ARTICLE

Behavioral responses of satellite tracked Blainville's beaked whales (*Mesoplodon densirostris*) to mid-frequency active sonar

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Abstract

The vulnerability of beaked whales (Family: Ziphiidae) to intense sound exposure has led to interest in their behavioral responses to mid-frequency active sonar (MFAS, 3–8 kHz). Here we present satellite-transmitting tag movement and dive behavior records from Blainville's beaked whales (*Mesoplodon densirostris*) tagged in advance of naval sonar exercises at the Atlantic Undersea Test and Evaluation Center (AUTEC) in the Bahamas. This represents one of the largest samples of beaked whales individually tracked during sonar operations (n = 7). The majority of individuals (five of seven) were displaced 28–68 km after the onset of sonar exposure and returned to the AUTEC range 2–4 days after exercises ended. Modeled sound pressure received levels were available during the tracking of four individuals and three of those individuals showed declines from initial maxima of 145–172 dB re 1 μPa to maxima of 70–150 dB re 1 μPa following displacements. Dive behavior data from tags showed a continuation of deep diving activity consistent with foraging during MFAS exposure periods, but also suggested reductions in time spent on deep dives during initial exposure periods. These data provide new insights into behavioral responses to MFAS and have important implications for modeling the population consequences of disturbance.

1 | INTRODUCTION

The highly tuned acoustic sensory systems of toothed whales (Odontoceti) evolved in marine soundscapes was predominantly influenced by surface waves, geological processes, and animal-produced sounds (Hildebrand, 2009). However, the introduction of anthropogenic noise sources such as vessel engines, naval sonar, seismic air guns, pile drivers, and underwater explosives have substantially changed the soundscapes experienced by marine mammals (Au, 2012; Hildebrand, 2009; McDonald, Hildebrand, Wiggins, & Ross, 2008). Intense underwater noise may disrupt cetacean behavior patterns (e.g., Aguilar de Soto et al., 2006; Dähne et al., 2013; DeRuiter et al., 2013; Goldbogen et al., 2013; Pirotta et al., 2012; Tyack et al., 2011) and induce physiological responses (Rolland et al., 2012) that may ultimately affect population health. Of particular concern, considerable evidence supports a causative link between specific beaked whale (family Ziphiidae) atypical mass stranding events and naval exercises employing mid-frequency active sonar (MFAS, 3–8 kHz) systems (Cox et al., 2006; D'Amico et al., 2009; Filadelfo et al., 2009; Frantzis, 1998).

Beyond the exposure conditions correlated with stranding events, there is additional concern that MFAS exposure may disrupt beaked whale foraging behavior and movement patterns, with potential energetic and reproductive consequences (e.g., Aguilar de Soto et al., 2006; Claridge, 2013; McCarthy et al., 2011; Moretti et al., 2014; New, Moretti, Hooker, Costa, & Simmons, 2013; Tyack et al., 2011). The United States' Marine Mammal Protection Act requires an understanding of how these sublethal disturbances or harassments may translate to impacts on population processes (Dolman & Jasny, 2015; Harris et al., 2018). As part of an overall effort to assess the Population Consequences of Acoustic Disturbance (PCAD/PCoD; Harwood et al., 2016; King et al., 2015; National Research Council, 2005; New et al., 2014), recent studies have attempted to quantify sound exposure thresholds that induce behavioral responses (Miller et al., 2014; Moretti et al., 2014) and describe the nature of those reactions (Southall, Nowacek, Miller, & Tyack, 2016). These studies have focused particularly on Blainville's beaked whales (*Mesoplodon densirostris*), Cuvier's beaked whales (*Ziphius cavirostris*), and northern bottlenose whales (*Hyperoodon ampullatus*), three species that are frequently involved in sonar-associated mass stranding events (D'Amico et al., 2009; Filadelfo et al., 2009; Simmonds & Lopez-Jurado, 1991) and appear to show a high behavioral sensitivity to sonar exposure relative to other marine mammals (Southall et al., 2016).

Under the PCAD/PCoD conceptual framework, one of the first steps in understanding population consequences of acoustic disturbance is to "characterize the ways in which human activities may disturb members of the population" (King et al., 2015). One hypothesized route by which MFAS exposure may affect beaked whale behavior, and ultimately population processes, is through displacement away from sonar sources. This has been hypothesized to mimic a generalized predator avoidance response (Frid & Dill, 2002), possibly based on confounding MFAS with the sounds produced by killer whales (*Orcinus orca*) in a similar frequency range (Harris et al., 2018; Tyack et al., 2011; Zimmer & Tyack, 2007). Current evidence from passive acoustic monitoring indicates declines in the number of *M. densirostris* vocal groups (i.e., groups of whales undertaking coordinated foraging dives using echolocation clicks) during naval exercises within an intensively ensonified central area of the U.S. Navy's Atlantic Undersea Test and Evaluation Center (AUTEC) range in the Bahamas (McCarthy et al., 2011; Tyack et al., 2011). This response has been followed by gradual repopulation by vocal groups from outside the range after sonar activity has ceased. Both patterns suggest the displacement of vocal groups away from the core area of MFA exposure. Based on this reduction of group vocal periods, a dose–response type of risk model was fitted to quantitatively assess the probability of behavioral disruption at different levels of sound pressure received levels (RL) (Moretti et al., 2014). Importantly

however, this form of data cannot directly discriminate the silencing of whales from displacement away from sonar activity and both responses have been observed in beaked whales during exposure to sonar (DeRuiter et al., 2013; Miller et al., 2015; Tyack et al., 2011). Also, while these data are informative about changes in echolocation within the geographic boundaries of the AUTEC passive acoustic hydrophone array, they do not provide direct information on changes in diving behavior consistent with foraging.

If beaked whales are displaced, they likely incur direct energetic costs of moving away from sonar sources, which may be substantially increased if flight is more rapid than least-cost travel velocities (Williams et al., 2017). Beyond these direct costs, Moretti et al. (2014) further posits that if beaked whales are displaced into areas where prey availability or catchability may be lower, then energy intake would decrease. For example, Benoit-Bird, Southall, and Moline (2016) examined deep prey fields in and around the Southern California Antisubmarine Warfare Range in relation to the distribution of *Z. cavirostris* obtained using the Navy's hydrophone array. They reported a general agreement between *Z. cavirostris* distribution and the distribution bathypelagic cephalopod prey, and postulated that the displacement of *Z. cavirostris* individuals to adjacent areas would reduce prey availability. Comparable heterogeneity of space use by beaked whale vocalizing groups (likely composed of *M. densirostris* and *Z. cavirostris*) has been demonstrated on the AUTEC range (Hazen, Nowacek, Laurent, Halpin, & Moretti, 2011). However, the implications of this heterogeneity for the foraging consequences of displacement have yet to be fully established. Hazen et al. (2011) faced challenges in drawing a direct linkage between spatial habitat use patterns and the distribution of beaked whale prey, because of the limited ability of near-surface bioacoustic instruments to measure the lower-mesopelagic and bathypelagic prey fields utilized by *M. densirostris* and *Z. cavirostris*.

A second hypothesized route by which MFAS exposure may affect beaked whale population processes is through the disruption of foraging dive cycles. *M. densirostris* has been shown to prematurely cease echolocation and foraging vocalizations during foraging dives and to ascend slowly in a direction away from sound sources, following initial exposure to simulated MFAS (Tyack et al., 2011). Moretti et al. (2014) further posits that if this disruption of foraging dives continues during extended sonar exposure, then energy intake would decrease in proportion to the number of "lost" dives. DeRuiter et al. (2013) and Falcone et al. (2017) examined data from tags placed on *Z. cavirostris* in Southern California and both found an increase in the duration of interdive intervals, as well as increased duration of dives following exposure to MFAS. Likewise, Stimpert et al. (2014) and Miller et al. (2015) document similar responses in *H. ampullatus* and Baird's beaked whale (*Berardius bairdii*).

Beaked whales may be particularly sensitive to this type of interruption of foraging dive cycles because of their comparatively large investment of time and energy into each foraging dive, when contrasted with other toothed whales (New et al., 2013; Joyce et al., 2017). This substantial time and energy investment likely relates to the use of anaerobic metabolism to extend bottom times during exceptionally deep and prolonged foraging dives (Joyce et al., 2017; Tyack, Johnson, Soto, Sturlese, & Madsen, 2006).

There remain important parameterization challenges in applying PCAD/PCoD models to better understand the repercussions of naval sonar exposure in beaked whale populations. In particular, where empirical data on behavioral and physiological responses is lacking, this conceptual framework can be forced to fall back on expert elicitation (Harwood et al., 2016; King et al., 2015; New et al., 2014). This study seeks to better inform particularly "Step 3" in the PCAD/PCoD framework as delineated by King et al. (2015), by using opportunistic observational data from medium-duration satellite-transmitting tags to document "measurable behavioral responses" to MFAS exposure. In particular, these tags can provide an individual (Lagrangian) behavioral perspective that has been unavailable in previous fixed passive acoustic studies (e.g., McCarthy et al., 2011; Moretti et al., 2010; Tyack et al., 2011). These tags also recorded data over long time periods in the presence of MFAS, providing information at time scales (e.g., days and weeks) that are highly relevant to the hypothesized displacement and foraging interruption responses of beaked whales (Tyack et al., 2011). The specific behavioral responses that we attempt to quantitatively and/or qualitatively examine in this study include: (1) were *M. densirostris* individuals displaced away from core areas of MFAS exposure?; (2) if so, where and how far did *M. densirostris* individuals travel?; (3) at what sound pressure RL did movements of individuals begin and cease during MFAS exposure?; (4) did individuals continue to exhibit cycles of deep dives

consistent with foraging during MFAS exposure?; and (5) did the deep dives of individuals reach comparable depths during MFAS exposure?

2 | METHODS

2.1 | Field data collection

Between 2009 and 2015, tags were deployed on *M. densirostris* individuals within and near AUTEC in the Tongue of the Ocean (TOTO) region of the Bahamas, prior to multivessel naval exercises that exposed these beaked whales to intense MFAS during "Submarine Commanders Courses" (SCC; McCarthy et al., 2011; see 2.4 Sonar Data below). Beaked whales were localized in real time using passive acoustic detection of echolocation clicks on an array of bottom-mounted hydrophones on the AUTEC range (Jarvis, Morrissey, Moretti, DiMarzio, & Shaffer, 2014; Moretti, Morrissey, DiMarzio, & Ward, 2006). These locations were relayed in real-time to boat-based observers and a tagging team on a 6.8 m rigid-hulled inflatable boat. This collaborative field approach greatly increased the opportunities for locating animals for tag deployments, which is particularly challenging given the cryptic surface behavior and long dives of beaked whales (Tyack et al., 2006).

The small satellite-transmitting tags attached to *M. densirostris* individuals consisted of two Platform Terminal Transmitter (PTT) instrument models both designed in the Low Impact Minimally Percutaneous External Electronics Transmitter configuration. SPOT model tags (49 g, AM-S240A-C, Wildlife Computers Inc., Redmond, WA) returned telemetry locations as well as an indirect proxy of dive behavior *via* summarized temperature readings. The more advanced SPLASH model tags (55 g, Mk-10, Wildlife Computers Inc.) transmitted telemetry locations as well as direct measurements of dive depths summarized at the level of single dives (in contrast to the higher-resolution dive records of archival time-depth recorders). Both tag models were attached on or near the dorsal fins of free-ranging (i.e., unrestrained) *M. densirostris* individuals from distances of 5–25 m using crossbows or black powder guns. The tag attachment consisted of 4–6.5 cm surgical grade titanium darts that penetrated into skin and connective tissue of the dorsal fin (Tyack et al., 2011). The sexes and age classes of tagged individuals were assessed based on sexually dimorphic characteristics where present, and in certain cases where skin biopsy material was available from an individual, sex was also confirmed using genetic methods (Morin, Nestler, Rubio-Cisneros, Robertson, & Mesnick, 2005; Rosel, 2003).

2.2 | Movement analyses

Both SPOT and SPLASH models transmitted a series of messages via the Argos system (www.Argos-system.org) when satellites were overhead during *M. densirostris* surface intervals. A maximum likelihood track of *M. densirostris* movement over the transmission life of each tag, was estimated from irregularly spaced Argos Kalman-filtered Doppler location fixes (McClintock, London, Cameron, & Boveng, 2015) using a continuous time correlated random walk (CTCRW) model (Johnson, London, Lea, & Durban, 2008). These CTCRW movement models were fitted in the R package *crawl* (version 2.1; Johnson, 2017) and enabled the explicit incorporation of location error ellipse extent and shape as well as process uncertainty in the correlated random walk parameters. Using a fitted CTCRW model for each track we predicted maximum likelihood (ML) location of each individual (1) at regular 30-min intervals for the calculation of displacement distances and (2) corresponding to the time-stamp of each sonar ping in tracks where sound pressure RL data was available. We estimated utilization distributions (UD) from CTCRW tracks following a data augmentation approach outlined by Johnson, London, and Kuhn (2011). This involved simulating 1,000 paths at regular 30-min intervals from the estimated posterior distribution of each CTCRW track model and then counting the simulated points that fell within each cell of a raster grid. Polygons were calculated such that 50% and 90% of simulated points fell within the defined contours, representing 50% and 90% UD. Displacement distances within tracks and distances of individuals from the edge and/or center of the AUTEC range were calculated as geodesic distances based on the WGS84 geoid model using the R package *geosphere* (Hijmans et al., 2016).

2.3 | Dive analyses

In addition to telemetry information, the transmissions of PTT tags to the Argos system included moderate- to coarse-resolution dive behavior information derived from either temperature (SPOT) or pressure and wet/dry (SPLASH) sensors. High-resolution environmental sensor measurements were summarized internally within SPOT and SPLASH tags into discrete messages that optimized transmission over bandwidth- and time-limited connections to the Argos satellite system. SPLASH tag dive behavior records were received in the form of durations and maximum depth reached (accuracy: ±1% of recorded depth) per dive that exceeded 15 m depth (dives <15 m were combined with surface time). The duration of each dive was measured by the SPLASH tag wet-dry sensors as the time interval between successive dry measurements. SPOT tags returned dive information in the form of histograms summarizing the proportion of time spent in 12 user-defined temperature bins (<4°C, 4–5.9°C, 6–7.9°C, 8–9.9°C, 10–11.9°C, 12–13.9°C, 14–15.9°C, 16–17.9°C, 18–19.9°C, 20–21.9°C, 22–23.9°C, and ≥24°C). These time-at-temperature (TAT) summaries provided a useful indirect proxy of time spent in different depth ranges, when interpreted in a context of local oceanography (Joyce, Durban, Fearnbach, Claridge, & Ballance, 2016). The median depths of the isotherms defining TAT bin boundaries (e.g., 4°C, 6°C, 8°C...24°C) were estimated within our Bahamas study area from hydrographic profile data assimilated from a variety of instruments, including ship-based conductivity temperature depth sensors, animal-borne sensors (e.g., SPLASH tags), and autonomous profiling floats (see Joyce et al., 2016).

To interpret TAT summaries, we drew on previous studies that documented *M. densirostris* dive behavior using high-resolution archival digital acoustic recording tags (DTAG). These DTAG records have shown a strong differentiation in *M. densirostris* diving between short shallow "bounce" dives and comparatively deep and prolonged foraging dives (Tyack et al., 2006). During shallow "bounce" dives (sensu Tyack et al., 2006), *M. densirostris* are typically silent. During deeper and longer dives echolocation clicks characteristic of prey search and buzz vocalizations indicative of prey capture attempts are frequently recorded (Arranz et al., 2011; Hickmott & Tyack, unpublished data; Tyack et al., 2006). We have termed the latter category "deep dives consistent with foraging" because these dives typically have a foraging function (Arranz et al., 2011; Tyack et al., 2006) except during periods of acute disturbance (e.g., DeRuiter et al., 2013; Miller et al., 2015; Tyack et al., 2011). We use the qualifier "consistent" because our depth measurements and TAT summaries did not allow us to directly infer foraging behavior associated with these dives. In the Bahamas and elsewhere, *M. densirostris* buzz vocalizations have been recorded up to depths typically no shallower than 400 m (Arranz et al., 2011; Hickmott & Tyac, unpublished data; Tyack et al., 2006), whereas the maximum depth of "bounce" dives rarely exceeds 250 m (Baird et al., 2006; Tyack et al., 2006). Thus, as an index of the proportion of time occupied by deep dives consistent with foraging during each six-hour TAT summary period, we calculated proportion of time *M. densirostris* individuals spent below the 18°C isotherm. This isotherm corresponds to an estimated depth of 342.3 m (range: 191.2–462.9 m) in the Bahamas based on previous analyses (see Joyce et al., 2016).

2.4 | Sonar data

M. densirostris individuals in this study were exposed to MFAS over the course of several multi-ship MFAS exercises (McCarthy et al., 2011) that were part of four SCCs (May 2009, May 2012, November 2013, and November 2015). These antisubmarine warfare training exercises involved up to four surface ships and accompanying helicopter dipped sonar units seeking a submarine target (Moretti et al., 2014). Each exercise was further subdivided into individual scenarios when sonars were actively transmitting.

We were able to access unclassified information on sound pressure RLs estimated from a propagation model during the May 2012 and November 2015 SCC exercises. The study area over which sound pressure RLs were modeled was centered on the AUTEC range and covered the majority of TOTO and surrounding areas of the Great Bahamas Bank between 23.8°N and 25.3°N. During the May 2009 and November 2013 SCC exercises we were only able to access the start and end times of the MFAS exercise periods. It is also important to note that due to the opportunistic observational nature of this study, the AUTEC range was not exclusively quiet during the preexposure and

postexposure periods before and after SCC MFAS exercises. We had access to a list of dates on which sonar activity occurred on the range. During the run-up to and following SCC MFAS exercises in different years there were a mix of days with and without sonar activity. However this "routine" sonar activity differed substantially in the degree of exposure from the more intense exposure during SCC MFAS exercises when beaked whales were exposed to frequent repeated use of the most powerful form of MFAS source (e.g., 53C surface ships).

Estimated RLs, when available (i.e., 2012 and 2015), were modeled from standard source characteristics (e.g., location, depth, power output levels and beam patterns) of surface ship and helicopter deployed MFAS sources using the US Navy's Comprehensive Acoustic Simulation System Gaussian Ray Bundle (CASS/GRAB) propagation model (Weinberg & Keenan, 1996). Outputs from CASS/GRAB models were not validated in this study, however this validation has been undertaken for other naval ranges (DiMarzio, Jones, Moretti, Thomas, & Oedekoven, 2018) and comparable propagation model outputs have been applied in similar studies of beaked whale sonar exposure (e.g., McCarthy et al., 2011; Moretti et al., 2014). Root mean squared sound pressure RL were estimated for representative pings by the CASS/GRAB model over an approximately 1 km by 1 km (0.00992° longitude by 0.00903° latitude) resolution spatial grid and predictions corresponded to depths of 5 m and 100 m. Note that these representative pings were down sampled from the actual (classified) rate of ping transmission and represented approximately one in every two pings transmitted by the sonar sources. However, given the relatively coarse temporal resolution of satellite transmitting tag telemetry information this slight imprecision of ping timing likely had a negligible effect. Best estimates of RL exposure along *M. densirostris* tracks were sampled from the 5 m depth raster layer using maximum likelihood location predictions from CTCRW models corresponding to the time-stamp of each modeled ping. Variation in RL estimates resulting from the uncertainty in animal locations in the *x*- and *y*-dimensions was represented by sampling the 5 m depth raster layers using $n = 100$ simulated coordinates drawn from the CTCRW model posterior distributions at the time-stamp of each modeled ping. Note, that due to inconsistent availability of dive information within individual tag records and across individuals, we have not attempted to directly account for the complex nonlinear variation in sound pressure RLs in the *z*-dimension. *M. densirostris* are noted deep divers and thus during the considerable proportion of time spent away from the surface, near surface RL estimates at predicted animal locations provided a spatial index of relative exposure levels. The maximum cell value in each 5 m depth raster layer was used as an indication of sound pressure near the sonar source (e.g., surface ship or dipping helicopter) associated with each modeled ping.

3 | RESULTS

3.1 | Sampling

This study drew on Argos tag records from *M. densirostris* individuals ($n = 7$) that were exposed during the MFAS exercise phases of four different SCC exercises. The sample of individuals exposed to MFAS in this study skewed heavily towards adult females (five of seven), with a single adult male and single subadult of unknown sex (Table 1). This sample also included a tag record (Ptt: 93232) that was previously documented in Tyack et al. (2011). Of these seven tags, two individuals carried SPLASH (Mk10) model transmitters that relayed summarized records of dive depths. The remaining five tags were SPOT (AM-S240A-C) model transmitters and three of these tags recorded a proxy record of dive activity in the form of TAT histograms. On average the SPLASH transmitters operated for shorter durations (mean: 23 days, range: 18–28 days) than SPOT tags (mean: 47 days, range: 27–89 days). Of the seven tags that overlapped multiship MFAS phases of SCC exercises in time, three individuals (Ptt: 111670, 129715, and 129720) were exposed while initially located within or in close proximity (<2 km) to the AUTEC hydrophone array (Figure 1). Among the remaining four individuals that overlapped these periods of intensive MFAS use, two individuals were initially located northwest (NW) of the AUTEC range at CTCRW predicted distances of 10 km (Ptt: 93232) and 29 km (Ptt: 129721), while two other individuals were located south (S) and southeast (SE) of the range at predicted distances of 27 km (Ptt: 111664) and 73 km (Ptt: 129719), respectively.

TABLE 1 Satellite tag deployments on Blainville's beaked whales (*Mesoplodon densirostris*) that overlapped the mid-frequency active sonar (MFAS) phases of Submarine Commanders Courses (SCC) on the AUTEC range between 2009 and 2015. Tags are categorized by Argos transmitter type (SPOT and SPLASH), sex, and age class. The sexes and age classes of tagged individuals were assessed based on sexually dimorphic characteristics and in some cases using genetic information from skin biopsy material. Also noted are the overall duration of tag transmission, as well as the length of preexposure, MFAS exercise, and postexposure periods, and the month and year of the MFAS exercise.

Ptt	Tag type	Sex	Age class	Total duration (d)	Pre-MFAS (d)	MFAS (d)	Post-MFAS (d)	Exercise date
93232	SPOT	Adult	Male	26	6.3	3.4	16.5	May 2009
111664	SPLASH	Adult	Female	17	7.9	3.7	5.1	May 2012
111670	SPLASH	Adult	Female	27	7.6	3.7	15.5	May 2012
129715	SPOT	Adult	Female	27	14.5	2.9	9.2	Nov 2013
129719	SPOT	Subadult	Unknown	62	13.9	2.2	45.7	Nov 2015
129720	SPOT	Adult	Female	26	13.8	2.2	9.9	Nov 2015
129721	SPOT	Adult	Female	88	13.9	2.2	72.2	Nov 2015

3.2 | Displacement patterns

All three *M. densirostris* individuals (Ptt: 111670, 129715, and 129720) that were located within close proximity to the AUTEC hydrophone array at the start of MFAS operations moved away in a north-northwest (NNW) direction to CTCRW predicted maximum distances of 27, 31, and 43 km from edge of the range (54, 58, and 69 km from center of the range; Figure 2). Two additional individuals (Ptt: 93232 and 129721) that were initially estimated to be located 10 and 29 km NW of AUTEC at the onset of MFAS operations also moved away from AUTEC in a NNW direction, showing a movement pattern similar to that of individuals exposed within the range (Figure 1). In contrast, a single individual (Ptt 111664) situated 27 km S of AUTEC at the onset of sonar operations moved initially to the south, away from the range but then turned northwards towards the range and only diverted away to the SE after entering the southwest corner of the AUTEC range (Figure 1). An individual (Ptt 129719) that was initially located 73 km SE of AUTEC at the onset of the November 2015 exercise (not shown in Figure 1) also moved towards the range. Because of the considerable distance separating this individual from the range, its movements during this exercise fell outside the domain of RL modeling in this study. We also did not include this individual in further analyses of dive response because the bathymetric configuration of TOTO likely blocked a substantial, though currently unknown, proportion of the sound from AUTEC at Ptt 129719's locations during the exercise. Of the five individuals that were located within close proximity to the NW of AUTEC at the onset of MFAS operations, the average maximum displacement from the initial exposure location during the exercise was 44 km (range: 28–68 km; Figure 2). Following the cessation of the MFAS phases of SCC exercises, the three individuals (Ptt 111670, 129715, 129720) that were initially located in close proximity (<2 km) to the AUTEC hydrophone array, returned to the AUTEC range within 1.7, 3.9, and 1.8 days respectively.

The displacements undertaken by over half of the sampled individuals (*n* = 4) during the MFAS periods took these individuals outside of habitats that they had occupied during the tag recording periods prior to sonar exposure (see Figure 1 and Table 1). During the MFAS operations two individuals (Ptt 93232, 129721) were displaced almost entirely outside the 50% UD contour occupied prior to the exercise, showing 1.7% and 0% overlap between exposure and preexposure 50% UD polygons. In addition, Ptt 129720 was also displaced a further approximately 20 km NNW of the preexposure 50% UD polygon. Because of limited number of Argos fixes returned by Ptt 129715 during MFAS operations, the UD of this individual was too diffuse to compare preexposure and exposure UD. However, the maximum likelihood track of this individual (Figure 1) shows that this individual was also displaced outside of the
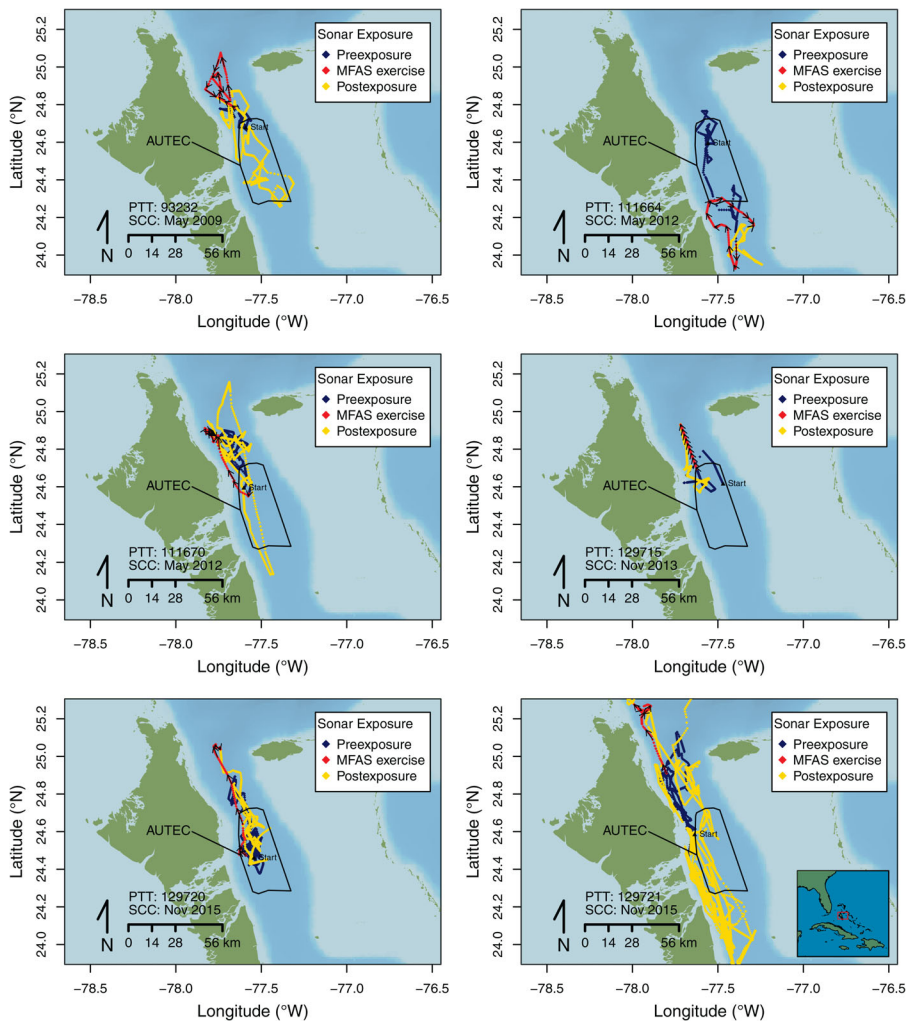
FIGURE 1 Maps of *Mesoplodon densirostris* tracks during preexposure (blue), mid-frequency active sonar (MFAS) exercises (red), and postexposure (yellow) phases of Submarine Commanders Courses (SCC) on the Atlantic Undersea Test and Evaluation Center (AUTEC) range (shown as a black polygon). Individual points represent maximum likelihood estimates of animal location at 30-min intervals from continuous time correlated random walk models, while black triangles show the initial tagging location and black arrows indicate direction of movement during MFAS exposure periods.

area occupied prior to sonar exposure. The 50% UD contour of Ptt 111670 during MFAS exposure only overlapped the preexposure 50% UD by 1.5%; however, this area was immediately adjacent to habitat occupied before the SCC exercise.

Ptt 111670 experienced a decline in maximum RLs at the CTCRW predicted tag locations from 169 dB re 1 μPa (*SD* 2.6 dB; units hereafter denoted as dB) to ~70 dB (*SD* 3.9 dB; approximately ambient RL) over course of the May 2012 exercise, while Ptt 129720 declined from 172 dB (*SD* 24.3 dB) to 145 dB (*SD* 0.88 dB) during November 2015 sonar operations (Figures 3a and 4a). Similarly, the maximum RL experienced by Ptt 129721, initially located an estimated 29 km NW of AUTEC, declined from 150 dB (SD 1.1 dB) to 133 dB (*SD* 0.9 dB) dB after a displacement of 45 km (Figure 4b). The increasing divergence between the maximum RL near source locations (yellow points in Figures 3a, 4a,b) and the maximum RL at the predicted locations of Ptt 111670, 129720, and 129721 (red diamonds in
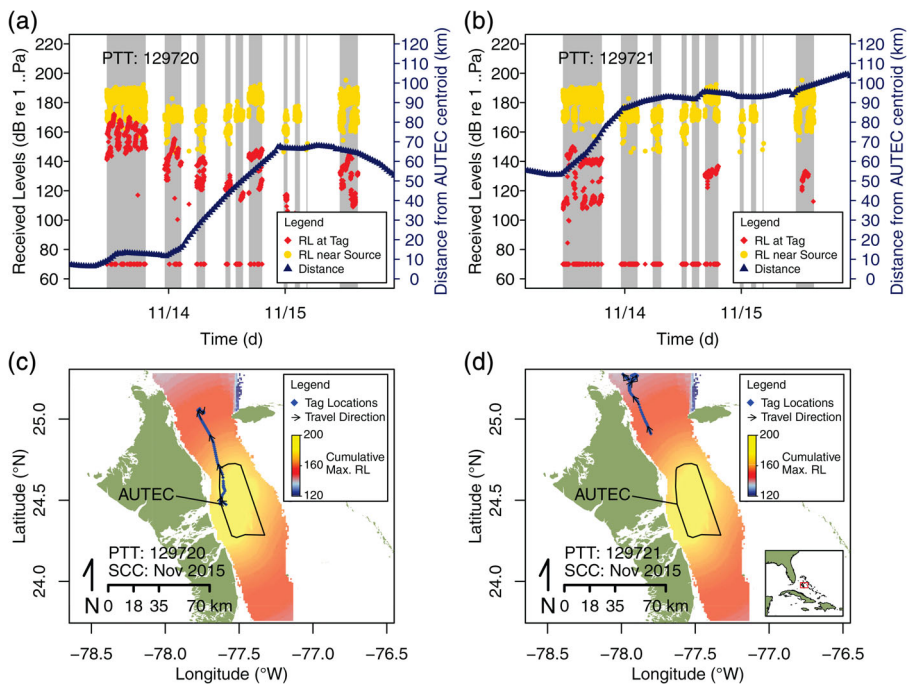
FIGURE 2 Time series of distances between tagged individuals (Ptt: 93232, 111664, 111670, 129715, 129720, 129721) and the center of the Atlantic Undersea Test and Evaluation Center (AUTEC) range before (blue), during (red), and after (yellow) mid-frequency active sonar (MFAS) exposure during Submarine Commanders Courses (SCC). Each time series has been realigned such that the start of the MFAS phase within each SCC aligns with a date-time stamp of 0 on the x-axis.
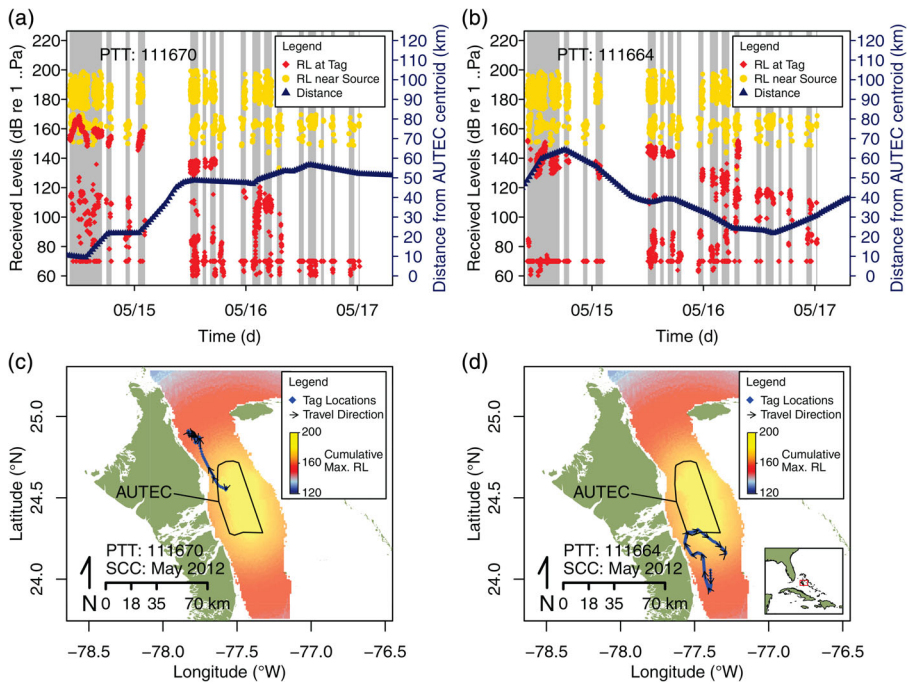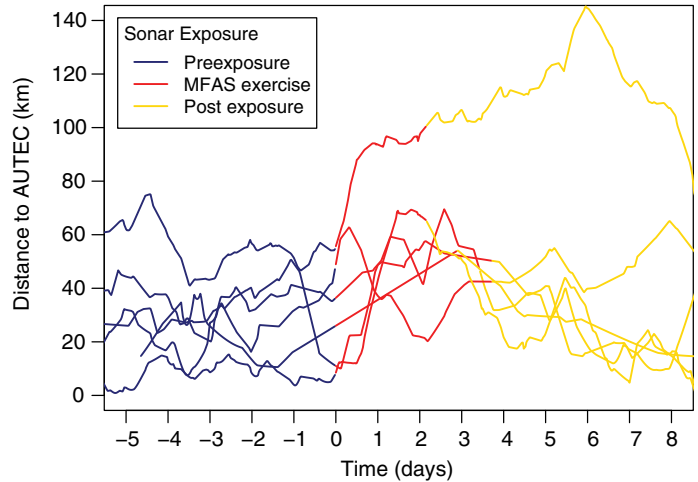
FIGURE 3 Time series (a and b) of modeled sound pressure received levels (RL) (1) at estimated tag locations (red diamonds), and (2) in the pixel nearest to the sonar source (yellow circles), as well as (3) distances between each individual whale and the center of the Atlantic Test and Evaluation Center (AUTEC) range (blue triangles) over the course of the May 2012 Submarine Commanders Course mid-frequency active sonar (MFAS) phase. Below are maps (c and d) showing the individual movements relative to the maximum RL within each grid cell over course of the MFAS exercise. Gray rectangles in the background of panels a and b denote scenarios, or periods of active sonar ping transmissions.

Figures 3a, 4a,b) was driven primarily by the increasing distance (blue triangles in Figures 3a and 4a,b) as these individuals moved away from sonar source locations as shown in Figures 3c, 4c,d. Changes in MFAS transmission intensity over the course of the 2012 MFAS exercise, particularly the cessation of 53C surface ship activity (i.e., the upper band of yellow points in Figure 3a,b) during the last six scenarios, also contributed to observed decline in RL at Ptt 111670

FIGURE 4 Time series (*a* and *b*) of modeled sound pressure received levels (RL) (1) at estimated tag locations (red diamonds), and (2) in the pixel nearest to sonar source (yellow circles), as well as 3) distances between each individual whale and the center of the Atlantic Undersea Test and Evaluation Center (AUTEC) range (blue triangles) over the course of the November 2015 Submarine Commanders Course mid-frequency active sonar (MFAS) phase. Below are maps (*c* and *d*) showing the individual movements relative to the maximum RL within each grid cell over course of the MFAS exercise. Gray rectangles in the background of panels *a* and *b* denote scenarios, or periods of active sonar ping transmissions.

locations. In contrast, Ptt 111664 experienced relatively consistent maximum sound pressure RL over the course of the May 2012 MFAS exercise (Figure 3), with an initial RL value of 152 dB (*SD* 34.5 dB) and an RL value at the end of sonar operations of 118 dB (*SD* 9.3 dB; Figure 3). This moderate decline was largely driven by the underlying sonar output levels (see above), as well as changes in the orientation of directional sonar sources (e.g., 53C surface ships), rather than the displacement of Ptt 111664, which actually moved closer to the sonar sources over much of this exercise.

3.3 | Dive patterns

The records of dive depth and dive duration returned by the two SPLASH tagged individuals (Ptt 111664 and 111670) contained substantial gaps in coverage. However, within the limited dive depth records returned by Ptt 111670, a secondary peak of dive activity in the 1,200–1,800 m depth range was detected within both the pre- and postexposure periods. During the MFAS exercise and the displacement of Ptt 111670 shown in Figure 1, dives to this deeper peak in excess of 1,200 m were not recorded (Figure 5). During the preexposure, postexposure, and MFAS phases of the Ptt 111664 dive record, we detected deep dives consistent with foraging primarily in the 700–1,200 m depth range and no clear differences in the vertical distribution of these presumed foraging dives were observed during MFAS operations (Figure 5). The TAT data from SPOT tags provided a less direct and less precise indication of absolute depths corresponding to these deep dives consistent with foraging, particularly for dive activity extending below the 6°C isotherm (approximately 1,030 m, range: 883–1,193 m) where the slope of
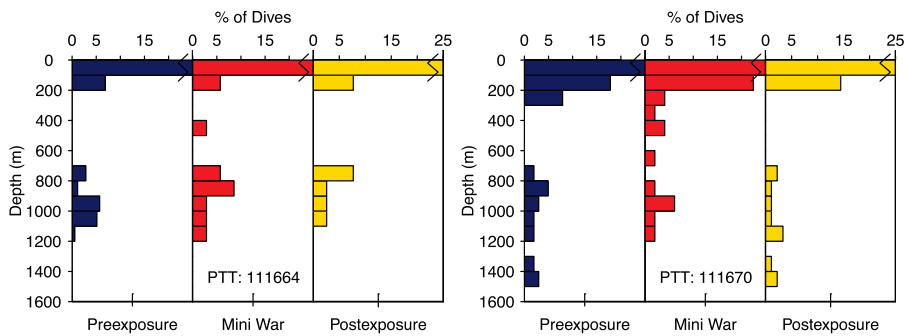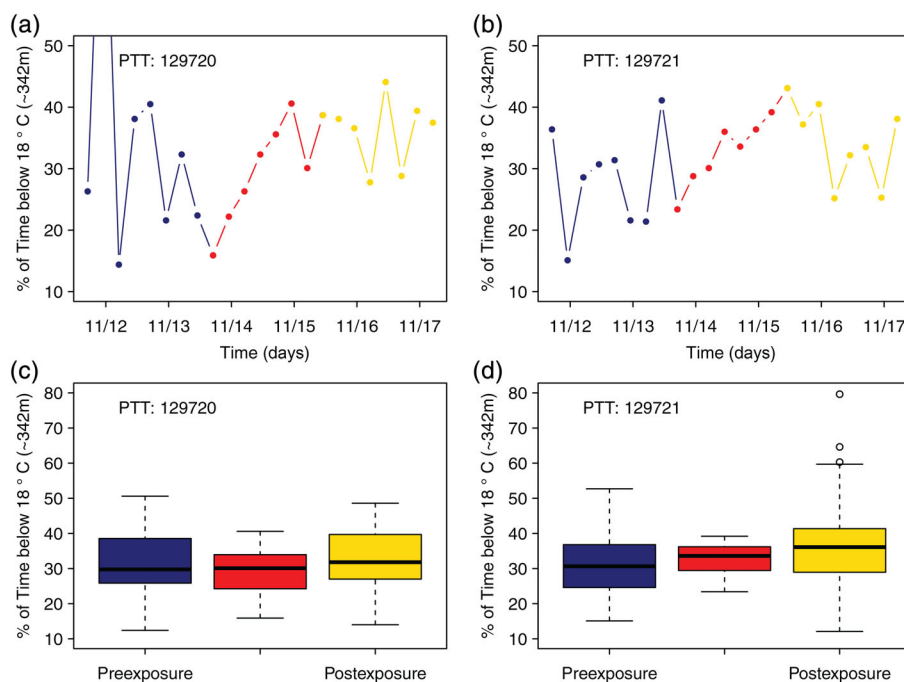
FIGURE 5 Histograms showing the maximum depths of dives recorded by two Blainville's beaked whales with SPLASH tags during preexposure (blue), MFAS operations (red), and postexposure (yellow) phases of the May 2012 Submarine Commanders Course.

temperature change with depth decreased markedly, resulting in much greater variation in isotherm depth between different hydrographic profiles (Joyce et al., 2016). With these important caveats in mind, the TAT data did not show a major shift in the depth distribution of deep dives consistent with foraging of Ptt 129720 or Ptt 129721 during the MFAS phase of the November 2015 SCC, relative to the variability exhibited in pre- and post-exposure periods.

When viewed in aggregate, TAT histograms returned by two SPOT tagged *M. densirostris* individuals (Ptt: 129720, 129721), show relatively consistent medians of 30.4% (median absolute deviance: 6.3) of time spent below the 18°C isotherm (i.e., on deep dives consistent with foraging) during the preexposure periods, compared with 31.2% (3.5) during the MFAS periods and 35.9% (6.6) during the postexposure periods (Figure 6a,b). However, examining this metric as a time series (Figure 6c,d), revealed that both Ptt 129720 and Ptt 129721 exhibited initial declines in the proportion of time allocated to dives consistent with foraging, spending 15.9% and 23.4% of time below the 18°C isotherm during the first 6-hr TAT summary of the November 2015 MFAS period, respectively. These initial declines were followed by nearly linearly increases in the proportion of time both Ptt 129720 and Ptt 129721 spent below the 18°C isotherm, as these individuals moved away from sonar sources during this exercise (Figure 1). By the end of the MFAS period, these proportions rose to 30.1% and 39.2%, respectively. Although, both individuals showed apparent increases, the range of variability during the MFAS phase fell within the overall range of variability seen during the pre- and postexposure periods (Figure 6). During the 5-day period after MFAS operations, the median proportions of time Ptt 129720 and Ptt 129721 spent below the 18°C isotherm were higher (30.2% and 36.8%, respectively) than during the 5-day period preceding the exercise (28.6% and 30.7%, respectively). Although our sample size for examining these behavior patterns was limited (*n* = 2), Ptt 129720 and Ptt 129721 were initially separated by 53 km at the start of the exercise, suggesting that the dive pattern changes were likely independent of one another.

4 | DISCUSSION

In this study we present opportunistically collected observational data on *M. densirostris* individual behavioral responses to frequent, repeated, and intense MFAS exposure during SCC naval exercises. Overall, we found clear and sustained displacement away from core areas of MFAS exposure in a substantial majority of tracked individuals. We also documented transient changes in dive depths and the proportion of time allocated to deep diving that were consistent with a response to sonar, however, the strength of evidence relating to these changes in dive behavior was less pronounced. These case studies represent "measurable behavioral responses" that can help inform ongoing

FIGURE 6 Time series (*a* and *b*) and boxplots (*c* and *d*) showing percentages of time spent below the 18°C isotherm by two Blainville's beaked whales with SPOT tags during preexposure (blue), mid-frequency active sonar (MFAS) operations (red), and postexposure (yellow) phases of the November 2015 Submarine Commanders Course (SCC). Time spent below this isotherm, which corresponds to a median estimated depth of 342.3 m (range: 191.2–462.9 m) in the Bahamas (see Joyce et al., 2016), was an indicator of the proportion of time spent on foraging dives. Note that the boxplot panels (*c* and *d*) summarize substantially longer preexposure and postexposure periods, than are shown in the zoomed period during MFAS operations in the time series panels (*a* and *b*).

efforts to model PCoD among beaked whales in the Bahamas and contribute to a coalescing global understanding of sonar impacts on marine mammals.

4.1 | Displacement response

The relatively small number of individuals tracked during SCC exercises in this study, as well as the unique geography and exposure history of *M. densirostris* on the AUTEC range, places important constraints on how much the results of this study may be generalized to overall population responses of *M. densirostris* to intense MFAS exposure. However, even the modest sample sizes of this effort add substantially to the number of beaked whales, in particular *M. densirostris*, that have been tracked under conditions of simulated or live sonar operations. The limited sample sizes in this study and in other efforts (e.g., DeRuiter et al., 2013; Falcone et al., 2017; Stimpert et al., 2015; Tyack et al., 2011) reflect the many challenges involved in deploying satellite-transmitting or archival tags on free-ranging beaked whales. These challenges include inconspicuous surfacing behavior and difficulties in approaching these animals during brief surface intervals between frequent and prolonged dives.

With these important caveats in mind, five of seven tagged *M. densirostris* individuals in this study showed clear and sustained displacements away from areas of intense naval sonar activity over the course of four separate MFAS exposure events. Displacements observed in two of these individuals began at initial distances of 10 and 29 km from the AUTEC range, suggesting that the area of disturbance related to MFAS multiship exercises may extend beyond the bounds of the AUTEC hydrophone array, where previous passive acoustic studies have documented behavioral

responses (e.g., McCarthy et al., 2011; Moretti et al., 2010; Tyack et al., 2011). These observed displacements also support the hypothesis of Moretti et al. (2014) that the cessation of group vocal periods in the central area of the AUTEC range during acoustically monitored SCC exercises (McCarthy et al., 2011; Moretti et al., 2010; Tyack et al., 2011) represents the movement of *M. densirostris* individuals away from the most intense areas of sonar exposure rather than the local silencing of groups and individuals. The displacements observed in five of the seven tagged individuals in this study were also consistent with the displacement responses seen over shorter durations in *M. densirostris* and *Z. cavirostris* instrumented with DTAGs and exposed to experimental sonar sources (DeRuiter et al., 2013; Tyack et al., 2011), as well as Argos tagged *Z. cavirostris* exposed to tactical MFAS (Falcone et al., 2017). Moreover, displacement is a general response seen in other odontocete species exposed to different types of intense noise (e.g., vessel engines; Aguilar de Soto et al., 2006; Pirotta et al., 2012), as well as in baleen whales (e.g., Goldbogen et al., 2013) and in terrestrial animals (e.g., Bayne, Habib, & Boutin, 2008; Francis, Ortega, & Cruz, 2009; Schaub, Ostwald, & Siemers, 2008).

Because of the observational nature of this study and the sample size limitations noted above, this study faced important constraints establishing a causative link between the documented displacement behaviors and MFAS exposure. Alternative hypotheses include random movements coincidental with naval exercises, or responses to other stimuli associated with naval exercises such as increased ship traffic associated with SCC operations. However, movements of Ptt 111670, 129720, and 129721 down RL gradients, were strongly suggestive of direct behavioral response to initial MFAS exposures between 150 dB and 172 dB. These initial exposure levels were greater than or equal to the 150 dB exposure level associated with a 50% chance of disturbance in the risk model of Moretti et al. (2014). We currently lack spatially explicit RL information from two of the four SCC exercises necessary to explicitly evaluate how two other individuals (Ptt 93232, 129715) moved with respect to sound pressure RL. However, based on both the similarity of naval operations during SCC exercises and the similarity of movement trajectories exhibited by Ptt 93232 and Ptt 129715, we can make an informed hypothesis that these individuals likely also experienced declines in RL as a result of their movements away from the AUTEC range.

The NNW direction of movement away from the AUTEC range exhibited by five of the individuals in this study was also consistent with previously documented displacement directions of *M. densirostris* vocal groups away from the central and eastern portion of the hydrophone array to the peripheral NW and SW corners (McCarthy et al., 2011; Tyack et al., 2011). The direction of displacement to the NNW was not wholly surprising given the confined underwater topography of the AUTEC region, which limits the possible routes of egress for *M. densirostris* individuals located in the northern half of AUTEC at the onset of an SCC event only to movements within an arc from the NW to the NE. However, it is also ecologically intriguing that these individuals generally displaced along the western shelf-slope of TOTO as opposed to the eastern side. The western area has been shown based on passive acoustic monitoring to experience heavier use by *M. densirostris* (Hazen et al., 2011) and is also consistent with an observation from Joyce et al. (2017) that *M. densirostris* typically spend a greater proportion of their time in habitats where the benthopelagic zone can be reached within the typical dive depth capacity of *M. densirostris* presumed foraging dives. This study shows that the distances some tagged individuals were displaced extended up to 43 km beyond the geographic boundaries of the AUTEC hydrophone array. This information will help better inform the direct costs associated with sonar-related displacements that can feed into energetic models of disturbance (e.g., New et al., 2013) and future PCAD/PCoD modeling efforts.

Intriguingly, one individual monitored during the May 2012 SCC exercise (Ptt 111664) did not displace away from sonar sources during the majority of the MFAS phase of this exercise. This individual, an adult female seen consistently at AUTEC in 5 years over the period 2007–2017 (DEC, unpublished data), was exposed to relatively consistent RL at or just below the 150 dB level at which Moretti et al. (2014) predicted a 50% chance disturbance, but was substantially above the 138 dB level at which Tyack et al. (2011) detected the interruption of foraging dive activity. Overall this suggests interindividual variability in responsiveness to sonar exposure, consistent with a portion of vocal groups remaining at the periphery of the AUTEC range during acoustically monitored naval exercises (Moretti et al., 2014). This also points to the potentially important role of exposure context and habituation in modulating

behavioral responses to naval sonar (Harris et al., 2018). Adult *M. densirostris* individuals, particularly adult females, in the Bahamas have been shown to display minimal natural dispersal (Claridge, 2013). Thus, each adult individual in the AUTEC area has likely experienced multiple major multivessel naval sonar exercises (typically held biannually) over the course of their lifetime, as well as frequent exposure to less intense sound sources such as helicopter dipped sonar systems. Behaviors seen in this habituated population may thus be atypical of behavioral responses of *M. densirostris* populations with less exposure history. McCarthy et al. (2011) and Tyack et al. (2011) showed at a population level that group vocal periods returned to the center of hydrophone array within 72 hr following the cessation of sonar exposure. This study found that individuals (*n* = 3) displaced from their initial locations on or close to the range did not return directly, taking between 1.7–3.9 days to return to the range.

4.2 | Dive response

The dive depths returned by the two SPLASH tagged individuals (Ptt 111664 and 111670) provided limited windows into the dive behaviors of *M. densirostris* during MFAS exposure because of substantial gaps in each time series. These gaps resulted primarily from (1) the brief and infrequent surfacing behavior of *M. densirostris*, (2) limited Argos satellite coverage within tropical latitudes, and (3) transmission bandwidth constraints. However, in the data that were received from Ptt 111670, we did not observe dives in the 1,200–1,800 m depth range during the MFAS exercise. During both pre- and postexposure periods, a secondary peak of deep dive activity consistent with foraging was observed within this depth range. This deep peak of dive activity has also been observed in the bimodal distribution of buzz vocalizations in ongoing DTAG sampling at AUTEC (Hickmott & Tyack, unpublished data). One possible explanation for this change might be a shift in the benthic depth of habitats to which Ptt 111670 was displaced, which could limit the range of possible foraging depths. However, during the NNW displacement of Ptt 111670 shown in Figure 1, this individual traversed habitats with an estimated median depth of 1,427 m, compared with median depths of 1,868 m and 1,638 m during pre- and postexposure periods. Consequently, exclusion from sufficiently deep habitats to continue diving to this deeper peak does not appear to be a sufficient explanation for the observed decrease in the median depth of presumed foraging dives. Because of the limited sample size, we cannot exclude the possibility that this difference in dive depths resulted from behavioral variation in response to prey distribution, or gaps in our data. Ongoing DTAG investigations (e.g., Hickmott & Tyack, unpublished data) may help inform whether these bimodal peaks represent switching between benthopelagic foraging dives and mesopelagic midwater foraging dives, as observed by Arranz et al. (2011). The deployment of multifrequency bioacoustic instruments on automated underwater vehicles (AUV) will also enable the measurement of prey density and composition within the lower mesopelagic and bathypelagic depths at which *M. densirostris* forages (Benoit-Bird et al., 2016; Dunlop et al., 2018; Southall, Benoit-Bird, Moline, & Moretti, 2019). These AUV bioacoustic surveys will hopefully illuminate whether important differences in prey availability or catchability exist between the AUTEC range and areas to which *M. densirostris* are displaced, as posited by Moretti et al. (2014).

An additional key finding of this study was that *M. densirostris* continued undertaking dive cycles consistent with foraging during MFAS exposure. However, there was internal variation in the proportion of time spent on deep dives consistent with foraging (i.e., <18°C) over the MFAS phase of the SCC exercises, that was suggestive of suppression of deep dive activity during the initial displacement response following the onset of MFAS exposure. This behavior pattern may correspond with the responses to experimentally simulated MFAS (at an RL of 138 dB) and pseudorandom noise seen in *M. densirostris* individuals instrumented with DTAGs (Tyack et al., 2011). After experimental sound exposure early in a foraging dive, these individuals ceased echolocation clicks and undertook prolonged slow ascents away from sound sources (Tyack et al., 2011). In the longer time series available through our tag TAT records, these initial drops were followed by nearly linear increases in time spent on deep dives over the course of extended displacements away from sonar sources. The reduced time allocated to deep dives consistent with foraging following initial sonar exposure may have also led to compensatory elevation of foraging dive activity during the postexposure period. Supporting this potential compensatory increase, the median proportion of time spent on deep dives

consistent with foraging was higher in the 5 days immediately following sonar exposure, relative to the preexposure periods in both Ptt 129720 and Ptt 129721. Determining whether these patterns within SCC exercises occurred by random chance or were more broadly typical of responses to sonar, was again limited by our small sample of individuals that successfully returned TAT histograms during MFA exercises (*n* = 2). We further lacked the continuity of dive records in our SPLASH tagged individuals or the resolution of individual dives in our TAT data to distinguish whether the initial response observed by Tyack et al. (2011), continued through the suppression of foraging dives early in the exposure period or simply through their increased spacing.

These findings have important implications for PCoD/PCAD assessments of disturbance. The disturbance response observed in archivally tagged *M. densirostris* (e.g., Tyack et al., 2011), along with reduction in the number of vocal groups on the AUTEC hydrophone array during major naval exercises (McCarthy et al., 2011; Moretti et al., 2010; Tyack et al., 2011), has led to a suggestion that foraging dives may be "lost" in response to MFAS exposure. This loss will be parameterized in PCoD/PCAD as a decrease in energy intake, with potential downstream effects on vital parameters (Moretti et al., 2014). Our results support this initial loss of presumed foraging time, but also suggest that *M. densirostris* individuals may have the ability to partially compensate by increasing the proportion of time spent at foraging depths following displacement. However, the foraging dive strategy of *M. densirostris*, which is hypothesized to partially rely on anaerobic respiration, may necessitate extended recovery periods between successive foraging dives. These recovery periods may constrain the ability of *M. densirostris* individuals to fully compensate for lost foraging time (Joyce et al., 2017; Tyack et al., 2006).

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