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Implementing conservation measures for the North Atlantic right whale: considering the behavioral ontogeny of mother-calf pairs

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Abstract

Understanding the behavioral ecology of a species is fundamental to effective conservation and management efforts. This study quantifies the behavioral ontogeny of North Atlantic right whale mother-calf pairs from birth to weaning spanning three critical habitat areas off the eastern coast of the United States and Canada. Data from 55 focal follows of 34 mother-calf pairs were collected from 2011 to 2015. Resting behaviors dominated the activity budgets for both mother and calf during the first 5 months, putting them at increased risk of vessel collisions. There was an increase in the proportion of active behaviors (travel, foraging, social activity) in both mother and calf as the calf matured. Importantly, the type of active behaviors, in particular surface skim feeding and surface active social behavior, meant that the risk of vessel collision to the pair did not decrease as the calf matured. Mother-calf right whale pairs showed very low calling rates on the calving grounds, suggesting that passive acoustic monitoring may not be an effective mitigation tool during the early months. However, calling rates increase once the pair leave the calving areas with both calf age and activity levels increasing, at which point passive acoustic monitoring becomes valuable. Protective measures need to take these rapid developmental changes throughout calf growth into account to improve the efficacy of protection measures for the endangered North Atlantic right whale and other species where behavioral ecology changes rapidly during maturation.

Introduction

Whaling has had a major impact on our oceans, removing at least 2/3 of all great whales from marine ecosystems (Roman *et al.*, 2014). As a result, the role that whales serve as key ecosystem engineers has been lost: as consumers, as prey, as vectors for nutrients and as detrital sources of energy and habitat in the deep sea (Roman *et al.*, 2014; Willis, 2014; Smith *et al.*, 2015). Since the ban on whaling, many species have shown a steady recovery in their population numbers, with some species even reproducing at unprecedented rates (e.g. 10–11% increase per year in humpback whales *Megaptera novaeangliae* off eastern Australia (Noad *et al.*, 2016)). However some species, such as the North Atlantic right whale (NARW) *Eubalaena glacialis*, are not recovering and the future of these species remains uncertain. Recognizing the driving factors that impede recovery and using science to inform conservation measures is essential in giving these populations a chance of survival.

NARWs are an endangered baleen whale species, hunted almost to extinction by the early 20th century. Despite a ban on whaling for this species imposed in 1935 (Tønnessen & Johnsen, 1982), the recovery rate of this population has been slow, around 2.8% per year between 1990 to 2010, with the population increasing from 295 to roughly 500 individuals (e.g. Knowlton, Kraus & Kenney, 1994; Waring *et al.*, 2016). However their population trajectory has been in decline since 2010, decreasing to an estimated 458 individuals (Pace, Corkeron & Kraus, 2017), leaving the NARW at a crisis point. The combination of a lower than expected birth rate and unsustainable levels of accidental mortality from anthropogenic sources, such as vessel collisions and entanglements, are driving this crisis (e.g. Kraus *et al.*, 2016; Brilliant *et al.*, 2017; Van der Hoop, Corkeron & Moore, 2017). Of concern is the disproportionate representation of calf and juvenile mortality from ship-strikes in this species (e.g. Moore *et al.*, 2004).

Over the past 30 years, NARWs have routinely calved in the waters off the southeastern United States during the winter months. Mother-calf pairs migrate north and are regularly observed feeding in the Great South Channel, Cape Cod Bay and Massachusetts Bay during the spring (Kraus & Rolland, 2007). During the summer months, when the calves reach about 8 months of age, NARWs are commonly found further north in Canadian waters, including the Bay of Fundy and Roseway Basin (Kraus & Rolland, 2007). However, recent changes in movement patterns of right whales within their known range (Davis *et al.*, 2017; Meyer-Gutbrod & Greene, 2018) are making their seasonal and spatial occurrence more unpredictable. This in turn makes it difficult to maintain an understanding of the anthropogenic risks they face. For species that show such large-scale movements, mothers and their dependent young are challenged by changing habitats during migration, exposing their calves to a wide range of ecological and anthropogenic threats along the way. It is thought that fewer than 100 reproductive females remain in the species (P. Corkeron, pers. comm.). Therefore, the need to conserve mother-calf pairs is paramount if this species stands any chance of survival.

Currently, passive acoustic monitoring (PAM) is used in a number of ways, including long-term monitoring of NARW occurrence throughout their range using fixed archival recordings (Davis *et al.*, 2017), as well as real-time fixed buoys and mobile platforms (Van Parijs *et al.*, 2009; Baumgartner *et al.*, 2013). This information is actively used to direct research efforts, understand changes in distribution, and mitigate vessel collisions (Van Parijs *et al.*, 2009; Davis *et al.*, 2017). The level of acoustic activity can vary depending on a species' behavior, habitat, age, sex and group composition. Understanding the behavioral and acoustic activity of mother-calf pairs is paramount to understanding when specific conservation measures directed at reducing anthropogenic impacts can be successful. In this study we quantify the surface and acoustic behaviors of NARW mother-calf pairs, tracking changes from birth onwards across their known habitat areas during the first year of the calf's life, with the goal of better understanding and mitigating vessel collision risk.

Materials and methods

Combined behavioral and acoustic data were collected from North Atlantic right whale (NARW) mother-calf pairs over five consecutive years, from 2011 to 2015. Field work was conducted in three separate right whale critical habitats. Efforts were focused during time periods when NARWs have previously been documented in these areas (Kraus & Kenney, 1991; NOAA, 2016): the southeastern United States (SEUS) NARW calving grounds between the months of January and March; and two subsequent foraging habitats, Cape Cod Bay (CCB), in the northeastern United States in April, and the Bay of Fundy (BOF), Canada between August and September (Fig. 1). Mother-calf pairs were present in the SEUS in all 5 years, CCB in 4 years and the BOF in 2 years (Table S1).

All behavioral observations and acoustic recordings were made using small boats (<8 m length) launched on fair--weather days (wind speed ≤10 knots and Beaufort sea state ≤3). In both the SEUS and CCB, visual sightings from concurrent aerial surveys directed at collecting photo identification information on NARWs aided in locating mother-calf pairs (Brown *et al.*, 2007; Gowan & Ortega-Ortiz, 2014). When no aerial survey information was available, mother-calf pairs were located opportunistically or via line transect surveys.

Photographs were taken to identify the mother based on individually distinct callosity patterns and other markings (Kraus *et al.*, 1986). Photographic identification (EGNO, individual NARW identification number) was confirmed at the end of each season by the New England Aquarium, which manages the NARW photo-identification catalog (Hamilton & Martin, 1999; http://rwcatalog.neaq.org).

Behavioral data collection

Continuous focal animal sampling was carried out by a dedicated observer for each mother-calf pair. This has been shown to be a reliable method for analyzing cetacean activity budgets and/or behavioral states (e.g. Mann, 1999; Karniski *et al.*, 2014). An ethogram was constructed to represent the complete activity budget of mother-calf pairs and behavioral states were considered mutually exclusive to one another (Table 1). The five behavioral states used are similar to those used for a previous study on the behavior of NARW mother-calf pairs (Hain *et al.*, 2013), as well as for other cetaceans including grey whales *Eschrichtius robustus* (Stelle, Megill & Kinzel, 2008), southern right whales *Eubalaena australis* (Taber & Thomas, 1982; Thomas & Taber, 1984), humpback whales (Cartwright & Sullivan, 2009; Zoidis *et al.*, 2014), and killer whales *Orcinus orca* (Ford, 1989). The duration of time spent in these key behavioral states was calculated for each focal follow to determine the overall activity budget.

Focal follows were conducted while attempting to maintain a distance of 50–200 m between the observation platform and the whales to minimize any impact on their behavior while remaining within range to record behavior with confidence. When conditions allowed, or a whale approached to <50 m, the engine was put into neutral or shut down completely. Behavioral data collection was suspended if the whales were >400 m from the vessel or if the Beaufort sea state was >4. As the behavioral development of the calf was the priority in this study, if the mother and calf separated, the calf became the focus of the follow and sampling for the mother was terminated until she returned within the sighting range.

Acoustic data collection

Acoustic recordings were made of the mother-calf pairs during each focal follow to determine call rates in each habitat. Two different methods were used for obtaining recordings depending on the behavior of the mother-calf pair (e.g. travelling or resting) and the habitat (shallow or

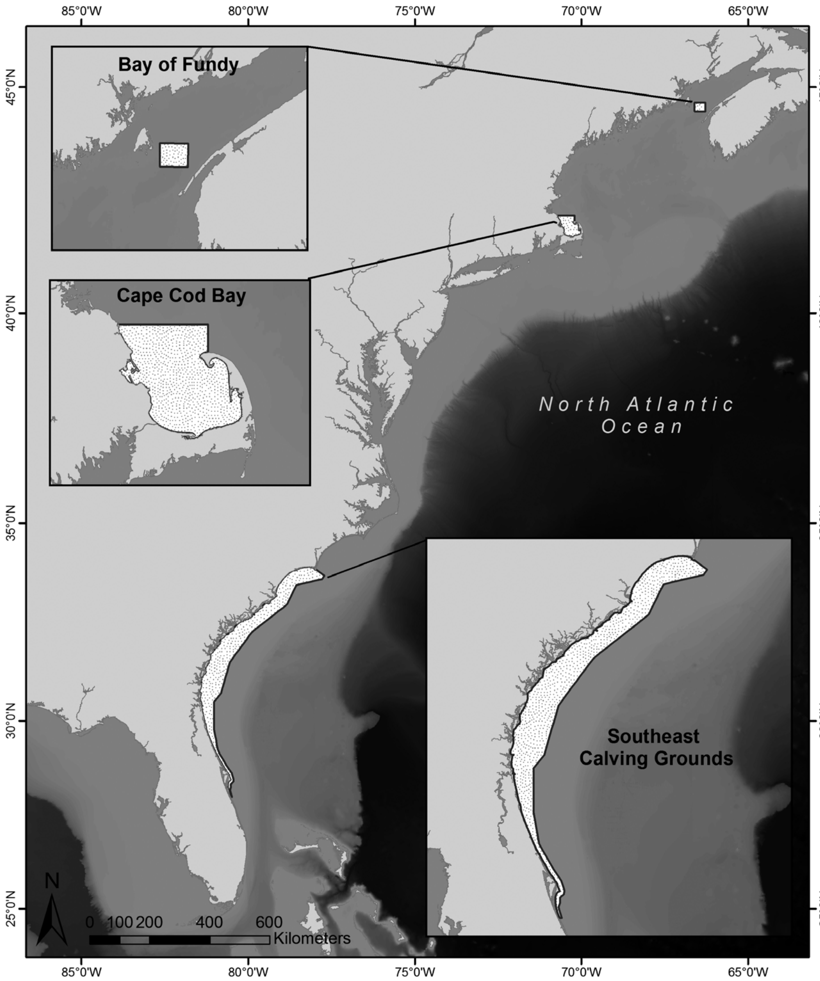

Figure 1 Location of the three critical habitat areas in which data collection occurred.

Table 1 The ethogram for North Atlantic right whale mother-calf pairs, consisting of five behavioral states recorded during focal follows

State	Definition	References
Rest	Resting motionless at the surface or just subsurface, and 'slow travel', with no change in heading or significant increase in speed.	Mann & Smuts, 1999; Stelle *et al.*, 2008; Hain *et al.*, 2013; Zoidis *et al.*, 2014
Nurse	Determined based on the calf's position relative to the mother's mammary slit while she is logging at the surface, and a common pattern of descending on one side and resurfacing on the opposite side of the mother.	Thomas & Taber, 1984; Hain *et al.*, 2013
Feed	High or low skim feeding evidenced by an open mouth, or subsurface feeding evidenced by long dives (up to 16 minutes) and a surfacing location in close proximity to the location of the initial dive.	Mayo & Marx, 1990; Baumgartner & Mate, 2003; Baumgartner, Mayo & Kenney, 2007
Travel	Directed forward active movement at a steady speed.	Thomas & Taber, 1984; Stelle *et al.*, 2008; Cartwright & Sullivan, 2009; Videsen *et al.*, 2017;.
Surface active/ play (SAP)	Increased activity at the surface, including participation in social activities such as surface active groups (SAGs), flipper and tail slapping, rolling, breaching, and interacting with other species or objects (*e.g.* the boat).	Würsig *et al.*, 1985; Ford, 1989; Baird *et al.*, 2002; Parks *et al.*, 2007; Stelle *et al.*, 2008; Hain *et al.*, 2013; Zoidis *et al.*, 2014

deep water). Depending on the hydrophone set-up, recordings were made using either an Edirol R-4 Pro 4-channel portable recorder (44.1 kHz sampling rate, 16-bit, frequency response 20 Hz–40 kHz (±3 dB)), or a Marantz PMD-661 hand-held solid-state recorder (44.1 kHz sampling rate, 16 bit, flat (±1 dB) frequency response 20 Hz–22 kHz).

For travelling behavior or in deeper water, recordings were made with either a three-element array or a single element hydrophone attached to a pole extended from the stern of the boat (HTI-96-MIN, High-Tech, Inc., flat (±1 dB) 2 Hz–30 kHz sensitivity, nominal −164 dB re: 1V/μPa). The three-element array was 90 m in length and the hydrophones were spaced 10 m apart at the tail end of the cable. The single element towed hydrophone was 20 m in length. Surgical tubing was used for stress relief at the attachment point to the pole in order to minimize self-noise when drag was applied to the cable. Towed recordings were only made when the vessel was travelling at speeds of 4–10 knots (most recordings at ~5 knots) to minimize the amount of flow noise in the recording. The 3-element hydrophone towed array was of sufficient weight that, when fully extended, the elements maintained a depth of at least 3 m while towing, and greater than 5 m when stationary. The single element towed hydrophone was weighted with 0.4–0.9 kg weights in order to maintain a similar depth as the array when towed and stationary. Observers on the vessel monitored the towing hydrophone visually to confirm that the hydrophone remained submerged during towing and aurally to assess the quality of the acoustic recording to make sure that cable strumming and/or flow noise levels were of an acceptable level.

During stationary behaviors, or in shallow habitats in the SEUS where water depth was often <10 m, dip hydrophones (HTI-96-MIN, High-Tech, Inc., flat (±1 dB) 2 Hz–30 kHz sensitivity, nominal −164 dB re: 1V/μPa) were deployed from spar buoys tethered to both sides of the boat. The drop hydrophones were weighted with 0.25 kg weights in order to keep the hydrophone vertical when attached to the spar buoy, and were deployed between 5 and 10 meters. For both the towed hydrophones and stationary hydrophones, the objective of the recordings was to detect tonal calls utilized for passive acoustic monitoring (Van Parijs *et al.*, 2009). Given that the source levels of these calls is estimated to exceed 147 dB_{rms} re 1 μPa (Parks & Tyack, 2005), and our recordings occurred <200 m from the whales, there was a low probability of missing a detection of any calls produced by the focal whale(s).

In 2014 and 2015, suction cup attached acoustic recording tags (Acousonde 3B, Greeneridge Sciences, Inc.) were used to collect data in CCB. These tags were equipped with sensors that record acoustic signals, pressure (depth), temperature, acceleration and magnetic field along three axes. Tags were programmed to sample audio at 25 kHz, with an anti-alias low pass filter setting to provide a flat (±3 dB) recording frequency range of 22 Hz–9.2 kHz. Additional sensors were sampled at 10 Hz.

All acoustic recordings were reviewed visually and aurally by an experienced acoustic technician using Raven Pro 1.5 (Cornell Bioacoustics Research Program, 2014 http://www.birds.cornell.edu/raven) software for the presence of NARW vocalizations (Parks *et al.*, 2011). The occurrence, timing, call type and number of calls produced were noted during each focal follow. The primary aim of the recordings was to assess the number of vocalizations detected in the presence of mother-calf pairs to inform passive acoustic monitoring, therefore no attempt was made to identify the caller (i.e. mother or calf). The behavioral sequencing was synced with the acoustic recordings; therefore each call could be assigned to an associated behavioral state. Only calls for which a behavioral state could be assigned were retained in subsequent analysis. Similar to the behavioral focal follows, if the mother and calf were in different behavioral states, the state of the calf was used to assign a behavioral state to the detected call.

Behavioral and acoustic analyses

Only focal follows >10 min duration were used in these analyses. Mother and calf were evaluated separately in order to obtain activity budgets for both individuals. To remain conservative, in a situation where a state was unclear to the observer, states were "turned off" and the animal(s) were not assigned to a state for that period of time. The cumulative time that an animal was unable to be assigned to a state was removed from the overall follow time to account for this. We then obtained percentages by dividing the time spent in the state by the adjusted focal follow time to determine relative time spent in each behavioral state.

For statistical comparisons of time spent in states, hours were used rather than proportions. This was done to reduce bias in the results as the observation times for focal follows were highly variable. To account for pseudoreplication (repeated measurements on the same mother-calf pair), non-normality and unbalanced sample sizes (unequal number and duration of follows in each habitat), linear mixed-effects models (LMMs) (Cnaan, Laird & Slasor, 1997) were used. Habitat was considered the fixed effect and whale ID and year were added as random effects. Models were run using restricted maximum likelihood estimates (REML) in order to provide unbiased estimates of the variance components. All analyses were conducted in R (R core team 2016) using the package lme4 (Bates *et al.*, 2015). Initial model results using Akaike information criterion (AIC) scores indicated that year was not an important variable, and it was subsequently removed from the analyses. Post hoc analyses on the LMMs were done using the package lsmeans (Lenth, 2016) and contrasts were done between all habitats using the Tukey method. The function lsmeans produces least squares means for contrasts based off of the model rather than raw data. This incorporates the other covariates of the model and is more appropriate for unbalanced designs (Lenth, 2016).

Call rates (calls per hour) were obtained by dividing the number of calls detected within a state or within a habitat by the total time of the behavioral follow or cumulative follow time for the season respectively. Mixed models were then used to analyze the calling rates between habitats and to assess the activity state in which vocalizations were predominantly detected. Habitat was set as the fixed effect, and whale ID and year were included as random effects. Year was removed from the model based on AIC scores during model development. Post hoc analyses using lsmeans were again used with contrasts between habitats and between states.

Results

A total of 64 focal follows were conducted between 2011 and 2015. Follows of less than 10 minutes in duration were discarded from further analysis, with 55 focal follows from 34 different mother-calf pairs, comprising 122.2 h of behavioral data used for analyses (Table S1). Thirteen pairs were followed on more than one occasion, with five repeat follows on one pair (catalog #3390). One mother (catalog #2040) was followed in two different years with subsequent calves (twice in 2011 and once in 2014). Seven pairs were followed in two habitats during the same year, although no pair was followed in all three habitats during a single year.

SEUS: 32 focal follows were conducted in the SEUS over the course of 5 years (average duration 2.2 ± 1.3 h), with 75.2 h of concurrent acoustic data collected. A total of 51 calls were recorded over the 5 years.

CCB: No data were obtained in CCB during 2012, but a total of 17 focal follows were conducted (average duration 2.0 ± 1.5 h) across the other 4 years, with 35.7 h of acoustic recordings. A total of 1175 calls were recorded over the 4 years.

BOF: NARW sightings declined precipitously between 2012 and 2015 in the BOF (Pettis & Hamilton, 2015). As a result, no data were collected on mother-calf pairs from 2013 to 2015 in this area. Six focal follows were conducted between 2011 and 2012 (average duration 3.1 ± 1.7 h), however one follow had to be dropped for a mother due to the short duration of the follow, leaving a total of five follows for mothers in the BOF and six for calves. A total of 20.3 h of acoustic data were collected in this habitat during the 2 years, with 1069 calls detected.

Behavioral activity budgets

The difference in time spent in specific behavioral states was compared for NARW mothers and their calves, however due to the very unbalanced sample sizes among habitats, especially in the BOF habitat, caution must be used in directly comparing percentages (Table 2). The activity budgets for mothers and calves were similar, with time spent in nurse and travel virtually identical across all habitats. Mixed models identified a statistically significant difference in the amount of time spent in *rest* and *feed* between mothers and calves in CCB only (Table S2). This was due to the increased amount of observed time feeding by mothers in this habitat and the lack of observations of feeding by the calves. No other statistically significant differences were observed in the time spent in each behavioral state when mothers were compared with calves.

For NARW mothers, *rest* dominated the activity budget in the SEUS, followed by *travel* and *nurse* (Fig. 2a, Table 2). No time was spent in *feed* on the calving grounds. The occurrences of *surface active/play* (*SAP*) in the SEUS were brief and infrequently observed, therefore they didn't constitute a measurable part of the activity budget. *Feed* was the principal state in CCB, followed by *rest*, *travel*, *SAP* and lastly *nurse*. In the BOF, *rest* was again the dominant activity for mothers, followed by the highest incidence of *travel* observed, and almost equal amounts of time spent in *feed* and *SAP*. *Nurse* again comprised a small percentage of the activity budget. Analysis from the mixed models showed a significant difference between the amount of time spent in *rest, nurse* and *feed* between the SEUS and CCB, and the amount of time spent in *travel* between the SEUS and both of the other habitats (Table S3).

As with mothers, the predominant activity for NARW calves in the SEUS was *rest*, followed by *travel* (Fig. 2b, Table 2). An almost equal amount of time was spent in *nurse* as in *SAP* for the calves in this habitat. No time was spent in *feed* in the SEUS. In CCB, *rest* was still the principal activity, and a similar amount of time was devoted to this state in this habitat as in the southeast. *Nurse* occurred at a low rate. *Feed* was observed once in CCB for calves, but the behavior was observed for <1 min, and so was not a measurable part of the overall activity budget. In CCB, *travel* and *SAP* made up a similar portion of the budget. *Rest* again made up the dominant activity in the BOF and *nurse* again comprised a small portion of the activity budget. No time was spent in *feed*. Time spent in *travel* was similar to time spent in *SAP*. When comparisons between habitats were made with the mixed models, the only significant difference was observed in the amount of time spent in *nurse* between the SEUS and CCB, and time spent in *travel* between the SEUS and the BOF (Table S4).

Calling behavior

A total of 2295 calls were detected across the entire the study period from 131.2 h of recordings, 75.2 h of which were in the SEUS, 35.7 h in CCB and 20.3 h in the BOF. Of the 2295 calls, 2059 were paired with behavioral sequencing data and subsequently used to assess calling rates/number of calls detected (Table 3). Both the calling rate (calls per hour) and production of calls increased as the calf aged, with the lowest

Table 2 Activity budgets of North Atlantic right whale mothers and calves in all three critical habitat areas showing percentage of total time spent in each behavioral state

State	SEUS (%)	CCB (%)	BOF (%)
Mom			
Rest	81	24	45
Nurse	9	3	4
Feed	0	54	11
Travel	10	13	30
SAP	0	6	10
Calf			
Rest	74	70	50
Nurse	8	3	3
Feed	0	0	0
Travel	10	13	27
SAP	8	14	20

SAP, surface active/play; SEUS, southeastern United States; CCB, Cape Cod Bay, Massachusetts, USA; BOF, Bay of Fundy, Canada.

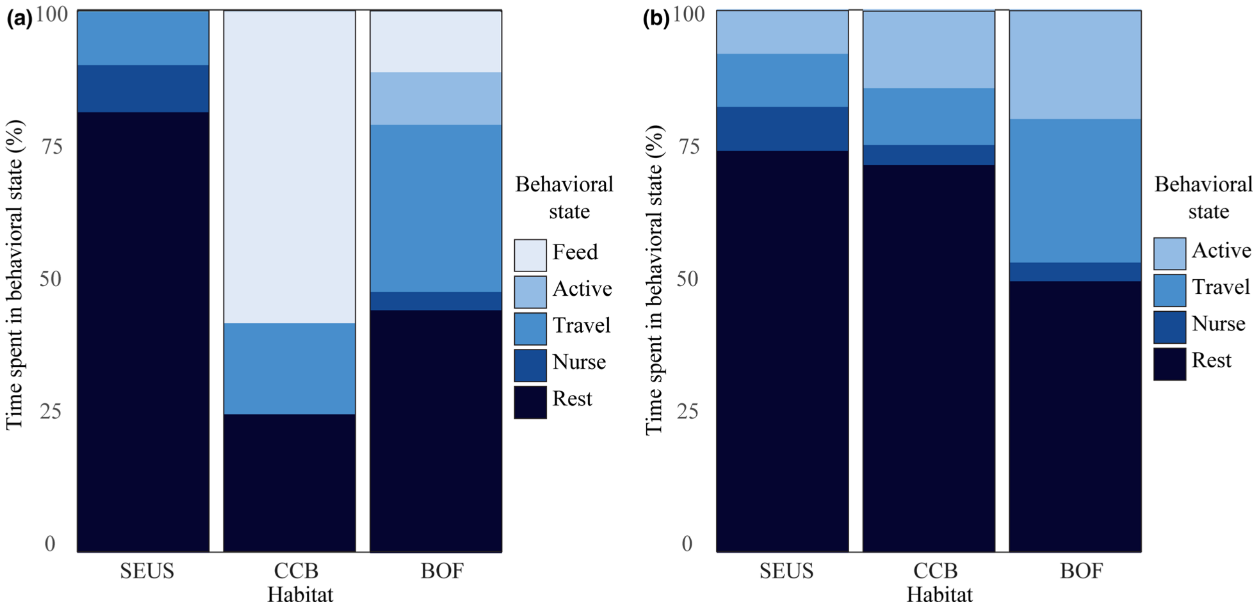

Figure 2 The activity budget of right whale mothers (a) and calves (b) in three habitat areas. SEUS, southeastern United States; CCB, Cape Cod Bay, Massachusetts, USA; BOF, Bay of Fundy, Canada. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

call rates recorded in the SEUS (total calls = 51; call rate lsmean = 1.1 ± 5.0), followed by CCB (total calls = 1175; call rate lsmean = 33.0 ± 7.5) and the BOF (total calls = 1069; call rate lsmean = 55.1 ± 11.0). There was a significant difference in the call rate between the SEUS and CCB, and the SEUS and the BOF (Table 3, Table S5).

When broken down by behavioral state, the lowest number of calls detected and the lowest call rates occurred during *nurse* (total calls = 25; call rate lsmean = 4.11 ± 7.0), followed by *travel* (total calls = 159; call rate lsmean = 6.5 ± 8.1) and *rest* (total calls = 548; call rate lsmean = 7.4 ± 6.5) (Table 3, Table S6). The highest number of vocalizations occurred during *SAP* (total calls = 1327; call rate lsmean = 65.6 ± 8.9), or times when the mother and calf were separated (Fig. 3). The call rate increased as the calf aged for all activity states with the exception of *SAP* between CCB and the BOF, however the only significant differences occurred in *rest* between the SEUS and the BOF, *rest* between CCB and the BOF, *nurse* between the SEUS and the BOF, *nurse* between CCB and the BOF, *SAP* between the SEUS and CCB, and *SAP* between the SEUS and the BOF (Table 3, Table S6). It should be noted that while it is possible that some calls were missed due to masking from flow noise, especially during times of travel, any calls that were missed would have been of such low amplitude that they would also likely be missed from any passive acoustic monitoring device due to the relatively close proximity of the whales to the hydrophone.

Discussion

This study demonstrates how the behavioral states of NARW mother-calf pairs alter over the course of their migration across the first 9 months of a calf's life. Similar to other marine mammals, the time calves spent resting decreased as they matured and they became more active, while mothers spent more time foraging (e.g. Kovacs, 1987; Cortez *et al.*, 2016). Of interest is that the extensive time periods spent in resting and nursing states reflect times that the whales are at the surface or just subsurface. These behaviors place the pair at an increased risk of ship strike, which may explain a high proportion of calves suffering from ship strike mortality in this species (e.g. Moore *et al.*, 2004). In addition, all of the behavioral observations were taken from the surface, so

Table 3 The total number of calls detected and the call rates (average calls per hour) of North Atlantic right whale mother-calf pairs in each behavioral state in the three habitat areas. As the behavioral state of the calf was used for the analysis on calling behavior, *feed* was not included

Habitat	Hours of acoustic recordings	Calls in *rest*	Calls in *nurse*	Calls in *travel*	Calls in *SAP*	Calls/hour (lsmean ± SE) in *rest*	Calls/hour (lsmean ± SE) in *nurse*	Calls/hour (lsmean ± SE) in *travel*	Calls/hour (lsmean ± SE) in *SAP*
SEUS	75.2	14	2	0	32	0.4 ± 3.5	0.2 ± 3.0	0 ± 6.2	5.1 ± 20.5
CCB	35.7	389	7	19	699	11.2 ± 4.7	3.3 ± 5.1	3.0 ± 11.2	142.6 ± 27.2
BOF	20.3	145	16	140	596	37.0 ± 9.0	25.3 ± 7.2	33.1 ± 12.6	135.2 ± 39.9

SAP, surface active/play; SEUS, southeastern United States; CCB, Cape Cod Bay, Massachusetts, USA; BOF, Bay of Fundy, Canada.

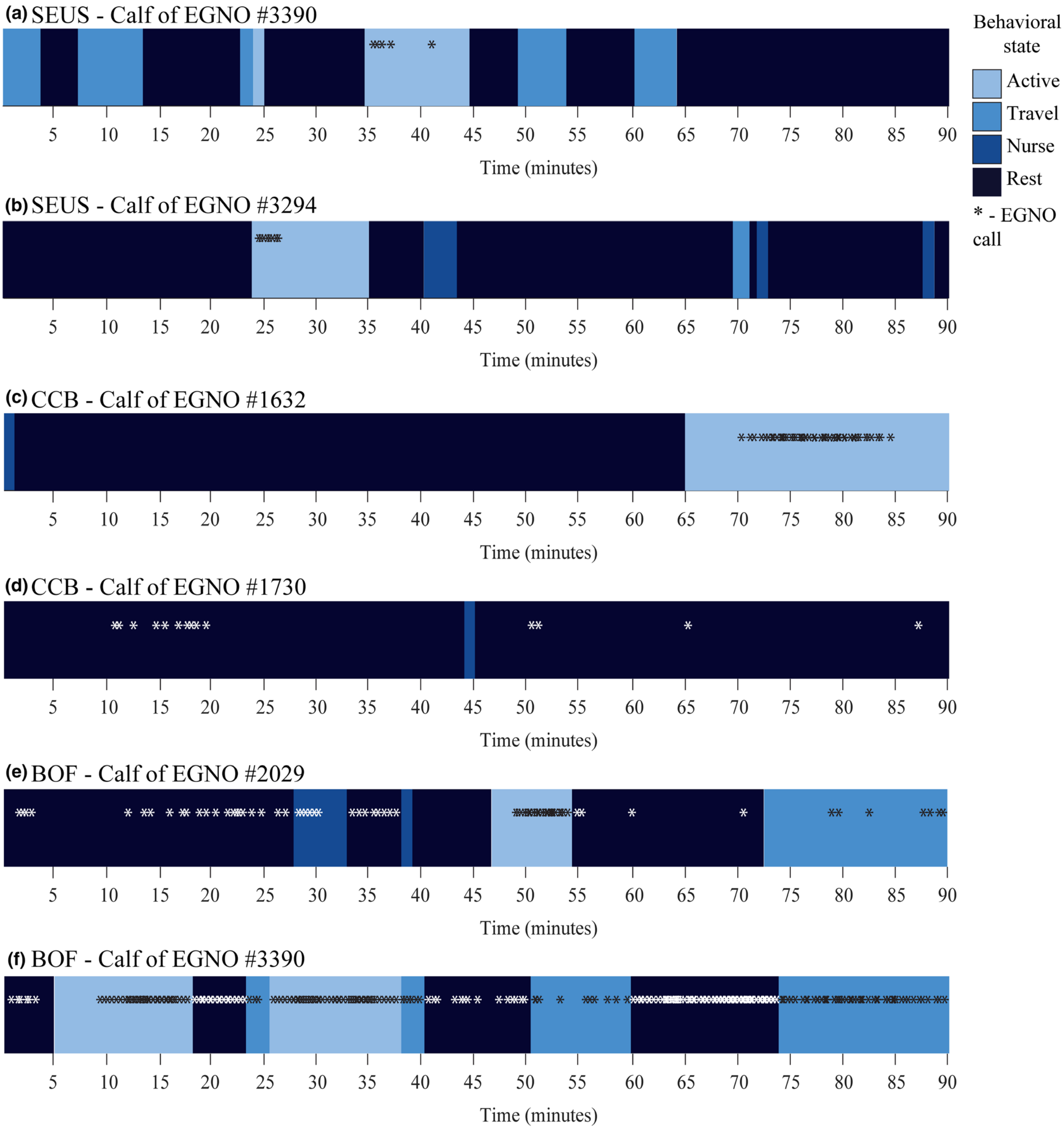

Figure 3 Example focal follows from calves in three study habitat areas, highlighting both the frequent state transitions and the changes in the time spent in certain behavioral states with age. Times of detected right whale vocalizations are marked with an * within the timeline. (a) calf of EGNO #3390, 5 February 2012 in the SEUS (b) calf of EGNO #3294, 21 January 2013 in the SEUS (c) calf of EGNO #1632, 17 April 2013 in CCB (d) calf of EGNO #1703, 30 April 2015 in CCB (e) calf of EGNO #2029, 17 August 2011 in the BOF (note that the mother and calf were separated from each other by hundreds of meters throughout most of this focal follow), and (f) calf of EGNO #3390, 3 September 2012 in the BOF. SEUS, southeastern United States; CCB, Cape Cod Bay, Massachusetts, USA; BOF, Bay of Fundy, Canada; EGNO, individual NARW identification number. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com]

particularly cryptic behaviors such as nursing are likely minimum estimates. However, as the same behavioral sequencing protocols were used in all habitats, there is not likely to be a directional bias between habitats for this state.

Ship strike risk differed for the mother and the calf depending on the habitat and the age of the calf. For example, mothers (81%) and calves (74%) were equally at risk when resting in the SEUS calving region. Calves remain vulnerable throughout the spring (CCB = 70%) while time spent near the surface decreased with age and independence from its mother (BOF = 50%). Once mothers enter CCB, their focus switches to foraging (54%) to replace the energetic expenditure of producing and rearing a calf (Lockyer, 1981; Kraus, Pace & Frasier, 2007). Although mothers make a switch to this more active behavior, NARWs in CCB tend to feed on near-surface prey patches, which keeps them at the surface and at risk of vessel collision (Mayo & Marx, 1990; Parks *et al.*, 2012). While on the summer foraging grounds (BOF), mothers switched back to spending the majority of their time resting (45%), however they increased their time spent in surface active groups (SAGs) (Kraus & Hatch, 2001; Parks *et al.*, 2007) (10%). In addition, they increased the amount of time spent traveling (30%), which is typically characterized by shallow dives in this area (Parks *et al.*, 2011). These behavior changes kept mothers near the surface where they remained at risk for vessel collisions.

The number of NARW calls detected and call rates were found to be highly variable and dependent on activity state. Very few calls were recorded from mother-calf pairs in the SEUS, however calling activity increased as the pair entered CCB and the BOF. Overall, the highest call rates were detected during *SAP*, despite the fact that mother-calf pairs spent a relatively small amount of time in this behavioral state. This pattern of calling behavior is consistent with call rates described from juvenile and adult NARWs from the BOF (Parks *et al.*, 2011). As the activity levels of calves increased over time, so did the number of calls emitted and the call rates. This is consistent with studies on the calling behavior of humpback whale mother-calf pairs showing increasing call rates over the course of the seasonal migration period (e.g. Dunlop, Cato & Noad, 2008; Videsen *et al.*, 2017).

Low calling rates in mother-calf pairs in the first months after birth likely serve as a method of limiting detectability by predators, while the close proximity of right whale mother-calf pairs during this period on the calving grounds allows for contact (visual or tactile) without the need for high amplitude vocalizations (Taber & Thomas, 1982; Hain *et al.*, 2013). Given the very low call rates in the SEUS, and the limited propagation of these calls in the shallow waters of this calving ground (Parks, Urazghildiiev & Clark, 2009; Soldevilla *et al.*, 2014), it is clear that relying solely upon acoustic cues as a method for detecting NARW mother-calf pairs to mitigate ship strike in the SEUS is insufficient. However, once they leave the calving grounds, PAM does become viable as a detection and mitigation strategy.

This study demonstrates that data on calling rates and behavioral activity states provide a valuable method for understanding NARW mother-calf detectability and risk exposure. As each individual moves between habitats, their risk levels and detectability using PAM change depending upon the behavior in which the whale is engaged. However, this risk does not necessarily decrease linearly as expected based on an increase in activity and remained high even outside of their calving habitat. As NARW distribution changes it will be important to understand how their behavioral states and communication changes as a result of the habitats that they utilize. Each one of these habitats may raise new vulnerabilities and concerns depending on the timing, age class, sex and behaviors for NARWs in the area.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. The focal follows of mother-calf North Atlantic right whale pairs during which behavioral data and acoustic recordings were collected across three different habitats.

Table S2. Results of lsmeans comparing time spent in each state per habitat between North Atlantic right whale calves and mothers, with a negative mean estimate and t-value indicating the mother spent less time in that state than the calf

Table S3. Results of lsmeans of hours spent in each behavioral state by habitat for North Atlantic right whale mothers with a negative mean estimate and t-value indicating the mother spent less time in that state in the first habitat of the two being compared

Table S4. Results of lsmeans comparing hours spent in each behavioral state per habitat for calves with a negative mean estimate and t-value indicating the calf spent less time in that state in the first habitat of the two being compared

Table S5. Results of lsmeans comparing call rates in each habitat, with a negative mean estimate and t-value indicating lower call rates were detected in the first habitat of the two being compared

Table S6. Results of lsmeans comparing call rates in each behavioral state per habitat, with a negative lsmean estimate and t-value indicating lower call rates were detected in the first habitat of the two being compared