Distribution, demography, and behavior of North Atlantic right whales (*Eubalaena glacialis*) in Cape Cod Bay, Massachusetts, 1998–2013

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ABSTRACT

The occurrence of North Atlantic right whales (*Eubalaena glacialis*) in Cape Cod Bay was documented during aerial surveys between 1998 and 2013. The seasonal occurrence remained relatively unchanged during the study, spanning the January through mid-May timeframe. The number of individual whales visiting the Bay was positively correlated with the increasing Best Cataloged Estimate (BCE), the number of photographed whales alive, with a maximum in 2011 of 56.9% (n = 277) of BCE. However, the rate of increase in number of individuals during the study was significantly greater than that of the BCE (difference in slope: 12.72; P < 0.01) suggesting that increased visitation to the Bay was due in part to a change in habitat preference. Although the demographic composition of whales observed during the study differed little from that of the cataloged whales, the proportion of calves born in the North Atlantic that were documented in the Bay increased significantly (P < 0.01). Models of random visitation demonstrated an individual preference for or rejection of the Bay by the right whales of the North Atlantic population.

Key words: *Eubalaena glacialis*, right whale, Cape Cod Bay, aerial survey, distribution, demography, behavior, cow/calf pairs, habitat preference.

The North Atlantic right whale (*Eubalaena glacialis*, hereafter “right whale”) is one of the rarest large whales in the world. Although small numbers of right whales may occasionally be found in the southern Gulf of Maine throughout the year, they

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regularly form feeding aggregations in Cape Cod Bay from early winter through mid-spring (Schevill et al. 1986, Winn et al. 1986, Hamilton and Mayo 1990, Payne et al. 1990). While the Bay has long been recognized as a significant feeding, socializing, and nursery area for right whales (Allen 1916, Schevill et al. 1986, Hamilton and Mayo 1990, Mayo and Marx 1990, Nichols et al. 2008), detailed information on the habitat use patterns and individual composition of the population visiting the Bay has been lacking. Here we report on the results of 16 yr of aerial surveys documenting the distribution, demography, and behavior of 468 individual right whales observed during the study.

Right whales were first documented in the Bay in the 1620s and were hunted commercially until the mid-19th century (Freeman 1862, Allen 1916, Watkins and Schevill 1982, Reeves et al. 1999). Studies of right whales in Cape Cod Bay began in 1955, when Watkins and Schevill (1979, 1982) recognized the importance of the Bay to the species. Among the areas where right whales aggregate along the east coast of North America, the Bay is unique because of its combination of shallow hydrography (<65 m) and the varied composition of the zooplanktonic food resources available to the whales (Mayo and Marx 1990).

The population of North Atlantic right whales is precariously low and its recovery has been sluggish for decades (Kraus et al. 2005, 2007). At the conclusion of our analyses in 2013, the best estimate of cataloged right whales was approximately 500 right whales (Pettis and Hamilton 2014) and the population growth rate for 1990 through 2010 was estimated at 2.8% (Waring et al. 2016, Pace et al. 2017), considerably lower than the 7% rate estimated for southern right whale (E. australis) populations in the Southern Hemisphere (IWC 2001). Ongoing research on North Atlantic right whales has concentrated on the individual and population level impacts of human activities, including mortality due to vessel strike and entanglements in fishing gear (Vanderlaan and Taggart 2007), and the effects of sublethal injuries on health and reproduction (Moore et al. 2007, Silber et al. 2010, Robbins et al. 2015, Rolland et al. 2016). Less extensive research has focused on the right whales’ habitat use (Nichols et al. 2008, Davies et al. 2015). However, there is no doubt that the future of the species remains in jeopardy. A recent population model reveals a decline in abundance to an estimated 458 (95% credible intervals 444–471) North Atlantic right whales in 2015 (Pace et al. 2017).

To date five seasonal high-use habitat areas for right whales have been identified in the North Atlantic (Kraus and Rolland 2007). In 1994 the eastern three-quarters of Cape Cod Bay was designated as one of three critical habitat areas in U.S. waters (Federal Register 59 FR 28793). Responding to issues impacting the whales in the Bay, in 1997 the Massachusetts Division of Marine Fisheries (MADMF), under federal court ruling, empaneled a team of scientists and managers to address the urgent need to document the right whales’ use of the Bay and to reduce vessel strikes and gear entanglement in state waters. The team’s deliberations resulted in the Massachusetts Large Whale Conservation Program establishing aerial surveys to monitor the presence, distribution, individual identification, and behavior of right whales. Data and associated analyses resulting from the surveys are reported here.

**METHODS**

The aerial survey of Cape Cod Bay began in 1997; however, data from the limited 1997 pilot study are not included in our analyses. During the surveys, trained observers documented individual right whale occurrence during 431 complete and
partial survey flights conducted annually between 1 January and 15 May from 1998 through 2013. The study season was chosen based on the time period identified from past research and the seasonal management measures instituted by the MADMF (322 Code Mass. Regs. § 12.00 [2013]) and the National Oceanic and Atmospheric Administration (U.S. Federal Register 2008, 2013).

Survey Methodology

Aerial survey protocols were designed using methodology developed by the Cetacean and Turtle Assessment Program (CeTAP) and modified for Cape Cod Bay surveys (Scott and Gilbert 1982; CeTAP 1982; Brown and Marx 1998; Brown et al. 2001, 2007; Knowlton and Brown 2007). Surveys were flown using twin engine, high wing Cessna 336 or 337 Skymaster aircraft at a minimum altitude of 229 m and a ground speed of approximately 185 km/h under Visual Flight Rules. Data were accepted for inclusion in the analysis if right whale identification was definite and confidence in the count was high, as outlined in the CeTAP protocols (CeTAP 1982). At the discretion of the flight crew, surveys were terminated if the estimated visibility was less than 3.7 km or the sea state was greater than Beaufort 5. For each complete survey flight, 15 east-west track lines were flown at 2.8 km intervals resulting in a total survey track line distance of 567 km as described in Clark et al. (2010) (Fig. 1).

The survey area was bounded by the land margins of Cape Cod, the mainland of Massachusetts, and the northern boundary of the Massachusetts state coastal waters, with whale sighting data extended northward of that boundary to latitude 42°7′N to correspond to the aerial survey track spacing of 2.8 km (Fig. 1). The narrow separation of survey tracks resulted in overlapping visual coverage of the entire Bay and photo-identification reduced the chance of counting individual whales more than once during a flight. The survey area included 89% of the 1994 designated Cape Cod Bay critical habitat (U.S. Federal Register 1994). Analyses presented in the results refer to the 1994 critical habitat boundaries that were in effect throughout this study before being modified in 2016 (U.S. Federal Register 2016). Sighting and photographic data were recorded following protocols described in Brown and Marx (2000) and Brown et al. (2007).

Distinctive right whale callosity patterns and scars photographed during surveys were used to identify individual whales (Payne et al. 1983, Kraus et al. 1986) by matching to photo collections maintained at the Center for Coastal Studies and subsequently confirmed by matching to the North Atlantic Right Whale Consortium Photo-Identification database (hereafter “the catalog”) archived and curated at the Anderson Cabot Center for Ocean Life at the New England Aquarium (NEAq, Boston, Massachusetts). Each individual whale in the catalog is associated with a rich database including a demographic profile and the photographic resighting information used to obtain the Best Catalog Estimate (hereafter “BCE”), the middle estimate of cataloged whales alive as reported in the annual NARWC report card (Pettis and Hamilton 2014). By identifying individual right whales photographed in Cape Cod Bay, their sighting history and distribution pattern could be compared to the catalog’s time series of individual sightings throughout the North Atlantic Ocean.

To analyze Cape Cod Bay right whale data in the context of population-wide parameters, we submitted a request to the North Atlantic Right Whale Consortium for access to demographic information for all cataloged whales, the yearly BCE
determined using techniques detailed in Pettis and Hamilton (2014) and yearly calving totals (Right Whale Consortium 2012).

**Data Analysis**

*Distribution*—Analyses were performed using statistical packages from the R Program (R Core Team 2014), unless otherwise noted below and tabulated in Appendix S1. To examine the right whale distribution throughout Cape Cod Bay and interannual spatial trends, we performed kernel density analyses with 12 natural breaks and manual classification using ArcMap 10.0 (ArcGIS version 10.0, Environmental Systems Research Institute, Inc., Redlands, CA) on right whale sighting locations recorded during complete surveys of the Bay, thereby minimizing partial-survey bias, and grouped into 4 yr periods. The center of right whale distribution

*Figure 1.* The Cape Cod Bay study area, with the 15 east-west aerial survey track lines, the 1994 boundary of the federally designated Cape Cod Bay Right Whale Critical Habitat area (dashed line), and the Massachusetts Coastal Zone boundary (gray line).
was determined by averaging latitude and longitude for sightings in the 4 yr periods and performing a multiple regression analysis to determine trends in location and movement of the center of distribution over the 16 yr of study.

Sightings per unit effort (SPUE) analyses were used to identify changes in the yearly whale distribution. The SPUE analyses were based upon counts of confirmed right whale sightings, regardless of the individual identification, thereby documenting spatial and temporal intensity of habitat use. The calculation of survey effort was based on total trackline distance surveyed, not including the cross tracks linking the east-west survey lines. We ran regression models to examine the trend in the yearly SPUE throughout the Bay, as well as to compare the trends inside and outside the western margin of the 1994 critical habitat management area, to identify spatial intensity changes in whale distribution. Best-fit models were determined by ANOVA and AIC analysis. In addition, we performed a Kendall’s rank correlation to identify the relationship between the SPUE inside and west of the 1994 critical habitat to determine if sightings in the western portion of the Bay were due to an increased number of whales, site-preference, or both.

Individual whales per unit effort (IPUE), based on uniquely identified individuals in a time period and area during both completed and partial surveys, was used to determine changes in the number of individuals in the Bay. Survey effort was based on total track line distance surveyed, not including cross tracks linking the east-west survey lines. We ran multiple regression models to determine the trends in the yearly IPUE and BCE and used Kendall’s rank correlation to determine the relationship between the IPUE and BCE (Appendix S2). To determine if the increase in IPUE was solely the result of the increase in population estimated by the BCE, the diffslope function in R was used to determine if the slopes of the IPUE and BCE between 2003 and 2013 increased at the same rate (Jurasinski 2012).

**Demographic and behavior pattern**—The age and sex of individual whales were determined by linking each whale identified through photo matching to demographic data provided in the catalog (Brown et al. 1994; Hamilton et al. 1995, 1998; Kenney 2001a). To investigate the difference in habitat use by demographic group, we performed beta regression analyses to identify the interannual trends in the sex and age ratio of whales visiting the Bay. G-test of goodness of fit with a Bonferroni correction was used to determine if the mean sex and age ratios differed from year to year (Hurd 2001, R Core Team 2014). For the comparisons, we used the sex ratio of 1:1 and age ratio of 3:1 based on the demographic ratios in the catalog for the study period. Additionally, G-test of independence analyses (log-likelihood ratio) were performed to determine if the mean sex and age ratios documented in Cape Cod Bay were similar to those in the catalog (Hurd 2001). The sex ratios used in the comparisons were based on the 16 yr study period, while age analysis was based on a 14 yr period (1998–2011).

To assess the importance of the Bay to cow/calf pairs, we ran a Spearman’s rank correlation on the yearly cow/calf pair sightings in the Bay compared to the total number of documented calves born in the North Atlantic (using the relationship defined in Knowlton et al. 1994). In addition, we performed a beta regression on the proportion of documented calves observed in the Bay to determine the trend in cow/calf pair visitation over the study period.

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For this study, behaviors for each whale observation were recorded as "surface and near-surface feeding," "social," "other," or "unreported." "Surface and near-surface feeding" was defined as an observation during which mouth open feeding behavior was documented at or beneath the surface. Social behavior was defined as whales in a Surface Active Group (SAG; Kraus and Hatch 2001, Parks et al. 2007) in which at least two individuals were rolling and touching at the surface, or whales that were approaching an established SAG. Any recorded behavior that did not fall into these two categories was placed in the "other" category, which included the less common behaviors such as logging, traveling, diving, breaching, and suckling. Whales with no recorded behavior were placed in the "unreported" category. Beta regression analysis was performed on the frequency of activities through each season to identify intra-seasonal trends in surface and near-surface feeding and SAG behavior during the study period.

Preferred use of the Bay—To determine if the individual right whales of the North Atlantic selectively chose Cape Cod Bay as a winter and early spring habitat, we tested the null hypothesis that the documented pattern of individual whale visitation was the result of a random selection by the cataloged individuals in the population. We compared the visitation pattern of individual whales documented in Cape Cod Bay with patterns of visitation generated by randomly sampling individuals of the cataloged North Atlantic population, using a sample size equal to that of the actual number of individual whales observed in a year, thus assuming a random choice to enter or bypass the Bay by the cataloged population. For this comparison, we selected from the entire catalog two age subsets of whales alive through all 16 yr of our study, those known to be juveniles (hereafter "initial juveniles"; n = 49) and those known to be adults ("adults"; n = 169) at the beginning of the study in 1998. Age subsets were used to determine if there were differences in habitat preference of the different age groups. Random samples were generated using the plyr package in R (Wickham 2011) by assigning randomly generated probabilities that each individual whale in a subset would be documented in the Bay during each year of the study. One thousand random samples were generated for each subset. If the randomly generated individual probability exceeded the year’s probability (i.e., the proportion of right whales observed during flights compared to the total number of right whales in the catalog for that year), then that right whale was modeled as absent from the Bay that year. Yearly random visitations were thereby generated for each whale in both subsets for each run of the model. The patterns of random visitation generated by each of the 1,000 models were compared with the observed right whale occurrence in Cape Cod Bay for each subset for each year. Fisher exact tests were performed to determine if the observed pattern of individual yearly visitation differed from that of each of the 1,000 random samples of each subset. Further, we compared the similarity of the observed visitation patterns of the two age subsets using Kendall’s rank correlation.

RESULTS

Throughout the study, the majority of right whales aggregated in eastern and southeastern Cape Cod Bay (Fig. 2). From 1998 through 2005, sightings along the western edge of the Bay, outside the western boundary of the 1994 critical habitat, were uncommon; in contrast sightings in this western area increased between 2006 and 2013 (Fig. 2). Although the calculated center of the geographic distribution
within the Bay shifted to the northwest during the study period, the movement was not significant ($R^2 = 0.7436, F_{1.5} = 8.702, P = 0.06$). While a significant increase in the occurrence of whales over the entire Bay was observed during the study ($R^2 = 0.4834, F_{1.14} = 13.1, P < 0.01$), the distribution of that increase was not uniform. The best fit model for the number of sightings outside the 1994 critical habitat was an exponential regression (AIC values: linear 60.35, polynomial 55.39, exponential 20.40), while the best fit model for the sightings inside the 1994 critical habitat was linear ($F_{14.13} = 1.8602, P = 0.20$). Further analysis focused on the comparison of the number of sightings inside and outside the 1994 critical habitat. Although changes in the SPUE inside and west of the critical habitat were significantly correlated (Kendall’s rank correlation $\tau = 0.376, P < 0.05$), the SPUE inside increased significantly at a constant rate.

Figure 2. The Kernel Density distribution of right whale sightings per square km from complete aerial surveys grouped in four year increments, with the 1994 boundary of the federally designated Cape Cod Bay Right Whale Critical Habitat area (dashed line).
The significant increase in SPUE outside the western edge of the 1994 critical habitat was exponential ($R^2 = 0.6003$, $F_{1,14} = 21.02$, $P < 0.01$).

The IPUE per survey date reflected a relatively regular pattern of the seasonal aggregation of whales in Cape Cod Bay (Fig. 3), one little changed from previous reports (Watkins and Schevill 1982, Hamilton and Mayo 1990, Nichols et al. 2008). Although variable throughout the study, over the 16 yr the mean IPUE was 0.73 individuals/100 km surveyed in January, usually remained low through February (mean IPUE = 1.76 whales/100 km), increased in March (mean IPUE = 3.47/100 km), reached a peak in April (mean IPUE = 7.17/100 km), and declined sharply in early May (mean IPUE = 1.16/100 km for the first 2 wk of May).

The IPUE in Cape Cod Bay over the 16 yr (Fig. 4) was positively correlated with the BCE (Kendall’s rank correlation $t = 0.527$, $P < 0.01$). From 1998 through 2001, a mean of 23.7% of the BCE was documented in the Bay. In 2002 and 2003, the IPUE/BCE ratio decreased to 3.9% ($n = 15$) and 5.6% ($n = 22$), respectively, then rose to a high of 56.9% in 2011 ($n = 277$), with a mean of 39% of the BCE for the period from 2010 through 2013. Although IPUE was declining through the early part of the study (Fig. 4) after the low in 2002 and 2003 beta regression analysis documented a significant increasing trend thereafter ($P < 0.01$). During the period of increase in IPUE from 2003 through 2013, the trend was significantly greater than the growth of the cataloged North Atlantic population reflected in the BCE (difference in slope: 12.72; $P < 0.01$), suggesting increasing preference for Cape Cod Bay.

Demographic analysis showed that adults were more common than juveniles during the study, with a mean of 72.6% adults and 27.5% juveniles (Appendix S3); however, the adult:juvenile ratio differed significantly from year to year ($G = 71.9356, \chi^2 \text{ df} = 15, P < 0.01$). Comparing our results with the expected 3:1 age ratio (Hamilton et al. 1998), individual year $G$-test of goodness of fit with a
Bonferroni correction indicated that 2005 and 2011 were adult-biased while 2008 through 2010 were juvenile-biased (Appendix S4), suggesting age preference in specific years. However, the mean Cape Cod Bay age ratio for the whole study period and the mean NARWC cataloged age ratio did not differ significantly ($G = 0.6985$, $\chi^2$ df = 1, $P > 0.05$), indicating that although there were years with age biases, overall the subpopulation visiting the Bay followed the cataloged population’s age ratio. No significant trends in the proportion of age groups ($P > 0.05$) were present.

Males were more common than females during the study, with a mean of 58% males and 38% females (Appendix S3); however, the sex ratios varied significantly from year to year ($G = 38.9215$, $\chi^2$ df = 15, $P < 0.01$). An individual $G$-test of goodness of fit with a Bonferroni correction identified four out of 16 yr that were male biased (2008, 2009, 2011, and 2012; Appendix S5), but no years that were female biased; the overall mean sex ratio throughout the study was significantly different from a 1:1 ratio ($G = 4.1973$, $\chi^2$ df = 1, $P < 0.01$). In addition, there was no significant difference between the mean sex ratio in our data and the mean live cataloged sex ratio (1998–2011), ($G = 1.4769$, $\chi^2$ df = 1, $P > 0.05$). Beta regression analysis showed a decrease in the proportion of females in the Bay during the study ($P < 0.05$) and a positive trend in the proportion of unknown sex ($P < 0.01$), the latter likely a reflection of the increased number of juveniles for which sex had not yet been determined. As more demographic data from juvenile whales become available, the portion of unknown sex seen in recent years will likely decrease. When proportions were based on the total number of known-sex individuals in the Bay during the study period, no trends were observed.

The frequency of right whale cow/calf pair sightings was analyzed to determine their association with the Bay. Cow/calf pairs were usually observed in April or May, 3–5 mo after birthing off the Florida and Georgia coasts, with the average first sighting of a calf of the year in Cape Cod Bay on 6 April. The percentage of calves observed in the Bay during the year they were born ranged from 0% to 40%, (mean = 12.7%). We identified a significant positive correlation between the
number of cow/calf pairs documented in the Bay and the total documented number of calves of the year reported to the catalog (Spearman’s rank correlation $r = 0.683$, $P < 0.01$). A beta regression analysis showed a significant increasing trend in the proportion of the total documented calves born and those observed in the Bay ($P < 0.01$).

During the study period, the highest proportion of identified behaviors was in the "surface and near-surface feeding" category, (42.3%–95.7%), with two exceptions. In 2002 and 2012, “social category” had the highest proportion of recorded behaviors (100% of sightings $n = 12$ and 53.0% of sightings $n = 179$, respectively); however, 2002 was likely biased due to small sample size ($n = 35$). Beta regression analysis showed a significant increasing trend in “surface and near-surface feeding” behavior both through the study season (January–May) and during the entire study period (1998–2013) ($P < 0.01$); however, there was no significant trend in observations of SAG and other behavioral categories during the study. When removing the small sample sizes of 2002 and 2003, the trends through the entire study period remain unchanged for each category.

The comparison of the random visitation models with the documented visitation by individually identified whales suggests a population for which more than half had a nonrandom association with Cape Cod Bay. Observed patterns of visitation by individual adult right whales differed significantly from 75.5% of their corresponding random models (Fisher’s exact test $P < 0.01$). The random models for the adult subset produced a peak visitation frequency at 3–4 yr and a mean model prediction of three whales (2%) not being observed in the Bay during the 16 yr of study. In comparison, the observed adult frequency peaks were at 2 and 8 yr and 38 (22%) of the whales were not observed in the Bay during the study (Fig. 5A). In addition, the mean model prediction for frequent visitors (8 or more years) was 2 adult individuals (1%) while 28 (17%) adult whales were actually observed visiting frequently during the entire study period.

Observed patterns of visitation by initial juveniles differed significantly from 74.2% of their corresponding random models (Fisher’s exact test, $P < 0.01$). The random models of the initial juvenile subset had a peak visitation frequency between 5 and 6 yr and a mean model prediction that all 49 of the initial juvenile whales would be observed at least once in Cape Cod Bay. In comparison, three (6%) initial juveniles were not observed during the study. However, the initial juvenile observations showed a departure from the random models similar to that of the adult subset, with the observed peak visitation frequency at 2, 8, and 11 yr. The prediction of frequent initial juvenile visitors (8 or more years) was 6 (12%) individuals, while 15 (31%) initial juveniles were documented during the study period.

A comparison of the patterns of return to the Bay of the two age subsets revealed a significant positive correlation between the observed patterns of adult and initial juvenile visitation (Kendall’s rank correlation, $r = 0.47$, $P < 0.05$).

**DISCUSSION**

The information collected during the 16 yr of study supports the long-held observation that Cape Cod Bay is an important habitat for North Atlantic right whales. The regularity of the seasonal return of the whales to the Bay to feed, socialize, and suckle their calves is a reflection of the Bay’s annual value to the species, a value affirmed in 2016 when the boundaries of the critical habitat area designated in 1994 were expanded to include the entire Bay and surrounding waters (U.S.
Figure 5. The frequency distribution of the number of years individual whales were observed in Cape Cod Bay for adult (A; n = 169) and initial juvenile (B; n = 49) right whales during the 16 yr of study (bold line) compared with the modeled random distribution of yearly individual occurrence generated from 1,000 model runs for each age group. Note: The y-axis scales in A and B are different.
Federal Register 2016). Although the timing of the whales’ peak residency in the Bay has remained relatively unchanged, dramatic annual variations in the number of whales identified during our study and subtler changes in their distribution suggests plasticity in their habitat use patterns that could impact management efforts over time.

The importance of the Bay to the right whale population may be gauged by comparing the yearly Best Catalog Estimate (BCE) with the yearly IPUE in the Bay. That the increase in the IPUE since 2003 was significantly greater than that of BCE is an indication that the increased number of individual whales visiting the Bay during the latter part of the study period was not principally a reflection of population growth, but of a selection by an increasingly large segment of the North Atlantic population.

Since feeding dominates the right whales’ activities in the Gulf of Maine (Baumgartner et al. 2007) their foraging behavior likely leads to the formation of aggregations of whales at several spatial scales (Kenney 2001b, Baumgartner et al. 2007). We suggest that increases in the number of individual right whales coming to Cape Cod Bay in the winter and early spring is influenced by changes in the distribution and quality of the food resources in the region, resulting in the selection of Cape Cod Bay over other potential North Atlantic feeding areas. Although our study cannot examine changes over multidecadal time periods, the observed pattern of yearly IPUE during the study may be part of a cycle in the quality and distribution of the food resources in the region influenced by the cyclic changes in meteorology and oceanography (Pershing et al. 2005, Kenney 2007, Davies et al. 2015). Further, it is likely that variation in the quality of the food resources has been the most influential factor mediating the right whales’ habitat choice and has resulted in the dramatic changes in the IPUE, as suggested by increases in the frequency of observed feeding events during the latter part of the study.

In addition to documenting an increase in the number of individual right whales visiting the Bay, we observed a trend toward expansion in their spatial distribution reflected in a significant ($P < 0.01$) increase in the SPUE beyond the western boundary of the critical habitat management area during the latter part of the study, in contrast with the early years of the study when the SPUE was high in the eastern half of the Bay and uniformly low in the west (Hamilton and Mayo 1990, Nichols et al. 2008). While a preference for the eastern portion of the Bay was apparent throughout the study, the shift in distribution toward the west illustrates the importance of considering the plasticity of the whales’ responses to zooplankton resources when developing management plans. We hypothesize that the expansion of the right whale’s distribution in Cape Cod Bay was due to a combination of factors including the increase in the total number of individuals visiting the Bay and changes in the environmental processes controlling the distribution and aggregation of zooplankton (Kenney 2007, Simmonds and Isaac 2007).

Although the age and sex ratios of right whales documented in Cape Cod Bay were similar to those of the cataloged North Atlantic population during the study period (Hamilton et al. 1998, Pettis and Hamilton 2014), significant biases identified during several years (Appendix S4, S5) may have resulted from either the transition to a skewed ratio (in the case of the present sex ratio, i.e., males > females) or a demographic selection during the latter part of the study. With the coincident demographic bias and a significant increase in both the proportion of near-surface feeding and the number of individual whales using the Bay, it is likely that the influence of changes in the attractiveness of the food resources had a widespread
effect on the distribution of whales throughout the region. Hence, we hypothesize that the enriched feeding environment may both attract greater numbers of individuals and result in a preference by demographic groups with the specific energetic demands identified by Fortune et al. (2013).

Our behavioral observations support previous research that identifies Cape Cod Bay as an area of social and nursery activity for the species (Hamilton and Mayo 1990, Kraus and Kenney 1991, Nichols et al. 2008). While the role of SAGs appears to have a broad functional basis (e.g., mating, play, practice mating, and maintenance of social bonds) (Parks et al. 2007), the observations of social activity throughout the winter and early spring complement the identification of the Bay as a multi-use critical habitat. For example, in 2012, a year of warmer water temperatures not suited for abundant zooplankton, the dominant behavior was social activity. Based on an estimated gestation period of 12–13 mo Best (1994) and Kraus et al. (2007) hypothesized that conception occurs in the winter months; therefore, the Bay may also be part of the regional mating ground proposed by Cole et al. (2013).

The positive correlation between the number of cow/calf pairs observed in the Bay with the number of documented calves born supports the recognition of the Bay as a nursing area as suggested by Mead (1986) and Hamilton and Mayo (1990). The increasing proportion of cow/calf pairs utilizing the Bay is evidence of the importance of its protected habitat to the recovery of the species. Comparable to the increase in the proportion of the cataloged population visiting the Bay, the increase in proportion of the calves is likely influenced by the dietary needs of the cow and may play an important role in habitat selection for cow/calf pairs (Fortune et al. 2013).

The comparison of random models with the observed patterns of individual whale visitation (Fig. 5A, B) rejects the null hypothesis and demonstrates that the cataloged population of North Atlantic right whales was not randomly represented in Cape Cod Bay. Instead, the population identified in the catalog was composed of individuals with distinctly different affinities for Cape Cod Bay as revealed by a continuum of visitation patterns, from those that showed a significant preference for the Bay to those that conspicuously avoided it, similar to the findings of Schaeff et al. (1993) describing cows bringing calves to the Bay of Fundy. The similar visitation patterns of the initial juvenile and adult subsets suggests that the association with the Bay may start early in life and extend into adulthood, comparable to the geographic preference of cows and calves reported by Malik et al. (1999), Kraus and Rolland (2007), Valenzuela et al. (2009) and Carroll et al. (2015). However, the differences in the visitation patterns between the subsets also suggest that the initial juvenile subset had a stronger affinity for the Bay or had not exploited other winter and early spring feeding areas perhaps known to older whales. Although fluctuations in IPUE combined with an increase in feeding activity during the study suggest responses to changes in the attractiveness of the Bay, the pattern of selection for or against the Bay by individual whales remained detectable throughout all of the comparisons with random models, implying an individual-based association between the whales and the Cape Cod Bay habitat not wholly influenced by food resource availability.

Our observations demonstrate the significance of Cape Cod Bay to the right whale population, by documenting the regular annual occurrence of an increasing number of individual whales and the role that the Bay plays as a feeding, socializing, and nursery for the species. The changes in habitat use patterns we have identified
present a challenge to conservation management, suggesting that stewardship of the right whales will require an adaptive and nimble system capable of identifying and responding to changes in patterns of right whale distribution, behavior, and habitat selection. Variations in the distribution and behavior of whales may profoundly and irregularly impact the management and mitigation of threats to the large portion of the remaining North Atlantic population that visits Cape Cod Bay, presenting a moving target for conservation and recovery efforts. Furthermore, while the management of known threats to right whales within Cape Cod Bay has been reactive to changing human activities and to variations in the occurrence patterns of right whales, habitat areas beyond the Bay will require expanded management incorporating an assessment of changing environmental parameters in order to protect emergent right whale aggregation areas and migratory corridors.

ACKNOWLEDGMENTS


Our sincere thanks to our pilots and mechanics C. Lofland, the late J. Ambroult, J. O’Brien, S. Ridlon, J. Williams, the late P. Kibler, J. Chronic, T. Howard, B. Payne, J. Greenhalgh, G. Breen, and R. Bisbee.

Sighting and life history data were used with permission from the North Atlantic Right Whale Consortium. The Logger 2000 data logging program was made available by the International Fund for Animal Welfare.

This study was carried out under NOAA Scientific Permits to Take Marine Mammals No 1014 (1998–1999), No 633-1483-01 (1999–2001), No 633-1483-02 (2002), No 633-1483-04 (2003–2005), No 633-1763-0 (2005–2008), No 633-1763-01 (2009), and No 14603 (2009–2013). Funding was provided by the Division of Marine Fisheries, Commonwealth of Massachusetts, NOAA-NMFS, the Massachusetts Environmental Trust, and by private donations.

LITERATURE CITED


Received: 16 June 2017
Accepted: 19 January 2018

SUPPORTING INFORMATION

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12511/suppinfo.

Appendix S1. Statistical tests and results.

Appendix S2. IPUE and BCE for the North Atlantic right whale in Cape Cod Bay.

Appendix S3. Demographic and behavior proportions for the North Atlantic right whale in Cape Cod Bay.

Appendix S4. Comparison of age class ratios based on a 3:1 ratio using a G-test of goodness of fit with Bonferroni corrected P-values.

Appendix S5. A comparison of sex ratios based on a 1:1 ratio using a G-test of goodness of fit with Bonferroni corrected P-values.