Ultrasound detection by clupeiform fishes

David A. Mann
Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida 34236 and Tucker-Davis Technologies, 4637 NW 6th Street, Gainesville, Florida 32653

Dennis M. Higgs
Department of Biology, University of Maryland, College Park, Maryland 20742

William N. Tavolga
Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida 34236

Marcy J. Souza and Arthur N. Popper[a)]
Department of Biology, University of Maryland, College Park, Maryland 20742

(Received 18 December 2000; revised 26 February 2001; accepted 5 March 2001)

It has previously been shown that at least one species of fish (the American shad) in the order clupeiforms (herrings, shads, and relatives) is able to detect sounds up to 180 kHz. However, it has not been clear whether other members of this order are also able to detect ultrasound. It is now demonstrated, using auditory brainstem response (ABR), that at least one additional species, the gulf menhaden (*Brevoortia patronus*), is able to detect ultrasound, while several other species including the bay anchovy (*Anchoa mitchilli*), scaled sardine (*Harengula jaguana*), and Spanish sardine (*Sardinella aurita*) only detect sounds to about 4 kHz. ABR is used to confirm ultrasonic hearing in the American shad. The results suggest that ultrasound detection may be limited to one subfamily of clupeiforms, the Alosinae. It is suggested that ultrasound detection involves the utricle of the inner ear and speculate as to why, despite having similar ear structures, only one group may detect ultrasound. © *2001 Acoustical Society of America.* [DOI: 10.1121/1.1368406]

PACS numbers: 43.80.Lb, 43.66.Cb [WA]

I. INTRODUCTION

Until recently, all studies of hearing in fishes have reported that the hearing bandwidth generally extends from below 100 Hz to approximately 1000 Hz in fishes without specializations for sound detection and to perhaps as high as 5000 to 7000 Hz in species that have specializations that enhance bandwidth and sensitivity (e.g., Fay, 1988; Popper and Fay, 1999). However, a number of peer reviewed and ''gray literature'' reports over the past 10 years have suggested that certain fishes, including a number of members of the taxonomic order clupeiforms (herrings, shads, anchovies, and relatives), may be able to detect ultrasonic signals to as high as 126 kHz (ESEERCO, 1991; Dunning *et al.*, 1992; Nestler *et al.*, 1992; Con Edison, 1994; Ross *et al.*, 1995, 1996). Other studies on the Atlantic cod (*Gadus morhua*), a species in a different taxonomic order (Gadiformes), suggested that this species could detect ultrasound at almost 40 kHz (Astrup and Møhl, 1993, 1998; Astrup, 1999).

We previously performed a set of classical conditioning experiments on one of the species reportedly capable of detecting high frequencies, the American shad (*Alosa sapidosomma*), and demonstrated that it could detect pure tones to over 180 kHz (Mann *et al.*, 1997, 1998). We suggested that ultrasound detection may be associated with a specialization of the utricle in the clupeiform ear (also see Nestler *et al.*, 1992). The utricular specializations include a unique arrangement of the utricular sensory epithelium and the presence of an air-filled bulla closely associated with this ear region.

One of the issues related to ultrasound detection is the extent to which it is found among the clupeiforms. Several of the earlier papers suggested, based on nonquantitative measures, that other members of the genus *Alosa* are able to detect ultrasound. However, there is also some evidence that two other clupeiforms, the bay anchovy (*Anchoa mitchilli*) and possibly the Atlantic herring (*Clupea haregus*), may not respond to these high frequencies (Schwarz and Greer, 1984; Dunning *et al.*, 1992; Nestler *et al.*, 1992; Con Edison, 1994). Since all of these species have air-filled auditory bullae in the utricle, it became important to test whether ultrasound detection is ubiquitous among this order, or whether it remains a specialization of only a few species.

In order to test the hypothesis that not all clupeiforms can detect ultrasound, we used the auditory brainstem response (ABR) to measure sound detection abilities of several taxonomically diverse members of this order. The ABR technique has been used successfully with fishes and shows thresholds for sound detection that are generally similar to those measured by traditional classical conditioning tests (Kenyon *et al.*, 1998; Yan *et al.*, 2000). We chose to perform ABR measurements rather than classical conditioning because the fragility of many clupeiforms makes it difficult to keep the fish alive long enough to complete classical conditioning training and recording. We also tested goldfish (*Carassius auratus*) as a control to determine if ABR responses were to spurious signals associated with the ultrasonic stimulus. The goldfish is a good control for the acoustic system

[a)]Author to whom correspondence should be addressed. Electronic mail: AP17@umail.umd.edu

Downloaded 08 Jul 2010 to 160.36.195.182. Redistribution subject to ASA license or copyright; see http://asadl.org/journals/doc/ASALIB-home/info/terms.jsp

since this species does not detect sounds above about 3 kHz, and this has been confirmed in many studies (Jacobs and Tavolga, 1967; Fay, 1988), including our earlier studies on American shad (Mann *et al.*, 1997, 1998).

II. METHODS

A. Fish

The species used in this study were the bay anchovy (*Anchoa mitchilli*) ($n=15$; 25–30 mm standard length), scaled sardine (*Harengula jaguana*) ($n=16$, 80–120 mm standard length), gulf menhaden (*Brevoortia patronus*) ($n=10$; 37–54 mm standard length), Spanish sardine (*Sardinella aurita*) ($n=2$; 90–110 mm standard length), American shad ($n=11$; 75–90 mm standard length), and goldfish (*Carassius auratus*) ($n=2$, 60 mm standard length). Large numbers of scaled sardine and bay anchovy were used because we were not always able to get an entire audiogram from an individual fish. We were only able to collect two Spanish sardines, but neither of these showed a response to ultrasound.

American shad were obtained from the PEPCO Chalk Point Generating Station (Chalk Point, MD) aquaculture facility and held at the University of Maryland fish colony, while the other species were obtained at the Mote Marine Laboratory, Sarasota, FL. Work on American shad and goldfish was approved by the Institutional Animal Care and Use Committee (IACUC) of the University of Maryland (UMD). Procedures with the other species were approved by the IACUC of the Mote Marine Laboratory (MML).

B. ABR testing

Testing of American shad and goldfish was performed at UMD, while work on the other species was performed at MML. It was not possible to do all of the studies at one location since the fish were obtained at different sites and transporting fish between locations would have been impossible due to the difficulty in keeping the fish alive. However, in order to ensure comparable procedures at both sites, ABR testing was carried out using identical hardware systems from Tucker-Davis Technologies using the BioSig software. The most significant difference in the two setups was tank size (19-liter circular tank, 30 cm deep at UMD) and (40 $\times$50-cm^2 rectangular tank, 30 cm deep at MML). However, this difference is not likely to have affected the data since the signals were calibrated in the same manner, as described later in this work. In addition, one of us (DAM) participated in the experiments at both locations in order to make sure that there were no differences in experimental detail. It is important to note that sound was calibrated as sound pressure level, and that acoustics in small tanks are different from free-field where there are presumably fewer reflections.

Auditory brainstem response were collected in response to repeated presentations of tone pip stimuli. Low-frequency tones ($<$20 kHz) were generated with an underwater speaker (University Sound UW-30). High-frequency tones ($>$20 kHz) were generated with an ITC-1042 underwater transducer. Signals were amplified with either a McIntosh amplifier (UMD) or with a Hafler amplifier (MML). Tone pips were 20 ms in duration, gated on and off with a Hanning window, and presented at 9 per second with the TDT system. Low-frequency tone pips were generated with a 6-μs sample period. Ultrasonic tone pips were generated with a 5.2-μs sample period. At UMD tone pips were calibrated with an LC-10 hydrophone (calibration sensitivity of -208.6 *re*: 1 V/μPa; ± 3 dB 0.1–180 kHz, omnidirectional). At MML, calibrations were performed with a Reson TC4013 hydrophone (calibration sensitivity of -211 dB *re*: 1 V/μPa; $\pm$ 3 dB 1 Hz to 170 kHz, omnidirectional). The hydrophone was positioned in the fish holder without the fish and the output was calibrated on an oscilloscope. Calibrations of the tone pips were performed by peak equivalent calibration. This entailed first calibrating continuous tones as rms SPL, and then the tone pips were presented using the identical signal parameters. Spectral analyses were also performed on acquired signals to ensure that there was no significant harmonic distortion (total harmonic distortion was less than 2% at all frequencies).

For ABR testing the fish was held approximately 10 cm underwater and a recording electrode was placed subcutaneously along the midline just behind the brain, and a reference electrode was placed subcutaneously along the midline just behind the eyes. A ground electrode was either placed in the muscle behind the reference electrode, or in the water adjacent to the fish. Signals from the electrodes were amplified using a digital biological amplifier (TDT DB4/HS4) and low-pass filtered at 10 kHz, high-pass filtered at 8 Hz, and notch-filtered at 60 Hz. Amplification was typically between 50 000 and 100 000.

The ABR responses were acquired by averaging 50 ms of the signal from the electrode from the onset of the tone pip. The ABRs were obtained after 50–200 averages depending on the species. ABRs with 50 averages were used for the bay anchovy, because they did not survive more than about 15 min in the tank. ABRs with 100–200 averages were used for the gulf menhaden, scaled sardine, Spanish sardine, American shad, and goldfish.

C. ABR threshold calculation

Auditory brainstem response thresholds were determined from the data by measuring the peak response at each frequency and level. A threshold criterion was determined based on an estimation of background noise from trials to low sound level presentations (all trials less than 100 dB SPL at both experimental sites). The criterion was set at the level of the 95th percentile for these nondetection trials (i.e., the level below which 95% of the trials fell), or if few trials were run at low levels, at the maximum positive or negative peak for these nondetection trials. To be considered above threshold, the peak level had to be higher than the criterion on two consecutive trials. Linear interpolation between the level before and after the criterion was used to calculate the threshold. Thresholds from 5 of the 11 American shad were measured by hand as the lowest sound pressure level that gave a repeatable response, because the signal-to-noise ratio did not allow an accurate measurement using the peak method de-

Downloaded 08 Jul 2010 to 160.36.195.182. Redistribution subject to ASA license or copyright; see http://asadl.org/journals/doc/ASALIB-home/info/terms.jsp

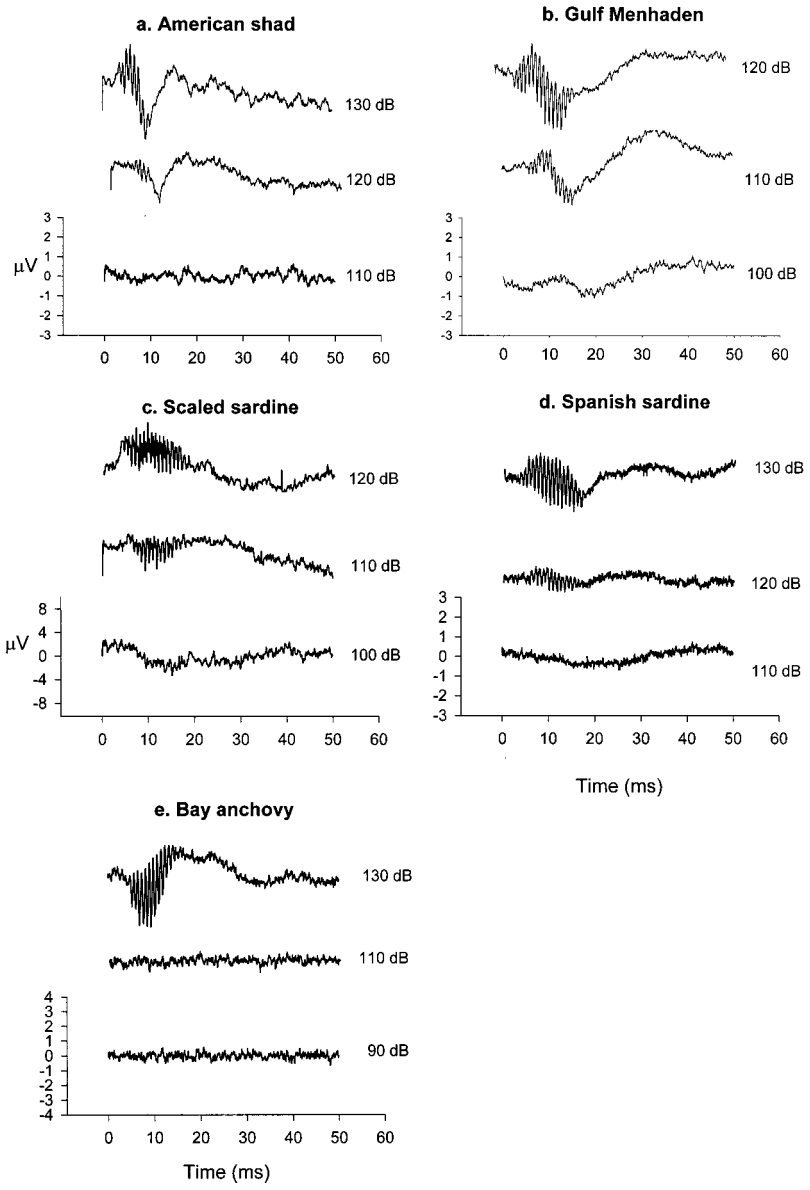

FIG. 1. ABR waveforms in response to 600-Hz sounds presented at several levels for (a) American shad, (b) gulf menhaden, (c) scaled sardine, (d) Spanish sardine, and (e) bay anchovy.

scribed above. The thresholds from these fish were not significantly different than those measured from the other six American shad using the peak method.

III. RESULTS

The ABR waveforms obtained in response to low-frequency sound and ultrasound presentation all show a negative trough at about 10 ms after the beginning of sound presentation. The ABR from the low-frequency sound presentation also has a higher-frequency component that is twice the frequency of the tone stimulus, which is typical of fish ABRs.

All species responded to low-frequency sound presentation (Fig. 1), while only American shad and gulf menhaden showed responses to ultrasound presentation from 40 to 80 kHz (Figs. 2 and 3). The other species did not respond to ultrasound presentation at sound pressure levels up to 180 dB SPL, but they showed a consistent ABR to low-frequency stimulation. The voltage of the ABR in response to ultrasound in the American shad and gulf menhaden was about the same as the voltage of the ABR to low-frequency sound for all species tested (Figs. 1 and 2). Therefore, we should have been able to detect a response to ultrasound in the other species had the ability to detect such sounds been present.

The low-frequency thresholds (below 10 000 Hz) were similar for all species, with thresholds around 120–130 dB SPL (Figs. 4 and 5). The ultrasonic thresholds for American shad were around 155 dB SPL and the ultrasonic thresholds for gulf menhaden were about 180 dB SPL (Fig. 4).

The ABR thresholds obtained for the American shad were in the range of 0 to 15 dB higher than the behavioral thresholds obtained in a previous study (Figs. 4 and 5), but showed a similar trend of better sensitivity at low frequencies than at ultrasonic frequencies. However, some of the lowest thresholds to ultrasound presentation (e.g., one American shad showed thresholds at 40 kHz of 130 dB) were as low as the detection thresholds for low frequency sound (Figs. 1 and 2).

Trials with low-frequency stimulation were run both before and after trials with ultrasound to ensure that the low-

Downloaded 08 Jul 2010 to 160.36.195.182. Redistribution subject to ASA license or copyright; see http://asadl.org/journals/doc/ASALIB-home/info/terms.jsp

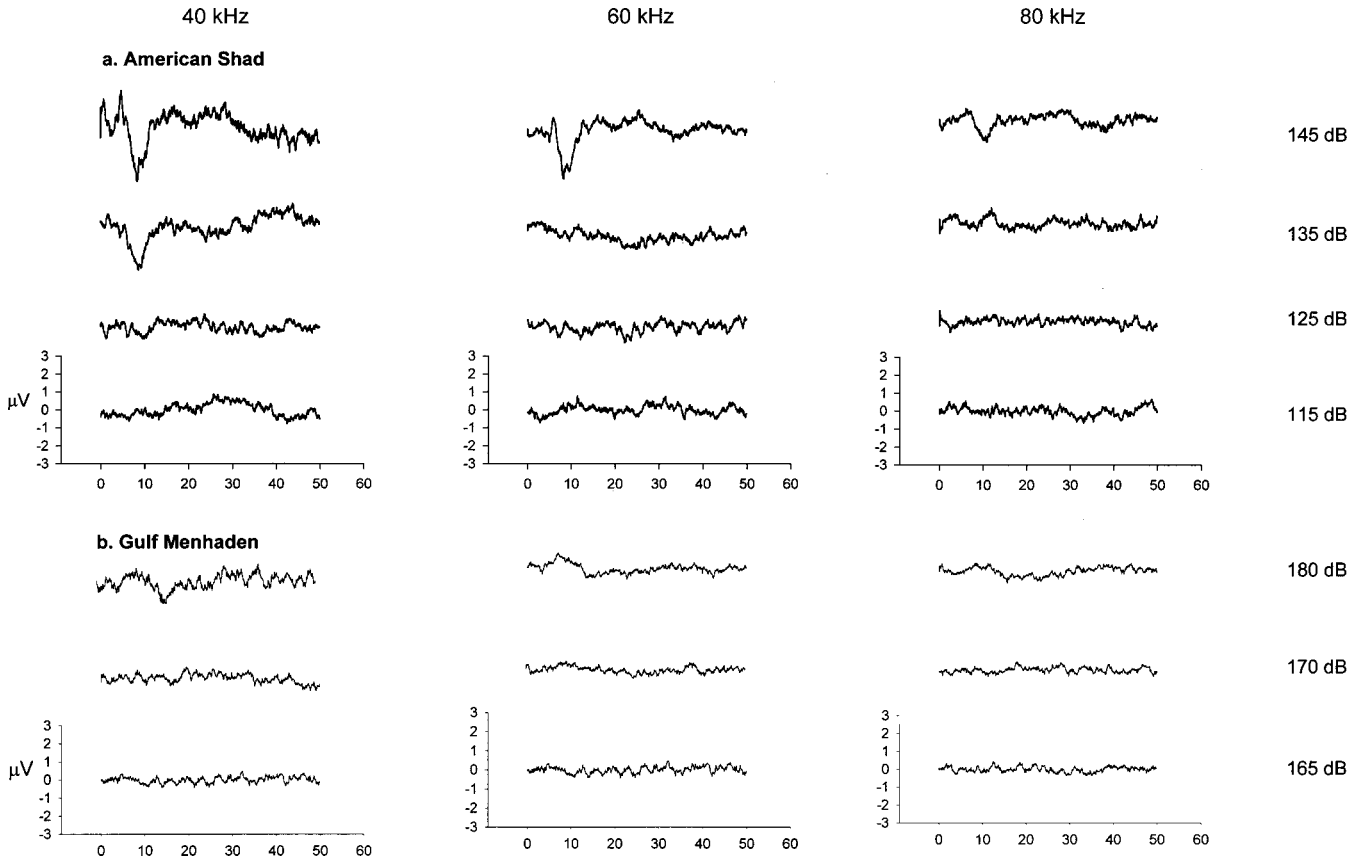

FIG. 2. ABR waveforms in response to 40-, 60-, and 80-kHz ultrasound presented at several levels for species that are able to detect ultrasound: (a) American shad and (b) gulf menhaden.

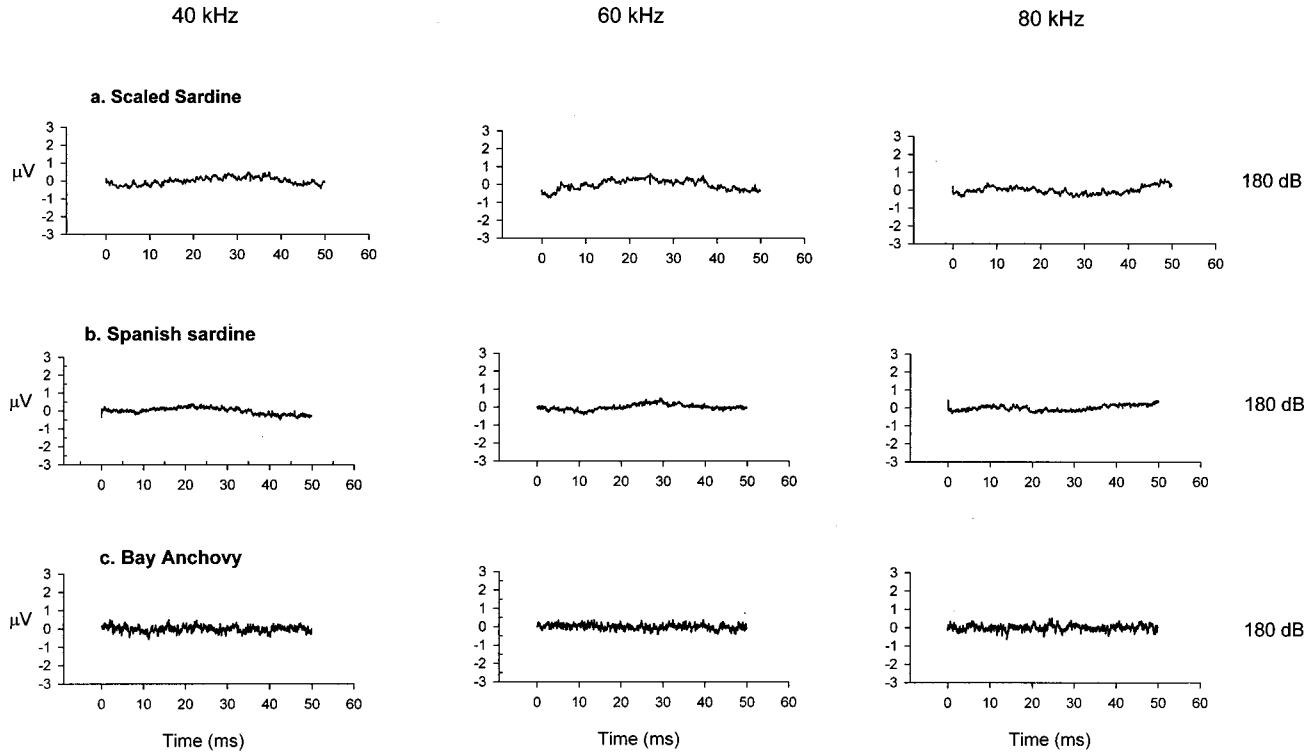

FIG. 3. ABR waveforms in response to 40, 60, and 80 kHz and at 180 dB for species that do not detect ultrasound: (a) scaled sardine, (b) Spanish sardine, and (c) bay anchovy. Arrows at 10 ms indicate troughs in ABR.

Downloaded 08 Jul 2010 to 160.36.195.182. Redistribution subject to ASA license or copyright; see http://asadl.org/journals/doc/ASALIB-home/info/terms.jsp

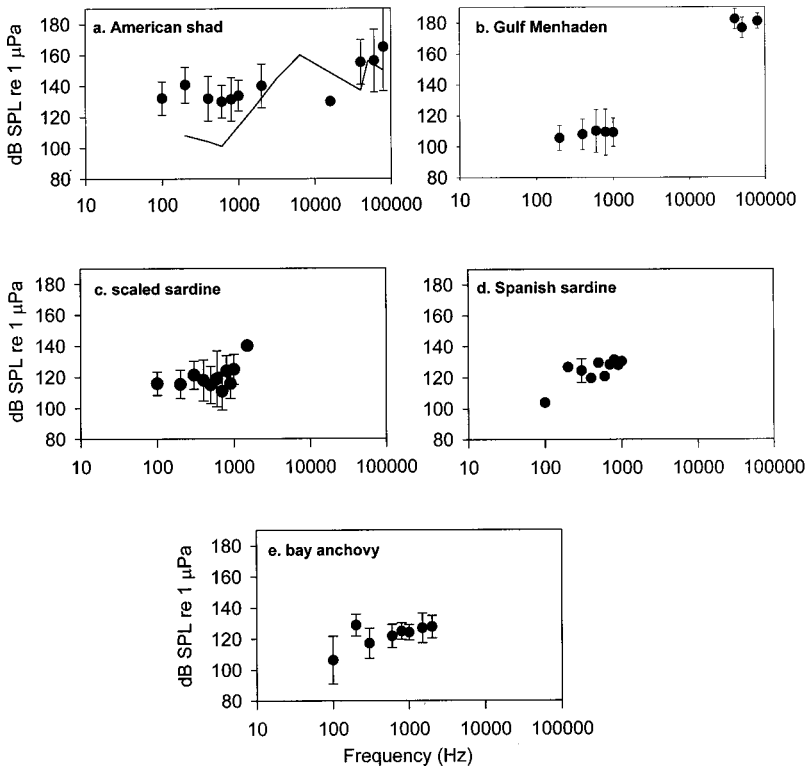

FIG. 4. Audiogram for (a) American shad, (b) gulf menhaden, (c) scaled sardine, (d) Spanish sardine, and (e) bay anchovy determined from ABRs. Data shown are mean values ±1 standard deviation. The behavioral audiogram for American shad determined by classical conditioning is plotted as a solid line in (a) (Mann *et al.*, 1998).

frequency ABR was consistent. Controls were also run with goldfish and dead clupeiform fishes to confirm that the ABR responses were not artifacts. There was never a positive ABR with dead fish, and goldfish controls did not respond above 4 kHz. Only two goldfish controls were run because there was no evidence of artifacts with dead fish or either of the goldfish. Also, the clupeoids that did not respond to ultrasound serve as a control for artifactual responses to ultrasound presentation.

IV. DISCUSSION

This study has demonstrated that a member of a second genus of clupeiform fish, the gulf menhaden, is able to detect ultrasonic signals, and it has also demonstrated that there are members of other genera of this order that cannot detect ultrasound. This study also demonstrated that even those species that do not detect ultrasound are able to detect sound to at least 4000 Hz (although they are not particularly sensitive), putting them into the general classification of hearing ''specialist'' (Popper and Fay, 1973, 1999). This is noteworthy since several other investigators have suggested that clupeiforms could only detect sounds to around 1–2 kHz (e.g., Enger, 1967; Sorokin *et al.*, 1988).

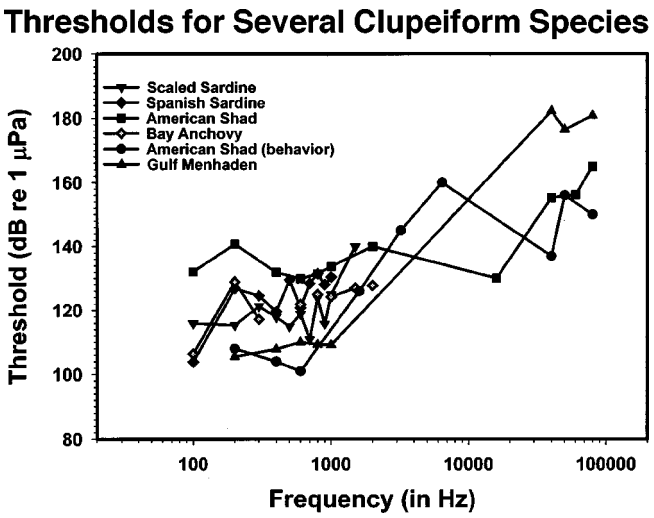

FIG. 5. Combined plot of audiograms for each of the species studied with ABR as well as behavioral data for the American shad (Mann *et al.*, 1998).

A. Evolution of ultrasound detection

One of the most interesting questions related to the discovery of ultrasound detection in fishes is how and why this capability arose. We previously hypothesized that this ability may have been an exaptation (= preadaptation) that evolved before there were echolocating predators, because all clupeids have the auditory bullae and specializations in the utricle (Mann *et al.*, 1997). We had assumed, incorrectly, that all clupeoids could detect ultrasound. These new findings of clupeoids that cannot detect ultrasound are important because they will allow us to investigate the mechanism and evolution of ultrasound detection in closely related species.

While we can only speculate, it is possible that the bulla and specialized utricle arose early in the evolution of clupeiforms and may have been a mechanism by which these fish could detect relatively higher frequency sounds (in the range of 1–4 kHz) than fishes without such specializations, or aided the fish in some other way, as suggested by Denton *et al.* (1979). An analogous event is likely to have occurred in the Otophysan fishes where the presence of the Weberian ossicles enables most of these species (e.g., goldfish and catfish) to detect sounds to 3 kHz or a bit higher (Fay, 1988). The detection of these higher frequencies may have been in response to the ancestors of both groups of fishes living in

Downloaded 08 Jul 2010 to 160.36.195.182. Redistribution subject to ASA license or copyright; see http://asadl.org/journals/doc/ASALIB-home/info/terms.jsp

shallow waters where low-frequency sounds attenuate very rapidly, but where higher frequencies carry greater distances (Rogers and Cox, 1988). In order for these fishes to glean information from any significant distance, they would only have been able to use higher frequencies, and this would have been a strong selective pressure for the evolution of specializations that enabled the fish to detect the biologically relevant sounds.

Since we now have shown that not all clupeiforms detect ultrasound, it is reasonable to suggest that while the evolution of the specialized utricle may have been responsible for hearing specializations, these adaptations do not immediately lead to the ability to detect ultrasound. Thus, we propose that the evolution of ultrasound detection in a number of clupeiforms of the subfamily Alosinae, including American shad and gulf menhaden, could have been under the selective pressures of echolocating *Tursiops*, which produce high-level (up to 220 dB *re* 1 μPa at 1 m) ultrasonic echolocation clicks (Au, 1993). In effect, the presence of the specialized utricle, if this is indeed the structure involved with ultrasound detection, may be viewed as an exaptation that could readily evolve into an ultrasound-detecting device, at least in some clupeiforms. It is interesting to question, however, why all members of this order did not evolve the same capability given that they are also prey of echolocating cetaceans. It is also important to note that there are several other subfamilies in the Clupeidae that remain to be tested.

B. Mechanism of ultrasound detection

One of the most interesting questions to ask is how ultrasound detection is performed in American shad and gulf menhaden. While we are not yet able to directly answer this question, the ABR data do provide us some potential insight into this issue. We previously argued (Mann *et al.*, 1997, 1998) that while it is possible that these fishes have evolved a new mechanism for ultrasound detection not involving an ear, the parsimonious argument is that detection involves the ear (see also Nestler *et al.*, 1992). The ABRs to both low-frequency sound and ultrasound showed a similar trough at 10 ms, suggesting that they are utilizing at least some of the same brain pathways. Furthermore, virtually all other animals, vertebrate and invertebrate, that detect ultrasound use an ear or earlike structure for ultrasound detection (e.g., Sales and Pye, 1974; Au, 1993; Grinnell, 1995; Hoy, 1999). Cod, *Gadus morhua*, is reported to be able to detect ultrasound, but only at high sound levels (185–200 dB *re* 1 μPa), and it has been suggested that receptors other than the ear are potentially being overstimulated (Astrup, 1999).

Clearly the potential mechanism thought to be involved in the cod is possible for clupeids. However, the clupeiform utricle has several unique features as compared to all other vertebrates and so it becomes a candidate for ultrasound detection in these species (e.g.,Wohlfhart, 1936; O'Connell, 1955; Denton *et al.*, 1979; Popper and Platt, 1979). The utricular sensory epithelium in the clupeiforms is divided into three distinct regions, the middle of which is suspended above a fluid-filled space that is separated by a thin membrane from an otic air bubble known as the auditory bulla that connects via a thin tube to the swim bladder (e.g., Denton *et al.*, 1979; Blaxter *et al.*, 1981a, b; Best and Gray, 1982). While earlier investigators suggested that this specialization may be associated with detection of changes in pressure as the fish moved to different depths (e.g., Denton *et al.*, 1979; Gray and Denton, 1979), it has been suggested that, instead, it may be an adaptation for high-frequency hearing (e.g., above 20 kHz) (Nestler *et al.*, 1992; Mann *et al.*, 1997, 1998). Moreover, we have suggested that the middle of the three sensory regions may be involved in ultrasound detection (Mann *et al.*, 1998), and this is supported by observations that there are defined differences in the utricular epithelium and its support in the American shad, an ultrasound detector, and the bay anchovy, a species that does not detect ultrasound (e.g., the middle macula of shad is more loosely suspended in shad than in anchovy; Higgs and Popper, in prep.). Ultimately, direct neurophysiological recordings from the ear and brain will be needed to prove the mechanism of ultrasound detection.

C. Practical applications

The behavioral response of various *Alosa* species to ultrasound presentation has been observed in the field and used to repel them from power plant intakes (e.g., Dunning *et al.*, 1992; Nestler *et al.*, 1992; Ross *et al.*, 1996). Our results showing that other clupeiforms, such as the bay anchovy, do not respond to ultrasound suggest that behavioral responses to ultrasound may be limited to a few species, perhaps only to members of the subfamily Alosinae, and thus limit the broad applicability of ultrasound in controlling clupeiform impingement.

The response of several *Alosa* species to ultrasound may also impact the fishing industry. There is evidence that acoustic sound sources (known as pingers) placed on fishing nets to reduce the by-catch of harbor porpoises (pingers presumably ''alert'' the porpoise to the presence of the nets) also reduced the catch of clupeids (Kraus *et al.*, 1997; see also Goodson, 1997). Kraus *et al.* (1997) suggested that the reason the harbor porpoise by-catch was reduced may have been because they were chasing clupeids that were deterred from the nets, and that the pingers were only indirectly influencing dolphin by-catch by reducing the number of clupeids in the vicinity of the nets. This becomes particularly important since Gulf and Atlantic menhaden are among the most important commercial fishes. In 1997–1998, 1.7 billion pounds were caught in the United States, accounting for 21% of all fish landings, and making menhaden the second largest commercial catch in the United States (NMFS, 1999). Given that these fishes account for such a large proportion of the fish catch, pingers on these nets might be very useful for deterring dolphins, although they may also serve to deter menhaden and ultimately affect the commercial catch of these species.

ACKNOWLEDGMENTS

This work was supported by Grant No. DC03936 from the National Institute of Deafness and Other Communicative Disorders of NIH. We thank Randy Wells and Doug Nowacek for help with organizing fish testing at MML. All

Downloaded 08 Jul 2010 to 160.36.195.182. Redistribution subject to ASA license or copyright; see http://asadl.org/journals/doc/ASALIB-home/info/terms.jsp

experiments comply with the ''Principles of animal care,'' Publication No. 86-23, revised 1995, of the National Institutes of Health and were under the supervision of the Institutional Animal Care and Use Committees of each institution involved in the study.

Astrup, J. (**1999**). ''Ultrasound detection in fish—a parallel to the sonar-mediated detection of bats by ultrasound-sensitive insects?'' Comp. Biochem. Physiol. A **124**, 19–27.

Astrup, J., and Møhl, B. (**1993**). ''Detection of intense ultrasound by the cod *Gadus morhua*,'' J. Exp. Biol. **182**, 71–80.

Astrup, J., and Møhl, B. (**1998**). ''Discrimination between high and low repetition rates of ultrasonic pulses by the cod,'' J. Fish Biol. **52**, 205–208.

Au, W. W. L. (**1993**). *The Sonar of Dolphins* (Springer-Verlag, New York).

Best, A. C. G., and Gray, J. A. B. (**1982**). ''Morphology of the utricular recess in the sprat,'' J. Mar. Biol. Assoc. U.K. **60**, 703–715.

Blaxter, J. H. S., Denton, E. J., and Gray, J. A. B. (**1981a**). ''Acousticolateralis systems in clupeid fishes,'' in *Hearing and Sound Communication in Fishes*, edited by W. N. Tavolga, A. N. Popper, and R. R. Fay (Springer, New York), pp. 39–59.

Blaxter, J. H. S., Denton, E. J., and Gray, J. A. B. (**1981b**). ''The auditory bullae-swimbladder system in late stage herring larvae,'' J. Mar. Biol. Assoc. U.K. **61**, 315–326.

Con Edison (**1994**). ''Evaluation of underwater sound to reduce impingement at the Arthur Kill Station, final report'' (Consolidated Edison Co., New York).

Denton, E. J., Gray, J. A. B., and Blaxter, J. H. S. (**1979**). ''The mechanics of the clupeid acousticolateralis system, frequency responses,'' J. Mar. Biol. Assoc. U.K. **59**, 27–47.

Dunning, D. J., Ross, Q. E., Geoghegan, P., Reichle, J. J., Menezes, J. K., and Watson, J. K. (**1992**). ''Alewives in a cage avoid high-frequency sound,'' North Am. J. Fish. Man. **12**, 407–416.

Enger, P. S. (**1967**). ''Hearing in herring,'' Comp. Biochem. Physiol. **22**, 527–538.

ESEERCO (Empire State Electric Energy Research Corporation) (**1991**). ''Responses of white perch, striped bass, alewives, spottail shiners, golden shiners, and Atlantic tomcod in a cage to high and low frequency underwater sounds generated by an electronic fish startle system,'' ESEERCO Project EP89-30, Amherst, New York.

Fay, R. R. (**1988**). ''Hearing in vertebrates, a psychophysics databook'' (Hill-Fay Assoc., Winnetka, IL).

Goodson, A. D. (**1997**). ''Developing deterrent devices designed to reduce the mortality of small cetaceans in commercial fishing nets,'' Mar. Fresh. Behav. Physiol. **29**, 211–236.

Gray, J. A. B., and Denton, E. J. (**1979**). ''The mechanics of the clupeid acoustico-lateralis system, low frequency measurements,'' J. Mar. Biol. Assoc. U.K. **59**, 11–26.

Grinnell, A. D. (**1995**). ''Hearing in bats, An overview,'' in *Hearing by Bats*, edited by A. N. Popper and R. R. Fay (Springer, New York), pp. 1–36.

Hoy, R. R. (**1999**). ''Acute as a bug's ear, An informal discussion of hearing in insects,'' in *Comparative Hearing, Insects*, edited by R. R. Hoy, A. N. Popper, and R. R. Fay (Springer, New York), pp. 1–17.

Jacobs, D. W., and Tavolga, W. N. (**1967**). ''Acoustic intensity limens in the goldfish,'' Anim. Behav. **15**, 324–335.

Kenyon, T. N., Ladich, F., and Yan, H. Y. (**1998**). ''A comparative study of hearing ability in fishes, the auditory brainstem response approach,'' J. Comp. Physiol. A **182**, 307–318.

Kraus, S. D., Read, A. J., Solow, A., Baldwin, K., Spradlin, T., Anderson, E., and Williamson, J. (**1997**). ''Acoustic alarms reduce porpoise mortality,'' Nature (London) **388**, 525.

Mann, D. A., Lu, Z., and Popper, A. N. (**1997**). ''A clupeid fish can detect ultrasound,'' Nature (London) **389**, 341.

Mann, D. A., Lu, Z., Hastings, M. C., and Popper, A. N. (**1998**). ''Detection of ultrasonic tones and simulated dolphin echolocation clicks by a teleost fish, the American shad (*Alosa* sapidissima),'' J. Acoust. Soc. Am. **104**, 562–568.

National Marine Fisheries Service (NMFS) (**1999**). ''Fisheries of the United States, 1998,'' NMFS Office of Science and Technology/Fisheries Statistics and Economics Division.

Nestler, J. M., Ploskey, G. R., Pickens, J., Menezes, J., and Schilt, C. (**1992**). ''Responses of blueback herring to high-frequency sound and implications for reducing entrainment at hydropower dams,'' N. Am. J. Fish. Man. **12**, 667–683.

O'Connell, C. P. (**1955**). ''The gas bladder and its relation to the inner ear in *Sardinops caerulea* and Engraulis mordax,'' Fish. Bull. **56**, 505–533.

Popper, A. N., and Fay, R. R. (**1973**). ''Sound detection and processing by fish, A critical review,'' J. Acoust. Soc. Am. **53**, 1515–1529.

Popper, A. N., and Fay, R. R. (**1999**). ''The auditory periphery in fishes,'' in *Comparative Hearing, Fish and Amphibians*, edited by R. R. Fay and A. N. Popper (Springer, New York), pp. 43–100.

Popper, A. N., and Platt, C. (**1979**). ''The herring ear has a unique receptor pattern,'' Nature (London) **280**, 832–833.

Rogers, P. H., and Cox, M. (**1988**). ''Underwater sound as a biological stimulus,'' in *Sensory Biology of Aquatic Animals*, edited by J. Atema, R. R. Fay, A. N. Popper, and W. N. Tavolga (Springer-Verlag, New York), pp. 131–149.

Ross, Q. E., Dunning, D. J., Menezes, J. K., Kenna, M. J., Tiller, G. (**1995**). ''Reducing impingement of alewives with high-frequency sound at a power plant on Lake Ontario,'' N. Am. J. Fish. Man. **15**, 378–388.

Ross, Q. E., Dunning, D. J., Thorne, R., Menezes, J. K., Tiller, G. W., and Watson, J. K. (**1996**). ''Response of alewives to high-frequency sound at a power plant intake on Lake Ontario,'' N. Am. J. Fish. Man. **16**, 548–559.

Sales, G., and Pye, D. (**1974**). *Ultrasonic Communication by Animals* (Chapman and Hall, London).

Schwarz, A. L., and Greer, G. L. (**1984**). ''Responses of Pacific Herring, *Clupea harengus pallasi*, to some underwater sounds,'' Can. J. Fish. Aquat. Sci. **41**, 1183–1192.

Sorokin, M. A., Donskoi, S. V., and Lebedeva, A. N. (**1988**). ''Sound reception in clupeidae,'' Biologiya Morya **2**, 34–40.

Wohlfhart, T. A. (**1936**). ''Das ohrlabyrinth der sardine (*Clupea pilchardus* Walb.) und seine beziehungen zur zchwimmblase und seitenlinie,'' Z. Morphol. Oekol. Tiere **31**, 371–410.

Yan, H. Y. Y., Fine, M. L., Horn, N. S., and Colón, W. E. (**2000**). ''Variability in the role of the gasbladder in fish audition,'' J. Comp. Physiol. A **186**, 435–445.

Downloaded 08 Jul 2010 to 160.36.195.182. Redistribution subject to ASA license or copyright; see http://asadl.org/journals/doc/ASALIB-home/info/terms.jsp