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Acoustic pressure and particle motion thresholds in six sciaenid fishes

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SUMMARY

Sciaenid fishes are important models of fish sound production, but investigations into their auditory abilities are limited to acoustic pressure measurements on five species. In this study, we used auditory brainstem response (ABR) to assess the pressure and particle acceleration thresholds of six sciaenid fishes commonly found in Chesapeake Bay, eastern USA: weakfish (Cynoscion regalis), spotted seatrout (Cynoscion nebulosus), Atlantic croaker (Micropogonias undulatus), red drum (Sciaenops ocellatus), spot (Leiostomus xanthurus) and northern kingfish (Menticirrhus saxatilis). Experimental subjects were presented with pure 10 ms tone bursts in 100 Hz steps from 100 Hz to 1.2 kHz using an airborne speaker. Sound stimuli, monitored with a hydrophone and geophone, contained both pressure and particle motion components. Sound pressure and particle acceleration thresholds varied significantly among species and between frequencies; audiograms were notably flatter for acceleration than pressure at low frequencies. Thresholds of species with diverticulae projecting anteriorly from their swim bladders (weakfish, spotted seatrout, and Atlantic croaker) were typically but not significantly lower than those of species lacking such projections (red drum, spot, northern kingfish). Sciaenids were most sensitive at low frequencies that overlap the peak frequencies of their vocalizations. Auditory thresholds of these species were used to estimate idealized propagation distances of sciaenid vocalizations in coastal and estuarine environments.

Supplementary material available online at http://jeb.biologists.org/cgi/content/full/211/9/1504/DC1

Key words: animal communication, hearing, particle acceleration, particle velocity, Sciaenidae, soniferous.

INTRODUCTION

Sound in water is composed of two physically linked components, propagating scalar pressure waves and directional particle motion, which differ in the pathways through which they reach the inner ears of fishes (Fay and Popper, 1975). The otoliths of all fishes are biological accelerometers that directly detect the particle motion components of sound as a result of inertial differences between sensory epithelia and otoliths (Lu and Xu, 2002; Popper and Fay, 1993). Additionally, the pressure component of sound may be detected indirectly by some fishes via accessory anatomical structures that transform sound pressure waves into particle displacements (Popper and Fay, 1993).

Fishes are categorized as hearing ‘specialists’ and ‘generalists’ on the basis of anatomy, the ability to detect the pressure component of sound, and the range of detectable bandwidth. Hearing specialist species have evolved projections of the swim bladder or skeletal connections that enable the indirect re-radiation of the pressure component of sound as particle displacement capable of stimulating the inner ear (Fay and Popper, 1974; Popper and Fay, 1999). Thus hearing-specialist fishes, which include groups such as clupeids, otophysans, mormyrids and osphronemids, may use both direct (particle motion) and indirect (pressure transduction) mechanisms to enhance their hearing sensitivity and extend their detectable auditory bandwidth (Mann et al., 1997; Popper and Fay, 1993; Yan, 1998; Yan and Curtssinger, 2000). By contrast, hearing generalist fishes lack such specialized structures coupling pressure-to-displacement transducers to the otic capsule, resulting in attenuation of the signal and reduced stimulation of the ear via sound pressure (Casper and Mann, 2006). The unaided organs of the inner ear of hearing generalists are thought to be fairly insensitive to the indirect transduction of sound pressure (Sand and Karlsen, 2000; Yan et al., 2000); direct particle motion stimulation of the otoliths is likely more relevant to these fishes (Lu and Xu, 2002; Casper and Mann, 2006). However, few studies have examined the hearing thresholds of fishes with respect to both pressure and particle motion sensitivity (Myrberg and Spires, 1980; van den Berg, 1985; Lovell et al., 2005; Casper and Mann, 2006).

Sciaenid fishes are model organisms of teleost bioacoustics (Ramcharitar et al., 2006a; Roundtree et al., 2006), but comparatively little is known about their auditory abilities. Sciaenid saccular otoliths are enlarged relative to most fishes, and their morphology and proximity to the swim bladder vary widely (Chao, 1978; Ramcharitar et al., 2001). Both hearing specialists and generalists have been identified within the family (Ramcharitar et al., 2004; Ramcharitar et al., 2006b). Unfortunately, the pressure detection abilities of less than two percent of the 270 sciaenid species have been described [Atlantic croaker, spot, weakfish, black drum, silver perch (Ramcharitar, 2003)], and the particle motion sensitivity of these fishes has not been examined. Comparative work on sciaenid fishes has great potential to elucidate form-and-function relationships in the teleost auditory system (Ramcharitar, 2003). We therefore performed auditory brainstem response experiments using a hydrophone and geophone to categorize the pressure and particle acceleration detection thresholds of six sciaenid fishes. The simultaneous recording of the pressure and particle motion...
components of sound stimuli allowed us to express audiograms with respect to both. The former allows us to compare our data to previously published results for sciaenid fishes (Ramcharitar and Popper, 2004; Ramcharitar et al., 2006b); the latter allows comparison to recent studies examining particle motion thresholds in other fishes (Casper and Mann, 2006; Mann et al., 2007).

MATERIALS AND METHODS

Experimental animals and design

Weakfish (Cynoscion regalis Bloch and Schneider 1801), spotted seatrout (Cynoscion nebulosus Cuvier 1830), Atlantic croaker (Micropogonias undulatus Linnaeus 1766), red drum (Sciaenops ocellatus Linnaeus 1766), spot (Leiostomus xanthurus Lacepede 1802) and northern kingfish (Menticirrhus saxatilis Bloch and Schneider 1801) were captured in Chesapeake Bay, eastern USA, using hook and line (Table 1). Animals were maintained in recirculating 1855 l aquaria at 20±1°C (winter months) or 25±2°C (summer months) and fed a combination of frozen Atlantic menhaden (Brevoortia tyrannus), squid (Loligo sp.) and commercially prepared food (AquaTox flakes; Zeigler, Gardners, PA, USA).

Experimental and animal care protocols were approved by the College of William and Mary’s Institutional Animal Care and Use Committee, protocol no. 0423, and followed all relevant laws of the United States. Auditory brainstem response (ABR) experiments were conducted on six animals of each species. All subjects were immobilized animals were suspended within a rectangular chamber by the submersed, omnidirectional hydrophone. Auditory brainstem response (ABR) is a non-invasive recording of the neural activity in the eighth cranial nerve and brainstem in response to synchronized acoustic stimuli (Corwin et al., 1982; Kenyon et al., 1998). The ABR experimental setup and procedure followed that of others (Kenyon et al., 1998). A speaker (model: TDT, Inc., Gainesville, FL, USA) and BioSig software were used to produce sound stimuli.

Recording of vertebrate ABR waveforms in anaesthetized and/or immobile subjects is a common practice to minimize the obscuring effect of muscular noise on ABR recordings (Hall, 1992; Kenyon et al., 1998; Casper et al., 2003). Sedated and immobilized animals were suspended within a rectangular 61×31×16.5 cm Plexiglas tank using foam straps, leaving <1 mm of the top of the head protruding from the water. Subjects were ventilated (1 l min−1) with filtered, oxygenated, and temperature-controlled seawater (25±2°C). At the conclusion of each experiment, fishes were euthanized with a massive i.m. dose of sodium pentobarbital (~300 mg kg−1).

Auditory brainstem response

Auditory brainstem response (ABR) is a non-invasive recording of the neural activity in the eighth cranial nerve and brainstem in response to synchronized acoustic stimuli (Corwin et al., 1982; Kenyon et al., 1998). The ABR experimental setup and procedure followed that of others (Kenyon et al., 1998). A speaker (model: 40-1034, 27.5 cm in diameter, Radio Shack, Fort Worth, TX, USA), suspended in the air, was mounted 1.5 m directly above the test subject. Two platinum wire needle electrodes (model: F-E7, 10 mm tip, Grass Technologies, West Warwick, RI, USA) were placed subdermally along the midline of each subject: the active electrode was positioned above the medulla, and the reference electrode in the dorsal musculature above the operculum. The system was grounded to the water of the experimental tank via a 6 cm×26 cm stainless steel plate. An omnidirectional hydrophone (Reson A/S, Slangerup, Denmark; sensitivity: −211 dB re: 1V/µPa) was suspended with rubber straps 25 mm below the water surface (i.e. the depth of a subject’s otic capsule) and positioned within 2.5 mm of the right opercle-preopercle margin of each subject to measure the sound pressure level of the stimulus and ambient noise.

In the absence of an anechoic chamber, all experiments were conducted in a concrete laboratory. We produced a stochastic differential white noise signal to characterize the echoes resulting from all reflective surfaces at the hydrophone positioned next to the subject. A custom Fourier/inverse Fourier transform algorithm (MATLAB version 6.5, Mathworks, Inc., Natick, MA, USA) was used to analyze these recordings and add to each frequency’s pure tone stimulus the appropriate signals needed to destructively interfere with any recorded echoes. Any alteration to the sound field in the laboratory since the last echo-cancellation (i.e. movements, small changes in the tank water level, etc.) required us to re-echo-cancel before proceeding. Visual examination of stimulus waveforms recorded by the hydrophone during ABR experiments (Fig. 1) confirmed that our echo-cancelled stimuli were very similar to pure tone waveforms used in other fish hearing experiments (Kenyon et al., 1998).

A Tucker-Davis Technologies System II (TDI, Inc., Gainesville, FL, USA) and BioSig software were used to produce sound stimuli.

Table 1. Species, sample size, standard length (SL) and mass of the six sciaenid fishes investigated in this study

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>SL (mm)</th>
<th>Mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cynoscion regalis</td>
<td>6</td>
<td>230–315</td>
<td>190–460</td>
</tr>
<tr>
<td>Cynoscion nebulosus</td>
<td>6</td>
<td>225–515</td>
<td>165–730</td>
</tr>
<tr>
<td>Micropogonias undulatus</td>
<td>6</td>
<td>230–485</td>
<td>185–790</td>
</tr>
<tr>
<td>Sciaenops ocellatus</td>
<td>6</td>
<td>305–555</td>
<td>585–955</td>
</tr>
<tr>
<td>Leiostomus xanthurus</td>
<td>6</td>
<td>115–381</td>
<td>65–405</td>
</tr>
<tr>
<td>Menticirrhus saxatilis</td>
<td>6</td>
<td>200–305</td>
<td>140–325</td>
</tr>
</tbody>
</table>

Fig. 1. Sample 500 Hz waveforms: (A) a pure tone 500 Hz stimulus waveform, (B) an echo-cancelled 500 Hz stimulus and (C) a 500 Hz signal that was not echo-cancelled. B and C were recorded in our experimental chamber by the submersed, omnidirectional hydrophone.
Sound pressure level (SPL) was measured by hydrophone, and mean SPLs of these recordings (in hydrophone (sensitivity: –200·dB re: 1V/H9262 Pa) containing two built-in units: a piezoelectric, omni-directional pressure-velocity probe (Mk. 2, Acoustech Corp, Philadelphia, PA, USA) and a bi-directional moving-coil geophone (sensitivity: 0.112 V cm⁻¹ s⁻¹). The outer housing of this probe was secured in place of the fish ~25 mm below the water surface with rubberized clamps, and the inner unit of the probe, designed to approximate neutral buoyancy, moved freely in response to our sound stimuli. The omnidirectional hydrophone was suspended by rubber straps to within 2 mm of the pressure-velocity probe. This setup enabled the simultaneous recording of the sound pressure and particle velocity components of the entire range of our experimental stimuli. Subsequently and separately, measurements of particle displacements were recorded in three orthogonal orientations (sensu Casper and Mann, 2006). The vertical component (z axis) of particle velocity had substantially greater amplitudes than the x (horizontal: head-to-tail) or y axes (left to right) at each frequency and attenuation (Table 2). This vertical axis was therefore considered most appropriate for expressing thresholds and plotting particle acceleration audiograms.

The otolithic organ systems of fishes are thought to act as accelerometers, and particle motion audiograms have been increasingly expressed in units of acceleration (Kalman, 1988; Fay and Edds-Walton, 1997; Casper and Mann, 2006). Therefore, particle velocity (m s⁻¹) was quantified as above for acoustic pressure, and velocity values were converted to particle acceleration using Eqn 1:

\[ A = u^2 \pi F, \]

where \( A \) is the particle acceleration (m s⁻²), \( u \) is the particle velocity (m s⁻¹) and \( F \) is the frequency (Hz) (see Table S1 in supplementary material).

### Table 2. Particle accelerations in three orthogonal Cartesian directions and for the magnitude of the three directions combined

<table>
<thead>
<tr>
<th>Frequency (Hz)</th>
<th>x-axis acceleration (m s⁻²)</th>
<th>y-axis acceleration (m s⁻²)</th>
<th>z-axis acceleration (m s⁻²)</th>
<th>Magnitude of particle acceleration (m s⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>0.015</td>
<td>0.010</td>
<td>0.182</td>
<td>0.033</td>
</tr>
<tr>
<td>200</td>
<td>0.018</td>
<td>0.061</td>
<td>0.578</td>
<td>0.370</td>
</tr>
<tr>
<td>300</td>
<td>0.064</td>
<td>0.082</td>
<td>1.17</td>
<td>1.38</td>
</tr>
<tr>
<td>400</td>
<td>0.080</td>
<td>0.096</td>
<td>1.01</td>
<td>1.04</td>
</tr>
<tr>
<td>500</td>
<td>0.094</td>
<td>0.129</td>
<td>0.428</td>
<td>0.206</td>
</tr>
<tr>
<td>600</td>
<td>0.113</td>
<td>0.109</td>
<td>0.670</td>
<td>0.473</td>
</tr>
<tr>
<td>700</td>
<td>0.141</td>
<td>0.114</td>
<td>0.482</td>
<td>0.266</td>
</tr>
<tr>
<td>800</td>
<td>0.168</td>
<td>0.125</td>
<td>0.510</td>
<td>0.304</td>
</tr>
<tr>
<td>900</td>
<td>0.184</td>
<td>0.115</td>
<td>0.305</td>
<td>0.140</td>
</tr>
<tr>
<td>1000</td>
<td>0.219</td>
<td>0.124</td>
<td>0.362</td>
<td>0.194</td>
</tr>
<tr>
<td>1100</td>
<td>0.218</td>
<td>0.206</td>
<td>0.413</td>
<td>0.260</td>
</tr>
<tr>
<td>1200</td>
<td>0.168</td>
<td>0.249</td>
<td>0.339</td>
<td>0.205</td>
</tr>
</tbody>
</table>

*(sensu Casper and Mann, 2006).

Sound pressure level (SPL) was measured by hydrophone, and mean SPLs of these recordings (in dB re: 1 µPa) were: x axis (116.7 dB), y axis (116.3 dB), z axis (119.7 dB). The x axis was considered to be anterior–posterior along each subject’s body whereas the y axis was considered to be lateral (right–left) relative to the subject. Particle acceleration was calculated from the particle velocity measured by the geophone for stimulus acoustic sound pressures. The speaker was mounted in air 1.5 m directly above each test subject. Most of the acoustic energy was along the vertical (z) axis coming from directly above test subjects. The magnitude of particle acceleration (m s⁻²) was calculated as \( \sqrt{x^2+y^2+z^2} \).
Statistical analyses

Auditory thresholds are ideally analyzed with repeated measures ANOVA designs because thresholds at different frequencies are non-independent within individual subjects (Underwood, 2002). Considering responses of an individual fish to be independent across frequencies constitutes pseudoreplication (Hurlbert, 1984); valid analyses of such data require that the nature of within-individual autocorrelation is explicitly understood. Inadequate consideration of the variance-covariance structure resulting from repeated measures may result in biased estimates of the variance of fixed effects (Littell et al., 2006). Pressure and particle acceleration thresholds were therefore analyzed separately using two-way repeated measures ANOVAs with a priori contrasts to investigate whether hearing varied between the six sciaenid species and among frequencies. All statistical analyses were conducted using SAS v 9.1 (SAS Institute, Cary, NC, USA). The model for these analyses is given in Eqn 2:

\[ Y_{ijk} = \mu + \alpha_i + \beta_j + \delta_{ik} + \epsilon_{ijk}, \]

where \( Y_{ijk} \) is the value of the response variable (threshold) for the \( i \)th species, \( j \)th frequency, and the \( k \)th level of their interaction; \( \mu \) is the overall mean of threshold for all species:frequency combinations; \( \alpha_i \) is the species (fixed factor); \( \beta_j \) is the frequency (fixed factor); \( \delta_{ik} \) is the species:frequency interaction; \( \epsilon_{ijk} \) is the...
random error term associated with the observation at each combination of the $i$th species, the $j$th frequency, and the $k$th level of their interaction.

We fitted models with three candidate covariance structures (unstructured, compound symmetry, and first order autoregressive [AR(1)]) to the pressure and particle acceleration threshold data. In the unstructured model (UN), each covariance between measures was estimated individually, allowing the data to dictate the appropriate covariance structure. The second covariance structure, compound symmetry (CS), assumed equal covariances between all pairs of observations. The final covariance structure, first order autoregressive [AR(1)], assumed that the correlation between observations is a function of their lag in space or time; adjacent observations are more likely to be correlated than those taken further apart (Littell et al., 2006). As a simple example involving the relationship between evoked potentials at 200, 300 and 900 Hz, the UN model would calculate the variance–covariance of every pair of observations individually, the AR(1) model would assume that evoked potentials at 200 and 300 Hz are likely more similar than responses at 200 versus 900 Hz, whereas the CS model would assume equal covariance.

After models were fitted to data, the appropriate covariance structure was selected using Akaike’s information criterion (AICc):

$$AIC_c = -2\ln(L) + 2p + 2(p+1)/(n-p-1),$$

where $AIC_c$ is Akaike’s information criterion for small sample size, $L$ is the value of the likelihood function at its maximum, $n$ is sample size (threshold of each fish of each species at each frequency), and $p$ is the number of estimated parameters. AICc is a parsimonious measure that strikes a balance between model simplicity and complex overparameterization (Burnham and Anderson, 2002). The small-sample adjustment ($AIC_c$) is recommended when the ratio of sample size to the number of parameters is less than 40 (Burnham and Anderson, 2002).

**RESULTS**

The ABR waveforms and audiograms for sound pressure and acceleration were species-specific, but with some commonalities. Auditory evoked potentials of the six sciaenid fishes (Fig. 2) generally began 10–15 ms after stimulus onset and were complete by 30 ms (≥400 Hz) or 50 ms (100–300 Hz). Waveform latency varied inversely with frequency and sound pressure level. Sound pressure, particle velocity, and acceleration audiograms of all species (Fig. 3 A–C) exhibited lowest thresholds at low frequencies (100–500 Hz). Velocity and acceleration audiograms were notably flatter at low frequencies. AICc values supported the selection of the first order autoregressive [AR(1)] covariance model for both pressure and particle acceleration analyses (Table 3), supporting the assumptions of the AR(1) model. Visual inspection of sciaenid audiograms (Fig. 3) confirms inferences based on AICc; ABR responses at adjacent frequencies were therefore more similar to each other than responses at distant frequencies.

Two-way repeated measures ANOVAs demonstrated significant differences between species for both pressure ($F_{3,48}=3.17, P=0.02$) and particle motion (velocity: $F_{5,51}=3.85, P=0.003$; acceleration: $F_{5,52}=3.00, P=0.02$) thresholds. Sound pressure thresholds of spot were significantly higher ($F_{1,35}=5.05, P=0.03$) than those of other sciaenids from 300–700 Hz. Among species with swim bladders, thresholds of those with anteriorly projecting diverticulae (weakfish, spotted seatrout and Atlantic croaker) did not differ from those species without diverticulae (red drum and spot; pressure: $F_{1,35}=2.35, P=0.13$). Surprisingly, thresholds of northern kingfish were among the lowest at higher frequencies (>600 Hz) even though the swim bladder atrophies in the adults we studied. Detection thresholds varied inversely with frequencies for both pressure ($F_{11,312}=53.01, P<0.001$) and particle motion (velocity: $F_{11,317}=78.47, P<0.0001$; acceleration: $F_{11,315}=129.24, P<0.0001$). Interactions of species and frequencies were significant for both pressure ($F_{55,310}=3.31, P<0.0001$) and particle motion (velocity: $F_{55,314}=8.48, P<0.0001$; acceleration: $F_{55,314}=9.77, P<0.0001$) and are visually evident in the crossing of species-specific curves within audiograms (Fig. 3A–C).

**DISCUSSION**

All fishes are able to directly detect the particle motion components of sound, yet fish auditory thresholds are generally assessed only for sound pressure levels (Popper and Fay, 1993). Few studies...
have examined hearing thresholds of fishes with respect to both pressure and particle motion sensitivity (Myrberg and Spires, 1988; van den Berg, 1985; Lovell et al., 2005; Casper and Mann, 2006). Moreover, direct particle motion simulation of the otoliths may be more relevant to hearing generalist fishes than the detection of sound pressure (Fay and Popper, 1975; Popper and Fay, 1993). In this study, we measured thresholds and expressed audiograms of six sciaenid fishes in terms of both sound pressure and acceleration using an omnidirectional hydrophone and a bi-directional geophone. Our experiments are the first to assess particle motion thresholds in sciaenid fishes and include first reports of pressure audiograms for spotted seatrout, red drum, and northern kingfish.

Sound stimuli during fish audition experiments contain both pressure and particle motion (Parvulescu, 1967; Lu et al., 1996; Casper and Mann, 2006). Small experimental tanks can have complex particle motion and sound pressure fields, potentially compromising laboratory investigations unless both components of sound stimuli are measured (Kalmijn, 1988; Popper and Fay, 1993). Placing stimulus-generating speakers in air rather than water purportedly reduces the particle motion (Kenyon et al., 1998). Our results, however, demonstrate that speakers in air can produce notable particle motion fields (Table 2). Similar conclusions were reached by others (Casper and Mann, 2006). Particle displacements in small tanks are complex, and for an equal sound pressure level they may be greater in tanks than in an unbounded body of water (Parvulescu, 1967; Rogers and Cox, 1988). General comparisons across studies may be complicated by differences in the location of the sound source in air versus water, the proximity of subjects to the sound source and air-water interfaces (Fay and Edds-Walton, 1997). Such concerns demonstrate the utility of routine particle motion assessment of experimental sound stimuli. Submersible units capable of generating and measuring particle motion are available (Casper and Mann, 2007a; Casper and Mann, 2007b). Future fish audition experiments should attempt to measure and report both the pressure and particle motion components of their experimental stimuli if possible (Popper and Fay, 1993; Casper and Mann, 2006).

The frequency range detected by the six sciaenids we studied was similar to those of other hearing generalist fishes (100 to <2000 Hz) (Popper and Fay, 1993; Kenyon et al., 1998; Ramcharitar, 2003; Ramcharitar and Popper, 2004; Ramcharitar et al., 2006b). Pressure detection thresholds of sciaenid fishes were significantly lower at low frequencies from 100–300 Hz. Our mean pressure thresholds for spot, weakfish and Atlantic croaker, obtained with a speaker in air, averaged about 6 dB higher than those obtained by others using a speaker in water (Ramcharitar and Popper, 2004; Ramcharitar et al., 2006b). Whether the different results are a consequence of speaker location/type, different levels of background noise, individual variation due to the use of larger animals in our study, or a combination of these factors, is unclear. Overall, our results generally support the conclusion of Ramcharitar et al. (Ramcharitar et al., 2006b) that enhanced swim bladder–otolith relationships within the Sciaenidae can improve auditory sensitivity. Among sciaenids bearing swim bladders, those possessing diverticulae (weakfish, spotted seatrout and Atlantic croaker) had generally but not significantly lower pressure thresholds than species lacking diverticulae (spot and red drum). Swim bladders lacking mechanical coupling to the otic capsule may not enhance sound pressure detection (Yan et al., 2000).

Surprisingly, however, we found the lowest sound pressure thresholds at higher frequencies (800–1100 Hz) in northern kingfish, a species with low hair cell densities and swim bladder atrophy in adults (Chao, 1978; Ramcharitar et al., 2001). Since species lacking swim bladders are unlikely to detect sound pressure (Casper and Mann, 2006; Mann et al., 2007), lower ‘pressure’ thresholds of kingfish at higher frequencies are most likely a response to particle motion during the simultaneous presentation of pressure and particle motion stimuli.

Otoliths are biological accelerometers most sensitive to particle motion on their longitudinal axis (Lu and Xu, 2002), and the larger otoliths of sciaenid fishes may confer higher sensitivity to the particle motion components of low frequency sounds (Lychakov and Rebane, 1993; Ramcharitar et al., 2006b). Our particle acceleration audiograms demonstrate significantly greater sensitivity at low frequencies (Fig. 3C) and are comparable to results obtained with elasmobranchs (Casper and Mann, 2006). Sciaenid species with enhanced connections between the swim bladder and otic capsule (Atlantic croaker, spotted seatrout, weakfish) may be able to obtain different information from the acoustic particle motion and sound pressure fields (van den Berg, 1985; Ramcharitar et al., 2001). By contrast, sciaenid fishes lacking connections between these organ systems (spot, red drum) are more likely to be responsive solely to particle motion fields (Ramcharitar, 2003). Similar conclusions have been reached for elasmobranch and teleost fishes lacking swim bladders (Mann et al., 2007; Casper and Mann, 2006). Adult kingfish (lacking swim bladders) used in our study probably detect acoustic particle motion rather than pressure. The situation is less clear for juvenile kingfish, which do have swim bladders that are distant from the otic capsule (Chao, 1978; Ramcharitar, 2003). Unfortunately, little is known about ontogenetic differences in pressure and particle motion discrimination in most fishes, including sciaenids.

A better understanding of particle motion thresholds in fishes is required, particularly with respect to hearing relative to the direction of stimulus (sensu Fay and Edds-Walton, 1997). In our study, maximum particle displacement occurred along the vertical axis (Table 2). But are sciaenids most sensitive to particle motion on this axis? Spawning aggregations, which involve chorusing fish juxtaposed in close proximity (Mok and Gilmore, 1983; Ramcharitar et al., 2006a; Gilmore, 2003), more likely stimulate otoliths in a horizontal direction. Although density and orientation of hair cell bundles in sciaenid fishes differ among species (Ramcharitar, 2003), a better understanding of particle motion thresholds in fishes is required as a basis for further research.
identify and manage their spawning habitats in environments with ever-increasing anthropogenic noise (Wahlberg and Westerberg, 2005; Ramcharitar et al., 2006a; Vasconcelos et al., 2007). Sciaenid bioacoustics therefore remains a fruitful research avenue and critical link between sensory physiology and behavioral ecology (Popper et al., 2005; Ramcharitar et al., 2006a; Roundtree et al., 2006). Such research promotes multidisciplinary syntheses that can mechanistically link processes from the cellular to the individual to the population level in support of fisheries management.

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Hearing in sciaenids


