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Evoked potential audiograms of the nurse shark (*Ginglymostoma cirratum*) and the yellow stingray (*Urobatis jamaicensis*)

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Abstract The hearing thresholds of the nurse shark, *Ginglymostoma cirratum*, and the yellow stingray, *Urobatis jamaicensis*, were measured using auditory evoked potentials (AEP). Stimuli were calibrated using a pressure-velocity probe so that the acoustic field could be completely characterized. The results show similar hearing thresholds for both species and similar hearing thresholds to previously measured audiograms for the lemon shark, *Negaprion brevirostris*, and the horn shark, *Heterodontis francisi*. All of these audiograms suggest poor hearing abilities, raising questions about field studies showing attraction of sharks to acoustic signals. By extrapolating the particle acceleration thresholds into estimates of their equivalent far-field sound pressure levels, it appears that these sharks cannot likely detect most of the sounds that have attracted sharks in the field.

Keywords Elasmobranch · Hearing · Audiogram · Auditory Evoked Potential · Particle acceleration

Introduction

Audition in elasmobranchs has been widely reviewed (Wisby et al. 1964; Popper and Fay 1977; Corwin 1981a, 1989; Myrberg 2001; Hueter et al. 2004), but very few experiments have been conducted during the last two decades. Early experiments included measurements of the hearing thresholds of several species (Kritzler & Wood 1961; Olla 1962; Banner 1967; Nelson 1967; Kelly and Nelson 1975; Casper et al. 2003), examinations of the anatomy involved in sound detection (Tester et al. 1972; Fay et al. 1974; Corwin 1977), mapping the auditory neural pathways (Barry 1987), and field attraction experiments to determine what sounds attract sharks in their natural environments (Nelson and Gruber 1963; Richard 1968; Myrberg et al. 1969; Nelson et al. 1969; Myrberg et al. 1972; Myrberg 1978). Despite this vast literature, the overall hearing abilities of this subclass of fishes remain largely unknown.

Of the five species of elasmobranchs tested, only two studies measured hearing thresholds with reference to particle motion, the lemon shark (Banner 1967) and the horn shark (Kelly and Nelson 1975), while the rest measured the pressure sensitivity of the sharks (Kritzler and Wood 1961; Nelson 1967; Casper et al. 2003). Sound consists of a propagating sound pressure wave and directional particle motion (for general reviews see Kalmijn 1988; Rogers and Cox 1988; Bass and Clark 2003; Bass and McKibben 2003). In order to detect sound pressure, a pressure-to-displacement transducer, such as the swim bladder found in many teleosts, is required. Without any kind of air-filled cavity the otolith organs can theoretically only detect particle motion, which appears to be the

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case in all elasmobranchs. Particle motion is a directional stimulus that drops off quickly as the distance from the sound source increases.

The audiograms of the lemon shark and horn shark show frequency sensitivity from 20 Hz to 1,000 Hz with best sensitivities at lower frequencies. In general, their hearing is not very sensitive in comparison to fishes with peripheral hearing adaptations, such as the goldfish (Fay 1988). Shark hearing sensitivity is more similar to fishes without swimbladders or other accessory hearing structures, all of which can only detect particle motion.

In the 1960s and 1970s several scientists used powerful speakers (US Navy J9 and J11) to transmit a wide variety of sound stimuli into the water in an attempt to determine what kind of sounds attract sharks in their natural environment (Nelson and Gruber 1963; Richard 1968; Nelson et al. 1969; Myrberg et al. 1969; Myrberg et al. 1972). These researchers found that when playing variably pulsed sounds, especially at low frequencies, sharks appeared to be attracted to and would orient to these sounds from distances as far as 250 m from the speakers. These results appear contradictory to laboratory experiments that have suggested poor hearing sensitivity. Additionally, shark ear anatomy indicates they should only detect particle motion, which attenuates quickly as the distance from a sound source increases. These obvious discrepancies indicate that there is still much unknown about the hearing abilities of elasmobranchs and that further research in this sensory modality of elasmobranchs is needed.

The goals of this experiment were to measure the hearing sensitivity of the nurse shark, *Ginglymostoma cirratum*, and the yellow stingray, *Urobatis jamaicensis*, to compare their thresholds to those of other elasmobranchs previously tested. These fishes belong to two orders of elasmobranchs, Orectolobiformes and Myliobatiformes, in which hearing has never been measured. *G. cirratum* was one of the many species of sharks that appeared when sounds were played in several of the field experiments (Richard 1968; Myrberg et al. 1969; Nelson et al. 1969) and the resulting thresholds obtained in this experiment can be used to determine how far the nurse shark can detect sounds from a source and relate the data to that found in the field experiments. Hearing tests were conducted using the auditory evoked potential method (AEP), a neurophysiological method of recording evoked potentials from the brain in response to acoustic stimuli (Kenyon et al. 1998). This method has been used to measure hearing thresholds in the little skate, *Raja erinacea*, and results obtained from this technique were similar to those measured with operant conditioning (Casper et al. 2003).

Materials and methods

Five each of *G. cirratum* (0.70–1.28 m standard length) and *U. jamaicensis* (0.15–0.24 m disc width) were caught with large nets while snorkeling in the water (0.5–3 m) surrounding the Florida Institute of Oceanography's Florida Keys Marine Lab (Long Key, Florida) during July of 2003. The fishes were held either in holding lagoons (sharks) or in cement tanks (rays) and fed pieces of squid. The cement lagoon used for hearing tests was 37 m × 15 m with an island (15 m × 2 m) found in the middle (Fig. 1A), and had circulating water pumped from the bay just north of the lab. All experiments were conducted in the narrow canal between the island and the land surrounding the southern portion of the lagoon where the water depth was 1.05 m. The sides of the canal were sloped at an angle with curved borders leading to a flat bottom of cement (Fig. 1B). Experimental procedures followed guidelines for the care and use of animals approved by the Institutional Animal Care and Use Committee at University of South Florida.

Each test fish was submerged in water containing MS-222 (tricaine methanosulfate, Fisher) for less than 1 minute and was then placed in stiff plastic mesh holders (2.54 cm × 2.54 cm holes). These holders were tightened with tie wraps that were tight enough to keep the fish from moving, but did not affect breathing. The restrained fish was then suspended from an aluminum bridge (stretching over the lagoon to the island) using bungee cords 0.5 m below the water's surface. The transducer (Aquasonic Tactile Sound Underwater Speaker, Clark Synthesis, Littleton, CO USA) was hung with a bungee cord from a rope tied across the lagoon 1 m from the head of the fish. The rope was tied at both ends onto pieces of rebar that were sunk into the ground outside the channel to keep any vibrations from the speaker isolated from the test fish.

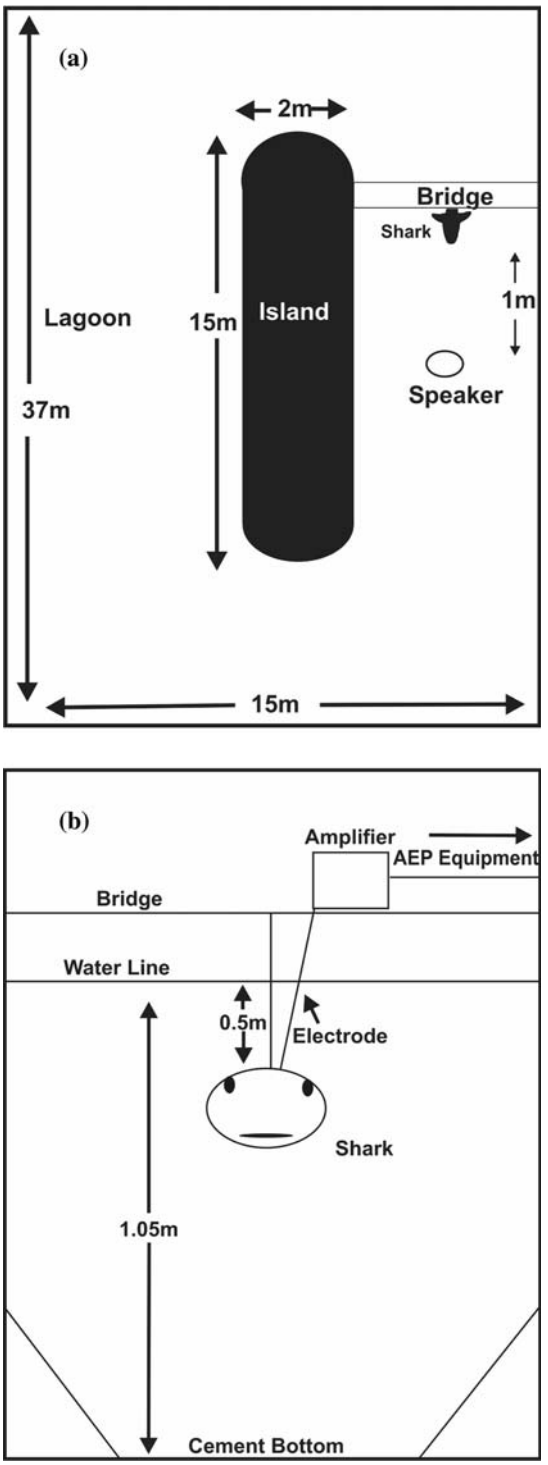

Fig. 1 (**A**) Overhead view of the lagoon setup. (**B**) Cross-sectional view looking directly at the shark. Figures not drawn to scale

Wire electrodes (12 mm × 28 Ga low profile needle electrode, JARI Electrode Supply, Gilroy, CA USA) were placed subdermally 1cm posterior to the endolymphatic pores (recording electrode), in the dorsal musculature near the dorsal fin (reference electrode) and free in the water (ground electrode). The electrodes were connected to a pre-amplifier (TDT HS4) which was then connected by a fiber-optic cable to a TDT (Tucker Davis Technologies, Gainesville, FL USA) evoked potential workstation with BioSig software.

Sounds were 50 ms pulsed tones shaped with a Hanning window and were presented with a 70 ms presentation period (14/second). Test frequencies ranged from 100 Hz to 2,000 Hz, but AEP signals were only obtained from fishes up to 1,000 Hz. Sounds were attenuated in 6 dB steps beginning at the loudest level that could be generated at each frequency. The AEP waveforms were digitized at 25 kHz and averaged between 100 and 1,000 times (Fig. 2A). More averages are needed as the signal moves closer to the threshold in order to pull the signal out of the noise floor.

A 2,048-point Fast Fourier Transform (FFT) was used to analyze the AEP signals in the frequency domain. The entire 70 ms window was FFT transformed because in many of the lower frequencies that were tested the recorded signal took up the entire window so this was done at every frequency to remain consistent. An AEP was determined to be present if the signal showed a doubling of the sound frequency (e.g., 400 Hz peak when the signal played was 200 Hz) with a peak at least 3 dB above the noise floor. The noise floor is estimated from the AEP power spectrum with a window of 100 Hz around the doubling frequency (i.e., 50 Hz on each side of the peak) (Fig. 2B). This frequency doubling occurs in all low frequency fish AEP testing (Mann et al. 2001; Egner and Mann 2005).

Following all hearing tests the fish was removed and replaced with a pressure/velocity probe (Acoustech Corporation, Philadelphia, PA USA) that was positioned where the head of the fish had been. The probe contained a velocity geophone (sensitivity 9.36 mV/cm/s, bandwidth 100 Hz–1 kHz) and a hydrophone (sensitivity: −186.1 dB re 1 V/μPa, bandwidth 10 Hz–2 kHz), which could simultaneously record sound pressure and particle velocity. Calibration with the geophone was performed in all

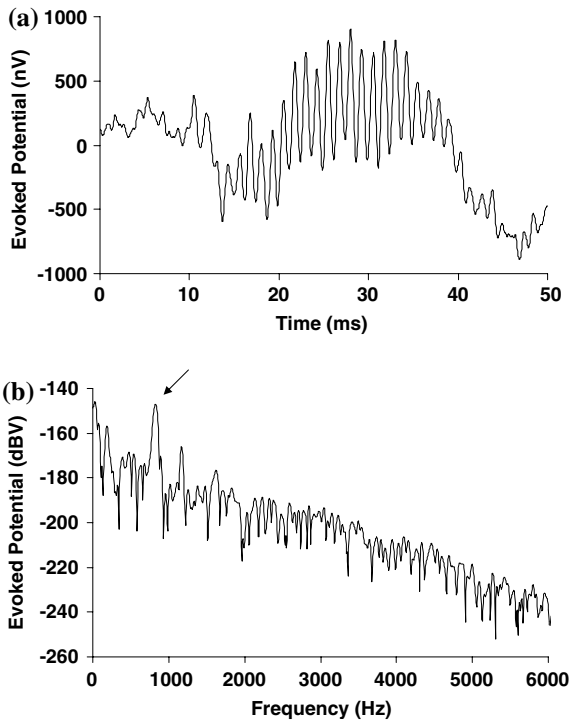

Fig. 2 (**A**) Example of the 400 Hz AEP of a nurse shark in the time domain with particle acceleration at 1.34 m/s^2. (**B**) 2,048-point Fast Fourier Transform (FFT) of the same AEP from a nurse shark in response to a 400 Hz sound. The arrow indicates the frequency doubling peak which occurs at 800 Hz. A positive detection is when the peak (at twice the frequency played) is at least 3 dB above the noise floor. The noise floor is estimated from the AEP power spectrum with a window of 100 Hz around the doubling frequency

orientations (0° horizontal (*X*-axis), 90° horizontal (*Y*-axis), and vertical (*Z*-axis)) and all calibrations are computed as Root Mean Square (RMS). Many researchers have suggested that the hair cells in the inner ear of fishes acts as an accelerometer and therefore detect the particle acceleration of sound (Kalmijn 1988; Fay and Edds-Walton 1997; Bass and McKibben 2003). Therefore, all audiograms have hearing thresholds shown in units of particle acceleration (m/s^2). Particle velocities can be converted to accelerations by multiplying the recorded velocity with [$2\pi \times$ frequency]. Background noise was also measured and was consistently below 10^{-6} m/s^2.

A two-way repeated measures ANOVA (SigmaStat) was used to compare frequency responses between the nurse shark and yellow stingray to determine if the two species had similar hearing thresholds at each frequency.

Results

AEP audiograms of *G. cirratum* and *U. jamaicensis* are plotted along with the audiograms obtained from the lemon shark, *Negaprion brevirostris* (Banner 1967) and the horn shark, *Heterodontus francisi* (Kelly and Nelson 1975) (Fig. 3). Both species had their most sensitive hearing at 300 Hz and 600 Hz. The hearing thresholds were not significantly different between the nurse sharks and yellow stingray at

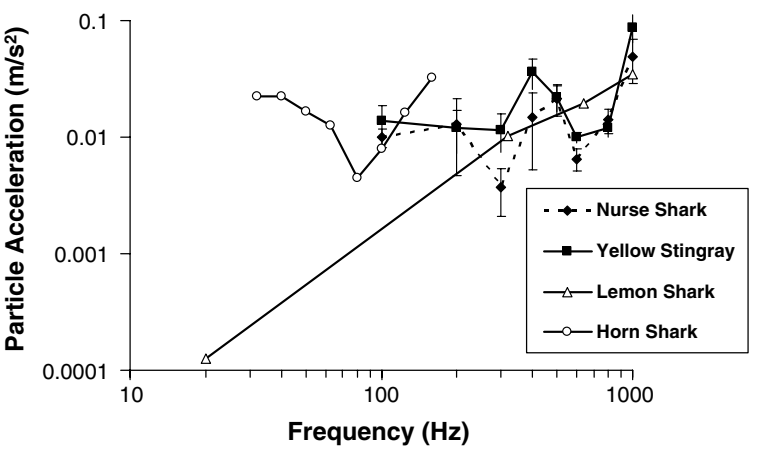

Fig. 3 Particle acceleration audiograms obtained for the nurse shark and yellow stingray. The thresholds are the particle accelerations recorded from the *X*-axis. The accelerations in the *Y* and *Z* directions were much smaller than the *X* leaving the overall magnitude of all three directions approximately equal to the *X* direction. Data from the lemon shark (Banner 1967) and the horn shark (Kelly and Nelson 1975) are plotted for comparison. Standard error bars are included for nurse shark and yellow stingray audiograms

Table 1 Particle velocity thresholds as recorded from the geophone and the converted particle accelerations (velocity × (2π × frequency)) and corresponding sound pressures recorded simultaneously with the hydrophone

Nurse Shark	Recorded particle velocity (m/s)	Converted particle acceleration (m/s^2)	Corresponding Sound Pressure (dB re 1 μPa)
100 Hz	7.18×10^{-5}	0.0099	147.15
200 Hz	4.68×10^{-5}	0.0129	139.40
300 Hz	8.97×10^{-6}	0.0037	136.44
400 Hz	2.65×10^{-5}	0.0147	147.83
500 Hz	3.13×10^{-5}	0.0216	137.89
600 Hz	7.80×10^{-6}	0.0065	134.21
800 Hz	1.27×10^{-5}	0.0141	135.24
1,000 Hz	3.51×10^{-5}	0.0486	146.29
Yellow Stingray		Particle Acceleration (m/s^2)	Corresponding Sound Pressure (dB re 1 μPa)
100 Hz	9.89×10^{-5}	0.0137	153.05
200 Hz	4.39×10^{-5}	0.0124	147.76
300 Hz	2.79×10^{-5}	0.0116	139.45
400 Hz	6.57×10^{-5}	0.0363	151.60
500 Hz	3.20×10^{-5}	0.0221	143.48
600 Hz	1.19×10^{-5}	0.0099	140.23
800 Hz	1.09×10^{-5}	0.0121	141.01
1,000 Hz	6.33×10^{-5}	0.0875	151.07

Thresholds are determined from the *x*-axis component of the sound field as the *y* and *z* axes yielded much smaller particle accelerations (See Table 2)

any frequency ($P > 0.05$) (Table 1). The average nurse shark threshold at 600 Hz was about 1.5 times more sensitive than the stingray. Based on visual inspection, the audiograms of the nurse shark and yellow stingray are fairly similar to the horn shark and lemon shark at the same frequencies tested, with the only obvious difference being the nurse shark having greater sensitivity at 600 Hz compared to the other elasmobranchs. The audiograms for both the nurse shark and yellow stingray and the sound propagation measurements are plotted using the horizontal component (*x*-axis) of particle acceleration as measured by the geophone–hydrophone probe. For clarification, the *x*-axis would be the along-body axis (head to tail), the *y*-axis is sound left-right axis on the fish, and the *z*-axis is the up-down axis. The vertical and 90° directions (*y*- and *z*-axes, respectively) yielded much smaller particle accelerations compared to the horizontal direction at each frequency (Table 2).

Table 2 Directional particle accelerations in each of the three Cartesian directions as well as the magnitude of the three directions combined, measured with the geophone for sound presentations at threshold levels for one of the nurse sharks

Frequency (Hz)	*X*-axis acceleration (m/s^2)	*Y*-axis acceleration (m/s^2)	*Z*-axis acceleration (m/s^2)	Magnitude of particle acceleration (m/s^2)
100	0.0067	0.0001	0.0017	0.0069
200	0.0035	0.0003	0.0007	0.0036
300	0.0008	0.0001	0.0002	0.0008
400	0.0076	0.0002	0.0015	0.0077
500	0.0203	0.0016	0.0042	0.0208
600	0.0060	0.0003	0.0011	0.0061
800	0.0190	0.0065	0.0044	0.0206
1,000	0.0346	0.0239	0.0088	0.0430

These data show that most of the acoustic energy was along the *X*-axis, which is equivalent to the direct path (straight line from the transducer to the shark's head). The *Y*-axis would be sound coming from the left or right of the shark's head, and the *Z*-axis would be sound coming from above the shark's head. The magnitude is calculated by the following equation: $\sqrt{(X^2+Y^2+Z^2)}$

Discussion

The hearing thresholds for the nurse shark and yellow stingray do not differ greatly from the thresholds obtained from the horn shark or the lemon shark, suggesting that these species have a similar range and sensitivity of hearing. The only obvious difference in hearing is the very low threshold at 20 Hz in the lemon shark, suggesting that future elasmobranch hearing experiments should include frequencies at least as low as 20 Hz. Corwin (1978) states that active, piscivorous elasmobranchs could have more developed hearing abilities compared to benthic species, because of slight modifications in the ear anatomy between ecomorphotype, though this does not appear to play a role with these species. The overall auditory anatomy of elasmobranchs is fairly similar among species, with differences primarily in numbers of hair cells, hair cell polarities and size of the macula neglecta epithelium (Corwin 1978). While it is possible that these variations could affect hearing thresholds, it is more likely that they play a larger role in directional hearing abilities (Corwin 1978). Thus, it seems probable that all elasmobranchs should have relatively similar hearing ranges and thresholds.

It has been suggested (Mann et al. 2001) that audiograms obtained using AEP can underestimate hearing sensitivity compared to behavioral testing procedures. Therefore, if there are differences between the two testing methods, it is possible that the actual hearing thresholds of these species could be low enough to detect the field attraction sounds. However, Casper et al. (2003) found similar thresholds in a skate measured with operant methods and AEPs. Kenyon et al. (1998) also found similar thresholds for goldfish when comparing their AEP data to previously existing behavioral thresholds and lower AEP thresholds than behavioral in the oscar. Future experiments in which audiograms obtained using both AEP and classical conditioning for the same shark will be needed to determine if the AEP method does underestimate the hearing abilities.

Another consideration involves the sound field in the lagoon. The largest component of sound came from directly in front of the fishes (Table 2), thereby stimulating hair cells which were polarized in that direction. Very little is known about the hair cell polarizations of the inner ear of elasmobranchs. The only data for the sacculus, utricle and lagena are from two skates, *Raja ocellata*, (Barber and Emerson 1980) and *Raja clavata* (Lowenstein et al. 1964). Most elasmobranch inner ear research has focused on the macula neglecta (Tester et al. 1972, Corwin 1977, Corwin 1978, Barber et al. 1985). The saccular macula contains predominantly dorsal/ventral polarized cells with a smaller portion of the macula oriented in the anterior/posterior direction. The utricular macula has mostly anterior/posterior polarized cells with some dorsal/ventral. The utricular macula and macula neglecta have all dorsal/ventral polarized cells. Experimental evidence (Lowenstein and Roberts 1951) has shown that the utricle and lagena are predominantly equilibrium receptors whereas the sacculus and macula neglecta are the most likely acoustic/vibration detectors. This evidence combined with the known polarizations of the hair cells of these end organs in the two skates suggests that most acoustic stimulation in elasmobranchs would occur for sounds above and below the fish (as was suggested by Corwin 1981b), with less stimulation from the front and back, as occurred in this current experiment. To resolve the question about whether elasmobranches respond equally to sound from all directions requires testing the response of elasmobranchs to sounds (or vibration) along different axes.

These results can also be compared to the field attraction experiments conducted by Myrberg and others (Richard 1968; Myrberg et al. 1969; Nelson et al. 1969). Nurse sharks were attracted in several of the experiments by low frequency, pulsed sounds. Particle accelerations were not measured, but sound pressure levels were recorded, which can be used to estimate the accompanying particle acceleration. In a planar propagating wave the sound pressure is proportional to the acoustic impedance multiplied by the particle velocity, $p = \rho c v$, where, p = pressure (Pa); ρ = density of medium (1,030 kg/m3); c = speed of sound in the medium (1,500 m/s); v = particle velocity (m/s).

The particle velocity (again using the values obtained from the x-axis direction of particle motion) can then be differentiated to calculate the particle acceleration. Using this relationship we can calculate the equivalent sound pressures in the far field that would be required to produce particle accelerations measured at threshold for the sharks. Although this equation can only work with a plane propagating wave, it provides a useful approximation of sound pressures that would produce equivalent particle

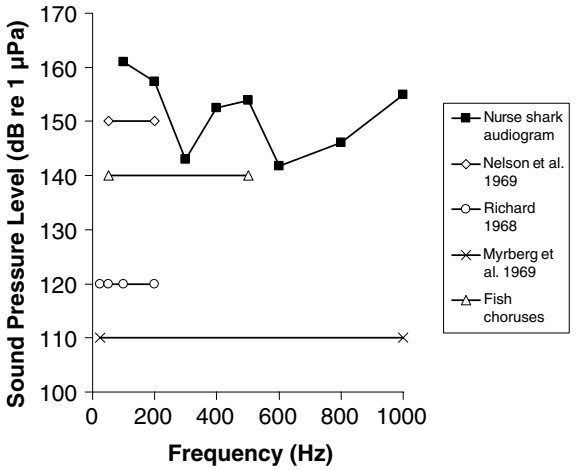

Fig. 4 The sound pressure needed to produce particle accelerations equivalent to the nurse shark audiogram in a plane propagating wave (square symbols). The sound pressure levels used in the field attraction experiments as well as the average sound pressure level of a sciaenid fish spawning chorus (Locascio and Mann 2005) are plotted for comparison. Distances from the sound source to the hydrophone for measurements of SPL were 1m for Richard (1968), Nelson et al. (1969) and this project, while they were made at 18.5 m for Myrberg et al. (1969). Sound pressure audiograms for the nurse sharks are calculated from the recorded velocities using the equation $P = \rho cV$ (where p = pressure (Pa), ρ = density of the medium (1,030 kg/m^3), c = speed of sound in medium (1,500 m/s), V = velocity (m/s)). The pressures were then log transformed to convert to sound pressure levels (dB re 1 μPa). The sound levels from this experiment as well as the fish spawning choruses and Nelson et al. (1969) are based on RMS levels. Richard (1968) and Myrberg et al. (1969) sound levels are based on spectrum levels

accelerations within the hearing range of the nurse sharks at large distances from the source (Fig. 4). Based on these equivalent pressures, it would appear that the sound pressures that were played in the field attraction experiments should not have been loud enough to attract nurse sharks (one of the species observed in many of the attraction experiments) given the AEP data, illustrating a discrepancy between these attraction experiments and the hearing thresholds measured in this study. Maximum sound levels that were used in the field attraction experiments reached 150 dB re 1 μPa (Nelson et al. 1969) from 50 to 200 Hz, which are below the projected SPL thresholds of the nurse shark. However it should be noted that this experiment did not test for hearing thresholds at frequencies as low as those played in the field attraction experiments (frequencies below 100 Hz) and it is impossible to know from what distances the sharks could even be detecting the sounds (at least 25 m with Myrberg et al. (1969), 20–30 m for Nelson et al. (1969) and unknown for Richard (1968)). Natural ambient sound levels also rarely reach the loudest levels played in these attraction experiments. Among the loudest of these natural sounds are fish choruses, which are typically around 140 dB SPL rms from 50 to 500 Hz (Locascio and Mann 2005). Therefore, the more likely stimulus for shark hearing are fish swimming nearby, which may leave large, low frequency hydrodynamic fields (dipole in nature) that can be detected by the ear and lateral line (Kalmijn 1988). Actual measurements of particle acceleration in the field to determine how far it propagates are critical for estimating how far a shark could be from a sound source and still detect it.

Future experiments need to address these differences including further testing of hearing in species which were attracted to sounds in the field. Audiograms from only four species of elasmobranchs are not sufficient for quantifying the hearing abilities of an entire subclass of fishes. Furthermore, very little is known about the propagation of sound particle acceleration in different environments. Equations and models might be able to predict these physical parameters in open ocean environments, but actual field measurements, especially in shallow water systems, will provide the data needed to compare the results of the attraction studies with those of the laboratory experiments. The technology exists now for measuring particle motion in the field as well as the laboratory and must be used for all future hearing experiments involving hearing generalists which cannot detect sound pressure.

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References

Banner A (1967) Evidence of sensitivity to acoustic displacements in the lemon shark, *Negaprion brevirostris* (Poey). In: Cahn PH (ed) Lateral line detectors. Indiana University Press, Bloomington, pp 265–273

Barber VC, Emerson CJ (1980) Scanning electron microscopic observations on the inner ear of the skate, *Raja ocellata*. Cell Tissue Res 205:199–215

Barber VC, Yake KI, Clark VF, Pungur J (1985) Quantitative analyses of sex and size differences in the macula neglecta and ramus neglectus in the inner ear of the skate, *Raja ocellata*. Cell Tissue Res 241:597–605

Barry MA (1987) Afferent and efferent connections of the primary octaval nuclei in the clearnose skate, *Raja eglanteria*. J Comp Neurol 266:457–477

Bass AH, Clark CW (2003) The physical acoustics of underwater sound communication. In: Simmons AM, Popper AN, Fay RR, (eds) Acoustic communication. Springer-Verlag, New York, pp 15–64

Bass AH, McKibben JR (2003) Neural mechanisms and behaviors for acoustic communication in teleost fish. Prog Neurobiol 69:1–26

Casper BM, Lobel PS, Yan HY (2003) The hearing sensitivity of the little skate, *Raja erinacea*: a comparison of two methods. Environ Biol Fishes 68:371–379

Corwin JT (1977) Morphology of the macula neglecta in sharks of the genus *Carcharhinus*. J Morphol 152:341–362

Corwin JT (1978) The relation of inner ear structure to the feeding behavior in sharks and rays. Scan Electron Micros II:1105–1112

Corwin JT (1981a) Audition in elasmobranchs. In: Tavolga WN, Popper AN, Fay RR (eds) Hearing and sound communication in fishes. Springer-Verlag, New York, pp 81–102

Corwin JT (1981b) Peripheral auditory physiology in the lemon shark: evidence of the parallel otolithic and non-otolithic sound detection. J Compar Physiol 142:379–390

Corwin JT (1989) Functional anatomy of the auditory system of sharks and rays. J Exp Zool – Suppl 2:62–74

Egner SA, Mann DA (2005) Auditory sensitivity of sergeant major damselfish *Abudefduf saxatilis* from post-settlement juvenitle to adult. Mar Ecol Prog Ser 285:213–222

Fay RR (1988) Hearing in vertebrates: a psychophysics databook. Hill-Fay Associates, Winnetka

Fay RR, Edds-Walton PL (1997) Directional response properties of saccular afferents of the toadfish, *Opsanus tau*. Hearing Res 111:1–21

Fay RR, Kendall JI, Popper AN, Tester AL (1974) Vibration detection by the macula neglecta of sharks. Comp Biochem Physiol 47A:1235–1240

Hueter RE, Mann DA, Maruska KP, Sisneros JA, Demski LS (2004) Sensory biology of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR, (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, pp 325–368

Kalmijn AD (1988) Hydrodynamic and acoustic field detection. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory biology of aquatic animals. Springer-Verlag, New York, pp 83–130

Kelly JC, Nelson DR (1975) Hearing thresholds of the horn shark, *Heterodontus francisci*. J Acoust Soc Am 58:905–909

Kenyon TN, Ladich F, Yan HY (1998) A comparative study of hearing ability in fishes: the auditory brainstem response approach. J Compar Physiol A 182:307–318

Kritzler H, Wood L (1961) Provisional audiogram for the shark, *Carcharhinus leucas*. Science 133:1480–1482

Locascio JV, Mann DA (2005) Effects of hurricane charley on fish chorusing. Biol Lett 1:362–365

Lowenstein O, T.Roberts DM (1951) The localization and analysis of the responses to vibration from the isolated elasmobranch labyrinth. A contribution to the problem of the evolution of hearing in vertebrates. J Physiol 114:471–489

Lowenstein O, Osborne MP, Wersäll J (1964) Structure and innervation of the sensory epithelia in the thornback ray (*Raja clavata*). Proce Roy Soc London B 160:1–12

Mann DA, Higgs DM, Tavolga WN, Souza MJ, Popper AN (2001) Ultrasound detection by clupeiform fishes. J Acoust Soc Am 109:3048–3054

Myrberg AA Jr (1978) Underwater sound – its effect on the behaviour of sharks. In: Hodgson ES, Mathewson RF, (eds) Sensory biology of sharks, skates and rays. Government USPrinting Office, Washington, DC

Myrberg AA Jr (2001) The acoustical biology of elasmobranchs. Environ Biol Fishes 60:31–45

Myrberg AA Jr, Banner A, Richard JD (1969) Shark attraction using a video-acoustic system. Marine Biol 2:264–276

Myrberg AA Jr, Ha SJ, Walewski S, Banbury JC (1972) Effectiveness of acoustic signals in attracting epipelagic sharks to an underwater sound source. Bull Marine Sci 22:926–949

Nelson DR (1967) Hearing thresholds, frequency discrimination, and acoustic orientation in the lemon shark, *Negaprion brevirostris* (Poey). Bull Marine Sci 17:741–768

Nelson DR, Gruber SH (1963) Sharks: attraction by low-frequency sounds. Science 142:975–977

Nelson DR, Johnson RH, Waldrop LG (1969) Responses to Bahamian sharks and groupers to low-frequency, pulsed sounds. Bull South Calif Acad Sci 68:131–137

Olla B (1962) The perception of sound in small hammerhead sharks, Sphyrna lewini. Thesis MS, University of Hawaii

Popper AN, Fay RR (1977) Structure and function of the elasmobranch auditory system. Am Zool 17:443–452

Richard JD (1968) Fish attracted with low-frequency pulsed sound. J Fish Res Board Can 25:1441–1452

Rogers PH, Cox M (1988) Underwater sounds as a biological stimulus. In: Atema J, Fay RR, Popper AN, Tavolga WN, (eds) Sensory biology of aquatic animals. Springer-Verlag, New York, pp 131–149

Tester AL, Kendall JI, Milisen WB (1972) Morphology of the ear of the shark genus *Carcharhinus*, with particular reference to the macula neglecta. Pac Sci 26:264–274

Wisby WJ, Richard JD, Nelson DR, Gruber SH (1964) Sound perception in elasmobranchs. In: Tavolga WN (ed) Marine bio-acoustics. Pergamon Press, New York, pp 255–267