OCS Study
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Sea Turtle Acoustic Ecology: Addressing Priority Data Gaps in Knowledge of Sea Turtle Hearing Sensitivity

U.S. Department of the Interior
Bureau of Ocean Energy Management
Sterling, VA

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DISCLAIMER

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ABOUT THE COVER

Hawksbill sea turtle swimming underwater. Credit: U.S. Fish and Wildlife Service

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List of Abbreviations and Acronyms

AEP	auditory evoked potential
ASA	Acoustical Society of America
BOEM	Bureau of Ocean Energy Management
cm	centimeter(s)
CMAST	Center for Marine Science and Technology
dB	decibel
dL	deciliter
Hz	hertz
KBSTRRC	Karen Beasley Sea Turtle Rescue and Rehabilitation Center
kg	kilogram(s)
L	liter
mg	milligram
min	minute
mmol	millimole
NCSU	North Carolina State University
NOAA	National Ocean and Atmospheric Administration
NSF	National Science Foundation
ONR	Office of Naval Research
PCV	packed cell volume
RCC	Rosalie Conservation Center
RL	received level
RMS	root mean square
SLR	simple linear regression
SPL	sound pressure level
TDT	Tucker-Davis Technologies
TS	total solids
µPa	micropascal(s)

1 Introduction

In 2014, a working group funded by the National Oceanic and Atmospheric Administration (NOAA), National Science Foundation (NSF), Office of Naval Research (ONR), and Acoustical Society of America (ASA) convened to establish sound exposure guidelines for fishes and sea turtles (Popper et al., 2014). The group provided a review of literature on the biological significance of sound, hearing sensitivity, anthropogenic noise sources, and noise impacts. In doing so, they identified a number of data gaps that were limiting factors in the establishment of exposure guidelines for sea turtles. They concluded with a set of interim guidelines until further research fills these data gaps. Among their recommended research priorities, they identified the need to determine the hearing sensitivity of all sea turtle species across all life stages.

Sea turtles inhabit temperate, tropical, coastal, and offshore marine environments. These habitats are subject to anthropogenic noise from shipping, military, and energy development activities (Hildebrand 2009). Noise at various levels has the potential to affect marine organisms by causing direct physical injury, inducing temporary or permanent threshold shifts in hearing sensitivity, inducing metabolic stress, disrupting behavior, displacing individuals from preferred locations, and masking biologically important sounds needed for prey detection, predator evasion, and navigation (Rako-Gospić and Picciulin, 2019).

In coastal and offshore habitats, seismic surveys pose a risk of repeated high amplitude exposures to marine life over large spatial and temporal scales (Estabrook et al., 2016; Wiggens et al., 2016), the effects of which remain poorly understood (Elliot et al., 2019). Impact and vibratory pile driving are also sources of high amplitude noise, albeit localized to smaller areas in shelf waters. Shipping, while not as loud, is continuous and omnipresent in many shelf waters (Hildebrand, 2009; Estabrook et al., 2016; Wiggens et al., 2016; Rice et al., 2014). Additional, intermittent sources of high amplitude noise that occur in both shelf and oceanic habitats include military sonar and explosives (Hildebrand, 2009; Accomando et al., 2024).

The biological significance, or role of sound for sea turtles, and the extent to which they may be affected by anthropogenic noise, is currently not well understood. A number of studies have demonstrated behavioral responses of sea turtles to anthropogenic noise sources (O'hara and Wilcox, 1990; McCauley et al., 2000; DeRuitter and Doukara, 2012; Kastelien et al., 2023). Over the past decade, knowledge of the hearing capabilities of sea turtles has greatly advanced. Previous studies of hearing in loggerhead (*Caretta caretta*) (Bartol et al., 1999; Lavender et al., 2014; Martin et al., 2012), green (*Chelonia mydas*) (Piniak et al., 2016; Ridgway et al., 1969), and leatherback (*Dermochelys coriacea*) (Dow Piniak et al., 2012) sea turtles revealed hearing capabilities up to 1,600Hz, with greatest sensitivities falling between 100 and 500Hz. However, very little hearing data exist for several species and age classes. These data gaps limit our ability to accurately assess potential impacts to all life stages and species of sea turtles from anthropogenic sound and to develop successful mitigation measures.

Our current knowledge suggests that sea turtles can detect much of the low-frequency, high-intensity anthropogenic sound in the ocean, including pile driving, low-frequency active sonar, and oil and gas exploration and extraction. The apparent low-frequency specialization of sea turtle hearing is reason for concern that they may be impacted by anthropogenic noise. Anthropogenic noise primarily occurs at low frequencies due to the physical nature of sound sources and the propagation efficiency of low-frequency sound in water (Richardson, 1995; Hildebrand 2009).

The objective of this study is to fill known data gaps and provide audiograms of four sea turtle species at the juvenile life stage: green, Kemp's ridley (*Lepidochelys kempii*), hawksbill (*Eretmochelys imbricata*), and loggerhead. All four species are listed as either threatened or endangered under the U.S. Endangered Species Act (NMFS and USFWS 1991, 1993, 1998, 2008, 2013, 2015, 2023; Conant et al., 2009; Seminoff et al., 2015) and vulnerable, endangered, or critically endangered by the International Union for Conservation of Nature (Casale and Tucker, 2017; Mortimer and Donnelly, 2008; Seminoff, 2023; Wibbels and Bevan, 2019). During post-hatchling and small juvenile stages, these sea turtle species occupy pelagic habitats, with greatest concentrations occurring at the convergence zones of sea surface currents. During juvenile and adult life stages, they generally inhabit coastal waters from shoreline to the shelf break, with variation occurring across individuals and species (Plotkin 2003; Bolten 2003). While habitat use of juvenile sea turtles overlaps significantly with anthropogenic noise, previous data on underwater hearing sensitivity of these species at this life stage either do not exist or are based on data from very few individuals.
In this study, we measured the underwater hearing sensitivity of 14 green, 13 Kemp's ridley, 6 hawksbill, and 14 loggerhead sea turtles—all at the juvenile life stage. The resulting audiograms provide a necessary tool for assessing and managing the potential impacts of noise occurring in their habitats.

2 Methods

Sea turtles were either wild-caught at the juvenile life stage (greens, Kemp's ridleys, and loggerheads), caught as hatchlings and raised in captivity (hawksbills and loggerheads), or sourced from rehabilitation facilities and tested after they were deemed fit for release (greens and Kemp's ridleys). Green sea turtles ranged in weight from 2.3 to 7.2kg and in straight carapace length from 26.6 to 38.0cm. Kemp's ridley sea turtles ranged in weight from 0.9 to 10.4kg and in straight carapace length from 17.2 to 41.2cm. Hawksbill sea turtles ranged in weight from 1.6 to 2.2kg and in curved carapace length from 26.6 to 29.0cm. Loggerhead sea turtles ranged in weight from 0.8 to 14.1kg and in straight carapace length from 17.6 to 44.0cm (Table 1). We measured hearing in green and Kemp's ridley sea turtles at both the North Carolina State University Center for Marine Science and Technology (CMAST) and the Karen Beasley Sea Turtle Rescue and Rehabilitation Center (KBSTRRC), hawksbill sea turtles were tested at the Rosalie Conservation Center (RCC), and loggerhead sea turtles at CMAST.

2.1 Pretest and Posttest Veterinary Methods

Team veterinarians performed physical exams and blood analyses prior to hearing tests to ensure turtles enrolled in the study were in good health (Tristan & Norton 2017). Blood was drawn from the external jugular vein (dorsal cervical sinus) for measurement of packed cell volume (PCV, by centrifugation), plasma total solids (TS, by refractometry), blood gases and plasma chemistries (pH, pO2, pCO2, bicarbonate, total CO_2, sodium, potassium, ionized calcium, and glucose, by iSTAT 1 point of care analyzer [Abbott, Green Oaks, Illinois] with CG8+ cartridges [Zoetus, Parsippany, New Jersey]) and lactate (Lactate Plus Meter, Nova Biomedical). Blood analyses were repeated immediately following hearing tests to assess physiologic impact of the testing procedures.

We manually restrained all turtles restrained with elastic self-adhering tape (VetWrap 3M Animal Care Products, St. Paul, Minnesota) wrapping the forelimbs to the marginal carapace, swaddled in a cloth bag with a drawstring closed loosely around the neck, and secured to a sliding platform that could be raised and lowered between the hearing test depth and the surface for breathing (Figure 1). A subset of turtles was also lightly sedated with midazolam (n = 14, 0.5–2.0mg/kg IM) or dexmedetomidine (n = 3, 10–15mcg/kg IM), at the veterinarian's discretion, to improve subject compliance and reduce myogenic artifact from movement, without sacrificing the turtles' voluntary airway control.

After lowering to hearing test depth, we initially brought turtles to the surface every minute for breaths, or whenever they showed intentional signs of wanting a breath (e.g., head and shoulder movements, raising head, presence of a bubble at the nares). If no breath was taken spontaneously, the turtle's beak would be lifted to encourage a breath. If still no breath was taken after the beak-lift assist, the turtle was slid back down to hearing test depth until the next scheduled lift. Surfacing intervals were gradually lengthened or shortened throughout the procedures to find the turtle's natural spontaneous respiratory rate under the test conditions. Data collection had to be paused when turtles were surfaced, so finding the longest interbreath (surfacing) interval that would not be unexpectedly interrupted by vigorous movements of breathing intension signs helped to maximize the productive data collection time within the overall test period. Interbreath intervals ranged from 0.75–5.00 min and were adjusted up or down within the test period as needed. The target hearing test period was capped at 1 hour, with occasional brief extensions to complete a test frequency if the turtle was visually assessed to be doing well throughout the test period. Following testing, all turtles were successfully released as planned.

Our methodology follows protocols developed to collect underwater hearing sensitivity data in freshwater and marine turtles (Christiansen et al., 2013; Dow Piniak, 2012; Dow Piniak et al., 2012; Harms et al., 2014; Harms et al., 2009, Piniak et al., 2016). Subjects were tested under North Carolina Wildlife Resources Endangered Species Permits 22ST42 and 23ST42, NOAA National Marine Fisheries Service Permit 21233-03, and NC State Institutional Animal Care and Use Protocol 20-438 and 23-382.

2.2 Auditory Evoked Potential Measurements

To measure hearing, we recorded auditory evoked potentials (AEP) in response to tonal pulses 50ms in duration and ranging from 50 to 1,600Hz. This rapid, non-invasive technique has been used to measure hearing in a diverse array of taxa including fishes, squid, seabirds, odontocetes, manatees, pinnipeds, sharks and sea turtles (Casper and Mann, 2006; Dow Piniak et al., 2012; Mann et al., 2005; Mooney et al., 2009; Piniak et al., 2016). We used a Tucker-Davis Technologies (TDT) workstation (Tucker-Davis Technologies, Inc. Alachua, Florida USA) consisting of an RX6 signal generator, an RX6 signal receiver, and BioSigRP analysis software.

Outgoing signals were amplified with a Samson Servo 120a speaker amplifier (Samson Technologies, Corp. Hicksville, New York USA) and played through a Diluvio AQ339 underwater speaker (Clark Synthesis, Littleton, Colorado USA). Incoming signals from electrodes were amplified using a TDT Medusa4Z electrode amplifier.

We conducted tests in circular tanks of 183cm diameter and 91cm water depth at CMAST, 152cm diameter and 76cm water depth at KBSTRRC, and 216cm diameter and 99cm water depth at RCC. Turtles were submerged to depths (surface to ear) ranging from 23 to 29cm at all testing sites and positioned at distances (speaker to ear) ranging from 91 to 104cm at CMAST, from 71 to 84cm at KBSTRRC, and from 103 to 107cm at RCC (Figure 1). Water temperatures matched source waters of the sea turtles as closely as possible in order to minimize thermal stress and ranged from 19.6°C to 27.2°C during testing of green, from 22.5°C to 28.6°C during testing of loggerhead, from 19.2°C to 28.3°C during testing of Kemp's ridley and from 25.1°C to 25.6°C during testing of hawksbill sea turtles.

We positioned electrodes subdermally under the frontoparietal scale on top of the head (signal), in subcutaneous tissue between the neck and shoulder (reference), and in the tank water (ground). Stimulus signals were initially presented at sound pressure levels (SPL) above hearing threshold and decreased by steps of 6dB until thresholds were reached at each frequency. The TDT workstation presented tone pulses at each SPL and frequency, and the responses were averaged until an AEP was observable, or up to 1,000 times. Example AEPs for a green sea turtle (subject 4937) are shown in Figure 2. We measured root mean square (RMS) SPLs (re 1µPa) at the midline location of each test subject's head using an HTI-96-Min hydrophone (High Tech, Inc., Gulfport, Mississippi USA) connected directly to the TDT workstation. We measured ambient noise levels (with no signal present) at the same location. Testing was restricted to approximately one hour depending on the subjects' vital rates. We were therefore limited in the number of frequencies that could be measured for each individual.

Table 1: Summary of all test subjects.

Date Tested	Subject ID	Species	Weight (kg)	Length (cm)	History	Restraint
13-Apr-22	Mauvelous	*C. mydas*	4.8	33.1	Rehabilitated	Manual
3-May-22	Lilac	*C. mydas*	4.4	31.6	Rehabilitated	Midazolam/Manual
8-Sep-22	Bittersweet	*C. mydas*	7.2	36.3	Rehabilitated	Midazolam/Manual
17-Aug-22	4891	*C. mydas*	2.5	27.7	Wild-caught	Midazolam/Manual
17-Aug-22	4892	*C. mydas*	2.3	27.0	Wild-caught	Midazolam/Manual
21-Aug-22	4893	*C. mydas*	6.1	38.0	Wild-caught	Midazolam/Manual
21-Aug-22	4900	*C. mydas*	2.5	28.0	Wild-caught	Midazolam/Manual
21-Aug-22	4904	*C. mydas*	2.9	28.0	Wild-caught	Midazolam/Manual
28-Aug-22	4803	*C. mydas*	2.6	27.3	Wild-caught	Midazolam/Manual
28-Aug-22	4899	*C. mydas*	5.4	34.7	Wild-caught	Midazolam/Manual
28-Aug-22	4905	*C. mydas*	3.1	29.0	Wild-caught	Midazolam/Manual
23-Jul-23	4934	*C. mydas*	2.5	27.4	Wild-caught	Manual

Date Tested	Subject ID	Species	Weight (kg)	Length (cm)	History	Restraint
29-Jul-23	4937	*C. mydas*	3.3	29.5	Wild-caught	Manual
29-Jul-23	4940	*C. mydas*	2.3	26.6	Wild-caught	Manual
5-Feb-22	Turtledove	*L. kempii*	1.8	22.8	Rehabilitated	Manual
13-Apr-22	Leaper	*L. kempii*	3.3	25.8	Rehabilitated	Manual
13-Apr-22	Pocus	*L. kempii*	10.4	41.2	Rehabilitated	Manual
3-May-22	Aquamarine	*L. kempii*	4.0	32.0	Rehabilitated	Manual
8-Sep-22	Limeapalooza	*L. kempii*	4.8	31.1	Rehabilitated	Midazolam/Manual
29-Jul-23	Gypsum	*L. kempii*	2.8	26.4	Rehabilitated	Manual
14-Aug-22	4888	*L. kempii*	2.3	24.9	Wild-caught	Manual
16-Aug-22	4890	*L. kempii*	2.0	23.4	Wild-caught	Manual
19-Aug-22	4894	*L. kempii*	4.0	31.4	Wild-caught	Midazolam/Manual
30-Aug-22	4818	*L. kempii*	2.6	28.0	Wild-caught	Midazolam/Manual
10-Jul-23	4933	*L. kempii*	0.9	17.2	Wild-caught	Manual
23-Jul-23	4930	*L. kempii*	3.4	27.8	Wild-caught	Manual
9-Aug-23	4923	*L. kempii*	2.2	26.8	Wild-caught	Manual
27,28-Mar-23	Kiki	*E. imbricata*	1.9	28.1*	Captive-raised	Manual
23,28-Mar-23	SuzieMarie	*E. imbricata*	1.9	26.8*	Captive-raised	Manual
25-Mar-23	Ettafaye	*E. imbricata*	2.2	29.0*	Captive-raised	Dexmedetomidine/Manual
25-Mar-23	Beetlejuice	*E. imbricata*	1.7	27.4*	Captive-raised	Dexmedetomidine/Manual
23-Mar-23	Mimosa	*E. imbricata*	2.1	28.0*	Captive-raised	Dexmedetomidine/Manual
27,28-Mar-23	Vaughn	*E. imbricata*	1.6	26.6*	Captive-raised	Manual
8-Jul-23	Gorganzola	*C. caretta*	1.1	18.3	Captive-raised	Manual
8-Jul-23	Ricotta	*C. caretta*	1.0	19.2	Captive-raised	Manual
8-Jul-23	Meunster	*C. caretta*	0.8	17.8	Captive-raised	Manual
9-Jul-23	Paneer	*C. caretta*	0.8	18.1	Captive-raised	Manual
9-Jul-23	Mozarrella	*C. caretta*	1.0	19.7	Captive-raised	Manual
9-Jul-23	Swiss	*C. caretta*	0.9	18.1	Captive-raised	Manual
9-Jul-23	Parmesan	*C. caretta*	1.0	18.9	Captive-raised	Manual
12-Jul-23	Goat	*C. caretta*	0.9	17.6	Captive-raised	Manual
12-Jul-23	Feta	*C. caretta*	1.1	18.9	Captive-raised	Manual
12-Jul-23	Cheddar	*C. caretta*	0.9	18.3	Captive-raised	Manual
10-Aug-23	4954	*C. caretta*	14.1	44.0	Wild-caught	Manual
12-Aug-23	4965	*C. caretta*	13.4	44.0	Wild-caught	Manual
10-Nov-22	CC1	*C. caretta*	2.3	23.5	Wild-caught	Manual
10-Nov-22	CC2	*C. caretta*	3.1	27.1	Wild-caught	Midazolam/Manual

Note: Subjects that underwent more than one test have test have two dates reported. Length measurements are of straight carapace length. Curved carapace length measurements are indicated with an asterisk.

Figure 1. Auditory testing of a juvenile Kemp's ridley sea turtle at the Karen Beasley Sea Turtle Rescue and Rehabilitation Center.
Relative positions of the sea turtle and speaker (left). Electrode placement for measuring AEP (right). Signal electrode (red) was placed subcutaneously under the frontoparietal scale on top of the head. Reference electrode (white) was placed subcutaneously between the neck and shoulder. Ground electrode (not shown) was suspended in the tank water.

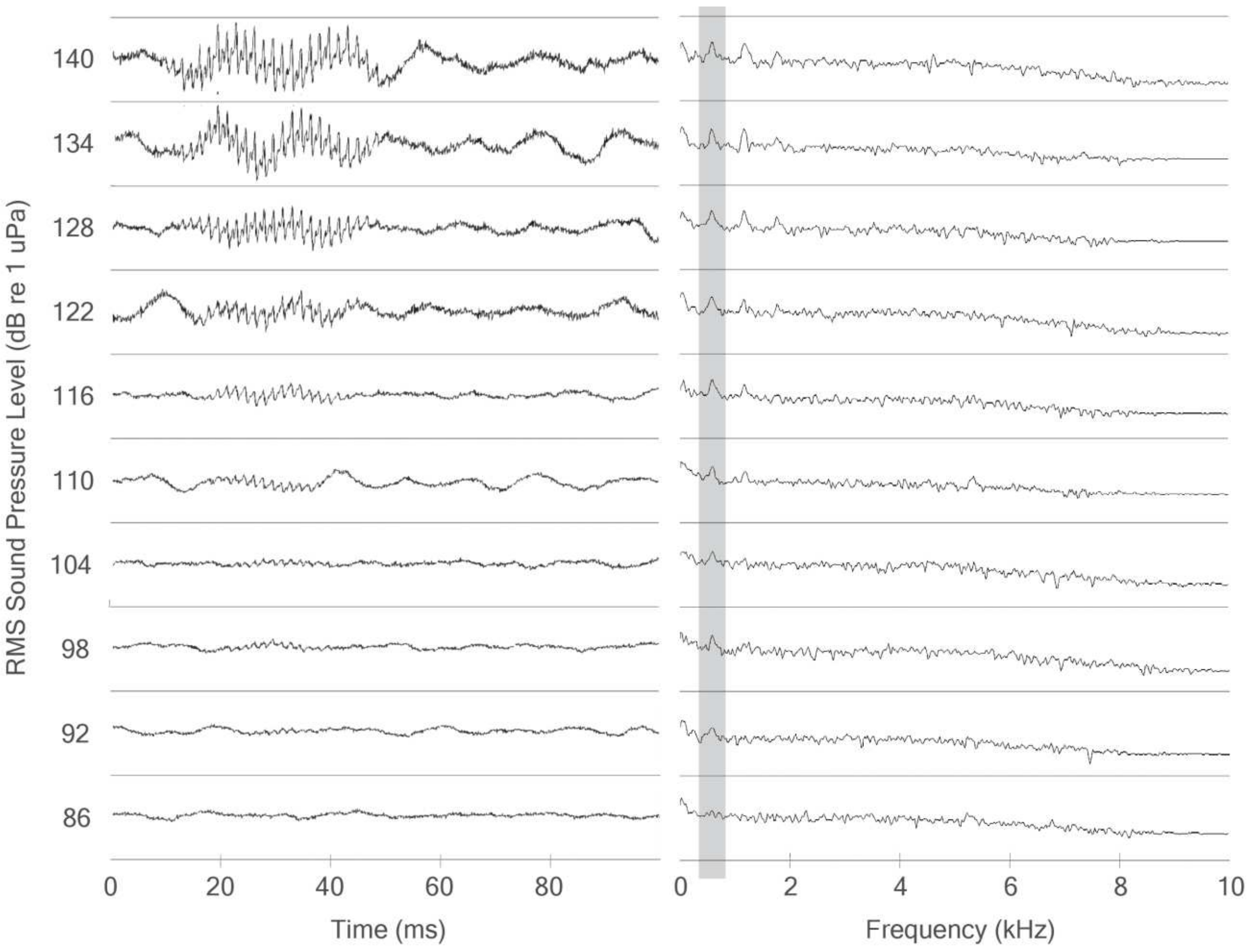

Figure 2. AEP measurements represented in the time domain (left) and frequency domain (right) during exposure to 300Hz tonal pulses.
The sound pressure level at the test subject was initially 140dB (re 1 µPa). This level was reduced in steps of 6dB until the hearing threshold was reached at 92dB. Note that no AEP response was detected at 86dB. A peak at 600Hz (twice the stimulus frequency) is visible in the frequency domain plots and highlighted in grey. | Test subject: 4937 | Species: *Chelonia mydas*

2.3 Statistical Analysis

To determine if rehabilitation history and/or use of sedation affected hearing sensitivity, we applied a Kenward-Roger F test to compare a complex linear mixed model (where threshold was the response variable, rehabilitation history, sedation, and frequency were fixed effects, and turtle ID was a random effect) to a nested, simple linear mixed model (where rehabilitation history and sedation were not included). The covariates rehabilitation history and sedation were binary variables, while frequency was categorical. Because water temperatures were evenly distributed across test subjects, and unique to each turtle ID, we allowed their potential effect to remain embedded in the random effect of turtle ID for these models. We tested the validity of this model assumption by confirming that the random effects were normally distributed using Q-Q plots. We conducted analysis using the statistical software package R (version 4.4.1 The R Foundation for Statistical Computing 2024). After testing for the effects of rehabilitation history and sedation, we examined the influence of water temperature on hearing thresholds by plotting simple linear regressions (SLR) at each frequency across test subjects.

3 Results

3.1 Hearing Sensitivity

No significant differences in hearing sensitivity resulting from rehabilitation history or use of sedation were detected when comparing the nested complex and simple linear mixed models (Kenward-Roger F test: green turtle $p = 0.43$; Kemp's ridley turtle $p = 0.96$; Hawksbill turtle $p = 0.85$; loggerhead turtle $p = 0.14$). Data from all test subjects within each species were therefore pooled to create the following composite audiograms (Figures 3, 4, 5 and 6) and averaged auditory thresholds (Table 2). Individual audiograms and threshold tables are presented in Appendix A.

Three instances of statistically significant ($p < 0.05$) correlations between temperature and hearing threshold occurred: 1) a positive correlation in which threshold increased (sensitivity decreased) as temperature increased (SLR: Temperature Range = 19.6–22.7°C, $\beta = 4.10$, $r^2 = 0.67$, $p = 0.007$) at 400Hz in the green sea turtle, 2) a negative correlation in which threshold decreased (sensitivity increased) as temperature increased (SLR: Temperature Range = 20.2–27.2°C, $\beta = -4.57$, $r^2 = 0.71$, $p = 0.04$) at 600Hz in the green sea turtle, and 3) a negative correlation in which threshold decreased (sensitivity increased) as temperature increased (SLR: Temperature Range = 19.4–28.3°C, $\beta = -2.71$, $r^2 = 0.62$, $p = 0.02$) at 600Hz in the Kemp's ridley sea turtle. All other regressions showed no statistical significance. Appendix B provides linear regressions of hearing sensitivity at each frequency across subjects tested at different temperatures. No regression analysis was conducted for hawksbill sea turtles as water temperature was constant (25.1-25.6°C) across all test subjects.

3.1.1 Green Sea Turtles

We recorded AEPs in 14 juvenile green sea turtles (11 wild-caught, 3 rehabilitated). AEPs were detected between 50 and 800Hz. Peak sensitivity occurred between 200 and 400Hz, followed by a steep decline in sensitivity at frequencies above 400Hz (Table 2, Figure 3). Thresholds varied by as little as 5dB across test subjects ($n = 4$) at 300Hz, to as much as 31dB across test subjects ($n = 6$) at 600Hz. The lowest received level (RL) for a single individual shown to evoke an auditory response was 78dB (re 1µPa) at 200Hz. The lowest RL averaged across all test subjects at a given frequency was 87dB (re 1µPa) at 200Hz and 400Hz. No responses were detected at 1,200Hz (max RL = 163dB) and 1,600Hz (max RL = 154 to 165dB). Mean ambient noise levels during testing decreased with frequency from 74dB (re 1µPa^2/Hz) at 50Hz to 46dB (re 1µPa^2/Hz) at 1,600Hz (Figure 3).

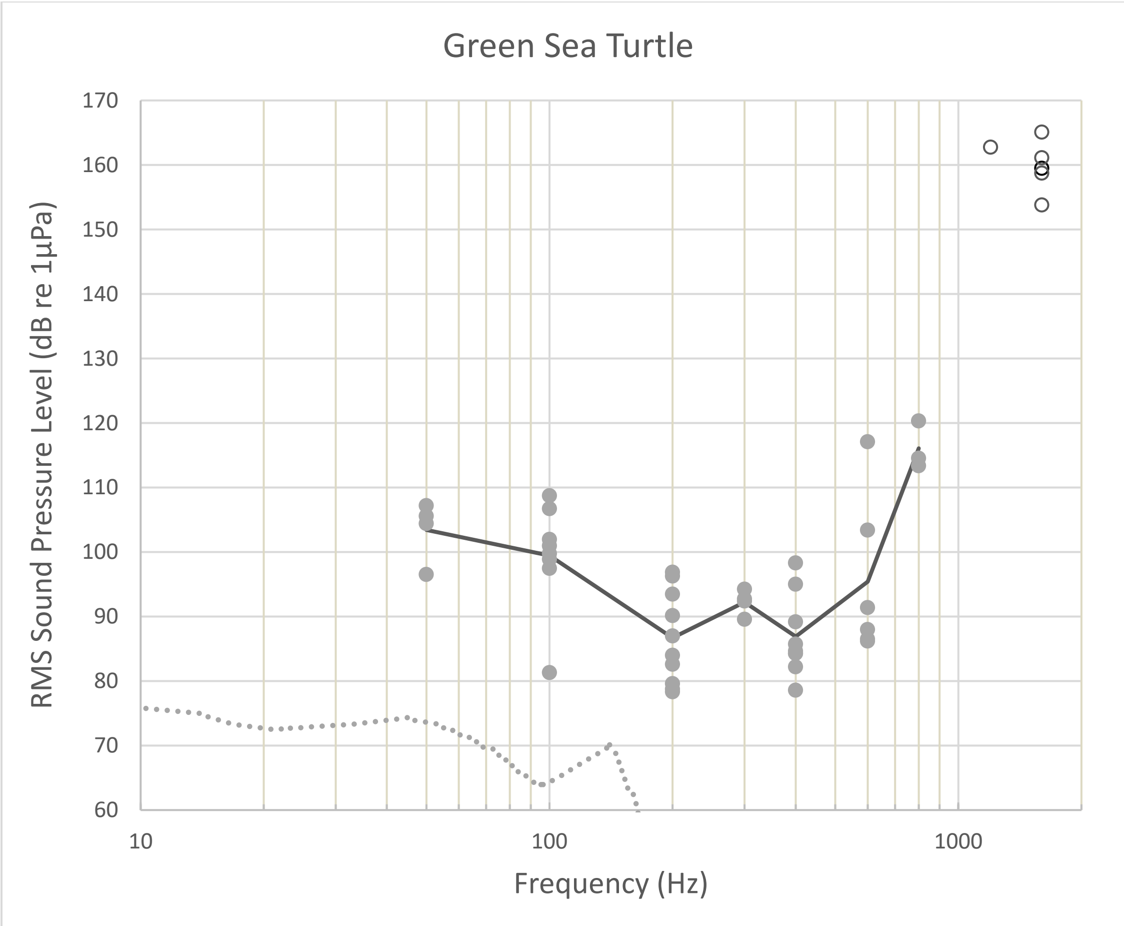

Figure 3**. Auditory thresholds of green sea turtles.**
Grey circles represent thresholds of individual test subjects. Open circles represent the maximum SPLs tested with no AEP responses. Solid line represents the mean auditory threshold at each frequency. Dotted line represents the mean spectrum level background noise (dB re 1µPa^2/Hz).

3.1.2 Kemp's Ridley Sea Turtles

We recorded AEPs in 13 juvenile Kemp's ridley sea turtles (7 wild-caught, 6 rehabilitated). AEPs were detected between 50 and 800Hz. Peak sensitivity occurred between 200 and 300Hz. A steep decline in sensitivity occurred at frequencies above 400Hz (Table 2, Figure 4). Thresholds varied by as little as 4dB across test subjects (n = 2) at 50Hz, to as much as 33dB across test subjects (n = 8) at 600Hz. The lowest RL for a single individual shown to evoke an auditory response was 86dB (re 1µPa) at 200Hz. The lowest RL averaged across all test subjects at a given frequency was 100 dB (re 1µPa) at 300Hz. No responses were detected at 1,200Hz (max RL = 143dB) and 1,600Hz (max RL = 143 to 165dB). Mean ambient noise levels during testing decreased with frequency from 77dB (re 1µPa^2/Hz) at 50Hz to 42dB (re 1µPa^2/Hz) at 1,600Hz (Figure 4).

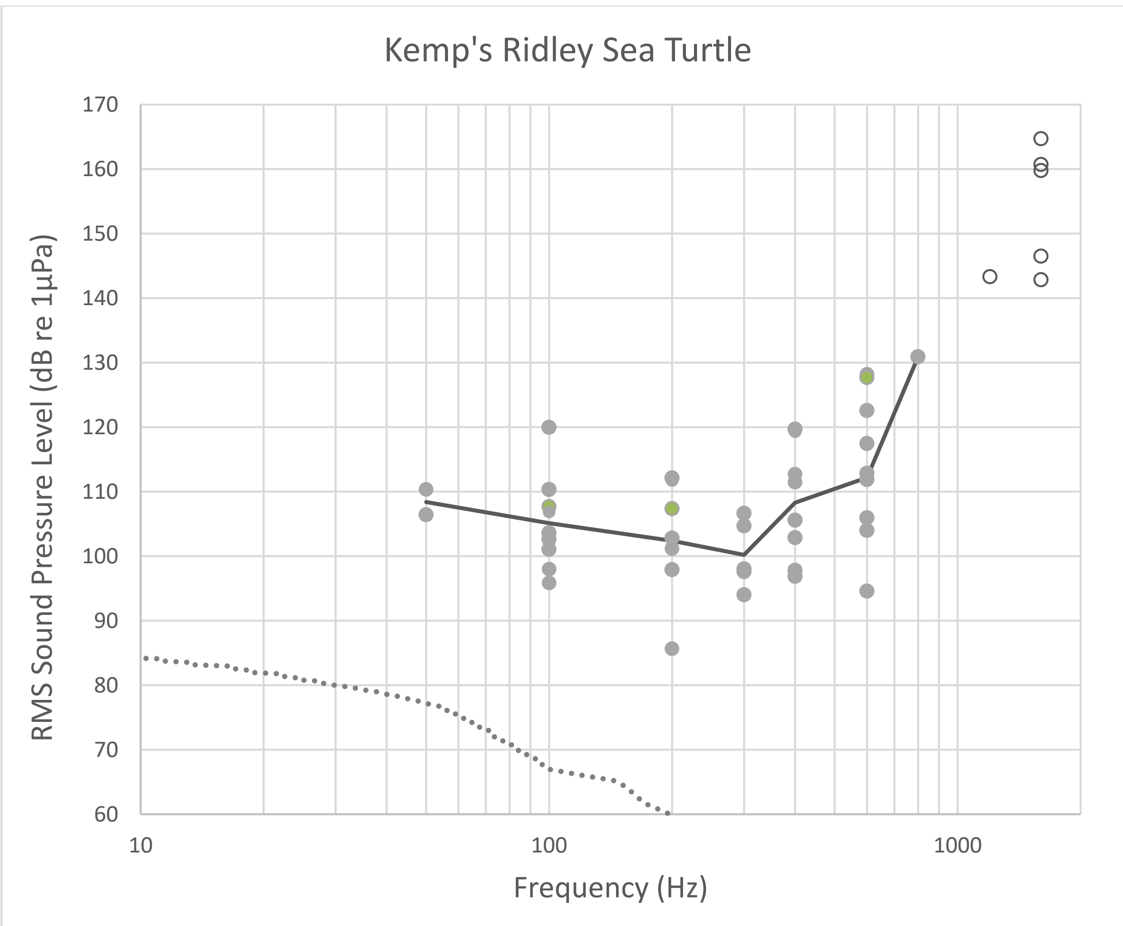

Figure 4. Auditory thresholds of Kemp's ridley sea turtles.
Grey circles represent thresholds of individual test subjects. Open circles represent the maximum SPLs tested with no AEP responses. Solid line represents the mean auditory threshold at each frequency. Dotted line represents the mean spectrum level background noise (dB re 1µPa^2/Hz).

3.1.3 Hawksbill Sea Turtles

We recorded AEPs in six hawksbill sea turtles (all of which were captive-raised). AEPs were detected between 50 and 800Hz. Peak sensitivity occurred between 200 and 400Hz (Table 2, Figure 5). A steep decline in sensitivity occurred at frequencies above 600Hz. Thresholds varied by as little as 5dB across test subjects (n = 4) at 800Hz, to as much as 20dB across test subjects (n = 3) at 50Hz. The lowest RL for a single individual shown to evoke an auditory response was 83 dB (re 1μPa) at 300 and 400Hz. The lowest RL averaged across all test subjects at a given frequency was 85dB (re 1μPa) at 400Hz. No responses were detected at 1,600Hz (max RL = 150 to 158dB). Mean ambient noise levels during testing decreased with frequency from 49dB (re $1\mu Pa^2$/Hz) at 50Hz to 41dB (re $1\mu Pa^2$/Hz) at 1,600Hz (Figure 5).

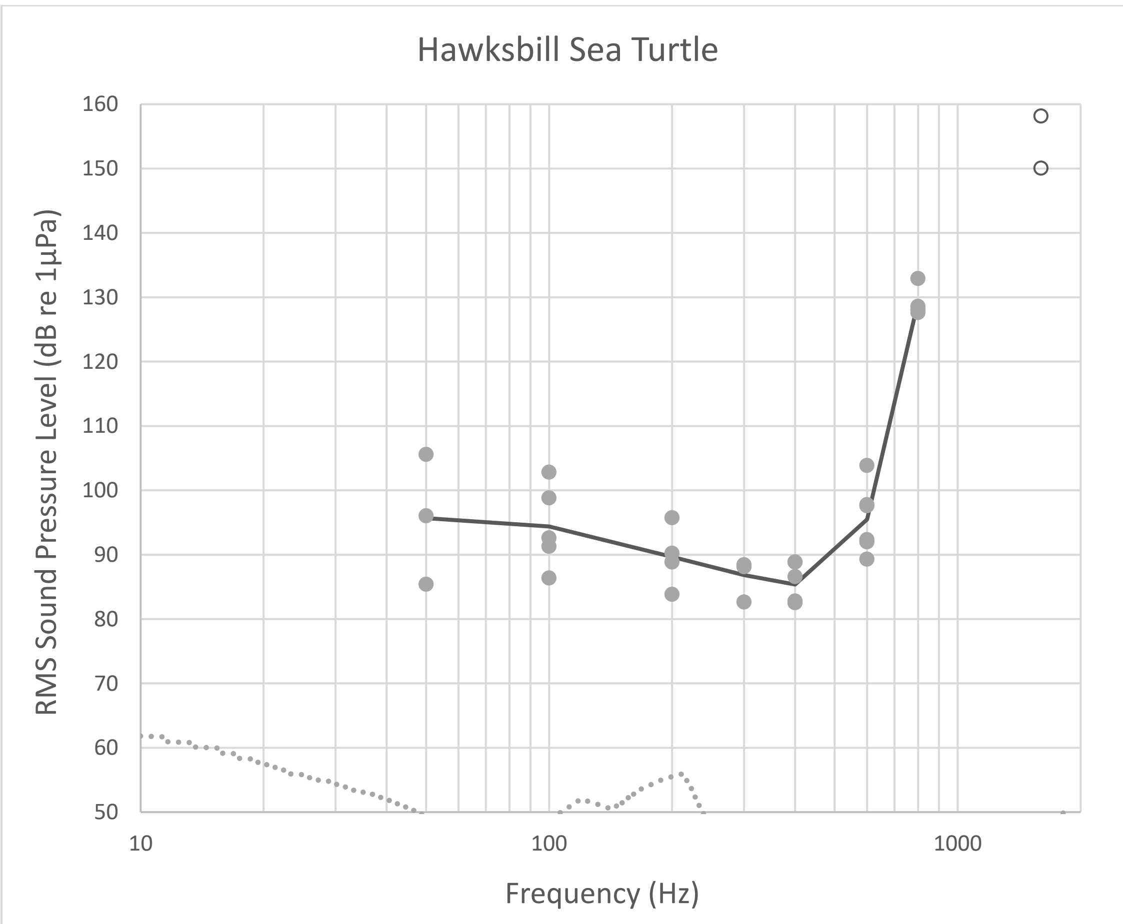

Figure 5. Auditory thresholds of hawksbill sea turtles.
Grey circles represent thresholds of individual test subjects. Open circles represent the maximum SPLs tested with no AEP responses. Solid line represents the mean auditory threshold at each frequency. Dotted line represents the mean spectrum level background noise (dB re $1\mu Pa^2$/Hz).

3.1.4 Loggerhead Sea Turtles

We recorded AEPs in 14 juvenile loggerhead sea turtles (4 wild-caught, 10 captive-raised). AEPs were detected between 50 and 600Hz. Peak sensitivity occurred below 400Hz where the audiogram remained relatively flat down to 50Hz (Table 2, Figure 6). A decline in sensitivity occurred at frequencies above 400Hz. Thresholds varied by as little as 13dB across test subjects (n = 3) at 600Hz, to as much as 34dB across test subjects (n = 10) at 400Hz. The lowest RL for a single individual shown to evoke an auditory response was 84dB (re 1µPa) at 200Hz. The lowest RL averaged across all test subjects at a given frequency was 95dB (re 1µPa) at 200 Hz. No responses were detected at 800Hz (max RL = 122 to 140dB) and 1,600Hz (max RL = 150 to 153dB). Mean ambient noise levels during testing decreased with frequency from 70dB (re 1µPa^2/Hz) at 50Hz to 40dB (re 1µPa^2/Hz) at 1,600Hz (Figure 6).

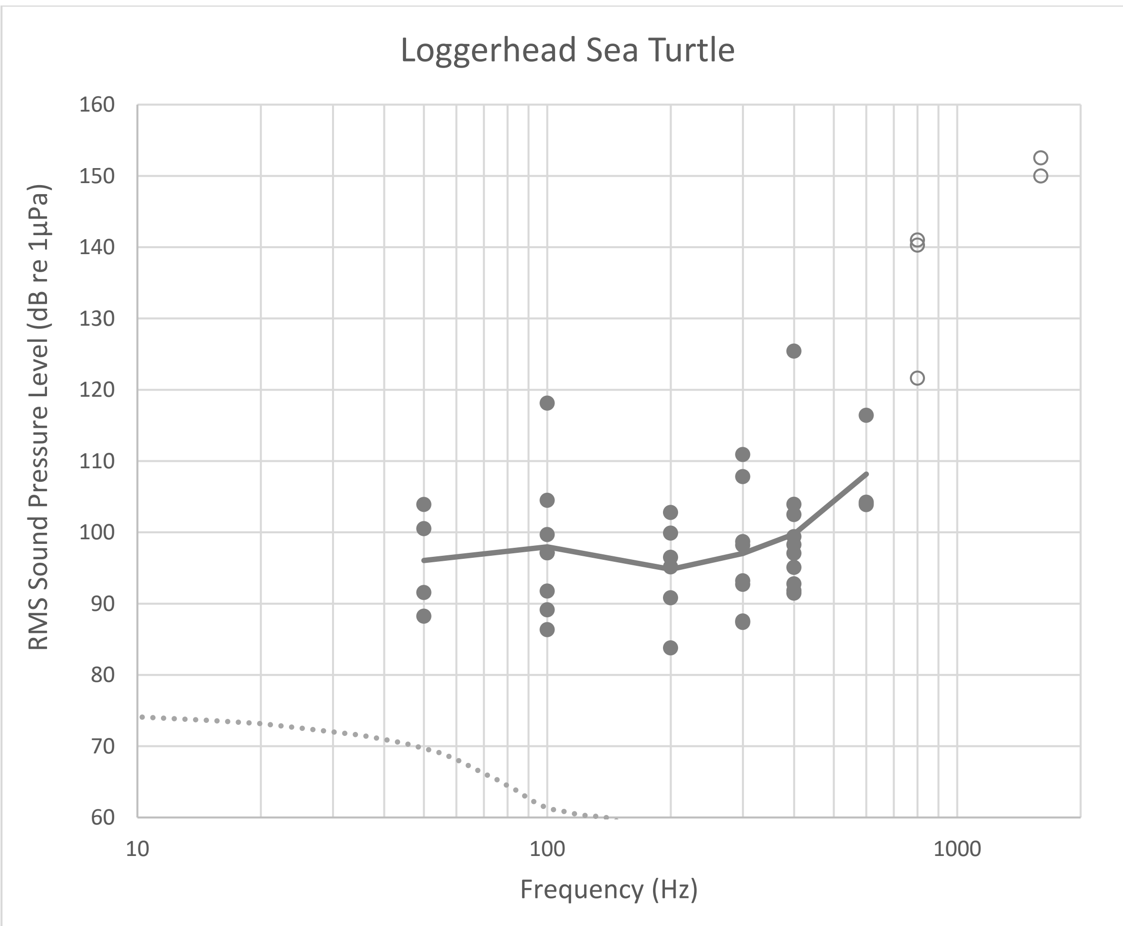

Figure 6. Auditory thresholds of loggerhead sea turtles.
Grey circles represent thresholds of individual test subjects. Open circles represent the maximum SPLs tested with no AEP responses. Solid line represents the mean auditory threshold at each frequency. Dotted line represents the mean spectrum level background noise (dB re 1µPa^2/Hz).

Table 2. Mean auditory thresholds (SPLrms dB re 1uPa) of each species at each frequency.

Species	50Hz	100Hz	200Hz	300Hz	400Hz	600Hz	800Hz
Green	103 (4)	99 (8)	87 (10)	92 (4)	87 (9)	95 (6)	116 (3)
Kemp's ridley	108 (2)	105 (9)	102 (8)	100 (5)	108 (8)	112 (8)	131 (1)
Hawksbill	96 (3)	94 (5)	90 (4)	87 (4)	85 (6)	95 (6)	129 (4)
Loggerhead	96 (4)	98 (8)	95 (6)	97 (8)	100 (10)	108 (3)	-

Note: The number of individuals tested at each frequency is given in parentheses.

3.2 Veterinary Findings

When all turtles were combined (wild, rehabilitation, captive-reared, greens, ridleys, loggerheads, hawksbill, manual restraint, sedation), plasma TS increased significantly during AEP testing by a mean of 0.14g/dL ($p = 0.0077$), and ionized calcium increased significantly by a mean of 0.03mmol/L ($p = 0.0285$), which are clinically irrelevant amounts, and no individual turtles had changes of clinical relevance in these two analytes. Lactate increased significantly by a mean of 1.06mmol/L ($p = 0.0008$), which is clinically insignificant. However, four turtles (three greens and one Kemp's ridley) experienced increases of >5mmol/L, which is clinically relevant (though minor compared with gill net interactions) (Snoddy et al., 2010) and even some routine physical examination changes (Mones et al., 2021), and one green sea turtle started at 10.3mmol/L and increased to 17.4mmol/L.

Blood pH decreased significantly by a mean of 0.0506 ($p = 0.0173$), also clinically insignificant, however one decreased from 7.622 to 6.887, the same green sea turtle as noted above with the high lactate values. This blood pH at the conclusion of the AEP testing is comparable to that of turtles entangled in gill nets. This reflects the fact that it had already expended substantial buffering capacity to counteract its high initial lactate (it had the lowest initial bicarbonate value, at 19.5mmol/L) incurred during initial capture and transport. No other turtle had a blood pH shift of clinical importance.

Glucose increased significantly by a mean of 26.9mg/dL ($p < 0.0001$), which is clinically relevant, and represents a classic adrenocortical-mediated stress response. Plasma corticosterone changes would likely support this conclusion (although timing could differ and be missed in our samples), and we could consider running those banked samples for corticosterone, pending validation of a corticosterone assay using sea turtle plasma. No values were clinically concerning as short-term changes. No differences were observed in these values between sedation and manual restraint groups at either time point.

3.2.1 Green Sea Turtles

Green turtle lactate increased by a mean difference of 3.57, but this difference was not quite statistically significant ($p = 0.0803$). Three green turtles had plasma lactate increases of more than 5mmol/L, which is clinically relevant. Green turtle glucose increased significantly by a mean difference of 22.7mg/dL ($p = 0.0021$). This is clinically significant, but with no clinically concerning values.

3.2.2 Kemp's Ridley Sea Turtles

Kemp's ridley lactate increased significantly by a mean difference of 1.39mmol/L ($p = 0.0015$) while pH actually increased significantly by a mean difference of 0.0524. These differences are not clinically significant, and only one turtle had an increase in lactate more than 3mmol/L. Kemp's ridley glucose increased significantly by a mean difference of 25.9mg/dL ($p = 0.0005$). This is clinically significant, but with no clinically concerning values as short-term changes.

3.2.3 Hawksbill Sea Turtles

Hawksbills had statistically significant but clinically insignificant changes in PCV (mean increase of 2.3L/L, $p = 0.0469$), plasma TS (mean increase of 0.47g/dL, $p = 0.0020$), pH (mean increase of 0.0663, $p = 0.0059$), and pCO_2 (mean increase of 4.5mmHg, $p = 0.0137$). The differences in PCV and TS were driven by a single outlier with initial values suggesting either a laboratory error or unrecognized lymph contamination. Blood glucose increased significantly by a mean difference of 33.4mg/dL ($p < 0.0001$), which is clinically significant but with no clinically concerning values as short-term changes.

3.2.4 Loggerhead Sea Turtles

Loggerhead lactate did not differ significantly following AEP testing, and no values were clinically concerning. PCV decreased significantly by a mean difference of 1.01L/L ($p = 0.0049$), but this difference is not clinically relevant. Loggerhead glucose increased significantly by a mean difference of 24.3mg/dL ($p < 0.0001$), which is clinically significant but with no clinically concerning values as short-term changes.

4 Discussion

These results suggest the four species are most sensitive to low frequencies (with greatest hearing sensitivity occurring from approximately 100 to 400Hz), followed by a decrease in sensitivity somewhere between 400 and 600Hz, and lowest sensitivity above 1,000Hz. The findings are similar to general trends reported in previous AEP studies (Bartol et al., 1999; Lavender et al., 2014; Martin et al., 2012; Piniak et al., 2016; Dow Piniak et al., 2012) (Table 3).

There are, however, key differences between the results of this study and those preceding it. We found hearing thresholds in the green, Kemp's ridley, and hawksbill sea turtles to be lower than previously reported. We also detected hearing capabilities in the Kemp's ridley sea turtle over a broader range than previously reported. Conversely, we detected hearing capabilities in the green, loggerhead, and hawksbill sea turtle over a narrower range that previously reported. These differences may be due to variation across study designs or variation across individual test subjects. Factors that may affect study outcomes are discussed in the following sections.

Table 3. Summary of hearing sensitivity studies conducted on sea turtles.

Species/Age Class	Method	Location of Sound Source	Location of Head	Measured Hearing Range (Hz)	Range of Greatest Sensitivity (Hz)	Lowest Hearing Threshold (dB re 1µPa)	Sample Size	Source
Green Sea Turtle								
Juvenile	AEP	aerial	partially submerged	100–800	600–700	94	2	Bartol & Ketten, 2006
Sub-adult	AEP	aerial	partially submerged	100–500	200–300	91	6	Bartol & Ketten, 2006
Juvenile	AEP	underwater	underwater	50–1,600	200–400	93	5	Piniak et al., 2016
Juvenile	***AEP***	***underwater***	***underwater***	***50–800***	***200–400***	***87***	***14***	***This Study***
Loggerhead Sea Turtle								
Post-hatchling juvenile	AEP	underwater	underwater	50–1,100	50–400	119	13	Lavender et al., 2014
Post-hatchling juvenile	Behavior	underwater	underwater	50–1,000	100–400	95	8	Lavender et al., 2014
Adult	AEP	underwater	underwater	100–1,131	100–400	110	1	Martin et al., 2012
Adult	Behavior	underwater	underwater	50–800	100–400	98	1	Martin et al., 2012
Juvenile	***AEP***	***underwater***	***underwater***	***50–600***	***50–400***	***95***	***14***	***This Study***

Species/Age Class	Method	Location of Sound Source	Location of Head	Measured Hearing Range (Hz)	Range of Greatest Sensitivity (Hz)	Lowest Hearing Threshold (dB re 1µPa)	Sample Size	Source
Kemp's Ridley Sea Turtle								
Juvenile	AEP	aerial	partially submerged	100–500	100–200	110	2	Bartol & Ketten, 2006
Juvenile	***AEP***	***underwater***	***underwater***	***50–800***	***200–300***	***100***	***13***	***This Study***
Hawksbill Sea Turtle								
Hatchling	AEP	underwater	underwater	50–1,600	200–400	88	10	Dow Piniak, 2012
Juvenile	***AEP***	***underwater***	***underwater***	***50–800***	***200–400***	***85***	***6***	***This Study***
Leatherback Sea Turtle								
Hatchling	AEP	underwater	underwater	50–1,200	100–400	84	11	Dow Piniak et al. 2012

4.1 AEP and Behavioral Testing Paradigms

The use of electrophysiological methods in this study was necessary in order to obtain data from a large number of test subjects in a consistent and efficient manner. It has been shown however, that psychophysical methods can be more sensitive in determining hearing thresholds of sea turtles (Martin et al., 2012; Lavender et al., 2014). Such experiments require many months or years of training and subsequent testing, often with only a small subset of subjects achieving adequate response reliability. The results from this study fill a critical data gap regarding the overall hearing range and frequencies of greatest sensitivity. However, the absolute hearing thresholds of the four species may be lower than what can be detected through measurements of AEPs (Popper et al., 2014; Sisneros et al., 2016). Therefore, the results presented here should be considered a conservative estimate of absolute hearing thresholds.

4.2 Temperature Effects

To reduce stress, temperatures in the test tanks were matched to the open water temperatures or rehabilitation tank temperatures that the subjects were sourced from. This resulted in differences in body temperature across test subjects. New research, published during the third year of this study by Wang et al. (2022), revealed that body temperature can affect hearing sensitivity in the freshwater turtle *Trachemys scripta elegans*. Temperature may therefore have played a role in the hearing sensitivities of the four marine species measured here. The effect size however is unclear. In this study we measured each test subject once, without repeating tests at varying body temperatures. Within the limited temperature ranges of this study, regression analysis of the data showed mixed results, with no statistical significance at most frequencies. Of the regressions with statistical significance, both positive and negative correlations were found: one positive (over a very limited temperature range [3.1°C]) and two negative (over a wider range of temperatures [7.0 and 8.9°C]). Random (temperature-independent) variation in hearing sensitivity across individuals may have obscured temperature effects in these regressions. Future studies should include repeated measurements of the same test subjects at different temperatures to quantify the relationship between hearing threshold and temperature at each frequency.

4.3 Masking Effects

Laboratory noise was minimized to the greatest extent possible during testing. Among the test frequencies, noise levels were greatest at 50Hz where they fell below measured hearing thresholds by at least 23dB in the green, 30dB in the Kemp's ridley, 36dB in the hawksbill, and 18dB in the loggerhead, sea turtle. Background noise levels decreased with increasing frequency, leaving a larger gap between measured hearing thresholds and noise levels above 50Hz. It is unclear whether acoustic masking occurred at any frequencies. As noted in Martin et al. (2012), there is a complete absence of published critical ratio (threshold to noise) data pertaining to sea turtles. Critical ratio studies of other nonmammalian vertebrates show variation across species and across frequencies within species. For example, Wysocki and Ladich (2005) found threshold to noise ratios (T/N) to increase with frequency from 9.7dB (at 200Hz) to 25dB (at 2000Hz) in *Carassius auratus* and from 9.6dB (at 100Hz) to 31.1dB (at 800Hz) in *Lepomis gibbosus*. Simmons (1988) reported critical ratios of 18dB (at 1,000Hz) with a rate of increase of 4dB/octave in *Rana catesbeiana*. Future studies should measure the critical ratios of sea turtle hearing across frequencies to determine if masking played a role in the outcome of all previously published sea turtle audiograms and to establish minimum requirements for ambient noise levels during future hearing tests.

4.4 Electromagnetic Artifacts at High SPLs

When driving the speaker at high wattage, the electromagnetic field produced by the speaker interfered with AEP measurements. This occurred at 1,200 and 1,600Hz where hearing sensitivity was poor in the test subjects and high SPLs would be needed to determine hearing thresholds. We therefor reported the highest SPLs tested in which no electromagnetic interference occurred, and no AEP was detected. Hearing thresholds fall somewhere above these levels.

4.5 Health Effects of Study Conditions

Underwater AEP testing requires restraint amounting to forced submergence, versus technically much simpler but less representative in-air testing. Despite these test conditions, this study demonstrates that with firm manual restraint constraining foreflipper movement, with or without light sedation, and with frequent predictable surface access for breathing, impacts on sea turtle blood gases, lactate and plasma biochemistry are negligible, far less than gill net entanglement (Snoddy et al., 2010), and even less than routine physical examinations (Mones et al., 2021).

4.6 Conclusion

This study demonstrates that green, Kemp's ridley, hawksbill, and loggerhead sea turtles at the juvenile life stage have hearing sensitivities within the frequency band where most anthropogenic noise occurs. While the audiograms presented here provide critical information on sea turtle hearing, it should be noted that actual hearing sensitivities may be lower than what is detectable through AEP measurements. The results presented here should be treated as a conservative estimate of absolute hearing thresholds.

The effects of noise on sea turtles at the individual or population level remain unknown. Future studies should aim to determine how sea turtles use sound in the natural environment and how this may be disrupted in the presence of noise. Investigations of both physiological and behavioral responses to noise are needed. The results presented here provide necessary foundational knowledge of sea turtle hearing for such studies.

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Appendix A: Individual Hearing Thresholds

A.1 Green Sea Turtles

Table A.1. Individual hearing thresholds (SPLrms dB re1µPa) of the 14 green sea turtle test subjects at each frequency.

Turtle ID	Water Temperature (°C)	50Hz	100Hz	200Hz	300Hz	400Hz	600Hz	800Hz	1,200Hz	1,600Hz
4803 *Cm**	22.7	-	102	93	-	95	-	-	-	>159
4891 *Cm**	19.6	-	100	97	-	84	-	-	>163	>161
4892 *Cm**	19.6	-	81	79	-	84	-	-	-	-
4893 *Cm**	20.2	-	-	80	-	86	-	-	-	-
4899 *Cm**	20.4	-	107	96	-	82	-	-	-	>159
4900 *Cm**	20.2	-	99	87	-	85	117	-	-	>165
4904 *Cm**	20.2	97	109	78	-	79	-	-	-	-
4905 *Cm**	22.4	-	101	83	-	89	103	-	-	>154
4934 Cm	27.2	104	-	-	94	-	86	113	-	-
4937 Cm	23.6	-	-	-	92	-	86	120	-	-
4940 Cm	23.5	106	-	-	90	-	91	115	-	-
Bittersweet *Cm**	24.0	-	-	-	93	-	88	-	-	-
Lilac *Cm**	22.3	-	97	90	-	98	-	-	-	-
Mauvelous *Cm*	23.3	107	-	84	-	-	-	-	-	-
Mean	**-**	**103**	**99**	**87**	**92**	**87**	**95**	**116**	**-**	**-**

Note: Subjects that were sedated during testing are indicated with an asterisk. Genus and species (*Chelonia mydas*) are indicated by *Cm*.

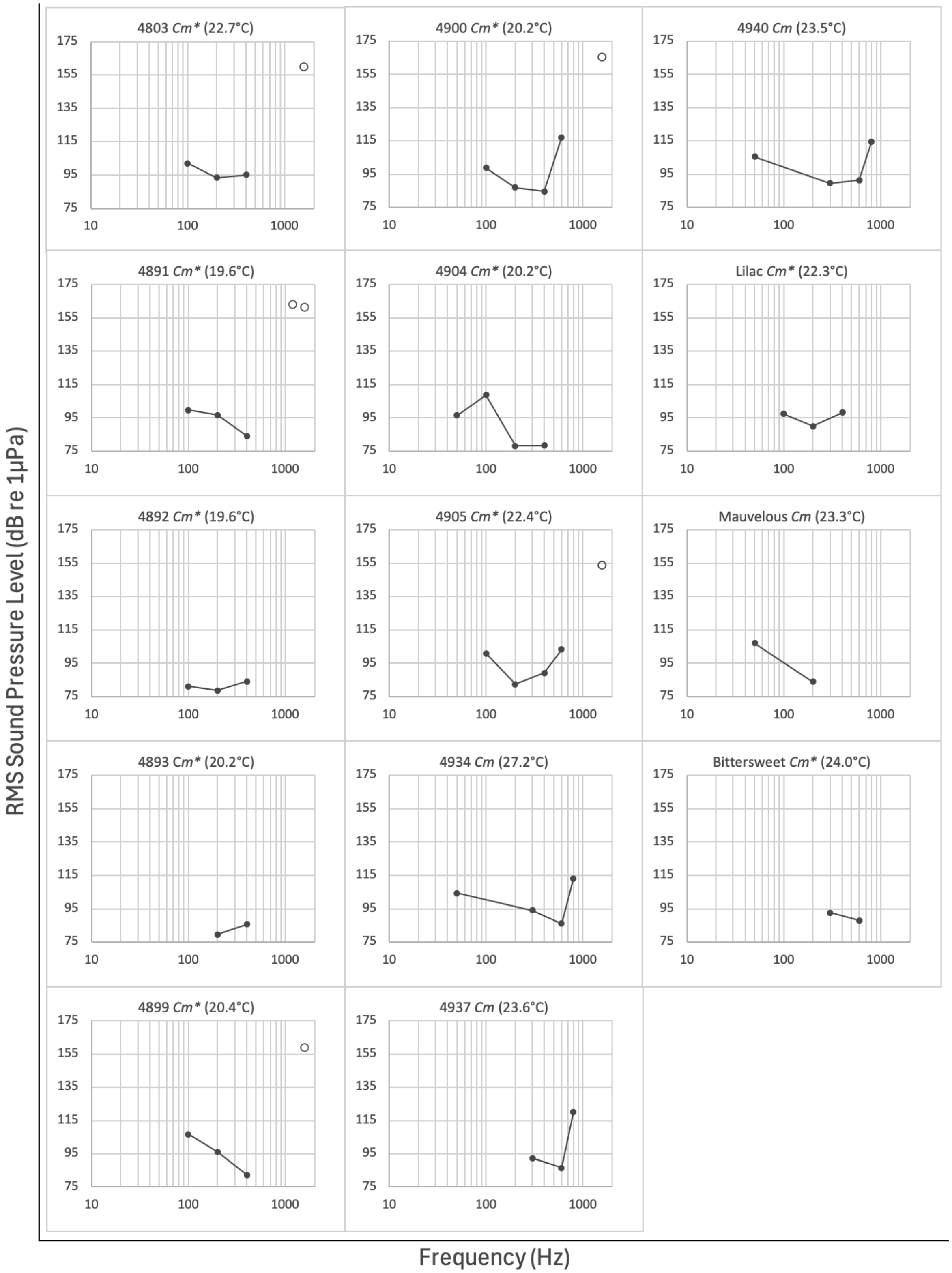

Figure A.1. Individual audiograms of the 14 green sea turtle test subjects.
Solid circles represent measured hearing thresholds. Open circles represent the maximum SPL tested with no AEP response. Water temperatures are provided in parentheses. Subjects that were sedated during testing are indicated with an asterisk. Genus and species are indicated by Cm.

A.2 Kemp's Ridley Sea Turtles

Table A.2. Individual hearing thresholds (SPLrms dB re 1μPa) of the 13 Kemp's ridley sea turtle test subjects at each frequency.

Turtle ID	Water Temperature (°C)	50Hz	100Hz	200Hz	300Hz	400Hz	600Hz	800Hz	1,200Hz	1,600Hz
4818 *Lk**	23.0	110	98	86	-	111	-	-	-	>161
4888 *Lk*	19.4	-	96	101	-	113	128	-	-	-
4890 *Lk*	19.2	-	108	107	-	-	-	-	-	-
4894 *Lk**	20.0	-	110	103	-	120	-	-	-	-
4923 *Lk*	28.3	-	-	-	98	-	104	131	-	-
4930 *Lk*	27.4	-	120	112	107	-	113	-	-	-
4933 *Lk*	28.0	-	103	-	98	98	95	-	-	>147
Aquamarine *Lk*	22.3	-	-	100	-	97	112	-	-	-
Gypsum *Lk*	25.0	106	-	-	94	-	-	-	-	-
Leaper *Lk*	23.4	-	104	98	-	106	123	-	-	>165
Limeapalooza *Lk**	24.0	-	-	-	105	-	106	-	>143	>143
Pocus *Lk*	23.2	-	107	112	-	119	-	-	-	>160
TurtleDove *Lk*	23.7	-	101	-	-	103	117	-	-	-
Mean	**-**	**108**	**105**	**102**	**100**	**108**	**112**	**131**	-	-

Note: Subjects that were sedated during testing are indicated with an asterisk. Genus and species (*Lepidochelys kempii*) are indicated by *Lk*.

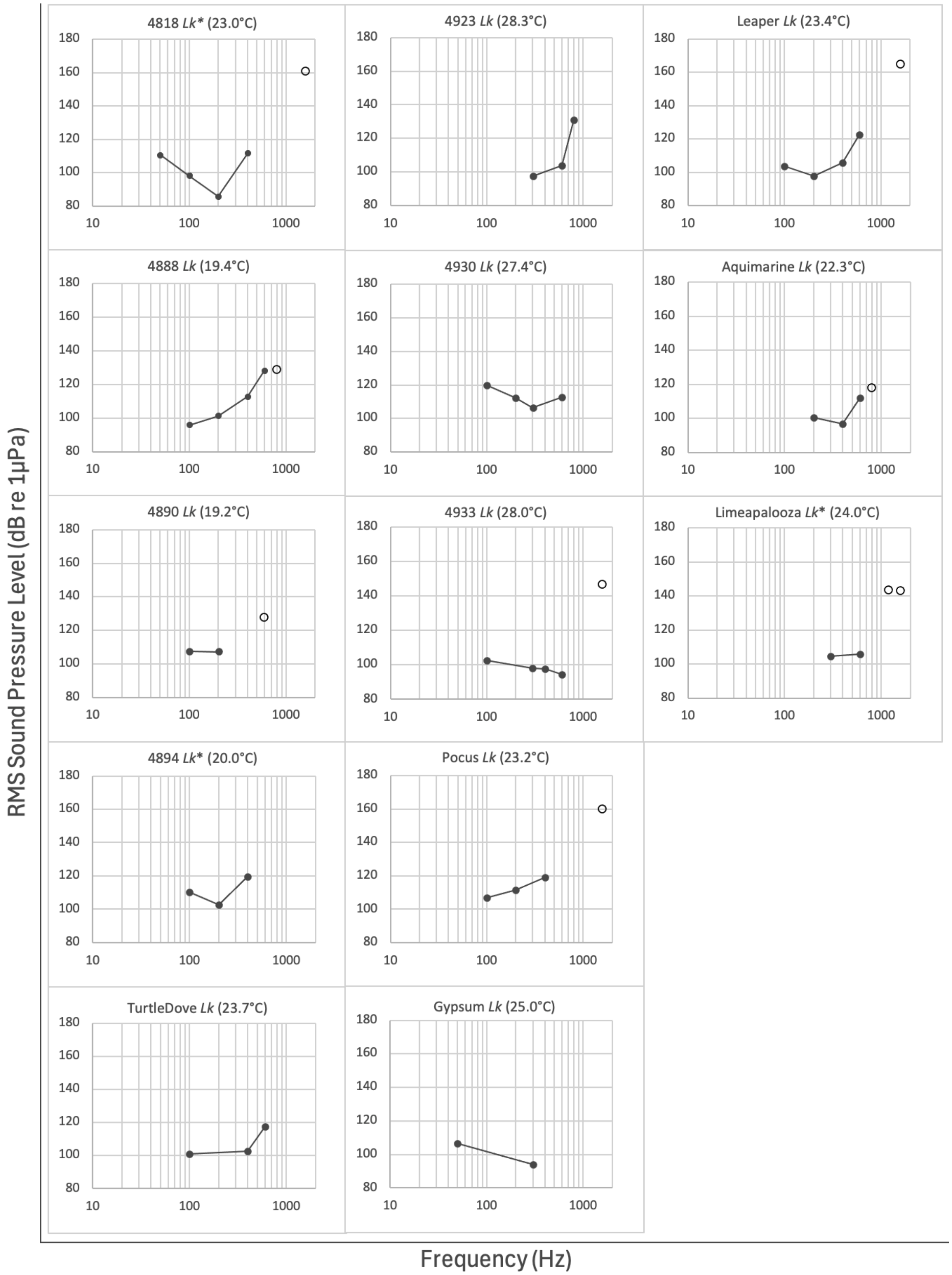

Figure A.2. Individual audiograms of the 13 Kemp's ridley sea turtle test subjects.
Solid circles represent measured hearing thresholds. Open circles represent the maximum SPL tested with no AEP response. Water temperatures are provided in parentheses. Subjects that were sedated during testing are indicated with an asterisk. Genus and species are indicated by *Lk.*

A.3 Hawksbill Sea Turtles

Table A.3. Individual hearing thresholds (SPLrms dB re 1µPa) of the six hawksbill sea turtle test subjects at each frequency.

Turtle ID	Water Temperature (°C)	50Hz	100Hz	200Hz	300Hz	400Hz	600Hz	800Hz	1,600Hz
Kiki *Ei*	25.1	-	103	89	88	89	104	129	>158
SusieMarie *Ei*	25.4	106	-	96	88	83	98	-	-
Ettafaye *Ei*	25.2	85	93	84	83	83	92	-	>150
Beetlejuice *Ei*	25.6	-	91	-	-	89	92	128	-
Mimosa *Ei**	25.6	-	99	-	-	83	98	128	-
Vaughn *Ei*	25.1	96	86	90	88	87	89	133	-
Mean	**-**	**96**	**94**	**90**	**87**	**85**	**95**	**129**	**-**

Note: Subjects that were sedated during testing are indicated with an asterisk. Genus and species (*Eretmochelys imbricata)* are indicated by *Ei*.

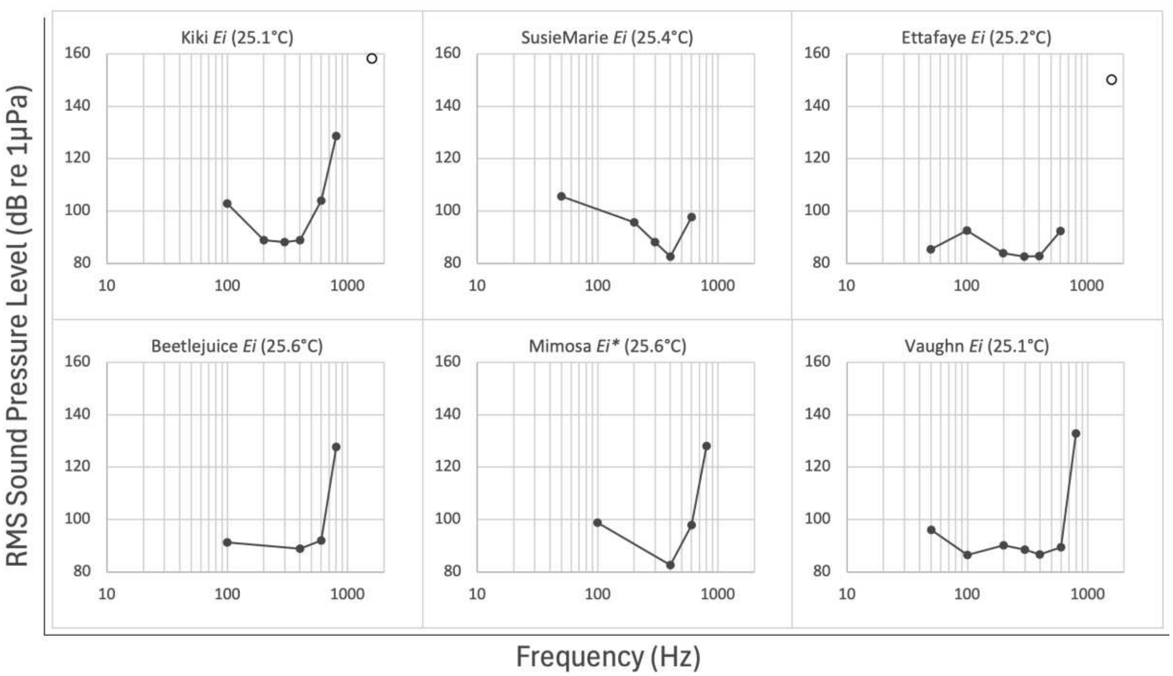

Figure A.3. Individual audiograms of the six hawksbill sea turtle test subjects.
Solid circles represent measured hearing thresholds. Open circles represent the maximum SPL tested with no AEP response. Water temperatures are provided in parentheses. Subjects that were sedated during testing are indicated with an asterisk. Genus and species are indicated by *Ei*.

A.4 Loggerhead Sea Turtles

Table A.4. Individual hearing thresholds (SPLrms dB re 1µPa) of the 14 individual loggerhead sea turtle test subjects at each frequency.

Turtle ID	Water Temperature (°C)	50Hz	100Hz	200Hz	300Hz	400Hz	600Hz	800Hz	1,600Hz
4954 Cc	24.8	-	100	103	111	-	-	>140	-
4965 Cc	26.2	-	-	-	87	92	-	-	-
CC1 Cc	22.5	-	-	84	-	95	104	-	-
CC2 Cc*	22.9	-	104	100	-	125	-	-	-
Cheddar Cc	28.2	-	-	-	98	-	-	>141	-
Feta Cc	27.9	-	97	-	99	-	-	-	>150
Goat Cc	28.4	-	89	-	88	-	-	-	-
Gorgonzola Cc	25.6	-	118	-	93	104	116	>122	-
Mozzarella Cc	28.6	-	-	-	108	97	-	-	>153
Muenster Cc	26.0	104	-	96	93	99	104	-	-
Paneer Cc	27.9	101	86	-	-	98	-	-	-
Parmesan Cc	28.3	88	-	-	-	91	-	-	-
Ricotta Cc	26.0	-	97	91	-	93	-	-	-
Swiss Cc	28.3	92	92	95	-	102	-	-	-
Mean	**-**	**96**	**98**	**95**	**97**	**100**	**108**	**-**	**-**

Note: Subjects that were sedated during testing are indicated with an asterisk. Genus and species (*Caretta caretta*) are indicated by *Cc*.

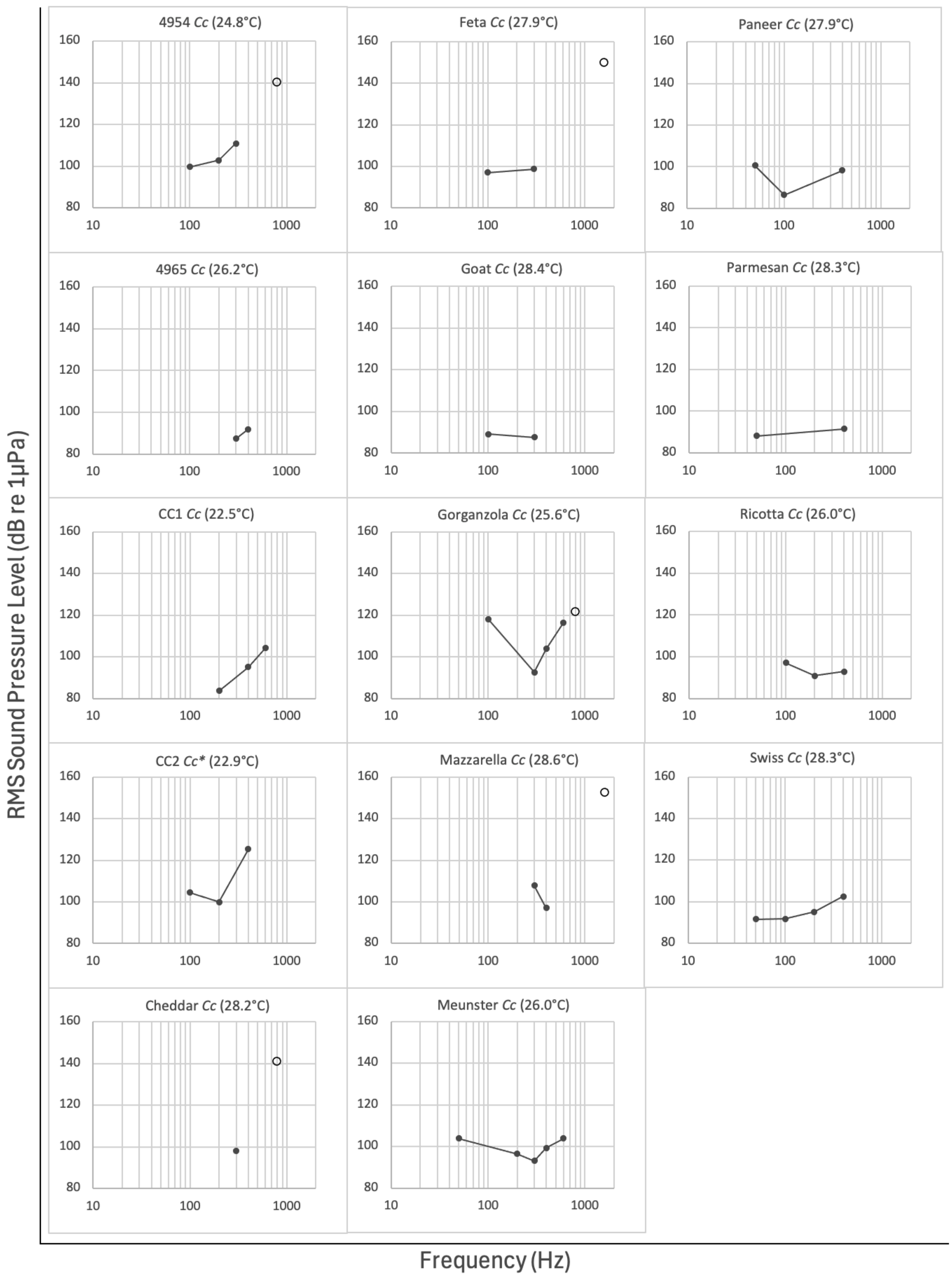

Figure A.4. Individual audiograms of the 14 loggerhead sea turtle test subjects.
Solid circles represent measured hearing thresholds. Open circles represent the maximum SPL tested with no AEP response. Water temperatures are provided in parentheses. Subjects that were sedated during testing are indicated with an asterisk. Genus and species are indicated by *Cc*.

Appendix B: Temperature Effects

B.1 Green Sea Turtles

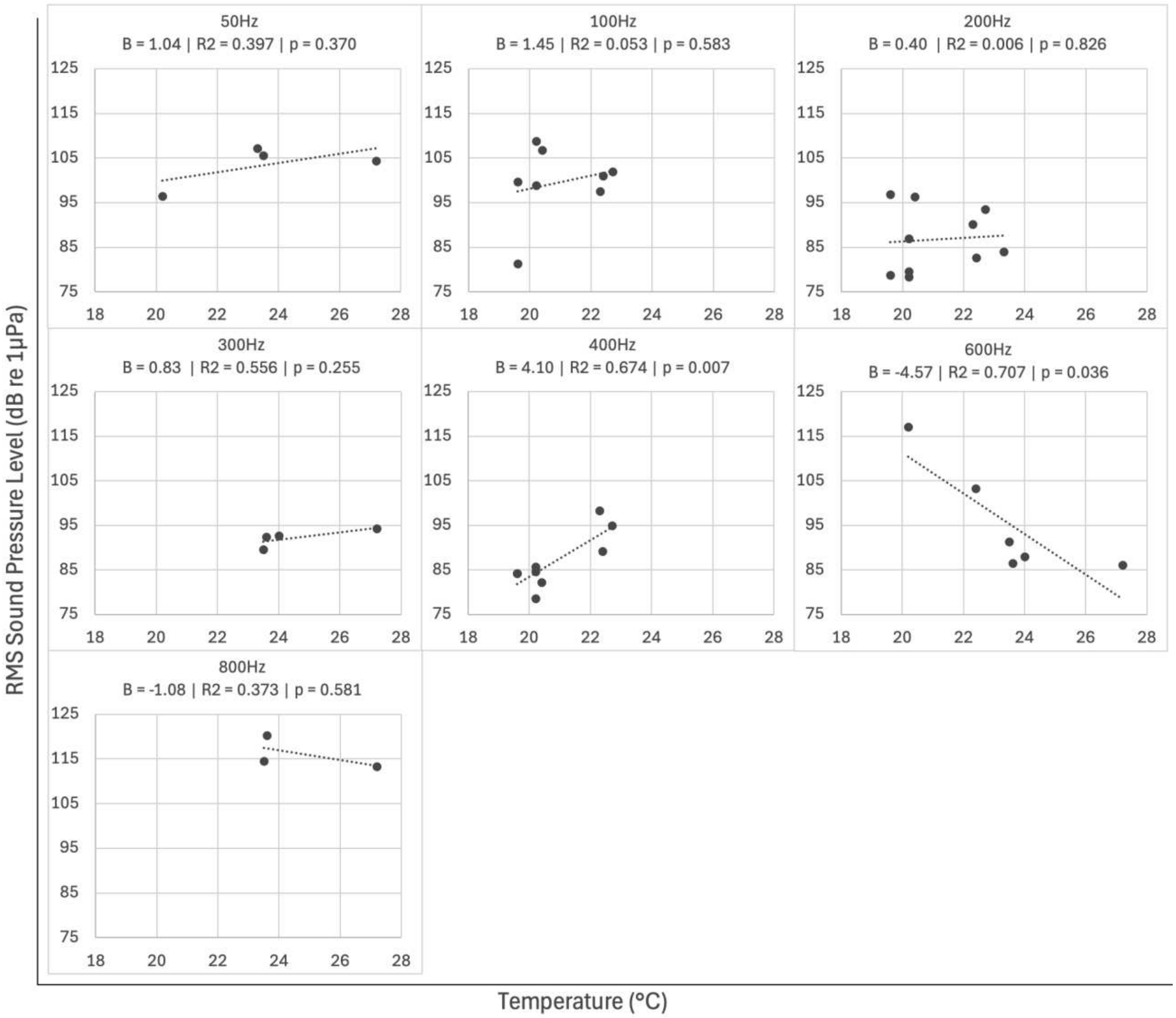

Figure B.1. Linear regression plots of green sea turtle hearing threshold vs temperature at each frequency.
Grey circles represent auditory thresholds of individual test subjects. A statistically significant ($p < .05$) positive correlation occurred at 400Hz. A statistically significant ($p < .05$) negative correlation occurred at 600Hz.

B.2 Kemp's Ridley Sea Turtles

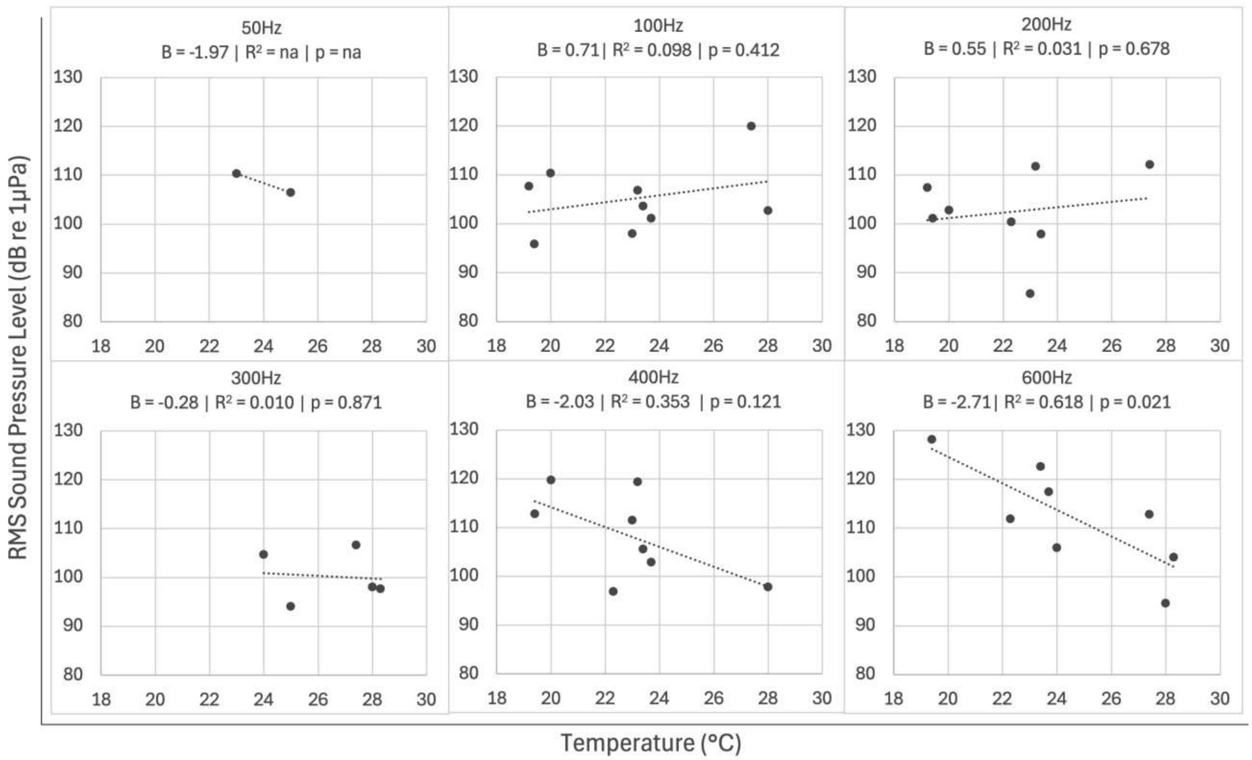

Figure B.2. Linear regression plots of Kemp's ridley sea turtle hearing threshold vs temperature at each frequency.
Grey circles represent auditory thresholds of individual test subjects. A statistically significant ($p < .05$) negative correlation occurred at 600Hz.

B.3 Loggerhead Sea Turtles

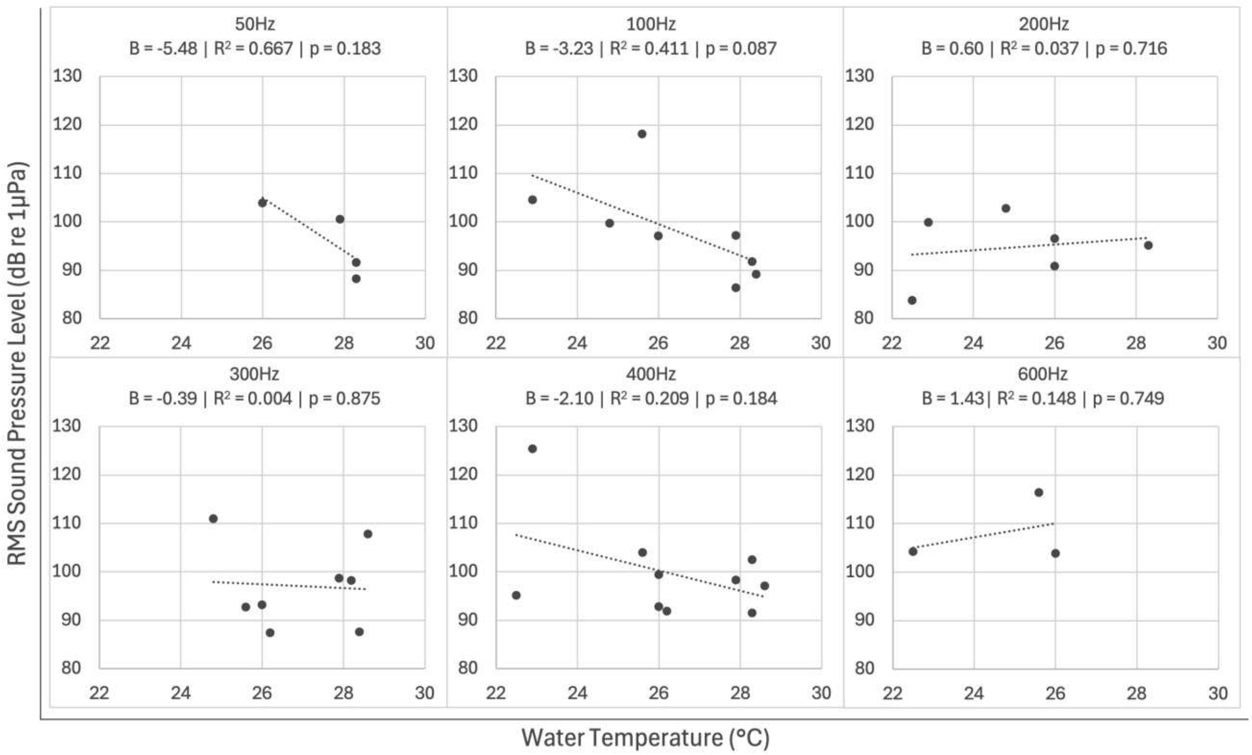

Figure B.3. Linear regression plots of loggerhead sea turtle hearing threshold vs temperature at each frequency.
Grey circles represent auditory thresholds of individual test subjects. No statistically significant ($p < .05$) correlations were present.

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