Vol. 46: 35–48, 2021
https://doi.org/10.3354/esr01141

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published September 23

Dive behavior of North Atlantic right whales on the calving ground in the Southeast USA: implications for conservation

Julia R. G. Dombroski[1,*], Susan E. Parks[1], Douglas P. Nowacek[2,3]

[1]Syracuse University, Department of Biology, Syracuse, NY 13244, USA
[2]Duke University, Nicholas School of the Environment, Marine Lab, Beaufort, NC 28516, USA
[3]Duke University, Pratt School of Engineering, Durham, NC 27708, USA

ABSTRACT: The North Atlantic right whale *Eubalaena glacialis* is a Critically Endangered whale whose habitat overlaps with areas of high human use. On feeding grounds, aspects of its behavior increase the vulnerability of this species to anthropogenic threats such as entanglement in fishing gear and vessel strikes. On the calving ground, natural dive behavior and the implications for conservation efforts in this species remain to be evaluated. In this study, we used 102.17 h of tag data collected over 15 deployments of archival tags on 14 individuals to describe the dive behavior of right whales in the Southeast USA. Lactating females spent up to 80% of the time at depths ≤3.5 m, leading to increased risk of vessel strike compared to other whale groups that spent a maximum of 30% of the time at those depths in this habitat. Non-lactating whales had significantly deeper maximum dive depths (12.1 m) than lactating females (7.3 m) and spent more time in the bottom phase of dives, closer to the sea floor (45 vs. 37% of the dive duration, respectively). Time spent closer to the sea floor increases the probability of interaction with fishing gear. Therefore, these dive data are useful to justify seasonal closures of fishing activity on the calving ground to protect both lactating and non-lactating whales. Opportunistic comparisons revealed that diel period, calf presence and calf age affect dive behavior of female right whales. In the face of the impacts of anthropogenic mortality on right whale populations, these results will aid vessel strike and entanglement risk assessment on the Southeast USA calving ground.

KEY WORDS: Ship-strike · Entanglement · Underwater movement · Subsurface behavior · Diel trend · Mother–calf behavior

1. INTRODUCTION

The North Atlantic right whale *Eubalaena glacialis* (hereafter right whale) is a Critically Endangered species. The right whale population has had a declining trend since 2010 and as of 2019, fewer than 400 individuals are estimated to remain alive (Pace et al. 2017, Cooke 2020). This severe population decline is linked to changes in prey concentration, low reproductive rate and increased mortality from interactions with human activities (Caswell et al. 1999, Corkeron et al. 2018, Meyer-Gutbrod & Greene 2018). The main anthropogenic threats to right whale survival are vessel strike and entanglement in commercial fishing gear (Kraus et al. 2005, Kenney 2018). Interactions with fishing gear have left visible scars on over 80% of the cataloged individuals in the population (Knowlton et al. 2012, Pettis et al. 2018), and the highest per capita rate of vessel strike among baleen whale species has been reported in right whales (Laist et al. 2001). Between 2003 and 2018, 70 right whale mortalities were documented throughout the range of the species. Of the 43 cases for which cause of death was determined, 58% were due to

*Corresponding author: dombroski.julia@gmail.com

Publisher: Inter-Research · www.int-res.com

entanglement and 42% were due to vessel strike (Sharp et al. 2019). Adult females and dependent male calves are disproportionately represented in the vessel strike mortality data (van der Hoop et al. 2013), leading to the hypothesis that behavioral differences of this important segment of the population put them at increased risk of lethal interactions with anthropogenic activities (Cusano et al. 2019).

To support effective management efforts to protect right whales from entanglement and vessel strikes, data on right whale dive and surface intervals affecting water column usage are urgently needed. On foraging grounds, prey distribution within the water column is known to strongly influence dive depth of right whales, leading to differences in potential risks to individuals. For example, in Cape Cod Bay, USA, right whales have been documented to swim and feed just subsurface, where they are at increased risk of collisions with vessels (Mayo & Marx 1990, Parks et al. 2012, Baumgartner et al. 2017). In summer months, right whales often spend increased time at deeper depths while foraging, reducing the risk of vessel collisions, but potentially increasing risk of entanglement with bottom-associated fishing gear (Baumgartner & Mate 2003, Baumgartner et al. 2017, Hamilton & Kraus 2019). Differences in dive behavior between mother–calf pairs and other age/sex classes have been documented on foraging grounds. For instance, right whale mother–calf pairs are more vulnerable to vessel strikes than other age/sex classes due to longer surface intervals in the Bay of Fundy (Baumgartner & Mate 2003). These changes in diving behavior not only affect the risk from vessels and fishing gear but can also impact the detectability of whales from visual surveys. For example, the visual detectability of right whales in Cape Cod Bay from vessels is strongly affected by dive depth, with surface skim-feeding whales easier to detect than subsurface feeding whales (Parks et al. 2012, Ganley et al. 2019).

Right whales migrate along the east coast of the USA and Canada between higher latitude deep-water feeding grounds and a lower latitude shallow-water calving ground (Kraus et al. 2005). While right whale dive behavior is generally associated with prey distribution in the water column on the foraging grounds (Baumgartner & Mate 2003, Parks et al. 2012, Baumgartner et al. 2017), less is known about right whale dive behaviour during migration or on the calving ground. Neither adult nor juvenile right whales have been observed feeding and are presumed to fast during migration and while on the calving ground (Fortune et al. 2013) where the average depth is only ~40 m, with peak right whale sightings at depths between 10 and 20 m (Keller et al. 2012). Despite the lack of observed feeding behavior and shallow water depths, right whales still dive below the surface on the calving ground.

Limited data on the dive behavior and surface intervals of right whales on the calving ground have been published (Hain et al. 1999). Currently, the only details available on the subsurface dive behavior of right whales on the calving ground come from 2 entangled non-lactating individuals (van der Hoop et al. 2017). Both whales showed changes in dive behavior to compensate for the increased drag and buoyancy imposed by the fishing gear and the telemetry buoys used to track animals (van der Hoop et al. 2014, 2017). When entangled, the whales glided for shorter periods of time, exhibited shorter dives and more variable fluke stroke amplitude than after they were freed (van der Hoop et al. 2017). After being partially disentangled, one of the whales took statistically longer and deeper dives with the maximum depth of most dives corresponding to the estimated sea floor depth (van der Hoop et al. 2014). Due to the effects of the entanglement and the sedatives administrated as part of the disentanglement operations, dive behavior of these individuals is unlikely to reflect the natural behavior of the species, even after whales were partially freed from gear.

The objective of our study was to describe the typical range of right whale dive behavior and surfacing intervals on the calving ground. This information is key to assess the detection probabilities and to design the most effective monitoring methods while better assessing the risk of vessel strikes and entanglement for right whales based on their behavior on the calving ground.

2. MATERIALS AND METHODS

2.1. Data collection

Digital acoustic recording tags (DTAG-2; Johnson & Tyack 2003) were attached to right whales from rigid-hull inflatable research vessels in January and February of 2006, 2014, 2015 and 2016 on the Southeast USA (SEUS) calving ground. The tags were deployed using a handheld 8.6 m long carbon-fiber pole and were attached to the dorsal surface of right whales via 4 silicone suction cups (60 mm diameter). After tagging, opportunistic focal follows were conducted to identify the behavioral state and events of tagged whales or mother–calf pairs in which only the mother was tagged. Focal follows were conducted while maintaining a minimum distance of 50 m between the observation platform and the focal animals to minimize effects on behavior. Behavioral states included traveling, resting, nursing or social behaviors which were defined in detail by Cusano et al. (2019). Tags were tracked for recovery after detachment through radio tracking of a built-in VHF transmitter. Individual identification for tagged animals was provided by the North Atlantic Right Whale Consortium Photo-identification Database (NARWC 2019). The reproductive state of individuals on the day of tagging was determined as: lactating when adult females were accompanied by a calf <1 yr old; pregnant when individuals were unaccompanied adult females that were subsequently sighted within 10 d accompanied by a young calf (<1 yr); juveniles when whales were estimated to be ≥1 and <9 yr, with no sightings with calves before or during the calving season (NARWC 2019). For lactating females sighted on the calving ground before giving birth, calf age (d) was estimated based on the time elapsed between the last sighting without a calf and the day of tag deployment as described by Root-Gutteridge et al. (2018). Juveniles and pregnant whales were grouped into a 'non-lactating' group for some analyses as indicated in Section 3.

The DTAG-2 polyethylene housing was 21 cm long and 10.5 cm wide. Devices weighed 330 g in air and were approximately 20 g buoyant in water. The DTAG-2 contained hydrophones, 3-axis magnetometer, and accelerometer, temperature and pressure sensors that were programmed to synchronously record data. For this study, only non-acoustic sensor data were used. These data were collected at a sampling rate of 50 Hz. Post-processing included sensor data decimation to 5 Hz and correction of tag orientation relative to the body frame of the whale using MATLAB scripts (Johnson & Tyack 2003; animaltags.org). Datasets generated during this study are available at GitHub: https://github.com/DombroskiJulia/Dombroskietal_ESR_RightWhaleDiveBehaviorSEUS.

Time–depth profiles of tagged whales (dive profiles) were generated from calibrated pressure data with an accuracy of ±0.5 m. Dives were defined as departures from the surface ≥3.5 m which corresponds to the average diameter of adult female right whales (Miller et al. 2012) plus the intrinsic error of the pressure sensor. The time of tag detachment from the whales was identified through inspection of both the sensor and audio records. The first and last dives in each record were disregarded from analysis to minimize the effect of the tagging approach on behavior and to prevent including incomplete dives in the analysis (Hooker et al. 2001, Nowacek et al. 2004). The pressure record was used to calculate percent time spent at the surface (depths ≤3.5 m) and at depth (depths >3.5 m). From the processed sensor data, we generated pitch and roll (rotation angles around the lateral and longitudinal axis, respectively) and heading to infer the body orientation of the tagged whale (Johnson & Tyack 2003).

2.2. Dive behavior and activity level

To describe dive behavior, the following parameters were extracted from dives using the MATLAB tag analysis tools from animaltags.org: total dive duration, surface interval, dive rate, maximum depth, bottom time, descent rate, ascent rate and average ascent and descent pitch. Total dive duration was calculated based on total time from departure to return to the surface. Surface interval was calculated as the time between surfacing and the start of the subsequent dive. Dive rate was calculated by dividing the dive count by duration of deployment used in the analysis (tag-on time minus duration of first and last dives). For each dive, maximum depth (max depth) was obtained. Max depth was defined as deepest depth reached during a dive and was used to obtain bottom time for each dive. Bottom time was defined as time spent within 85% of max depth. Descent and ascent phases were defined as sustained motion to and from depth as observed from the pressure record. Ascent and descent rates were calculated based on total vertical distance traveled divided by travel time. Ascent and descent average pitch were calculated for each dive. Average ascent and descent pitch were defined as average pitch angle (rotation angle around the transverse axis) displayed during ascent and descent, respectively. Summary statistics (median, mean and SD) of dive parameters were calculated for all analyzed dives within a deployment. Dive parameters were compared between deployments on lactating and non-lactating whales (pregnant and juvenile) using a 2-tailed Mann-Whitney *U*-test for independent samples. Additional opportunistic comparisons were made between dive behavior of 2 lactating females with young (23 d old) and older (70 d old) calves and 1 individual (EgNO 3101) who was tagged both while pregnant and after her calf was born. All statistical analyses were carried out in R Software (R Core Team 2019).

The roll record was visually inspected for below-surface (depth >3.5 m) roll events, and events >2π rad (a full revolution along the longitudinal axis of the whale) were counted for each tag. Minimum specific acceleration (MSA, m s^{-2}) was used as a proxy for overall activity level (Simon et al. 2012, Bejder et al. 2019) for comparisons of behavior for EgNO 3101, who was tagged once while pregnant and again while lactating within the same season. MSA was calculated by subtracting the overall acceleration by gravitation from the norm of 3 axes of the DTAG accelerometer for these 2 deployments (Simon et al. 2012).

2.3. Diel trend

To investigate diel differences in dive behavior, dives from tags that remained attached until after astronomical twilight were divided into daytime dives (before astronomical twilight) and night-time dives (after astronomical twilight). Twilight time for the location and time at which tags were deployed was obtained from the United States Naval Observatory (https://www.usno.navy.mil/USNO). Dive statistics were calculated separately for day and night-time dives and compared using a 2-tailed Mann-Whitney *U*-test for independent samples.

2.4. Temperature distribution

The temperature record of the DTAGs was used to measure the range of water temperatures experienced by the tagged whales. To determine whether dive behavior had thermoregulatory benefits, water temperatures at the surface (≤3.5 m) and at depth (>3.5 m) were compared using a Mann-Whitney *U*-test. Significant statistical differences between temperatures recorded at the surface and at depth could indicate a thermoregulatory function.

3. RESULTS

3.1. Data collection

Sensor data were collected from 15 tags deployed on 14 individuals (10 lactating, 3 juvenile and 2 pregnant right whales, including 1 whale tagged when pregnant and again when lactating). Calves were not tagged during this study. Deployment details and summary dive statistics are presented in Table 1. On average, tags remained attached for 6.81 ± 6.57 h

Table 1. Summary of DTAG deployments on right whales between 2006 and 2016 on the calving ground in the Southeast USA (SEUS), including deployment identification (Dep ID: 2-letter abbreviation of the Latin binomial, 2 digits of the year in which tagging occurred followed by the corresponding Julian Day and a letter indicating deployment order). EgNO is the unique whale ID from the North Atlantic right whale consortium (NARWC) identification database. Reproductive state (J: juvenile, P: pregnant, L: lactating) on the day of tagging as well as the individual sex were obtained from NARWC. Sighting data from NARWC were used to estimate calf age (na: not applicable; –: data not available). Total deployment duration corresponds to total time when tags were attached to whales (e.g. tag-on time). Analyzed time is the total time used in the analysis (i.e. total deployment time minus the duration of the first and last dives). Dive count corresponds to overall number of complete dives found and analyzed in that deployment (first and last dives were excluded from analysis). Dive rate was obtained by dividing dive count by the analyzed duration

Dep ID	EgNO	Reproductive state/sex (age in yr)	Estimated calf age (d)	Total deployment duration (h)	Analyzed duration (h)	Dive count	Dive rate (dives h^{-1})
eg06_021a	3442	J/M (2)	na	1.36	1.31	17	13.0
eg06_024a	3323	J/M (3)	na	1.69	1.63	23	14.1
eg06_024e	3430	J/F (2)	na	0.88	0.46	6	13.0
eg06_028a	1151	P/F (>26)	na	18.57	18.55	140	7.5
eg14_040a	2123	L/F (23)	30	1.52	1.42	14	9.8
eg14_041a	2040	L/F (24)	55	5.50	5.23	57	10.9
eg14_049a	3157	L/F (13)	23	11.63	11.15	59	5.3
eg14_056a	2645	L/F (18)	70	5.74	5.36	40	7.5
eg15_052a	3292	L/F (13)	–	23.04	22.81	163	7.1
eg16_025a	3101[a]	P/F (15)	na	4.97	4.79	38	7.9
eg16_030a	3405	L/F (12)	–	3.41	3.02	15	5.0
eg16_031a	1281	L/F (>35)	–	6.60	6.29	47	7.5
eg16_032a	1810	L/F (>28)	–	1.70	1.62	11	6.8
eg16_048a	3101[a]	L/F (15)	22	4.98	4.80	26	5.4
eg16_053a	3317	L/F (13)	–	10.52	10.31	60	5.8
Total				102.17	98.80	716	

[a]In 2016, EgNO 3101 was first tagged when she was pregnant. 23 days later on that same year, she was tagged again while accompanied by a calf

(average ± SD). Deployment duration ranged from 0.88 to 23.4 h. Tag detachments occurred due to interactions with calves, active surface behaviors, rapid underwater movements or due to pre-programmed release time. Focal follow duration ranged from 1.00 to 2.68 h. Lactating females interacted only with their respective calves, and pregnant females were not observed to interact with other whales. Juveniles were observed interacting with other whales in surface active groups.

Overall, whales spent up to 84% of the analyzed deployment duration with their dorsal surface at depths ≤3.5 m (Fig. 1). Median percent time spent at the surface (depths ≤3.5 m) was 44%, with a mean of 48 ± 21%. For deployments on juveniles (eg06_021a, eg06_024a, eg06_024e), the tag was within the surface layer (depths ≤3.5 m) on average 30% of the time; on pregnant females, 32% (eg06_028a, eg16_025a); and on lactating females (eg14_040a, eg14_041a, eg14_049a, eg14_056a, eg16_030a, eg16_031a, eg16_032a, eg16_048a, eg16_053a), 57% of the analyzed deployment duration.

3.2. Dive behavior and activity level

Dive parameters are summarized by lactation state (lactating and non-lactating [juveniles and pregnant whales]) in Fig. 2. There were no statistical differences between the median surface interval (lactating = 133 s; non-lactating = 123 s) (Mann-Whitney U = 48 015, n_1 = 221, n_2 = 480, p > 0.05, 2-tailed) or median dive duration (lactating = 274 s; non-lactating = 300 s) (U = 533 371, n_1 = 222, n_2 = 481, p > 0.05) between groups. All other dive parameters were statistically different between lactating and non-lactating whales. Lactating females had significantly shorter bottom times (lactating = 74 s; non-lactating = 100 s) (U = 60 211, n_1 = 222, n_2 = 481, p < 0.05) and shallower max depths of dives than non-lactating whales (lactating = 7.3 m; non-lactating = 12.1 m) (U = 71 590, n_1 = 222, n_2 = 481, p < 0.05). Median descent pitch (lactating = 0.4 rad; non-lactating = –0.3 rad) (U = 63 792, n_1 = 222, n_2 = 481, p < 0.05) and ascent pitch (U = 76 523, n_1 = 222, n_2 = 481, p < 0.05) significantly differed between lactating and non-lactating whales (lactating = –0.1 rad; non-lactating = –0.05 rad). For both lactating and non-lactating whales, median descent pitch was steeper than the median ascent pitch. Notably, the median ascent pitch was negative for all whales, meaning that they were likely buoyantly returning to the surface in most cases, rather than actively swimming up in the water column. Higher median ascent (lactating = 0.01 m s^{-1}; non-lactating = 0.1 m s^{-1}) (U = 65 601, n_1 = 222, n_2 = 481, p < 0.05) and descent rates (lactating = 0.09 m s^{-1}; non-lactating = 0.2 m s^{-1}) (U = 81 172, n_1 = 222, n_2 = 481, p < 0.05) were observed from tags deployed on non-lactating animals. Dive parameters for each deployment are summarized in Table S1, and parameters grouped by lactation state (lactating and non-lactating) are summarized in Table S2 in the Supplement at www.int-res.com/articles/suppl/n046p035_supp.pdf. Dive profiles for all deployments are presented in Fig. S1.

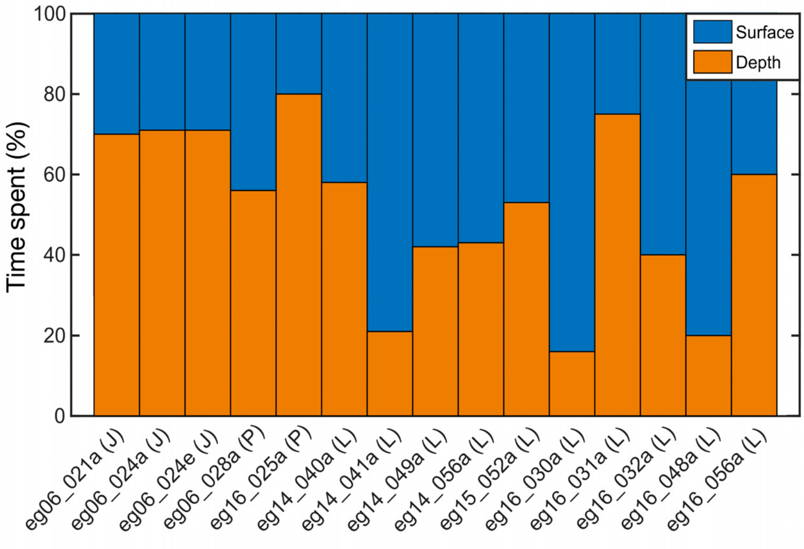

Fig. 1. Percent time spent near or at surface (depths ≤3.5 m, blue) and at depth (depth >3.5 m, orange) in 15 DTAG deployments on North Atlantic right whales on the Southeast US calving ground. Deployments are identified by deployment ID (see Table 1) and a letter corresponding to the reproductive state of the tagged individual (J: juvenile; P: pregnant; L: lactating)

Below-surface full-rotational rolls were recorded in the bottom phase of dives in 7 out of the 15 deployments. Deployments eg15_052a, eg16_031a and eg16_048a had 1 full rotational roll each; deployment eg06_024a had 2; eg16_053a had 5; eg16_025a had 8; and eg06_028a had a total of 10 full rotational rolls during dives.

The average percentages of time spent in the ascent/descent and bottom phase of dives for each deployment are summarized in Fig. 3. Overall bottom time (time spent within 85% of max depth of each dive) represented between 12 and 80% of total dive duration. On average, lactating females spent 37% of dive duration in the bottom phase of dives, whereas

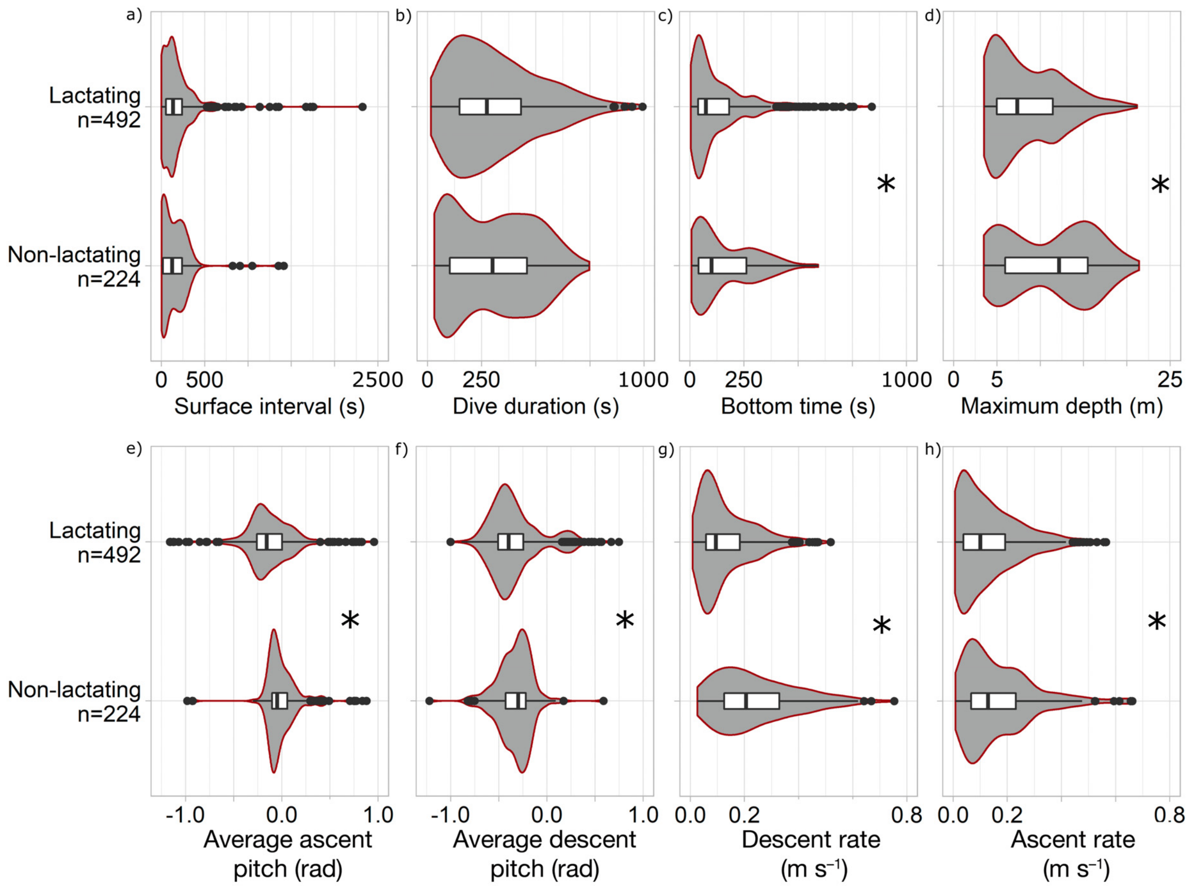

Fig. 2. Distribution of (a) surface interval, (b) dive duration, (c) bottom time, (d) maximum depth, (e) average ascent pitch, (f) average descent pitch, (g) descent rate and (h) ascent rate for DTAG deployments on lactating and non-lactating (juvenile and pregnant) right whales on the Southeast US calving ground between 2006 and 2016. Data represented as box plots with additional violin plot (gray shaded area) to illustrate the kernel probability density. Left and right sides of the box delimit 25th and 75th quartiles, respectively. The box covers the interquartile interval (IQI), where 50% of data is found. Vertical line inside the box represents the median. Whiskers mark values whithin 1.5 times IQI range bellow the 25th interval and above the 75th interval. Black dots represent values >1.5 times and <3 times the IQI in either side of the box. Asterisks represent statistical significance ($\alpha = 0.05$; Mann-Whitney U-test)

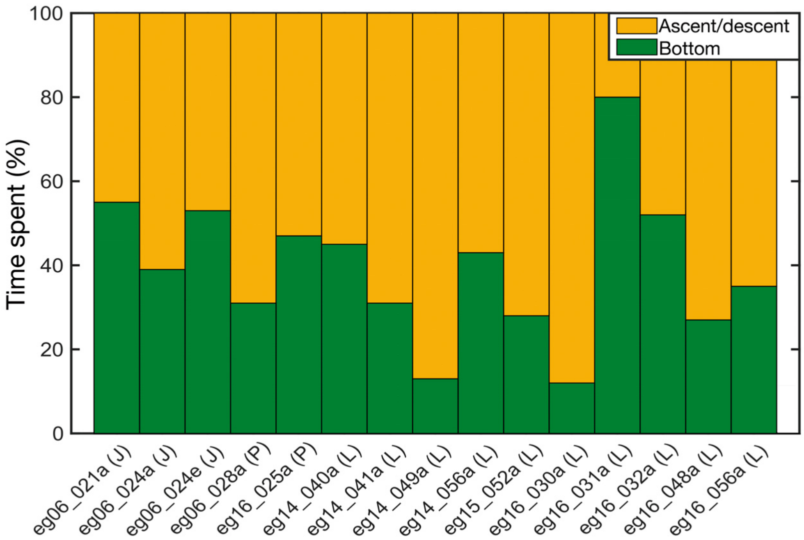

Fig. 3. Time spent (%) on the bottom (green) and in the ascent/descent phases of dives (yellow) for 15 DTAG deployments on right whales on the Southeast US calving ground. Deployments are identified as in Fig. 1

non-lactating females spent on average 45% of dive duration in the bottom phase. Table S3 summarizes percent time spent at the surface, in ascent/descent and in the bottom phase of dives for each deployment.

In 2014, eg14_049a, a female accompanied by a calf with an estimated age of 23 d, had a lower dive rate than eg14_056a, a female accompanied by a calf 70 d old (5.64 vs. 7.46 dives h^{-1}

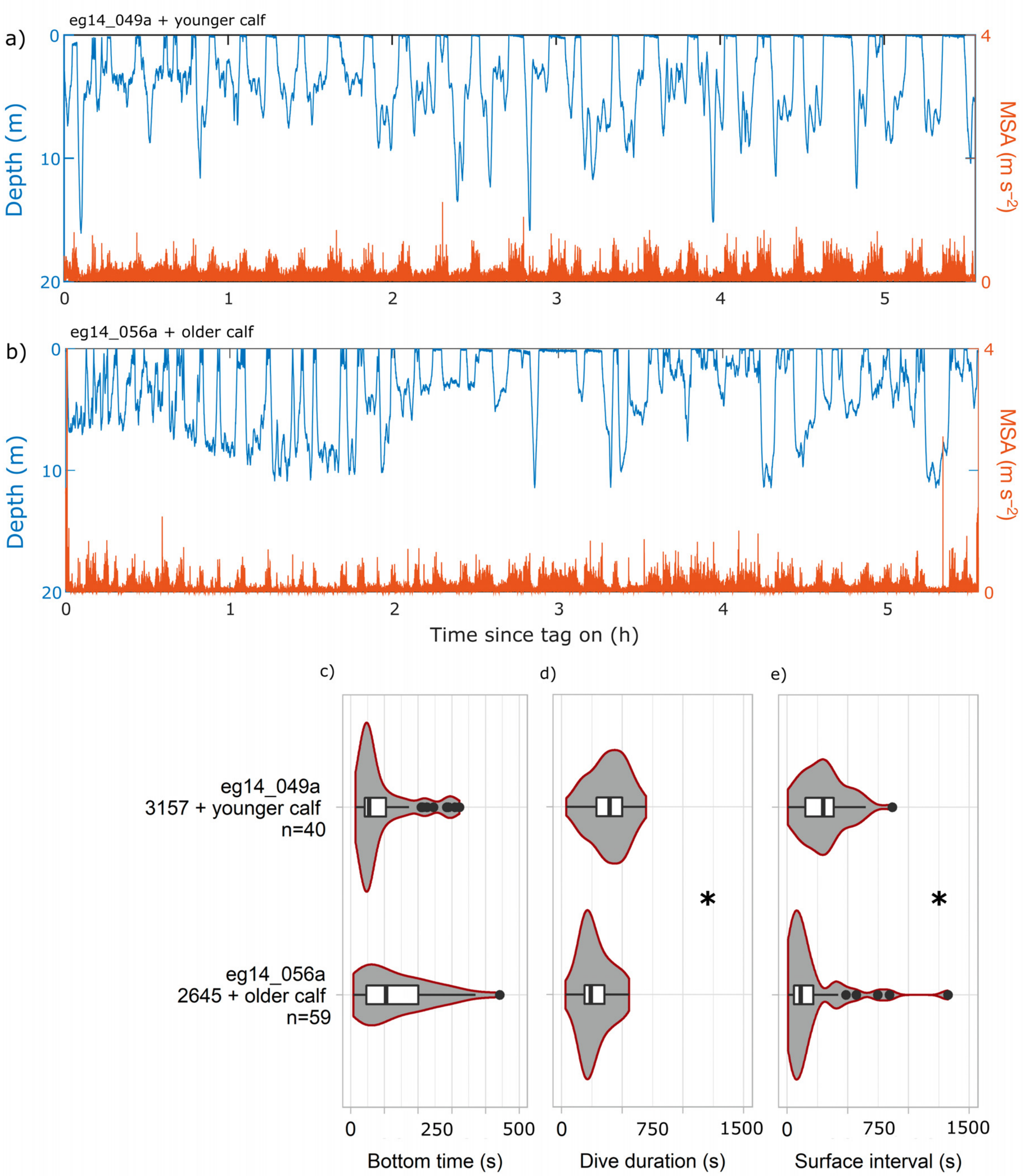

Fig. 4. Dive profiles (blue) and minimum specific acceleration (MSA, m s^{-2}) (orange) for deployments (a) eg14_049a, a lactating female with a 23 d old calf and (b) eg14_056a, a lactating female with a 70 d old calf. Distribution of (c) bottom time, (d) dive duration and (e) surface interval revealed that eg14_056a had longer surface intervals and dives than eg14_049a, suggesting that calf age can alter dive behavior of females. Data for eg14_049a were truncated to the duration of data from eg14_056a only in this figure to illustrate data at similar time scales. Data representation as in Fig. 2

respectively, Fig. 4). Overall median surface interval was longer for the deployment on the female with the youngest calf (eg14_049a, 270 s), than for the female with the older calf (eg14_056a, 111 s, U = 1593, n_1 = 59, n_2 = 40, $p < 0.05$). Median bottom time was shorter for eg14_049a (55 s) than for eg14_056a (105 s) but was not statistically different (U = 904.5, n_1 = 59, n_2 = 40, $p > 0.05$). The bottom phase of the dives corresponded to only 13% of the overall duration of the analyzed dives, and the median dive duration was significantly longer for the whale accompanied by the younger calf (390 s vs. female with older calf = 240 s, U = 1659, n_1 = 59, n_2 = 40, $p < 0.05$).

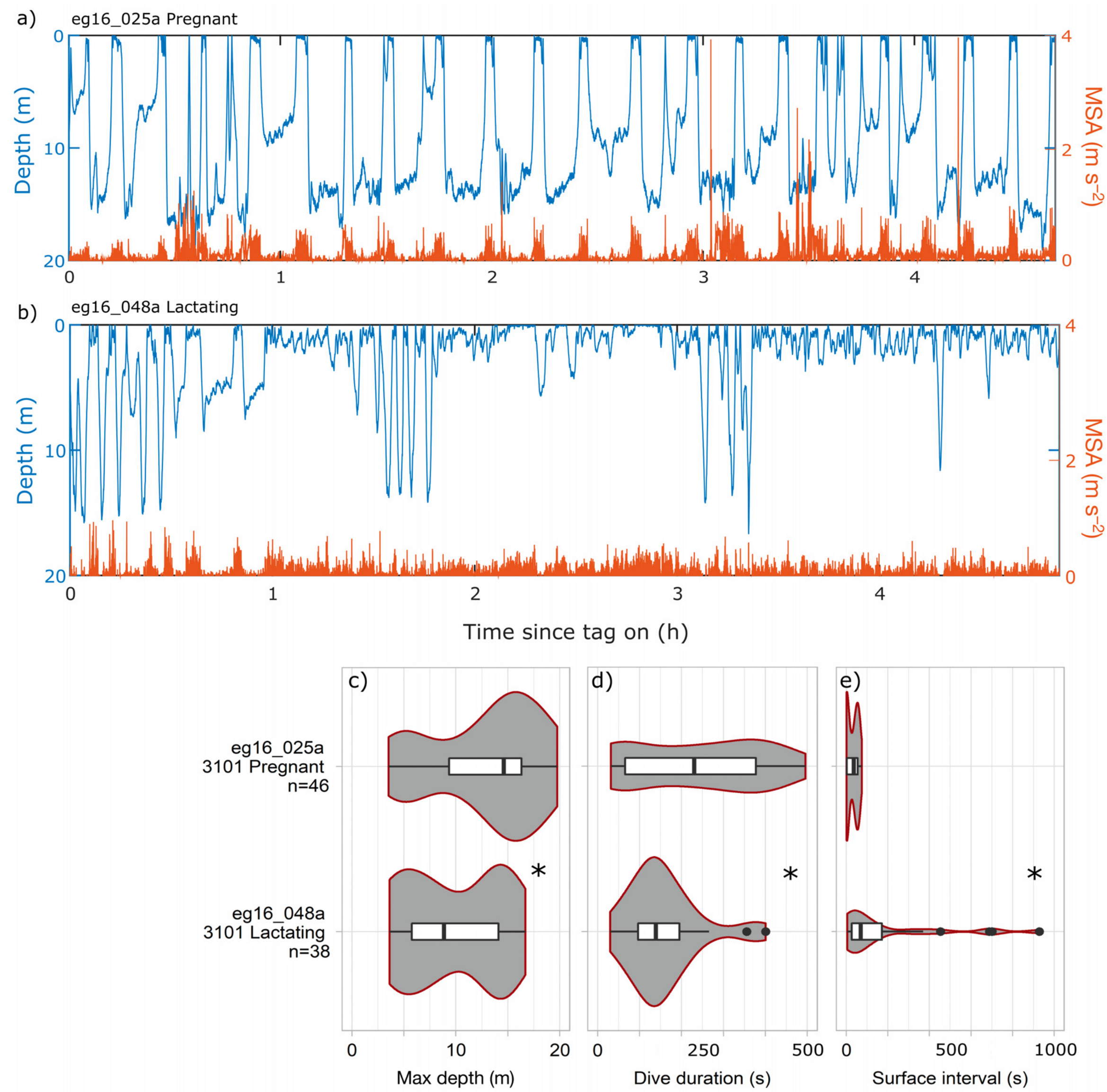

Fig. 5. Dive profiles (blue) and minimum specific acceleration (MSA, m s^{-2}) (orange) of EgNO 3101 tagged (a) when pregnant and (b) when lactating. Note consistent MSA values for the lactating state, indicating prevalence of low energy behavior for this deployment. Distribution of (c) maximum depth, (d) dive duration and (e) surface interval revealed that calf presence modified the dive behavior of this female, shortening her surface interval and dive duration. Data representation as in Fig. 2

In 2016, EgNO 3101 was tagged twice: once when she was pregnant (deployment eg16_025a) and again 23 d later, when she was lactating (eg16_048a, Fig. 5). Both deployments yielded similar analysis duration (~4.8 h). The overall dive rate was slightly higher during pregnancy than during lactation (7.93 vs. 5.41 dives h^{-1}, respectively, Table 1). However, median surface interval was ~50% shorter (pregnant = 88 s, lactating = 171 s) ($U = 212$, $n_1 = 38$, $n_2 = 26$, $p < 0.05$) and median dive duration was ~35% longer when EgNO 3101 was pregnant (390 s) than when she was accompanied by a calf (140 s, $U = 744$, $n_1 = 38$, $n_2 = 26$, $p < 0.05$). Bottom time represented a smaller proportion (27 vs. 47%) of her dives, and median max depth was ~60% shallower when lactating (8.8 m) than when she was pregnant (14.6 m, $U = 680$, $n_1 = 38$, $n_2 = 26$, $p < 0.05$), showing clear modifications in dive behavior when EgNO 3101 was accompanied by a calf in comparison to when she was pregnant.

3.3. Diel pattern

In 4 deployments (eg06_028a, eg14_049a, eg15_52a and eg16_053a), tags remained attached to whales past astronomical twilight. For these deployments,

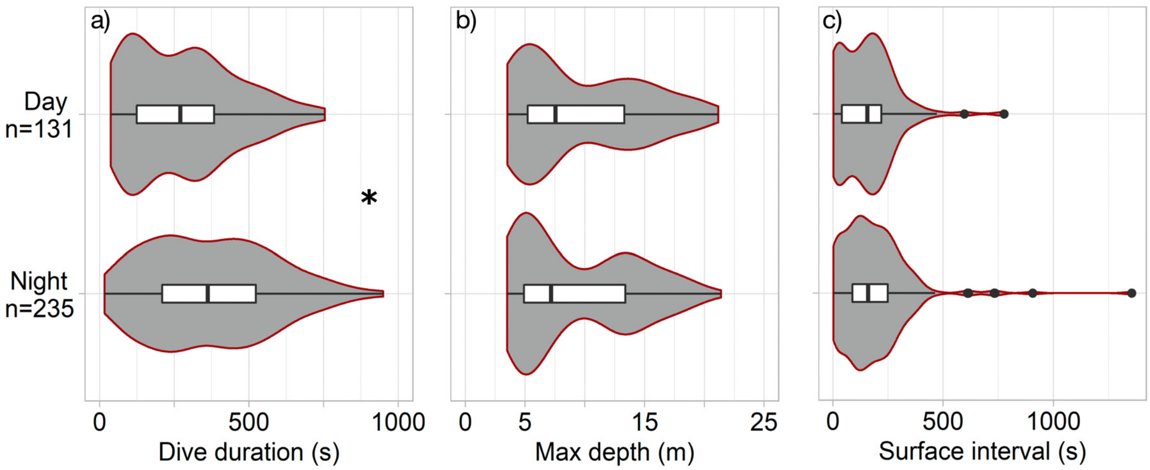

Fig. 6. Distribution of (a) dive duration, (b) maximum dive depth and (c) surface interval for day and night dives for deployments eg06_028a(P), eg14_049a (L), eg15_52a(L) and eg16_053a(L). Data representation as in Fig. 2

dive count, dive rate and descriptive statistics (median, minimum–maximum, mean and SD) for dive duration, max depth and surface interval were calculated separately for day and night (before and after the astronomical twilight, respectively, Tables S4 & S5). Independently of lactation state, dive rates were higher during the day and dive duration was longer at night (day = 307 s, night = 358 s) ($U = 25156$, $n_1 = 254$, $n_2 = 169$, $p < 0.05$). There was no significant difference between dive depth between day (8.2 m) and night (7.1 m) ($U = 20101$, $n_1 = 254$, $n_2 = 169$, $p > 0.05$; Fig. 6; Tables S4 & S5) or surface interval (day = 164 s, night = 170 s; $U = 21933$, $n_1 = 254$, $n_2 = 169$, $p > 0.05$).

3.4. Temperature distribution

Whales spent most of the time in waters with temperatures between 13 and 16°C. Temperature at the surface (16°C) was not significantly different than water temperature at depth (15°C) ($U = 124.7$, $n_1 = 456{,}935$, $n_2 = 848{,}595$, $p > 0.05$) across all deployments. The overall distribution of temperature values can be found in Fig. S2.

4. DISCUSSION

In general, the risk of vessel strike for a right whale is associated with vessel size, speed and route and the time a whale spends within the risk zone that comprises the draft of the vessel and the hydrodynamic zone below its hull (Silber et al. 2010, Laist et al. 2014, McKenna et al. 2015). The depth extension of this risk zone depends on factors associated with vessel size and movement as well as the size and movement of the animal (McKenna et al. 2015). In the waters where our study was conducted, there are both shallow-draft recreational vessels and deep-draft, full ocean-going cargo and container vessels that approach to the port of Jacksonville, FL, bisecting the study area. While the draft of recreational vessels can reach ~2 m, the port of Jacksonville docks large cargo and container vessels with a maximum draft of ~12 m (https://www.jaxport.com/). Seasonal speed restrictions for these large (≥19.8 m long) vessels are in effect during the calving season to reduce vessel strike probability and lethality; however, the more time a whale spends close to the surface, the more likely it is to be within the risk zone of the draft and the more likely it is to be struck by a vessel (Laist et al. 2014, McKenna et al. 2015). Results from our study show that lactating females spend significantly more time at depths close to the surface (on average 57 % and up to 84 % of tag deployment duration) than pregnant females and juveniles, and therefore within the draft of large vessels, which are more likely to be involved in deadly collisions with large whales (Laist et al. 2001, 2014, McKenna et al. 2015). These results indicate that lactating females and their calves are at higher risk of being struck by vessels than other whales on the calving ground due to increased time spent in the riskiest portion of the water column. This result supports previous observations of a disproportionate number of vessel strike mortalities associated with female–calf pairs (van der Hoop et al. 2013). Lactating females likely spend more time at the surface due to the typical right whale mother–calf pair behavior on the calving ground (e.g. Hain et al. 2013, Cusano et al. 2019).

On their respective calving grounds, baleen whale mother–calf pairs engage in behaviors that demand low energetic investment (e.g. southern right whales *Eubalaena australis*: Taber & Thomas 1982, Burnell & Bryden 1997; humpback whales *Megaptera novaeangliae*: Cartwright & Sullivan 2009, Bejder et al. 2019). Previous studies of right whale mother–calf pairs off the SEUS found that their predominant behavioral state was resting (Hain et al. 2013, Cusano et al. 2019), comprising 81 and 74% of the female and calf activity budget, respectively (Cusano et al. 2019). Right whales usually rest at the surface and in shallow water depths (Hain et al. 2013, Cusano et al. 2019). Therefore, it is likely that lactating females spend more time close to the surface than juvenile whales and pregnant females due to the prevalence of resting behavior in this habitat. This hypothesis is supported by the MSA measurements that indicate consistent low activity levels for lactating females.

The time right whales spend in different portions of the water column affects detection probability for visual monitoring methods and therefore can impact local abundance estimates (Ganley et al. 2019). To be detected by visual surveys, whales must be visible (available within the visual detection range). In order to be visible, they must be within the surface layer and/or break the surface water line (Ganley et al. 2019). However, although not visible (e.g. when below the surface layer) and therefore not available to be detected, whales might still be present in the area (availability bias; Marsh & Sinclair 1989). Lactating females spend more time at the surface and consequently they will be available for detection more frequently. On the other hand, juveniles and pregnant whales spend more time below the surface, and therefore are less likely to be detected by visual monitoring methods even when present in the habitat. Addressing the variability in availability bias across whale groups is key to robustly estimating detection probability and right whale abundance on the calving ground and in other habitats.

We are not aware of any fishery currently operating or permitted in the SEUS during the calving period. Therefore, entanglement in fishing gear and/or floating groundlines is not an imminent threat to right whales on the calving ground. Yet, the information presented here underscores the importance of current seasonal closures of fishing activity and the floating groundline ban. That is because aspects of right whale dive behavior could potentially increase risk of entanglement in this habitat. For instance, diving close to the sea floor can increase the risk of whales becoming entangled in floating groundlines (Hamilton & Kraus 2019, Howle et al. 2019). Groundlines connect bottom traps and, in the case of floating trap lines, can arch up to 5 m above the sea floor. While diving on the calving ground, right whales spent on average 40% of the dive cycle in the bottom phase, within 85% of the max depth reached during a dive. Therefore, when taking deep dives in the shallow water depths of the calving ground, whales would be swimming within the arch of floating groundlines, increasing risk of entanglement, if these were to be found in the calving habitat. Moreover, computer models suggest that performing rolls near the sea floor also increases the probability of entanglement (Howle et al. 2019). Because pregnant females and juveniles perform deeper dives and spend more time in the bottom phase of dives, the risk of entanglement in floating groundlines might be higher for these groups. For both lactating and non-lactating whales, the display of barrel-rolls in the bottom phase of dives could represent increased entanglement risk in floating ground lines. Deeper dives by non-lactating whales could also indicate that these individuals use deeper parts of the calving grounds more frequently than lactating whales and would therefore be at greater risk of entanglement if floating groundlines were being used in the SEUS. Should future management consider allowing fishery activity in the area while right whales are present, our results suggest that alternatives to floating groundlines, such as ropeless gear and/or sinking groundlines, would be the best options to reduce risk of entanglement in the area.

Water depth is one of the physical factors associated with right whale distribution on the calving ground. In this habitat, higher sighting rates occur in water depths between 10 and 20 m (Keller et al. 2006, 2012, Gowan & Ortega-Ortiz 2014). In comparison to feeding grounds, where water depths can reach 200 m, the slope of the continental shelf on the calving ground is more gradual and waters are considerably shallower. In this study, median maximum dive depth ranged from 5 to 16 m. Therefore, as suggested by van der Hoop et al. (2017), dive depth is likely constrained by the maximum depths of the habitat. However, it is important to note that habitat depth at the location of each dive is not available for the deployments considered here and that the absolute distance between the whale and the seafloor is therefore unknown.

Temperature is also associated with right whale distribution in the SEUS (Keller et al. 2006, 2012, Gowan & Ortega-Ortiz 2014). Due to the presence of Gulf Stream waters on the outer shelf (41–71 m), temperatures are cooler in the inner shelf region (0–40 m). Right whales are more frequently sighted in inner shelf waters, where surface temperatures range from 13 to 15°C. Accordingly, in this study, right whales were instrumented with DTAGs on the inner shelf; the temperature registered by the tags ranged from 10 to 19°C with a median temperature of approximately 14°C. The lack of significant difference between temperatures at the surface and at depth is consistent with descriptions of the oceanographic properties of the calving ground, characterized by a well-mixed water column (Keller et al. 2012). Similar surface and at-depth temperature also suggest that there are no thermoregulatory benefits of diving in this habitat.

Right whales are amongst the most positively buoyant of baleen whales. Due to their positive buoyancy, as Nowacek et al. (2001) observed on feeding grounds, right whales there had to invest more energy actively swimming during the descent phase of dives to overcome this buoyancy and could then glide with reduced energy expenditure during the final ascent phase of dives. Differences in energy investment between the descent and ascent phases can result in differences in the time whales take to travel to and from the bottom of a dive. On the calving ground, the ascent and descent rates were similar for lactating females. The same relationship was observed in right whales in the Bay of Fundy, Canada, where ascent rates were equal to or greater than descent rates (Nowacek et al. 2001). For non-lactating whales on the calving ground, however, median descent rates were greater than ascent rates. Average descent pitch angles were steeper than average ascent pitch for both lactating and non-lactating whales. On the calving ground, as well as in other habitats, right whale buoyancy can affect the risk of vessel strikes (Nowacek et al. 2001). On the feeding grounds in the Bay of Fundy, right whales started their buoyancy-driven ascent glides at depths >30 m (Nowacek et al. 2001). On the calving ground, right whales would then be buoyant even when diving to the maximum dive depth recorded in this study (21.3 m). Nowacek et al. (2001) postulated that this increased buoyancy could lead to reduced maneuverability, thereby decreasing the chances of right whales effectively avoiding vessels when on a collision course. Silber et al. (2010) modeled the hydrodynamics of whale–vessel collisions and found that buoyancy is indeed a factor affecting the risk of vessel strike.

Overall, dive behavior of lactating right whales differed from that of non-lactating individuals. Despite the small sample size, our results suggest that the dive behavior of lactating females is altered by calf presence and calf age. In our opportunistic comparison between 2 individuals tagged in 2014, the lactating female with the younger calf exhibited lower dive rates and longer surface intervals. This observation is consistent with visual observations of decreased time spent at the surface resting as right whale calves mature (Cusano et al. 2019). For the individual (EgNO 3101) tagged when pregnant and subsequently as a lactating female in 2016, the presence of the calf led to longer dives and longer surface intervals. We acknowledge that in both of these comparisons, we only have a single exemplar and suggest that additional research is needed to establish whether these observed trends represent true differences related to calf age and presence.

As documented for other cetacean species, lactating baleen whales are solely responsible for the extensive parental care required by calves, who often attempt to mimic the dive behavior of females (Whitehead & Mann 2000, Bejder et al. 2019). However, calves lack the physiological capacity and motor skills necessary to take deep dives, to travel long distances and to maneuver underwater like an adult (Szabo & Duffus 2008, Bejder et al. 2019). Therefore, lactating baleen whales have been documented to change their behavior to accommodate the limited skills and to maintain proximity with their calf (Taber & Thomas 1982, Tyson et al. 2012, Miketa et al. 2018). These changes in behavior include changes in the activity budget, habitat use and water column use (Taber & Thomas 1982, Thomas & Taber 1984, Tyson et al. 2012, Miketa et al. 2018, Bejder et al. 2019). Lactating right whales on the calving ground may spend time at or near the surface to remain close to their young calves as they develop skills necessary to swim for as long, and dive for as long and as deep, as adults.

As the calves develop, females are expected to gradually change their dive behavior, taking longer dives and spending less time at the surface (Miketa et al. 2018). The preliminary observations from our study showed that the lactating female with the older calf had shorter surface intervals, shorter dives and spent more time in the bottom phase of dives than the female with the younger calf. Longer deployment attachments on lactating females throughout calf development, as well as deployments on calves, will provide further information to assess changes in female and calf behavior associated with calf development and behavioral ontogeny.

Night dive data obtained from 3 individuals suggest that right whales might exhibit diel differences in dive behavior on the calving ground. Overall, dive rate was lower, dives were longer, and median max depth was deeper in nighttime dives than in daytime dives. Diel differences in dive behavior have been reported for right whales on feeding grounds and for other baleen whale species such as blue whales *Balaenoptera musculus*, humpback whales, Bryde's whales *B. edeni*/*brydei* and fin whales *B. physalus* (Calambokidis et al. 2007, Friedlaender et al. 2013, Baumgartner et al. 2017, Izadi et al. 2018, Keen et al. 2019). In most cases, diel changes in the dive behavior were associated with changes in prey distribution. North Atlantic right whales were not observed feeding on the calving ground (Fortune et al. 2013). Therefore, it is highly unlikely that the observed diel trend is associated with prey distribution and foraging efficiency. Diel differences in dive behavior can also result from variability in activity levels between day and night.

5. CONCLUSION

In this paper, we explored dive behavior of the Critically Endangered North Atlantic right whale on the calving ground. We described aspects of the dive behavior of this species with important conservation implications. Differences in dive behavior between lactating and non-lactating whales indicate that monitoring methods should account for different detection availability of these whale groups. While lactating females are at greater risk of vessel strikes because they spend more time at the surface, pregnant females and juvenile whales reach greater depths when diving, underscoring the importance of seasonal closures of high-risk fishing activities on the calving ground. Calf presence, calf age, and diel period were shown to affect the diving behavior of females. We hope that these data will inform protection and monitoring efforts for right whales on the calving ground in the Southeast USA.

Acknowledgements. We thank the North Atlantic Right Whale Consortium for access to whale identification and sighting data used in this study. Funding was provided by the Office of Naval Research and the US Fleet Forces Command and managed by Naval Facilities Engineering Command Atlantic as part of the US Navy Marine Species Monitoring Program. North Atlantic Right Whale Consortium, NOAA Southeast Science Center, Oceanworks Group, New England Aquarium, Georgia Department of Natural Resources, and the Florida Fish and Wildlife Conservation Commission were instrumental with right whale sightings and logistical support. We also thank the following people who helped with data collection: Lisa Conger, Dana Cusano, Julian Dale, Heather Foley, Alex Loer, Jessica McCordic, Rett Newton, Nicola Quick, Zach Swaim, Danielle Waples and Chen-Yi Wu. Data were collected under NMFS permit 17355-01 issued to Dr. P. Corkeron. Tagging was conducted under US National Marine Fisheries Service permit 17355-01. Methods were approved by the Institutional Animal Care and Use Committees of Duke University and Syracuse University.

LITERATURE CITED

Baumgartner MF, Mate BR (2003) Summertime foraging ecology of North Atlantic right whales. Mar Ecol Prog Ser 264:123–135

Baumgartner MF, Wenzel FW, Lysiak NSJ, Patrician MR (2017) North Atlantic right whale foraging ecology and its role in human-caused mortality. Mar Ecol Prog Ser 581:165–181

Bejder L, Videsen S, Hermannsen L, Simon M, Hanf D, Madsen PT (2019) Low energy expenditure and resting behaviour of humpback whale mother–calf pairs highlights conservation importance of sheltered breeding areas. Sci Rep 9:771

Burnell SR, Bryden MM (1997) Coastal residence periods and reproductive timing in southern right whales, *Eubalaena australis*. J Zool (Lond) 241:613–621

Calambokidis J, Schorr GS, Steiger GH, Francis J and others (2007) Insights into the underwater diving, feeding, and calling behavior of blue whales from a suction-cup-attached video-imaging tag (Crittercam). Mar Technol Soc J 41:19–29

Cartwright R, Sullivan M (2009) Behavioral ontogeny in humpback whale (*Megaptera novaeangliae*) calves during their residence in Hawaiian waters. Mar Mamm Sci 25:659–680

Caswell H, Fujiwara M, Brault S (1999) Declining survival probability threatens the North Atlantic right whale. Proc Natl Acad Sci USA 96:3308–3313

Cooke JG (2020) North Atlantic right whale. *Eubalaena glacialis* (errata version published in 2020). The IUCN Red List of Threatened Species 2020: e.T41712A162001243. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T41712A178589687.en

Corkeron P, Hamilton P, Bannister J, Best P and others (2018) The recovery of North Atlantic right whales, *Eubalaena glacialis*, has been constrained by human-caused mortality. R Soc Open Sci 5:180892

Cusano DA, Conger LA, Van Parijs SM, Parks SE (2019) Implementing conservation measures for the North Atlantic right whale: considering the behavioral ontogeny of mother–calf pairs. Anim Conserv 22:228–237

Fortune SME, Trites AW, Mayo CA, Rosen DAS, Hamilton PK (2013) Energetic requirements of North Atlantic right whales and the implications for species recovery. Mar Ecol Prog Ser 478:253–272

Friedlaender AS, Tyson RB, Stimpert AK, Read AJ, Nowacek DP (2013) Extreme diel variation in the feeding behavior of humpback whales along the western Antarctic Peninsula during autumn. Mar Ecol Prog Ser 494:281–289

Ganley LC, Brault S, Mayo CA (2019) What we see is not what there is: estimating North Atlantic right whale *Eubalaena glacialis* local abundance. Endang Species Res 38:101–113

Gowan TA, Ortega-Ortiz JG (2014) Wintering habitat model for the North Atlantic right whale (*Eubalaena glacialis*) in the Southeastern United States. PLOS ONE 9:e95126
Hain JHW, Ellis SL, Kenney RD, Slay CK (1999) Sightability of right whales in coastal waters of the southeastern United States with implications for the aerial monitoring program. In: Garner GW, Amstrup SC, Laake JL, Manley BFJ, McDonald LL, Robertson DG (eds) Marine mammal survey and assessment methods. A.A. Balkema, Rotterdam, p 191–207
Hain JHW, Hampp JD, McKenney SA, Albert JA, Kenney RD (2013) Swim speed, behavior, and movement of North Atlantic right whales (*Eubalaena glacialis*) in coastal waters of northeastern Florida, USA. PLOS ONE 8:e54340
Hamilton PK, Kraus SD (2019) Frequent encounters with the seafloor increase right whales' risk of entanglement in fishing groundlines. Endang Species Res 39:235–246
Hooker SK, Baird RW, Al-Omari S, Gowans S, Whitehead H (2001) Behavioral reactions of northern bottlenose whales (*Hyperoodon ampullatus*) to biopsy darting and tag attachment procedures. Fish Bull 99:303–308
Howle LE, Kraus SD, Werner TB, Nowacek DP (2019) Simulation of the entanglement of a North Atlantic right whale (*Eubalaena glacialis*) with fixed fishing gear. Mar Mamm Sci 35:760–778
Izadi S, Johnson M, de Soto NA, Constantine R (2018) Night-life of Bryde's whales: ecological implications of resting in a baleen whale. Behav Ecol Sociobiol 72:78
Johnson MP, Tyack PL (2003) A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE J Oceanic Eng 28:3–12
Keen EM, Falcone EA, Andrews RD, Schorr GS (2019) Diel dive behavior of fin whales (*Balaenoptera physalus*) in the Southern California Bight. Aquat Mamm 45:233–243
Keller CA, Ward-Geiger LI, Brooks WB, Slay CK, Taylor CR, Zoodsma BJ (2006) North Atlantic right whale distribution in relation to sea-surface temperature in the southeastern United States calving grounds. Mar Mamm Sci 22:426–445
Keller CA, Garrison L, Baumstark R, Ward-Geiger LI, Hines E (2012) Application of a habitat model to define calving habitat of the North Atlantic right whale in the southeastern United States. Endang Species Res 18:73–87
Kenney RD (2018) What if there were no fishing? North Atlantic right whale population trajectories without entanglement mortality. Endang Species Res 37:233–237
Knowlton AR, Hamilton PK, Marx MK, Pettis HM, Kraus SD (2012) Monitoring North Atlantic right whale *Eubalaena glacialis* entanglement rates: a 30 yr retrospective. Mar Ecol Prog Ser 466:293–302
Kraus SD, Brown MW, Caswell H, Clark CW and others (2005) North Atlantic right whales in crisis. Science 309:561–562
Laist DW, Knowlton AR, Mead JG, Collet AS, Podestà M (2001) Collisions between ships and whales. Mar Mamm Sci 17:35–75
Laist DW, Knowlton AR, Pendleton D (2014) Effectiveness of mandatory vessel speed limits for protecting North Atlantic right whales. Endang Species Res 23:133–147
Marsh H, Sinclair DF (1989) Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. J Wildl Manag 53:1017–1024
Mayo CA, Marx MK (1990) Surface foraging behaviour of the North Atlantic right whale, *Eubalaena glacialis*, and associated zooplankton characteristics. Can J Zool 68: 2214–2220
McKenna MF, Calambokidis J, Oleson EM, Laist DW, Goldbogen JA (2015) Simultaneous tracking of blue whales and large ships demonstrates limited behavioral responses for avoiding collision. Endang Species Res 27:219–232
Meyer-Gutbrod EL, Greene CH, Davies KT (2018) Marine species range shifts necessitate advanced policy planning: the case of the North Atlantic right whale. Oceanography 31:19–23
Miketa ML, Patterson EM, Krzyszczyk E, Foroughirad V, Mann J (2018) Calf age and sex affect maternal diving behaviour in Shark Bay bottlenose dolphins. Anim Behav 137:107–117
Miller CA, Best PB, Perryman WL, Baumgartner MF, Moore MJ (2012) Body shape changes associated with reproductive status, nutritive condition and growth in right whales *Eubalaena glacialis* and *E. australis.* Mar Ecol Prog Ser 459:135–156
NARWC (North Atlantic Right Whale Consortium) (2019) North Atlantic right whale consortium sightings database. Anderson Cabot Center for Ocean Life at the New England Aquarium, Boston, MA
Nowacek DP, Johnson MP, Tyack PL, Shorter KA, McLellan WA (2001) Buoyant balaenids: the ups and downs of buoyancy in right whales. Proc R Soc B 268:1811–1816
Nowacek DP, Johnson MP, Tyack PL (2004) North Atlantic right whales (*Eubalaena glacialis*) ignore ships but respond to alerting stimuli. Proc R Soc B 271:227–231
Pace RM III, Corkeron PJ, Kraus SD (2017) State–space mark–recapture estimates reveal a recent decline in abundance of North Atlantic right whales. Ecol Evol 7: 8730–8741
Parks SE, Warren JD, Stamieszkin K, Mayo CA, Wiley D (2012) Dangerous dining: surface foraging of North Atlantic right whales increases risk of vessel collisions. Biol Lett 8:57–60
Pettis HM, Pace RM III, Hamilton PK (2018) North Atlantic right whale consortium annual report card. Report to the North Atlantic right whale consortium, November 2018. NARWC, Boston, MA. https://www.narwc.org/uploads/1/1/6/6/116623219/2018report_cardfinal.pdf
R Core Team (2019) R: a language and environment for statistical computing (version 3.6.0). R Foundation for Statistical Computing, Vienna
Root-Gutteridge H, Cusano DA, Shiu Y, Nowacek DP, Van Parijs SM, Parks SE (2018) A lifetime of changing calls: North Atlantic right whales, *Eubalaena glacialis*, refine call production as they age. Anim Behav 137:21–34
Sharp SM, McLellan WA, Rotstein DS, Costidis AM and others (2019) Gross and histopathologic diagnoses from North Atlantic right whale *Eubalaena glacialis* mortalities between 2003 and 2018. Dis Aquat Org 135:1–31
Silber GK, Slutsky J, Bettridge S (2010) Hydrodynamics of a ship/whale collision. J Exp Mar Biol Ecol 391:10–19
Simon M, Johnson M, Madsen PT (2012) Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. J Exp Biol 215: 3786–3798
Szabo A, Duffus D (2008) Mother–offspring association in the humpback whale, *Megaptera novaeangliae*: following behaviour in an aquatic mammal. Anim Behav 75:1085–1092
Taber SM, Thomas PO (1982) Calf development and mother–calf spatial relationships in southern right whales. Anim Behav 30:1072–1083
Thomas PO, Taber SM (1984) Mother–infant interaction and

behavioral development in southern right whales, *Eubalaena australis*. Behaviour 88:42–60
Tyson RB, Friedlaender AS, Ware C, Stimpert AK, Nowacek DP (2012) Synchronous mother and calf foraging behaviour in humpback whales *Megaptera novaeangliae*: insights from multi-sensor suction cup tags. Mar Ecol Prog Ser 457:209–220
van der Hoop JM, Moore MJ, Barco SG, Cole TVN and others (2013) Assessment of management to mitigate anthropogenic effects on large whales. Conserv Biol 27:121–133
van der Hoop JM, Moore M, Fahlman A, Bocconcelli A and others (2014) Behavioral impacts of disentanglement of a right whale under sedation and the energetic cost of entanglement. Mar Mamm Sci 30:282–307
van der Hoop JM, Nowacek DP, Moore MJ, Triantafyllou MS (2017) Swimming kinematics and efficiency of entangled North Atlantic right whales. Endang Species Res 32:1–17
Whitehead H, Mann J (2000) Female reproductive strategies of cetaceans: life histories and calf care. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, IL, p 219–246

Editorial responsibility: Sascha Hooker, St. Andrews, UK
Reviewed by: 3 anonymous referees

Submitted: May 13, 2019
Accepted: June 14, 2021
Proofs received from author(s): September 8, 2021