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Leatherback sea turtles (*Dermochelys coriacea*) react to impulsive sounds

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Many marine ecosystems, including in the Northwest Atlantic, are expected to experience a sudden and sustained increase in underwater noise due to ocean development. To investigate the response of sea turtles to impulsive sounds, specifically those generated from seismic surveys, we equipped leatherback sea turtles at a seasonal foraging ground in coastal Massachusetts with data loggers to record video footage, sound, depth, and location. We then exposed the tagged turtles to a controlled short burst (0.25 ms), broad frequency (~ 300—1200 Hz), high intensity (sound source level of 221 dB re 1μPa) impulsive sound produced by a seismic sparker towed from a vessel. We collected a mean (± SD) of 109.4 ± 35.3 min of footage from 13 leatherbacks across four days in 2023, with the sparker exposure lasting 52.2 ± 11.6 min per turtle. Underwater peak sound pressure level of frequencies within the hearing range of leatherbacks (100—1200 Hz) were between ~ 128.5—176.2 dB during the tag deployments. We assessed the effects of peak sound pressure level on turtle behavior metrics and found that there was a significant effect on tortuosity, dive duration, and probability of foraging from the sound intensity coinciding with the emitted impulsive sound, while swim speed was more correlated with proximity to the sparker vessel regardless of sound intensity level. Probability of foraging declined by ~ 64% during the exposure period. These behavioral shifts along with their potential to decrease individual fitness, should be considered when evaluating the environmental impacts of intense acoustic stimuli on sea turtles.

Keywords Foraging, Dive duration, Tortuosity, Sound pressure level, Seismic sparker, Anthrophony

Sound travels through water approximately four times faster than through air[1], and ocean turbidity and effects of current can impair vision and chemical senses. This makes sound detection an important sensory capability for aquatic species ranging from simpler organisms like cnidarians through more complex animals such as whales and dolphins. Many animals intentionally produce sounds ranging between 10—20,000 Hz to communicate, navigate, or forage[2]. Sounds produced through natural biological and geological processes can be masked or altered by human-generated sounds, or anthrophony[2]. Ecological research on soundscapes and anthrophony has lagged considerably relative to other sensory studies despite its pervasiveness and potential deleterious effects for many organisms. For example, over the past 50 years, the increase in shipping has contributed to an approximately 32-fold rise in low frequency noise within shipping lanes, ports, and surrounding waters[2]. Furthermore, since the development of sonar in the 1920s, seismic surveys, which introduce impulsive sounds of short, high-intensity bursts to many marine environments[3], have become increasingly common and are necessary for the construction of offshore energy structures, such as oil and gas platforms and wind turbines[4].

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Increases in anthrophony can cause hearing loss, altered behavior, masking of acoustic communications, and strandings of marine animals[2].

The development, operation, and decommissioning of wind farms in the Northwest Atlantic Ocean is expected to introduce a range of new sounds that can be disruptive to marine life, including both low frequency and impulsive sounds[5]. Impulsive sounds are characterized as a rapid increase in sound pressure over a very short time across a broad frequency range, creating a much sharper and intense acoustic profile[6]. Research has identified that impulsive sounds can be more damaging to an animal's ability to hear than continuous noise[7]. During wind turbine pre-construction and maintenance inspection, geophysical seismic surveys are required to map the benthic and sub-benthic geology using impulsive sounds capable of deep seafloor penetration[8]. Acoustic arrays commonly used for seismic surveys are one of the loudest anthropogenic sound sources, typically employing 18 – 48 air guns that produce impulsive sounds ranging from below 100 Hz to 20,000 Hz[9] at an intensity of ~ 260 dB re 1 μPa, with little loss of intensity through depths reaching 7—11 km[10,11]. Turbine installation requires drilling and pile-driving, and the corresponding hammer strikes for setting a monopile into the sediment also creates impulsive sounds. Each monopile requires approximately 500 to 5,000 hammer strikes ranging from 15 to 60 impulsive strikes per minute[12], creating peak sound pressure levels (SPL) of 205 dB re 1 μPa within 100 m of the strike and a detectable range above background noise of nearly 70 km[13].

Sea turtle responses to acute stimuli, particularly while in water, have not been well researched[14]. Only a few studies have investigated the scope of sea turtle hearing while underwater[6,15–17] and even fewer have verified that hearing capabilities in sea turtles may remain consistent for some species between hatchling and juvenile age classes[18]. In tank experiments, sea turtles tend to exhibit negative reactions when exposed to low-frequency sounds within their hearing range (~ 50—1,600 Hz)[16,18–22]. For example, Lendhart[19] identified a noticeable shift in loggerhead behavior towards remaining at or near the surface of the water when exposed to sounds below 80 Hz. Lendhart et al.[20] continued this study by exposing loggerhead and Kemp's ridley turtles to 430 Hz sounds and noticed a more profound reaction, with turtles exhibiting a 'ballistic head contraction' and 'rapid flipper activation'. Tank experiments by Samuel et al.[21] identified a similar response from sea turtles to US Naval sonar of similar low frequency ranges. However, sounds generated for studies within tanks are likely to be distorted due to reverberation and resonance[23], and turtle responses may not mimic behavior in the wild. Samuel et al.[21] measured the in-water ambient noise within a small estuary system that has a seasonal presence of sea turtles and found a considerable amount of low frequency sound in the environment associated with increased anthropogenic activities. Habituation from constant exposure to ambient sounds within their peak hearing range, however, may potentially diminish turtle behavioral responses to these stimuli over time, and, in some cases, increase the risk of dangerous interactions for the turtle. For example, diamondback terrapins exhibit a similar hearing range to sea turtles, but in a high traffic lagoon, they did not seem to respond to boat noises below 140 dB re 1 μPa and between 400 – 600 Hz leaving them vulnerable to boat strikes[24].

Leatherback sea turtles are listed as endangered throughout their range by the US Endangered Species Act (ESA)[25]. They are a highly migratory species traveling thousands of kilometers each year, and in the Western Atlantic, leatherbacks will routinely swim from Caribbean and South American nesting beaches to Canadian and northern US foraging grounds and back[26–28]. These turtles experience an extreme range of habitats with some individuals seasonally residing on the continental shelf overlapping with areas designated for marine industrial development in the Northwest Atlantic[27,28], while others move through the open ocean diving to depths of up to 1,200 meters[29]. Although these large animals can perform extreme dives and migrations, their diet is limited to gelatinous zooplankton[30]. As a result, small changes to the ecosystem that are disruptive to jellyfish production, distribution, or the leatherbacks' ability to forage on them can have population-scale consequences[31]. For example, due to the high volume of food required for leatherbacks to maintain their large size, reduction in their foraging success could reduce their ability to migrate and reproduce. This has been suggested as a contributing factor hindering the recovery of the Eastern Pacific leatherback compared to the Western Atlantic population[32,33]. Well known anthropogenic threats to leatherbacks include fisheries impacts, vessel strikes, and nesting beach disturbances[34]; however, little research has been conducted on the non-lethal disruptions to leatherback behavior from stochastic, short-term disturbances, including from acoustic stimuli. To investigate this in situ, we exposed leatherback sea turtles, equipped with high-resolution motion sensing suction-cup tags, to impulsive sound generated by a seismic survey sparker at a productive foraging ground where this species is known to seasonally aggregate. The effects of this type of acoustic stimuli on the fine-scale movement and feeding patterns of leatherback sea turtles were assessed to investigate possible impacts from marine development on this endangered species.

Results

In total, we exposed 13 tagged leatherback turtles to impulsive sound via the sparker, with 12 returning over 10 min of acoustic and dive data pre- and during exposure (Figs. 1, 2 and Supplementary A). We recovered footage from the same 12 turtles, however, the camera shifted position on two individuals, making the footage difficult to annotate regarding foraging events during the sparker exposure period. Seven turtles transmitted location data allowing for mapping and analysis (Fig. 3). We recorded 109.4 ± 35.3 min (mean ± SD) of footage from each turtle, for a total of 1,422 min, and sparker exposure lasted 52.2 ± 11.6 min per turtle (Table 1). Throughout the tag deployments, peak SPL of frequencies within the hearing range of leatherbacks (100—1200 Hz) were between 128.5—176.2 dB.

Results from the Generalized Linear Mixed Model (GLMM) comparing swimming speed by distance from the sparker vessel to whether the sparker was on or off showed that the distance from the sparker vessel was the only significant effect, and the best fitting model removed the effect of the sparker (Fig. 4a). This suggested that the higher swimming speeds near the vessel were probably related to avoidance of the vessel, and the direction of movement may have been away from the path of the sparker vessel. The GLMM for tortuosity, however,

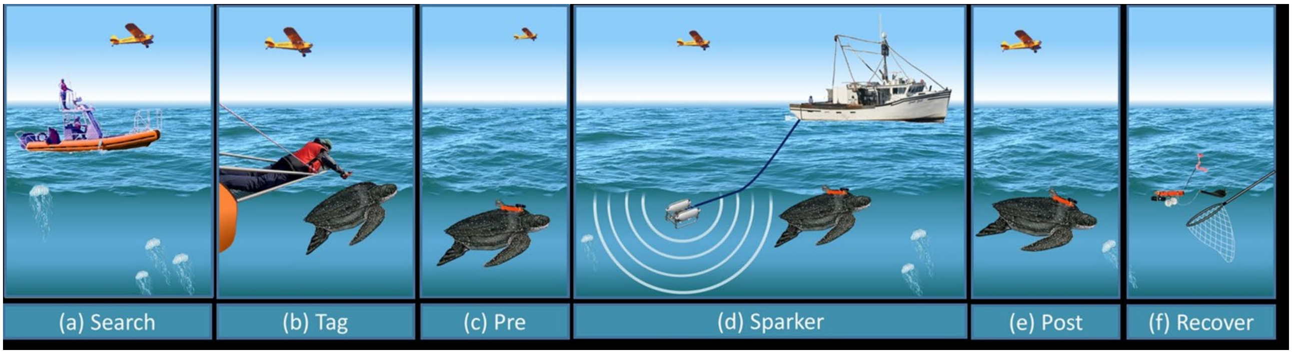

Fig. 1. Visualization of the research methods. **a**) Prior to deployment we would first search for turtles using boat and aerial-based observers. **b**) Tag would be deployed directly from the vessel without capture of the turtle. **c**) Turtle was given time to acclimate to the tag. **d**) Turtles were exposed to the sparker towed by a separate vessel. **e**) Turtles were allowed to reacclimate after exposure during the remaining time for the tag release to activate. **f**) Tag was recovered manually from the tagging vessel.

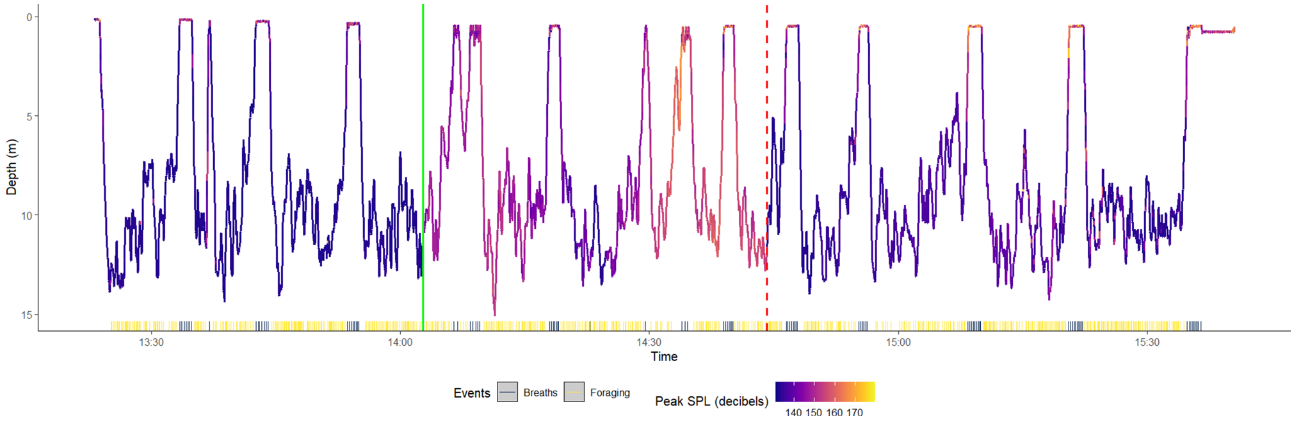

Fig. 2. Full time series of dives, annotated foraging and breathing events, and peak SPL recorded by tag deployed on DC.11 as an example of the data acquired from each deployment. The green line is the start of the sparker exposure period and the red dashed line is the end.

identified that there was a significant interaction between distance from the sparker vessel and whether the sparker was on or off (Fig. 4b). In the absence of impulsive sound exposure (i.e. while the sparker was off), distance to the vessel had no effect on tortuosity. When the sparker was on, turtle movement was straighter while farther from the sound source; however, data were sparse for observations far from the tagged animals because the intention of the study was to remain close to the turtles during the exposure period.

There was a positive relationship between dive durations and dive depth (deeper dives were longer). Controlling for this depth effect, increasing average peak SPL values were correlated with shorter dives, suggesting a negative effect starting at ~ 141 dB (Figs. 5a and b). Similarly, the logistic regression comparing the probability of foraging with depth and peak SPL showed significant, independent relationships with each explanatory variable (Figs. 6a and b). We counted 266.9 foraging events hr^{-1} (0.07 events sec^{-1}) for all turtles combined. When peak SPL was below 141 dB, foraging rate was 333.0 events hr^{-1} (0.09 events sec^{-1}), while above 141 dB, at which the GAM identified a negative effect on dive duration, foraging decreased to 129.7 events hr^{-1} (0.04 events sec^{-1}). The probability of a foraging event per second increased from ~ 0.04 to ~ 0.15 across the depth range observed, while the probability of a foraging event per second decreased from a high of ~ 0.11 to minimum of ~ 0.04 as peak SPL increased, a reduction of 63.6%. This was also evident in the foraging suitability results, which indicated that turtle foraging effort was not centered around the optimal foraging depth interval of 18–21 m, but rather the lower peak SPL (Figs. 6c and d).

Discussion

Understanding the ways that environmental variables influence animal behavior is typically complicated by individual variability and complex interactive effects. Relationships between movement patterns and oceanographic variables, such as temperature, ocean currents, and measures of productivity are often correlated to explain behavior at the macroscale[32,33,35]. As a highly migratory species, the data collection techniques available for assessing the impacts of environmental drivers on leatherback sea turtles are frequently limited by

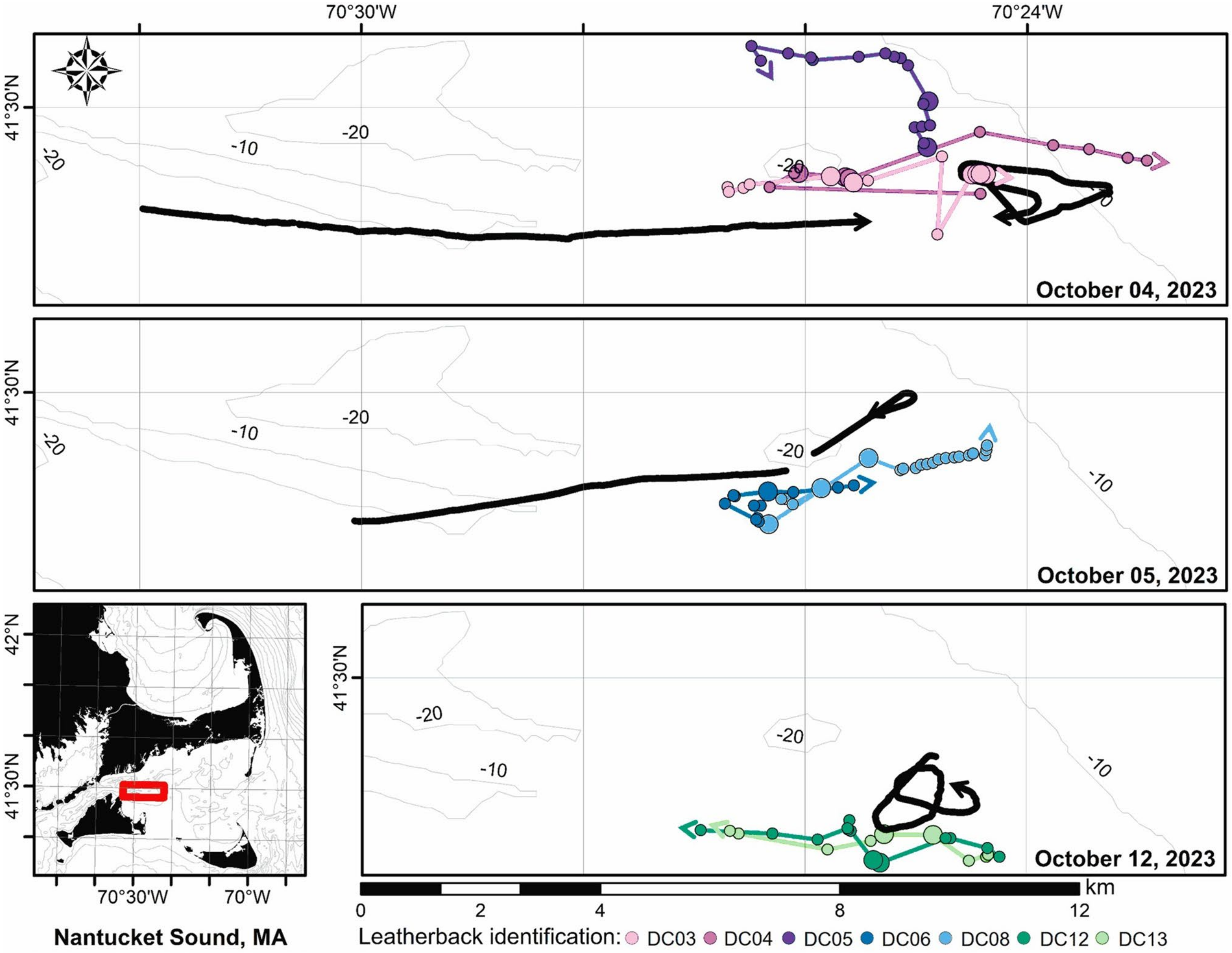

Fig. 3. Map of the seven turtles that recorded location data along with the vessel path while the sparker was on (solid black lines in each map). Negative numbers represent the isobaths. Size of circles for each turtle represents the location data transmitted while the sparker was off (small circles) or on (large circles).

ID	Date	Deployment duration (min)	Sparker duration (min)	Footage (min)	TDR data	GPS data
DC.01	21–09-2023	112	82	110	YES	NO
DC.02	04–10-2023	113	43	100	YES	NO
DC.03	04–10-2023	151	54	124	YES	YES
DC.04	04–10-2023	216	63	144	YES	YES
DC.05	04–10-2023	224	45	10	NO	YES
DC.06	05–10-2023	160	56	147	YES	YES
DC.07	05–10-2023	195	56	120	YES	NO
DC.08	05–10-2023	152	56	118	YES	YES
DC.09	05–10-2023	133	56	77	YES	NO
DC.10	12–10-2023	157	42	120	YES	NO
DC.11	12–10-2023	132	42	103	YES	NO
DC.12	12–10-2023	169	42	112	YES	YES
DC.13	12–10-2023	137	42	137	YES	YES

Table 1. Summary data for all tag deployments.

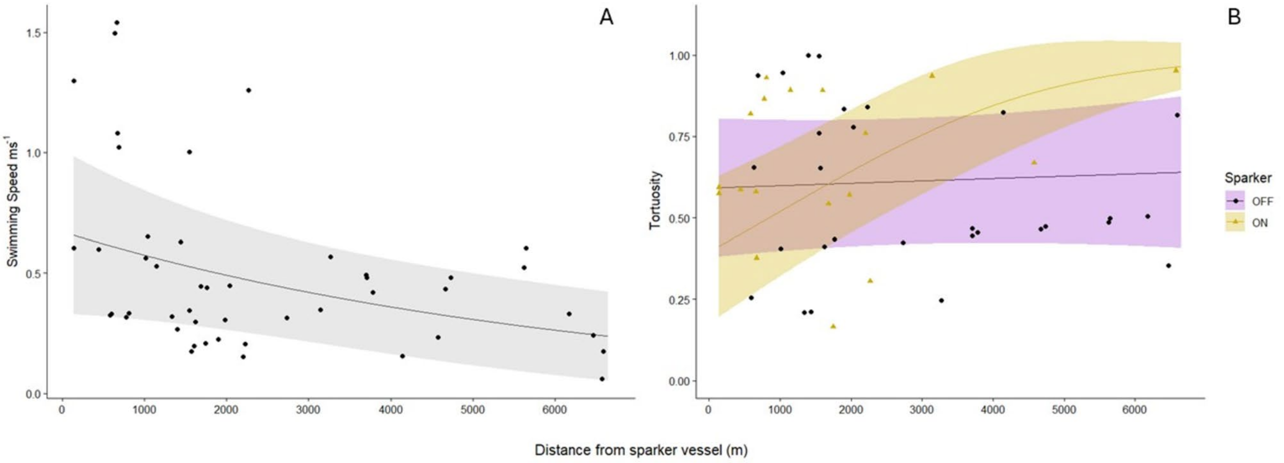

Fig. 4. **a**) Swimming speed in relation to distance from sparker vessel. **b**) Swim tortuosity in relation to distance from vessel and distinguished by sparker on (gold) and off (grey). Shaded areas around the lines represent the 95% confidence intervals.

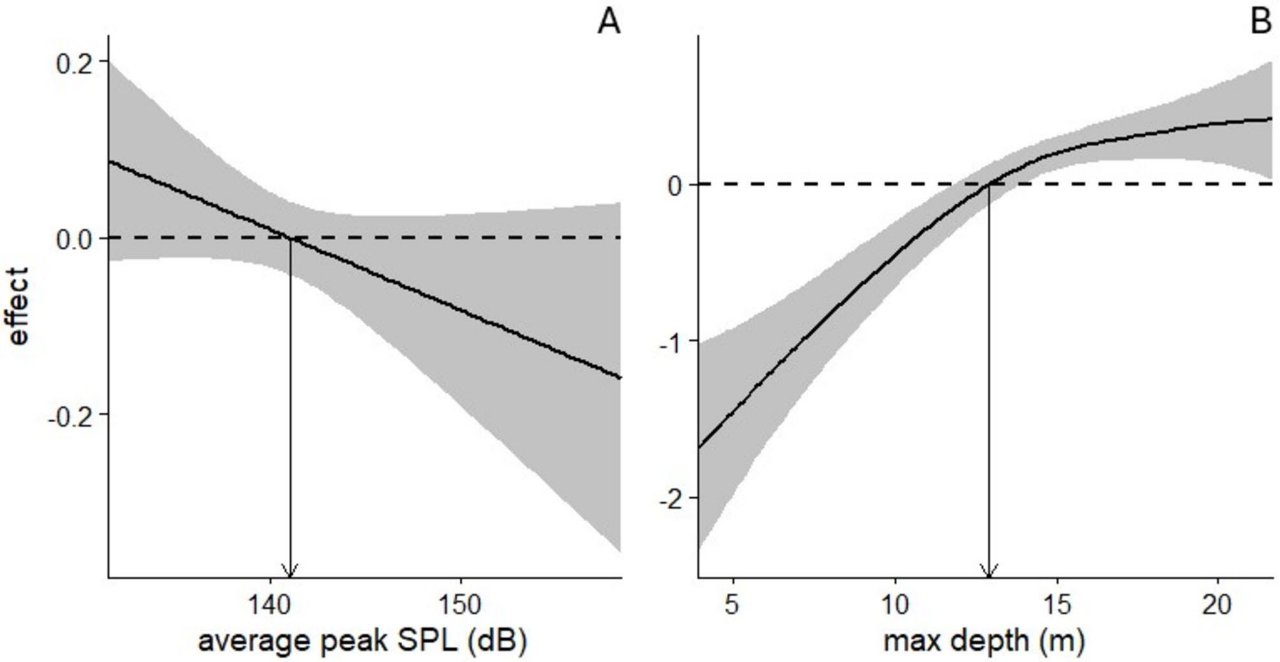

Fig. 5. GAM outputs representing the population effect on dive duration from **a**) average peak SPL and **b**) max dive depth treating turtle as a random effect. Shaded areas around the lines represent the 95% confidence intervals. The effect of average peak SPL crosses zero around 141 decibels, and the effect of maximum depth crosses zero around 13 m.

insufficient spatial resolution across long distances. Because of this, effects from anthrophony, among other highly localized variables, have remained a difficult ecosystem component to integrate. This is further complicated by the often-transient occurrence of these effects that require long-term *in-situ* monitoring[36,37]. While the present study occurred over a relatively short time period (~ 35 h among the 13 turtles tagged) within a small area (~ 5 km^2), the fine-scale approach used to determine effects of impulsive sound exposure on leatherback behavior is an important first step for addressing these research gaps.

The high-resolution sampling from the tag sensors combined with our ability to deploy these data loggers with minimal interaction to the leatherback proved a complementary set of methods for assessing potential impacts from impulsive sound exposure on turtle movement and foraging. The minimally invasive method allowed for recording near-natural behavior without requiring time for the study animal to acclimate to the tagging process[38,39]. Leatherbacks resumed foraging during the immediate dive post tag deployment, and

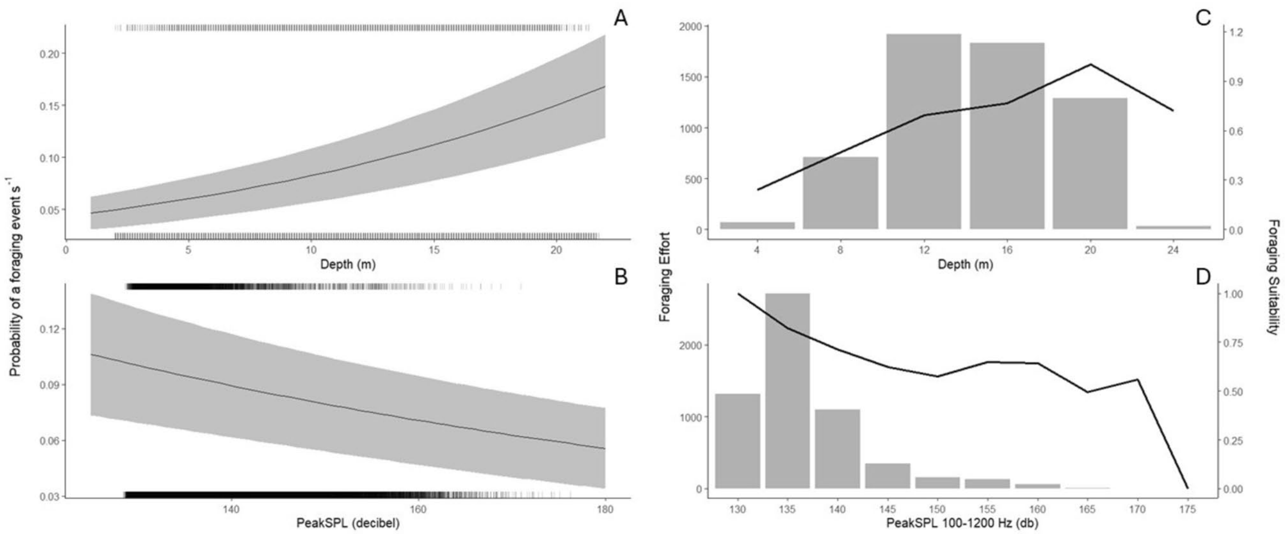

Fig. 6. Probability of foraging related to **a**) depth and **b**) peak SPL, shaded areas around the lines represent the 95% confidence intervals. Foraging effort (grey bars) equal to the total number of foraging events along with foraging suitability (black line) related to **c**) depth and **d**) peak SPL.

foraging rates during these initial dives were generally higher than during the sparker exposure. While the presence of the tagging vessel didn't seem to limit foraging as we continued maneuvering within the area to tag additional leatherbacks prior to the start of the exposure, the larger sparker vessel did seem to yield increased swimming speed of the tagged leatherbacks that were nearby. Distance to the sparking vessel also had an effect on tortuosity, although this seemed more related to the sparker rather than the vessel, because when the sparker was off the predicted tortuosity was nearly the same at all distances from the vessel. The predicted tortuosity when the sparker was on, however, shows increasing straightness with increased distance from the sparker. This relationship should be interpreted with some caution as it was not well supported by data 3–5 km from the sparker, and it was likely influenced by a single point that was > 6 km from the sparker. A more meandering turtle path near an active sparker could be related to turtles orienting to determine the direction of the dynamically moving sound source (i.e., the sparker vessel). While straighter turtle paths farther from the sparker vessel could be attributed to the attenuation of directional changes needed to increase distance between the turtle and the sparker. Because we did not record high sound intensity associated with the vessels when compared to the peak SPL from the sparker (which was much louder), and the study site was immediately adjacent to the Nantucket ferry channel, with numerous recreational fishing vessels additionally present within the area, it seems the drive to forage here outweighed wariness of nearby vessel traffic for the leatherbacks tagged during this study.

The ~ 64% decrease in the probability of foraging associated with the increase in peak SPL levels was an important finding that supported interpretation of the reductions in tortuosity and dive duration while the sparker was on. This indicates that exposure to impulsive sound can impact foraging and seems to suggest that leatherbacks do respond to auditory stimuli which, if loud enough, can disrupt their prevailing behavior. In addition, the foraging suitability models showed a much closer fit with the peak SPL compared with depth, suggesting that leatherbacks were potentially selecting quieter areas in the water column to forage rather than depth where prey volume was optimal. Regardless, all turtles were tagged within a 5 km^2 area over the course of several days of sparker operation without forcing the dense aggregation of leatherbacks elsewhere. However, our experiments only lasted on average ~ 110 min per day, and so it is unclear how a short-term behavior response might translate to changes in individual fitness or population level effects if the sound exposure lasted several hours or days as is expected during the preparation and construction of turbines[13].

Residency at the small study area within Nantucket Sound may have been caused by the extreme density of jellyfish that often move through the site from August through October, potentially making this area a particularly important foraging ground for leatherbacks along their seasonal migratory path. For turtle species with strong site fidelity, they may acclimate to constant anthrophony instead of finding a new location, which can yield dire consequences as seen in terrapins that regularly were struck by boats instead of avoiding them in a nearshore lagoon[24]. Leatherbacks are already at risk of vessel strikes[40], and although in the Western Atlantic region less than 5% of live leatherbacks examined had injuries associated with boats, this may be due to the low survival rate from this type of anthropogenic interaction[41]. Loud, low frequency sounds created by ocean development may be an additional disruption to leatherbacks that could affect their ability to detect and respond to threats.

Using videography, we confirmed that nearshore Massachusetts waters are a vital foraging ground[27,28,42] that may provide the prey densities required by this Western Atlantic population's caloric demands[43]. Compared to Eastern Pacific leatherbacks, the Western Atlantic population typically has a higher reproductive output requiring substantially more calories[43], such that a reduction in foraging success for the Western Atlantic turtles to Eastern Pacific levels could extend remigration intervals by nearly five years resulting in much lower reproductive output[31]. During this study, we calculated that leatherbacks ate ~ 267 jellyfish hr^{-1}, which was similar to previous research in the region (~ 187 jellyfish hr^{-1})[44], however, was substantially higher than the average foraging rate at a more northern site (16 jellyfish hr^{-1}, Nova Scotia, Canada)[45]. This higher consumption rate may be indicative of lower quality or smaller prey, attempts to increase energy reserves, and/or other variables influencing metabolic demands in preparation for periods of fasting that may occur during migration[46]. Regardless, with nearly all of their dive periods committed to foraging, leatherbacks in this region may not be able to find a different foraging site with less disruptive conditions and equally high prey availability, thereby sacrificing fitness gains.

Leatherbacks frequent many areas of the nearshore waters of the Northwest Atlantic including habitats with active and planned marine development, including wind farm construction and lease areas slated for future construction[27,28,42]. Over the next several decades, anthrophony in the region is likely to increase considerably, and remain elevated for the foreseeable future. These changes are particularly relevant to leatherbacks and other sea turtles as the acoustic properties from the combination of large boat traffic, seismic surveys, construction, turbine operation, and decommissioning will coincide with the low frequency hearing ranges of these animals[12]. Based on our study, the consequences of impulsive sounds could cause leatherbacks to reduce foraging success as feeding rates may slow down or distributions may shift to areas with less disruptive acoustics. However, with this species considered Endangered in the region, and already threatened by a range of anthropogenic interactions[40,41,47], the additive impacts of acoustic stress may be more consequential than what was documented in our scaled approach[24]. In this study, we only interacted with turtles that were actively foraging within an area already influenced by a lot of anthropogenic sound from vessel traffic, and as a result it is unclear what the response would have been if their prevailing behavior had been something different, or within an area containing fewer prey resources or less ambient noise. Additional in situ research to obtain high resolution data, more comprehensive population and impact monitoring, and improved understanding of acclimatization are necessary to establish baseline information, estimate population level impacts, and inform mitigation options.

Methods

All methods were approved by a National Oceanographic and Atmospheric Administration (NOAA) Endangered Species Act (ESA) Sect. 7 consultation and carried out in accordance with ESA Permit #23,639 issued to Coonamessett Farm Foundation, Inc. Tagging methods were also approved by the National Marine Fisheries Service (NMFS) Atlantic Institutional Animal Care and Use Committee (IACUC) and carried out in accordance with Protocol #Atlantic IACUC-2020–001. Methods and results are presented following as closely as possible to the ARRIVE guidelines for reporting animal research[48].

Within Nantucket Sound, Massachusetts, we tagged 13 turtles and exposed them to an impulsive sound generated by a seismic sparker (Applied Acoustics Dura-Spark L80) that remained just below the water surface while towed behind a 50 ft diesel-engine fishing vessel. Tagging occurred over the course of four days at-sea in the early autumn of 2023 (Sept 21, Oct 4, 5, and 12). The sparker emitted, at a one-second interval, a high intensity (300 Joules) pulse lasting 0.25 ms, with a sound source level of 221 dB re 1µPa, and a frequency range between ~ 300 Hz and ~ 1,200 Hz. This device is designed to be towed by a vessel for seismic surveys within nearshore or freshwater environments less than 200 m deep.

Turtle tagging followed protocols specified in Rogers et al.[38] for deployment of the HiCAS (High Resolution Camera and Satellite). In summary, the tagging process started with first locating a turtle through spotting from the tagging boat and an airplane. Then once an individual was found, we followed it as best we could from plane and boat until it took a breath. While at the surface, we slowly approached the turtle from behind with the tagging boat and deployed the data logger by hand directly onto the leatherback without capturing or restraining the animal. Through this technique, the interaction of deploying the tag does not seem to yield a disruption in the prevailing foraging behavior[38]. Throughout the study, we used two types of HiCAS data loggers and recorded behavior of the turtles before, during, and after the exposure of the seismic sparker. All tags consisted of a Paralenz dive camera that recorded video, sound, depth and temperature, and a Holohil radio transmitter to aid in relocating the tag for recovery. Some tags were also equipped with location capabilities, either through only a GPS transmitter (Acbotics Acsense) or both a GPS and Argos transmitter (Wildlife Computers Mk10). The Acsense was also equipped with an HTI 96 hydrophone (High Tech Inc.) with a known sensitivity (-201 dB re: 1 V/µPa), that we used to calibrate the SPL values from the paired Paralenz dive cameras recordings.

Turtles were tagged prior to 13:00 to provide enough remaining daylight hours for tag recovery after the 2 – 3-h deployment period. Once tag deployments were completed, we started the sparker exposure period. The seismic sparker was towed from a separate vessel instead of the tagging boat due to the space and power requirements of the device and to allow the tagging vessel to continue monitoring the turtles. Ideally the sparker vessel was in the vicinity of the tagged turtles when the exposure period began, however, when the sparker vessel arrived after turtles were already tagged, the sparker was started while the vessel was enroute. Upon arrival, the sparker vessel conducted long passes either in a straight line across the area or in a more dynamic pattern to ensure the sparker remained in proximity to the turtles. For each controlled exposure, we towed the sparker within the top five meters of the water column at ~ 4 knots (~ 2 m/s), which is the typical protocol for conducting seismic surveys with this tool[8]. The sparker vessel recorded GPS points on their on-board chart plotter to later compare vessel track and position to the turtles' via the GPS data collected from the tags.

Turtle derived GPS data were used to calculate swimming speed between surface intervals, and tortuosity, or movement path efficiency, throughout the tagging period. Tortuosity is measured on a 0 – 1 scale, with zero being the most tortuous and one the straightest. GPS positions for tagged turtles relative to the path of the sparker vessel were plotted using ArcGIS 10.8. GLMMs, with the individual considered as a random effect, were used to compare swimming speed and tortuosity by distance from the sparker vessel and whether the sparker was on or off. The GLMMs were fit as loglinear, and normal distributions using the log and identity links. Assumptions of the models were met and models were reduced using backward selection to remove terms that were not significant and did not improve model fit based on the Akaike information criterion (AIC).

Variable	Event type	Description
Inter- and intra- species observations		
Fish	Point	Fish species present, event marked for every new species identified
Jellyfish	Point	At each 1 min interval after deployment, footage stopped to count the number of jellyfish by species in the frame
Acoustic characteristics		
Abnormal noise	Point	Event to mark any noise of interest other a boat or sparker
Boat noise	Point	Recorded noise most likely to be a boat
Sparker off	State	Sparker noise cannot be identified in the recording
Sparker on	State	Sparker noise can be identified in the recording
Tag characteristics		
Tag Off	State	Tag not on the turtle either prior to or after deployment
Tag On	State	Tag is on the turtle
Above water	State	During deployment, tag is above the surface of the water
Underwater	State	During deployment, tag is fully submerged
Turtle behavior		
Breaths	Point	Event marked for each breath
Foraging	Point	Event marked for each foraging incident with modifier to indicate jellyfish species consumed
Other relevant events		
Boats	Point	Boats in view while above surface, including sparker, tagging, or other vessels
Miscellaneous	Point	Point event to account for any other incident worth noting

Table 2. Ethogram used to annotate video footage. State events are measured by duration and frequency, while point events are measured by frequency only.

For characterizing foraging and dive behavior, we first annotated all video footage by following an ethogram developed using the behavioral observation research interactive software, BORIS (see Table 2 for full ethogram and definitions)[49]. In addition to calculating foraging and breathing events per minute, and a relative density of jellyfish in view, the annotations were used to segment the raw time-depth recordings (TDRs) into dives and surfacings. A surfacing was defined as a bout of successive 'Above water' events where the time difference between those events was less than 30 s. A dive, then, was the complement of a surfacing, with the additional constraint that the turtle was below 2 m. Once dives and surfacings were defined, durations were extracted along with maximum depth and average peak SPL. We also calculated foraging suitability per 4 m depth bin and at 5 dB SPL intervals (between 130—175 dB) by dividing the number of foraging events by the time spent within the range of these conditions. As a result, a suitability value close to 1 meant near continuous foraging within a depth or SPL range.

For interpreting behavior in relation to sparker exposure, we grouped all turtle data based on the time when the sparker was on or off, and focused on the received sound frequency exposures between 100 – 1,200 Hz. We limited the frequencies to this range to both match the hearing capabilities of leatherbacks[22] and the acoustic properties of the sparker which reached a low of between 100—300 Hz. To reduce artificially inflated peak SPL readings due to excessive noise at the water surface (i.e. water splashing the hydrophone), and ensure that all sounds included in the analysis occurred while underwater, we excluded SPL data recorded during surfacings.

Effects of average peak SPL on dive duration, maximum dive depth, and foraging probability were analyzed using a combination of generalized additive models and logistic regression. Generalized additive models[50,51] were used to model dive duration (mins) as a function of the maximum dive depth (m) and average peak SPL (dB). A total of 12 models were fitted to the data, with 2 models being supported by AIC (ΔAIC values <2). The 2 supported models were nested, only excluding the average peak SPL variable. Logistic regression was used to predict the probability of foraging per one-second interval, including fixed effects for peak SPL and dive depth (which directly affected peak SPL), with a random effect of individual turtles. The logistic regression was fit as a binomial distribution using the logit link in the 'glmer' package from the statistical software R (Version 4.4.1)[52]. Assumptions of the models were met and models were reduced using backward selection to remove terms that were not significant and did not improve model fit based on the Akaike information criterion (AIC). In addition to the model outputs, suitability indices were produced for the significant effects identified to describe the frequencies of the habitat conditions (peak SPL and depth) where foraging success occurred relative to foraging effort.

Data availability

Data can be made available upon request to the corresponding author.

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Author contributions

All authors meaningfully contributed to the study design, field work, data analysis, and manuscript preparation. More specifically, HH, EF, and SP designed the camera tags. SP, KC, LC, RR, JH, HH deployed the tags on leatherbacks and RM, FD, and VO ran the sparker. SP, KC, VO, and RM annotated all footage. RM, JH, EF, HH and NC conducted analysis and created the figures. SP, RM, and JH wrote the manuscript, while remaining authors provided critical feedback.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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