnham et al. 2004).

Right-truncation at 3000 m results in overlap in strip half-widths between adjacent tracklines, but this does not bias abundance estimates (Buckland 2006). To test the sensitivity of abundance estimates to overlapping strip half-widths, we fit models for April of each year, which is a subset of data with a high sample size and high availability. For this test we used a right-truncation distance of 1398 m, the point at which the 2 strip half-widths met. We found no consistent direction in bias and the difference in abundance estimates between models with a right-truncation of 3000 m and 1389 m was less than 15% in most years (n = 15). However, we were unable to achieve adequate goodness-of-fit for 3 of the 20 years, most likely due to low sample size in these years.

2.3. Time in view

The time in view is the amount of time a whale is visible to an observer and is a function of the field of view (the observer's visual range forward and aft of the airplane), airplane speed, and altitude (Laake et al. 1997). To calculate the time in view, 13 transects laid out between 446 and 2910 m from a navigation buoy were flown up to 6 times at both 228 and 304 m altitude. Observers marked the time when they observed the buoy forward of the airplane, perpendicular to the airplane, and as the buoy left their view aft of the airplane. The first model, fit in a Bayesian framework, tested for a difference in the effect (α) of altitude and the effect (β) of distance (x) on time in view (t):

$$t = \alpha[\text{altitude}] + \beta x \tag{2}$$

Posterior distributions of the parameters for this and all Bayesian models in this paper were obtained by Hamiltonian Monte Carlo resampling using the 'rethinking' package in R (R Core Team 2009, Mc-

Elreath 2015). Bayesian models were used to allow for future updating of estimates as more data become available. We used the Gelman-Rubin criterion to check for model convergence and visually inspected all trace plots. To interpret the results from the Bayesian analyses, we used the confidence likelihood terminology used by the Intergovernmental Panel on Climate Change (IPCC 2007). A weakly informative normal prior with mean = 91 and standard deviation (SD) = 40 was used for α which centers the time in view distribution at 91 s with 95% probability between 9 and 171 s, which encompasses all of our data points. A normal vague prior with mean = 0 and SD = 100 was used for β allowing for the conservative possibility of no influence of distance on time in view by allowing the slope to equal 0, but the SD allows for the possible slopes to vary widely. Finally, a weakly informative half-Cauchy prior [0, 10] was used for σ to ensure that the lower limit of the SD of the mean takes on a positive value, and is wide enough to give the model a starting value, while the thick tail of the half-Cauchy distribution will not rule out reasonable parameter estimates. There was strong support for no difference in the effect (α) of altitude on time in view (see Section 3); consequently, we fit a pooled model of the effect of distance on time in view. To determine time in view, the field of view (the forward and aft angles of view) was calculated using the mode of the posterior distribution of β in the model:

$$\tan\theta = \beta \cdot \text{Speed} \tag{3}$$

Since the flat windows used for this study result in a blind spot directly beneath the airplane, we assumed perfect detection would occur at 100 m ($g[100] = 1$), not 0 m; therefore, we evaluated t at 100 m. Assumptions about the size of the blind spot have varied in other similar studies (Hain et al. 1999, Forcada et al. 2004, Andriolo et al. 2006, Gómez de Segura et al. 2006, Gowan & Ortega-Ortiz 2014, Robertson et al. 2015). The mode of the posterior distribution of α from the time in view linear model was used to determine $t(100)$ as:

$$t(x) = \alpha + \frac{x \cdot \tan\theta}{\text{speed}} \tag{4}$$

2.4. Availability correction

We measured availability bias using 61.8 h of data on dive and surface times collected from 87 focal follows (focal follows as defined by Friedlaender et al. 2009) on 22 d during the 2016 and 2017 seasons. The amount of time spent in the field each month was weather-dependent, resulting in an increasing number of follows as the season progressed (Table S1 in the Supplement at www.int-res.com/articles/suppl/n038p101_supp.pdf). Focal follows were conducted from a 12 m vessel, during which whales were approached up to a distance of 50 m; we stayed with an individual or group of whales in association (as defined by Whitehead 1983) for up to 60 min, collecting photographs of each individual. To avoid pseudoreplication, photographs were matched to the North Atlantic Right Whale Consortium photo-identification database curated at the Anderson Cabot Center for Ocean Life at the New England Aquarium (NEAq). As a result, no individuals were used more than once in the analysis. Surface time was defined as the period when the individual or at least one animal in the group were at the surface, and dive times were when no whales were at the surface (Laake et al. 1997, Hain et al. 1999). Submergences, presumably shallow, which occurred between breaths were categorized as surface time. Animals beneath the surface may still be visible from an aerial platform, depending on depth and water turbidity (see Section 4). Using dive time data from 2016 and 2017 to estimate availability for 1998 through 2017 assumes that diving behavior has remained consistent from 1998 through 2017. Prey availability influences dive behavior, and a change in the seasonal transition of the 3 main zooplankton taxa may influence availability estimates. Analyses of zooplankton abundance in CCB indicate trends in the seasonal transition have remained relatively steady from 1999 to 2010 (Stamieszkin et al. 2010).

To determine if a monthly availability correction was needed, we fit a normally distributed linear model with percent surface time (PST) as function of month in a Bayesian framework and evaluated differences in the posterior distributions of intercepts. A normal vague prior with mean = 50 and SD = 20 was used for α, which centers the PST at 50 but allows it to move anywhere between 10 and 90. A uniform vague prior [0, 100] was used for σ to constrain the lower limit of the SD of the mean to be positive but it is wide enough as to not constrain the model, and the uniform distribution allows for all parameters to be equally likely.

Laake et al. (1997) determined that the average probability $a(x)$ that an animal at perpendicular distance x will be at the surface and within the observer's field of view can be estimated as:

$$a(x) = \frac{\bar{s}}{\bar{s}+\bar{d}} + \frac{\bar{d}\left[1-\exp\left(\frac{-t(x)}{\bar{d}}\right)\right]}{\bar{s}+\bar{d}} \tag{5}$$

where s and d, time spent at and beneath the surface, respectively, are bootstrapped 1000 times and evaluated using t at 100 m.

Distributions for monthly abundance estimates (that is, the estimated abundance from a survey flown in a given month) were calculated by combining 1000 bootstrap values, both from the distance sampling abundance distribution and from the availability correction distribution.

2.5. Calibrating indicators of abundance to estimates of abundance

The relationships between SPUE, as well as counts of whales, with abundance are correlated, since they are all based on the same data. We used non-parametric Kendall correlation to measure this correlation. With the purpose of using SPUE or counts of whales as indicators of abundance, we developed a calibration equation. To do so, we used 2 regression analyses with abundance as the dependent variable and SPUE or counts of whales, respectively, as predictor variables, and month as an interaction effect. Monthly SPUE values were calculated by dividing the monthly number of right whales by the monthly trackline distance surveyed. Counts of whales used in this comparison were the monthly means of total whales sighted in each survey.

2.6. Trends in abundance

To examine trends in abundance from 1998 through 2017, we ran general least squares (GLS) models with time as a covariate on each of 1000 bootstrap samples from monthly abundance distributions to generate 1000 possible abundance trajectories from 1998 through 2017. In order to compare abundance trends in CCB with abundance trends for the population, we ran GLS models on each of 1000 bootstrap samples from the yearly month of peak abundance distributions to generate 1000 possible abundance trajectories from 1998 through 2017.

3. RESULTS

3.1. Time in view

The 84% overlap in posterior distributions of model intercepts for each altitude indicates it is likely that time in view did not differ between the 2 altitudes (Fig. S1 in the Supplement). With time in view pooled at the 2 altitudes, time in view increases with distance (Fig. 1). The estimated time in view at 100 m, the effective trackline, was 51.22 s. We tested the sensitivity of the model results to changes in the prior distributions. Changing the prior for α from a normal distribution with mean = 91 s and SD = 40 s to a normal distribution with mean = 40 s and SD = 40 s had a minimal effect on the estimate for α which changed from 51 to 54 s. Changing the priors did not affect the estimate for β. To test the sensitivity of the availability estimates to the value of α, we used the mean surface and dive times to calculate availability (Table S1). There was a positive (0.18–2.6%) change in the monthly availability estimates when α was changed from 51 to 54 s.

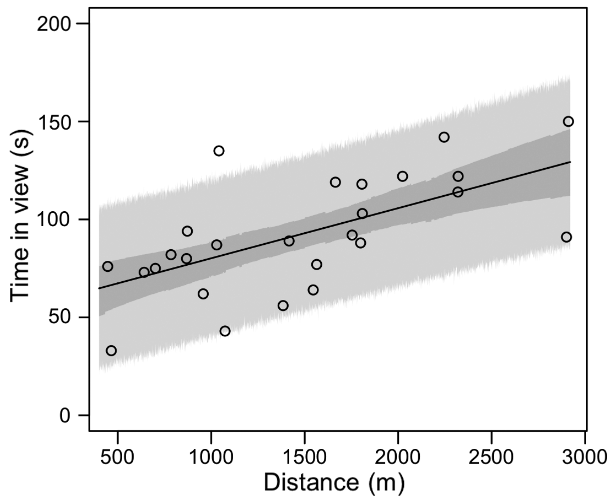

Fig. 1. Relationship between a North Atlantic right whale's distance from the trackline and the time in an observer's view; time in view is dependent on the whale's distance from the trackline: slope = 0.03 (m s^{-1}). Dark gray shading: 89% highest posterior density intervals = [0.02, 0.04]. Light gray shading: 89% percentile intervals. Open circles: data points

3.2. Availability correction

Percent surface time from focal follows are presented in Fig. 2 (January: 16%; February: 34%; March: 31%; April: 55%). Mean surface and dive times are presented in Table S1. Overlap in the posterior distributions of monthly intercepts from the Bayesian linear model (Fig. 3) show that PST during February and March are more likely than not to be the same (65.4% overlap), but that it is likely all other pairs of months are different (19% overlap in the distributions for January and February, 26.5% over-

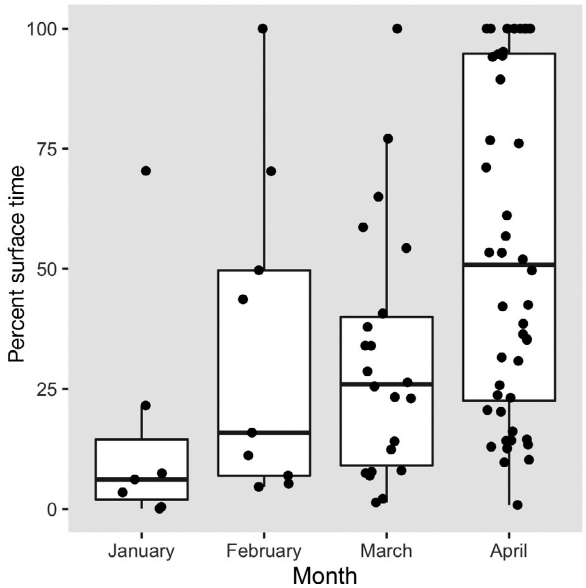

Fig. 2. Percent surface time of North Atlantic right whales binned by month. Points are values for individual focal follows. Sample size for January = 7, February = 10, March = 22, April = 48. The lower and upper bounds of the box mark first and third quartiles. The whiskers extend to the smallest and largest values within the 1.5× interquartile range

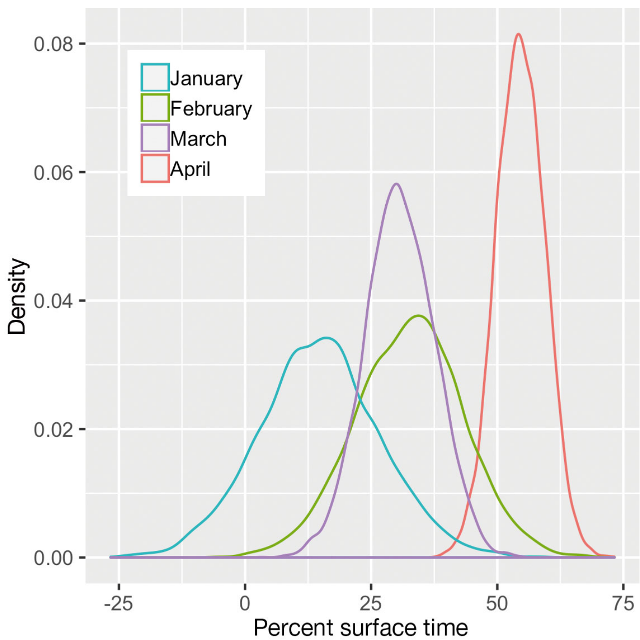

Fig. 3. Posterior distributions of monthly percent surface time of North Atlantic right whales for the linear model testing the relationship between percent surface time and month

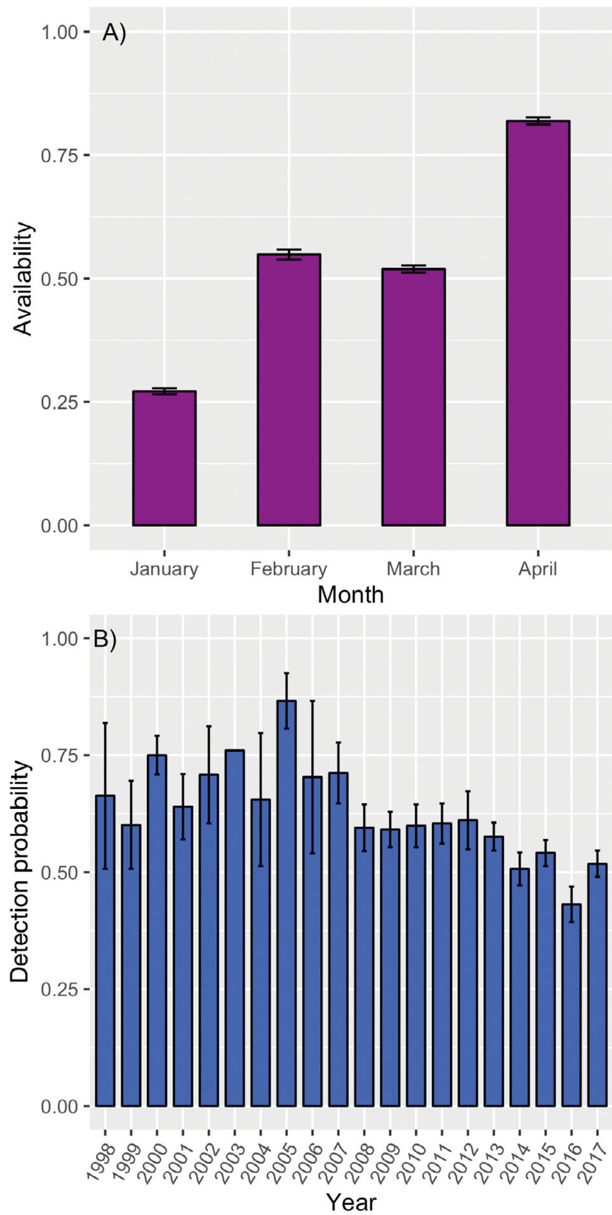

Fig. 4. (A) Monthly probability of a North Atlantic right whale being available due to dive behavior (±SE) and (B) annual detection probability estimates (±SE) for the survey platform

lap for January and March, 0.6% overlap for January and April, 5.8% overlap for February and April, and 0.5% overlap for March and April). Thus, availability fluctuates throughout the season (Fig. 4A, Table S1).

To test the influence of the prior distribution for α on the conclusions from the model, we compared a normally distributed prior with mean = 50 and SD = 20, and a normally distributed prior with mean = 25 and SD = 40. The choice of prior slightly changed the overlap in the posterior distributions, but the conclusions of the model did not change. Availability estimates were lowest for January (0.27) and increased through April (0.91) (Fig. 4A, Table S1).

3.3. Distance sampling

The annual detection functions (Fig. 5, Table S2) all showed adequate goodness-of-fit ($p > 0.05$), except for 2003. The average probability of detection ($\hat{P}_a$) ranged from 0.43 in 2016 to 0.87 in 2005 (Fig. 4B, Table S2).

Timing of peak abundance varied annually (Fig. 6). In some years (n = 8), right whales were first observed in January, increased to peak abundance by March, held steady or decreased in April, and declined sharply in May. In other years (n = 8), peak abundance occurred in April rather than March. Outliers from either pattern occurred in 1998, with peak abundance in February, and 2015, with the peak in May.

3.4. Calibrating indicators of abundance to estimates of abundance

There was a strong correlation between monthly SPUE values and abundance (Kendall's rank correlation $\tau = 0.84$, $p < 2.2 \times 10^{-16}$), and between counts of whales and abundance (Kendall's rank correlation $\tau = 0.81$, $p < 2.2 \times 10^{-16}$). Fig. 6 allows a comparison of abundance estimates, counts of whales, and SPUE across the study period. Although general patterns were similar, correcting for the combined effect of incomplete detection due to distance from the trackline and availability bias creates a discrepancy between abundance estimates and both SPUE and counts of whales, especially early in the season. However, conditional on month, SPUE and counts of whales both had a significant linear relationship with abundance (SPUE: $p < 0.01$, $R^2 = 0.93$, slopes: January = 32 646, $p < 0.01$, February = 17 818, $p = 0.06$, March = 19 952, $p < 0.01$, April = 13543, $p < 0.01$, May = 17 147, $p = 0.05$; Fig. 7A; counts of whales: $p < 0.01$, $R^2 = 0.88$, slopes for counts of whales: January = 6.06, $p < 0.01$, February = 4.3, $p = 0.02$, March = 4.50, $p < 0.01$, April = 2.6, $p < 0.01$, May = 2.0, $p = 0.04$, Fig. 7B).

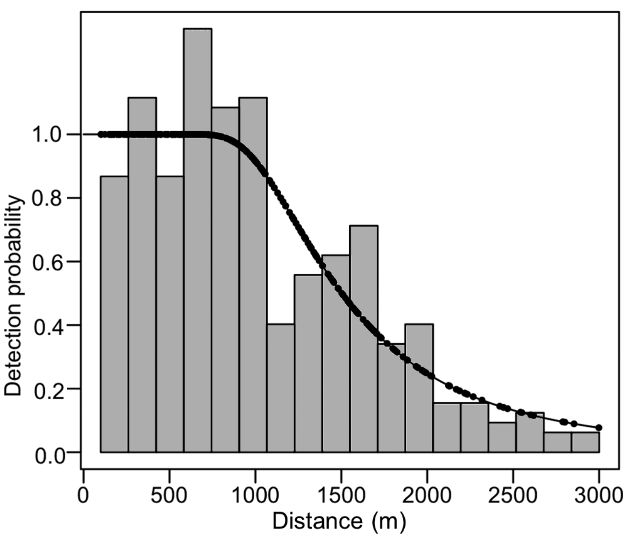

Fig. 5. Detection function of North Atlantic right whales for 2015. The detection function (black line) is the probability of detecting a whale with increasing distance from the trackline. Bars: frequency of sightings at binned distances; black dots: whale sightings

3.5. Trends in abundance

The GLS model on bootstrapped yearly samples revealed a positive trend in abundance with a mode of 4.9 whales yr^{-1} (2.5% quantile: 2.7, 97.5% quantile: 9.17; Fig. 8). This translates to an increase of 98 whales in estimated abundance over the period of 1998 to 2017 in CCB. The GLS model on bootstrapped samples from the yearly month of peak abundance revealed a positive trend in peak abundance of 11.71 whales yr^{-1} (2.5% quantile: 4.8, 97.5% quantile: 26.07). This translates to a 10% yr^{-1} increase in estimated abundance in the month of peak abundance over the period of 1998 to 2017 in CCB.

4. DISCUSSION

This study is the first to quantify abundance of right whales in CCB and seasonal fluctuations in right whale availability bias, and to analyze long-term abundance trends for this area. CCB is an area of seasonally high right whale density and is of recognized importance to the population, where effective management is critical (Mayo et al. 2018). One major result, with immediate relevance to the function of right whale aerial surveys in CCB, is that there are large variations in whale availability through the season. Over the 2 yr of focal-follow data, our range of availability estimates varied threefold across months. Low availability results in a downward bias in perceived abundance. Bias per se may not be problematic if it is constant, as the relationship between a biased indicator and the true quantity will not change (Hiby 1999). Variable biases, however, cause the indicator to be an unreliable measure. Availability issues have also been highlighted in previous studies of right whales. Acoustic monitoring in CCB has detected right whales on days when aerial

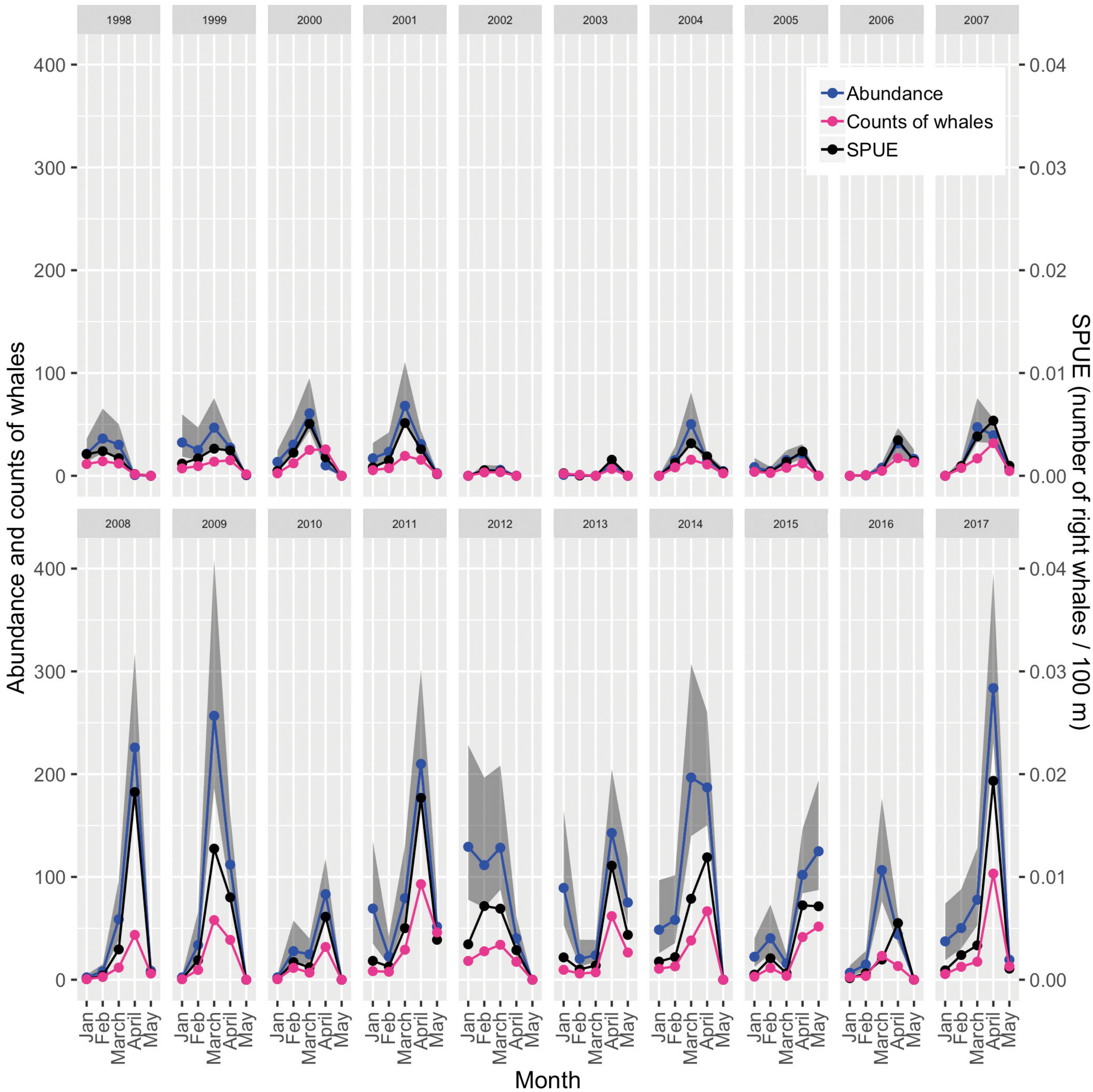

Fig. 6. North Atlantic right whale abundance estimates, sightings per unit effort (SPUE), and counts in Cape Cod Bay by month for each year. Blue points: median of the distribution of bootstrapped abundance; gray shaded regions: 1st and 3rd quartiles of the distribution; black points: SPUE; pink points: counts of right whales divided by the number of surveys in each month. There was no survey effort in May 2002

surveys found none (Clark et al. 2010). Likewise, right whale aerial surveys in the southeast US, although effective for describing distribution, have resulted in imprecise daily estimates due to low availability (Hain et al. 1999). Variation in availability has been reported for numerous other taxa. Availability varied with water temperature and depth for loggerhead and green sea turtles (Thomson et al. 2012), air temperature and time of day for Hermann's tortoises *Testudo hermanni* (Couturier et al. 2013), and group size for humpback whales *Megaptera novaeangliae* (Hodgson et al. 2017) and elk *Cervus elaphus* (Samuel et al. 1987). For right whales, the major shifts in availability through the season, repre-

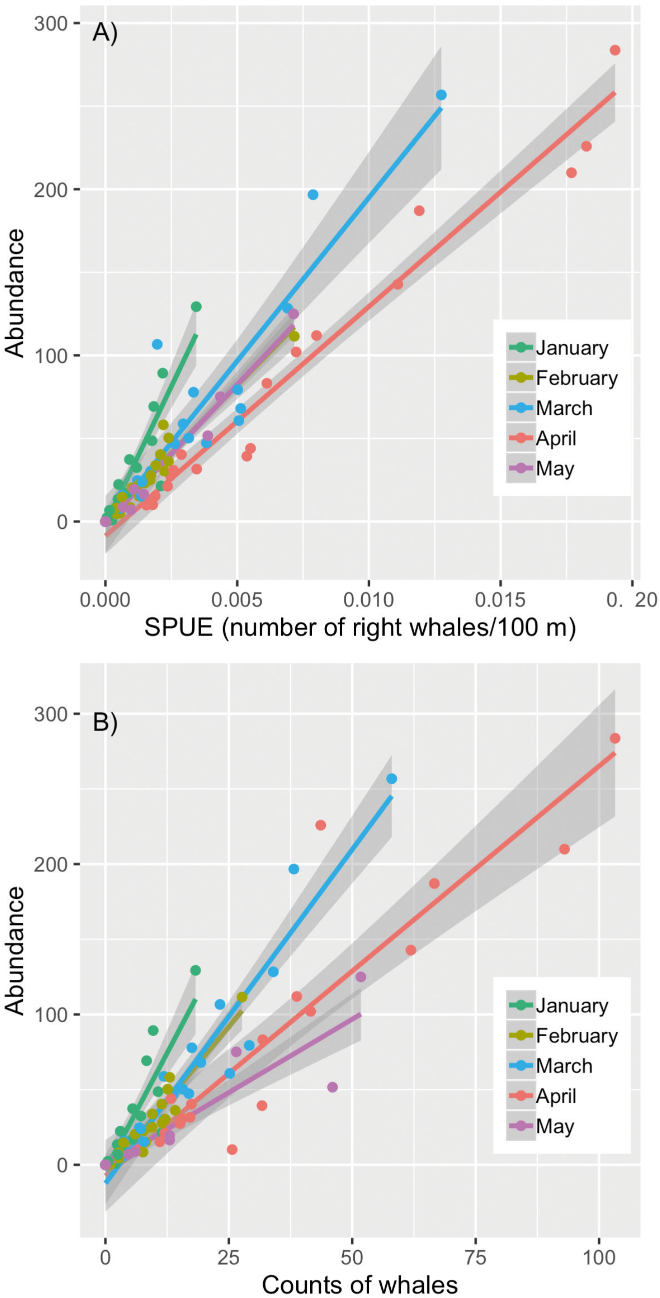

Fig. 7. Slopes of relationships between monthly abundance estimates of North Atlantic right whales and (A) sightings per unit effort (SPUE) and (B) counts of whales

sented by the month in our study, need to be factored into assessments of abundance, and therefore into the timing of management plans, such as seasonal fisheries closures and ship speed restrictions.

Survey detection probability varied 2-fold across the 1998 to 2017 observation period, likely due to a wide range of factors including weather conditions and changes in observers. In other studies, sea state, platform, and group size were factors that influenced detection probability, and these factors varied by species (Gómez de Segura et al. 2006, Friday et al. 2013). Perception bias, the failure to detect all animals that are available on the transect line, was not addressed directly in this study. To estimate only this component of bias, additional information is required by additional observer teams (Marsh & Sinclair 1989, Laake & Borchers 2004). This study did not have access to these methods, and therefore we were unable to estimate this bias and the influence of its causes. Studies of small marine mammals have found availability bias to far outweigh perception bias (Marsh & Sinclair 1989), and in the case of large whale aerial surveys, it is likely that perception bias would similarly be exceeded by availability bias (Carretta et al. 2000, Laake & Borchers 2004, Roberts et al. 2016).

In order to increase accuracy in estimates of availability and abundance across the range of the right whale — information that is imperative to the management of the species — more information about right whale diving behavior throughout its range and variation across the seasons is crucial. Several cetaceans exhibit season-specific and habitat-specific diving behavior (e.g. sperm whales, Jaquet et al. 2000; minke whales *Balaenoptera acutorastrata*, Stockin et al. 2001). On Stellwagen Bank and in the Great South Channel, right whales had a shorter mean surface time (2.58 min; CeTAP 1982) than in CCB (8.11 min; Table S2), while the range of mean surface times in CCB (0.8–13.35 min) extends the range reported in other areas (2.14–11.09 min) (CeTAP 1982, Nieukirk 1992, Winn et al. 1995, Hain et al. 1999, Baumgartner & Mate 2003, Roberts et al. 2016). Monthly mean dive times collected in CCB (1.30–8.83 min) are within the range of reported estimates (0.87–12.17 min). However, mean dive times fail to describe the full variability of right whale diving behavior; in CCB, some dives we observed in our focal follows lasted more than 30 min. Heterogeneity in dive time data is a result of variation in whale foraging strategies in a number of cetacean species (Jaquet et al. 2000, Stockin et al. 2001, Baumgartner et al. 2017), and the function of CCB as a major feeding area is likely the reason for the heterogeneity in right whales (Hamilton & Mayo 1990, Mayo et al. 2018). During the winter months, *Centropages* spp. and *Pseudocalanus* spp. are the dominant copepods and can aggregate in layers close to the sea floor (Leeney et al. 2009). Abundance of *Calanus finmarchicus* increases throughout the season, peaking in April with the formation of dense surface patches

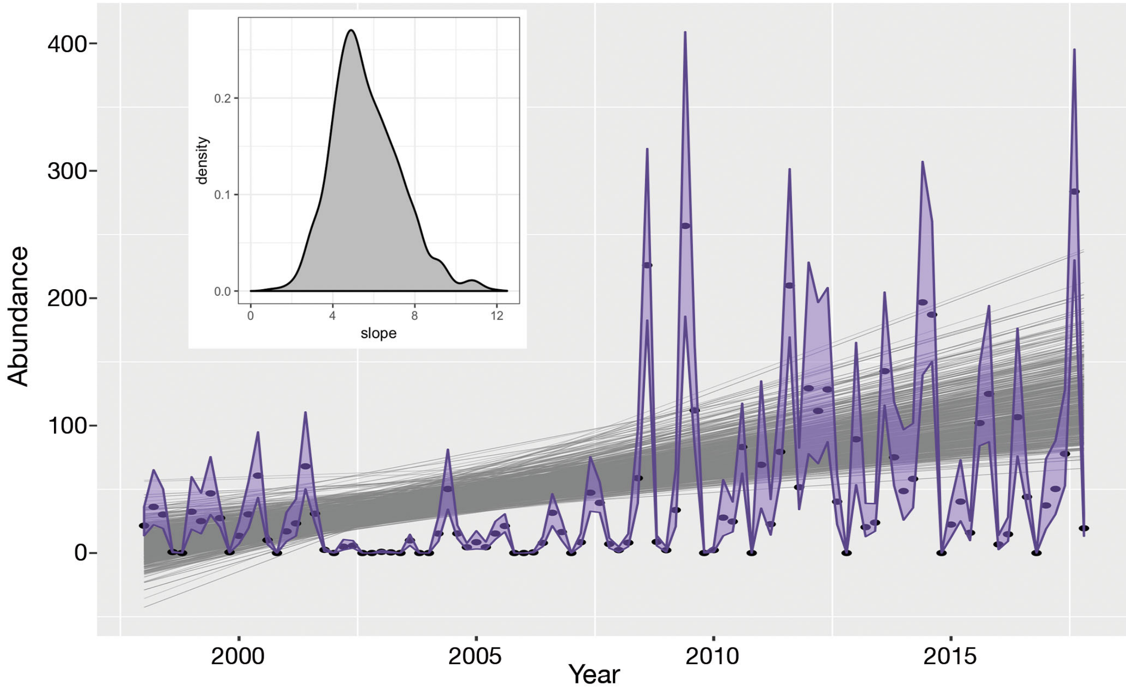

Fig. 8. Trends in North Atlantic right whale abundance. Points: medians of the distribution of monthly abundance estimates; purple shaded regions: 1st and 3rd quartiles of the distribution; gray lines: fits from 1000 bootstrapped general least squares models. Inset displays the distribution of possible trends (the distribution of slopes of the gray lines) in right whale abundance from the bootstrapped models

(Pendleton et al. 2009). Diving depths of right whales in tagging studies were found to have a strong relationship with depths of high zooplankton concentrations (Baumgartner & Mate 2003, Parks et al. 2012, Baumgartner et al. 2017). By responding to changes in the vertical zooplankton distribution, whales in CCB spend little time at the surface during winter months with surface time increasing in spring. It is thus essential to factor intra-seasonal variation in whale availability into the calculation of abundance estimates, particularly during January and February when long dives result in a reduction in availability compared with April.

The long-term data set available on right whales in CCB has allowed for a comparison between counts of whales, SPUE, and abundance, thereby providing valuable insight for other studies that use measures of relative abundance as a proxy for abundance. Our study demonstrates that SPUE and counts of whales are biased indicators of the number of whales present in CCB, and that this bias changes throughout the season. For several years there were strikingly more right whales utilizing the area than SPUE or counts of whales suggested. The difference between abundance and indicators of abundance is most conspicuous in extreme cases (e.g. April 2017) but the conditional effect of month, which represents changing seasonal availability, is crucial in January and February when few right whales are sighted; correcting for low availability reveals that many more whales are visiting CCB during those months than are observed. Comparing our abundance estimates with counts of whales and SPUE (Hamilton & Mayo 1990, Nichols et al. 2008, Mayo et al. 2018) also revealed an important difference in seasonality compared to assessments based on SPUE and counts of whales: in 10 of the 20 years, peak seasonal abundance appears to occur in March, rather than in April as previously reported. Furthermore, sporadic surveys and opportunistic sightings in CCB have documented right whales in December (Nichols et al. 2008). If availability in December is similar to that of January through March, more whales are present than has been assumed — and critically, the season over which right whales use CCB is longer than previously believed.

This study was limited by a number of conditions imposed by the survey protocols. During aerial surveys, some sightings were not independent — that is, some whales were sighted because they were in proximity of previously sighted whales, which can cause an upward bias in abundance estimates; data are now being collected in such a way as to allow for the removal of these sightings for future abundance estimates. During focal follows, submerged whales and submerged whales producing fluke prints were classified as diving animals, as was perceived from a ship-based platform. However, the aerial survey team can sometimes observe submerged whales, and fluke prints may alert observers to the presence of whales. Based on our results, in 2017 observers began noting cues for breaking the trackline. Of the survey sightings from 2017 that were included in this analysis, 8% were of submerged whales, which would have been calculated as unavailable; this results in an inflated abundance estimate. Furthermore, the depth of submerged whales and water turbidity likely influence availability (Laake et al. 1997, Laake & Borchers 2004). Pollock et al. (2006) noted the logistical problems of correcting for variables which can fluctuate for each sighting (e.g. turbidity) in aerial surveys of dugongs *Dugong dugon*, and Richard et al. (1994) found that life-sized models of narwhals *Monodon monoceros* and belugas *Delphinapterus leucas* at 10 m deep were visible during photo-analysis. For right whales in CCB, the issue of availability while submerged is likely most problematic in March when a large proportion of whales are subsurface feeding (Parks et al. 2012), possibly imparting an upward bias to our abundance estimates. Roberts et al. (2016) pointed out there are spatial and temporal variations in right whale dive times. In using dive time data from 2016 and 2017 to calculate availability for the entire time series, we have assumed that there were no drastic changes in dive times from 1998 through 2017. Ideally, data on diving behavior should be collected yearly and those availability estimates would then be applied to that year's abundance estimates; however, this was not an option for aerial survey data that had already been collected from 1998–2015 without corresponding dive-time data. The analyses concerning PST and time in view were conducted in a Bayesian framework which is an inherently iterative process; the posterior distributions from the 2016 and 2017 PST and time in view data can therefore be used as priors for future attempts at estimating availability. This strategy allows for every data point to be used, whether it was collected in the current year or not, which may be particularly beneficial in January and February when weather can preclude obtaining large sample sizes of dive-time data.

The seasonal shifts in availability and the resulting adjustments of abundance estimates have serious conservation ramifications. Entanglements and ship-strikes are the primary anthropogenic causes of deaths for right whales (Knowlton & Kraus 2001, Knowlton et al. 2012), and conservation policies in CCB were crafted to protect right whales from those risks when SPUE is high. However, anchored trap gear is permitted in the month of January (Massachusetts Division of Marine Fisheries 2016), a month of low SPUE but one during which our results indicate substantial numbers of whales use CCB in some years, increasing the risk of entanglement. Similarly, the higher-than-perceived whale abundance in January, February, and March means that more animals may be at risk of ship-strike during those months than previously thought. In addition, whales tend to feed at or just below the surface in March and April, and are thus more vulnerable (Parks et al. 2012, Baumgartner et al. 2017). Moreover, the unquantified presence of right whales in December is not currently addressed by either fishing or shipping policies. Seasonal management areas (SMAs), aimed at slowing vessels to reduce ship-strikes, begin in January for CCB, and March for some parts of the study area east of Cape Cod (NOAA 2013). Conservation plans for CCB aimed at reducing right whale mortality will be most effective if they are grounded in abundance estimates.

The increasing trend in the use of CCB by right whales will exacerbate these conservation issues. The positive abundance trend reinforces similar findings based on the number of individuals per unit effort (Mayo et al. 2018) that indicate increased use of CCB over the last decade. Right whale abundance increased significantly in CCB from 1998 through 2017, outpacing the growth of the population. Pace et al. (2017) estimated an overall population increase of 2.8% yr^{-1} from 1990 to 2010, and a decline of 5% from 2010 to 2015. In contrast, our abundance estimates indicate a mode of 4% annual increase in abundance for the later period (2010–2015) in CCB and a 10% annual increase in the month of peak abundance from 1998 through 2017. Underlying reasons for this positive trend in CCB are poorly understood and could stem from improved plankton resources in the Bay or poorer or less predictable alternative feeding grounds. Regardless of the causes for this trend, CCB is an increasingly important right whale habitat and the management of entanglement and ship strike risk in CCB will play a significant role in the protection and recovery of the species.

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