INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6” x 9” black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.
AN EXPERIMENTAL AND THEORETICAL INVESTIGATION OF THE MECHANICS OF THE GOLDFISH PERIPHERAL AUDITORY SYSTEM

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

By

James J. Finneran, B.S., M.S.

The Ohio State University

1997

Dissertation Committee:

Dr. Mardi C. Hastings, Adviser
Dr. Donald R. Houser
Dr. Chia-Hsiang Menq

Approved by

Mardi C. Hastings
Adviser
Department of Mechanical Engineering
ABSTRACT

Despite the progress made in establishing the capabilities of the auditory system in several species of fish, significant questions remain regarding how sound reaches the ear and the nature of the coupling between the ear and various accessory structures. In this research, experimental measurements and theoretical modeling were used to examine the mechanical behavior of the peripheral auditory system of the goldfish (*Carassius auratus*).

The experiments consisted of measuring the *in vivo* motion of the swimbladder, Weberian ossicles, and otoliths of an anesthetized and tethered fish, in response to an acoustic stimulus, using a noninvasive ultrasonic measurement system. The experimental results show strong coupling between the swimbladders, tripus, and saccule. At low frequencies, the swimbladders, Weberian ossicles, and otoliths move with the same amplitude and phase as the fish's body. At higher frequencies, multiple resonances occur in most swimbladder responses. The swimbladder resonance also appears in the sagitta response; the sagitta displacement ranges from 1 to 10 nm/Pa. The results of only a few tests indicate motion of the lagenar otolith, while no data show movement of the utricular otolith.

The mathematical model of the dynamics of the goldfish peripheral auditory system is the first such model to include the swimbladder, Weberian apparatus, and saccule (including the hair cell ciliary bundles). The saccule model features only translation of the otolith in the direction of hair cell orientation. The model predicts the correct amplitude and phase relationships between the two swimbladder chambers and shows the coupling
observed between the anterior swimbladder and the tripus. The model also predicts a high-pass filter effect due to the tunica externa compliance; however, the model low frequency cut-off seems insufficient to prevent a change in depth from overstimulating the Weberian apparatus. The model predicts a sagitta displacement on the order of 10 nm/Pa. Above 50 Hz, the relative displacement between the sagitta and sensory epithelium is primarily due to the Weberian apparatus. The phase relationships between the sagitta and sensory epithelium displacements vary with location of the acoustic source.
ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Mardi Hastings, for advice and guidance throughout this work. I also wish to thank Dr. Arthur Popper for critically reading and commenting on this manuscript. I also thank Dr. Donald Houser and Dr. Chia-Hsiang Menq for serving on my dissertation committee. Finally, I wish to thank Corrie Derenburger for help in conducting the experimental measurements and analyzing the data.

This work was supported by the Office of Naval Research, Grant Number N00014-94-1-0337.
VITA

May 26, 1967  Born - Columbus, Ohio

1990  B.S. Mechanical Engineering, The Ohio State University

1991  M.S. Mechanical Engineering, The Ohio State University

1990–Present  Graduate Research Associate, The Ohio State University

PUBLICATIONS


**FIELDS OF STUDY**

**Major Field:** Mechanical Engineering

**Studies in:** Bioacoustics, Ultrasound, System Dynamics
TABLE OF CONTENTS

Abstract .......................................................................................................................... ii
Acknowledgments .......................................................................................................... iv
Vita ....................................................................................................................................... v
List of Figures ..................................................................................................................... xi
List of Tables .................................................................................................................... xxi

Chapters:

1. Introduction .............................................................................................................. 1
   A. Motivation ........................................................................................................ 1
   B. Background ...................................................................................................... 2
      1. Underwater sound ................................................................................... 2
      2. Structure of the goldfish ear .................................................................... 2
      3. Hearing mechanisms ............................................................................... 6
      4. Taxonomic information ............................................................................. 9
   C. Literature review ............................................................................................ 10
      1. Structure of the peripheral auditory system in bony fishes .................... 10
      2. Mechanics of the peripheral auditory system in bony fishes .............. 11
      3. Models of the peripheral auditory system in bony fishes ...................... 14
         a. Swimbladder models ................................................................... 14
         b. Otolith models .......................................................................... 21
         c. Hair cell models ........................................................................ 21
   D. Overview of this study .................................................................................. 24

2. Noninvasive ultrasonic measurement system ......................................................... 26
   A. Principles ...................................................................................................... 26
      1. Amplitude measurement ........................................................................ 30
      2. Phase measurement ............................................................................... 31
         a. Effect of target reflection coefficient ............................................ 34
         b. Effect of low frequency target motion ........................................ 35
      3. Measurement verification and accuracy ............................................. 38
B. Spatial resolution ................................................................. 43
   1. Theoretical ........................................................................ 44
      a. Focused source only .................................................. 44
      b. Focused source and focused receiver ....................... 47
   2. Experimental ................................................................. 50

3. Acoustic waveguide .................................................................. 56
   A. Waveguide construction ..................................................... 59
   B. Waveguide performance: theoretical ................................. 60
      1. Phase velocity .......................................................... 60
      2. Attenuation ............................................................... 66
      3. Attenuated plane waves in a duct ................................. 68
         a. No reflected wave ............................................... 70
   C. Waveguide performance: experimental ............................... 72
      1. Radial behavior ........................................................ 72
      2. Axial behavior ........................................................ 74
      3. Phase velocity ......................................................... 78
      4. Attenuation ............................................................. 79
   D. Active control system ........................................................ 81
      1. Active control theory ............................................... 81
      2. Control methodologies ............................................. 84
      3. Pattern search method .............................................. 86
      4. Experimental implementation .................................. 87
      5. Comparison with unbounded plane progressive wave ....... 93

4. Experimental methods ............................................................. 96
   A. Experimental animals ........................................................ 96
   B. Experimental apparatus ..................................................... 99
      1. Waveguide setup ....................................................... 99
         a. Acoustic stimulus in the waveguide ....................... 103
      2. Pool setup .............................................................. 107
         a. Acoustic stimulus in the pool ................................. 110
   C. Experimental procedure .................................................. 111
   D. Data reduction .............................................................. 114
   E. Measurement threshold and accuracy ............................... 118
      1. Measurement threshold ............................................ 118
      2. Measurement accuracy ............................................. 121

5. Experimental results ............................................................. 123
   A. Introduction .................................................................... 123
      1. Representative data ................................................ 123
      2. Test replication and measurement accuracy ................. 132
   B. Anterior and posterior swimbladders ............................... 138
      1. Fish mass, length, and bladder dimensions ................. 138
      2. Body surface vs. swimbladder wall ......................... 142
      3. Multiple resonances ............................................... 147
      4. Comparison of anterior and posterior responses ........... 150
      5. Swimbladder resonance frequency and damping .......... 151
   C. Tripus and Weberian ossicles ........................................ 154
6. Peripheral auditory system model development ................................................. 166
   A. Model overview .................................................................................. 166
      1. Effect of acoustic particle velocity .................................................. 167
      2. System model inputs and material properties ............................... 169
   B. Model for the goldfish swimbladder ................................................... 170
      1. Single DOF radial motion ................................................................. 170
      2. Two DOF radial motion ................................................................. 179
      3. Swimbladder material properties .................................................... 185
   C. Model for the Weberian apparatus ....................................................... 192
      1. Tunica externa model ................................................................. 192
      2. Weberian ossicle model .............................................................. 197
      3. Fluid canal model ....................................................................... 199
      4. Coupled swimbladder/Weberian apparatus system ....................... 202
      5. Weberian apparatus material properties ........................................ 202
   D. Model for the saccule ......................................................................... 212
      1. Single DOF saccule model ............................................................ 212
      2. Saccule model material properties ............................................... 218
   E. Summary ............................................................................................. 222

7. Auditory system model results ..................................................................... 224
   A. Source and fish geometry ............................................................... 224
   B. Baseline results ................................................................................ 229
   C. Parameter effects study ...................................................................... 241
      1. Swimbladder subsystem ................................................................. 242
      2. Weberian apparatus subsystem ..................................................... 248
      3. Saccule subsystem ...................................................................... 257
   D. Model and experimental comparison .................................................. 259
   E. Effect of fish mass, bladder ratio, and source location ......................... 266
      1. Fish mass and bladder ratio ......................................................... 266
      2. Source location ........................................................................... 270
   F. Summary ............................................................................................. 274

8. Conclusions and recommendations ............................................................ 276
   A. Ultrasonic measurement system ......................................................... 276
   B. Low-frequency test environment ....................................................... 277
   C. Experimental measurements ............................................................. 278
   D. Auditory system model ...................................................................... 281

Appendices:
   A. Waveguide fabrication drawings ....................................................... 284
   B. Experimental test parameters ............................................................ 289
   C. Auditory system model source code .................................................. 295
Bibliography

311
**LIST OF FIGURES**

1.1 Medial view of the right ear of the goldfish, *Carassius auratus*, a member of the series Otophysi and family Cyprinidae (Modified from Popper and Coombs, 1980) ................................................................. 3

1.2 SEM of a group of hair cell ciliary bundles on the saccular macula of the Hawaiian squirrel-fish, *Adioryx xantherythrus* (From Popper, 1983). The length of the black bar is 1 μm .................................................. 5

1.3 Hair cell orientation patterns from the goldfish saccule and lagena. A – anterior, D – dorsal (Modified from Platt, 1977) ............................................................ 5

1.4 Block diagram of the three hearing mechanisms ............................................................................. 6

1.5 Dorsal view of an otophysan fish showing the relationship between the swimbladder, Weberian ossicles, and inner ear. The fourth ossicle, the claustrum, is not visible (Modified from Chardon and Vandewalle, 1992) ............ 8

1.6 Taxonomic relationship among members of the superorder Ostariophysi, showing the families of the order Cypriniformes. The goldfish belongs to the family Cyprinidae, which also includes carp, minnows, tench, and barbels (Nelson, 1984) .......................................................................................... 10

1.7 Gating spring model for mechanoelectric transduction in hair cells (From Hudspeth and Markin, 1994). (a) At the resting state transduction channels tend to remain closed. (b) After bending towards the kinocilium, gating springs stretch and tend to keep gates open, allowing Ca²⁺ and K⁺ ions to enter the cell .................................................................................................................. 22

1.8 Mechanical model for the bending response of a bullfrog saccular ciliary bundle (From Howard and Hudspeth, 1987) .............................................................. 24

2.1 Noninvasive ultrasonic measurement system ................................................................................. 27

2.2 Calculation of source-target-receiver path length for motion (a) along the transducer bisector, (b) orthogonal to the transducer axes, and (c) perpendicular to the bisector. The thick lines indicate the source-target-receiver path d' ........................................................................................................... 28
2.3 Received ultrasonic spectrum from a goldfish anterior swimbladder showing the relationship between the carrier and the sidebands. For this case the low frequency source was 400 Hz and the ultrasonic source frequency was 15 MHz..........................32

2.4 Change in \(\sin(2k_y d)\) as a function of the change in distance \(d\) from the ultrasonic source/receiver to the target, for a 15-MHz carrier frequency and an initial distance of 19 mm..........................................................................................35

2.5 DC component of phase detector output experimentally measured as a function of carrier frequency for a balloon target..........................36

2.6 Action of carrier frequency adjustment for (a) \(\phi_R = 0\) and (b) \(\phi_R = \pi\)..................37

2.7 Experimental setup used to evaluate the ultrasonic measurement system.................39

2.8 Detailed view of the accelerometer, acrylic post, and electromechanical shaker..................................................39

2.9 Measured displacement amplitude (from the ultrasonic system) vs. the "actual" displacement amplitude (from the accelerometer) at 1000 Hz.................41

2.10 Measured displacement phase (from the ultrasonic system) vs. the "actual" displacement phase (from the accelerometer) at 1000 Hz.................41

2.11 Measured displacement phase \(\phi\): acoustic pressure for a 20-mm diameter balloon..................................................................................43

2.12 Coordinate system for a single focused ultrasonic source.................................44

2.13 Axial behavior for three focused ultrasonic source configurations.................47

2.14 Coordinate system for the ultrasonic field..................................................48

2.15 Theoretical receiver fields for the ultrasonic measurement system of Fig. 2.14 showing the (a) \(u_1-u_3\), (b) \(u_1-u_4\), and (c) \(u_2-u_3\) contour planes. The lines represent the \(-3, -6, -10, -20, \) and \(-30\) dB contour levels \(re:\) maximum amplitude........................................................................51

2.16 Experimental setup for ultrasonic sample volume measurements.................52

2.17 Experimental receiver fields for the ultrasonic measurement system of Fig. 2.14 showing the (a) \(u_1-u_3\), (b) \(u_1-u_4\), and (c) \(u_2-u_3\) contour planes. The lines represent the \(-3, -6, -10, -20, \) and \(-30\) dB contour levels \(re:\) maximum amplitude..........................54

2.18 Sample volume dimensions at 15 MHz as functions of the bisected angle........55

3.1 System block diagram for active sound absorption within a duct .................58
3.2 Simplified representation of the position of the waveguide within the water channel .................................................................................................................59
3.3 Waveguide geometry and cylindrical coordinates ..........................................................60
3.4 Comparison of the more exact model of Easwaran and Munjal with the model of Junger for a water-filled steel tube immersed in water. EM - Easwaran and Munjal (1995); JU - Junger (1955) ..............................................................................67
3.5 Theoretical phase velocity (Junger's analysis) as a function of frequency for 6.35-mm thick acrylic tubes with inside diameters of 13, 18, and 23 cm ..........67
3.6 Theoretical impedance ratio for plane traveling waves within the waveguide ......72
3.7 Experimental setup for radial SPL measurements ..........................................................73
3.8 Experimentally measured radial SPL for 25, 100, 400, 600, and 800 Hz ....74
3.9 Experimental setup for axial SPL measurement ..........................................................75
3.10 SPL measured along the waveguide longitudinal axis ................................................76
3.11 Acoustic impedance ratio measured along the waveguide longitudinal axis. Top - real part; bottom - imaginary part..........................................................77
3.12 Phase velocity as a function of frequency within the waveguide. The theoretical curve is based on the model of Junger (1955) ..................78
3.13 The attenuation in the waveguide was estimated using two techniques. At high frequencies (a), pressure data were fitted with Eq. (3.40). At lower frequencies (b), pressure minima were fit to Eq. (3.47).............................80
3.14 Attenuation as a function of frequency in the waveguide. The functions used for the curve-fit are given in Eq. (3.48) ..................................................81
3.15 One-dimensional model of active control in the waveguide ..................................82
3.16 Example of a performance surface for active impedance control in a cylindrical duct. The vertical axis is 20 log_{10}(MSE); the horizontal axes are the real and imaginary parts of the source input ratio Q. ..................................................85
3.17 Flowchart for the pattern search method ..............................................................88
3.18 Active control system hardware ..........................................................................89
3.19 Progress of the optimization routine at 25 Hz ..................................................89
3.20 Effect of hydrophone spacing on active control system performance .................91
3.21 Acoustic impedance ratio measured with and without active control. Top - real part; bottom - imaginary part ..........................................................92
3.22 Reflection coefficient measured with and without active control .................93

3.23 Real and imaginary parts of the normalized acoustic impedance measured using the desired value from Eq. (3.62) in the active control system ...............95

4.1 Medial-lateral and dorso-ventral radiographs for a 36.1-g goldfish (GF017). The bar length is 1 cm. ASB – anterior swimbladder; PSB – posterior swimbladder; TR – tripus; LA – lagenar otolith; UT – utricular otolith ..........98

4.2 Behavioral audiograms for the goldfish. JT – Jacobs and Tavolga (1967); PS – Popper (1971b), small fish (45–48 mm); PL – Popper (1971b), large fish (110–120 mm) ......................................................................................98

4.3 Orientation of the waveguide and the ultrasonic measurement system ............100

4.4 Detailed view of the ultrasonic transducer configuration within the waveguide .............................................................................................................101

4.5 Experimental setup for tests within the waveguide ...........................................102

4.6 Example of the acoustic pressure measured within the waveguide test section. (a) average sound pressure level; (b) pressure phase re: primary source input ...........................................................................................................105

4.7 Representative sample of the (rms) acoustic particle velocities measured within the waveguide test section .................................................................106

4.8 Waveguide test section showing the location and sizes of the openings cut to allow access for the ultrasonic transducers and the fish. Dimensions are in millimeters ..................................................................................107

4.9 Geometry and layout of the plastic pool used for high frequency testing ..........108

4.10 Experimental setup used for high frequency tests in the pool ..............................109

4.11 Example of the measured acoustic pressure in the pool at the location of the fish. (a) average sound pressure level; (b) pressure phase re: primary source input ...........................................................................................................110

4.12 Representative sample of the (rms) acoustic particle velocities measured in the pool at the location of the fish .................................................................111

4.13 View from the x-z camera during testing of fish GF016 .................................113

4.14 Effect of target motion amplitude on signal detectability for the same carrier amplitude. (a) Sideband is above the noise so the motion may be measured. (b) With the same carrier amplitude, a lower amplitude motion may produce a sideband below the noise floor .................................................................119

xiv
4.15 Effect of carrier amplitude on signal detectability for the same target motion amplitude. (a) Sideband is below the noise so the motion may not be measured. (b) With a larger carrier amplitude, the same amplitude motion may produce a sideband above the noise floor...

4.16 Minimum detectable target motion, in terms of normalized velocity, for different carrier amplitudes

5.1 Normalized velocity measured from the swimbladders of goldfish GF016. ASB - anterior swimbladder; PSB - posterior swimbladder

5.2 Normalized velocity for the tripus and saccular otolith of goldfish GF016. TR - tripus; SA - saccular otolith

5.3 Normalized velocity for the lagenar and utricular otoliths of goldfish GF016. LA - lagenar otolith; UT - utricular otolith

5.4 Normalized velocity measured from the swimbladders of goldfish GF004. ASB - anterior swimbladder; PSB - posterior swimbladder

5.5 Normalized velocity for the tripus, lagenar, and saccular otoliths of goldfish GF004. TR - tripus; SA - saccular otolith; LA - lagenar otolith

5.6 Normalized velocity measured from the anterior swimbladder of goldfish GF756 showing the variation of response with repeated testing. The legend text indicates the test code for each data set (see Appendix B)

5.7 Summary of the normalized velocity measured from a lead target measuring 150 x 150 x 60 mm. The symbols represent 18 individual sets of experimental data obtained between Sept. 1996 and Feb. 1997. The thick line is the estimated accuracy for zero normalized velocity (see Table 4.1)

5.8 Normalized velocities measured from the anterior swimbladder, jaw, skull, and backbone of goldfish GF024. ASB - anterior swimbladder

5.9 Normalized velocity amplitude measured from the anterior swimbladder and skull of goldfish GF017. ASB - anterior swimbladder

5.10 Normalized velocity amplitude measured from the anterior swimbladder and tail muscle of goldfish GF757. ASB - anterior swimbladder

5.11 Standard body length vs. mass for the goldfish tested. The solid curve is a least squares fit to the data, given in Eq. (5.1)

5.12 Swimbladder radii vs. fish mass. The solid curve is the least squares fit to the anterior swimbladder data, given by Eq. (5.2)

5.13 Bladder ratio vs. goldfish mass

5.14 Percent volume (in ml/g) vs. the average mass of each goldfish tested
6.3 Relative magnitudes of the tissue damping and radiation damping factors from Eq. (6.32), for $\mu = 5 \times 10^5$ N/m$^2$; $\eta = 1.25 \times 10^5$ N/m$^2$; $R_j = 5$ mm; $R_o = 10$ mm ......................................................................................................... 177

6.4 Mechanical system analogous to the system described by Eq. (6.31) .................. 178

6.5 Geometry of the 2-DOF model for the goldfish swimbladder ....................... 179

6.6 Mechanical system model for the coupled swimbladders............................ 180

6.7 Example of least squares curve-fit to uncoupled swimbladder data. The data are from the anterior swimbladder of fish GF016, measured using the waveguide setup................................................................. 189

6.8 Example of least squares curve-fit to uncoupled swimbladder data. The data are from the posterior swimbladder of fish GF004, measured using the pool setup ..................................................................................... 190

6.9 Simplified representation of a section through the anterior swimbladder ...... 193

6.10 Surface of the anterior swimbladder tunica externa showing the slit .......... 194

6.11 Mechanical system representation of the tunica externa sliding motion. WB – Weberian apparatus subsystem................................................................. 196

6.12 Detailed view of the Weberian ossicles (Modified from Krumholz, 1943)....... 197

6.13 Lumped parameter mechanical system model of the Weberian ossicles ....... 198

6.14 Fluid system model for the Weberian apparatus fluid canals ....................... 200

6.15 Lumped parameter circuit representation of the fluid canal system ............. 201

6.16 Experimental creep test data from Alexander (1961b), along with the linear least squares fit of Eq. (6.89). The curve-fit parameters are $A_m = 3 \times 10^6$ m$^2$/N and $n = 0.26$; $R^2 = 0.893$ ......................................................... 204

6.17 Geometric models used to estimate the rotational inertia of the (a) tripus, (b) intercalarium, and (c) scaphium ................................................................. 205

6.18 Transverse slice through the goldfish labyrinth. LA – lagena, TC – transverse canal, SA – saccule, RM – release membrane................................. 211

6.19 Rigid shell model for the saccular capsule. TC – transverse canal, RM – release membrane................................................................. 211

6.20 Equivalent mechanical systems showing how the $N_{hc}$ hair cell ciliary bundles and otolithic membrane elements may be replaced by the sums $N_{hc}Z_{hc}(t)$ and $N_{hc}Z_{cm}(t)$ ..................................................................................... 213

6.21 Mechanical system 1-D model for the saccule ............................................ 214
6.22 Mechanical system model for a hair cell ciliary bundle ...........................................220

7.1 Configuration of the goldfish and the acoustic source. ASB – anterior swimbladder; PSB – posterior swimbladder ........................................................225

7.2 Block diagram for the auditory system model ........................................................228

7.3 Normalized velocity for the swimbladders and tripus using the baseline model parameters. asb – anterior swimbladder; psb – posterior swimbladder; ptr – posterior region of the tripus; atr – anterior region of the tripus.....................................................................................................................230

7.4 Normalized velocity for the tripus, intercalarium, and scaphium using the baseline model parameters. atr – anterior region of tripus; ic – intercalarium; sc – scaphium ........................................................................................................231

7.5 Transfer functions relating the Weberian ossicle velocities to the anterior swimbladder radial velocity ..............................................................232

7.6 Normalized displacements for the saccule model. Xsg – sagitta; Xse – sensory epithelium; Xrel – relative displacement; Pa – acoustic pressure ...........235

7.7 Individual components of sagitta displacement due to the sensory epithelium motion and fluid flow entering the saccule [see Eqs. (6.116)-(6.119)].
Xsg1, xsg1(ω); Xsg2, xsg2(ω)................................................................................236

7.8 Transfer functions relating the relative motion xrel(ω) to the sensory epithelium displacement and the fluid displacement entering the saccule. Hse – Hse(ω); Hsa – Hsa(ω). Also see Eqs. (6.112) and (7.13) .....................239

7.9 Individual components of the relative displacement between the sagitta and sensory epithelium due to the direct, indirect, and Weberian paths for a monopole source 1-m in front of the goldfish. dir – direct path normalized displacement; ind – indirect path normalized displacement; web – Weberian path normalized displacement .................................................................240

7.10 Effect of the tissue shear moduli on the anterior swimbladder response.
u1low, μ1 = 1×10^6 N/m^2; u2low, μ2 = 5×10^6 N/m^2; u1high, μ1 = 1×10^4 N/m^2; u2high, μ2 = 5×10^6 N/m^2 ..................................................243

7.11 Effect of the tissue shear moduli on the posterior swimbladder response.
u1low, μ1 = 1×10^6 N/m^2; u2low, μ2 = 5×10^6 N/m^2; u1high, μ1 = 1×10^4 N/m^2; u2high, μ2 = 5×10^6 N/m^2 ..................................................244

7.12 Effect of the tissue loss factors on the anterior swimbladder response.
u1low, η1/ω = 5 N·s/m^2; u2low, η2/ω = 5 N·s/m^2; u1high, η1/ω = 500 N·s/m^2; u2high, η2/ω = 500 N·s/m^2 ..................................................245

7.13 Effect of the tissue loss factors on the posterior swimbladder response.
u1low, η1/ω = 5 N·s/m^2; u2low, η2/ω = 5 N·s/m^2; u1high, η1/ω = 500 N·s/m^2; u2high, η2/ω = 500 N·s/m^2 ..................................................246
7.14 Normal and uncoupled responses of the anterior and posterior swimbladders. asb – anterior swimbladder; psb – posterior swimbladder ........247

7.15 Effect of tunica extema compliance on the response of the anterior portion of the tripus. Atelow, $A_{a} = 3\times10^{-7}$ m$^3$/N; Atehigh, $A_{a} = 6\times10^{-6}$ m$^3$/N ..............249

7.16 Effect of tunica extema compliance on the normalized relative displacement. Atelow, $A_{a} = 3\times10^{-7}$ m$^3$/N; Atehigh, $A_{a} = 6\times10^{-6}$ m$^3$/N ..........................250

7.17 Effect of the tunica extema thickness $h_{u}$ on the tripus normalized velocity. hTElow, $h_{u} = 0.1$ mm; hTEhigh, $h_{u} = 0.2$ mm.................................251

7.18 Effect of the ligament stiffness $k_{l_t}$ on the tripus normalized velocity. KL1low, $k_{l_1} = 4\times10^4$ N/m; KL1high, $k_{l_1} = 7.5\times10^5$ N/m ..................252

7.19 Effect of the transverse canal diameter $d_{f_3}$ on the normalized velocity of the fluid entering the saccule. d3low, $d_{f_3} = 0.0025$; d3high, $d_{f_3} = 0.01$ ......254

7.20 Effect of saccular chamber compliance on the velocity of the fluid entering the saccule. Cf3high, $c_{f_3} = 2\times10^{-16}$ m$^3$/Pa; Cf3low, $c_{f_3} = 3\times10^{-18}$ m$^3$/Pa; noRM, $c_{f_3} = 2\times10^{-18}$ m$^3$/Pa........................................255

7.21 Effect of saccular chamber compliance on the normalized relative displacement. Cf3high, $c_{f_3} = 2\times10^{-16}$ m$^3$/Pa; Cf3low, $c_{f_3} = 3\times10^{-18}$ m$^3$/Pa; noRM, $c_{f_3} = 2\times10^{-18}$ m$^3$/Pa........................................256

7.22 Effect of varying the sagitta equivalent radius $R_{s_1}$ on the relative displacement between the sagitta and the sensory epithelium. Rsglow, $R_{s_1} = 0.25$ mm; Rsghigh, $R_{s_1} = 1.0$ mm......................................258

7.23 Comparison of the model anterior swimbladder response with the normalized velocity measured from the anterior swimbladder of goldfish GF756. Symbols – experimental; line – model..............................261

7.24 Comparison of the model posterior swimbladder response with the normalized velocity measured from the posterior swimbladder of goldfish GF756. Symbols – experimental; line – model..............................262

7.25 Comparison of the model and experimental (GF756) results for the tripus normalized velocity. Symbols – experimental; line – model .........................264

7.26 Comparison of the model and experimental (GF756) results for the sagitta normalized displacement. Symbols – experimental; line – model .........................265

7.27 Effect of goldfish mass on the anterior swimbladder response. mass10, $m_{s_1} = 10$ g; mass60, $m_{s_1} = 60$ g; mass100, $m_{s_1} = 100$ g.........................267

7.28 Effect of goldfish mass on the normalized relative displacement between the sagitta and the sensory epithelium. mass10, $m_{s_1} = 10$ g; mass60, $m_{s_1} = 60$ g; mass100, $m_{s_1} = 100$ g.................................268
7.29 Effect of the bladder ratio on the posterior swimbladder normalized velocity.
Gbr1, $G_{br} = 0.25$; Gbr2, $G_{br} = 0.5$; Gbr3, $G_{br} = 1.0$; Gbr4, $G_{br} = 1.3$ ....... 269

7.30 Individual components of the normalized relative displacement due to the
direct, indirect, and Weberian paths for a monopole source 10-m in front of
the goldfish. dir – direct path; ind – indirect path; web – Weberian path .......... 271

7.31 Individual components of the normalized relative displacement due to the
direct, indirect, and Weberian paths for a monopole source 1-m behind the
goldfish. dir – direct path; ind – indirect path; web – Weberian path .......... 272

7.32 Individual components of the normalized relative displacement due to the
direct, indirect, and Weberian paths for a monopole source 10-m behind the
goldfish. dir – direct path; ind – indirect path; web – Weberian path .......... 273

A.1 Waveguide assembly drawing ................................................................. 285
A.2 Flange detail drawing .................................................................................. 286
A.3 Gasket detail drawing .................................................................................. 287
A.4 Support block assembly drawing ............................................................... 288
### LIST OF TABLES

2.1 Accuracy, resolution, and threshold estimates for the amplitude and phase measurement systems ................................................. 42

3.1 Hydrophone spacings for the active control system .................................. 91

4.1 Measurement system accuracy expressed in terms of the normalized displacement and velocity .................................................. 122

5.1 Summary of the results for the swimbladder wall/body surface comparison. The values indicate the number of responses from the body surface which were in-phase/out-of-phase, or of equal/lower amplitude than that of the bladder wall. Based on a total goldfish of 11 goldfish .................................. 145

5.2 Summary of multiple resonance data .................................................. 147

5.3 Comparison of anterior and posterior swimbladder responses .................. 151

5.4 Comparison of anterior swimbladder and tripus responses ....................... 157

6.1 Geometric and material properties for the 2-DOF swimbladder model .......... 186

6.2 Estimated shear moduli and loss factors for the 2-DOF swimbladder model .... 191

6.3 Geometric and material properties for the tunica extema model ................. 203

6.4 Lever-arm lengths for the Weberian ossicles, as shown in Fig. 6.13 ............ 206

6.5 Mechanical impedances for the Weberian ossicle ligaments ....................... 207

6.6 Dimensions for the Weberian apparatus fluid canals ................................ 208

6.7 Fluid properties for the Weberian apparatus canals .................................. 209

6.8 Material properties and dimensions for the saccule model ....................... 218

6.9 Parameter values for the ciliary bundle model of Fig. 6.30 ....................... 222
B.1 Table of experimental test parameters. ASB – anterior swimbladder; PSB – posterior swimbladders; TR – tripus; LA – lagenar otolith; SA – saccular otolith; UT – utricular otolith; WG – waveguide; x – structure was located and data collected; † – no useful data was obtained; ‡ – data was collected from the outer body surface.

289
CHAPTER 1

INTRODUCTION

A. Motivation

Aquatic animals possess complex and highly evolved sensors which enable them to exploit mechanical stimuli found underwater. Fish rely almost exclusively on passive systems such as the ear, which is the principal sensor for acoustic signals.

For its size, a fish ear is an extremely sensitive acoustic sensor. Behavioral conditioning techniques have shown that some fish possess auditory thresholds as low as 50 dB \( (re: 1 \mu Pa) \) with bandwidths up to 3 kHz (Popper and Fay, 1993). Furthermore, fish are able to discriminate between pure tones with frequency differences from 4 to 7\% (Jacobs and Tavolga, 1968; Fay, 1989a) and between pure tones with intensity differences as low as 1.5 dB (Jacobs and Tavolga, 1967; Fay, 1989b). Several species of fish are also known to be able to determine the direction of a sound source within 10 to 20\° in azimuth and elevation (Schuijf, 1975; Hawkins and Sand, 1977; Schuijf and Buwalda, 1980).

Despite the progress made in establishing the capabilities of the fish auditory system, the details of how the auditory system accomplishes the signal detection and analysis remain poorly understood. In addition, significant questions remain regarding exactly how sound reaches the fish ear and the nature of the coupling between the ear and various accessory structures. In this study, experimental measurements and theoretical modeling have been used to examine the mechanical behavior of the peripheral auditory system of the goldfish \( (Carassius auratus) \). Determination of the mechanical function of the
peripheral auditory system and development of an accurate model may provide a foundation for future development of an actual microelectromechanical sensor that could “hear” as well as a fish.

\section*{B. Background}

1. \textit{Underwater sound}

   Most fish possess traditional vertebrate sensory organs that provide for sight, hearing, touch, taste, and smell (Reinert, 1992). Sound has certain advantages over the other sensory signals, however, especially when environmental conditions are unsuitable for visual or chemical communication. The effectiveness of visual stimuli underwater is limited by low light levels and contrast attenuation at increasing distances. Chemical signals propagate slowly, are directional only when water flow is directional, and are easily diffused by water currents. Underwater sound, however, has a high speed of propagation, low attenuation, and directional properties. Because of its low attenuation and the ability of sound speed gradients in the ocean to channel sound (so that it may propagate without interacting with the surface or bottom), sound is the only sensory stimulus that allows long range transmission underwater (Rogers and Cox, 1988).

2. \textit{Structure of the goldfish ear}

   Fish do not possess an outer or middle ear as in mammals, however they do have an inner ear. Figure 1.1 shows the inner ear of the goldfish, \textit{Carassius auratus}, a member of the series Otophysi. The inner ear consists of a membranous system of contiguous ducts and pouches filled with liquid endolymph (Platt and Popper, 1981). The ear contains three semicircular canals and three otolith organs: the utricle, the saccule, and the lagena. A seventh sensory organ, the macula neglecta, is present in some species but its function is
unknown in bony fish (Popper and Fay, 1993). The semicircular canals and the utricle are collectively referred to as the *pars superior* and are generally considered to be vestibular organs (Platt, 1983). The saccule and the lagena are known as the *pars inferior* and are thought to be the sound receptors in most fishes (Popper, 1983). There may, however, be some functional overlap between the three otolith organs (Popper and Fay, 1993).

![Diagram of the goldfish ear](image)

**Figure 1.1** Medial view of the right ear of the goldfish, *Carassius auratus*, a member of the series Otophysi and family Cyprinidae (Modified from Popper and Coombs, 1980).

Each otolith organ contains a single, dense, calcium carbonate stone or otolith suspended in a fluid-filled pouch or sac (Carlström, 1963). The saccular, lagenar, and utricular otoliths are also known as the sagitta, asteriscus, and lapillus, respectively (Chardon and Vandewalle, 1991). The size and shape of the otoliths are species-specific,
with the saccular otolith showing much greater variation than that of the lagena (Popper, 1983). On the wall of each otolithic chamber lies a sensory epithelium, or macula, which contains mechanoreceptive hair cells innervated by the a branch of the eighth nerve (Platt and Popper, 1981; Popper, 1983). Each hair cell has a bundle of hair-like cilia that project into the otolithic chamber, where they are coupled to the otolith through a gelatinous otolithic membrane (Platt and Popper, 1981; Steinacker et al., 1990; Popper and Fay, 1993).

Figure 1.2 is a scanning electron micrograph (SEM) of a group of hair cell ciliary bundles. Each bundle consists of a single, long, eccentrically placed kinocilium and a number of shorter, graded stereocilia. Bending of the hair cell ciliary bundle causes nerve impulses to be sent to the brain. The greatest response occurs when the bundle is bent along an axis toward the kinocilium, while a displacement in any other direction produces a response that is a cosine function of the direction relative to that of the main axis through the kinocilium (Hudspeth and Corey, 1977; Popper, 1983). Bending of the hair cell ciliary bundles is believed to occur through a shearing action caused by relative motion between the otolith and the macula.

Hair cells occur in groups, with all of the hair cells within a particular group having their kinocilia oriented in the same direction, as shown in Fig. 1.2. Figure 1.3 shows the hair cell orientation patterns for the goldfish saccule and lagena (Platt, 1977). As relative motion occurs between each otolith and sensory epithelium, arrays of differently oriented hair cells from the otolithic organs in both ears may provide detailed information about the direction and pathway of motion (Schuijf and Buwalda, 1980; Popper et al., 1988; Rogers et al., 1988; Popper and Fay, 1993).
FIGURE 1.2 SEM of a group of hair cell ciliary bundles on the saccular macula of the Hawaiian squirrel-fish, *Adioryx xantherythrus* (From Popper, 1983). The length of the black bar is 1 μm.

FIGURE 1.3 Hair cell orientation patterns from the goldfish saccule and lagena. A – anterior, D – dorsal (Modified from Platt, 1977).
3. Hearing mechanisms

There are generally considered to be at least two paths through which sound gets to the fish ear: the direct path, which is common to all fish, and the indirect path, which occurs only in fish with a swimbladder (a gas-filled chamber located in the abdominal cavity and primarily used to regulate buoyancy). In addition, a third path exists in some fish, known as hearing specialists, which possess auxiliary structures believed to enhance audition. In the case of the Otophysi, which possess specialized vertebrae known as the Weberian ossicles, this third path will be referred to as the "Weberian path." The three paths for the goldfish are illustrated in Fig. 1.4 and described below.

![Diagram of the three hearing mechanisms](image)

**Figure 1.4** Block diagram of the three hearing mechanisms.

The direct path operates as follows. Since the density of a fish is roughly the same as that of the surrounding water, it can be expected that any impinging acoustic wave will tend to carry the entire fish along with it at the same amplitude and frequency (Dijkgraaf, 1960). The otoliths, which are about three times as dense as the rest of the fish, will move...
with an amplitude and phase different from that of the rest of the fish, including the sensory macula. This relative motion between otolith and macula results in bending of the hair cell ciliary bundles.

In the indirect path, acoustic pressure acting on the swimbladder, which is much more compressible than water, will cause the swimbladder walls to vibrate. The vibrating swimbladder will then act as a new sound source whose acoustic particle motion will stimulate the otolithic organs in a manner similar to the direct path (von Frisch, 1938; van Bergeijk, 1964; Fay and Popper, 1974).

The Weberian path is found only in fish which contain Weberian ossicles, a series of bones found in members of the series Otophysi. The Weberian ossicles consist of three or four specialized vertebrae which mechanically couple the swimbladder to the fluids of the inner ear (Watson, 1939). Figure 1.5 illustrates the relationship between the swimbladder, the Weberian ossicles, and the ear. The largest ossicle, the tripus, connects posteriorly to the swimbladder and anteriorly via a ligament to the second ossicle, the intercalarium, which in turn is connected via a ligament to the third ossicle, the scaphium (Chranilov, 1927; Chranilov, 1929). The tripus, intercalarium, and scaphium are connected to the vertebral column through relatively compliant cartilaginous processes, thus each ossicle may rotate about the connection point (Alexander, 1962; Popper, 1971a). A fourth ossicle, the claustrum, is present in some species (Popper, 1983). The scaphium, and claustrum when present, are imbedded in the cartilaginous walls of the sinus impar, a fluid-filled canal which projects anteriorly and communicates with the transverse canal, which directly opens into the left and right saccular chambers (Evans, 1925; Watson, 1939; Krumholz, 1943; Alexander, 1962; Jenkins, 1977).

The Weberian apparatus is believed to operate as follows (Chranilov, 1929; Alexander, 1966). Acoustic pressure acting on the swimbladder causes the swimbladder walls to expand and contract. The swimbladder contains two walls; the inner wall, the
tunica interna, is complete, while the outer wall, the tunica externa, has a longitudinal slit in it. Chranilov (1929) suggested that the tunica interna stretches with swimbladder expansion; the tunica externa does not stretch, but instead slides over the tunica interna. As the edges of the slit in the tunica externa move farther apart, the ossicles rotate forward. When the swimbladder contracts, the sequence is reversed: the edges of the slit in the tunica externa move closer and the ossicles move backwards.

FIGURE 1.5 Dorsal view of an otophysan fish showing the relationship between the swimbladder, Weberian ossicles, and inner ear. The fourth ossicle, the claustrum, is not visible (Modified from Chardon and Vandewalle, 1992).

Expansion of the swimbladder will thus cause forward motion of the ossicles and fluid flow into the saccule. Similarly, compression of the swimbladder will cause fluid
flow out of the saccule. The saccular otolith features delicate wing-like projections or flutes which lie in the path of the fluids within the transverse canal (Wohlfahrt, 1932; von Boutteville, 1935; von Frisch, 1936; von Frisch, 1938). Fluid motion due to Weberian ossicle motion is therefore likely to cause relative motion between the saccular otolith and the sensory epithelium.

Furukawa and Ishii (1967a, 1967b) reported that in goldfish the ventral fluting of the saccular otolith is attached to a thin membraneous portion of the ventro-medial wall of the saccular capsule. This thin region of the saccular capsule is also described in goldfish by deBuret (1929), von Boutteville (1935), and Alexander (1966), and in certain catfishes by Jenkins (1977), who used the term release membrane. Furukawa and Ishii (1967a, 1967b) hypothesized that any fluid flow into the saccular chamber could easily displace the release membrane and cause a dorso-ventral motion of the saccular otolith.

Regardless of how sound reaches the ear, sound can only be detected if it causes bending of the hair cell ciliary bundles. In the direct path the acoustic particle motion is the stimulus that brings about relative motion between otolith and macula. Acoustic pressure is the stimulus for both the indirect and Weberian paths. This dual sensitivity of the fish auditory system makes it important to know the nature of the acoustic field near the fish in order to meaningfully interpret any experimental results. Care must be taken in designing an experimental apparatus so that the character of the sound field is controllable, or at least known (Parvulescu, 1964; Parvulescu, 1967).

4. Taxonomic information

Regarding hearing, the most often discussed species of bony fish are members of the series Otophysi, which is part of the superorder Ostariophysi (Popper and Fay, 1993). The Otophysi represent a group of about 6,000 (mostly freshwater) species that possess Weberian ossicles, including the orders Cypriniformes (minnows, goldfish, carp),
Siluriformes (catfish), Characiformes (characins), and Gymnotiformes (knifefish). The Ostariophysi include the Otophysi plus the series Anotophysi (order Gonorynchiformes), a group of fishes that have primitive Weberian ossicles but an ear similar to other non-otophysans. Figure 1.6 shows the orders contained within the superorder Ostariophysi, along with the relationship of the family Cyprinidae, which contains the goldfish, to the other families of the order Cypriniformes.

FIGURE 1.6 Taxonomic relationship among members of the superorder Ostariophysi, showing the families of the order Cypriniformes. The goldfish belongs to the family Cyprinidae, which also includes carp, minnows, tench, and barbels (Nelson, 1984).

C. Literature review

1. Structure of the peripheral auditory system in bony fishes

The earliest significant study of the structure and function of the swimbladder was that of Weber (1820), in which he described the fish ear and speculated on the function of the small ossicles, since known as the Weberian ossicles, that connect the swimbladder to the inner ear. Early investigators of the morphology of the swimbladder include Bridge and Haddon (1889, 1893) and Chranilov (1929), who examined members of the Siluriformes,
Evans (1925) and Chranilov (1927), who studied members of the Cypriniformes, and Watson (1939), who detailed the origins of the Weberian ossicles in the goldfish.

Additional studies on the structure and function of the swimbladder have been carried out by Jones and Marshall (1953) and Alexander (1959a, 1959b, 1959c, 1961a, 1966). The structure of the complete Weberian apparatus has been examined by Alexander (1962) for the Cypriniformes, while the morphology of the Weberian ossicles has been described by Krumholz (1943) for the Cypriniformes and Siluriformes, and by Popper (1971a) for the Characiformes (Genus: Astyanax).

Early experiments, such as those of Manning (1924) and von Frisch and Stetter (1932), were successful in identifying the otolithic organs of the inner ear as the site of acoustic reception in fishes. Descriptions of the chemical composition of the otoliths for a number of species have been provided by Carlström (1963), while Wohlfahrt (1932), von Frisch (1936), Adams (1940), Jenkins (1977), and Platt and Popper (1981), among others, have examined the structure of the otoliths in various otophysan fish.

2. Mechanics of the peripheral auditory system in bony fishes

Few authors have directly investigated the mechanics of the swimbladder, Weberian ossicles, or otoliths. Of the work that has been done, the majority has relied upon intrusive or post mortem procedures, or has been performed in complex acoustical environments; thus little credible data exists, especially at lower frequencies.

The first direct investigation of the mechanics of the otoliths was that of DeVries (1950). In this study, X-ray photography was used to measure the displacements of the otoliths in intact fish heads. Both static displacements due to gravitational forces and vibrations due to oscillating forces were investigated. Results showed that the response of the saccular otolith was nearly critically damped. For a 30-g ruff (a non-otophysan) the natural frequency of the saccular otolith was estimated to be 40 Hz.
Alexander (1961b) examined the viscoelastic properties of isolated samples from the tunica interna and tunica externa of several species of Cyprinidae. Alexander noted that the tunica externa of the anterior swimbladder sac was highly extensible at low frequencies, but the rate of stretching was limited by a high viscosity. The tunica interna behavior was completely elastic. The high extensibility of the tunica externa at low frequencies was believed to create a high-pass filter effect: the tunica externa would stretch at low frequencies, but at higher frequencies, where the tunica externa was inextensible, it would not stretch but instead slide over the tunica interna and cause motion of the Weberian ossicles. In this fashion, the Weberian apparatus would be insensitive to low frequency pressures such as those resulting in a change of depth.

In a post mortem procedure, Popper (1974) used a probe microphone inserted into the anterior chamber of the goldfish swimbladder to measure the sound pressure level (SPL) within the swimbladder during acoustic stimulation. Results showed that the swimbladder had a flat response from 50 to 2000 Hz.

Using holographic measurement techniques, Vaitulevich and Ushakov (1974), Vaitulevich (1979), and Altman et al. (1984) examined the behavior of the swimbladder in the carp. These experiments required removal of the lateral wall of the fish and exposure of the swimbladder. Regions of maximum vibration in isolated swimbladders were found to coincide with the approximate location of the attachment of the tripodes. In addition, a change in elastic properties was observed following death of the fish.

A laser light scattering approach was used by Clarke et al. (1975) to examine the swimbladder of the goldfish. These tests were performed post mortem with the swimbladder partially exposed. Results of this method showed a sharp decrease in swimbladder response above 1000 Hz. A change in response was also observed due to post mortem aging effects.
Sand and Michelsen (1978) used a laser vibrometry technique to measure the movement of different parts of the perch saccular otolith during horizontal vibration of the fish along its longitudinal axis. These post mortem experiments required the brain to be removed, fluids to be drained from the saccular chamber, and the saccular otolith to be exposed and painted, in order to increase reflectivity. Fluid moved back into the saccular chamber (its origin was unknown), but removal of the brain likely affected the results. Complex vertical motions of the otolith were observed with stimulation at frequencies above 40 Hz, along with a displacement node near the center of the otolith.

Rogers and Hastings (1989) developed a noninvasive ultrasonic technique to measure in vivo the acoustically induced vibrations of the peripheral auditory organs in the goldfish. Their results confirmed that the response of the swimbladder to acoustic pressure is transmitted through the Weberian ossicles to the saccular otolith. A high-pass filter effect was also observed which may have been the result of the mechanism proposed by Alexander (Cox, 1987; Cox and Rogers, 1987). The resonance frequencies observed during post mortem experiments were significantly lower than those in vivo, again indicating a dramatic change in material properties upon death of the animal. These experiments were conducted in a relatively small tank (0.5 x 0.5 x 0.9 m), however, which caused erratic variations in the particle velocity at the location of the fish and erratic fluctuations in the measured frequency responses below 500 Hz. This same apparatus was also used by Zhou (1992) and Lewis (1994), who measured the in vivo response of the swimbladder in both goldfish and oscars (Astronotus ocellatus). Their results showed the existence of a double resonance in the goldfish response, attributed to the two-chambered goldfish swimbladder.

Lychakov (1992) analyzed the significance of the inter-specific differences in the size and shape of the otoliths. This work indicated that the otolith masses and the ratio between the masses of the different otoliths show regular patterns of variation, depending
on the mode of life of the fish. Also, regardless of species, the ratio between the otolith mass and its area of projection on the macula can be described by different power equations in the three otolithic organs.

3. Models of the peripheral auditory system in bony fishes

a. Swimbladder models. Models for teleostean swimbladders may be broadly classified into two groups: those interested in predicting the characteristics of high-frequency sound scattered from the swimbladder, and those dealing with the swimbladder's interaction with low-frequency sound and the swimbladder's contribution to hearing. This study is primarily concerned with the latter.

The goal of most low-frequency models is to find the scattered pressure as a function of the incident acoustic pressure. The results are usually presented in terms of the scattering cross-section $\sigma_s$, defined as

$$\sigma_s(\omega) = 4\pi R^2 \frac{|P_s(\omega)|^2}{|P_i(\omega)|^2},$$

(1.1)

where $R$ is the swimbladder radius, $P_s(\omega)$ is the scattered pressure amplitude, and $P_i(\omega)$ is the incident acoustic pressure amplitude (Kinsler et al., 1982). The ratio of scattered to incident pressure may be expressed in a form analogous to that of a single degree-of-freedom (1-DOF) mechanical system:

$$\frac{P_s(\omega)}{P_i(\omega)} = \frac{C_s}{(\omega_n^2 / \omega^2 - 1) + j\delta(\omega)},$$

(1.2)

where $C_s$ is a constant, $\omega_n$ is the undamped natural frequency, and $\delta(\omega)$ is the damping factor. The damping factor is written as an explicit function of frequency to distinguish it
from the damping factor at resonance, $\delta_a$. The damping factor is related to the damping ratio $\zeta(\omega)$ by the equation

$$\zeta(\omega) = \frac{\delta(\omega)}{2}(\omega_n/\omega).$$

The quality factor $Q$ is the reciprocal of the damping factor at resonance, or

$$Q = \frac{1}{\delta_n}.$$  

Early swimbladder models, such as those used by Alexander (1966, 1968), approximated the swimbladder as a free spherical air bubble. From Minnaert (1933), the natural frequency for a free spherical air bubble in water is

$$\omega_n = \frac{1}{R}(3\gamma P_o / \rho_w)^{1/2},$$

where $\gamma$ is the ratio of specific heats for air, $P_o$ is the hydrostatic pressure at the bubble, $\rho_w$ is the density of water, and $R$ is the mean bubble radius.

Damping of the free air bubble occurs from sound radiation, heat conduction, and viscous losses (Devin, 1959). The total damping factor is thus the sum of the individual contributions of the radiation, thermal, and viscous damping components:

$$\delta(\omega) = \delta_{rad}(\omega) + \delta_{th}(\omega) + \delta_{visc}(\omega).$$

From Devin (1959), the radiation damping factor $\delta_{rad}$ is
the thermal damping factor $\delta_{th}$ is

$$
\delta_{th}(\omega) = \frac{3(\gamma - 1)}{R} \left( \frac{\kappa_a}{2\rho_a c_{p,a}} \right)^{1/2} \left( \frac{\omega_a}{\omega} \right),
$$

and the viscous damping factor $\delta_{vis}$ is

$$
\delta_{vis}(\omega) = \frac{4 \xi_w}{\rho_w R^2 \omega},
$$

where $\kappa_a$ is the thermal conductivity of air, $\rho_a$ is the density of air, $c_{p,a}$ is the specific heat at constant pressure for air, $\xi_w$ is the dynamic viscosity of water, and $c_w$ is the speed of sound in water.

Experimental measurements of the resonance frequency and damping of intact swimbladders in living fish, however, do not generally agree with the free spherical air bubble model. At depths less than 200 m, experimental values for the resonance frequency and damping are both higher than predicted (Batzler and Pickwell, 1970; McCartney and Stubbs, 1971; Sand and Hawkins, 1973; Løvik and Hovem, 1979). Accordingly, the spherical gas bubble model has been modified by several authors to include additional stiffness and damping terms.

Andreeva (1964), McCartney and Stubbs (1971), and Ye and Farmer (1994) all modeled the swimbladder as a spherical elastic shell surrounding an air cavity. In each of these models the shell, which represents the tissue surrounding the swimbladder, has a complex shear modulus $\mu$, defined as
Values for the complex shear modulus at frequencies between 3 and 14 kHz were obtained by Lebedeva (1965) from post mortem measurements on tissues from several different species. The shear modulus $\mu$ ranges from $10^6$ to $10^8$ N/m$^2$; the loss factor $\eta$ is between 0.2 and 0.3. Lebedeva's data for $\mu$ correlate reasonably well with $\omega^2$. Although Andreeva (1964), McCartney and Stubbs (1971), and Ye and Farmer (1994) all used an elastic shell model, their models differ regarding the thickness of the shell.

Andreeva (1964) modeled the surrounding tissue as being infinitely thick. The resonance frequency of her model is

$$\omega_n = \frac{1}{R} \left( \frac{3\gamma P_o + 4\mu}{\rho_w} \right)^{1/2}. \quad (1.11)$$

The radiation and thermal damping are identical to the spherical air bubble; however, the viscous damping is replaced by a fish tissue damping $\delta_f(\omega)$, given by

$$\delta_f(\omega) = \frac{4\eta}{\rho_w R^2 \omega^3}. \quad (1.12)$$

At shallow depths and low frequencies, the tissue damping factor is much larger than the radiation and thermal damping factors (Andreeva, 1964).

McCartney and Stubbs (1971) used a thin-walled spherical shell with mean radius $R$ and an excess internal pressure $P_{x}$. For this model

$$\mu = \mu + j\eta. \quad (1.10)$$
\[ \omega_n = \frac{1}{R} \left[ \frac{3\gamma(P_0 + P_3) + 4\mu(3t_{sb}/R)}{\rho_w} \right]^{1/2} \]  

(1.13)

and

\[ \delta_f(\omega) = \frac{4\eta}{\rho_w R^2 \omega^2} \left( \frac{3t_{sb}}{R} \right), \]  

(1.14)

where \( t_{sb} \) is the shell thickness.

Ye and Farmer (1994) used a spherical shell with a finite thickness to model the swimbladder. The shell has an inner radius \( R_i \), outer radius \( R_o \), and Lamé constants \( \lambda \) and \( \mu \). The resonance frequency and tissue damping factor are

\[ \omega_n = \frac{1}{R_o} \left( \frac{3\gamma P_0 / E + 4\mu D}{\rho_w} \right)^{1/2} \]  

(1.15)

and

\[ \delta_f(\omega) = \frac{4\eta D}{\rho_w R_o^2 \omega^2}, \]  

(1.16)

respectively, where

\[ E = \frac{4\mu + (2\mu + 3\lambda) e^3}{6\mu + 3\lambda}, \]  

(1.17)

\[ D = \frac{2\mu + 3\lambda(1 - e^3)}{6\mu + 3\lambda}, \]  

(1.18)
and $e = R/R_e$.

In contrast to the elastic shell models, Love (1978) modeled the swimbladder as a spherical fluid shell enclosing an air cavity which supports a surface tension. The shell is composed of a viscous, heat-conducting Newtonian fluid. The resonance frequency and tissue damping factor for this model are

$$\omega_n = \frac{1}{R} \left[ \frac{3\gamma P_0}{\rho_f} + \frac{2s_T}{\rho_f R} (3\gamma - 1) \right]^{1/2}$$

and

$$\delta_f(\omega) = \frac{2s_T}{\rho_f R^2 \omega_n},$$

respectively, where $s_T$ is the surface tension, $\rho_f$ is the density of the shell fluid, and $\xi_f$ is the dynamic viscosity of the fluid shell.

Feuillade and Nero (1996) combined the elastic solid and fluid shell models. Their model features an air cavity surrounded by a thin (1-mm), inner elastic shell, which is itself surrounded by a viscous fluid shell. They also added a variation of $\mu$ with depth.

deMunck and Schellart (1987) used a prolate spheroid air bubble to model the acoustic field scattered from the swimbladder. Their model has

$$\omega_n = \left[ \frac{3\gamma P_0}{a_1(a_1^2 - a^2)} \rho_w \ln\left(\frac{a_1 + a}{a_1 - a}\right) \right]^{1/2}$$

and
where $2a$ is the interfocal distance and $a_i$ is the half-major axis. The tissue stiffness was neglected; the tissue damping was based on experimental data of $Q$ in the range of 0.9–1.6 (deMunck and Schellart, 1987).

Although the 1-DOF model works well for many fish possessing a single-chambered swimbladder, goldfish and other Cypriniformes have swimbladders consisting of two-chambers (Evans, 1925). Zhou (1992) and Lewis (1994) demonstrated the inadequacy of a 1-DOF model to fit the measured amplitude response of the goldfish swimbladder. In particular, the measured response of the goldfish swimbladder may exhibit twin peaks in the amplitude due to the individual resonances of the two swimbladder chambers. Also, Lewis (1994) demonstrated that if the shear modulus is a function of $\omega^2$, then Andreeva’s model predicts an overdamped system for small goldfish. Although not specifically stated, this result is also applicable to the models of McCartney and Stubbs (1971), and Ye and Farmer (1992), since all three have similar equations for the resonance frequency (they differ only by a multiplier). Experimental measurements show a swimbladder resonance for even small goldfish (Cox, 1987), therefore this represents a major problem with using Lebedeva’s data in conjunction with the 1-DOF elastic shell model for the goldfish.

Zhou (1992) and Lewis (1994) also compared the measured amplitude response of the goldfish swimbladder to that of a two degree-of-freedom (2-DOF) model consisting of two coupled spherical air bubbles. Zhou (1992) showed that the 2-DOF model accurately predicts the response measured from two closely spaced balloons and may predict the double resonance appearing in the measurements from a goldfish swimbladder. The absence or presence of the double resonance was attributed to the distance between the two

$$\delta_{rad}(\omega) = \frac{2\omega R/c}{\ln\left(\frac{a + a_i}{(a - a_i)}\right)}$$ (1.22)

where $2a$ is the interfocal distance and $a_i$ is the half-major axis. The tissue stiffness was neglected; the tissue damping was based on experimental data of $Q$ in the range of 0.9–1.6 (deMunck and Schellart, 1987).
balloons: at a large spacing the two balloons are uncoupled and respond individually; at a very small spacing the system behaves as a single balloon. Only at intermediate distances did the system exhibit the coupled response.

**b. Otolith models.** A simple lumped parameter model of otolith mechanics was proposed by deVries (1950, 1956). The otolith is represented by a lumped mass $m_o$ of density $\rho_o$ immersed in water. The displacement of the otolith is $x_o$ and the displacement of the wall of the otolithic chamber is $x$. The equation relating the otolith and otolithic chamber displacements is

$$x_o(\omega) = \frac{(\rho_o/\rho_o - 1)m_o\omega^2}{k_o - m_o\omega^2 + j\omega b_o}x(\omega),$$

where $m_o$ is the effective mass of the otolith and surrounding fluid ($m_o \approx 1.3 m_o$), $b_o$ is the effective viscous damping, and $k_o$ is the stiffness of the structures coupling the otolith to the sensory epithelium.

**c. Hair cell models.** Mechanics of the ciliary bundles may be interpreted on both the macromechanical and micromechanical levels. In terms of macromechanics, the mechanical properties of the ciliary bundles and their coupling to the otolithic membrane affect the motion of the otolith. In this case the stiffness and damping of the hair cell ciliary bundles are desired. On a micromechanical level, the mechanoelectric transduction is of primary interest, thus a microelectromechanical model is needed to describe the mechanisms controlling bending of the ciliary bundle and depolarization of the hair cell.

Figure 1.7 illustrates the gating spring model, a micromechanical model for the mechanoelectric transduction by hair cells (Hudspeth and Markin, 1994). In this model, one or more transduction channels exist near the tip of each stereocilium. Each channel has
a gate to regulate the flow of ionic current into the hair cell. Each gate is connected to the adjacent stereocilium through a "gating spring" which lies along the axis of the ciliary bundle toward the kinocilium. Figure 1.7(a) shows the resting state, where the gate is closed. Each gate actually swings open and closed during the resting state, due to the influence of thermal buffeting by surrounding molecules, and is open approximately 20% of the time (Hudspeth, 1985). When the hair bundle is deflected towards its kinocilium, as in Fig. 1.7(b), the stereocilia in successive ranks slide over one another, stretching the gating springs. Each gate still swings open and closed, but now the gating spring force acts on the gate, causing it to spend more of its time open. As a result, a larger current flows through each gate and the cell is depolarized (Hudspeth, 1985).

![Gating Spring Model](image)

**FIGURE 1.7** Gating spring model for mechanoelectric transduction in hair cells (From Hudspeth and Markin, 1994). (a) At the resting state transduction channels tend to remain closed. (b) After bending towards the kinocilium, gating springs stretch and tend to keep gates open, allowing Ca\(^{2+}\) and K\(^+\) ions to enter the cell.
The gating spring model was proposed in accordance with experimental evidence indicating that transduction is localized to the hair bundle top, that the transduction is too rapid to permit the intervention of second messengers, and that a displacement of stereocilia exerts a tensile force on a linkage connected to the conduction channel (Hudspeth, 1985). After the model was first presented, anatomical experiments confirmed the existence of fine filaments linking each stereocilium to the flank of the next adjacent longer stereocilium along the axis of symmetry (Pickles et al., 1984).

Since the appearance of the gating spring model, several researchers have measured the mechanical bending stiffness of hair cell ciliary bundles. Howard and Ashmore (1986) found that each hair cell ciliary bundle behaves approximately like an ideal pivot about its insertion point on the macula. The stiffness $K_{hc}$ of each bundle is given by

$$K_{hc} = \frac{N_s K_s}{h_z^2},$$

where $N_s$ is the number of stereocilia, $h_z$ is the height above the cuticular plate, and $K_s$ is the pivotal stiffness per stereocilium, estimated to be $0.49 \times 10^{-15}$ N-m/rad.

Howard and Hudspeth (1987) measured the response of bullfrog saccular hair cell ciliary bundles to a step input in bending displacement along the main axis. These experiments showed the hair cell ciliary bundles to have viscoelastic properties and to exhibit stress relaxation. The authors suggested a three-element lumped parameter model consisting of a series spring (the gating spring) and damper in parallel with a second spring representing the stereociliary pivot. Figure 1.8 shows the proposed model and the mean values measured for each element. These values were confirmed by Jaramillo and Hudspeth (1993), who performed relaxation tests on ciliary bundles from the bullfrog saccule using a more sophisticated experimental apparatus.
Kachar et al. (1990) modeled the otolithic membrane as a rigid body and added an additional spring in parallel to the arrangement in Fig. 1.8, in order to represent subotolothic filaments present at the level of the ciliary bundles.

D. Overview of this study

Although much is known about the structure of the peripheral auditory system, little reliable data has been obtained regarding the mechanics of the system, mainly because previous studies have used invasive or post mortem procedures, or been performed in complex acoustic environments or within the acoustic nearfield. Models of the auditory system have focused individually on the swimbladder, otoliths, or hair cells. No models exist for the complete peripheral auditory system.

The purpose of this study was to theoretically and experimentally examine the mechanical function of the goldfish peripheral auditory system in an effort to better understand how the initial transduction of acoustic to electrical energy occurs in the peripheral auditory organs. This involved two main objectives: (1) to experimentally measure the amplitude and phase response of the goldfish swimbladder, Weberian ossicles, and otoliths in response to acoustic plane waves at frequencies down to 10 Hz, and (2) to
develop a mathematical model for the goldfish peripheral auditory system including the swimbladder, Weberian apparatus, and the saccule. To accomplish the former required completion of two additional tasks: development of a suitable acoustic environment for testing at frequencies down to 10 Hz, and modification of an existing ultrasonic measurement technique to allow phase angle measurement.

The experiments consisted of anesthetizing and tethering individual fish within a low-frequency sound field. Two experimental setups were used to cover the frequency range 10 to 3000 Hz. At the lower frequencies, the sound field was generated using two low frequency acoustic sources flanged to an acoustic waveguide. This system used an active control technique to achieve traveling wave conditions at frequencies down to approximately 10 Hz. At higher frequencies, tests were conducted in a vinyl swimming pool with the fish located in the direct field of the acoustic source. In either case, as the fish was insonified by the low frequency source, the frequency responses of the swimbladder, Weberian ossicles, and otolith organs were measured using an ultrasonic system previously developed for noninvasive measurement of acoustically induced vibrations in biological tissue. The system was capable of measuring in vivo vibrational amplitudes as small as 1.5 nm with a spatial resolution on the order of 0.5 mm. The measurement system was further modified in this study to allow phase angle as well as amplitude measurement.

This document is organized as follows. The details of the ultrasonic measurement system are presented in Chapter 2. Chapter 3 describes the acoustic waveguide and active control scheme. The experimental apparatus and results are described in Chapters 4 and 5, respectively. Chapters 6 and 7 detail the peripheral auditory system model. Finally, Chapter 8 presents conclusions and recommendations for future research.
CHAPTER 2

NONINVASIVE ULTRASONIC MEASUREMENT SYSTEM

Noninvasive ultrasonic techniques are routinely used to examine internal structures of living organisms. These techniques rely upon acoustic impedance mismatches within the organism to scatter or reflect sound and generate echoes. The swimbladder, Weberian ossicles, and otoliths of the goldfish each provides an acoustic impedance mismatch significant enough to scatter incident ultrasonic waves; therefore, these structures may be successfully examined with an ultrasonic system.

This study employed an ultrasonic technique developed by Rogers and Hastings (1989) to measure the amplitude of acoustically-induced vibrations. It has been expanded here to include both amplitude and phase measurement.

A. Principles

If a fish is placed within a sound field of low frequency \( \omega_L \) \( ( = 2\pi f_L ) \), the organ being investigated will vibrate with a displacement \( x_L(t) \) given by

\[
x_L(t) = X_L \cos(\omega_L t - \phi_L),
\]

where \( X_L \) and \( \phi_L \) are the displacement amplitude and phase, respectively, and \( t \) is time. The goal of the measurement system is to find \( X_L \) and \( \phi_L \) as functions of the low frequency \( \omega_L \).
Figure 2.1 shows the main components of the ultrasonic measurement system. The included angle is defined as $2\beta$, and it is assumed that the angle between each transducer axis and the transducer bisector has a magnitude of $\beta$. The ultrasonic source generates continuous waves of ultrasound at the source or carrier frequency $\omega_s \ (= 2\pi f_s)$. Ultrasound incident upon the target is scattered back to a separate ultrasonic receiver, which converts any received pressure to a voltage. If the ultrasonic receiver is assumed to be uniformly sensitive to pressure, then the receiver output in volts, $e_r(t)$, may be written as

$$e_r(t) = K_s R P_i \cos[\omega_s t - \phi_r]$$  \hspace{1cm} (2.2)

where $K_s$ is a constant, $R$ is the pressure reflection coefficient magnitude, $P_i$ is the pressure amplitude incident on the target, and $\phi_r$ is the phase of the received ultrasound (relative to the phase of the transmitted ultrasound).
The received phase is the product of the wave number and the source-target-receiver path length, plus the pressure reflection coefficient phase. For a stationary target, the received phase is

$$\phi_r = 2k_Hd + \phi_R, \quad (2.3)$$

where $k_H$ is the ultrasonic wave number ($k_H = \omega_H/c_w$, where $c_w$ is the sound speed in water), $d$ is the distance to the target from both the source and the receiver, and $\phi_R$ is the pressure reflection coefficient phase. If the target is moving, the received phase is time-dependent and the received ultrasound is phase-modulated. For target motion along the transducer bisector, as shown in Figs. 2.1 and 2.2(a), the source-target-receiver path length $d'(t)$ is

$$d'(t) = 2\left[d^2 + x_L^2(t) + 2dx_L(t)\cos\beta\right]^{1/2}. \quad (2.4)$$

![FIGURE 2.2](image)

FIGURE 2.2 Calculation of source-target-receiver path length for motion (a) along the transducer bisector, (b) orthogonal to the transducer axes, and (c) perpendicular to the bisector. The thick lines indicate the source-target-receiver path $d'$. 
Assuming $x_L(t)$ is harmonic with a small amplitude, Eq. (2.4) may be replaced by the Taylor series linear approximation about $x_L(t) = 0$:

$$d'(t) = 2d + 2x_L(t) \cos \beta. \quad (2.5)$$

For motion in a direction orthogonal to the plane of the transducer longitudinal axes, as shown in Fig. 2.2(b), the source-target-receiver path length is

$$d'(t) = 2\left[d^2 + x^2_L(t)\right]^{1/2}. \quad (2.6)$$

or, using the linearized approximation about $x_L(t) = 0$

$$d'(t) \approx 2d. \quad (2.7)$$

This is the same path length for the stationary target, so the system is insensitive to motion in this direction. For motion within the plane of the transducer axes, perpendicular to the bisector, as shown in Fig. 2.2(c), the path length is

$$d'(t) = \left[d^2 + x^2_L(t) - 2dx_L(t)\sin \beta\right]^{1/2} + \left[d^2 + x^2_L(t) + 2dx_L(t)\sin \beta\right]^{1/2}, \quad (2.8)$$

which again reduces to Eq. (2.7) if the linear approximation is used. Therefore, for small target motions, the measurement system is only sensitive to displacement components in the direction of the transducer bisector.

For target motion along the bisector having the displacement given by Eq. (2.1), the received phase may be approximated as
Substituting Eq. (2.9) into Eq. (2.2) yields

\[
e_r(t) = K_x R P_i \cos(\omega_H t - 2k_H d - 2k_H X_L \cos(\omega_L t - \phi_L) - \phi_R)
\]  

(2.10)

for the receiver output in volts. The measurement system objective is to extract the target displacement amplitude \(X_L\) and phase \(\phi_L\) from the received ultrasonic signal. The displacement amplitude may be directly obtained from the received signal using a high frequency spectrum analyzer. Phase measurement, however, is more complicated since \(\omega_L\) is typically only a small fraction of \(\omega_H\) and the amplitudes associated with acoustic vibrations are small. The specific techniques used to measure the amplitude and phase are discussed next.

1. Amplitude measurement

The ultrasonic technique for amplitude measurement has been described previously (Cox, 1987; Cox and Rogers, 1987; Rogers and Hastings, 1989) and will only be briefly summarized. Since \(k_H X_L\) is small, Eq. (2.10) may be written as

\[
e_r(t) = K_x R P_i [\cos(\omega_H t - 2k_H d - \phi_R) + 2k_H X_L \cos(\omega_L t - \phi_L) \sin(\omega_H t - 2k_H d - \phi_R)]
\]  

(2.11)

Expanding Eq. (2.11) and neglecting the constant phase term \((-2k_H d - \phi_R)\) yields

\[
e_r(t) = K_x R P_i \{\cos(\omega_H t) + k_H X_L \cos \beta \sin[(\omega_H + \omega_L)t - \phi_L] + k_H X_L \cos \beta \sin[(\omega_H - \omega_L) t + \phi_L]\}
\]  

(2.12)
Equation (2.12) shows that the effect of the low frequency vibration is to introduce sidebands into the received echo spectrum. The sidebands are located at the frequencies \((\omega_H + \omega_L)\) and \((\omega_H - \omega_L)\) and each has an amplitude of \(k_p X_L \cos \beta\) relative to the high frequency carrier amplitude. By measuring the ratio of the sideband amplitude \(E_{\text{sideband}}\) to the carrier amplitude \(E_{\text{carrier}}\), the amplitude \(X_L\) of the low frequency vibration may be determined from

\[
\frac{E_{\text{sideband}}}{E_{\text{carrier}}} = k_p X_L \cos \beta \tag{2.13}
\]

or

\[
X_L = \frac{E_{\text{sideband}}}{E_{\text{carrier}}} \frac{c_0}{\omega_H} \sec \beta . \tag{2.14}
\]

With a 15-MHz transmitter and a spectrum analyzer with a dynamic range of 80 dB, the smallest measurable displacement is about 1.5 nm.

Figure 2.3 shows the signal received from a goldfish anterior swimbladder vibrating at 400 Hz using a 15-MHz ultrasonic source. The relationship between the carrier and sidebands can be seen, as well as the large dynamic range of the HP 3585B spectrum analyzer. For this case the amplitude ratio \(E_{\text{sideband}} / E_{\text{carrier}}\) is approximately −68 dB and \(\beta = 30^\circ\), thus, from Eq. (2.9), \(X_L = 7.3\) nm.

It should be pointed out that the target motion depends on the intensity of the low frequency acoustic field, therefore the measured target displacement must always be normalized with respect to the actual parameters of the low frequency field.

**2. Phase Measurement**

Since the low frequency source operated at only a small fraction of the ultrasonic frequency, phase measurement required demodulating the receiver output. The goal of the
demodulation is to shift the carrier and sidebands from being centered about \( \omega_H \) to being centered about zero. This moves the sideband formerly occurring at \((\omega_H + \omega_L)\) to \(\omega_L\), where it may be examined with conventional instrumentation.

![Received ultrasonic spectrum from a goldfish anterior swimbladder showing the relationship between the carrier and the sidebands. For this case the low frequency source was 400 Hz and the ultrasonic source frequency was 15 MHz.](image)

Many demodulation techniques rely on the principle of frequency mixing, that is, when two periodic signals are mixed or multiplied the resulting signal has components at the sum and difference frequencies of the inputs:

\[
\cos(\omega_1 t) \times \cos(\omega_2 t) = \cos[(\omega_1 - \omega_2) t] + \cos[(\omega_1 + \omega_2) t] + \text{[higher order terms]}.
\] (2.15)
Low-pass filtering removes the components at and above the sum frequency, leaving the difference term only. If \( \omega_1 = \omega_H + \omega_L \) (the phase-modulated signal) and \( \omega_2 = \omega_H \) (the carrier), the filtered mixer output will simply be \( \cos(\omega_2 t) \).

For this study, phase demodulation was achieved using a phase detector consisting of a double-balanced mixer and low-pass filter. The phase detector output is a time-varying dc signal proportional to the cosine of the instantaneous phase difference between two inputs. For the actual detector used here (Mini-Circuits model ZRPD-1), the phase detector output \( e_p(t) \) was

\[
e_p(t) = -K_p \cos(\phi_1 - \phi_2),
\]

where \( \phi_1 \) and \( \phi_2 \) are the phases of the applied inputs and \( K_p \) is the phase detector maximum dc output (Scientific Components, 1992). If the ultrasonic carrier and receiver signals are the phase detector inputs, the output is

\[
e_p(t) = -K_p \cos(\phi_1),
\]

or

\[
e_p(t) = -K_p \cos[2k_H d + 2k_H X_L \cos \beta \cos(\omega_L t - \phi_L) + \phi_R].
\]

Since \( k_H X_L \) is small, the phase detector output may be expanded and written as

\[
e_p(t) = -K_p \cos(2k_H d + \phi_R) + K_p \sin(2k_H d + \phi_R) 2k_H X_L \cos \beta \cos(\omega_L t - \phi_L),
\]

which is of the form
The phase \( \phi_L \) is therefore obtained by measuring the phase of \( e_q(t) \). In practice \( e_q(t) \) will contain components at frequencies other than \( \omega_L \), so some sort of frequency selectively must be employed when measuring \( \phi_L \). This may be easily accomplished with a digital signal analyzer or a lock-in amplifier. When using live subjects, however, subtle complications, are introduced by the target reflection coefficient phase and by any low frequency target motions.

a. Effect of target reflection coefficient. The phase detector output depends on the phase of the received ultrasound. If the Weberian ossicles and otoliths are assumed to be rigid, then \( \phi_R = 0 \) (Kinsler et al., 1982) and Eq. (2.19) reduces to

\[
e_q(t) = K_x \cos(2k_H d) + K_y \sin(2k_H d)2k_H X_L \cos\beta \cos(\omega_L t - \phi_L) .
\] (2.21)

The swimbladder is an excellent example of a pressure-release surface, thus \( \phi_R = \pi \) (Rogers and Cox, 1988) and Eq. (2.19) reduces to

\[
e_q(t) = K_x \cos(2k_H d) - K_y \sin(2k_H d)2k_H X_L \cos\beta \cos(\omega_L t - \phi_L) .
\] (2.22)

or

\[
e_q(t) = K_x \cos(2k_H d) + K_y \sin(2k_H d)2k_H X_L \cos\beta \cos(\omega_L t - \phi_L \pm \pi) .
\] (2.23)

The measured phase of the swimbladder must therefore be corrected by \( \pm \pi \). The phase of other structures does not require any such correction.
b. Effect of low frequency target motion. Careful examination of Eq. (2.19) reveals a more serious source of error than that mentioned above. The term $2k_fd$, although nominally a constant, may show some variation due to small target motions (e.g., due to respiration) or a slow drift in carrier frequency. Because of the large magnitude of $k_f$, small changes in $d$ may result in sizable changes in $\sin(2k_fd)$, as shown in Fig. 2.4. If the change in $2k_fd$ causes $\sin(2k_fd)$ to change sign, then the measured phase will be shifted by $\pm \pi$.

![Graph showing the change in $\sin(2k_fd)$ as a function of the change in distance $d$ from the ultrasonic source/receiver to the target, for a 15-MHz carrier frequency and an initial distance of 19 mm.]

The values of $\omega_f$ and $d$ influence the chance of spurious phase shifts occurring; the worst case would be if $k_fd = n\pi$, where $n$ is an integer. In this case $\sin(2k_fd)$ approaches zero and any deviation is likely to cause a sign change. To minimize the occurrence of these phase shifts, the carrier frequency was adjusted in order to make

$$2k_fd = (2n - 1)\pi/2, \quad n = 1, 2, 3, \ldots$$

(2.24)
This was accomplished by monitoring the dc component of the phase detector output, $e_{dc}$, using a digital volt meter (DVM) and adjusting $\omega_H$ to drive $e_{dc}$ to zero. From Eqs. (2.21) and (2.22),

$$e_{dc} = \pm K_r \cos(2k_H d),$$

(2.25)

which is illustrated in Fig. 2.5.

![Graph showing the dc component of phase detector output as a function of carrier frequency.](image)

FIGURE 2.5 DC component of phase detector output experimentally measured as a function of carrier frequency for a balloon target.

If $e_{dc} = 0$ then $\sin(2k_H d) = \pm 1$, where small changes will be less harmful than if $\sin(2k_H d) = 0$. The adjustment to $\omega_H$ was performed according to the following rule:

- If $|e_{dc}| > 0$ then decrease $\omega_H$.
- If $|e_{dc}| < 0$ then increase $\omega_H$.  

36
The adjustment to $\omega_H$ has the added benefit of making the phase measurement insensitive to the target reflection coefficient phase. If $\phi_R = 0$, then $e_{dc} = +K_q \cos(2k_Hd)$ [Eq. (2.21)] and the adjustment moves $2k_Hd$ towards $\pi/2$, where $\sin(2k_Hd) = +1$. This is illustrated in Fig. 2.6(a). If $\phi_R = \pi$, then $e_{dc} = -K_q \cos(2k_Hd)$ [Eq. (2.22)] and the adjustment moves $2k_Hd$ towards $3\pi/2$, where $\sin(2k_Hd) = -1$ [Fig. 2.6(b)]. Therefore, regardless of the reflection coefficient phase, proper adjustment of $\omega_H$ simplifies Eq. (2.19) to

$$e_q(t) = K_q 2k_H X_L \cos \beta \cos(\omega_L t - \phi_L),$$

(2.26)

and no phase correction is necessary.

![Diagram](image)

**FIGURE 2.6** Action of carrier frequency adjustment for (a) $\phi_R = 0$ and (b) $\phi_R = \pi$.

The adjustment to $\omega_H$ was performed at each low frequency $\omega_L$ tested. The resulting adjustments to $\omega_H$ were always less than 40 kHz, which represents a change in $\omega_H$ of only 0.27%. All calculations were based upon the actual carrier frequency used.
Although Eq. (2.20) implies that the phase detector output may also be used to measure the target amplitude, this is impractical, for in vivo measurements with the current setup, because \( \sin(2k_d d) \) is not absolutely known. For phase measurement, precise knowledge of \( \sin(2k_d d) \) is not required—only that it will not change sign.

3. Measurement verification and accuracy

The measurement process was verified using the arrangement of Fig. 2.7, in which the system was used to measure the amplitude and phase of an acrylic post excited by an electromechanical shaker operating at a constant frequency. The amplitude and phase measured with the ultrasonic system were compared to the “actual” amplitude and phase, obtained from a calibrated accelerometer (PCB model 352B22), which was also mounted to the acrylic post. Figure 2.8 shows the details of the shaker and accelerometer mountings. The shaker was placed above the waterline, with only a portion of the acrylic post and the accelerometer located underwater. A thin latex sheath was used to cover and seal the region of the post located underwater. To insure that the ultrasonic system and accelerometer were both sensing the same motion, the ultrasonic transducers were actually focused on the accelerometer housing, rather than the post. The orientation was such that the directions of positive displacement were identical for each measurement device.

The high frequency carrier, supplied by an HP 33120A function generator operating near 15 MHz, was split into two signals: one was used to drive the ultrasonic source, the other was used as the reference signal in the phase detector. The ultrasonic receiver output was amplified and split into two signals: one applied as the second input to the phase detector and the other input to the HP 3585B spectrum analyzer. The spectrum analyzer was used to measure the displacement amplitude from the ultrasonic system. The phase detector output
FIGURE 2.7 Experimental setup used to evaluate the ultrasonic measurement system.

FIGURE 2.8 Detailed view of the accelerometer, acrylic post, and electromechanical shaker.
was low-pass filtered and input to a Stanford Research Systems SR 850 lock-in amplifier. The lock-in amp was used to measure the displacement phase from the ultrasonic measurement system.

The shaker was driven from one output of a National Instruments DSP 2200 computer board; the second DSP 2200 output generated a signal at the same frequency, to be used as the reference input to both the lock-in amp and one input channel of the DSP board. The accelerometer output was connected through a power supply/signal conditioner (PCB model 482A16) to the second input channel of the DSP board, which was used to sample the accelerometer signal and measure its amplitude and phase. The arrangement allowed the phase angles measured from both the ultrasonic system and the accelerometer to share a common reference.

To assess the performance of the amplitude measurement scheme, the voltage amplitude input to the shaker was varied in discrete steps as the ultrasonic system and accelerometer measured the resulting motion amplitude. To assess the performance of the phase measurement system, the shaker input voltage phase was varied with respect to the phase reference signal as the ultrasonic system and accelerometer measured the resulting motion phase. These tests were repeated for a number of frequencies.

Figure 2.9 shows the measured displacement amplitude vs. the actual displacement amplitude, at 1000 Hz. The symbols represent the experimental data; the solid line is a least squares linear fit to the data. The slope of the linear fit is 1.038, with $R^2 = 0.9972$. These data show that the displacement amplitude obtained with the ultrasonic measurement system agrees with that measured with the accelerometer and that the amplitude measurement is linear.

Figure 2.10 shows the measured displacement phase vs. the actual displacement phase, again at 1000 Hz. The symbols are the experimental data; the solid line is a least
FIGURE 2.9 Measured displacement amplitude (from the ultrasonic system) vs. the "actual" displacement amplitude (from the accelerometer) at 1000 Hz.

FIGURE 2.10 Measured displacement phase (from the ultrasonic system) vs. the "actual" displacement phase (from the accelerometer) at 1000 Hz.
squares linear fit to the data. For the data of Fig. 2.10, the slope is 1.003 and $R^2 = 0.9999$, which indicates that the displacement phase obtained with the ultrasonic system agrees with that measured with the accelerometer and that the phase measurement is linear.

Data analogous to that of Figs. 2.9 and 2.10 were used to estimate the accuracy of the amplitude and phase measurement schemes. Table 2.1 summarizes the results. The accuracy estimates are based on the ±3σ limits (Doebelin, 1983). Because the HP 3585B analyzer relies on a logarithmic amplitude scale, the amplitude resolution is a percentage of the displacement amplitude; i.e., at any particular displacement amplitude, a 1.2% change is necessary to produce a detectable change in the measurement system output.

<table>
<thead>
<tr>
<th>Amplitude measurement</th>
<th>Phase measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>accuracy (±3σ limits)</td>
<td>± 4.2 nm</td>
</tr>
<tr>
<td>resolution</td>
<td>1.2%</td>
</tr>
<tr>
<td>threshold</td>
<td>1.5 nm</td>
</tr>
<tr>
<td></td>
<td>± 3.0 deg</td>
</tr>
<tr>
<td></td>
<td>&lt; 1 deg</td>
</tr>
</tbody>
</table>

**TABLE 2.1** Accuracy, resolution, and threshold estimates for the amplitude and phase measurement systems.

As a final check of the phase measurement system, the phase response of a 20-mm diameter balloon was measured in response to an acoustic stimulus. Figure 2.11 shows the measured displacement phase as a function of frequency. The phase reference is the acoustic pressure at the target. Positive displacement is defined as away from the ultrasonic system (see Fig. 2.1), which in this case corresponds to *inward* radial motion. With the exception of the very lowest frequency, the data fit the expected 2nd order system behavior well. At low frequencies the input and output are in-phase; above resonance the input and
output are $180^\circ$ out-of-phase. The resonance frequency of a spherical air bubble with the same volume as the balloon is near 330 Hz, which agrees with the phase data. Deviation from the expected behavior is caused by the non-uniform balloon wall thickness, nonspherical shape, viscoelasticity of the balloon wall, and the method by which the balloon was suspended.

![Phase vs Frequency Graph](image)

FIGURE 2.11 Measured displacement phase re: acoustic pressure for a 20-mm diameter balloon.

B. Spatial resolution

The spatial resolution of the ultrasonic measurement system is determined by the size of the ultrasonic sample volume. The sample volume may be thought of as the three-dimensional volume enclosed within the intersection of the beams from each ultrasonic transducer; it is also known as the crossed volume (Baker and Yates, 1973). The sample volume for the noninvasive ultrasonic measurement system was examined both theoretically and experimentally.
1. Theoretical

The theoretical sample volume size for the ultrasonic system was investigated by first examining the theoretical field of a focused source, then modifying the theory to include both a focused source and a focused receiver.

a. Focused source only. The source has a projected radius \( a \) and is spherically concave with radius of curvature \( A \), as shown in Fig. 2.12. The source is assumed to be axisymmetric with a uniform velocity over its surface. Polar coordinates \((r, \theta)\) are used with the origin at the transducer center.

![Figure 2.12 Coordinate system for a single focused ultrasonic source.](image)

If the source is gently curved and has a radius larger than the wavelength, the pressure at \((r, \theta)\) may be expressed in terms of the Rayleigh integral

\[
p(r, \theta) = \frac{jk \rho_w c_w v_x}{2\pi} \int_S \frac{e^{-jk r'}}{r'} dS. \tag{2.27}
\]

where \( \rho_w \) is the density of water, \( c_w \) is the sound speed in water, \( v_x \) is the normal component of the source surface velocity, \( S \) is the area of the radiating surface, and \( r' \) is
the distance from the target to the incremental area \( dS \) on the transducer surface (O'Neil, 1949; Madsen et al., 1981; Djelouah et al., 1991; Chen et al., 1993). The double integral of Eq. (2.27) has been reduced to a single integral and solved numerically by various authors (Penttinen and Luukkala, 1976; Madsen et al., 1981; Lucas and Muir, 1982).

A computationally more advantageous solution may be obtained, however, by reducing the single integral solution to a summation in terms of cylindrical Bessel functions using the Lommel integrals (Born and Wolf, 1980; Chen et al., 1993). Modifying the nomenclature of Chen et al. (1993), the normalized pressure \( \xi(r, \theta) \), defined as

\[
\xi(r, \theta) = \frac{p(r, \theta)}{\rho_c c_0 v},
\]

is

\[
\xi(r, \theta) = \frac{j k_m a^2}{r} e^{-\mu r} F(Y, Z),
\]

where

\[
Y = \frac{k_m a^2}{r} \left(1 - \frac{r}{A} \cos \theta\right),
\]

and

\[
Z = k_m a \sin \theta.
\]

The exact form of the function \( F(Y, Z) \) depends on the normalized coordinates \( Y \) and \( Z \). Closed form solutions are available at the focal point, within the focal plane, and along the source axis:
\[ F(Y,Z) = \begin{cases} 
0.5, & Y = 0, Z = 0 \text{ (focal point)}, \\
\frac{J_n(Z)}{Z}, & Y = 0, Z \neq 0 \text{ (focal plane)}, \\
\frac{1 - e^{-j\pi Y}}{jY}, & Z = 0, Y \neq 0 \text{ (source axis)}, 
\end{cases} \tag{2.32} \]

where \( J_n \) is the Bessel function of the first kind of order \( n \) (Chen et al., 1993). For off-axis locations, the solutions are expressed in terms of infinite sums of Bessel functions. For \( |Y/Z| < \sqrt{2} \),

\[ F(Y,Z) = \frac{e^{-j\pi Y}}{Y} \left[ \sum_{n=0}^{\infty} (-1)^n \left( \frac{Y}{Z} \right)^{2n+1} J_{2n}(Z) + j \sum_{n=0}^{\infty} (-1)^n \left( \frac{Y}{Z} \right)^{2n+2} J_{2n+2}(Z) \right], \]

\[ |Y/Z| < \sqrt{2}. \tag{2.33} \]

For \( |Y/Z| \geq \sqrt{2} \), Eq. (2.33) may converge slowly and the following alternate form is used:

\[ F(Y,Z) = -j \frac{Z^2}{2Y} \left[ 1 + e^{-j \left( \frac{Z^2}{2Y} \right)} \sum_{n=0}^{\infty} (-1)^n \left( \frac{Z}{Y} \right)^{2n} J_{2n}(Z) + j \sum_{n=0}^{\infty} (-1)^n \left( \frac{Z}{Y} \right)^{2n+1} J_{2n+1}(Z) \right], \]

\[ |Y/Z| \geq \sqrt{2}. \tag{2.34} \]

Although Eqs. (2.33) and (2.34) contain infinite summations, these may be replaced by finite summations \( \sum_{n=0}^{N} \), where \( N \) is chosen so that the normalized pressure is calculated within an acceptable degree of accuracy. For the entire range of \( |Y/Z| \), a truncation error \( \varepsilon < 0.01 \) can be achieved using \( N = 7 \) (Chen et al., 1993).

To illustrate the axial beams of a single transducer, Eqs. (2.29)-(2.32) were used to find the normalized axial pressure for three 6.35 mm diameter source configurations: (1)
focused at 19 mm and operated at 15 MHz, (2) focused at 19 mm and operated at 20 MHz, and (3) focused at 25 mm and operated at 20 MHz. Figure 2.13 shows the results. As the focal range decreases, the amplitude at the focus, or the sensitivity, increases and the beam width decreases (the spatial resolution increases). Both sensitivity and spatial resolution are improved by increasing the frequency; however, at high frequencies RF interference and sound attenuation may degrade performance.

FIGURE 2.13 Axial behavior for three focused ultrasonic source configurations.

b. Focused source and focused receiver. The complete ultrasonic measurement system features two focused ultrasonic transducers, arranged so that their axes intersect at their focal points, as shown in Figs. 2.1 and 2.14(a). The transducer axes lie within the $u_1$-$u_2$ plane. The observation point $Q$ may be located with reference to the global coordinates $u = (u_1, u_2, u_3)$, the local coordinates $(r_1, \theta_1)$, which are referenced to the ultrasonic source, or the local coordinates $(r_2, \theta_2)$, which are referenced to the ultrasonic receiver, as shown in Fig. 2.14(b).
The pressure incident on an infinitesimal target located at point $u$ is

$$p_i(u) = p(r_i, \theta_i).$$  \hspace{1cm} (2.35)

The average pressure over the surface of a target with area $A_r$ located at point $u$ is the integral of Eq. (2.35) over the area of the target, divided by the target area:

$$p_i(u) = \frac{1}{A_r} \int \int p(r, \theta) \, dT ,$$  \hspace{1cm} (2.36)

or, in terms of the normalized pressure $\zeta(r, \theta)$ of Eq. (2.28)

$$p_i(u) = \frac{\rho_s c \mu}{A_r} \int \int \zeta(r, \theta) \, dT .$$  \hspace{1cm} (2.37)

The finite target size is included to allow comparison with experimental measurements of the spatial resolution.
If the target is assumed to be a small, rigid reflector, and the incident wave is considered locally plane, then the target will act as a spherical source with velocity $v_r$.

$$v_r = \frac{-p_r(u)}{\rho_w c_w}.$$  \hspace{1cm} (2.38)

Substituting Eq. (2.37) into Eq. (2.38) yields

$$v_r = \frac{-v}{A_r} \int \zeta(r, \theta) \, dT.$$ \hspace{1cm} (2.39)

If reciprocity is assumed to hold, then the output voltage amplitude from a reversible transducer receiving waves emitted from $u$ is proportional to the pressure amplitude at $u$ resulting from transmission of the same waves by the reversible transducer acting as a source (Weight and Hayman, 1978). The output voltage $e_r(u)$ from the ultrasonic receiver due to a target located at $u$ may therefore be written as

$$e_r(u) = K_p \rho(r_2, \theta_2),$$ \hspace{1cm} (2.40)

or

$$e_r(u) = K_p \rho_w c_w v_r \zeta(r_2, \theta_2),$$ \hspace{1cm} (2.41)

where $K_p$ is a constant. Substituting Eq. (2.39) into Eq. (2.41) gives

$$e_r(u) = -K_p \rho_w c_w \frac{v}{A_r} \zeta(r_2, \theta_2) \int \zeta(r_1, \theta_1) \, dT.$$ \hspace{1cm} (2.42)

The normalized receiver output, $E_r(u) = e_r(u)/\rho_w c_w v_r$, is
\[ E(u) = K \xi(r_2, \theta_2) \int \int \xi(r_1, \theta_1) \, dT, \tag{2.43} \]

where \( K \) is a constant. The theoretical spatial resolution of the system is obtained by solving Eq. (2.43) in a point-by-point fashion. The normalized pressures \( \xi(r_1, \theta_1) \) and \( \xi(r_2, \theta_2) \) are obtained from Eqs. (2.29)–(2.34).

Equation (2.43) was solved for a 6.35 mm diameter source and receiver focused at 19 mm and operated at 15 MHz. The included angle \( 2\beta \) was 60°. The target was assumed to be circular with a diameter of 0.2 mm. The results are presented in Figs. 2.15(a)–(c) as contour plots of the normalized receiver output in dB re: the maximum amplitude.

2. Experimental

The sample volume size was measured experimentally using the setup shown in Fig. 2.16. The ultrasonic source and receiver were 6.35 mm diameter immersion transducers focused at 19 mm (Panametrics V317-SU F0.75). Each transducer had a resonance at approximately 20 MHz. The source and receiver were both mounted to search tubes (Krautkramer Branson model ST-015) and immersed in water. The source search tube was attached to a manual positioning system (not shown in Fig. 2.16) which allowed motion in the \( u_2 \) direction and rotation about the vertical. The receiver was attached to a manual positioning system (not shown in Fig. 2.16) which allowed linear motion along the three coordinate axes and rotation about the vertical. The source was driven directly from an HP 33120A function generator operating at 15 MHz. The receiver output passed directly into an HP 3585B spectrum analyzer, which was connected to a 486 DX2/66 personal computer (PC) via an HP 82335 GPIB interface board.
FIGURE 2.15 Theoretical receiver fields for the ultrasonic measurement system of Fig. 2.14 showing the (a) $u_1-u_3$, (b) $u_1-u_4$, and (c) $u_2-u_4$ contour planes. The lines represent the $-3, -6, -10, -20, \text{ and } -30 \text{ dB contour levels re: maximum amplitude.}$
FIGURE 2.16 Experimental setup for ultrasonic sample volume measurements.

The target was a 0.2 mm diameter brass wire aligned so that its front face was parallel to the $u_2$-$u_3$ plane and its length was parallel to the $u_1$-axis. The target was mounted on a search tube and immersed in fresh water. The target search tube was attached to a motorized positioning system (Aerotech ATS-100 series) which allowed motion along the three coordinate axes. The PC controlled the positioning system via a Unidex 500 motion control board. The entire measurement process was controlled by software written in LabVIEW, by National Instruments.

The initial alignment between the source, receiver, and target was accomplished using the following procedure. First, the source was operated in pulse-echo mode using a Panametrics 5052UA ultrasonic analyzer and the target was moved until the observed time-delay between the transmitted pulse and the received echo corresponded to a distance equal to the source focal length. The target was then moved along each axis to maximize the received echo amplitude. After maximizing the received echo from the ultrasonic source,
the target was held fixed while the ultrasonic receiver was operated in pulse-echo mode. The receiver was then moved until the target was at a distance equal to the receiver focal length and a maximum amplitude echo was observed. Next the system was configured as in Fig. 2.16 and the target moved until a maximum amplitude was obtained from the ultrasonic receiver. This point of maximum received amplitude was designated as the origin of the coordinate system. The angle $2\beta$ was measured after alignment.

After alignment, the target was moved point-by-point through a $2 \times 2$ mm grid of points in each of the $u_1$-$u_2$, $u_2$-$u_3$, and $u_3$-$u_1$ planes. At each point, the receiver amplitude was recorded from the HP 3585B.

Figure 2.17 shows the experimental contour plots for the receiver field of the ultrasonic measurement system operated at 15 MHz with $2\beta = 60^\circ$. The data are presented in dB re: the maximum receiver amplitude in each plane. The general appearance of the experimental contours is similar to the theoretical results of Fig. 2.15.

The experiments were repeated with $2\beta = 50^\circ$ and $70^\circ$. The sample volume dimensions were then estimated from the $-3$ dB contour lines in each plane and compared to the theoretical predictions based on Eq. (2.43). Figure 2.18 illustrates the variation of each sample volume dimension with the bisected angle. The symbols are the experimental data; the lines are the theoretical predictions.

Figure 2.18 shows that the size of the sample volume in the $u_3$ direction is independent of the angle; it depends only on the ultrasonic source and receiver dimensions. The length in the $u_2$ direction is also nearly independent of bisected angle. Only in the $u_1$ direction (along the bisector) is the change with angle significant. As the angle increases, the sample volume depth decreases. Therefore in order to reduce the sample volume depth, the bisected angle should be increased.
FIGURE 2.17 Experimental receiver fields for the ultrasonic measurement system of Fig. 2.14 showing the (a) $u_1$-$u_2$, (b) $u_1$-$u_3$, and (c) $u_2$-$u_3$ contour planes. The lines represent the $-3$, $-6$, $-10$, $-20$, and $-30$ dB contour levels relative to maximum amplitude.
For this study a nominal value of $50^\circ$ was chosen (the exact angle can only be measured after alignment). At 15 MHz, this results in approximate sample volume dimensions of $0.5 \times 0.2 \times 0.2$ mm. For the goldfish used in this study, the swimbladder dimensions are on the order of 10–20 mm, while the Weberian ossicles and otoliths are on the order of 1–5 mm. The spatial resolution of the system is therefore sufficient to allow multiple, independent samples from the swimbladder, Weberian ossicles, and otoliths.
CHAPTER 3

ACOUSTIC WAVEGUIDE

The ultrasonic measurement system described in the preceding chapter measures the target motion in response to some low frequency sinusoidal excitation. In this study, the low frequency excitation was accomplished by insonifying the target with an underwater acoustic source operating within the 10–3000 Hz range.

At low frequencies the long acoustic wavelength in water normally rules out conventional testing in rectangular aquarium-type tanks. Ideally, experiments would be conducted in an acoustic free field or anechoic chamber; however, an anechoic chamber would need to have dimensions at least on the order of a wavelength and to be lined with relatively long, sound-absorbent wedges. Diffuse sound fields are often used for tests; however, according to design standards a properly designed reverberant chamber has a volume equal to three times the wavelength cubed with a height: width: length ratio of 2:3:5 (ANSI S1.21-1972). Even at 50 Hz, in water such a chamber would have dimensions of 28 x 42 x 70 m. In addition, it is unlikely that an object relatively small compared to the wavelength, such as a fish, would experience the diffuse field.

In this study, a cylindrical acoustic waveguide with an active termination was used to generate a plane traveling wave within the 10–400 Hz frequency range. A traveling wave is a desirable stimulus because the relationship between the acoustic pressure and particle velocity is well known. Also, waves from any real source approach plane waves as the distance from the source increases (Rogers and Cox, 1988).
The waveguide was constructed of acrylic tubing, which is relatively flexible compared to water. This resulted in much larger attenuation and lower sound speed (and hence shorter wavelength) than normally encountered in open water or in a rigid duct. These conditions helped to achieve anechoic end conditions by reducing the amplitude of waves reflected from the waveguide exit. In a previous study using a 12-cm inside diameter (i.d.) acrylic tube with a wall thickness of 3.2 mm, the sound speed was about 20% of the value for open water, and anechoic conditions were approximately realized at frequencies above 300 Hz (Finneran and Hastings, 1995; Hastings et al., 1996).

The objectives of this study, however, required anechoic conditions at frequencies down to 10 Hz. At these low frequencies, passive sound absorbing methods generally do not work. This is because passive absorption techniques require a viscous termination whose thickness is a sizable part of a wavelength (Parvulescu, 1967). As the wavelength of the sound increases, so does the required length of the passive termination. As part of a previous study, a 6-m termination of metal wool (approximately 64 kg/m³) failed to have any effect on the measured sound field within a 12-cm i.d. acrylic waveguide, even at 300 Hz. A passive absorbing termination was therefore considered impractical for this study and an active termination, featuring a second acoustic source, was necessary.

The use of a secondary source to absorb sound was originally proposed by Olson and May (1953) and has been demonstrated within ducts by various authors (Parvulescu, 1961; Guicking and Karcher, 1984; Orduña-Bustamante and Nelson, 1992). These systems generally follow the block diagram shown in Fig. 3.1. The desired value is a mathematical expression representing the sensor output if the incident sound is completely absorbed at the secondary source. The controller acts upon the error signal, along with a reference signal correlated to the primary source input, to generate the secondary source.
input. Essentially, the controller provides a gain and phase adjustment to the secondary source so that the impedance at the secondary source is equal to the medium characteristic impedance (Parvulescu, 1967).

Active terminations may also be used to synthesize other end conditions (van den Berg and Schuijf, 1985; Buwalda, 1981; Cahn et al., 1969; Weiss, 1967; Parvulescu, 1967). This is particularly useful with regards to studies on fish hearing: since the auditory system is sensitive to both pressure and particle velocity, it may be desirable to generate a pressure or velocity node/antinode at the fish's location.

Plane wave propagation in the waveguide, however, is limited at high frequencies by the i.d. of the waveguide. Also, as the frequency increases, the active control system performance degrades. Therefore, above approximately 400 Hz, experiments were conducted in a 2.4-m diameter, vinyl-walled swimming pool. A brief discussion of the pool system is in Chapter 4, Section B.
This chapter begins with an overview of the waveguide construction. Next, the theoretical performance and experimental behavior of the waveguide are discussed. Finally, the active control scheme is covered in detail.

A. Waveguide construction

The waveguide was fabricated from 18-cm i.d., 6.35-mm thick acrylic tube. Acrylic flanges were cut and attached to individual sections of tube, allowing the sections to be bolted together for a total length of approximately 14 m. At 0.1-m intervals along the length of the waveguide, 9.5-mm holes were drilled to allow hydrophone access. At the location of the test section, larger openings were made to provide access for the ultrasonic measurement system. Underwater sound projectors (NRL Type J-13) were flanged to each end of the waveguide.

The assembled waveguide was supported on concrete blocks placed within an in-ground water channel in Robinson Lab, Room 1030. Figure 3.2 is a simplified representation of the water channel and the position of the waveguide. The assembled waveguide was filled with water and submerged in the water-filled channel. The channel

![Figure 3.2](image-url)

**FIGURE 3.2** Simplified representation of the position of the waveguide within the water channel.
measured approximately 15 x 1.2 x 1 m. Water in the channel was continuously filtered, except during testing. Appendix A contains more detailed drawings related to the waveguide fabrication.

B. Waveguide performance: theoretical

1. Phase velocity

The waveguide is represented by a circular cylindrical tube or shell, shown in Fig. 3.3. The tube is filled with a fluid having a density $\rho$ and unbounded sound speed $c$, and immersed in a fluid with density and unbounded sound speed $\rho_e$ and $c_e$, respectively. Both fluids are assumed to be stationary and non-viscous. The outer fluid is assumed to be unbounded, thus waves may only travel away from the waveguide and into the outer medium. The tube itself is assumed to be homogeneous, isotropic, and elastic.

The equations of motion for the tube may be written in vector form as

$$
(\lambda + 2\mu) \nabla(\nabla \cdot \mathbf{w}) - \mu \nabla \times (\nabla \times \mathbf{w}) = \rho \frac{\partial^2 \mathbf{w}}{\partial t^2} ,
$$

where $\mathbf{w} = (w_r, w_\theta, w_z)$ is the wall displacement, $\lambda$ and $\mu$ are the Lamé constants, and $\rho$ is the tube density (Easwaran and Munjal, 1995). Although $\mathbf{w}$ is a function of $(r, \theta, x, t)$, for
the sake of clarity this is not explicitly shown in Eq. (3.1) or any of the following equations. Solutions to Eq. (3.1) may be written in terms of a scalar potential $\phi$ and vector potential $\psi = (\psi_r, \psi_\theta, \psi_\phi)$ such that

$$w = \nabla \phi + \nabla \times \psi.$$  \hspace{1cm} (3.2)

Substitution of Eq. (3.2) into Eq. (3.1) gives

$$\nabla^2 \phi = \frac{1}{c_L^2} \frac{\partial^2 \phi}{\partial t^2},$$  \hspace{1cm} (3.3)

and

$$\nabla^2 \psi = \frac{1}{c_T^2} \frac{\partial^2 \psi}{\partial t^2},$$  \hspace{1cm} (3.4)

where the longitudinal (or dilatational) wave speed $c_L$ is (Redwood, 1960; Easwaran and Munjal, 1995)

$$c_L = \sqrt{\frac{\lambda + 2\mu}{\rho}},$$  \hspace{1cm} (3.5)

and the transverse (or shear) wave speed $c_T$ is (Easwaran and Munjal, 1995; Redwood, 1960)

$$c_T = \sqrt{\frac{\mu}{\rho}}.$$  \hspace{1cm} (3.6)
Assuming harmonic time dependency of the form $e^{i\omega t}$, traveling waves in the $x$-direction and standing waves in the $r$-direction, a set of potentials which satisfies Eqs. (3.3) and (3.4) is

$$
\phi = \left[ C_1 H_n^{(1)}(qr) + C_2 H_n^{(2)}(qr) \right] \cos(n \theta) e^{i(\omega t - kr)},
$$  
\hspace{1cm} (3.7)

$$
\psi_r = \left[ C_3 H_{n+1}^{(1)}(sr) + C_4 H_{n+1}^{(2)}(sr) \right] \sin(n \theta) e^{i(\omega t - kr)},
$$  
\hspace{1cm} (3.8)

$$
\psi_\theta = -\left[ C_3 H_{n+1}^{(1)}(sr) + C_4 H_{n+1}^{(2)}(sr) \right] \cos(n \theta) e^{i(\omega t - kr)},
$$  
\hspace{1cm} (3.9)

$$
\psi_x = \left[ C_5 H_n^{(1)}(sr) + C_6 H_n^{(2)}(sr) \right] \sin(n \theta) e^{i(\omega t - kr)},
$$  
\hspace{1cm} (3.10)

where $C_1 - C_6$ are arbitrary complex constants, $k$ is the wave number in the longitudinal direction,

$$
q^2 = \left( \frac{\omega}{c_j} \right)^2 - k^2, \hspace{1cm} (3.11)
$$

$$
s^2 = \left( \frac{\omega}{c_f} \right)^2 - k^2, \hspace{1cm} (3.12)
$$

and $H_n^{(1)}$ and $H_n^{(2)}$ are Hankel functions of order $n$ of the first and second kind, respectively (Easwaran and Munjal, 1995).

If appropriate boundary conditions are applied to Eqs. (3.3) and (3.4), along with equations describing the motions of the inside and surrounding fluids, the result will consist of a system of eight homogeneous equations, which may be written in matrix form. For nontrivial and unique solutions, the determinant of the coefficient matrix must vanish. Setting the determinant of the coefficient matrix equal to zero thus enables one to find, for a
given frequency and mode number, the sound speed within the tube. This requires the solution of an $8 \times 8$ determinant with complex roots. Rather than pursue the numerically intensive task of solving this system, simplified forms of the above equations were used for the case of an axisymmetric thin shell (Junger, 1955; Junger and Rosato, 1954).

For the simplified model, the waveguide is considered to be a thin, axisymmetric, circular cylindrical shell with a mean radius $a$ and half-thickness $h$. The wall displacements in the $r$ and $x$-directions are

$$w_r(x,t) = W_r(x)e^{i(\omega t - kx)}$$  \hspace{1cm} (3.13)

and

$$w_x(x,t) = W_x(x)e^{i(\omega t - kx)} ,$$  \hspace{1cm} (3.14)

respectively. The equations of motion may then be written as

$$-\rho \omega^2 w_r(x,t) = -\frac{E}{1-v^2} \left( -\frac{jv}{a} k w_x(x,t) + \frac{w_x(x,t)}{a^2} \right) - \frac{E h^2}{6(1-v^2)} \left( 2k^4 w_r(x,t) + \frac{2+v}{1-v} \frac{w_x(x,t)}{a^4} \right)$$

$$+ \frac{p_i(a,x,t)}{2} \left( \frac{1}{h} - \frac{1-2v}{a(1-v)} \right) - \frac{p_o(a,x,t)}{2} \left( \frac{1}{h} + \frac{1-2v}{a(1-v)} \right) \hspace{1cm} (3.15)$$

and

$$-\rho \omega^2 w_x(x,t) = -\frac{E}{1-v^2} \left( k^2 w_x(x,t) + \frac{jv}{a} k w_r(x,t) \right) , \hspace{1cm} (3.16)$$

where $E$ is Young's modulus, $v$ is Poisson's ratio, $p_i(a,x,t)$ is the pressure in the fluid inside the tube, evaluated at $r = a$; and $p_o(a,x,t)$ is the pressure in the fluid outside the tube, evaluated at $r = a$ (Junger, 1955; Junger and Rosato, 1954; Kennard, 1953). Equations
(3.15) and (3.16) may be manipulated to arrive at a frequency equation which is independent of $w_j(x,t)$

$$w_\nu(x,t) \left[ -\frac{a^2 \omega^2}{c_t^2} + \frac{v^4 k^2}{s^2} + \frac{1}{6} \left( \frac{h}{a} \right)^2 \left( 2k^2 a^4 + \frac{2+v}{1-v} \right) \right] = \frac{a p_t(a,x,t)}{2pc_t^2} \left( \frac{a}{h} - \frac{1-2v}{1-v} \right) - \frac{a p_o(a,x,t)}{2pc_t^2} \left( \frac{a}{h} + \frac{1-2v}{1-v} \right). \quad (3.17)$$

Waves in the inner and outer mediums may be expressed in terms of the velocity potentials $\phi_1(r,x,t)$ and $\phi_2(r,x,t)$, respectively, given by

$$\phi_1(r,x,t) = C_i J_0(q_ir)e^{i(\omega-\kappa z)}, \quad (3.18)$$

and

$$\phi_2(r,x,t) = C_o H_0^{(2)}(q_or)e^{i(\omega-\kappa z)}, \quad (3.19)$$

where $C_i$ and $C_o$ are arbitrary complex constants,

$$q_i^2 = (\omega/c_i)^2 - k^2, \quad (3.20)$$

$$q_o^2 = (\omega/c_o)^2 - k^2, \quad (3.21)$$

and $J_n$ is the Bessel function of the first kind of order $n$ (Easwaran and Munjal, 1995; Redwood, 1960). From Eqs. (3.18) and (3.19) and the boundary conditions

$$v_\nu(a,x,t) = w_\nu(x,t) \quad (3.22)$$

and

$$v_o(a,x,t) = w_o(x,t). \quad (3.23)$$
where $v_{i}(r,x,t)$ and $v_{o}(r,x,t)$ are the radial components of the acoustic particle velocities in the inner and outer mediums, respectively, the pressures on either side of the tube wall are

$$p_{i}(a,x,t) = -\frac{\rho_{i} \omega^3}{q_{i}} \frac{J_{0}(a \alpha)}{J_{1}(a \alpha)} w_{i}(a \alpha),$$

and

$$p_{o}(a,x,t) = -\frac{\rho_{o} \omega^2}{q_{o}} \frac{H_{0}^{(2)}(q_{o} \alpha)}{H_{1}^{(2)}(q_{o} \alpha)} w_{o}(a \alpha).$$

Finally, substituting Eqs. (3.24) and (3.25) into Eq. (3.17) yields the characteristic equation for the motion of the tube

$$-\frac{a^2 \omega^2}{c_{T}^2} + \frac{v^2 k^2}{s^2} + \left[ \frac{h - \frac{1}{6} (\frac{h}{a})^2 (2k^4 a^4 + \frac{2 + v}{1 - v})}{2q_{i} \rho_{i} c_{i}^2 J_{1}(q_{i} \alpha)} \right] a + \left[ \frac{\omega^2 \rho_{o} a}{2q_{o} \rho_{o} c_{o}^2} \frac{H_{0}^{(2)}(q_{o} \alpha)}{H_{1}^{(2)}(q_{o} \alpha)} \frac{1}{h} \right] \frac{a}{1 - 2v} + \frac{1}{2q_{i} \rho_{i} c_{i}^2 J_{1}(q_{i} \alpha)} \frac{1}{1 - 2v} = 0.$$  

At each frequency, this transcendental equation may be solved for the axial wave number $k$ corresponding to the lowest (quasi plane-wave) mode, which is the only mode of interest here. The phase velocity $c$ within the waveguide is related to the axial wave number $k$ by

$$c = \omega / k.$$  

If the inside and outside fluids are the same and $c < c_{i}$, then the roots of Eq. (3.26) are real (Junger, 1955), which enables one to pursue a straightforward root-finding strategy. It should be noted that the variable $c$, without a subscript, indicates the phase velocity in the waveguide and is a function of frequency. The variables $c_{i}$, $c_{o}$, and $c_{\omega}$ are assumed to be
constants and indicate the unbounded wave speeds for the fluid inside the waveguide, the fluid outside the waveguide, and water. For this study, \( c_i = c_o = c_w \).

Figure 3.4 compares the phase velocity obtained using the simple model described above with that of the more exact model (Easwaran and Munjal, 1995) for a water-filled steel tube immersed in water. The properties of the steel tube are: \( a = 28.6 \text{ mm}, h = 3.2 \text{ mm}, E = 211 \text{ GPa}, v = 0.3, \rho = 7800 \text{ kg/m}^3 \). The properties of the inner and outer fluid media are \( \rho_i = \rho_o = 1000 \text{ kg/m}^3 \) and \( c_i = c_o = 1482 \text{ m/s} \). At low frequencies the simple model gives a slightly higher velocity (about 1%) than the exact model. This is probably due to the thin-walled assumption being violated. For this case the ratio \( a/h = 8.9 \); the thin-walled assumption normally requires \( a/h > 10 \), so the simple model may be inaccurate here. At higher frequencies the agreement is satisfactory. Because of the close agreement between the two models, and the relative simplicity of Junger's analysis, Junger's method [Eq. (3.26)] was used for the remainder of this study.

Figure 3.5 illustrates the variation of phase velocity with frequency for 6.35-mm thick acrylic tubes with diameters of 13, 18, and 23 cm. Material properties for acrylic are from Read and Dean (1978). The phase velocities are between 20–25% of the sound speed in open water.

2. **Attenuation**

Sound propagating inside the waveguide is attenuated by absorption within the fluid and at the waveguide walls, and by radiation into the surrounding medium. Attenuation inside the waveguide is accounted for through the use of a complex wave number \( k \) defined as

\[
 k = \frac{\omega}{c} - j\alpha ,
\]  

(3.28)
FIGURE 3.4 Comparison of the more exact model of Easwaran and Munjal with the model of Junger for a water-filled steel tube immersed in water. EM - Easwaran and Munjal (1995); JU - Junger (1955).

FIGURE 3.5 Theoretical phase velocity (Junger's analysis) as a function of frequency for 6.35-mm thick acrylic tubes with inside diameters of 13, 18, and 23 cm.
where the attenuation coefficient $\alpha$ represents the dissipation of acoustic energy as sound travels down the waveguide. For an unbounded medium $\alpha$ is proportional to $\omega^5$; for propagation within a narrow duct, wall effects dominate and $\alpha$ is proportional to $\omega^{1/2}$ (Kinsler et al., 1982; Pierce, 1989). For wide ducts, $\alpha$ is proportional to $\omega^{1/2}$ at low frequencies and to $\omega^3$ at higher frequencies (Pierce, 1989). For this study, the waveguide falls between the narrow and wide duct conditions.

### 3. Attenuated plane waves in a duct

Most applications of acoustic waves in ducts deal with rigid, air-filled ducts, where the attenuation is negligible. For an acrylic duct in water, the attenuation is not negligible, thus some of the acoustic relations commonly used for rigid ducts must be re-examined.

For plane wave propagation within the waveguide, the pressure is

$$p(x,t) = \left[ Ae^{i\alpha(L-x)} + Be^{-i\alpha(L-x)} \right] e^{i\omega t}$$

and the axial particle velocity is

$$v(x,t) = \frac{k}{\rho \omega} \left[ Ae^{i\alpha(L-x)} - Be^{-i\alpha(L-x)} \right] e^{i\omega t}$$

where $A$ represents the forward wave, $B$ represents the reflected wave (Kim and Prasad, 1992), $x$ is the distance from the source, and $L$ is the length of the waveguide. The pressure reflection coefficient $R(x)$ is defined as the ratio of the reflected pressure to the incident pressure. From Eq. (3.29),

$$R(x) = \frac{B}{A} e^{-i2\alpha(L-x)}$$

68
The ratio of acoustic pressure to particle velocity is the specific acoustic impedance

\[ z(x) = \frac{p(x,t)}{v(x,t)}. \]  \hspace{1cm} (3.32)

If the specific acoustic impedance is divided by the medium characteristic impedance, the acoustic impedance ratio \( \zeta(x) \) is obtained:

\[ \zeta(x) = \frac{z(x)}{\rho_c c} = \frac{p(x,t)}{\rho_c c v(x,t)}. \]  \hspace{1cm} (3.33)

From Eqs. (3.29)-(3.33), the impedance ratio for the waveguide is

\[ \zeta(x) = \frac{k \left[ 1 + R(x) \right]}{k \left[ 1 - R(x) \right]}. \]  \hspace{1cm} (3.34)

Measurement of the reflection coefficient or impedance ratio normally requires two closely spaced hydrophones. If \( x_1 \) and \( x_2 \) are defined as the locations of hydrophone 1 and hydrophone 2, respectively, then the spacing between hydrophones, \( s \), is

\[ s = x_2 - x_1. \]  \hspace{1cm} (3.35)

and the midpoint between the two hydrophones, \( \bar{x} \), is

\[ \bar{x} = \frac{x_1 + x_2}{2}. \]  \hspace{1cm} (3.36)

The transfer function between hydrophones 1 and 2 is defined as
where \( P(x, \omega) \) is the Fourier Transform of \( p(x,t) \) and \(*\) indicates the complex conjugate.

From Eqs. (3.29)–(3.31) and Eq. (3.37), the transfer function is

\[
H(\bar{x}, \omega) = \frac{P(x_2, \omega) P^*(x_1, \omega)}{P(x_1, \omega) P^*(x_1, \omega)},
\]  

(3.37)

The transfer function, reflection coefficient, and impedance ratio are related by Eqs. (3.34) and (3.38), thus the transfer function may also be found as a function of the impedance ratio:

\[
H(\bar{x}, \omega) = \frac{\xi(\bar{x}, \omega)k / k - j \tan(kx/2)}{\xi(\bar{x}, \omega)k / k + j \tan(kx/2)}. 
\]  

(3.39)

\textit{a. No reflected wave.} For this study the desired acoustic stimulus is a plane traveling wave within the waveguide. This is achieved in theory by having an infinite length duct or perfectly absorbing termination, therefore no reflected wave is generated. If there is no reflected wave, then \( B = 0 \) and \( R(x) = 0 \). The expression for the pressure amplitude along the length of the waveguide is

\[
|P(x, \omega)| = P_0(\omega) e^{-\alpha x},
\]  

(3.40)

where \( P_0(\omega) \) is the pressure amplitude at \( x = 0 \). Equation (3.40) indicates that if there is no reflected wave the sound pressure level within the waveguide is a linear function of the distance \( x \) from the source. Substituting \( R(x) = 0 \) into Eq. (3.34) yields

70
or, expanding Eq. (3.41),

\[
\zeta(x, \omega) = \frac{k}{k^2 + \omega^2} + j \frac{k \alpha}{k^2 + \alpha^2}.
\]  \hspace{1cm} (3.42)

Normally, a plane traveling wave is described as having \( \zeta(x, \omega) = 1 \angle 0^\circ \); however, Eq. (3.42) shows that for non-zero attenuation this is not strictly true—the impedance ratio has a non-zero imaginary part and a real part less than one. Figure 3.6 is a plot of Eq. (3.42) versus frequency. If \( \alpha^2 \ll k^2 \), then Eq. (3.42) reduces to

\[
\zeta(x, \omega) = 1 + j \frac{\omega}{k},
\]  \hspace{1cm} (3.43)

thus the assumption that \( \text{Re}(\zeta) = 1 \) is actually reasonable, even with attenuation. With no reflected wave the transfer function reduces to

\[
H(x, \omega) = e^{-kx}.
\]  \hspace{1cm} (3.44)

Equation (3.44) is identical to the form for no attenuation, with the wave number \( k \) replaced with the complex wave number \( \mathbf{k} \).
FIGURE 3.6 Theoretical impedance ratio for plane traveling waves within the waveguide.

C. Waveguide performance: experimental

After fabrication of the waveguide was complete, experimental measurements were performed to evaluate the waveguide behavior without using active control. These experiments were specifically designed to provide information regarding (1) the highest frequency at which plane wave propagation was valid, (2) the lowest frequency, if any, at which traveling waves existed without active control, (3) the phase velocity, and (4) the attenuation.

1. Radial behavior

At sufficiently low frequencies, only plane waves will propagate down the waveguide. For a rigid-walled cylindrical duct, the frequency $f_c$ at which plane wave propagation is no longer valid is (Pierce, 1989; Munjal, 1987)

$$f_c = \frac{1.841 c}{2\pi a}.$$  \hspace{1cm} (3.45)
Using the theoretical phase velocity from Fig. 3.5, $f_0$ is approximately 850 Hz for a 18-cm i.d. tube; however, the rigid-wall assumption is not valid, so this must be regarded as only an estimate.

To experimentally measure the highest frequency at which the plane wave assumption is valid, the sound pressure level (SPL) was measured along the waveguide cross-section at several different frequencies. Figure 3.7 shows the experimental setup. A B&K 8103 miniature hydrophone was used to measure the acoustic pressure. The hydrophone output was amplified using a charge amp (Kistler Type 5010), then input to a National Instruments AT-DSP 2200 digital signal processing (DSP) board within a 486 DX2/66 PC. The DSP board was also used to generate a sine wave which was amplified and used to drive the J-13 underwater sound projector. A second J-13 was located at the far end of the waveguide, but was used as only a passive termination for this test. The measurement process was controlled by the PC using LabVIEW® software, by National Instruments.

![PERSONAL COMPUTER WITH DSP BOARD](image)

![AUDIO AMP](image)

![CHARGE AMP](image)

![J-13](image)

![HYDROPHONE](image)

![WAVEGUIDE](image)

**FIGURE 3.7** Experimental setup for radial SPL measurements.
Figure 3.8 shows the normalized SPL measured across the waveguide diameter, for frequencies of 25, 100, 400, 600, and 800 Hz. At each frequency, the data have been normalized to give 0 dB at \( r = 0 \). Any deviation from the zero dB level indicates departure from the plane wave assumption. At low frequencies the curves are flat, indicating plane waves. As the frequency increases, the measured pressure begins to deviate from the 0-dB baseline; at 600 Hz and above, the plane wave assumption is no longer valid.

2. **Axial behavior**

The acoustic pressure and pressure gradient were measured along the longitudinal axis of the waveguide in order to determine whether traveling waves or standing waves were present. If a traveling wave exists, the pressure is given by Eq. (3.40). If a standing wave exists, the axial pressure data will consist of a series of nodes and antinodes, with the distance between adjacent nodes equal to \( \lambda/2 \).

![Normalized SPL Measurement](image)

**FIGURE 3.8** Experimentally measured radial SPL for 25, 100, 400, 600, and 800 Hz.
Figure 3.9 shows the experimental setup used for the axial SPL measurements. Two B&K 8103 miniature hydrophones were moved in a point-by-point fashion along the length of the waveguide. At each location, the acoustic pressures were measured at several frequencies. The hydrophone outputs were amplified using two charge amps, then input to the National Instruments AT-DSP 2200 DSP board residing within the PC. The DSP board was also used to generate a sine wave, which was amplified and used to drive the J-13 underwater sound projector. A second J-13 was located at the far end of the waveguide, but acted only as a passive termination for these measurements. The measurement process was controlled by a virtual instrument developed within LabVIEW®. The acoustic particle velocity in the axial direction, \( V(x,\omega) \), was estimated from the measured (complex) pressures \( P(x_1, \omega) \) and \( P(x_2, \omega) \) and the hydrophone spacing \( s \) using a discretized form of Euler's Equation for harmonic functions:
Figure 3.10 shows the measured axial SPL at 12.5, 75, and 300 Hz. At high frequencies the data begin to approach the ideal behavior for a traveling wave. At low frequencies, standing waves are present. At 12.5 Hz, however, the data are somewhat misleading. When the acoustic wavelength is greater than twice the waveguide length, the standing wave pattern may no longer be present. Therefore, at very low frequencies, the acoustic impedance ratio is a better indicator of whether or not a traveling wave exists.

\[ V(\bar{x}, \omega) = -\frac{1}{j\rho_0 \omega} \frac{P(x_2, \omega) - P(x_1, \omega)}{s}. \] (3.46)

Figure 3.11 shows the acoustic impedance ratio measured along the waveguide. The data at 12.5 Hz now clearly show that a traveling wave does not exist; the impedance ratio at 12.5 Hz is primarily imaginary. At 350 Hz a traveling wave is approached, except at locations close to either the source or the termination.
FIGURE 3.11 Acoustic impedance ratio measured along the waveguide longitudinal axis. Top – real part; bottom – imaginary part.
3. Phase velocity

Two methods were used to experimentally measure the phase velocity. At low frequencies, with standing waves present, the distance between adjacent pressure nodes was measured. This distance equals $\lambda/2$. Since the wavelength, phase speed, and frequency are related by $\lambda = cf$, the phase velocity in the waveguide could be calculated since the frequency was known. At higher frequencies, when reflections are less significant, the time delay between the pressure incident on two closely spaced hydrophones was measured and used to calculate the phase velocity.

Figure 3.12 compares the experimentally measured phase velocity to the theoretical prediction from Section B. There is good agreement between the two. The phase velocity in the waveguide is approximately 370 m/s at frequencies below 200 Hz; this is about 25% of the unbounded sound speed in water.

![Figure 3.12 Phase velocity as a function of frequency within the waveguide. The theoretical curve is based on the model of Junger (1955).](image-url)
4. Attenuation

Attenuation in the waveguide was also measured using two different methods, depending on whether standing waves or traveling waves were present. When traveling waves were present, a function having the form of Eq. (3.40) was fitted (using a linear regression technique) to the axial pressure data. This is illustrated in Fig. 3.13(a). At low frequencies, the attenuation was estimated by fitting the equation

\[ P_L = \alpha(L-x), \]  

(3.47)

where \( P_L \) is the pressure at the antinode closest to \( x = L \), to the measured pressure minima (Kinsler et al., 1982), as illustrated in Fig. 3.13(b).

Figure 3.14 shows the measured attenuation as a function of frequency. The symbols represent the experimental data and the solid line is a curve fit to the data. At low frequencies the data were best fit by a function of the form \( f^{1/2} \), while at high frequencies a function of the form \( f^2 \) provided a better fit. The curve in Fig. 3.14 has the form

\[
\alpha = \begin{cases} 
0.011 f^{1/2}, & f < 100 \text{ Hz}, \\
0.088 + 1.73 \times 10^{-6} f^2, & f \geq 100 \text{ Hz}.
\end{cases}
\]  

(3.48)

The 100 Hz transition point was located by trial and error in order to get the best fit. The results of Fig. 3.14 imply that below 100 Hz the waveguide wall effects are dominant and above 100 Hz the attenuation varies as in the unbounded medium; however, the attenuation values here are much larger than those typically encountered in open water.
FIGURE 3.13 The attenuation in the waveguide was estimated using two techniques. At high frequencies (a), pressure data were fit with Eq. (3.40). At lower frequencies (b), pressure minima were fit to Eq. (3.47).
D. Active control system

Although active control of sound in ducts is relatively common today (Elliott and Nelson, 1993), most applications involve active noise control, where the acoustic pressure is minimized at some location or the sound propagating down a duct is canceled or reflected back towards the source, so that it does not propagate downstream. For this study, the objective is not to minimize pressure, but to use the secondary source to absorb the incident sound by matching the impedance at the waveguide exit to the medium characteristic impedance. This is known as active impedance control.

1. Active impedance control theory

To examine how a second acoustic source can be used to absorb sound, the waveguide is modeled as a straight duct with cross-sectional area $A_e$ and length $L$, as
shown in Fig. 3.15. The primary source is located at $x = 0$ and the secondary source is located at $x = L$. The volume velocities of the primary and secondary sources are $Q_1$ and $Q_2$, respectively, and their electrical inputs are $E_1$ and $E_2$, respectively.

If the frequency is below 600 Hz, only plane waves will propagate in the waveguide and the pressure and particle velocity are given by Eqs. (3.29) and (3.30). Applying the boundary conditions

\begin{align}
\nu(0, t) &= \frac{Q_1}{A_c} e^{i\omega t} \tag{3.49} \\
\nu(L, t) &= \frac{Q_2}{A_c} e^{i\omega t} \tag{3.50}
\end{align}

to Eq. (3.30) allows one to solve for $A$ and $B$. Equations (3.29) and (3.30) may then be used to find the acoustic impedance ratio at any point within the tube:

\[ \zeta(x, \omega) = \frac{-jk \cos k(L - x) - Q \cos kx}{k \sin k(L - x) + Q \sin kx} \tag{3.51} \]

where $Q = Q_2/Q_1$. At the waveguide exit,
\[ \zeta(L, \omega) = -\frac{jk - Q \cos kL}{k - Q \sin kL}. \] (3.52)

There is a one-to-one correspondence between \( Q \) and \( \zeta(L, \omega) \), thus manipulation of \( Q \) allows any desired ratio to be obtained (Bobber, 1962). For an anechoic termination, \( \zeta(L, \omega) = k/k \), thus

\[ Q_{\text{anechoic}} = e^{-jkl}. \] (3.53)

If the attenuation is zero, then Eq. (3.53) requires the secondary source to have the same motion as the primary source, delayed by the time it takes the sound to travel from the primary source to the secondary source.

Rather than manipulate the acoustic impedance ratio directly, it is more useful to define an error signal so that when the error signal is zero, anechoic conditions exist. For active impedance control a suitable error is

\[ E(\bar{x}, \omega) = H(\bar{x}, \omega) - H_{12}(\bar{x}, \omega), \] (3.54)

where \( E(\bar{x}, \omega) \) is the error, \( H(\bar{x}, \omega) \) is the transfer function measured between two hydrophones located at \( x_1 \) and \( x_2 \), and \( H_{12}(\bar{x}, \omega) \) represents the ideal transfer function between hydrophones 1 and 2 (Orduña-Bustamante and Nelson, 1992).

For a plane traveling wave

\[ H_{12}(\bar{x}, \omega) = e^{-k\bar{x}}. \] (3.55)
Manipulation of Eqs. (3.34)-(3.37) and Eq. (3.44) allows one to solve for the error in terms of $Q$:

\[ H(\bar{x},\omega) = \frac{\cos k(L-x_i) - Q \cos kx_i}{\cos k(L-x_i) - Q \cos kx_i} e^{ikx}. \]  

(3.56)

If the mean squared error (MSE), defined as $|E(\bar{x},\omega)|^2$, is plotted as a function of the real and imaginary parts of $Q$, a hypersurface, known as the performance surface, is generated. An example of a performance surface for active impedance control in a duct is shown in Fig. 3.16. The objective of the controller in Fig. 3.1 is to adjust $E_2$ so as to move the error towards the minimum point on the performance surface, that is, to minimize the MSE. This has been done by various authors using different techniques.

2. Control methodologies

Beatty (1964) used a theoretical relationship analogous to Eq. (3.53) to derive $Q_{\text{anechoic}}$ for a water-filled steel tube. Using the theoretical value, anechoic conditions were obtained at 1000 Hz and 1600 Hz.

Guicking and Karcher (1984), Guicking et al. (1985), and Karcher (1982) used a two-microphone technique to separate the standing wave field into incident and reflected wave components. A signal proportional to the incident wave was passed through a control filter and used to drive the secondary source. Reflection coefficients less than 0.05 were obtained from 100 to 800 Hz in air. For best results, however, the control filter required manual adjustment at each frequency. Curtis et al. (1990) manually adjusted the amplitude and phase of a secondary source to achieve anechoic end conditions in an air-filled duct.

A substantial improvement over earlier techniques was presented by Orduña-Bustamante and Nelson (1992), who used a time-domain adaptive control scheme featuring the filtered-x LMS algorithm to provide an absorbing termination in an air-filled tube. The
adaptive nature of the controller allowed use with periodic, random, and transient signals. Anechoic end conditions were achieved from 30 to 330 Hz.

![Performance Surface](image)

FIGURE 3.16 Example of a performance surface for active impedance control in a cylindrical duct. The vertical axis is $20 \log_{10}(\text{MSE})$; the horizontal axes are the real and imaginary parts of the source input ratio $Q$.

Although the adaptive controller used by Orduña-Bustamante and Nelson (1992) is well-suited for creating absorbing terminations in ducts, it was considered more complicated than necessary for this study. Here the primary source input is well known and consists of a single frequency. The controller is only required to automatically adjust the amplitude and phase of the secondary source to minimize the error signal. This can be
done without resorting to adaptive methods if the problem is treated as one of multivariable optimization. In this case the independent variables are the real and imaginary parts of $Q$ (or $E_2$ if $E_1$ is fixed), while the dependent variable is the MSE.

3. Pattern search method

Optimization routines may be classified as search methods, which require function evaluation only, or gradient methods, which also require the Jacobian gradient vector (Adby and Dempster, 1974). Because the performance surface in this case consists of circular contours (see Fig. 3.16), any search technique is likely to eventually reach the minimum. For this study the pattern search technique was chosen for several reasons. It is robust in the presence of noise and tends to follow the line of steepest descent (Elliott et al., 1987). Also, the pattern search technique has been successfully used in experimental studies to minimize the sound pressure of single frequency fields in enclosures (Elliott et al., 1987, Nelson and Elliott, 1987; Bullmore et al., 1985).

The pattern search takes incremental steps, called pattern moves, after suitable directions have been found by local exploration. If the search progresses well, the step size is increased; otherwise the step size is reduced. When the step size is reduced below a set value, the search is ended (Adby and Dempster, 1974).

Local exploration is performed by searching each coordinate direction to find a local minimum near the current base point. If the local exploration fails to find a new local minimum, the result is known as an undefined direction and a new local exploration is begun closer to the base point.

A pattern move consists of a single step to a new base along a line from the previous local minimum through the current local minimum. The step size of the pattern move is determined by the progress of the search. Each successful pattern move results in a doubling of the step size. Each unsuccessful pattern move halves the step size. Movement
to a new base is not carried out if the function evaluation at the new base is greater than the previous local minimum. In this case the base is rejected and a new pattern is begun from the previous local minimum (Adby and Dempster, 1974).

Figure 3.17 is a flowchart illustrating the operation of the pattern search. The successive base points are represented by the vector \( \mathbf{n} = [\text{Re}(Q) \text{ Im}(Q)] \), where \( \mathbf{n}_0 \) is the initial base point and \( \mathbf{n}_i \) is the base point after \( i \) iterations. The variables \( \delta \) and \( m \) are the step size and the number of times the step size has been halved, respectively. The local exploration for the \( i^{th} \) iteration defines a new local minimum \( \mathbf{n}_{Ai} \) and updates the search direction vector \( \mathbf{N} \). If \( \mathbf{N} \neq 0 \) and the function evaluation at the new local minimum is less than the value at the previous minimum, \( f(\mathbf{n}_{Ai}) < f(\mathbf{n}_{Ai-1}) \), a pattern move is made to a new base. Otherwise the increments are halved and a new pattern begun. After halving \( M \) times, the search is terminated and the answer given by the current value of \( \mathbf{n} \).

4. Experimental implementation

Figure 3.18 shows the individual elements of the active control system. Two NRL Type J-13 underwater sound projectors acted as the primary and secondary sources. Two hydrophones (B&K 8103) were located near the test section. The hydrophone outputs passed into separate charge amplifiers (Kistler Type 5010) and then into the analog inputs of a National Instruments AT-DSP 2200 DSP board within a 486 DX2/66 PC. The measured transfer function between the two hydrophones was corrected for phase mismatch according to ASTM E 1050-90 (American Society for Testing and Materials, 1990). The two analog outputs of the DSP board went into separate channels of an audio amplifier (Crown Power Tech 1) and then to the primary and secondary sources. The pattern search algorithm was implemented in software using a custom virtual instrument written in LabVIEW®. Figure 3.19 shows the progress of the optimization routine at 25 Hz.
FIGURE 3.17 Flowchart for the pattern search method.
FIGURE 3.18 Active control system hardware.

FIGURE 3.19 Progress of the optimization routine at 25 Hz.
Performance of the active control system was assessed by measuring the impedance ratio $\zeta(\bar{r}, \omega)$ at a fixed location as a function of the frequency. Operation at high frequencies was limited (according to ASTM E 1050-90) by the requirement that

$$s \ll \frac{c}{2f}.$$  (3.57)

For $s = 0.1 \text{ m}$, the maximum frequency is near 500 Hz. ASTM E 1050-90 states no precautions regarding a minimum acceptable hydrophone spacing at low frequencies; however, Schroeder (1994), using an air-filled aluminum impedance tube, reported problems at low frequencies if the microphone spacing was too small. Similar problems were expected for the water-filled acrylic waveguide.

To investigate the low frequency performance, the impedance ratio was measured (after optimization) as a function of hydrophone spacing. Figure 3.20 shows the results for 12.5 Hz, 18.75 Hz, and 25 Hz. The data indicate that at 25 Hz a spacing of 0.8 m is adequate, while at 12.5 Hz a spacing of more than 1 m is required. Overall, three different hydrophone spacings were used; Table 3.1 lists the spacings used and the frequency range for each.

Figures 3.21 and 3.22 give the results for the active control system. Overall the control system was very successful in absorbing the incident sound and providing anechoic end conditions. The reflection coefficient was less than 0.05 from 12.5 to 500 Hz.
FIGURE 3.20 Effect of hydrophone spacing on active control system performance.

<table>
<thead>
<tr>
<th>Spacing (m)</th>
<th>Frequency range (Hz)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.8</td>
<td>$f &lt; 38$</td>
</tr>
<tr>
<td>0.4</td>
<td>$38 \leq f \leq 112$</td>
</tr>
<tr>
<td>0.1</td>
<td>$f &gt; 112$</td>
</tr>
</tbody>
</table>

TABLE 3.1 Hydrophone spacings for the active control system.
FIGURE 3.21 Acoustic impedance ratio measured with and without active control. Top – real part; bottom – imaginary part.
FIGURE 3.22 Reflection coefficient measured with and without active control.

5. Comparison with unbounded plane progressive wave

After successful optimization of the secondary source, or at frequencies where a traveling wave exists without active control, the impedance ratio within the waveguide is given by Eq. (3.41),

$$\zeta(x, \omega) = \frac{k}{\kappa}, \quad \text{(3.41)}$$

which indicates that the acoustic particle velocity for a traveling wave within the waveguide is

$$V(x, \omega) = \frac{P(x, \omega)}{\rho c} \left( \frac{k}{\kappa} \right). \quad \text{(3.58)}$$

For a plane progressive wave in open water the attenuation is negligible below 10 kHz, thus the particle velocity is
If the waveguide is water-filled, then \( \rho_i = \rho_w \), however, the phase velocity in the waveguide is only about one-fourth of the unbounded sound speed; therefore, for the same acoustic pressure, a traveling wave in the waveguide will have a particle velocity magnitude about four times larger than that of a traveling wave in open water. Because the goldfish auditory system is sensitive to both pressure and particle velocity, this may affect the interpretation of experimental data.

To get around this, a new desired value may be used in place of Eq. (3.55). The goal of the controller is now to generate a wave with

\[
\frac{P(\vec{x},\omega)}{\rho_w c_w V(\vec{x},\omega)} = \frac{k}{k}.
\]

Thus the ideal impedance ratio at \( \vec{x} \) is

\[
\zeta_{12}(\vec{x},\omega) = \frac{c_w}{c} \left( \frac{k}{k} \right).
\]

From Eq. (3.39) the desired transfer function \( H_{12}(\vec{x},\omega) \) can be found from \( \zeta_{12}(\vec{x},\omega) \):

\[
H_{12}(\vec{x},\omega) = \frac{c_w/c - j \tan(ks/2)}{c_w/c + j \tan(ks/2)}.
\]

Using this new value for \( H_{12}(\vec{x},\omega) \), the active control experiments were repeated, again using the setup shown in Fig. 3.18. To assess the controller's performance the acoustic impedance was measured and then normalized by dividing by \( \rho f_c \), rather than
\( \rho c \), as in Fig. 3.21. Figure 3.23 shows the measured normalized impedance ratio as a function of frequency. The symbols represent the experimental data; the solid lines indicate the ideal performance, that is, the impedance ratio with zero error. The results are very close to the ideal behavior. For the experiments on the goldfish, the desired value of Eq. (3.62) was used to generate the low frequency field. This results in a plane traveling wave within the waveguide with a pressure/velocity ratio equal to that of a plane progressive wave in open water.

![Figure 3.23](image.png)

**FIGURE 3.23** Real and imaginary parts of the normalized acoustic impedance measured using the desired value from Eq. (3.62) in the active control system.
CHAPTER 4

EXPERIMENTAL METHODS

The experiments consisted of anesthetizing and tethering individual fish within an underwater, low-frequency sound field. As each fish was insonified by the low-frequency source, the frequency responses of the swimbladders, Weberian ossicles, and otoliths were measured using the ultrasonic measurement system described in Chapter 2. The experiments were performed in an acoustic waveguide at frequencies between approximately 10 Hz and 400 Hz, and within a small swimming pool at frequencies up to 3000 Hz. The two test apparatus were physically unique, yet shared some common instrumentation and equipment. At least one day was normally required to switch from operating within one apparatus to operating within the other. The tests within the waveguide and pool were therefore not run simultaneously, or even consecutively. Typically, one apparatus was used for a period of several weeks before changing to the other apparatus. This means that some fish may not have been tested in both apparatus.

This chapter describes the experimental apparatus and procedure, including the methods used to reduce the data. The experimental results are presented in Chapter 5.

A. Experimental animals

Experiments were conducted on 61 goldfish obtained from suppliers in central and southern Ohio. Masses and standard body lengths, measured from the tip of the snout to the base of the caudal fin, ranged from 14 to 77 g and 79 to 138 mm, respectively. The
smaller fish, however, were difficult to properly anesthetize (without overdosing). In addition, it was very difficult to find the desired structures in the early tests; therefore, meaningful, in vivo data were obtained only from 22 individuals, most in the 30 to 70 g range. Appendix B includes a complete listing of the test sequence.

Fish were kept in community aquaria until tested. To allow repeated identification of specific individuals, fish were tagged using nylon thread and numbered plastic discs (Floy-Tag Co. Fingerling Tag). For each fish it was necessary to remove a portion of the operculum in order to allow the ultrasound to penetrate to the lagena and saccule. This minor procedure had no noticeable effect on the animal’s health; the fish swam and fed normally after the procedure and did not show any visible signs of stress. Over time the operculum regenerated. All experiments were approved by the Animal Care and Use Committee at The Ohio State University.

Radiographs of individual fish were obtained and used to assist in locating specific organs during testing. Figure 4.1 illustrates medial-lateral and dorso-ventral radiographs from a 36.1-g goldfish. The anterior and posterior swimbladders appear as dark areas. Because they are much denser than bone, the lagenerated and utricular otoliths are also apparent. The saccular otolith is not visible, due to its small size and location medial to the lagena.

The sound pressure level generated by the low-frequency source(s) was chosen to be above the goldfish auditory threshold, yet below the level at which the auditory system would be damaged. In addition, the noise floor in the waveguide was measured near 100 dB re: 1μPa, so the SPL needed to be above this value to achieve a good signal-to-noise ratio. Behavioral audiograms for the goldfish, shown in Figure 4.2, indicate that the auditory threshold is within 50–75 dB re: 1μPa between 50 and 2000 Hz (Popper, 1971b; Jacobs and Tavolga, 1967). Temporary threshold shifts have been observed in goldfish exposed to 149 dB re: 1μPa for 4 h (Popper and Clarke, 1976); actual physical damage to
FIGURE 4.1 Medial-lateral and dorso-ventral radiographs for a 36.1-g goldfish (GF017). The bar length is 1 cm. ASB - anterior swimbladder; PSB - posterior swimbladder; TR - tripus; LA - lagenar otolith; UT - utricular otolith.

FIGURE 4.2 Behavioral audiograms for the goldfish. JT - Jacobs and Tavolga (1967); PS - Popper (1971b), small fish (45-48 mm); PL - Popper (1971b), large fish (110-120 mm).
the auditory organs has been detected in goldfish subjected to SPLs of 189–200 dB re: 1\mu Pa (Hastings, 1995). Hastings (1991) cites 150 dB re: 1\mu Pa as being an apparently safe upper limit. For this study a nominal value of 10 Pa was chosen; this results in an SPL of 140 dB re: 1\mu Pa, which meets the above criteria.

B. Experimental apparatus

1. Waveguide setup

At frequencies between 10 and 400 Hz, experiments were conducted in the acoustic waveguide described in Chapter 3. Figure 4.3 shows the position of the ultrasonic measurement system relative to the waveguide and water channel. Figure 4.4 is a more detailed view showing the orientation of the ultrasonic transducers within the waveguide. The ultrasonic source and receiver were 6.35-mm diameter immersion transducers focused at 19 mm (Panametrics V317-SU F0.75). Each transducer was broadband (\(Q \approx 2.9\)) with a resonance at approximately 20 MHz. The source and receiver were both mounted to search tubes (Krautkramer Branson model ST-015) and immersed in water. The source search tube was attached to a manual positioning system which allowed motion in the x-direction and rotation about the vertical; the receiver was attached to a manual positioning system which allowed linear motion along all three coordinate axes and rotation about the vertical. Alignment between the ultrasonic source and receiver was accomplished according to the procedure outlined in Chapter 2 and was verified each day of testing. It was necessary to cut openings in the waveguide to provide access for the ultrasonic transducers (and to allow positioning of the target). The effect of these openings is discussed below, in the subsection entitled “Acoustic stimulus in the waveguide.”
FIGURE 4.3 Orientation of the waveguide and the ultrasonic measurement system.
Figure 4.4 shows the complete experimental setup for tests conducted in the waveguide, with the waveguide itself omitted for clarity. All experiments were coordinated through a custom virtual instrument written in LabVIEW* running on a 486 DX2/66 PC. A National Instruments AT-DSP 2200 digital signal processing board was used to generate the primary and secondary source waveforms. These signals were amplified (Crown Power-Tech 1 audio amp) and used to drive the acoustic sources: two NRL Type J-13 underwater sound projectors flanged to the ends of the 14-m long waveguide. At frequencies above 150 Hz, audio transformers (Altech model 15300) were used to improve the impedance match between the amplifier and the J-13 sound projectors.

The ultrasonic carrier output from the HP 33120A function generator was split using a 0° power splitter (Mini-Circuits model ZRPD-1). One signal was amplified and used to drive the ultrasonic source; the other carrier signal was used as the reference in the phase detector. Voltage into the ultrasonic source was approximately 10 Vrms. The exact
carrier frequency was adjusted during data collection, as described in Chapter 2, in order to eliminate a possible 180° phase error due to target motion. The resulting carrier frequencies were within 14.95 ± 0.40 MHz.

FIGURE 4.5 Experimental setup for tests within the waveguide.
The ultrasonic receiver output was amplified in two stages: first through the receiver section of a Panametrics 5052UA ultrasonic analyzer (40 dB maximum gain), then through a Mini-Circuits model ZFL-500LN low-noise amplifier (20 dB maximum gain). The amplified signal was then split (again using a 0° power splitter) and input to both the phase detector and the HP 3585B spectrum analyzer. The spectrum analyzer directly measured the relative amplitude between the ultrasonic carrier and sidebands. The phase detector output was low-pass filtered and input to a digital voltmeter (HP 34401A) and also to the Stanford Research SR 850 lock-in amplifier. The lock-in amp measured the phase of the phase detector output with respect to the primary source input signal; in other words, the lock-in amp measured the target displacement phase with respect to the primary source input. The voltmeter was used as part of the closed-loop adjustment of the carrier frequency, as described in Chapter 2, Section A.2.b.

Anesthetic solution was gravity-fed from an 18.9-L reservoir through plastic tubing and discharged near the fish’s head. The anesthetic flow rate was monitored and adjusted using a ball-type flowmeter with a built-in valve (Gilmont model F-4001). The fish itself was suspended from a motorized positioning system (Aerotech ATS-100 series) so that the organ being investigated was within the ultrasonic sample volume. The PC controlled the positioning system via a Unidex 500 motion control board. The entire measurement process was controlled through an interface written in LabVIEW®.

a. Acoustic stimulus in the waveguide. The active control system described in Chapter 3 was used to optimize the secondary source amplitude and phase at each frequency so that a traveling wave existed. Optimization was performed about once a week, without a fish present. The resulting values for the primary and secondary source amplitude and phase were then used for all experiments carried out until the next optimization.
After optimizing the secondary source, the low-frequency field was examined with a B&K 8103 miniature hydrophone to determine the local acoustic stimulus presented to the fish: the acoustic pressure and particle velocity within the ultrasonic sample volume. Because a fish's swimbladder scatters significant amounts of sound, this procedure was always performed without a fish present. The hydrophone was mounted to the motorized positioning system and moved throughout a 16-mm cube centered at the sample volume. The acoustic pressure amplitude and phase (re: primary source input) were measured at 15 discrete points within this cube: the center, the eight corners, and the six face-centers. The measured pressures within each face of the cube were averaged and used, along with the average pressure from the other parallel cube face, to estimate the acoustic particle velocity in the corresponding direction according to Eq. (3.46). The pressure at the sample volume was taken as the average of the 15 measured pressures. Mapping the low frequency field in this manner was performed after each new optimization.

Figure 4.6 shows a representative sample of the acoustic pressure typically measured within the waveguide test section. Although an attempt was made to scale the primary source amplitudes in order to generate a constant pressure at the fish, it was impossible to generate equal pressures at all frequencies. At high frequencies the J-13 impedance mismatch with the audio amplifier and the high attenuation within the waveguide made it more difficult for the secondary source to absorb the incident sound unless the primary source amplitude was reduced. At low frequencies, the J-13 response was the limiting factor. In addition, it was impossible to predict exactly how the active control scheme would adjust the secondary source, thus some fluctuation of the measured pressure from the desired value was inevitable. It should also be pointed out that the phase in Fig. 4.6(b) is the phase of the pressure referenced to the primary source input, thus the amplifier and source characteristics are also present.
FIGURE 4.6 Example of the acoustic pressure measured within the waveguide test section. (a) average sound pressure level; (b) pressure phase re: primary source input.

Figure 4.7 shows an example of the local acoustic particle velocities typically measured at the location of the sample volume in the waveguide test section. The velocities measured within the 16-mm space of the sample volume show considerable differences from the “global” particle velocities measured (using two fixed hydrophones) after optimization of the secondary source. These differences are attributed to the openings in the waveguide which allowed access for the ultrasonic transducers and positioning of the fish. These openings created relatively large, local pressure gradients in their vicinity, leading to particle velocities much larger than anticipated, especially at the lower frequencies.
Figure 4.8 shows the sizes and locations of the openings cut in the waveguide. An attempt was made to keep these as small as possible, however the size of the ultrasonic search tubes and the freedom required to position the target put a lower limit on the size of the openings. The search tube openings were not covered in order to prevent direct mechanical coupling between the waveguide and the ultrasonic transducers. The target opening was left uncovered to allow positioning of different targets within the sample volume. Covering the opening after positioning the fish, just prior to collecting data, was not practical since any disturbance was likely to move the target out of the ultrasonic sample volume.
FIGURE 4.8 Waveguide test section showing the location and sizes of the openings cut to allow access for the ultrasonic transducers and the fish. Dimensions are in millimeters.

2. Pool setup

At higher frequencies, where the waveguide plane wave assumption begins to break down and the active control system does not function properly, experiments were performed in a vinyl-walled swimming pool having a diameter of 2.4 m and a depth of 0.4 m. Figure 4.9 shows the geometry of the pool and location of the test apparatus. The complete experimental setup, shown in Fig. 4.10, is nearly identical to that used in the waveguide (shown in Fig. 4.5). One difference is that there is no secondary source. In early experiments, the primary source was a University Sound UW-30 underwater loudspeaker; this was later replaced with an NRL J-9 underwater sound projector. The measured frequency responses appeared to be insensitive to the particular choice of acoustic source; however, the J-9 produced a more uniform acoustic field at lower frequencies.
FIGURE 4.9 Geometry and layout of the plastic pool used for high frequency testing.
Because of the relatively small volume of the pool, the anesthetic flow system was not used; it was determined that the flow system would result in an unacceptable buildup of anesthetic, unless frequent water changes were performed. It took several days to degas and equilibrate the water in the pool after each water change, making frequent water changes problematic. To compensate for the absence of the anesthetic flow, the fish were
placed in a deeper state of anesthesia before testing. The net result was that fish tested in
the pool could not be kept anesthetized as long as those tested in the waveguide. This
restriction was not a major problem.

**a. Acoustic stimulus in the pool.** The acoustic pressure and particle velocity in the
pool were measured using the same procedure as in the waveguide. Figure 4.11 shows a
representative sample of the pressure amplitude and phase measured at the test location.

![Image of graphs showing pressure amplitude and phase](image)

**FIGURE 4.11** Example of the measured acoustic pressure in the pool at the location of the
fish. (a) average sound pressure level; (b) pressure phase re: primary source input.
Figure 4.12 shows the corresponding acoustic particle velocity along the three coordinate axes. At the lower frequencies, the axial velocity is very large but decreases with frequency. At higher frequencies, the axial velocity \( V_x(\omega) \) approaches the plane wave value, but then begins to deviate. These deviations are probably due to the relatively shallow depth of the water and reflections from the wall of the pool.

![Graph showing acoustic particle velocities](image)

**FIGURE 4.12** Representative sample of the (rms) acoustic particle velocities measured in the pool at the location of the fish.

**C. Experimental procedure**

Animals were anesthetized before testing by immersion in a 1:2500 (1 g in 2500 ml \( \text{H}_2\text{O} \)) solution of MS-222 (ethyl \( m \)-aminobenzoate) for approximately 2–2.5 h, depending on the size. Fine thread was then inserted through the fleshy region of the back, dorsal to the spinal cord, and used to tether the animal from a support post attached to the motorized positioning system. Metal washers or nuts were added to a separate loop of thread hung
from the animal to keep it from floating. The fish was then submerged in the test apparatus. As the fish was being positioned, its body, mouth, and throat were visually inspected for air bubbles; any existing bubbles were gently cleared. Each fish was oriented facing the (primary) source, with its longitudinal axis aligned with the source axis. The ultrasonic system was placed to map the right side of the animal, measuring motion in the medial-lateral direction.

For tests in the waveguide, anesthetic was administered through plastic tubing located near the head. The anesthetic concentration was approximately 1:12000, again depending on the fish’s size, and the flow rate was adjusted from 5 to 17 ml/min depending on the fish’s size, total time under anesthetic, and behavior. The flow was turned on before testing began, to allow some buildup of anesthetic, and turned off before any data collection. Using this procedure it was possible to keep goldfish anesthetized and motionless for up to 5 h. Animals that regained consciousness during testing were removed from the test apparatus and immersed in anesthetic until respiration again ceased, upon which they were returned to the test fixture.

After lowering to a position in front of the ultrasonic transducers, the fish was positioned to locate the individual auditory organs. The correct location of each organ was based on the physical location of the sample volume and the strength of the returned echo. Two CCD video cameras (Sony XC-75) were used to give views of the $x$-$z$ and $x$-$y$ planes (see Fig. 4.4), with the location of the sample volume in each view marked on a video monitor. Thus it was possible to estimate where the sample volume was positioned on the fish. Figure 4.13 shows the view from the $x$-$z$ camera, which was located underwater behind the ultrasonic transducers. With practice, locating the anterior and posterior swimbladders was very easy; finding the tripus and other Weberian ossicles, and especially the otoliths, proved much more difficult. Often the correct location could only be verified after the fact by examining the measured response.
Locating the various organs was also assisted by operating the ultrasonic transducers in pulse-echo mode using a Panametrics 5052UA ultrasonic analyzer. Operating a single transducer in pulse-echo mode revealed any reflective surfaces within the geometric limits of the transducer beam. Operating both transducers in "pitch-and-catch" mode revealed any interfaces within the intersection of the transducer beams. The time delay between the emitted pulse and each received echo is related to the distance between the ultrasonic source and the structure that caused the echo. The amplitude of each echo is related to the impedance mismatch between the structure and water. The pulse-echo
technique therefore made it possible to estimate the depth and composition of various structures within the fish's body. This technique, used in conjunction with a radiograph, proved extremely valuable in locating the otoliths.

Once an organ was located, the displacement amplitude and phase were measured as described in Chapter 2. The collection of data from a specific location took 10 to 15 minutes, after which the search was resumed for the next organ. After collecting data from all of the organs that could be found, the fish was placed in fresh water and respirated by gently stroking the ventral side of the body and forcing water over the gills until steady respiration resumed. For fish whose operculum had been partially removed, recovery was also assisted by allowing fresh water to flow directly over the exposed gill. Most fish over 30-g completely recovered after testing and showed no adverse effects as a result of the anesthetic. This allowed replication of the experiments for many of the fish; however, the difficulty involved in locating the smaller organs sometimes prevented multiple sets of data from being acquired.

D. Data reduction

The first step in reducing the data was to correct for any motion of the ultrasonic transducers. Any relative motion between the ultrasonic source and receiver will modulate the received phase and be perceived as motion of the target. To quantify this effect, the amplitude and phase of a 150 × 150 × 60 mm lead target were measured. The lead should remain motionless within the acoustic field, thus any measured displacement indicates motion of the ultrasonic transducers or the target support post.

The measured target displacement $x_p(\omega)$ is

$$x_p(\omega) = X_p(\omega)e^{j[\phi_p(\omega)-\phi(\omega)]}, \quad (4.1)$$
where \( X_r(\omega) \) is the measured displacement amplitude, \( \phi_r(\omega) \) is the measured displacement phase, and \( \phi_s(\omega) \) is the primary source input phase. The bold type is used to emphasize that \( x_r(\omega) \) is complex. Adopting the notation that \( \phi'(\omega) \) indicates a phase referenced to the primary source input, Eq. (4.1) may be written as:

\[
x_r(\omega) = X_r(\omega) e^{i\phi_r(\omega)}.
\]

(4.2)

Similarly, the displacement measured from the lead is

\[
x_{pb}(\omega) = X_{pb}(\omega) e^{i\phi_{pb}(\omega)}.
\]

(4.3)

The actual target displacement \( x_L(\omega) \) was found by subtracting the motion of the lead from the measured target motion:

\[
x_L(\omega) = x_r(\omega) - x_{pb}(\omega).
\]

(4.4)

The target displacement may also be written using the amplitude \( X_L(\omega) \) and phase \( \phi_L(\omega) \):

\[
x_L(\omega) = X_L(\omega) e^{i\phi_L(\omega)}.
\]

(4.5)

where

\[
X_L(\omega) = |x_r(\omega) - x_{pb}(\omega)|,
\]

(4.6)

\[
\phi_L(\omega) = \angle[x_r(\omega) - x_{pb}(\omega)],
\]

(4.7)
and $\angle$ indicates "the phase of." Even after subtracting the displacement of the lead, some low frequency data revealed peaks or notches in the measurements common to all locations tested. These data indicated a waveguide or test apparatus resonance and were normally excluded from the results.

The measured displacement depended on the strength of the stimulus presented to the fish. It was therefore necessary to normalize the measured target motion using the actual acoustic pressure and/or particle velocity. The acoustic stimulus presented to the fish was known from the mapping of the low frequency acoustic field. The measured average (rms) pressure at the test site was

$$p_{\text{ave}}(\omega) = P_{\text{ave}}(\omega) e^{i\phi(\omega)}, \quad (4.8)$$

and the measured (rms) acoustic particle velocity was

$$v(\omega) = [v_x(\omega), v_y(\omega), v_z(\omega)], \quad (4.9)$$

where

$$v_x(\omega) = V_x(\omega) e^{i\phi_x(\omega)}, \quad (4.10)$$

$$v_y(\omega) = V_y(\omega) e^{i\phi_y(\omega)}, \quad (4.11)$$

and

$$v_z(\omega) = V_z(\omega) e^{i\phi_z(\omega)}. \quad (4.12)$$
Regardless of the test setup, the acoustic pressure and particle motion were both significant at the location of the fish, so the acoustic energy density was used to normalize the target motion. Acoustic energy density is defined as

$$E(\omega) = \frac{1}{2} \rho_w V_y^2(\omega) + \frac{1}{2} \rho_w \left[ \frac{P_{\text{tot}}(\omega)}{\rho_w c_w} \right]^2.$$  (4.13)

The velocity component $V_y(\omega)$ was used, rather than the overall velocity magnitude, since the ultrasonic system is only sensitive to motion in the y-direction.

Target motion amplitudes are presented in Chapter 5 in terms of the normalized velocity $W(\omega)$, which is defined as the target velocity divided by $\rho_w c_w \sqrt{E(\omega)/\rho_w}$, or

$$W(\omega) = \frac{\omega X_y(\omega)}{\rho_w c_w \sqrt{E(\omega)/\rho_w}},$$  (4.14)

and has units of (m/s)/Pa. Since the target motion was harmonic, the phase of the target velocity was obtained by adding $90^\circ$ to the displacement phase, $\phi'_x(\omega)$. The target velocity phase was then normalized by subtracting the phase of the acoustic pressure at the target, $\phi'_p(\omega)$, to yield the normalized velocity phase $\phi'_w(\omega)$:

$$\phi'_w(\omega) = \phi'_x(\omega) + 90^\circ - \phi'_p(\omega).$$  (4.15)

In some cases it was more illustrative to use the normalized displacement amplitude $D(\omega)$,

$$D(\omega) = \frac{X_y(\omega)}{\rho_w c_w \sqrt{E(\omega)/\rho_w}},$$  (4.16)

which has units of m/Pa, and the normalized displacement phase $\phi'_d(\omega)$.
\[ \phi_B(\omega) = \phi_L(\omega) - \phi_P(\omega). \] (4.17)

The experimental results for the motion of the various auditory organs are presented as plots of the normalized velocity (or normalized displacement) amplitude and phase vs. frequency.

**E. Measurement threshold and accuracy**

**1. Measurement threshold**

In order to obtain a valid amplitude or phase measurement, the ultrasonic measurement system requires that the sideband be above the noise floor of the HP 3585B spectrum analyzer. This means that, for a specific carrier amplitude, motion amplitudes below a certain value will not produce a sideband large enough to be above the noise, and will therefore not be detected. This idea is illustrated in Fig. 4.14. In Figs. 4.14(a) and 4.14(b), both carrier signals have the same amplitude; however, the motion amplitude for the target in Fig. 4.14(a) is large enough to produce a measurable sideband, while that of Fig. 4.14(b) is not. For the carrier signal shown, the motion amplitude of Fig. 4.14(b) is therefore below the measurement threshold and is not detectable. However, the target motion of Fig. 4.14(b) may be detected if the carrier amplitude is increased. This is illustrated in Fig. 4.15. In Fig. 4.15(a) the sideband is below the measurement threshold. In Fig. 4.15(b), using the same target motion amplitude, the carrier amplitude has been increased enough to move the sideband amplitude above the noise, so that it may now be measured.

The measurement threshold thus depends on both the amplitude of the target motion and the amplitude of the ultrasonic carrier. For a target such as a swimbladder, which provided a large reflected signal and thus a large carrier amplitude, a small target
FIGURE 4.14 Effect of target motion amplitude on signal detectability for the same carrier amplitude. (a) Sideband is above the noise so the motion may be measured. (b) With the same carrier amplitude, a lower amplitude motion may produce a sideband below the noise floor.

FIGURE 4.15 Effect of carrier amplitude on signal detectability for the same target motion amplitude. (a) Sideband is below the noise so the motion may not be measured. (b) With a larger carrier amplitude, the same amplitude motion may produce a sideband above the noise floor.
motion could still yield a relatively large amplitude sideband. For small, irregularly shaped targets deep within the goldfish body, such as the otoliths, the reflected signal amplitudes were lower, the carrier amplitudes were lower, and therefore larger motions were required in order to be detected.

If the noise level is known, it is possible to calculate, for a given carrier amplitude, the minimum target motion amplitude which will produce a sideband just above the noise floor. Using Eq. (4.14) and the acoustic field data of Figs. 4.6, 4.7, 4.11, and 4.12, the minimum detectable target displacement was converted to units of normalized velocity. Figure 4.16 shows this estimated minimum detectable normalized velocity as a function of frequency for several different carrier amplitudes.

![Graph showing minimum detectable target motion as a function of frequency for different carrier amplitudes.](image)

**FIGURE 4.16** Minimum detectable target motion, in terms of normalized velocity, for different carrier amplitudes.

Figure 4.16 indicates that as the carrier amplitude decreases, the minimum detectable velocity amplitude increases. In addition, all of the curves increase dramatically at high frequencies. Typical carrier amplitudes were as follows: swimbladder, 500–700
mV; tripus, 200–400 mV; lagenar otolith, 100–500 mV; saccular and utricular otoliths, 80–150 mV. The family of curves in Fig. 4.16 were calculated using estimated noise floor levels and the acoustic field data of Figs. 4.6, 4.7, 4.11, and 4.12. Since the acoustic field properties varied somewhat, and the noise floor was estimated from isolated measurements, the curves in Fig. 4.16 must be regarded only as estimates of the minimum detectable velocity amplitudes for a given carrier. The main usefulness of Fig. 4.16 is that it allowed a direct comparison between the estimated minimum detectable velocity (as a function of frequency) and the actual experimental data. Also, the phase measurement produced erratic results when the motion amplitude was near the measurement threshold. Figure 4.16 is therefore useful to determine when the measured target amplitude is so low that erratic phase data may result.

2. Measurement accuracy

The experimental data are presented in Chapter 5 in terms of the normalized velocity and normalized displacement, defined in Eqs. (4.14)–(4.17). It is therefore advantageous to present the amplitude accuracy estimates from Chapter 2, Section A.3, in terms of the normalized velocity and normalized displacement. Typical rms pressures measured in the test section averaged 140 dB re: 1μPa, or 10 Pa (see Figs. 4.6 and 4.11); therefore, in terms of the normalized displacement, the accuracy is approximately ± 0.42 nm/Pa. In terms of normalized velocity, the accuracy is a function of frequency. At 1000 Hz, the estimated accuracy is ± 2.6 (μm/s)/Pa. These accuracy estimates are summarized in Table 4.1.
<table>
<thead>
<tr>
<th>Estimated accuracy (±3s limits)</th>
</tr>
</thead>
<tbody>
<tr>
<td>normalized displacement</td>
</tr>
<tr>
<td>± 0.42 nm/Pa</td>
</tr>
<tr>
<td>normalized velocity (1000 Hz)</td>
</tr>
<tr>
<td>± 2.6 (μm/s)/Pa</td>
</tr>
</tbody>
</table>

Table 4.1 Measurement system accuracy expressed in terms of the normalized displacement and velocity.
CHAPTER 5

EXPERIMENTAL RESULTS

This chapter presents the results of the experimental measurements of the response of the goldfish swimbladders, Weberian ossicles, and otoliths. The data is presented in terms of the normalized velocity and normalized displacement, which are defined in Chapter 4, Section D. This chapter begins by introducing some representative experimental data, then follows with more detailed, individual discussions of the swimbladder, Weberian ossicle, and otolith data. Appendix B contains a complete listing of the individual test details, such as the date, fish tag number, and which organs were located. All of the data presented is in vivo.

A. Introduction

1. Representative experimental data

Figures 5.1–5.3 plot the response of the swimbladders, tripus, and otoliths for goldfish GF016 (53.7 g; 125.7 mm). Figure 5.1 shows the normalized velocity measured from the anterior and posterior swimbladders. The top plot displays the amplitude, in (μm/s)/Pa; the bottom plot shows the phase, in degrees (relative to the acoustic pressure phase). This plotting convention is followed in all of the normalized velocity plots presented. Data from approximately 10–400 Hz was collected using the waveguide setup; data from approximately 200–3000 Hz was collected using the pool setup. In the region of overlapping frequencies, one would ideally expect the data points to coincide. However,
FIGURE 5.1 Normalized velocity measured from the swimbladders of goldfish GF016. ASB – anterior swimbladder; PSB – posterior swimbladder.
FIGURE 5.2 Normalized velocity for the tripus and saccular otolith of goldfish GF016. TR – tripus; SA – saccular otolith.
since the data was necessarily collected on different days, and the response of a single organ on an individual fish varied somewhat from test to test, there is no guarantee that the data will coincide. Also, since the ultrasonic system is only sensitive to motion along the transducer bisector, any differences in position or angular orientation of the fish from test to test will lead to discrepancies in the measured response.

In Fig. 5.1, the low and high frequency amplitude and phase data match reasonably well. At low frequencies, both bladders move with essentially the same amplitude and phase. The phase angles at low frequencies approach +90°, which corresponds to a displacement phase of 0° relative to the acoustic pressure. Positive displacement is defined in the direction away from the ultrasonic system, which means that the bladder wall moves radially inward in response to a positive acoustic pressure, as expected. At higher frequencies, the resonance of each bladder is visible. The amplitudes at resonance are roughly identical; however, the anterior bladder resonance frequency is higher than that of the posterior. The high frequency phase data confirms this as well. Above the resonance, the amplitudes decay and the phase angles flatten out just below -90°.

Figure 5.2 shows the normalized velocity measured from the tripus and saccular otolith (sagitta) of GF016. For these structures, no low frequency data was available. Both the tripus and sagitta responses show amplitude peaks near the swimbladder resonances. For this fish the tripus response has a larger peak amplitude. At low frequencies the tripus response lags that of the otolith by 90°; at higher frequencies the phase lag is smaller and the phase angle of each roughly approximates that of the anterior swimbladder.

Figure 5.3 is a plot of the normalized velocity measured from the lagenar and utricular otoliths in goldfish GF016. To allow comparison, Fig. 5.3 has the same scale as Figs. 5.1 and 5.2. At low frequencies, the two otoliths move with basically the same amplitude and phase as the anterior and posterior swimbladders. This type of low-frequency motion was observed in most structures (including the tail muscle and the jaw.
FIGURE 5.3 Normalized velocity for the lagenar and utricular otoliths of goldfish GF016. LA – lagenar otolith; UT – utricular otolith.
bone). Since the measured amplitudes are well above the measurement threshold at low frequencies, this appears to indicate motion of the fish as a whole (caused by the large particle velocities in the waveguide at low frequencies), rather than a response to the acoustic pressure.

At higher frequencies the lagenar otolith shows some response near the swimbladder resonances; however, motion of the utricular otolith does not differentiate itself from the gross motion of the fish. In fact, at high frequencies, the utricular otolith motion amplitude approaches the measurement threshold. The phase angle for the utricular otolith is very erratic. This behavior was observed in all of the phase angle measurements when the demodulated signal amplitude was near the phase measurement threshold (see Chapter 4, Section E).

Figures 5.4 and 5.5 show the responses measured from the swimbladders, tripus, and otoliths of goldfish GF004 (33.7 g; 100.2 mm). This particular fish was only tested once, using the pool setup, thus no low frequency data are available. Figure 5.4 shows the response of the anterior and posterior swimbladders. For this fish the posterior swimbladder has a higher resonance frequency and a lower amplitude at resonance than the anterior chamber. The phase relationship between the two also serves to emphasize the difference in resonance frequencies; although both phase angles begin near +90°, the posterior phase leads the anterior throughout the entire frequency range and begins its descent at a higher frequency. Both phase angles flatten near -90°; however, the anterior swimbladder phase drops again near 2000 kHz, which may correspond to a harmonic of the resonance frequency. Although the resonance frequencies and amplitudes at resonance are different, these data are otherwise similar to that of Fig. 5.1 and to most of the other swimbladder data obtained.

The anterior swimbladder response in Fig. 5.4 also illustrates the condition of multiple resonances, as previously reported by Zhou (1992) and Lewis (1994). This
FIGURE 5.4 Normalized velocity measured from the swimbladders of goldfish GF004. ASB – anterior swimbladder; PSB – posterior swimbladder.
FIGURE 5.5 Normalized velocity for the tripus, lagenar, and saccular otoliths of goldfish GF004. TR – tripus; SA – saccular otolith; LA – lagenar otolith.
phenomenon is attributed to the dual-chambered goldfish swimbladder: if the two chambers are of different sizes, each will have a unique resonance frequency. Since the bladders are in close proximity, direct coupling may exist and the response of one may influence the other.

Figure 5.5 shows the measured normalized velocity for the tripus, sagitta, and lagenar otoliths of goldfish GF004. The responses of the tripus and sagitta are in-phase and have nearly the same amplitude. The highest response for each occurs near the swimbladder resonance frequency; the tripus and saccular otolith phase angles also closely match those of the swimbladders. This behavior is also shown in Fig. 5.2 and implies strong coupling between the swimbladder and the Weberian ossicles and saccular otolith. In contrast to the saccular otolith, the lagenar otolith amplitude is near the minimum detectable amplitude for the carrier signal obtained, thus the lagenar otolith is essentially not moving in the medial-lateral direction. The lagenar otolith phase angle is not shown because the response amplitude is near the phase measurement threshold for much of the frequency range, thus the phase data are erroneous.

In many respects, the data of Figs. 5.1–5.5 are representative of the results for all of the goldfish tested. The response of each swimbladder shows a resonance, though the resonant frequency and amplitude at resonance of each bladder are not necessarily the same. In many cases, the posterior swimbladder amplitude was less than that of the anterior; this has also been experimentally observed by Lewis (1994). The tripus and sagitta are usually in-phase with one another, especially at frequencies near the swimbladder resonance, and move with similar amplitudes. In addition, the tripus is usually in-phase with the anterior swimbladder (or both bladders) which again indicates coupling between the anterior swimbladder and the Weberian ossicles. In contrast to the saccular otolith, the utricular otolith showed no measurable response in any of the fish
tested. The lagenar otolith had a measurable response in only a few fish tested; in the majority of fish the lagena was not moving with any measurable amplitude in the medial-lateral direction.

2. Test replication and measurement error

Figure 5.6 shows the normalized velocity measured from the anterior swimbladder of goldfish GF756 (60.4 g; 123.9 mm). Figure 5.6 includes two sets of data obtained using the waveguide setup and five sets from the pool. This plot, along with Figs. 5.1 and 5.2, reveals the variation in the measured response that may be observed in an individual fish tested multiple times. The degree of scatter in the experimental data is much greater than the measurement accuracy specified in Chapter 4, Section E.2 (Table 4.1). This indicates the existence of uncontrolled biological parameters—variations in the measured response due to the biological nature of the target. These variations may be due to respiration or other target motion, or changes in tissue properties from day to day. Scatter in the data may also be due to slight differences in the sample volume location or fish orientation, or gross changes in the target itself; for example, the swimbladder volume is, to some extent, controlled by the fish and may vary from test to test. Since the data is in vivo, some fluctuation is inevitable. To evaluate the extent of scatter in the data due to the in vivo nature of the tests, the response of a lead target is provided as a comparison.

Figure 5.7 shows the normalized velocity measured from the lead target, which measured 150 x 150 x 60 mm. Since the amplitudes are near the estimated measurement threshold (see Chapter 4, Section E), the phase data are not shown. The symbols represent 18 individual sets of experimental data, collected in both the waveguide and pool, over the period September 1996 to February 1997. The thick line represents the estimated amplitude accuracy for a normalized velocity of zero. This is intended to provide a comparison between the measurement error and the scatter in the lead response. The lead target is an
FIGURE 5.6 Normalized velocity measured from the anterior swimbladder of goldfish GF756 showing the variation of response with repeated testing. The legend text indicates the test code for each data set (see Appendix B).
inanimate object which, in theory, will not respond to the low-frequency acoustic stimulus. The effects of biological parameters, either due to low-frequency target motion (i.e., respiration), changes in tissue properties over a period of time, or other causes, should therefore not appear in the lead data and the scatter should fall within the measurement error. As indicated by the scale of the ordinate in Fig. 5.7, the amplitude of motion of the lead is much smaller than that of the goldfish swimbladders, Weberian ossicles, and otoliths. The majority of data in Fig. 5.7 also lie within the estimated accuracy limits for a normalized velocity amplitude of zero. Although some data points have a larger amplitude than the line representing the estimated accuracy, the scatter within the data does lie within

FIGURE 5.7 Summary of the normalized velocity measured from a lead target measuring $150 \times 150 \times 60$ mm. The symbols represent 18 individual sets of experimental data obtained between Sept. 1996 and Feb. 1997. The thick line is the estimated accuracy for zero normalized velocity (see Table 4.1).
the estimated accuracy bounds; thus, the scatter caused by uncontrollable biological parameters which is apparent in the goldfish data of Figs. 5.1–5.5 is not present in the lead response.

The lead target also has merit as an experimental control; a comparison between Figs. 5.1–5.5 and Fig. 5.7 illustrates the differences that exist between the measured responses of the peripheral auditory organs and those of the lead target. Other useful controls include structures within the fish not believed to be related to audition. These structures would include the skull, jawbone, backbone, and the muscular tissue at the base of the caudal fin.

Figure 5.8 shows the normalized velocity measured from the anterior swimbladder, jawbone, skull, and backbone of goldfish GF024 (37.4 g; 102.0 mm). At low frequencies, the amplitude and phase of the anterior swimbladder and jaw are nearly identical. These amplitudes are roughly an order of magnitude higher than that of the lead at these frequencies. These data seem to indicate that the entire fish moves in response to the acoustic stimulus at low frequencies, where the acoustic particle velocity is large. At higher frequencies, the anterior swimbladder amplitude is significantly larger than the amplitudes of the skull and backbone. In fact, because of the relatively low carrier amplitudes for the skull and backbone in this case—150 mV and 72 mV, respectively—the amplitudes for the skull and backbone are actually below the measurement threshold (see Fig. 4.16).

Figure 5.9 shows the normalized velocity amplitude measured from the anterior swimbladder and skull of goldfish GF017 (36.1 g; 104.7 mm). The swimbladder response clearly dominates the motion of the skull.

Figure 5.10 shows the normalized velocity amplitude measured from the anterior swimbladder and tail muscle of goldfish GF757 (19.3 g; 84.0 mm). Again, the response of the anterior swimbladder is significantly larger than that measured from the tail muscle.
FIGURE 5.8 Normalized velocities measured from the anterior swimbladder, jaw, skull, and backbone of goldfish GF024. ASB – anterior swimbladder.
FIGURE 5.9 Normalized velocity amplitude measured from the anterior swimbladder and skull of goldfish GF017. ASB – anterior swimbladder.

FIGURE 5.10 Normalized velocity amplitude measured from the anterior swimbladder and tail muscle of goldfish GF757. ASB – anterior swimbladder.
Overall, the amplitudes for the tail, jaw, skull, and backbone were low and were typically near the measurement threshold. The amplitudes of the motions of these structures are therefore similar to those of the lagenar and utricular otoliths, lower than those typically measured in the Weberian ossicles and saccular otolith, and much lower than those of the anterior and posterior swimbladder.

These comparisons are a form of measurement validation; they show that the motion amplitudes measured from the fish are much larger than the motion of a target (theoretically) at rest. The control data also show that the acoustic stimulus produces motions of the swimbladders, Weberian ossicles, and saccular otolith which are several orders of magnitude larger than the motions of various structures not believed to be related to audition.

As a final comment, it should be emphasized that the ultrasonic measurement system is only sensitive to motion in the direction of the bisector between the transducer longitudinal axes, which corresponds to the medial-lateral direction for the fish. Motion in any other direction will not be detected. Thus, the data must be interpreted with caution, especially with regards to the otoliths, which may undergo complex 3-D translation and rotation.

B. Anterior and posterior swimbladders

1. Fish mass, length, and bladder dimensions

The mass and standard body length of each fish were measured before each test. Swimbladder dimensions were also measured from 31 in vivo radiographs. The swimbladder major and minor axis dimensions were used to compute the volume of each chamber, assuming a prolate spheroidal shape. The radius of each bladder was then defined as the radius of a sphere with a volume equal to that estimated from the radiograph. The bladder ratio, which is defined as the ratio of the posterior swimbladder radius to the
anterior swimbladder radius, was calculated from the measured swimbladder dimensions. The percent volume, defined by Alexander (1959a) as the total swimbladder volume (ml) divided by the fish mass (g), was also computed.

Figure 5.11 is a plot of the average standard body length vs. the average mass for each goldfish tested. This data is represented reasonably well ($R^2 = 0.956$) by the equation

$$L_{g} = 30.92 m_{g}^{1/3}, \quad (5.1)$$

where $m_{g}$ is the goldfish mass (g) and $L_{g}$ is the standard length (mm). Figure 5.12 shows the swimbladder radii plotted against the average mass for each fish. Although each radius generally increases with increasing mass, as expected, neither set of data is represented particularly well by a simple equation. A least squares fit of a function of $m_{g}^{1/3}$ to the anterior data yields

$$R_{1} = 1.84 m_{g}^{1/3}, \quad (5.2)$$

with $R^2 = 0.329$, where $R_{1}$ is the anterior swimbladder radius in millimeters and $m_{g}$ is in grams.

The bladder ratio is plotted in Fig. 5.13. The large amount of scatter in the data illustrates the variability in the size of the posterior swimbladder with respect to the anterior. In the smaller fish the anterior is generally larger than the posterior, however in the larger fish this is not necessarily true.

Finally, Fig. 5.14 shows the how the percent volume varies with goldfish mass. Again a large amount of scatter exists in the data. The mean value is 4.45 (standard
FIGURE 5.11 Standard body length vs. mass for the goldfish tested. The solid curve is a least squares fit to the data, given in Eq. (5.1).

FIGURE 5.12 Swimbladder radii vs. fish mass. The solid curve is the least squares fit to the anterior swimbladder data, given by Eq. (5.2).
FIGURE 5.13 Bladder ratio vs. goldfish mass.

FIGURE 5.14 Percent volume (in ml/g) vs. the average mass of each goldfish tested.
deviation 1.0). This value is significantly less than that reported by Alexander (1959a), who gives values from 6.3–8.9 with a mean of 7.9. The difference may be due to the prolate spheroid model not accurately fitting the shape of the bladder.

2. Body surface vs. swimbladder wall

Before starting the experiments, it was expected that the largest amplitude echo would come from the air-water interface present at the swimbladder wall. At the body surface of the fish itself, little reflection was expected because of the similar acoustic impedances of the fish flesh and water. However, early data showed significant reflections occurring at the body wall of the fish. Figure 5.15 shows the ultrasonic pulse-echo response recorded from the anterior swimbladder of goldfish GF000. The first peak corresponds to the body wall of the fish; the second indicates the actual swimbladder wall. In this plot, the transducer focal point lies at 26 μs, so the bladder wall echo appears significantly larger than the echo from the body surface, which is far from the focus (see Figs. 2.12, 2.14, and 2.16). In fact, the echo from the bladder wall was normally of lower amplitude due to attenuation. Since the two echoes are sufficiently separated in time, the structures which produce the echoes may be examined individually with the ultrasonic measurement system.

Figure 5.16 is an oscilloscope trace of the pulse-echo response of the posterior swimbladder of GF000. As in Fig. 5.15, unique echoes exist which correspond to the body wall and the actual swimbladder wall.

Figure 5.17 shows the normalized velocity measured from the anterior swimbladder wall and the body surface of goldfish GF000. The filled symbols represent the individual sets of data collected from the bladder wall; the open symbols are from the body surface of the fish. The amplitude at the body surface is lower than at the bladder wall, but both structures move essentially in-phase with one another.
FIGURE 5.15 Oscilloscope trace of the pulse-echo response from the anterior swimbladder and body surface of goldfish GF000.

FIGURE 5.16 Oscilloscope trace of the pulse-echo response from the posterior swimbladder and body surface of goldfish GF000.
FIGURE 5.17 Normalized velocity for the anterior swimbladder and body wall of goldfish GF000. Top - amplitude; bottom - phase.
Figure 5.18 shows the normalized velocity measured from the fish's body lateral to the posterior swimbladder and from the posterior bladder wall itself. Similarly to the response from the anterior swimbladder, both the body surface and the bladder wall move in-phase with one another and the amplitude at the bladder wall is somewhat larger.

Data analogous to that of Figs. 5.17 and 5.18 were collected for the anterior and posterior swimbladders of 11 goldfish. The results are summarized in Table 5.1. Table 5.1 shows that for both the anterior and posterior swimbladders the body surface responses were always in-phase with the response of the bladder wall. Although the body surface amplitude was never observed to be greater than the bladder wall amplitude, the data are otherwise inconclusive and the amplitude at the body surface may be equal to or lower than that measured at the bladder itself.

<table>
<thead>
<tr>
<th>Bladder</th>
<th>Amplitude</th>
<th>Phase</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Equal</td>
<td>Lower</td>
</tr>
<tr>
<td>anterior</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>posterior</td>
<td>7</td>
<td>4</td>
</tr>
</tbody>
</table>

TABLE 5.1 Summary of the results for the swimbladder wall/body surface comparison. The values indicate the number of responses from the body surface which were in-phase/out-of-phase, or of equal/lower amplitude than that of the bladder wall. Based on a total goldfish of 11 goldfish.
FIGURE 5.18 Normalized velocity of the posterior swimbladder and body wall for goldfish GF000. Top – magnitude; bottom – phase.
3. Multiple resonances

The occurrence of multiple resonances in the swimbladder response was briefly mentioned in Section A and demonstrated in Fig. 5.4. One of the data sets in Fig. 5.17 also shows the double resonance; it is plotted independently in Fig. 5.19. In addition, another example of multiple resonances is illustrated in Fig. 5.20, which shows the normalized velocity from the anterior and posterior swimbladders of goldfish GF026 (14.3 g; 79 mm). For this particular test, the response of each bladder displays a double resonance. Figs. 5.4, 5.19, and 5.20 show multiple peaks in the amplitude corresponding to each individual resonance frequency. In addition, the phase angle often shows a slight "hump" at the location of each additional resonance.

Multiple resonances were not observed in every individual test. In fish where multiple resonances were observed, previous and/or subsequent tests often showed no multiple resonances, for example, as shown in Fig. 5.17. In attempt to quantify the occurrence of multiple resonances, the swimbladder data was classified according to whether multiple resonances were observed in the anterior response, the posterior response, both, or neither. This classification was performed on every individual test, and on the response measured from every individual fish. Data from the waveguide were excluded since the goldfish resonances were above the highest waveguide frequency. Table 5.2 summarizes the results of this classification.

<table>
<thead>
<tr>
<th></th>
<th>Anterior only</th>
<th>Posterior only</th>
<th>Both</th>
<th>Neither</th>
</tr>
</thead>
<tbody>
<tr>
<td>all tests</td>
<td>8</td>
<td>2</td>
<td>15</td>
<td>9</td>
</tr>
<tr>
<td>individual fish</td>
<td>8</td>
<td>0</td>
<td>9</td>
<td>2</td>
</tr>
</tbody>
</table>

TABLE 5.2 Summary of multiple resonance data.
FIGURE 5.19 Normalized velocity measured from the anterior swimbladder of GF000 showing multiple resonances.
FIGURE 5.20 Normalized velocity measured from the anterior and posterior swimbladders of goldfish GF026 showing multiple resonances. ASB – anterior swimbladder; PSB – posterior swimbladder.
The first row of Table 5.2 presents a numerical breakdown of all the relevant tests which showed multiple resonances in the anterior swimbladder, posterior swimbladder, both bladders, or neither bladder. The second row shows the number of individual fish which exhibited multiple resonances in the response of their swimbladder during any test conducted on them. The data of Table 5.2 imply that, for any given test, multiple resonances were relatively common. Almost every goldfish tested showed a multiple resonance at one time or another; in fact, the only two goldfish that did not show multiple resonances were only tested once, so it is uncertain if more tests would have yielded different results. Also, it seems that in most fish multiple resonances in the posterior would not occur without also being present in the anterior response. Because of the relatively small sample size (19 fish), the data of Table 5.2 are somewhat ambiguous; however, they do imply that the occurrence of multiple resonances is common.

Zhou (1992) attributed the absence or presence of multiple resonances to the spacing between the individual bladders: only at intermediate spacings would the bladders be coupled, yet still respond individually as opposed to a single bladder. In this study, the spacing between the bladders was estimated from radiographs to lie between 0.5–0.75 mm. This relatively small range of values for the spacing between bladders may explain why the occurrence of multiple resonances was common.

4. Comparison of anterior and posterior response

Table 5.3 summarizes the differences observed between the response of the anterior and posterior swimbladders in the 22 goldfish tested. The data labeled as N/A are from fish where only low-frequency data were available, or the occurrence of multiple resonances made comparison impossible. In the majority of the fish, the amplitude of the anterior swimbladder response was equal to or greater than that of the posterior. This observation agrees with Alexander (1966) and Lewis (1994). The resonance frequencies of the bladders
were often roughly equal; when the resonances were not the same, the posterior resonance frequency was typically higher than that of the anterior. Finally, the posterior swimbladder phase angle led the anterior phase angle in 13 of the 18 fish which produced valid data. The differences in the behavior of the two bladders are likely due to the differences in their structure. The anterior swimbladder contains two layers, with the outer one being viscoelastic (Alexander, 1961b). The Weberian ossicles may also influence the response of the anterior chamber. A higher stiffness, perhaps due to more surrounding tissue, could also explain the posterior swimbladder's typically lower amplitude, higher resonance, and leading phase angle.

<table>
<thead>
<tr>
<th></th>
<th>Higher amplitude</th>
<th>Higher resonance frequency</th>
<th>Leading phase angle</th>
</tr>
</thead>
<tbody>
<tr>
<td>anterior</td>
<td>11</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>posterior</td>
<td>3</td>
<td>6</td>
<td>14</td>
</tr>
<tr>
<td>equal</td>
<td>5</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>N/A</td>
<td>3</td>
<td>6</td>
<td>4</td>
</tr>
</tbody>
</table>

**TABLE 5.3 Comparison of anterior and posterior swimbladder responses.**

5. **Swimbladder resonance frequency and damping**

Although a smaller fish will generally have a higher resonance frequency than a larger fish (Cox, 1987), the masses and standard body lengths of fish used in this study—from 14 to 77 g and 79–138 mm, respectively—do not provide a large enough variation to indicate a clear relationship between fish size and swimbladder resonance frequency. For
this reason, the swimbladder resonance frequencies and quality factors at resonance ($Q$) are presented without any discussion regarding a relationship between these parameters and the fish size.

The resonance frequency and quality factor for each fish were estimated from the measured swimbladder responses. In fish where multiple resonances were observed, the peak having the lowest frequency (which was usually the peak with the largest amplitude) was used. In 2 tests, small peaks were observed before the largest amplitude peak (e.g., see Fig. 5.20); these were neglected. Figures 5.21(a) and 5.21(b) display the estimated resonance frequency vs. goldfish mass for the anterior and posterior bladders, respectively. The error bars indicate the standard deviations for fish that were tested more than once. For the anterior swimbladder, the resonance frequencies lie in the range 500–1250 Hz, with an average of 900 Hz and a standard deviation of 160 Hz. The posterior swimbladder resonance frequencies varied from roughly 500 to 1500 Hz, with an average of 1015 Hz and standard deviation of 205 Hz. These values compare favorably with those presented by Lewis (1991).

Figure 5.22 shows variation of the quality factor with goldfish mass for both the anterior and posterior swimbladders. For the anterior swimbladder, most of the values for $Q$ lie in the range 1–5, with a single fish having a $Q$ of 13. Excluding the highest and lowest values, the mean is 3.01 with a standard deviation of 1.18. For the posterior bladder, the range is 0.1–5, with a single high value at 10.5. Again excluding the highest and lowest values, the mean is 2.71 with a standard deviation of 0.92. These values compare favorably with values of 3.0, reported by Cox (1987), and 3.8–5.1 reported by Batzler and Pickwell (1970). Overall, the quality factor for the goldfish swimbladder is much smaller than that of the spherical air bubble; both bladders appear to have roughly the same damping.
FIGURE 5.21 Resonance frequency vs. goldfish mass for the (a) anterior swimbladder and (b) posterior swimbladder.

FIGURE 5.22 Quality factor vs. goldfish mass for the (a) anterior swimbladder and (b) posterior swimbladder.
C. Tripus and Weberian ossicles

Figures 5.23 and 5.24 present some representative data measured from the swimbladders and Weberian ossicles for two goldfish. Figure 5.23 shows the normalized velocity measured from the anterior swimbladder and Weberian ossicles in goldfish GF012 (38.8 g; 106.2 mm). The response of the tripus is shown in Fig. 5.23, as well as that of another Weberian ossicle, either the intercalarium or scaphium (it was impossible to distinguish between the two because of their size and relative positions). At low frequencies, the ossicle amplitudes generally match that of the anterior swimbladder, however, the phase shows quite a bit of scatter. At high frequencies, the tripus and Weberian ossicle are in-phase with the anterior swimbladder and show amplitude peaks near the swimbladder resonance. The amplitude and phase responses also indicate a second resonance in the swimbladder near 2000 Hz which is also present in the tripus and ossicle responses. The low and high-frequency phase data for the Weberian ossicle show roughly a 90° phase difference in the range of frequencies where the data overlap. This could mean that the measurements were taken at different spatial locations on the same ossicle, or that two separate ossicles were examined. In the case of the former, assuming the ossicle moves as a rigid body, the phase discrepancy indicates that the ossicle is undergoing some rotation, so that different regions on the ossicle have different phases.

Figure 5.24 shows the normalized velocity measured from the swimbladders and tripus of goldfish GF022 (32.4 g; 100.7 mm). Again, the tripus amplitude contains a peak which corresponds to the anterior swimbladder resonance. The tripus phase angle closely follows the anterior swimbladder phase, and both lag that of the posterior swimbladder.
FIGURE 5.23 Normalized velocity measured from the anterior swimbladder and Weberian ossicles of goldfish GF012. ASB – anterior swimbladder, TR – tripus, WB – unknown Weberian ossicle.
FIGURE 5.24 Normalized velocity measured from the anterior swimbladder and Weberian ossicles of goldfish GF022. ASB – anterior swimbladder, PSB – posterior swimbladder, TR – tripus.
Table 5.4 compares the response of the tripus with that of the anterior swimbladder. In almost every case the tripus response was of a lower amplitude, but showed an amplitude peak corresponding to the anterior swimbladder resonance. The tripus phase angle also usually matched the phase angle of the anterior swimbladder. These observations again indicate coupling between the anterior swimbladder and the tripus. In addition, in the few fish where the response of other Weberian ossicles were found, the tripus and other ossicles were found to have similar amplitudes and to be moving in-phase with one another. The Weberian ossicle data seem to indicate that the resonances of the individual ossicles are well above the frequencies tested. The Weberian ossicle apparatus therefore acts essentially as a spring for the frequencies considered in this study. The anterior swimbladder motion is transmitted to the tripus, although the amplitude is reduced. This is in contrast to the suggestion of Alexander (1966) that the motion of the swimbladder is amplified by the ossicle arrangement.

<table>
<thead>
<tr>
<th></th>
<th>Higher amplitude</th>
<th>Higher resonance frequency</th>
<th>Leading phase angle</th>
</tr>
</thead>
<tbody>
<tr>
<td>anterior swimbladder</td>
<td>14</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>tripus</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>equal</td>
<td>1</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td>N/A</td>
<td>7</td>
<td>7</td>
<td>8</td>
</tr>
</tbody>
</table>

TABLE 5.4 Comparison of anterior swimbladder and tripus responses.
D. Otoliths

Figure 5.25 illustrates the measured normalized velocity of the anterior swimbladder, lagenar otolith and saccular otolith of goldfish GF025 (20.7 g, 88.0 mm). The response of the saccular otolith mimics the anterior swimbladder response, only with a smaller amplitude. The phase of the saccular otolith motion shows a consistent lag with respect to that of the anterior swimbladder above 500 Hz. The amplitude of the lagenar otolith response is considerably smaller than that of the saccular otolith and essentially indicates no measurable motion. The lagenar otolith phase is similar to the saccular otolith phase, only with more scatter since the lagenar otolith amplitude is near the phase measurement threshold.

Figure 5.26 shows the measured normalized velocities of the tripus, lagenar and saccular otoliths of goldfish GF756. The tripus and saccular otolith have similar responses; the lagenar otolith is not moving with any measurable amplitude in the medial-lateral direction. The phase of the lagenar otolith response is not shown because the amplitude is close to the measurement threshold. Similarly to that of the Weberian ossicle in Fig. 5.23, the phase data for the saccular otolith show a 90–180° discontinuity between the low-frequency measurements in the waveguide and the high-frequency measurements in the pool. This is most likely the result of the measurements being taken at different locations along the saccular otolith, or of the fish being positioned with a slightly different attitude from one test to the next. In the latter case, if the fish is oriented with different degrees of yaw or roll the measurement system may be measuring a motion component other than the medial-lateral component. The former case implies that a relative phase angle exists between different locations along the saccular otolith. If the otolith moves as a rigid body, which seems likely, this relative phase angle could only occur if the otolith is experiencing rotation about the vertical.
Figure 5.27 shows the measured normalized velocities of the tripus, lagenar and saccular otoliths of goldfish GF026 (14.3 g; 79.0 mm). Again the tripus and saccular otoliths have similar responses with amplitudes above that of the lagenar otolith, which in this case does experience some motion. However, in this fish the lagenar otolith phase angle is dramatically different for the two data sets shown. In fact, the two sets show roughly a 180° phase shift throughout most of the frequency range. In this case the data were taken the same day with the same orientation of the fish, so the phase difference must be due to the difference in location of the measurement. As discussed above, the phase difference implies that the otolith is undergoing complex motion, including rotation.

The phase of the saccular otolith motion shown in Fig. 5.27 also possesses some unique features. Most of the observed phase angles of the saccular otolith matched those of the tripus; however, in Fig. 5.27 the saccular phase leads that of the tripus at low frequencies and lags that of the tripus by 360° at high frequencies. This type of response of the saccular otolith occurred in three of the fish tested and again, seems to indicate that the saccular otolith moves in a complicated fashion.

Figure 5.28 shows the normalized sagitta displacement for three goldfish. All three responses show a decline in amplitude at low frequencies, followed by a local minimum value. Beyond the minimum, the amplitude is essentially flat, until it begins to decline at high frequencies, above the swimbladder resonance. Within the flat region, the normalized amplitudes lie roughly between 1–10 nm/Pa.
FIGURE 5.26 Response measured from the tripus, saccular, and lagenar otoliths of GF756. TR – tripus, SA – saccular otolith, LA – lagenar otolith.
FIGURE 5.27 Normalized velocity measured from the tripus, saccular, and lagenar otoliths of goldfish GP026. TR - tripus, SA - saccular otolith, LA - lagenar otolith.
FIGURE 5.28 Normalized displacements for the saccular otoliths from goldfish GF026, GF016, and GF025.
It should be noted that the experimental measurements are for the medial-lateral direction only. The relationship between the transverse canals and saccular chambers implies a dorso-ventral component of motion input to the sagitta from the Weberian apparatus; in fact, the apical ciliary bundles of the saccular hair cells are roughly oriented to be sheared by motion in the dorso-ventral direction. Significant motions may therefore exist in directions other than the medial-lateral direction.

E. Summary

The data from the anterior and posterior swimbladders showed clear amplitude peaks corresponding to their resonance frequencies. Often, the response of a bladder contained multiple peaks which are believed to be related to the individual resonances of the two swimbladder chambers. The occurrence of multiple resonances in the swimbladders appears relatively common, having been observed in every fish tested more than once.

Significant reflection of the ultrasound was observed at the body wall of the fish. The response of the body surface was in-phase with the swimbladder, but often had a lower amplitude.

The response of the tripus was found to normally be in-phase with that of the anterior swimbladder, but have an amplitude lower than that of the bladder. The swimbladder resonance controlled the tripus response, which seems to indicate that the Weberian apparatus acts as a spring at low frequencies and transmits the swimbladder motion to the saccule.

The saccular otolith generally showed a response similar to that of the tripus, although at high frequencies the sagitta phase sometimes lagged the tripus phase by as much as 360°. In most cases the saccular otolith phase angle followed that of the anterior swimbladder and tripus. The amplitude of the saccular otolith response was similar to that of the tripus. The lagenar otolith was not moving with any measurable amplitude in the
majority of the tests; in those cases where it was moving, the amplitude was below that of the saccular otolith and the tripus. The utricular otolith showed no measurable motion in any of the tests. The normalized displacement amplitude of the sagitta in the medial-lateral direction was on the order of 1–10 nm/Pa.
CHAPTER 6
PERIPHERAL AUDITORY SYSTEM MODEL DEVELOPMENT

This chapter presents the derivation of the model for the goldfish peripheral auditory system and an explanation of how the various material properties and structure dimensions were obtained. The model results are presented in Chapter 7.

A. Model overview

The model for the peripheral auditory system consists of 3 major subsystems for the swimbladder, the Weberian apparatus, and the saccule. Subsystem models for the direct and indirect acoustic fields are also required. Figure 6.1 is a simplified block diagram which illustrates the relationships among the subsystems. All of the subsystem models are linear. Only the steady-state frequency response is considered; the models are not designed to accommodate other inputs, such as random or transient. This chapter details the development of the models for the major subsystems: the swimbladder, Weberian apparatus, and the saccule. The direct field and indirect field models are described in Chapter 7, Section A.

The total ciliary bundle shear consists of individual contributions from the three pathways discussed in Chapter 1: the direct path, the indirect path, and the Weberian path. The main goal of the model is to estimate the total ciliary bundle shear and the ciliary bundle
shear components caused by each of these contributions. The response of each swimbladder, the coupling between the anterior swimbladder and the Weberian apparatus, and the effects of various material and geometric properties are also of interest.

FIGURE 6.1 Simplified block diagram of the model subsystem relationships.

1. Effect of acoustic particle velocity

Assuming a linear system, where superposition is valid, the velocity $V(\omega)$ of any structure within the fish may be expressed as the sum of two terms, one due to the acoustic pressure, the other due to the acoustic particle velocity:

$$V(\omega) = H_p(\omega) P_a(\omega) + H_s(\omega) V_a(\omega),$$

(6.1)

where $H_p(\omega)$ is the transfer function between the structure velocity and the acoustic pressure, $H_s(\omega)$ is the transfer function between the structure velocity and the acoustic
particle velocity, $P_a(\omega)$ is the acoustic pressure, and $V_a(\omega)$ is the acoustic particle velocity. Since the acoustic impedance of a fish's body—$1.6 \times 10^6$ rayl (Ishimaru, 1978)—is nearly the same as that of the surrounding water ($\sim 1.5 \times 10^6$ rayl) the entire fish is assumed to move with the same amplitude and phase as the surrounding water; thus $H_f(\omega) = 1 \angle 0^\circ$. This argument is strengthened by the experimental data which show that the tissues surrounding the swimbladder move in-phase with the bladder wall. If $H_f(\omega) = 1 \angle 0^\circ$, then Eq. (6.1) may be written as

$$V_{\text{TOTAL}}(\omega) = V_{\text{REL}}(\omega) + V_a(\omega),$$

which states that the total velocity of a structure is equal to the velocity of the structure relative to the velocity of the fish's body, plus the velocity of the fish itself, which is assumed to equal the acoustic particle velocity $V_a(\omega)$.

In deriving the response of the swimbladder and Weberian apparatus, the main interest lies in finding the relative velocity between each element and the fish's body. This is because the coupling between the swimbladder and the Weberian apparatus relies on the change in swimbladder volume; translation of the fish will move the swimbladder, Weberian ossicles, and canal fluids together. Therefore, the acoustic pressure is considered the primary stimulus for the swimbladder and the goal of the model is to convert this pressure into radial motion of the bladder wall. The Weberian apparatus model uses the swimbladder motion as an input, so it also relies on the acoustic pressure as its primary input. The translation of the entire fish must be considered, however, when comparing the model predictions to the experimental data. It should be noted that it is the acoustic particle
velocity in the measurement direction that must be used in Eq. (6.2). In contrast to the swimbladder and Weberian apparatus models, the saccule model uses the absolute velocities, and so always requires the motion of the fish’s body as an input.

2. System model inputs and material properties

In addition to the acoustic pressure and particle velocity, the primary independent variables for the subsystem models are the goldfish mass and the bladder ratio, which is defined as the ratio of the posterior swimbladder radius to the anterior swimbladder radius. The mass was measured directly before each test; the bladder ratio was calculated using the swimbladder dimensions measured from in vivo radiographs. Relationships between these parameters are discussed and illustrated in Chapter 5, section B.1.

Most body dimensions and size-dependent parameters, with the exception of the posterior swimbladder radius, are assumed to be proportional to the length of the fish. The mean values for the mass and length are 34.4 g and 99 mm; these are considered as the baseline for the size of the fish. Baseline values for the anterior and posterior radii are 6 mm and 5 mm, respectively. Since no clear relationship exists between the bladder ratio and the mass, the bladder ratio is kept as an independent variable. The baseline value for the bladder ratio is 0.83 (standard deviation 0.22).

Before beginning the discussion of the individual subsystem models, a few words are in order concerning the geometric and material properties required for the model. Estimating these properties was one of the more difficult problems encountered in creating the model. For this reason, most parameters are specified as having a minimum, maximum, and baseline value. The minimum and maximum values allow one to estimate which parameter uncertainties are likely to have the most dramatic effect on the responses
predicted by the model. Some parameters, however, are either known to a high degree of accuracy, or are regarded as secondary for a parameter effect study, and are therefore only specified using the baseline value.

B. Model for the goldfish swimbladder

In modeling the two-chambered swimbladder of the goldfish, the first step is to develop a suitable 1-DOF model for each of the individual chambers, then couple the two 1-DOF models into a 2-DOF system. The goal in developing the 1-DOF model is to find the relationship between the acoustic pressure incident on the swimbladder and the resulting radial motion of the bladder wall. This is in contrast to the swimbladder models reviewed in Chapter 1, which derive the scattered pressure as a function of the incident pressure. For this reason, a new derivation is undertaken, based on the work of Ye and Farmer (1994).

1. Single DOF radial motion

The goldfish swimbladder consists of two air-filled bladders of roughly prolate spheroidal shape. Strasberg (1953) and Weston (1967) have shown that a non-spherical air bubble has an increased resonance frequency compared to a spherical bubble of the same volume. The effect is small, however, for prolate or oblate spheroids of nearly spherical shape. For example, an oblate or prolate spheroid with a major axis to minor axis ratio of 2 exhibits an increase in resonance of only about 2%. Measurements of goldfish bladder dimensions from radiographs revealed an average major/minor axis ratio of 1.44 (standard deviation 0.12) for the anterior swimbladder and 1.66 (standard deviation 0.33) for the posterior; therefore, the increase in resonance frequency for the goldfish should be negligible and the bladders may be modeled as spherical in shape. Each individual
swimbladder chamber is therefore modeled as a spherical elastic shell surrounding an air cavity. The shell has Lamé constants \( \lambda \) and \( \mu \), where \( \mu \) is defined as

\[
\mu = \mu + j \eta .
\] (6.3)

The parameters \( \mu \) and \( \eta \) are referred to as the shear modulus and the loss factor, respectively. Figure 6.2 illustrates the shell geometry.

The inner and outer radii may be expressed as functions of time using

\[
r_i(t) = R_i - \Delta R_i(t)
\] (6.4)

and

\[
r_o(t) = R_o - \Delta R_o(t) ,
\] (6.5)
respectively, where the mean inner and outer radii are $R_i$ and $R_o$, respectively, and the displacements at the inner and outer boundaries are $\Delta R_i(t)$ and $\Delta R_o(t)$, respectively. It should be noted that the displacements are defined positive for radially inward motion. The inner gas pressure $p_i(t)$ is assumed to be uniform throughout the air cavity and to consist of a mean value $P_i$ plus a perturbation pressure $\Delta P_i(t)$:

$$p_i(t) = P_i + \Delta P_i(t).$$

(6.6)

Similarly, the pressure outside the shell, $p_o(t)$, is

$$p_o(t) = P_o + \Delta P_o(t).$$

(6.7)

The equation of motion for the shell displacement $w(r,t)$ is

$$\left(\lambda_r + \mu \right) \nabla \left[ \nabla \cdot w(r,t) \right] + \mu \nabla^2 w(r,t) = \rho_s \frac{\partial^2 w(r,t)}{\partial t^2},$$

(6.8)

where $\rho_s$ is the shell density (Hunter, 1983). If the acoustic wavelength is large compared to the shell dimensions, the inside and outside pressures may be related using the static behavior of the shell (Ye and Farmer, 1994). Approximating the general case using the static behavior, the radial stress $\sigma_r(r,t)$ and radial displacement $w(t)$ in the shell are

$$\sigma_r(r,t) = (3\lambda_r + 2\mu)A - 4\mu \frac{B}{r^3}$$

(6.9)

and
respectively, where $A$ and $B$ are constants. Using the boundary conditions

\begin{align*}
\sigma_r(R_i,t) &= -p_i(t), \\
\sigma_r(R_o,t) &= -p_o(t), \\
w(R_i,t) &= -\Delta R_i(t), \\
w(R_o,t) &= -\Delta R_o(t),
\end{align*}

and

\begin{align*}
w(R_o,t) &= -\Delta R_o(t),
\end{align*}

the relationships between the inner and outer perturbation pressures and inner and outer displacements are found to be

\begin{align*}
\Delta P_o(t) &= C \Delta P_i(t) + 4\mu D \frac{\Delta R_i(t)}{R_i}, \\
\frac{\Delta R_o(t)}{R_o} &= -\frac{e^3 - 1}{3\lambda_r + 6\mu} \Delta P_o(t) + E \frac{\Delta R_i(t)}{R_i},
\end{align*}

where

\begin{align*}
C = & \frac{3\lambda_r + 2\mu}{3\lambda_r + 6\mu} + \frac{4\mu}{3\lambda_r + 6\mu} e^3.
\end{align*}
and \( e = R/R_0 \). The results of Eqs. (6.15)-(6.19) are identical to those of Ye and Farmer (1994), using the current the sign convention for the radial displacements.

If the compression of the gas within the swimbladder is assumed to be an adiabatic process, then the gas pressure \( P_g \) and volume \( v_g \) are related by the equation

\[
P_g v_g^\gamma = \text{constant}.
\]  

Taking the derivative of Eq. (6.20) yields

\[
dP_g = \frac{\gamma P_g}{v_g} dv_g.
\]  

The goldfish swimbladder has an excess internal pressure, so the initial gas pressure \( P_g = P_0 + P_{ex} \), where \( P_0 \) is the hydrostatic pressure and \( P_{ex} \) is the excess swimbladder pressure. The change in gas pressure from the initial state is \( dP_g = \Delta P_g(t) \). The initial volume for a spherical bladder is \( \frac{4}{3} \pi R_i^3 \). For small radial displacements, the change in volume is the surface area multiplied by the radial displacement, \( dv_g = -4\pi R_i^2 \Delta R_i \). Equation (6.21) may then be written as

\[
\Delta P_i(t) = 3\gamma (P_0 + P_{ex}) \frac{\Delta R_i(t)}{R_i}.
\]
Equations (6.15), (6.16), and (6.22) may be combined to express $\Delta R_s(t)$ as a function of the outer perturbation pressure $\Delta P_s(t)$, which is equal to the sum of the incident and scattered acoustic pressures:

\[
\Delta P_s(R_s, t) = P_i(R_s, t) + P_s(R_s, t),
\]

where $P_i(R_s, t)$ and $P_s(R_s, t)$ are the incident and scattered pressures at the outer shell surface, respectively.

Since the incident pressure has the form of a harmonic time signal, at this point it is convenient to switch to the frequency domain. The scattered pressure is assumed to be in the form of spherical waves, so

\[
P_s(r, \omega) = \frac{P_s(\omega)}{r} e^{-j\omega r}.
\]

The acoustic particle displacement associated with the scattered wave is

\[
\xi_s(r, \omega) = -\frac{1 + jkr}{\rho_0 \omega^2 r} P_s(r, \omega).
\]

At the outer shell surface the boundary condition

\[
\xi_s(R_s, \omega) = -\Delta R_s(\omega)
\]

holds, thus the scattered pressure at $r = R_s$ is
If the shell material is assumed to have properties similar to rubber, then \( \lambda_\tau >> \mu \) (Read and Dean, 1978). Also, for low frequencies, \((kR_0)^2 << 1\). Using these assumptions and making the necessary substitutions into Eq. (6.23), the incident acoustic pressure \( P_i(R_o, \omega) \) may be related to \( \Delta R_i(\omega) \) according to

\[
P_i(R_o, \omega) = \left[ \frac{\rho_e \omega^2 R_o^2 - j\rho_e \omega^2 kR_o^2}{1 + (kR_o)^2} \right] \frac{\Delta R_o(\omega)}{R_o}.
\]  

(6.27)

The natural frequency of this system is found by setting the real part of the braced term in Eq. (6.28) equal to zero and solving for \( \omega \). The result is

\[
\omega_n = \left[ \frac{3\gamma (P_e + P_{ex}) + 4\mu (1 - e^3)}{\rho_e R_i e^3} \right]^{1/2}. 
\]

(6.29)

By comparing Eq. (6.28) to Eq. (1.2), the damping factor is found to be the imaginary part of the term in braces in Eq. (6.28) divided by \( \rho_e R_i e^2 \), or

\[
\delta(\omega) = \frac{4\eta (1 - e^3)}{\rho_e R_i e^2 + kR_o}.
\]

(6.30)
The first term in Eq. (6.30) represents the tissue damping, while the second is the radiation damping; thermal damping has been neglected. Figure 6.3 illustrates the relative contribution of the radiation and tissue damping as functions of frequency. In this case the inner and outer bladder radii are 5 mm and 10 mm, respectively, and the shear modulus and loss factor are equal to $5 \times 10^5$ N/m$^2$ and $1.25 \times 10^5$ N/m$^2$, respectively, which are the mean values specified by Lebedeva (1965). The tissue damping clearly dominates until about 2 kHz; this is above the resonance of the smallest goldfish used in this study and near the upper frequency range of interest for the model. The radiation damping term is therefore neglected and the total damping approximated using only the tissue damping term.

![Graph of tissue and radiation damping factors](image)

FIGURE 6.3 Relative magnitudes of the tissue damping and radiation damping factors from Eq. (6.32), for $\mu = 5 \times 10^5$ N/m$^2$; $\eta = 1.25 \times 10^5$ N/m$^2$; $R_i = 5$ mm; $R_o = 10$ mm.

The system described by Eq. (6.28) is analogous to the mechanical system shown in Fig. 6.4. The equation describing the behavior of this system is

$$SP_e(\omega) = \left[ k_m - m \omega^2 + jb \omega \right] \Delta R(\omega)$$

(6.31)
where $S$ is the surface area, $m$ is the mass, $b$ is the damping coefficient, and $k_m$ is the stiffness. Putting Eq. (6.28) into the form of Eq. (6.31) requires that

$$m = S p R e,$$

$$k_m = S \frac{3\gamma (P_0 + P_x) + 4\mu (1 - \epsilon^3)}{R_i},$$

and

$$b = S \frac{4\eta (1 - \epsilon^3)}{R_i \omega}.$$

FIGURE 6.4 Mechanical system analogous to the system described by Eq. (6.31).

Equations (6.32)–(6.34) give values of the equivalent mass, stiffness, and damping, respectively, for the 1-DOF model of the swimbladder. As in the model of McCartney and Stubbs (1971), both the excess pressure and surrounding tissues tend to increase the stiffness and hence the resonance frequency.
2. Two DOF radial motion

The model for the two-chambered goldfish swimbladder consists of two elastic shells whose centers are separated by a distance $d_{12}$. Figure 6.5 shows the geometry of the system. The shell representing the anterior swimbladder has an inner radius $R_1$ and an outer radius $R_{a,1}$. The shell representing the posterior swimbladder has an inner mean radius $R_2$ and an outer mean radius $R_{a,2}$. The radial displacements of the inner shell surfaces are $\Delta R_1$ and $\Delta R_2$, respectively, which are defined as positive for radially inward motion.

![Diagram showing the geometry of the 2-DOF model for the goldfish swimbladder.](image)

**FIGURE 6.5** Geometry of the 2-DOF model for the goldfish swimbladder.

Each swimbladder chamber may be modeled as a mechanical system as in Fig. 6.4. A mechanical representation of the complete system is shown in Fig. 6.6 and consists of two 1-DOF systems coupled together through a spring and a damper. These coupling parameters represent the effect of one swimbladder on the response of the other. The effect of the posterior swimbladder on the anterior is modeled with the stiffness $k_{12}$ and damping $b_{12}$. The effect of the anterior on the posterior is modeled with the stiffness $k_{21}$ and damping $b_{21}$. It should be noted that $k_{12} \neq k_{21}$ and $b_{12} \neq b_{21}$. This treatment is analogous to that of Zhou (1992).
FIGURE 6.6 Mechanical system model for the coupled swimbladders.

The mass, stiffness, and damping of each swimbladder may be found by analogy with Eqs. (6.32)–(6.34). For the anterior swimbladder,

\[ m_i = S_i \rho R_i e_i, \]  

\[ k_i = S_i \frac{3\gamma (P_0 + P_{z_i}) + 4 \mu_i (1 - e_i^2)}{R_i}, \]  

and

\[ b_i = S_i \frac{4\eta_i (1 - e_i^2)}{R_i \omega}. \]
where $\mu_1$, $\eta_1$, and $P_{x1}$ are the shear modulus, loss factor, and excess pressure for the anterior swimbladder, respectively; $S_1$ is the anterior swimbladder surface area ($S_1 = 4\pi R_1^2$), and $e_1 = R_1/R_{o1}$. Similarly, for the posterior swimbladder,

$$ m_2 = S_2 \rho_2 R_2 e_2, \quad (6.38) $$

$$ k_2 = S_2 \frac{3\gamma (P_0 + P_{x2}) + 4\mu_2 (1 - e_2^2)}{R_2}, \quad (6.39) $$

and

$$ b_2 = S_2 \frac{4\eta_2 (1 - e_2^3)}{R_2 \omega}, \quad (6.40) $$

where $\mu_2$, $\eta_2$, and $P_{x2}$ are the shear modulus, loss factor, and excess pressure for the posterior swimbladder, respectively; $S_2$ is the posterior swimbladder surface area ($S_2 = 4\pi R_2^2$), and $e_2 = R_2/R_{o2}$. The choice of a unique shear modulus and loss factor for each bladder is based on observations that the posterior swimbladder is less extensible than the anterior (Evans, 1925; Alexander, 1959c; Alexander, 1966; Lewis, 1994).

To estimate the coupling parameters, the equations describing the response of the system in Fig. 6.6 are compared to equations presented by Zabolotskaya (1984) describing the motion of two closely-spaced gas bubbles. From the system of Fig. 6.6,

$$ \Delta \tilde{R}_1(t) + \frac{b_1 + b_{12}}{m_1} \Delta \tilde{R}_1(t) + \frac{k_1 + k_{12}}{m_1} \Delta R_1(t) - \frac{k_{12}}{m_1} \Delta R_2(t) - \frac{b_{12}}{m_1} \Delta \tilde{R}_2(t) = \frac{S_1}{m_1} P_0(t) \quad (6.41) $$

and
where the overhead dots signify time derivatives.

Zabolotskaya (1984) derived the response of two closely-spaced underwater air bubbles as functions of the incident acoustic pressure. His results may be written as

\[
\Delta \bar{R}_2(t) + \frac{b_1 + b_{12}}{m_2} \Delta \bar{R}_2(t) + \frac{k_2 + k_{12}}{m_2} \Delta R_2(t) - \frac{k_{12}}{m_2} \Delta R_1(t) - \frac{b_{12}}{m_2} \Delta \bar{R}_1(t) = \frac{S}{m_2} P_o(t),
\]

where \( \bar{R}_1 \) and \( \bar{R}_2 \) are the mean bubble radii; \( m_1, k_1, b_1, \) and \( m_2, k_2, b_2 \) are the mass, stiffness, and damping of bubbles 1 and 2, respectively; \( \Delta R_1 \) and \( \Delta R_2 \) are the radial displacements of bubbles 1 and 2, respectively, and \( d_{12} \) is the distance between the bubble centers. The parameters of Eqs. (6.43) and (6.44) are analogous to their counterparts of Eqs. (6.41) and (6.42).

Equations (6.43) and (6.44) may be manipulated to eliminate \( \Delta \bar{R}_2 \) from Eq. (6.43) and \( \Delta \bar{R}_1 \) from Eq. (6.44):

\[
\Delta \bar{R}_1(t) + \frac{b_1}{m_1} \Delta \bar{R}_1(t) + \frac{k_1}{m_1} \Delta R_1(t) + \frac{b_1 b_2}{d_{12} m_1} \Delta \bar{R}_2(t) - \frac{R_2 b_2}{d_{12} m_1} \Delta R_2(t) - \frac{R_2 k_2}{d_{12} m_1} \Delta R_2(t) = \frac{1}{\rho_o R_2} P_o(t),
\]

\[
\Delta \bar{R}_2(t) + \frac{b_2}{m_2} \Delta \bar{R}_2(t) + \frac{k_2}{m_2} \Delta R_2(t) + \frac{R_2^2}{d_{12} R_2} \Delta \bar{R}_1(t) = \frac{1}{\rho_o R_1} P_o(t).
\]
\[
\begin{align*}
\Delta \hat{R}_2(t) &+ \frac{b_2}{m_2 F} \Delta \hat{R}_1(t) + \frac{k_2}{m_2 F} \Delta R_1(t) - \frac{R_1 b_1}{d_{12} m_1 F} \Delta \hat{R}_1(t) \\
&- \frac{R_1 k_1}{d_{12} m_2 F} \Delta R_1(t) = \left( \frac{d_{12} - R_1}{d_{12} m_2 F} \right) P_2(t),
\end{align*}
\]  

(6.46)

where

\[
F = 1 - \frac{R_1 R_2}{d_{12}^2}.
\]  

(6.47)

To estimate \( k_{12} \) and \( b_{12} \), the \( \Delta R_3(t) \) and \( \Delta \hat{R}_2(t) \) terms, respectively, in Eq. (6.45) are set equal to the corresponding terms in Eq. (6.41). The results are

\[
\begin{align*}
\Delta R_3(t) &= \frac{d_{12} - R_1}{d_{12} m_2 F} P_2(t), \\
\Delta \hat{R}_2(t) &= \frac{d_{12} - R_1}{d_{12} m_2 F} P_2(t),
\end{align*}
\]  

(6.48)

and

\[
\begin{align*}
b_{12} &= G_{12} b_2, \\
k_{12} &= G_{12} k_2.
\end{align*}
\]  

(6.49)

where

\[
G_{12} = \frac{d_{12} R_2}{d_{12}^2 - R_1 R_2}.
\]  

(6.50)

Using a similar procedure with the \( \Delta R_1(t) \) and \( \Delta \hat{R}_1(t) \) terms in Eqs. (6.46) and (6.42), \( k_{21} \) and \( b_{21} \) are defined as

\[
\begin{align*}
k_{21} &= G_{21} k_1, \\
b_{21} &= G_{21} b_1.
\end{align*}
\]  

(6.51)
Once the individual mechanical elements of Fig. 6.6 have been defined, the complete response of the swimbladder system may be derived. To assist this, the following mechanical impedances are defined, using frequency domain notation:

\[
Z_{shl}(\omega) = j\omega m_1 + b_1 + k_1 / j\omega ,
\]

(6.54)

\[
Z_{shl}(\omega) = j\omega m_2 + b_2 + k_2 / j\omega ,
\]

(6.55)

\[
Z_{12}(\omega) = b_{12} + k_{12} / j\omega ,
\]

(6.56)

and

\[
Z_{21}(\omega) = b_{21} + k_{21} / j\omega .
\]

(6.57)

The system of Fig. 6.6 may then be described by the set of equations

\[
\left[ Z_{shl}(\omega) + Z_{12}(\omega) \right] V_{1}(\omega) - Z_{12}(\omega)V_{2}(\omega) = S_{1} P_{a}(\omega)
\]

(6.58)
and

\[-Z_{11}(\omega)V_1(\omega) + \left[Z_{12}(\omega) + Z_{11}(\omega)\right]V_1(\omega) = S_2 P_0(\omega), \tag{6.59} \]

where $V_1(\omega)$ is the anterior swimbladder radial velocity $[V_1(\omega) = j\omega \Delta R_1(\omega)]$ and $V_2(\omega)$ is the posterior swimbladder radial velocity $[V_2(\omega) = j\omega \Delta R_2(\omega)]$.

Equations (6.58) and (6.59) describe the radial motion of the 2-DOF swimbladder model. The coupling between the model for radial swimbladder motion and the Weberian ossicles is accomplished using a mechanical system model for the tangential motion of the anterior swimbladder tunica externa. It is assumed that the loading effect of the additional systems is negligible.

3. Swimbladder material properties

To actually compute the response of the 2-DOF swimbladder model it is necessary to fix the values of the many material and geometric properties in Eqs. (6.54)-(6.59). Some of these values are commonly known, others may be estimated from the literature, or from direct measurement. Some parameters, however, may only be estimated by fitting the response predicted by the theoretical model to responses determined experimentally.

Table 6.1 lists the some of the material properties and geometric constants used in the swimbladder model. Most parameters can only be estimated and are therefore given as an average value bracketed by the minimum and maximum estimated values. A more detailed explanation follows.

The gas inside the swimbladders is assumed to be air with the ratio of specific heats $\gamma = 1.4$. A shallow depth is also assumed, thus the hydrostatic pressure is approximately equal to atmospheric pressure. The effect of changing depth is not included in this model.
TABLE 6.1 Geometric and material properties for the 2-DOF swimbladder model.

Values for the anterior swimbladder radius and bladder ratio $G_{sr}$ were obtained from in vivo radiographs as described in Chapter 5, Section B. The spacing between the bladders, $h_{12}$, was also estimated from the radiographs to lie between 0.5 and 0.75 mm for the sizes of fish tested, with the average being about 0.60 mm. The spacing $d_{12}$ is

$$d_{12} = R_1 + R_2 + h_{12}. \quad (6.60)$$

Alexander (1959a) measured the excess swimbladder pressure in several Cypriniformes. For the goldfish, he reported values between 1.6 and 3.7 cm Hg with a mean of 2.4 cm Hg. These values were based on the assumption that the excess pressure in each bladder was equal, so identical values are specified for the anterior and posterior bladders.
The only available shear modulus data are from Lebedeva (1965). However, these data are from non-otophysans and do not cover the lower frequencies of interest here. As described in Chapter 1, these data also suffer from a problem with the elastic shell models in that no resonance will be predicted for small fish. For these reasons, it was necessary to estimate $\mu$ and $\eta$ for each bladder by fitting the model responses to the experimentally measured frequency response for each swimbladder.

The most obvious method of fitting the model to the experimental data is to simply fit the equations for the swimbladder velocities to the measured amplitude and phase. This results in a rather difficult curve-fit problem, however, due to the high order of $\omega$ and the fact that the equations are complex in nature. To simplify the curve-fit, the bladders were uncoupled and the response of each considered independently. This is accomplished experimentally by deflating one bladder and measuring the response of the other [see Derenburger (1997) and Derenburger et al. (1997) for the deflation procedure]. The measured response is in terms of the normalized velocity $W(\omega)$, therefore the theoretical motion must be converted to this form for comparison. Also, the translation of the fish's body tissues must be considered.

The equations for the uncoupled swimbladder velocities are

$$V_1(\omega) = \frac{S_1}{Z_{s1}(\omega)} P_s(\omega) - V_d(\omega) \quad (6.61)$$

and

$$V_2(\omega) = \frac{S_2}{Z_{s2}(\omega)} P_s(\omega) - V_d(\omega). \quad (6.62)$$
As discussed in Section A, the incident acoustic particle velocity has been included in the expression for the total motion of the bladders. The negative sign arises from the coordinate system definition (see Chapter 7, section A). The overall motion of each swimbladder consists of the motion due to the change in volume (caused by the pressure) and the motion due to translation of the fish's body (caused by the particle velocity). The particle velocity in Eqs. (6.61) and (6.62) is the component in the direction of motion that was measured, in this case the acoustic particle velocity in the medial-lateral direction.

Although the acoustic field at the test location (described in Chapter 4) consists of spherical waves at low frequencies, plane waves are assumed, in order to further simplify the analysis. For plane waves the pressure and velocity are related by \( P_a(\omega) = \rho_w c_w V_a(\omega) \); therefore, the acoustic energy density \( E(\omega) \) becomes

\[
E(\omega) = \rho_w \left[ \frac{P_a(\omega)}{\rho_w c_w} \right]^2.
\]

(6.63)

The normalized velocity is defined as the target velocity divided by \( \rho_w c_w \sqrt{E(\omega)/\rho_w} \). The theoretical normalized velocities for the uncoupled anterior and posterior swimbladders are thus

\[
W_1(\omega) = \frac{m_1 \omega^2 - k_1 - j\omega(b_1 - S_1 \rho_w c_w)}{\rho_w c_w(k_1 - m_1 \omega^2 + j\omega b_1)}
\]

(6.64)

and

\[
W_2(\omega) = \frac{m_2 \omega^2 - k_2 - j\omega(b_2 - S_2 \rho_w c_w)}{\rho_w c_w(k_2 - m_2 \omega^2 + j\omega b_2)}.
\]

(6.65)
The curve-fits were accomplished using a complex implementation of the least-squares technique (Adby and Dempster, 1974). The stiffness and damping were considered the independent variables; the other parameters in Eqs. (6.64) and (6.65) were held constant during the optimization. Once the stiffness and damping were established, the shear modulus and loss factor were found from Eqs. (6.35)–(6.40). The curve-fit procedure was implemented using in vivo data from the anterior swimbladders of four fish and the posterior swimbladders of six fish. Figures 6.7 and 6.8 illustrate the results of two curve-fits, one for data obtained in the waveguide test setup, the other for data from the pool setup.

**Figure 6.7** Example of least squares curve-fit to uncoupled swimbladder data. The data are from the anterior swimbladder of fish GF016, measured using the waveguide setup.
FIGURE 6.8 Example of least squares curve-fit to uncoupled swimbladder data. The data are from the posterior swimbladder of fish GF004, measured using the pool setup.

Curve-fits were attempted using stiffness and damping terms which were constant, linear, and quadratic functions of $\omega$. The best results were obtained when both the stiffness and damping were constant. This results in a constant shear modulus $\mu$ and a loss factor $\eta$ which is a linear function of frequency. The curve-fits were repeated for a number of different values of the shell ratio $e$. Values of $e$ based on the actual body wall thickness resulted in poor fits or no convergence. The best results were obtained with $e = 0.9$ for both bladders. This results in a relatively thin shell, which therefore must be interpreted as
the thickness of the tissues that contribute additional stiffness to the bladders, not the thickness of the surrounding body. This thin-walled shell approach agrees with the treatment of McCartney and Stubbs (1971).

In general, the curve-fits produced high loss factors (~1500 N/m^2) and low shear moduli values (~10^5 N/m^2) compared to the experimental data for the coupled bladders; this was probably because the waveguide data do not extend to frequencies above the resonance. Because of this, the baseline values for the loss factors were changed to 1000 N/m^2 for both bladders. The baseline shear moduli were estimated to be 1x10^6 N/m^2 for the anterior swimbladder and 5x10^5 N/m^2 for the posterior. The maximum and minimum values were also adjusted from the measured values to reflect the uncertainty in the data. Table 6.2 lists the resulting shear modulus and loss factor estimated for each bladder. It should be stressed that these values are only intended to be an estimate.

<table>
<thead>
<tr>
<th>Property</th>
<th>Minimum</th>
<th>Baseline</th>
<th>Maximum</th>
<th>Reference/Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>e_1</td>
<td>-</td>
<td>0.9</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>e_2</td>
<td>-</td>
<td>0.9</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>μ_1 (N/m^2)</td>
<td>1x10^4</td>
<td>1x10^5</td>
<td>1x10^5</td>
<td>-</td>
</tr>
<tr>
<td>μ_2 (N/m^2)</td>
<td>5x10^4</td>
<td>5x10^5</td>
<td>5x10^5</td>
<td>-</td>
</tr>
<tr>
<td>η_1/ω (N·s/m^2)</td>
<td>5</td>
<td>100</td>
<td>500</td>
<td>-</td>
</tr>
<tr>
<td>η_2/ω (N·s/m^2)</td>
<td>5</td>
<td>100</td>
<td>500</td>
<td>-</td>
</tr>
</tbody>
</table>

TABLE 6.2 Estimated shear moduli and loss factors for the 2-DOF swimbladder model.
C. Model for the Weberian apparatus

The model for the Weberian apparatus consists of lumped parameter mechanical models for the Weberian ossicles and fluid canals which are coupled to the 2-DOF swimbladder model described previously. The coupling is achieved using a phenomenological model for the sliding motion of the tunica externa.

1. Tunica externa model

As suggested by Chranilov (1929), it is assumed that the tunica interna is limited to stretching with swimbladder expansion, but that the tunica externa may not only stretch, but also slide over the tunica interna by virtue of the longitudinal slit it contains. Furthermore, the motion of the largest Weberian ossicle, the tripus, is assumed to follow the motion of the edges of the slit in the tunica externa.

Figure 6.9 shows a simplified representation of a transverse section through the anterior swimbladder. The mean radii of the tunica interna and tunica externa are $R_n$ and $R_m$, respectively. It is assumed that the connective tissues separating the two layers are incompressible and that the radial motion of each layer is equal to $\Delta R_i(t)$. The sliding motion of the tunica externa is denoted by the tangential displacement $\Delta T_i(t)$. The goal of this stage of the model is to relate the radial displacement $\Delta R_i(t)$ to the sliding displacement $\Delta T_i(t)$. It is assumed that the displacement of the posterior portion of the tripus is equal to $\Delta T_i(t)$.

The behavior of the tunica externa subsystem is idealized as follows: Acoustic pressure acts on the anterior swimbladder and causes the tunica interna and tunica externa to expand/contract. Expansion/contraction of the tunica externa then causes the stress $\sigma_m(t)$ [and thus the force $F_m(t)$] to change. The change in stress tends to make the tunica externa
slide over tunica interna in order to balance the forces. The sliding of the tunica externa is opposed by a frictional force $f_\ell(t)$. The effects of the tripus and swimbladder radial motion are ignored.

The equation of motion for the tunica externa is approximated as

$$F_\phi(t) - f_\ell(t) = m_\phi \Delta \Gamma_1(t), \quad (6.66)$$

where $m_\phi$ is the effective mass of the moving part of the tunica externa. If the tunica externa is assumed to be thin and the stress uniform across the thickness, then the relationship between the force $F_\phi(t)$ and the stress $\sigma_\phi(t)$ is

$$F_\phi(t) = 2\pi R_\phi h_\phi \sigma_\phi(t), \quad (6.67)$$

Figure 6.9 Simplified representation of a section through the anterior swimbladder.
where \( h_e \) is the tunica extema thickness. *Post mortem* experimental data for the tunica extema compliance are available for several Cypriniformes (Alexander, 1961b), therefore the tunica extema stress and strain are related through the complex compliance \( J_\mu(t) \):

\[
\sigma_\mu(t) = \frac{\varepsilon_\mu(t)}{J_\mu(t)}.
\] (6.68)

The tunica extema is viscoelastic, therefore the compliance is a function of time.

The strain is estimated as the change in surface area at time \( t \) divided by the initial surface area \( S_\mu(0) \), or

\[
\varepsilon_\mu(t) = \frac{S_\mu(t) - S_\mu(0)}{S_\mu(0)}.
\] (6.69)

The surface areas in Eq. (6.69) are approximated with the help of Fig. 6.10. The longitudinal slit in the tunica extema is approximated as circular in shape with a radius \( T_1 \).

![Diagram of the anterior swimbladder tunica extema showing the slit.](image)

**FIGURE 6.10** Surface of the anterior swimbladder tunica extema showing the slit.
If the slit radius $T_1$ is small relative to $R_\mu$, the tunica externa curvature within the circular slit area may be neglected. Also, since $\Delta R_1(t) \ll 1$ and $\Delta T_1(t) \ll 1$, the terms containing $\Delta R_1^2(t)$ or $\Delta T_1^2(t)$ may be neglected. The result for the strain is then

$$
\varepsilon(t) = \frac{8R_\mu \Delta R_1(t) - 2T_1 \Delta T_1(t)}{4R_\mu^2 - T_1^2}.
$$

(6.70)

The connective tissue within the gap between the tunica interna and tunica externa is modeled as an incompressible fluid with dynamic viscosity $\xi_L$. The tangential motion of the tunica interna is assumed to be zero and a linear velocity profile is assumed in the connective tissue. The frictional force $f_L(t)$ is then approximated as

$$
f_L(t) = \frac{2\pi R_\mu^2 \xi_L}{h_L} \Delta T_1(t),
$$

(6.71)

where $h_L$ is the gap thickness.

Substituting Eqs. (6.67), (6.68), (6.70), and (6.71) into Eq. (6.66) yields

$$
m_\mu \Delta T_1(t) = -\frac{2\pi R_\mu^2 \xi_L}{h_L} \Delta T_1(t) - \frac{4\pi R_\mu h_L T_1}{J_\mu(t)\left(4R_\mu^2 - T_1^2\right)} \left[\Delta T_1(t) - \frac{4R_\mu}{T_1} \Delta R_1(t)\right].
$$

(6.72)

Equation (6.72) may be written more concisely in the frequency domain:

$$
j_\omega m_\mu V_\tau(\omega) = Z_\mu(\omega)\left[2_\tau V_\omega(\omega) - V_\tau(\omega)\right] - Z_\tau V_\tau(\omega),
$$

(6.73)

where $V_\tau(\omega)$ is the tunica externa sliding velocity $V_\tau(\omega) = j_\omega \Delta T_1(\omega)$. 

195
The system of Eq. (6.73) has the mechanical analog shown in Fig. 6.11. The coupling to the anterior swimbladder occurs through the rigid, massless lever shown at the left of Fig. 6.11. The tunica extema mechanical impedance $Z_u(\omega)$ is shown graphically as a Voigt element, however, the actual form of $Z_u(\omega)$ depends on the functional form of $J_u(\omega)$. Although the effects of the tripus and other Weberian ossicles are neglected, the attachment point for the Weberian apparatus subsystem is shown.

\[ Z_u(\omega) = \frac{4\pi R_u h_u T_1}{j\omega J_u(\omega)(4R^2_u - T_1^2)}, \quad (6.74) \]

\[ G_r = \frac{4R_w}{T_1}, \quad (6.75) \]

and

\[ Z_L = \frac{2\pi R^2 e^5 h_L}{h_L}. \quad (6.76) \]

FIGURE 6.11 Mechanical system representation of the tunica extema sliding motion. WB – Weberian apparatus subsystem.
2. *Weberian ossicle model*

Figure 6.12 is a detailed view of the Weberian ossicles in the Cypriniformes. The posterior tip of the tripus is attached to the tunica extema. The individual ligaments are denoted L1–L4.

![Figure 6.12](image)

**FIGURE 6.12** Detailed view of the Weberian ossicles (Modified from Krumholz, 1943).

Figure 6.13 shows the mechanical system model for the Weberian ossicles. The tripus and intercalarium are represented by the rotational inertias $J_r$ and $J_w$. The scaphium and clastrum are assumed to move together as a rigid body with rotational inertia $J_{sc}$. The medial surface of the clastrum forms a part of the wall of the atrium sinus impar, thus the motion of the scaphium/clastrum body is opposed by the pressure within the sinus impar, $P_{si}(\omega)$. The cross-sectional (wetted) area of the clastrum is $A_{cr}$. The ossicles are free to rotate about pinned joints with the vertebrae; these joints are assumed to be frictionless. The ligaments L1 and L2 are represented by pure springs; ligaments L3 and L4 are represented by viscoelastic elements, shown graphically as Voigt elements. The effective lever arms for
the various forces are shown in Fig. 6.13 and denoted as \( \ell_1, \ell_2, \ell_3, \ell_{sc}, \ell_w, \) and \( \ell_{sc} \). The velocities indicated in Fig. 6.13 are defined at the lever-arm locations. The mass of the tunica externa is negligible compared to the inertia of the tripus.

Assuming small angular displacements of the rotational inertias, the equations for the system of Fig. 6.13 are written as

\[
Z_p(\omega)V_3(\omega) - Z_3(\omega)V_e(\omega) = -G_\ell G_T Z_w(\omega)V_1(\omega),
\]

(6.77)

\[
Z_w(\omega)V_e(\omega) - Z_L(\omega)V_3(\omega) - Z_L(\omega)V_e(\omega) = 0,
\]

(6.78)

and

198
where the mechanical impedances $Z_p(\omega)$, $Z_c(\omega)$, and $Z_{sc}(\omega)$ are defined as

\begin{align}
Z_p(\omega) &= j \omega \frac{J}{\ell_3^2} + G_1^2 Z_{L1}(\omega) + G_2^2 Z_{L2}(\omega) + G_3^2 Z_{L3}(\omega) + G_4^2 Z_L + Z_3(\omega), \\
Z_c(\omega) &= j \omega \frac{J}{\ell_1^2} + Z_{L3}(\omega) + Z_{L4}(\omega), \\
Z_{sc}(\omega) &= j \omega \frac{J}{\ell_{sc}^2} + Z_{L4}(\omega);
\end{align}

and

\begin{equation}
V_{sc}(\omega) = -\frac{1}{G_L} V_r(\omega),
\end{equation}

and $G_1 = \ell_1 / \ell_3$, $G_2 = \ell_2 / \ell_3$, and $G_L = \ell_L / \ell_3$. Equations (6.77)-(6.79) comprise the model for the Weberian ossicles.

3. *Fluid canal model*

Figure 6.14 shows the fluid component of the Weberian apparatus. It is modeled as a rigid-walled cylindrical pipe system with three geometrically different sections. The fluid within each section is treated as incompressible. Section 1 represents the sinus impar,
which contains perilymph. Section 2 represents the sinus endolymphaticus, which projects posteriorly into the sinus impar and contains endolymph. A thin membrane exists between the sinus impar and the posterior projection of the sinus endolymphaticus, thus fluid motion within the sinus impar may be transmitted to the sinus endolymphaticus. This membrane is neglected in the model; continuity of pressure and volume velocity is assumed at the junction. Section 3 represents the transverse canal, which connects the left and right saccular chambers to the sinus endolymphaticus and contains endolymph.

Figure 6.15 shows an equivalent circuit for the fluid system of Fig. 6.14. The acoustic wavelength is assumed to be large relative to the dimensions of the canals, thus the actual geometry of the system is neglected. The fluid sections have cross-sectional areas $A_{f,1}$, $A_{f,2}$, $A_{f,3}$, lumped fluid inertias $m_{f,1}$, $m_{f,2}$, $m_{f,3}$, and lumped fluid resistances $r_{f,1}$, $r_{f,2}$, $r_{f,3}$. Each saccular chamber has a fluid capacitance $c_{f,3}$. Finally, the pressure within each saccular chamber is $P_{sa}(\omega)$.

![Diagram of fluid system model for the Weberian apparatus fluid canals.](image)
FIGURE 6.15 Lumped parameter circuit representation of the fluid canal system.

Using the circuit of Fig. 6.15, the sinus impar pressure and scaphium velocity are related by the equation

\[ A_c V_s(\omega) - \frac{1}{Z_p(\omega)} P_s(\omega) = 0, \quad (6.84) \]

where the fluid canal system mechanical impedance \( Z_p(\omega) \) is defined as

\[ Z_p(\omega) = j\omega \left( 2m_{f,1} + 2m_{f,2} + m_{f,3} \right) + \left( 2r_{f,1} + 2r_{f,2} + r_{f,3} \right) + \frac{1}{j\omega c_{f,3}}. \quad (6.85) \]

The velocity of fluid entering the saccule, \( V_{sd}(\omega) \), is related to \( V_s(\omega) \) through

\[ V_{sd}(\omega) = \frac{A_{sl}}{A_{j,3}} V_s(\omega). \quad (6.86) \]
The pressure in the saccular chamber is related to the pressure in the sinus impar by

\[ P_{s}(\omega) = \frac{P_{i}(\omega)}{1 - \omega^2 c_{f,3} \left( 2m_{f,1} + 2m_{f,3} + m_{f,3} \right) + j \omega c_{f,3} \left( 2r_{f,1} + 2r_{f,3} + r_{f,3} \right)}. \] \tag{6.87}

4. Coupled swimbladder/Weberian apparatus system

When the Weberian apparatus model is coupled to the 2-DOF swimbladder with the tunica externa model, the resulting system is described by Eqs. (6.77), (6.78), (6.79), and (6.84). These equations may be manipulated to form a system of four equations, which is written in matrix form as

\[
\begin{bmatrix}
Z_u(\omega) & -Z_d(\omega) & 0 & 0 \\
-Z_u(\omega) & Z_u(\omega) & -Z_d(\omega) & 0 \\
0 & -Z_u(\omega) & Z_m(\omega) & A_{cl} \\
0 & 0 & A_{cl} & -1/Z_e(\omega)
\end{bmatrix}
\begin{bmatrix}
V_u(\omega) \\
V_e(\omega) \\
V_m(\omega) \\
P_i(\omega)
\end{bmatrix}
= -G_z G_T Z_u(\omega) V_d(\omega). \tag{6.88}
\]

Once the system of Eq. (6.88) has been solved, Eqs. (6.86) and (6.87) may be used to find the velocity and pressure within the saccular chamber.

5. Weberian apparatus material properties

Table 6.3 lists the values for the geometric properties of the tunica externa. The tunica externa mean radius is approximated as being equal to the anterior swimbladder radius \( R_1 \). The tunica externa thickness and gap thickness are estimated from dissected animals and from data presented by Alexander (1961b). The viscosity of the tissue within the gap between the tunica externa and tunica interna is estimated to lie within the range 0.01-1.0 N·s/m². The slit radius \( T_1 \) is estimated from measurements on dissected animals.

202
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Minimum</th>
<th>Baseline Value</th>
<th>Maximum</th>
<th>Reference/Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_{\infty}$ (mm)</td>
<td>—</td>
<td>$R_i$</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>$h_{\infty}$ (mm)</td>
<td>0.1</td>
<td>0.15</td>
<td>0.2</td>
<td>Alexander (1962, 1961b)</td>
</tr>
<tr>
<td>$h_i$ (mm)</td>
<td>0.05</td>
<td>0.1</td>
<td>0.2</td>
<td>Alexander (1962)</td>
</tr>
<tr>
<td>$\xi_i$ (N·s/m²)</td>
<td>0.01</td>
<td>0.1</td>
<td>1.0</td>
<td>—</td>
</tr>
<tr>
<td>$T_i/R_1$</td>
<td>0.1</td>
<td>0.2</td>
<td>0.3</td>
<td>—</td>
</tr>
<tr>
<td>$A_{\infty}$ (m²/N)</td>
<td>$3\times10^{-7}$</td>
<td>$3\times10^{-6}$</td>
<td>$6\times10^{-6}$</td>
<td>Alexander (1961b)</td>
</tr>
<tr>
<td>$n$</td>
<td>—</td>
<td>0.26</td>
<td>—</td>
<td>Alexander (1961b)</td>
</tr>
</tbody>
</table>

TABLE 6.3 Geometric and material properties for the tunica externa model.

To estimate the tunica externa compliance, a curve-fit was performed on creep test data from isolated samples of the tunica externa and tunica interna from several species of Cypriniformes (Alexander, 1961b). A least squares technique was used to fit a function of the form

$$J_c(t) = A_{\infty} \left( \frac{t}{t_0} \right)^n,$$

(6.89)

where $J_c(t)$ is the creep compliance and $A_{\infty}$ and $n$ are constants. The time $t$ was normalized by the constant $t_0 = 1$ s in order to keep the units of $J_c(t)$ and $A_{\infty}$ identical. Figure 6.16 shows the creep compliance data from several tench (Alexander, 1961b), along with the least squares fit to the data. The least squares solution yielded $A_{\infty} = 3\times10^{-6}$ m²/N and $n = 0.26$. The $R^2$ value was 0.893. Since Alexander's data were post mortem, it seems more likely that the in vivo compliance would be lower than the curve-fit result. The maximum and minimum compliance values were estimated with this in mind.
FIGURE 6.16 Experimental creep test data from Alexander (1961b), along with the linear least squares fit of Eq. (6.89). The curve-fit parameters are $A_w = 3 \times 10^4 \text{ m}^2/N$ and $n = 0.26$; $R^2 = 0.893$.

The frequency domain expression $J_s(\omega)$ was obtained by taking the Fourier transform of Eq. (6.89). The tunica externa compliance was estimated using the relationship between creep compliance and complex compliance (Findley et al., 1976):

$$J_s(\omega) = j\omega J_c(\omega),$$  \hspace{1cm} (6.90)

which gives

$$J_s(\omega) = \frac{A_w}{(j\omega \tau_b)^n},$$  \hspace{1cm} (6.91)

where $\Gamma$ is the gamma function.
The Weberian ossicle rotational inertias are estimated by modeling each ossicle as being composed of a number of simple geometric solids. The tripus model is shown in Fig. 6.17(a). The tripus thickness is assumed constant. The intercalarium model, shown in Fig. 6.17(b), consists of three circular cylinders fused together. The scaphium/claustrum body is modeled as the half-ellipsoid in Fig. 6.17(c).

![Geometric models](image)

**FIGURE 6.17** Geometric models used to estimate the rotational inertia of the (a) tripus, (b) intercalarium, and (c) scaphium.

The dimensions of the ossicles and the lever-arm lengths in Fig. 6.13 were estimated from direct examination of goldfish and from sketches and data presented by Chranilov (1929, 1927), Watson (1939), Alexander (1962), Weber (1820), and Krumholz (1943) for a number of different Cypriniformes. The density of the ossicles, \( \rho_{wb} \), is assumed to match that of fish bone, which was given by Alexander (1959b) as 1570–2040 kg/m\(^3\) for roach, carp, and dace. Table 6.4 lists the lever-arm lengths shown in Fig. 6.13. The lever arm lengths are given with respect to the length of the tripus; the tripus length is assumed proportional to the fish length.
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Minimum</th>
<th>Baseline</th>
<th>Maximum</th>
<th>Reference/Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\rho_{wb} \text{ (kg/m}^3\text{)}$</td>
<td>1570</td>
<td>1805</td>
<td>2040</td>
<td>Alexander (1959b)</td>
</tr>
<tr>
<td>$\ell_{r}/\ell_{rd}$</td>
<td>0.05</td>
<td>0.06</td>
<td>0.07</td>
<td>-</td>
</tr>
<tr>
<td>$\ell_{L}/\ell_{tr}$</td>
<td>0.5</td>
<td>0.62</td>
<td>0.71</td>
<td>-</td>
</tr>
<tr>
<td>$\ell_{1}/\ell_{tr}$</td>
<td>0.12</td>
<td>0.20</td>
<td>0.36</td>
<td>-</td>
</tr>
<tr>
<td>$\ell_{2}/\ell_{tr}$</td>
<td>0.14</td>
<td>0.15</td>
<td>0.17</td>
<td>-</td>
</tr>
<tr>
<td>$\ell_{3}/\ell_{tr}$</td>
<td>0.31</td>
<td>0.38</td>
<td>0.55</td>
<td>-</td>
</tr>
<tr>
<td>$\ell_{4}/\ell_{tr}$</td>
<td>0.16</td>
<td>0.20</td>
<td>0.29</td>
<td>-</td>
</tr>
<tr>
<td>$\ell_{5}/\ell_{tr}$</td>
<td>0.08</td>
<td>0.11</td>
<td>0.16</td>
<td>-</td>
</tr>
</tbody>
</table>

TABLE 6.4 Lever-arm lengths for the Weberian ossicles, as shown in Fig. 6.13.

Ligaments 1 and 2 are modeled as pure springs composed of collagen and elastin, respectively (Alexander, 1962), with

$$Z_{L1}(\omega) = k_{L1} / j\omega,$$  \hspace{1cm} (6.92)

and

$$Z_{L2}(\omega) = k_{L2} / j\omega.$$  \hspace{1cm} (6.93)

Ligaments 3 and 4 contain significant amounts of ichthyocol (Alexander, 1961b); therefore, their compositions are assumed to be similar to the tunica externa. To include the effects of the ichthyocol, L3 and L4 are modeled as pure springs (with the stiffness of L1) in parallel with an impedance based on the tunica externa impedance. Because the dimensions and
material properties of L3 and L4 are similar, it is assumed that \( Z_{L3}(\omega) = Z_{L4}(\omega) \). To account for the different geometry between the tunica externa and the ligaments, the tunica externa impedance is multiplied by the ligament form factor (defined as area/length) divided by the tunica externa form factor. For a swimbladder radius of 6 mm, the ratio of form factors is approximately 0.01, so

\[
Z_{L3}(\omega) = Z_{L4}(\omega) = k_{L1} / j\omega + 0.01Z_{a1}(\omega).
\] (6.94)

All four ligaments are assumed to have the same dimensions, which were estimated from several dissected specimens. The cross-section is approximated as rectangular, with average dimensions 0.20 × 0.47 mm; the average length is estimated as 0.53 mm. The elastic moduli for elastin and collagen are given by Fung (1993) as \( 6 \times 10^5 \) N/m² and \( 1 \times 10^9 \) N/m², respectively. The resulting values for each stiffness are displayed in Table 6.5.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Minimum</th>
<th>Baseline</th>
<th>Maximum</th>
<th>Reference/Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>( k_{L1} ) (N/m)</td>
<td>( 4 \times 10^4 )</td>
<td>( 1.8 \times 10^5 )</td>
<td>( 7.5 \times 10^5 )</td>
<td>–</td>
</tr>
<tr>
<td>( k_{L2} ) (N/m)</td>
<td>24</td>
<td>108</td>
<td>450</td>
<td>–</td>
</tr>
</tbody>
</table>

TABLE 6.5 Mechanical impedances for the Weberian ossicle ligaments.

Turning now to the fluid canal system, Table 6.6 lists the estimated diameter \( d_{f,n} \) and length \( \ell_{f,n} \) for each of the \( n \) sections of the fluid canal model. The dimensions are based on dissections and sketches presented by Chardon and Vandewalle (1991), Popper (1971a), and von Frisch (1938).
TABLE 6.6 Dimensions for the Weberian apparatus fluid canals.

The density and viscosity of perilymph (section 1) are from Money et al. (1971) for the pigeon. The density and viscosity of endolymph (sections 2 and 3) are from ten Kate and Kuiper (1970) who measured the properties of labyrinth fluids in the pike. Table 6.7 lists the density and dynamic viscosity for each of the fluid sections.

The Reynolds number for oscillatory fluid flow in a circular pipe is

$$R_e(\omega) = \frac{\rho_f d_f^2 \omega}{4 \xi_f}, \quad (6.95)$$

where $\rho_f$ is the fluid density, $d_f$ is the pipe diameter, and $\xi_f$ is the fluid dynamic viscosity (van Netten, 1991). For low frequencies, where $\omega < 32 \xi_f \rho_f^{-1}d_f^{-2}$ and $R_e(\omega) \ll 1$, the lumped resistance and inertance of the $n^{th}$ section are
TABLE 6.7 Fluid properties for the Weberian apparatus canals.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Minimum</th>
<th>Baseline</th>
<th>Maximum</th>
<th>Reference/Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \rho_{f,1} ) (kg/m(^3))</td>
<td>–</td>
<td>1008</td>
<td>–</td>
<td>Money et al. (1971)</td>
</tr>
<tr>
<td>( \xi_{f,1} ) (N·s/m(^3))</td>
<td>–</td>
<td>0.76(\times)10(^{-3})</td>
<td>–</td>
<td>Money et al. (1971)</td>
</tr>
<tr>
<td>( \rho_{f,2} ) (kg/m(^3))</td>
<td>1005</td>
<td>1010</td>
<td>1015</td>
<td>ten Kate and Kuiper (1970)</td>
</tr>
<tr>
<td>( \xi_{f,2} ) (N·s/m(^3))</td>
<td>1.12(\times)10(^{-3})</td>
<td>1.20(\times)10(^{-3})</td>
<td>1.28(\times)10(^{-3})</td>
<td>ten Kate and Kuiper (1970)</td>
</tr>
<tr>
<td>( \rho_{f,3} ) (kg/m(^3))</td>
<td>1005</td>
<td>1010</td>
<td>1015</td>
<td>ten Kate and Kuiper (1970)</td>
</tr>
<tr>
<td>( \xi_{f,3} ) (N·s/m(^3))</td>
<td>1.12(\times)10(^{-3})</td>
<td>1.20(\times)10(^{-3})</td>
<td>1.28(\times)10(^{-3})</td>
<td>ten Kate and Kuiper (1970)</td>
</tr>
</tbody>
</table>

\[
r_{f,n} = \frac{128 \xi_{f,n} \ell_{f,n}}{\pi d_{f,n}^2},
\]

and

\[
m_{f,n} = \frac{4 \rho_{f,n} \ell_{f,n}}{3 A_{f,n}},
\]

respectively, where \( A_{f,n} \), \( \xi_{f,n} \), and \( \rho_{f,n} \) are the cross-sectional area, fluid viscosity, and fluid density for the \( n \)th fluid canal section (Doebelin, 1972). At high frequencies, where \( \omega > 7200 \xi_f \rho_f^{-1}d_f^{-2} \) and \( R_s(\omega) \gg 1 \), the lumped resistance and inertance are

\[
r_{f,n}(\omega) = \frac{8 \ell_{f,n}}{\pi d_{f,n}^3} \left(2 \rho_{f,n} \xi_{f,n} \omega\right)^{1/2}
\]
respectively (Doebelin, 1972). At frequencies between the low and high values cited, linear interpolation was used to estimate the resistance and inertance.

Figure 6.18 is a magnified view of a transverse slice through the labyrinth of a goldfish which shows the relationship between the transverse canal and the saccular chambers. Also visible in Figure 6.18 is a thin region within the saccular capsule wall, which is taken to be analogous with the release membrane as described in the catfish by Jenkins (1977) and also reported in the goldfish by Furukawa and Ishii (1967a).

The compliance of the saccular capsule was estimated by modeling it as a rigid spherical shell. The release membrane was modeled as a thin circular membrane of radius $R_{rm}$ and thickness $t_{rm}$ which is attached to the floor of the saccular chamber, as shown in Fig. 6.19.

The maximum deflection of the release membrane, $\Delta y_{rm}(\omega)$, is estimated by modeling the release membrane as a uniformly loaded circular plate with clamped edges:

$$\Delta y_{rm}(\omega) = 0.171 \frac{R_{rm}}{E_{rm} \left( t_{rm} / R_{rm} \right)^2} \Delta P_{sa}(\omega),$$

(6.100)

where $E_{rm}$ is the release membrane elastic modulus (Vidosic, 1987). If the release membrane is assumed to deflect into an ellipsoidal shape, then the volume change $\Delta v_{sa}(\omega)$ and pressure change $\Delta P_{sa}(\omega)$ within the saccule are related using

$$\Delta v_{sa}(\omega) = 0.114\pi \frac{R_{rm}^3}{E_{rm} \left( t_{rm} / R_{rm} \right)^3} \Delta P_{sa}(\omega).$$

(6.101)

The compliance is the change in volume divided by the change in pressure, or

\[ c_{f,3} = 0.114 \pi \frac{R_{rm}^3}{E_{rm} (t_{rm} / R_{rm})^3}. \]  

(6.102)

Assuming that the saccular chamber wall has properties similar to collagen, Eq. (6.102) reduces to

\[ c_{f,3} = \frac{3.58 \times 10^{-10} R_{rm}^3}{(t_{rm} / R_{rm})^3} \text{ m}^3/\text{Pa}. \]  

(6.103)

If \( R_{rm} \) is on the order of 1.0 mm and \( (t_{rm} / R_{rm}) \) is roughly 0.24, \( c_{f,3} \) is on the order of \( 3 \times 10^{-17} \text{ m}^3/\text{Pa} \). Table 6.6 lists the estimated range of values for \( R_{rm} \), the ratio \( (t_{rm} / R_{rm}) \), and \( c_{f,3} \).

D. Model for the saccule

1. Single DOF saccule model

In the goldfish saccule, the sensory epithelium, or macula, lies roughly in a vertical plane with its longitudinal axis oriented at a 30° angle with respect to the rostral-caudal axis of the fish (Fay and Olsho, 1979; also see Fig. 1.3). The hair cell ciliary bundles are therefore assumed to be oriented 120° and -60° with respect to the rostral-caudal axis. For the 1-D model of the saccule, only translation of the otolith within a vertical plane, in the direction of the ciliary bundle orientation is considered.

The saccule is assumed to contain \( N_{hc} \) identical hair cells which are distributed uniformly across the macula. The mechanical impedance of a single hair cell ciliary bundle to shear along its axis is \( Z_{hc}(t) \). The hair cell ciliary bundles are coupled to the otolith
through the otolithic membrane, which is assumed to be homogeneous and isotropic. For the model, the otolithic membrane is divided into elemental regions which couple each individual ciliary bundle to the otolith. The mechanical impedance of each of these identical regions is $Z_{om}(t)$. Figure 6.20 illustrates how the $N_{hc}$ hair cells and otolithic membrane elements may be replaced by mechanical impedances representing the sum of the $N_{hc}$ individual elements. In Fig. 6.20, $m_o$ and $x_o(t)$ are the otolith mass and displacement, respectively, $x_{se}(t)$ is the displacement of the sensory epithelium or macula, and $x_{hc}(t)$ is the displacement of the hair cell ciliary bundle tip. Ciliary bundle shear occurs from the relative displacement $x_{hc}(t) - x_{se}(t)$.

![Equivalent mechanical systems](image)

**FIGURE 6.20** Equivalent mechanical systems showing how the $N_{hc}$ hair cell ciliary bundles and otolithic membrane elements may be replaced by the sums $N_{hc}Z_{hc}(t)$ and $N_{hc}Z_{om}(t)$.

Figure 6.21 shows the 1-D model for the saccule. The saccular otolith, or sagitta, has a density $\rho_{sg}$, volume $v_{sg}$, and mass $m_{sg}$ ( = $\rho_{sg}v_{sg}$). It is coupled to the sensory epithelium through the otolithic membrane and hair cell ciliary bundle mechanical impedances $Z_{om}(t)$ and $Z_{hc}(t)$, as illustrated in Fig. 6.20. It is assumed that there is no direct
connection between the otolith and the saccular chamber or the release membrane. The saccular chamber is filled with endolymph having a density $\rho_e$ and a dynamic viscosity $\xi_e$. Fluid displaced from the transverse canal enters the saccular capsule with a relative velocity $V_{se}(t)$, therefore the absolute velocity of endolymph in the saccule is $\dot{x}_{se}(t) - V_{se}(t)$. The displacements of the sagitta, hair cell ciliary bundles, and sensory epithelium are $x_{se}(t)$, $x_{hc}(t)$, and $x_{sa}(t)$, respectively. The main goal is to find the shearing displacement of the ciliary bundles, defined using the relative displacement $x_{rel}(t)$, where

$$x_{rel}(t) = x_{hc}(t) - x_{sa}(t).$$  \hspace{1cm} (6.104)

![FIGURE 6.21 Mechanical system 1-D model for the saccule.](image-url)
Since the acoustic impedance of a fish is roughly identical to that of the surrounding water, the sensory epithelium displacement will closely follow that of the surrounding water, which, within an acoustic field, is a harmonic function of time. The mechanical system model in Fig. 6.21 thus represents a body in an accelerated fluid. The sagitta therefore undergoes a “lift” force $f_L(t)$ in the direction of $\ddot{x}_s(t)$ equal to

$$f_L(t) = \rho_s v_{s\theta} \left[ \ddot{x}_s(t) - \dot{V}_{s\theta}(t) \right]. \quad (6.105)$$

(Prandtl, 1952) and a drag force $f_D(t)$ proportional to the relative acceleration between the otolith and the surrounding fluid and the “apparent” volume $v'_{s\theta}$ of the sagitta, which is the volume of the fluid displaced by the moving otolith (Prandtl, 1952):

$$f_D(t) = -\rho_s v_{s\theta} \left[ \ddot{x}_s(t) - \dot{x}_s(t) + \dot{V}_{s\theta}(t) \right]. \quad (6.106)$$

A negative sign is present since the drag force acts to oppose the lift force. The forces described by Eqs. (6.105) and (6.106) exist even if the endolymph is inviscid. Also acting on the otolith is a viscous drag force $f_v(t)$:

$$f_v(t) = -Z_{v\theta}(t) \left[ \ddot{x}_s(t) - \dot{x}_s(t) + V_{s\theta}(t) \right], \quad (6.107)$$

where $Z_{v\theta}(t)$ is the relationship between the viscous drag force and the relative velocity between the endolymph and the otolith. Finally, a reaction force exists due to the otolithic membrane, $f_{om}(t)$:

$$f_{om}(t) = -Z_{om}(t) \left[ \dot{x}_s(t) - \dot{x}_{om}(t) \right]. \quad (6.108)$$

215
where $Z_{om}(t)$ is the mechanical impedance of the otolithic membrane.

The equation of motion for the system of Fig. 6.21 is then written as:

$$f_e(t) + f_d(t) + f_v(t) + f_{om}(t) = m_{sg} \ddot{x}_{sg}(t). \quad (6.109)$$

Substituting Eqs. (6.105)–(6.108) into Eq. (6.109) yields

$$m_e \left[1 + \frac{Z_{ke}(t)}{Z_{om}(t)} \right] \ddot{x}_{rel}(t) + Z_{rel}(t) \left[1 + \frac{Z_{ke}(t)}{Z_{om}(t)} \right] \dot{x}_{rel}(t) + N_{he} Z_{he}(t) \dot{x}_{rel}(t)
$$

$$= -m_{sg} \left[1 - \rho_e / \rho_{sg} \right] \ddot{x}_{sg}(t) - \rho_{sg} \left( v_{sg} + v'_{sg} \right) \dot{v}_{sg}(t) - Z_{om}(t) V_{om}(t), \quad (6.110)$$

where the effective mass $m_e$, defined as the mass of the sagitta plus any entrained fluid, is

$$m_e = m_{sg} + \rho_e v'_{sg}. \quad (6.111)$$

Equation (6.110) is written more concisely in the frequency domain as

$$\bar{x}_{rel}(\omega) = - \frac{Z_m(\omega)}{Z_{sg}(\omega)} \bar{x}_{sg}(\omega) - \frac{Z_f(\omega)}{j \omega Z_{sg}(\omega)} \bar{V}_{om}(\omega), \quad (6.112)$$

where

$$Z_{sg}(\omega) = j \omega m_{sg} \left[1 + \frac{Z_{he}(\omega)}{Z_{om}(\omega)} \right] + N_{he} Z_{he}(\omega) + Z_{rel}(\omega) \left[1 + \frac{Z_{he}(\omega)}{Z_{om}(\omega)} \right], \quad (6.113)$$

$$Z_m(\omega) = j \omega m_{sg} \left[1 - \rho_e / \rho_{sg} \right], \quad (6.114)$$

216
\[ Z_f(\omega) = j\omega \rho_e (u_{s_k} + u'_{s_k}) + Z_{\text{vis}}(\omega). \]  

(6.115)

The value of \( V_{\text{vis}}(\omega) \) is known from the Weberian apparatus model. The value of \( x_{s_k}(\omega) \) is assumed to match the acoustic particle displacement in the surrounding water and will therefore depend on the character and location of the acoustic source.

Equations (6.105)–(6.109) may also be solved for \( x_{s_k}(\omega) \):

\[ x_{s_k}(\omega) = \frac{Z'_{s_k}(\omega)}{Z'_{s_k}(\omega) x_{s_k}(\omega) - \frac{Z_f(\omega)}{j\omega Z'_{s_k}(\omega)} V_{\text{vis}}(\omega),} \]  

(6.116)

where

\[ Z'_{s_k}(\omega) = j\omega m_e + N_{he} \frac{Z_{\text{om}}(\omega) Z_{he}(\omega)}{Z_{\text{om}}(\omega) + Z_{he}(\omega)} + Z_{vis}(\omega) \]  

(6.117)

and

\[ Z'_m(\omega) = j\omega \rho_e (u_{s_k} + u'_{s_k}) + N_{he} \frac{Z_{\text{om}}(\omega) Z_{he}(\omega)}{Z_{\text{om}}(\omega) + Z_{he}(\omega)} + Z_{vis}(\omega). \]  

(6.118)

Equation (6.116) may also rewritten as

\[ x_{s_k}(\omega) = x_{s_{1k}}(\omega) + x_{s_{2k}}(\omega), \]  

(6.119)

where \( x_{s_{1k}}(\omega) \) is the sagitta displacement due to the sensory epithelium displacement \( x_{s_k}(\omega) \) and \( x_{s_{2k}}(\omega) \) is the sagitta displacement due to the velocity of the fluid entering the saccular chamber, \( V_{s_k}(\omega) \).
2. Saccule model material properties

Table 6.8 lists most of the material and geometric properties for the saccule model. The otolith density is from deVries (1956). The sagitta mass is based on data from Furukawa and Ishii (1967a). The apparent volume is assumed to equal the otolith volume. The radius and length were estimated from direct measurements and from Adams (1940); it should be noted that the radius is larger than that which would be obtained using the volume of a cylinder and the density and mass of the otolith. The increase is attributed to the additional surface area presented to the fluid in the form of the extended flutes. The properties of endolymph are repeated from Table 6.7.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Minimum</th>
<th>Baseline</th>
<th>Maximum</th>
<th>Reference/Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\rho_{sg}$ (kg/m$^3$)</td>
<td>-</td>
<td>2930</td>
<td>-</td>
<td>deVries (1956)</td>
</tr>
<tr>
<td>$m_{sg}/m_{sf}$ (mg/g)</td>
<td>0.006</td>
<td>0.0085</td>
<td>0.01</td>
<td>Furukawa and Ishii (1967a)</td>
</tr>
<tr>
<td>$v'<em>{sg}/v</em>{sg}$</td>
<td>-</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>$R_{sg}$ (mm)</td>
<td>0.25</td>
<td>0.5</td>
<td>1.0</td>
<td>-</td>
</tr>
<tr>
<td>$L_{sg}/L_{sf}$</td>
<td>0.031</td>
<td>0.034</td>
<td>0.039</td>
<td>Adams (1940)</td>
</tr>
<tr>
<td>$\rho_e$ (kg/m$^3$)</td>
<td>1005</td>
<td>1010</td>
<td>1015</td>
<td>ten Kate and Kuiper (1970)</td>
</tr>
<tr>
<td>$\xi_e$ (N·s/m$^2$)</td>
<td>$1.12\times10^{-3}$</td>
<td>$1.20\times10^{-3}$</td>
<td>$1.28\times10^{-3}$</td>
<td>ten Kate and Kuiper (1970)</td>
</tr>
<tr>
<td>$N_{sg}/L_{sf}$ (HC/mm)</td>
<td>127</td>
<td>147</td>
<td>167</td>
<td>Platt (1977)</td>
</tr>
</tbody>
</table>

TABLE 6.8 Material properties and dimensions for the saccule model.

The sagitta is approximated as a circular cylinder with radius $R_{sg}$ and length $L_{sg}$, thus the relationship between the fluid velocity and the force on the cylinder, $Z_{fr}(\omega)$, may
be specified using the mechanical impedance of a circular cylinder immersed in a flowing viscous fluid. The flow is assumed to be uniform and the effects of the saccular chamber walls are ignored. Using the dimensionless frequency parameter $\omega_0$, defined as

$$\omega_0 = \frac{2 \xi}{\rho_s R_{is}^2}$$

(Freeman and Weiss, 1985), the cylinder mechanical impedance is then

$$Z_{ij}(\omega) = 2 \pi \xi L_{ij} \left[ \left( 1 + 2 \sqrt{\omega / \omega_0} \right) + j \omega / \omega_0 \left( 2 + \sqrt{\omega / \omega_0} \right) \right]$$

(Stokes, 1851).

The total number of hair cells present in the saccule, $N_{hc}$, is based on the data of Platt (1977), who provides a thorough account of the number, size, distribution, and orientation of the hair cell ciliary bundles in the goldfish saccule, utricle, and lagena. For a single 51-mm goldfish, Platt (1977) reported 7494 individual hair cells in the saccular macula. For the lagenar macula, he reported 3651 large-bundled hair cells in a 44-mm goldfish and 4852 in a 51-mm goldfish. The number of hair cells therefore appears to increase with the size (i.e., the age) of a fish. This statement is also supported by Lombarte and Popper (1994), and Popper and Hoxter (1984). Using the hair cell densities for the saccular macula of five goldfish (Platt, 1977), the average density is estimated as $336 \pm 33$ hair cells for an area of $100 \times 100 \mu m$, or $336 \pm 33$ HC/10^4μm^2. Using the average density and the total number of hair cells above, the macula area for a 51-mm fish is estimated as $(22.3 \pm 2.2) \times 10^4\mu m^2$. The manner in which the macula area scales with the
size of the fish is unknown, however, since the saccular macula is rather elongated, it is assumed that the macula area scales with the length of the fish. The proportionality constant relating $N_{hc}$ and $L_{w}$ is therefore $147 \pm 20 \text{ HC/mm}$.

The model for the individual hair cell ciliary bundles is based on those presented by Howard and Hudspeth (1987) and Benser et al. (1993), with a slight modification. The model of Howard and Hudspeth (1987), which is shown in Fig. 1.8, leads to problems because it predicts an instantaneous response to a step input. In fact, Corey and Hudspeth (1983) have shown that the time lag between an applied force stimulus and the resulting bundle deflection is on the order of $20-25 \mu s$ for a ciliary bundle from the bullfrog saccule. Therefore, the model of Fig. 1.8 was modified to include not only the subotolithic stiffness $k_{sof}$ as suggested by Benser et al. (1993), but also a damping, presumably also due to the presence of subotolithic filaments, which is in parallel with the subotolithic stiffness. The damping $b_{sof}$ also includes any viscous damping due to fluid drag on the bundle as it moves within the endolymph. The resulting model is displayed in Fig. 6.22.

![Mechanical system model for a hair cell ciliary bundle.](image)

FIGURE 6.22 Mechanical system model for a hair cell ciliary bundle.

The ciliary bundle itself is represented by a standard linear solid consisting of a damping $b_{cb}$ and two stiffnesses, one due to the stereociliary pivot ($k_{sp}$) and one arising
from the gating spring \( k_{gs} \). In parallel with the ciliary bundle elements exists a stiffness and damping caused by the presence of subotolithic filaments that connect the otolithic membrane to the sensory epithelium. Nonlinearities present in the ciliary bundle response are neglected.

The mechanical impedance for the ciliary bundle is

\[
Z_{hc}(\omega) = \frac{k_{gs} b_{cb}}{k_{gs} + j \omega b_{cb}} + \frac{k_{sp}}{j \omega} + \frac{k_{sof}}{j \omega} + b_{sof}. \tag{6.122}
\]

The damping \( b_{cb} \) was given by Howard and Hudspeth (1987) as approximately 6 \( \mu N \cdot s/m \) for saccular hair cells in the bullfrog. Benser et al. (1993) indicated that the ciliary bundle elements account for 50–70% of the total stiffness in Fig. 6.22, again for a bullfrog. Howard and Hudspeth (1987) stated that the gating spring stiffness is roughly 60% of the stereociliary pivot stiffness. Using this information and measured values for the total ciliary bundle stiffness \( k_{cb} \) (Benser et al., 1993), the magnitudes of the individual stiffnesses in Fig. 6.22 may be estimated. The subotolithic filament damping \( b_{sof} \) is estimated from the total ciliary bundle stiffness along with a time constant of 25 \( \mu s \) (Corey and Hudspeth, 1983). Table 6.9 summarizes the parameter values for the ciliary bundles.

The otolithic membrane is assumed to be perfectly rigid and to transmit the motion of the otolith evenly to all of the ciliary bundles. The otolith is therefore assumed to be fixed relative to the ciliary bundle tip; that is, the otolith motion is identical to the ciliary bundle tip motion. This is essentially the same treatment as in Kachar et al. (1990). Benser et al. (1993) experimentally demonstrated that the otolithic membrane in the bullfrog saccule does not move as a rigid body; when excited at a point location the response amplitude declined at successive points away from the stimulus. However, if the excitation of the otolithic membrane is assumed to be uniformly distributed, this effect is negligible.

221
Also, Corey and Hudspeth (1983) have shown that the phase lag produced by the otolithic membrane is negligible at the frequencies of interest here (time constant of 20 μs), thus the rigid body assumption may be justified. For the rigid body case, \( Z_{gb}(\omega) \rightarrow \infty \) and \( x_{gb}(\omega) = x_{bk}(\omega) \).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Minimum</th>
<th>Baseline Value</th>
<th>Maximum</th>
<th>Reference/Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>( k_{cb} ) (mN/m)</td>
<td>0.55</td>
<td>1.35</td>
<td>2.15</td>
<td>Benser et al. (1993)</td>
</tr>
<tr>
<td>( k_s/k_{cb} )</td>
<td>–</td>
<td>0.225</td>
<td>–</td>
<td>Howard and Hudspeth (1987)</td>
</tr>
<tr>
<td>( k_{sf}/k_{cb} )</td>
<td>–</td>
<td>0.375</td>
<td>–</td>
<td>Howard and Hudspeth (1987)</td>
</tr>
<tr>
<td>( k_{ro}/k_{cb} )</td>
<td>–</td>
<td>0.4</td>
<td>–</td>
<td>Benser et al. (1993)</td>
</tr>
<tr>
<td>( b_{cb} ) (μNs/m)</td>
<td>–</td>
<td>6</td>
<td>–</td>
<td>Howard and Hudspeth (1987)</td>
</tr>
<tr>
<td>( b_{rof} ) (μNs/m)</td>
<td>0.011</td>
<td>0.027</td>
<td>0.043</td>
<td>Corey and Hudspeth (1983) Benser et al. (1993)</td>
</tr>
</tbody>
</table>

TABLE 6.9 Parameter values for the ciliary bundle model of Fig. 6.22.

E. Summary

The goldfish peripheral auditory system model consists of three major subsystems which model the swimbladder, Weberian apparatus, and saccule. The goldfish swimbladders are modeled as a 2-DOF lumped mechanical system. The Weberian apparatus model uses a lumped mechanical arrangement for the ossicles and a rigid-walled, lumped cylindrical pipe network for the fluid canals. The coupling between the swimbladder and Weberian ossicles is achieved through a phenomenological model for the swimbladder tunica externa. The saccule model features only a single degree of freedom,
corresponding to translation of the otolith in the direction of hair cell orientation. The model results, parameter effects study, and a comparison with the experimental data are presented in Chapter 7.
CHAPTER 7

AUDITORY SYSTEM MODEL RESULTS

This chapter presents the results for the goldfish peripheral auditory system model derived in Chapter 6. The dynamic inputs to the system model consist of the acoustic pressure incident on the swimbladder and the acoustic particle velocity at the saccule. Therefore, to solve the model equations, the type and location of the acoustic source must first be specified. Following this, the baseline results are presented. These are followed by a study of the effects of the different model parameters and a comparison with the experimental data. Finally, the effects of changing the source location, fish mass, and bladder ratio are examined.

A. Source and fish geometry

Figure 7.1 illustrates the configuration for the goldfish and the acoustic source. The anterior and posterior swimbladders are located at \( \mathbf{r}_1 \) and \( \mathbf{r}_2 \), respectively. The point \( p \) may be located with respect to the acoustic source using the vector \( \mathbf{r}_p \), the anterior swimbladder using \( \mathbf{r}_{p/1} \), or the posterior swimbladder using \( \mathbf{r}_{p/2} \). Also shown in Fig. 7.1 is the right saccular coordinate system, which has the unit vectors \( \hat{s}_1, \hat{s}_2, \hat{s}_3 \). The \( \hat{s}_3 \) direction coincides with the direction of motion for the 1-DOF saccule model.

The acoustic field consists of the direct field due to the acoustic source plus the indirect field due to the sound scattered by the two swimbladder chambers. If the source is...
considered to be a monopole and the acoustic pressure incident on the anterior swimbladder is $P_a(\omega)$, then the direct field pressure at point $p$, $P_D(r_p,\omega)$, is

$$P_D(r_p,\omega) = \frac{r_1}{r_p} P_a(\omega) e^{-\beta(r,\eta)}, \quad (7.1)$$

where $r_1$ and $r_p$ are the lengths of the vectors $r_1$ and $r_p$, respectively. The direct field particle velocity at $p$, $v_D(r_p,\omega)$, is

$$v_D(r_p,\omega) = \frac{r_1}{r_p} \left[ 1 - \frac{j}{k r_p} \frac{P_a(\omega)}{\rho_w c_w} e^{-\beta(r,\eta)} \right] \hat{e}_p, \quad (7.2)$$

where $\hat{e}_p$ is a unit vector in the direction of $r_p$.

FIGURE 7.1 Configuration of the goldfish and the acoustic source. ASB – anterior swimbladder; PSB – posterior swimbladder.
The indirect field particle velocity is equal to the sum of the particle velocities in the scattered waves from the anterior and posterior bladders, or

\[ \mathbf{v}_i(r_p, \omega) = \mathbf{v}_{i,1}(r_{p/1}, \omega) + \mathbf{v}_{i,2}(r_{p/2}, \omega), \tag{7.3} \]

where \( \mathbf{v}_i(r_p, \omega) \) is the indirect field particle velocity, \( \mathbf{v}_{i,1}(r_{p/1}, \omega) \) is the indirect field particle velocity due to the anterior swimbladder, and \( \mathbf{v}_{i,2}(r_{p/2}, \omega) \) is the indirect field particle velocity due to the posterior swimbladder. To find each of the indirect field velocity vectors, it is assumed that the scattered field from each bladder consists of spherical waves.

For the anterior swimbladder, its scattered wave particle velocity, at the point \( p \), is

\[ \mathbf{v}_{i,1}(r_{p/1}, \omega) = \left[ 1 - \frac{j}{kr_{p/1}} \frac{A_i(\omega)}{\rho_c c_\omega r_{p/1}^2} e^{-j(k r_{p/1} + \phi_s)} \right] \hat{e}_{p/1}, \tag{7.4} \]

where \( r_{p/1} \) is the length of \( \mathbf{r}_{p/1} \), \( \hat{e}_{p/1} \) is a unit vector in the direction of \( \mathbf{r}_{p/1} \), and \( A_i(\omega) \) and \( \phi_s \) are constants to be determined by the boundary condition

\[ \mathbf{v}_{i,1}(R_1, \omega) = -V_i(\omega), \tag{7.5} \]

where the negative sign in Eq. (7.5) arises from the fact that \( \Delta R_i(\omega) \) is defined positive for radially inward motion. Substituting Eq. (7.5) into Eq. (7.4) yields

\[ \mathbf{v}_{i,1}(r_{p/1}, \omega) = \left[ -\frac{R_1^2}{r_{p/1}^2} \left( \frac{1}{1 + jk R_1} \right)^2 \left( \frac{1 + jkr_{p/1}}{1 + jkr_{p/1}} \right) V_i(\omega) e^{-j(k r_{p/1} + \phi_s)} \right] \hat{e}_{p/1}. \tag{7.6} \]

Similarly, for the posterior bladder,
\[ \mathbf{v}_{l,2}(r_{p/2}, \omega) = \left[ \frac{R_2^2}{r_{p/2}^2} \left( \frac{1 + jkr_{p/2}}{1 + jkR_2} \right) \mathbf{V}_2(\omega) e^{-i\sigma(r_{p/2} - r_1)} \right] \hat{\mathbf{e}}_{p/2}, \] (7.7)

where \( r_{p/2} \) is the length of \( r_{p/2} \) and \( \hat{\mathbf{e}}_{p/2} \) is a unit vector in the direction of \( r_{p/2} \).

The total acoustic particle velocity at \( p \) is the sum

\[ \mathbf{v}_d(r_p, \omega) = \mathbf{v}_d(r_p, \omega) + \mathbf{v}_{l,1}(r_{p/1}, \omega) + \mathbf{v}_{l,2}(r_{p/2}, \omega). \] (7.8)

If the point \( p \) is located at the saccule, then Eqs. (7.2), (7.6), (7.7) and (7.8) may be used to find the acoustic particle velocity at the saccule, with the values of \( r_{p/1} \) and \( r_{p/2} \) estimated from radiographs. The acoustic particle displacement at the saccule, \( x_\alpha(r_p, \omega) \), is

\[ x_\alpha(r_p, \omega) = \frac{1}{j\omega} \left[ \mathbf{v}_d(r_p, \omega) + \mathbf{v}_{l,1}(r_{p/1}, \omega) + \mathbf{v}_{l,2}(r_{p/2}, \omega) \right]. \] (7.9)

Assuming that the sensory epithelium moves with the same amplitude and phase as the acoustic wave in the water, then the sensory epithelium (vector) displacement equals \( x_\alpha(r_p, \omega) \), and the displacement component in the \( \mathbf{s}_3 \) direction, \( x_{\mathbf{s}_3}(\omega) \), is

\[ x_{\mathbf{s}_3}(\omega) = x_\alpha(r_p, \omega) \cdot \mathbf{s}_3. \] (7.10)

The transformation matrix from the \( \hat{\mathbf{e}}_1, \hat{\mathbf{e}}_2, \hat{\mathbf{e}}_3 \) coordinate system to the \( \hat{\mathbf{s}}_1, \hat{\mathbf{s}}_2, \hat{\mathbf{s}}_3 \) coordinate system is

\[
\begin{bmatrix}
\hat{s}_1 \\
\hat{s}_2 \\
\hat{s}_3
\end{bmatrix} =
\begin{bmatrix}
-\cos\theta_{s} & 0 & \sin\theta_{s} \\
0 & -1 & 0 \\
\sin\theta_{s} & 0 & \cos\theta_{s}
\end{bmatrix}
\begin{bmatrix}
\hat{e}_1 \\
\hat{e}_2 \\
\hat{e}_3
\end{bmatrix},
\] (7.11)
where $\theta_{sa} \approx 30^\circ$ (Fay and Olsho, 1979). Substituting the expression for $\hat{s}_3$ into Eq. (7.10) yields

$$x_{sa}(\omega) = \left[ \sin\theta_{sa} \quad 0 \quad \cos\theta_{sa} \right] x_a(r_p, \omega). \quad (7.12)$$

Figure 7.2 is a more detailed version of the model block diagram of Fig. 6.1 which includes the direct and indirect field components and the variables input to each of the subsystems. The model was numerically coded using MATLAB® (MathWorks, 1995). The MATLAB® script files and functions required for the model are listed in Appendix C.

FIGURE 7.2 Block diagram for the auditory system model.
B. Baseline results

Figures 7.3-7.7 present the model baseline results for a monopole source located 1-m in front of a 34.4-g goldfish with a bladder ratio of 0.83. Figure 7.3 shows the model results for the swimbladders and tripus. The data are presented in terms of the normalized velocity, defined in Eq. (4.14). The anterior and posterior swimbladders show similar resonance frequencies, with the anterior swimbladder having a larger amplitude at resonance. Both phase angles begin near +90° at low frequencies and end up near -90°. The amplitude of the motion of the tripus is significantly smaller than that of the swimbladders. The posterior region of the tripus has a small phase lead compared to the swimbladders; the anterior part of the tripus is 180° out-of-phase with respect to the posterior part, since the tripus is rotating. Compared to the bulk of the experimental data, the model amplitudes show the correct relationship and are of the same order of magnitude; the phase angles roughly correspond to those observed in the experimental data.

Figure 7.4 shows the model normalized velocities for the anterior part of the tripus, the intercalarium, and the scaphium. All three are in-phase and have similar amplitudes; the amplitude of the tripus is the largest, then the intercalarium. The phase angles for the swimbladder and Weberian ossicles confirm the expected operation of the Weberian apparatus: positive pressure causes inward radial motion of the anterior swimbladder, forward rotation of the ossicles, and fluid flow into the sinus impar.

Alexander (1961b) proposed that the viscoelastic properties of the tunica externa produce a high-pass filter effect. This would prevent low frequency pressure changes from causing displacement of the Weberian ossicles. To examine this, the transfer functions relating the Weberian ossicle velocities to the anterior swimbladder radial velocity are plotted in Fig. 7.5.
FIGURE 7.3 Normalized velocity for the swimbladders and tripus using the baseline model parameters. asb – anterior swimbladder; psb – posterior swimbladder; ptr – posterior region of the tripus; atr – anterior region of the tripus.
FIGURE 7.4 Normalized velocity for the tripus, intercalarium, and scaphium using the baseline model parameters. atr – anterior region of tripus; ic – intercalarium; sc – scaphium.
FIGURE 7.5 Transfer functions relating the Weberian ossicle velocities to the anterior swimbladder radial velocity.
The three transfer functions in Fig. 7.5 all show a high-pass effect with a low-frequency roll-off of 5 dB/decade and a flat phase angle throughout the frequency range shown. Although a high-pass filter effect is present, it seems that the filters are not sharp enough to prevent a change of depth from resulting in a significant input to the Weberian ossicles. If a change in depth results in a pressure input with frequency content up to only 0.05 Hz, the Weberian ossicle input will be roughly -20 dB relative to the same stimulus applied at 500 Hz. The pressure changes accompanying a change in depth are several orders of magnitude larger than those of an acoustic wave: a 1-m change in depth results in a pressure change of 9800 Pa, which is almost 200 dB re: 1μPa. It thus appears that the high-pass filters of Fig. 7.5 would not be able to prevent relatively large inputs from passing to the Weberian ossicles. However, it is likely that non-linearities neglected in the model prevent over-stimulation of the Weberian apparatus at low frequencies; for example, as the motions input to the ossicles increase, the ligament stiffnesses may increase accordingly. It may also be possible for the goldfish to transfer gas from the posterior to the anterior swimbladder (or the reverse) in order to keep the anterior swimbladder volume relatively constant within a range of depths. Alexander (1966) stated that proprioceptors in the bladder walls of Cyprinidae allow detection of swimbladder volume changes and Evans (1925) suggested that the swimbladder nerve and sphincter muscle arrangement appears to act as a mechanism for maintaining uniform pressure in the anterior swimbladder.

Figure 7.6 illustrates the model normalized displacements within the saccule. At low frequencies, the sensory epithelium and the sagitta move together, in-phase with the acoustic particle displacement, which, for spherical waves, is -180° out-of-phase with respect to the acoustic pressure. As the frequency increases, the sagitta motion decreases, reaches a null, then begins to increase in the opposite direction. At frequencies above the null point, the sagitta phase is relatively flat at -360°, until the swimbladder resonance. Above the null point, the sensory epithelium phase begins to approach -90° (the result for
plane waves); however, at higher frequencies the indirect field components begin to dominate the direct field particle displacement, and the phase begins to approach the swimbladder phase. Thus, at high frequencies, the sensory epithelium and sagitta are again in-phase.

The sagitta amplitude and phase response may be further clarified by examining the individual components of sagitta motion outlined in Eqs. (6.116)-(6.119): $x_{sg}(\omega)$, which is caused by the sensory epithelium displacement, $x_s(\omega)$, and $x_{sg}(\omega)$, which is caused by the fluid velocity entering the saccule, $V_{sg}(\omega)$. These components are plotted in Fig. 7.7. At low frequencies the sagitta motion is controlled by the sensory epithelium motion. At higher frequencies, the motion due to the fluid flow increases, until the two components have an equal amplitude (the curves intersect). Because the two components are 180° out-of-phase at low frequencies, the components cancel each other, producing a displacement null. At frequencies above the null point, the sagitta motion is controlled by the fluid flow entering the saccule, which has a 0° phase until the swimbladder resonance.

Returning to Fig. 7.6, the relative displacement between the sagitta and the sensory epithelium, $x_{re}(\omega) [= x_{sg}(\omega) - x_s(\omega)]$, has a relatively flat amplitude and phase angle (re: acoustic pressure), between ±45° for most of the low-frequency range, until the swimbladder resonance. Above the swimbladder resonance, the amplitude and phase angle decrease.

From approximately 50 to 400 Hz, Fig. 7.6 shows that the sagitta and relative displacements are in-phase with the acoustic pressure. Using the sign conventions of Fig. 6.21, this translates to dorsal sagitta (and hair cell ciliary bundle tip) motion in response to positive acoustic pressure. Above 400 Hz, a phase lag sets in, so that from 600–800 Hz the sagitta and relative displacement lags the acoustic pressure by 40–80°. These results may be compared to the experimental data of Furukawa and Ishii (1967a), who measured microphonic potentials in goldfish saccular afferent nerve fibers.
FIGURE 7.6 Normalized displacements for the saccule model. Xsg – sagitta; Xse – sensory epithelium; Xrel – relative displacement; Pa – acoustic pressure.
FIGURE 7.7 Individual components of sagitta displacement due to the sensory epithelium motion and fluid flow entering the saccule [see Eqs. (6.116)-(6.119)]. $X_{sg1}$, $x_{sg1}(\omega)$; $X_{sg2}$, $x_{sg2}(\omega)$.
Furukawa and Ishii (1967a) showed that, between 600 and 800 Hz, the microphonic potentials measured from nerve fibers innervating the dorsal portion of the macula were in-phase with the incident acoustic pressure. Microphonic potentials from nerve fibers innervating the ventral portion of the macula were out-of-phase with the pressure. From these data, Furukawa and Ishii concluded that the hair cell ciliary bundles are deflected dorsally in response to positive acoustic pressure and ventrally in response to negative acoustic pressure. Furukawa and Ishii (1967a) also reported a time delay of 0.1–0.2 ms between the pressure stimulus and the onset of the microphonic potential. Between 600 and 800 Hz this time delay corresponds to a phase lag of 20–60°. These data therefore indicates that the relative motion between the sagitta and sensory epithelium is generally in-phase with the acoustic pressure, but lags the acoustic pressure by 20–60° at frequencies between 600 and 800 Hz. These observations are in general agreement with the model results, which show the phase lag between \( x_{rel}(\omega) \) and the acoustic pressure to be 40–80° between 600 and 800 Hz.

Equation (6.112) may be written to express the relative displacement between the sagitta and the sensory epithelium as the sum

\[
x_{rel}(\omega) = H_{se}(\omega) x_{se}(\omega) + H_{sf}(\omega) \frac{V_{fs}(\omega)}{j\omega},
\]

(7.13)

where \( H_{se}(\omega) \) is the transfer function between the sensory epithelium displacement and the relative displacement, and \( H_{sf}(\omega) \) is the transfer function between the fluid displacement and the relative displacement. These transfer functions are displayed in Fig. 7.8 as functions of frequency. The frequency range in Fig. 7.8 has been extended to 1 Hz. At low frequencies, the slope of \( H_{sf}(\omega) \) is +20 dB/decade; the slope of \( H_{se}(\omega) \) is +40 dB/decade. At higher frequencies, above 10 Hz, both transfer functions have flat a amplitude ratio.
Figure 7.8 therefore indicates that the 1-DOF saccule model operates as a displacement sensor above 10 Hz. At low frequencies the saccule responds to the velocity of fluid entering the saccular chamber, and to the acceleration of the sensory epithelium. At low frequencies, the phase angle of $H_{s}(\omega)$ does not approach 0°, as might be expected, but rather -90°. This is a consequence of Stoke's Law, which dictates that at sufficiently low frequencies the force on an object moving in a viscous fluid is proportional to the relative velocity between the fluid and the object (Stokes, 1851). At low frequencies the object’s displacement will therefore be in-phase with the fluid velocity. For the saccule model the phase is -90°, not +90°, because of the sign conventions in Fig. 6.21.

Equation (7.13) shows that the relative displacement is the sum of the displacements due to the sensory epithelium motion and the motion of the fluid entering the saccule from the transverse canal. Taking this approach one step further, the total relative displacement $x_{r}(\omega)$ may be interpreted as the sum of the relative displacements between the sagitta and sensory epithelium due to each of the three hearing mechanisms: the direct path, the indirect path, and the Weberian path. Since the system model is linear, these individual components may be directly calculated and used to assess the relative contribution of each as a function of frequency.

Figure 7.9 shows the individual components of $x_{r}(\omega)$ due to the three hearing mechanisms for the model baseline parameters. The Weberian component dominates throughout most of the frequency range shown. The direct path has a strong influence only at low-frequencies, below 50 Hz. The indirect path component amplitude is larger than the direct path at frequencies near the swimbladder resonance, but still well below that of the Weberian component. The phase angles show the direct and Weberian components in-phase at low-frequencies, and the Weberian and indirect components 180° out-of-phase throughout the frequency range. It should be pointed out that these results apply only to the case of a monopole source 1-m in front of the fish. For closer source locations, the direct
FIGURE 7.8 Transfer functions relating the relative motion $x_{re}(\omega)$ to the sensory epithelium displacement and the fluid displacement entering the saccule. $H_{se}(\omega)$; $H_{sa} - H_{se}(\omega)$. Also see Eqs. (6.112) and (7.13).
FIGURE 7.9 Individual components of the relative displacement between the sagitta and sensory epithelium due to the direct, indirect, and Weberian paths for a monopole source 1-m in front of the goldfish. dir – direct path normalized displacement; ind – indirect path normalized displacement; web – Weberian path normalized displacement.
component would be expected to have a stronger influence; for sources farther away, the
direct component would be expected to have a weaker influence. These relationships are
examined in Section E of this chapter.

Based on Fig. 7.9, one would expect the removal of the swimbladder or the
Weberian ossicles to result in a severe loss of hearing sensitivity, up to approximately 40
dB. This was observed by Poggendorf (1952), who found a loss of 25–40 dB in hearing
sensitivity following removal of the tripus in the catfish. Fay and Popper (1974) also
reported a decline of 20–35 dB in sound pressure sensitivity after removal of the
swimbladder in goldfish. These data were obtained from behavioral conditioning
experiments.

C. Parameter effect study

Forty-two of the model parameters discussed in Chapter 6 were estimated using
minimum, baseline, and maximum values. For each of these parameters, the model was
run using the minimum and maximum values. The results were then compared to the
baseline results to determine the effect of each parameter on the model response. From this
preliminary study, 10 model parameters were identified as having a significant effect on the
model response. The remaining 32 parameters, when varied from the minimum to the
maximum estimated value, did not change the baseline model results. In this section, the
parameters which had a significant effect on the model response are discussed individually,
according to which model subsystem they belong to. Since the fish mass and bladder ratio
are considered to be independent variables, rather than model constants, their effects are
considered in a later section.
1. Swimbladder subsystem

The significant parameters for the swimbladder subsystem are the shear moduli $\mu_1$ and $\mu_2$, and the loss coefficients $\eta_1$ and $\eta_2$. Figures 7.10 and 7.11 show the effects of the shear moduli on the anterior and posterior swimbladder normalized velocities, respectively. Decreasing each shear modulus decreases the anterior swimbladder resonance frequency; increasing the shear moduli increases the resonance frequency. The same trend holds for the posterior swimbladder, except that when $\mu_2 = 5 \times 10^6$ N/m², the posterior response shows multiple peaks, similar to those observed experimentally. The phase angle also shows the characteristic "hump" associated with the second peak.

Figures 7.12 and 7.13 show the effects of the loss factors on the anterior and posterior swimbladder normalized velocities, respectively. Decreasing the loss factors increases the anterior swimbladder amplitude at resonance and sharpens the phase angle near resonance. Increasing the loss factors reduces the amplitude and reduces the sharpness of the phase angle near the resonance. Varying the loss factor values has a similar effect on the posterior response, except that when $\eta_1/\omega = 5$ N·s/m², the posterior response exhibits multiple peaks.

To examine the occurrence of multiple peaks more closely, the shear moduli were adjusted to $\mu_1 = 1 \times 10^6$ N/m² and $\mu_2 = 5 \times 10^6$ N/m², in order to widely separate the individual bladder resonances. Figure 7.14 shows the resulting anterior and posterior responses, plus the response of each swimbladder without the coupling terms defined in Eqs. (6.48)-(6.53). The uncoupled responses show clear amplitude peaks corresponding to the resonance frequency of each individual bladder. When the systems are coupled, the anterior resonance frequency shifts up, towards the posterior resonance frequency, and the posterior resonance frequency shifts down, towards the anterior resonance frequency. The coupled response of a bladder may contain two peaks, as in the posterior response of Fig. 7.14, one at a frequency corresponding to the anterior resonance, the other corresponding to the posterior resonance frequency.
FIGURE 7.10 Effect of the tissue shear moduli on the anterior swimbladder response. 
\( u_{\text{low}}, \mu_1 = 1 \times 10^4 \text{ N/m}^2; \) \( u_{\text{low}}, \mu_2 = 5 \times 10^4 \text{ N/m}^2; \) \( u_{\text{high}}, \mu_1 = 1 \times 10^6 \text{ N/m}^2; \) \( u_{\text{high}}, \mu_2 = 5 \times 10^6 \text{ N/m}^2. \)
FIGURE 7.11 Effect of the tissue shear moduli on the posterior swimbladder response. 
$u_{\text{low}}, \mu_1 = 1 \times 10^4 \text{ N/m}^2$; $u_{\text{low}}, \mu_2 = 5 \times 10^4 \text{ N/m}^2$; $u_{\text{high}}, \mu_1 = 1 \times 10^6 \text{ N/m}^2$; $u_{\text{high}}, \mu_2 = 5 \times 10^6 \text{ N/m}^2$. 

244
FIGURE 7.12 Effect of the tissue loss factors on the anterior swimbladder response. n1low, $\eta_1/\omega = 5$ N·s/m$^2$; n2low, $\eta_2/\omega = 5$ N·s/m$^2$; n1high, $\eta_1/\omega = 500$ N·s/m$^2$; n2high, $\eta_2/\omega = 500$ N·s/m$^2$. 

245
FIGURE 7.13 Effect of the tissue loss factors on the posterior swimbladder response. 
\( n1_{\text{low}}, \eta_1/\omega = 5 \text{ N·s/m}^2; \) \( n2_{\text{low}}, \eta_2/\omega = 5 \text{ N·s/m}^2; \) \( n1_{\text{high}}, \eta_1/\omega = 500 \text{ N·s/m}^2; \) \( n2_{\text{high}}, \eta_2/\omega = 500 \text{ N·s/m}^2. \)
FIGURE 7.14 Normal and uncoupled responses of the anterior and posterior swimbladders. asb – anterior swimbladder; psb – posterior swimbladder.
2. Weberian apparatus subsystem

The significant parameters for the Weberian apparatus subsystem are the tunica externa compliance $A_{se}$ and thickness $h_{se}$, Weberian ossicle ligament stiffness $k_{L1}$, transverse canal diameter $d_{y3}$, and the compliance of the saccular chamber, $c_{y3}$.

Figure 7.15 shows the effect of the tunica externa compliance on the normalized velocity of the (anterior portion of the) tripus. As the compliance increases, the tunica externa has more of a tendency to stretch with, rather than slide over, the tunica interna, thus the tripus amplitude decreases. If the compliance decreases, the tunica externa stretches less and slides more, thus the tripus motion amplitude increases. Varying the compliance constant $A_{se}$ has no effect on the tripus phase angle.

Figure 7.16 illustrates the effect of the tunica externa compliance on the normalized relative displacement between the sagitta and the sensory epithelium. As the compliance increases the relative displacement amplitude curve shifts down (lower amplitude). The relative displacement phase is unaffected by changes in the tunica externa compliance.

Figure 7.17 shows the effect of the tunica externa thickness $h_{se}$ on the normalized velocity of the anterior portion of the tripus. As the thickness increases, the tripus amplitude increases; the phase angle does not change. The effect of $h_{se}$ is therefore similar to that of $A_{se}$, but the direction of change is reversed: increasing $A_{se}$ decreases the tripus velocity amplitude, while increasing $h_{se}$ increases the tripus velocity amplitude. Otherwise, the curves generated by varying the tunica externa thickness will look similar to those generated by varying the tunica externa compliance.

Figure 7.18 shows the effect of varying the ligament stiffness $k_{L1}$ on the tripus response. Increasing the ligament stiffness reduces the tripus amplitude; decreasing the stiffness raises the tripus amplitude. The phase angle changes very little; decreasing the stiffness causes the phase to drop more rapidly above the swimbladder resonance. At frequencies below resonance the effects of varying the ligament stiffness are similar to those obtained upon changing the tunica externa compliance.
FIGURE 7.15 Effect of tunica externa compliance on the response of the anterior portion of the tripus. Atelow, $A_w = 3 \times 10^{-7}$ m$^2$/N; Atehigh, $A_w = 6 \times 10^{-4}$ m$^2$/N.
FIGURE 7.16 Effect of tunica externa compliance on the normalized relative displacement. Atelow, $A_w = 3 \times 10^{-7}$ m$^2$/N; Atehigh, $A_w = 6 \times 10^{-6}$ m$^2$/N.
FIGURE 7.17 Effect of the tunica externa thickness $h_w$ on the tripus normalized velocity. hTElow, $h_w = 0.1$ mm; hTEhigh, $h_w = 0.2$ mm.
FIGURE 7.18 Effect of the ligament stiffness $k_{\text{L}}$ on the tripus normalized velocity. KL1low, $k_{\text{L}} = 4 \times 10^4$ N/m; KL1high, $k_{\text{L}} = 7.5 \times 10^5$ N/m.
Figure 7.19 illustrates the effect of the transverse canal diameter $d_{i,3}$ on the normalized velocity of the fluid entering the saccule from the transverse canal. Since the fluid is assumed incompressible, changing the diameter simply scales the fluid velocity amplitude without affecting the phase angle. The fluid volume velocity is conserved throughout the Weberian apparatus canals, thus decreasing the transverse canal diameter results in an increase in the fluid velocity; increasing the transverse canal diameter causes a decrease in the velocity. Since the phase angle does not change as the parameter is varied, the results are again analogous to the effects of varying the tunica externa compliance.

Figures 7.17–7.19 show a change in the amplitude response of the tripus or canal fluid, respectively, with no (or very little) change in the phase angle of the response. The effects of the tunica externa thickness, ligament stiffness, and canal diameter are therefore analogous to those of the tunica externa compliance and curves generated by changing $h_{se}$, $k_{l1}$, or $d_{f,3}$ will resemble those obtained by varying the tunica externa compliance. Consequently, the effects of these parameters on the normalized sagitta displacement $x_s(\omega)$ and normalized relative displacement $x_{rel}(\omega)$ may be inferred from Figs. 7.15 and 7.16 if the directions of change are recognized: increasing $k_{l1}$ or $d_{f,3}$ has the same effect as increasing $A_{se}$; increasing $h_{se}$ has the same effect as decreasing $A_{se}$.

Figures 7.20 and 7.21 show the effects of the saccular chamber compliance $c_{f,3}$ on the transverse canal fluid velocity entering the saccule and the relative displacement between the sagitta and the sensory epithelium. In addition to the baseline, minimum, and maximum values from Table 6.6, the results are plotted for the case of no release membrane. In this case, the saccular chamber compliance is controlled only by the elasticity of the saccular chamber itself. If the chamber is modeled as a spherical shell, as in Fig. 6.19, the compliance is estimated to be approximately $2 \times 10^{-18} \text{m}^3/\text{Pa}$. 

253
FIGURE 7.19 Effect of the transverse canal diameter \( d_{j3} \) on the normalized velocity of the fluid entering the saccule. \( d_{3\text{low}}, d_{j3}/L_{u} = 0.0025; d_{3\text{high}}, d_{j3}/L_{u} = 0.01. \)
FIGURE 7.20 Effect of saccular chamber compliance on the velocity of the fluid entering the saccule. Cf3high, $c_{f,3} = 2 \times 10^{-16}$ m$^3$/Pa; Cf3low, $c_{f,3} = 3 \times 10^{-16}$ m$^3$/Pa; noRM, $c_{f,3} = 2 \times 10^{-18}$ m$^3$/Pa.
FIGURE 7.21 Effect of saccular chamber compliance on the normalized relative displacement. $C_{f3\text{high}}, c_{f,3} = 2 \times 10^{-16}$ m$^3$/Pa; $C_{f3\text{low}}, c_{f,3} = 3 \times 10^{-18}$ m$^3$/Pa; noRM, $c_{f,3} = 2 \times 10^{-18}$ m$^3$/Pa.
Figure 7.20 shows the effect of $c_{fs}$ on the transverse canal fluid velocity entering the saccule. A decrease in the compliance results in a decrease in the fluid velocity. Increasing the compliance causes an increase in the saccular compliance, thus fluid enters the saccule with a higher velocity. In this case a second resonance also appears in the response, indicated by the second amplitude peak and phase angle drop at high frequencies. Below this second resonance, the phase angle does not vary with changes in $c_{fs}$.

Figure 7.21 shows the effects of $c_{fs}$ on the relative displacement between the sagitta and the sensory epithelium. Varying the saccular chamber compliance causes a shift in the normalized displacement curves. As in the fluid velocity plot shown in Fig. 7.20, a second resonance also appears at the upper frequency range when the compliance is high. Below the second resonance, the phase angle does significantly change with changes in the saccular chamber compliance.

3. Saccule subsystem

When the saccule subsystem parameters were varied within the range of estimated values, none caused a significant change in the model response over the frequency range of interest. Some changes were observed at low frequencies due to changes in the equivalent sagitta radius $R_s$. Figure 7.22 shows the effect of $R_s$ on the relative displacement between the sagitta and the sensory epithelium. Interpretation of Fig. 7.22 is assisted by noting that the 1-DOF saccule model operates essentially as a displacement sensor. At low frequencies the relative displacement ramps upwards, levels off, and remains flat above approximately 10 Hz (see Fig. 7.7). The flat portion of the response is the usable range of the sensor. For the baseline saccule model, almost the entire range 10–5000 Hz is therefore within the “usable range” of the sensor. Changing $R_s$ shifts the point where the response levels off.
FIGURE 7.22 Effect of varying the sagitta equivalent radius $R_{sg}$ on the relative displacement between the sagitta and the sensory epithelium. Rs.low, $R_{sg} = 0.25$ mm; Rs.high, $R_{sg} = 1.0$ mm.
Changing the number of hair cells or the mechanical stiffness of each ciliary bundle, within the range of estimated values (see Figs. 6.29 and 6.31), does not cause a significant change in the response within the frequency range 10–5000 Hz. The bundle stiffness required an order of magnitude change before it created a change in the sagitta response similar to that caused by varying $R_{sg}$. It is possible that the system is designed to operate well above the saccular otolith resonance so that changes in the number or stiffness of the hair cells do not significantly affect the hearing ability of the fish; however, better estimates of the mechanical properties of the swimbladder and hair cell ciliary bundles are required before this can be stated with any certainty.

**D. Model and experimental comparison**

Figures 7.23–7.26 compare the model results with the experimental measurements of the normalized velocity from the swimbladders and tripus, and the normalized displacement from the sagitta. Rather than use a goldfish whose size matched the model baseline value, the experimental data were selected from the single fish which had been tested the most times. This allowed the model to be compared to a large amount of experimental data for the same fish. The experimental data in Figs. 7.23–7.26 are from goldfish GF756 (60.4 g; 123.9 mm). The model was adjusted by using a mass of 60.4 g and a bladder ratio of 0.96, which correspond to the mass and bladder ratio for GF756. The swimbladder shear moduli, loss factors, and the tunica externa compliance were also adjusted to better fit the experimental data. All of the parameters were within the estimated range of values after adjustment. For the model results the shear moduli and loss factors were as follows $\mu_1 = 5 \times 10^4$ N/m², $\mu_2 = 1 \times 10^6$ N/m², $\eta_1/\omega = 10$ N·s/m², and $\eta_2/\omega = 400$ N·s/m². The tunica externa compliance was adjusted down to $1 \times 10^{-5}$ m²/N.
Figure 7.23 compares the experimental and model results for the anterior swimbladder normalized velocity. The model response matches the resonance frequency and generally agrees with the experimental amplitude; however, the shape of the model curve is not quite sharp enough near the resonance. The phase data agree at low frequencies; at high frequencies the agreement is not quite as good. One cause for the discrepancy between the model and the experimental data may be the frequency dependency for the swimbladder shear moduli and loss factors. Unfortunately, without more data on the tissue material properties at audio frequencies, this may not be resolved.

Figure 7.24 compares the model and experimental normalized velocities for the posterior swimbladder. The model resonance frequency is low, but otherwise the agreement is good, especially the phase angle.

Figure 7.25 compares the model and experimental normalized velocities for the posterior part of the tripus. The amplitude agreement is very good; however, the phase angles show a consistent lag between the model and the experiment. This points to some problem with the model for the coupling between the anterior swimbladder and the tripus or in the tunica externa compliance itself.

Figure 7.26 shows the model results for the normalized sagitta displacement plotted along with the experimentally measured normalized sagitta displacement. The model phase angle has been shifted by +360° to match the experimental data at high frequencies. This is valid based on the data of Fig. 7.7, which shows the sagitta displacement in-phase with acoustic pressure near the swimbladder resonance. It must be emphasized that the model is designed to predict the dorso-ventral motion of the otolith, while the experiments measured the medial-lateral motion, so a high level of agreement is not expected; however, the results should agree within an order of magnitude. The model and experimental amplitudes are within an order of magnitude, and both show a roll-off at high frequencies with similar shape. The phase angles agree from approximately 100 Hz until roughly 1000 Hz, above
FIGURE 7.23 Comparison of the model anterior swimbladder response with the normalized velocity measured from the anterior swimbladder of goldfish GF756. Symbols – experimental; line – model.
FIGURE 7.24 Comparison of the model posterior swimbladder response with the normalized velocity measured from the posterior swimbladder of goldfish GF756. Symbols – experimental; line – model.
the swimbladder resonance. The notch present in the model amplitude does not show up in the experimental data; however most of the experimental data from the saccular otoliths, including that of Fig. 7.26, indicate a drop in amplitude near 300–500 Hz (see Fig. 5.29), without the accompanying phase shift predicted by the model. The model and experimental phase angles do not agree at low frequencies; however, this discrepancy may be due to the difference in the directions of the motions plotted in Fig. 7.26.

A comparison between Figs. 6.18 and 6.19 also helps to explain the discrepancy between the model predictions and the measured sagitta motion in the medial-lateral direction. Based on Figs. 6.18 and 6.19, the medial-lateral motion would be roughly 70% of the model predictions. The expected phase of the medial-lateral sagitta motion may also be estimated using Fig. 6.18. Positive pressure will cause swimbladder contraction and fluid flow out of the saccular chambers. This would be expected to cause the sagitta to move in a medial direction, which corresponds to positive phase for the ultrasonic measurement system configuration. Thus, the sagitta motion in the medial-lateral direction should be roughly in-phase with the acoustic pressure at low frequencies, and would not be expected to have a phase angle of ±180°.

Overall, the model agrees with the experimental data, within an order of magnitude, and shows many of the trends present in the experimental data, including the general relationship between the anterior swimbladder, posterior swimbladder, and tripus velocity amplitudes. The swimbladder phase angles match well; the measured tripus phase angle showed a persistent lead over the model. The model results for the sagitta are of the same order of magnitude as the experimentally measured displacements. This agreement is satisfactory, considering that the experiments were conducted in the medial-lateral direction and the model results are for the dorso-ventral direction.
FIGURE 7.25 Comparison of the model and experimental (GF756) results for the tripus normalized velocity. Symbols – experimental; line – model.
FIGURE 7.26 Comparison of the model and experimental (GF756) results for the sagitta normalized displacement. Symbols – experimental; line – model.
E. Effect of fish mass, bladder ratio, and source location

1. Fish mass and bladder ratio

Because the goldfish mass and bladder ratio are considered to be independent variables, rather than model constants, they were not included in the parameter effects study of Section B. However, the influence of these parameters on the model response may be important, and was therefore examined.

Figure 7.27 shows the effect of changing the goldfish mass on the anterior swimbladder response. Unlike the experimental data, which show no clear relationship between the goldfish size and the resonance frequency, the model predicts a clear drop in resonance frequency with increasing mass. Accompanying the drop in resonance frequency is also a drop in damping, which results in higher amplitude peaks and sharper phase angles near the resonance frequency. The experimental data showed no clear relationship between the swimbladder $Q$ and the fish mass. This is partly due to the lack of a clear relationship between the swimbladder size and the fish mass, but also probably due to variations in the shear moduli and loss factors between fish.

Figure 7.28 shows the effect of goldfish mass on the relative velocity between the sagitta and sensory epithelium. The response curves show a modest shift down in amplitude with increasing mass and also reflect the shift in the swimbladder resonance frequency. Aside from the shift in swimbladder resonance, the phase angles are unchanged.

Figure 7.29 shows the effect of the bladder ratio on the posterior swimbladder normalized velocity. As the bladder ratio changes, the change in resonance frequency is small, suggesting that the anterior swimbladder is exercising a large amount of control over the frequency of the posterior resonance. At high bladder ratios the amplitude at resonance increases, in agreement with the data of Fig. 7.27 showing an decrease in damping with an increase in fish (or swimbladder) size. Overall, the bladder ratio is not as significant as first suspected, since the coupling between the bladders tends to blur the individual responses.
FIGURE 7.27 Effect of goldfish mass on the anterior swimbladder response. mass10, \( m_f = 10 \) g; mass60, \( m_f = 60 \) g; mass100, \( m_f = 100 \) g.
FIGURE 7.28 Effect of goldfish mass on the normalized relative displacement between the sagitta and the sensory epithelium. mass10, $m_{sf} = 10$ g; mass60, $m_{sf} = 60$ g; mass100, $m_{sf} = 100$ g.
FIGURE 7.29 Effect of the bladder ratio on the posterior swimbladder normalized velocity. Gbr1, $G_{BR} = 0.25$; Gbr2, $G_{BR} = 0.5$; Gbr3, $G_{BR} = 1.0$; Gbr4, $G_{BR} = 1.3$. 

269
2. Source location

Figures 7.30–7.32, along with Fig. 7.8, may be used to make predictions about the effect of changing source location on the peripheral auditory mechanics. Figures 7.8 and 7.30 show the relative displacement components for a monopole source located 1-m and 10-m in front of the fish, respectively. Comparing the two cases reveals that at a larger source distance, the influence of the direct path diminishes, while the effects of the Weberian and indirect paths do not. This is because the direct path relies on the acoustic particle velocity as the input to the saccule; at larger distances from the source, the particle velocity decreases, which decreases the direct path component. Thus for large source distances, the Weberian path dominates throughout the entire frequency range. This condition would also be present in any experimental procedures where the fish is excited using a loudspeaker in air. Although the pressure waves in the air may couple to the water in a small tank at low frequencies by exciting the boundaries of the tank, this would not produce particle velocities as large as those accompanying an acoustic wave underwater at low frequencies close to a source (Parvulescu, 1964; Parvulescu, 1967).

Figures 7.31 and 7.32 show the relative displacement components for a monopole source located 1-m and 10-m behind the fish, respectively. The amplitude plots of Figs. 7.31 and 7.32 are the same as Figs. 7.8 and 7.30, respectively; however, the phase angles show different relationships. In particular, the direct component phase is shifted by 180° when the source is located behind the fish. With the source behind the fish, the direct and indirect path components are in-phase at low frequencies and 180° out-of-phase with the Weberian path component. These phase relationships may have a role in the directional hearing abilities.
FIGURE 7.30 Individual components of the normalized relative displacement due to the direct, indirect, and Weberian paths for a monopole source 10-m in front of the goldfish. dir – direct path; ind – indirect path; web – Weberian path.
FIGURE 7.31 Individual components of the normalized relative displacement due to the direct, indirect, and Weberian paths for a monopole source 1-m behind the goldfish. dir – direct path; ind – indirect path; web – Weberian path.
FIGURE 7.32 Individual components of the normalized relative displacement due to the direct, indirect, and Weberian paths for a monopole source 10-m behind the goldfish. dir – direct path; ind – indirect path; web – Weberian path.
F. Summary

The results for the auditory system model generally agree with the experimentally measured response of the swimbladders and tripus. The model predicts the correct amplitude and phase relationships between the swimbladders and shows the coupling observed between the anterior swimbladder and tripus. The model also predicts a high-pass filter effect due to the tunica externa compliance; however, the model low frequency roll-off of 5 dB/decade (see Fig. 7.5) is insufficient to prevent a change in depth from supplying a large amplitude input to the Weberian apparatus. It is speculated that another mechanism may exist to prevent changes in depth from affecting the Weberian apparatus performance.

For the sagitta, the model predicts that at low frequencies the sagitta moves in the same direction as the sensory epithelium, but at higher frequencies moves in response to the fluid entering the saccule from the transverse canal. The model results for the relative displacement between the sagitta and the sensory epithelium show the saccule response to be analogous to that of an inertial displacement sensor above approximately 10 Hz. The model results also agree with the data presented by Furukawa and Ishii (1967a) which show that the relative motion between the sagitta and the sensory epithelium lags the acoustic pressure by 20–60° from 600–800 Hz. The model predicts a sagitta amplitude on the order of 10 nm/Pa.

If the relative displacement is broken down into the components controlled by the direct, indirect, and Weberian paths, the Weberian path component dominates above 50 Hz and is roughly 40 dB larger than the others at frequencies above 100 Hz. This agrees with data showing a severe loss of hearing sensitivity after removal of the swimbladder or tripus (Poggendorf, 1952; Fay and Popper, 1974). The phase relationships between the direct component and the others change as the source is moved from the front to the back of the fish. Phase relationships such as this may influence directional hearing.
The swimbladder shear moduli, loss factors, and the tunica externa compliance seem to have the largest impact on the model results. Varying the number or stiffness of hair cell ciliary bundles does not change the saccule model results.
CHAPTER 8

CONCLUSIONS AND RECOMMENDATIONS

This study had four major objectives: (1) to modify the ultrasonic measurement technique developed by Rogers and Hastings (1989) to allow phase angle measurement, (2) to develop a suitable acoustic environment for testing at frequencies down to 10 Hz, (3) to experimentally measure the in vivo amplitude and phase response of the goldfish swimbladder, Weberian ossicles, and otoliths, and (4) to develop a mathematical model for the goldfish peripheral auditory system. These objectives were met with varying degrees of success.

A. Ultrasonic measurement system

The ultrasonic measurement system was successfully modified to include phase angle measurement. The phase measurement scheme used a phase detector circuit (consisting of a double-balanced mixer and low-pass filter) to demodulate the received, phase-modulated ultrasonic signal. This allowed the phase of the target motion to be measured with respect to the acoustic pressure. However, with this method, low-frequency motion of the target was found to cause a 180° phase ambiguity. This situation was resolved by using the average value of the phase detector output (measured with a dc voltmeter) to adjust the ultrasonic carrier frequency before each measurement. The addition of this feedback loop resolved the 180° phase ambiguity, but increased the time required for each measurement.
The spatial resolution of the ultrasonic system was also investigated in this study. Because of the relatively small size of the otoliths and Weberian ossicles, it was desired to improve the spatial resolution from previous studies. This was accomplished by using focused ultrasonic transducers and a frequency of 15 MHz; the resulting sample volume size was approximately $0.5 \times 0.2 \times 0.2$ mm.

There remains much room for improvement in the ultrasonic measurement system. The use of a phase-locked-loop (PLL) circuit may enable one to avoid the $180^\circ$ phase error without resorting to the time consuming carrier frequency adjustment used in this study. A PLL circuit may also make it possible to obtain an amplitude measurement without the use of the HP 3585B spectrum analyzer; this is desirable because of the high cost and large size of the HP 3585B. In addition, if the received ultrasound could be demodulated without introducing amplitude or phase ambiguities, transient and random testing would be possible. This would enable one to measure the response of the auditory organs to inputs that more closely resemble signals of biological relevance, such as transient signals.

**B. Low-frequency test environment**

The objective of developing a suitable acoustic environment for low frequency testing was only partially met. An active control scheme, based on the pattern search technique, was used to successfully generate plane traveling waves within a water-filled acrylic tube at frequencies down to 12.5 Hz. The pressure/velocity ratio within this acoustic waveguide was adjusted to give the same ratio as a plane progressive wave in open water. Therefore, in this respect, a controlled underwater acoustic environment was obtained, down to 12.5 Hz; however, for this study, it was necessary to cut openings in the waveguide to allow access for the fish and the ultrasonic transducers. The presence of these openings created relatively large pressure gradients and particle velocities in their vicinity and disrupted the plane traveling wave in the test section. It was therefore necessary to
normalize the measured frequency response data with the acoustic energy density at the location of the fish, which was estimated from measurements of the local acoustic pressure and particle velocity.

Although the presence of the openings prevented the acoustic waveguide from completely meeting the goals of this study, the waveguide, when used with the active control scheme, may be very useful for other types of auditory testing in fish. A similar acoustic waveguide, without the active control, was used in intense tone studies on the oscar (*Astronotus ocellatus*) (Finneran *et al*., 1995; Hastings *et al*., 1996). The current apparatus allows not only plane traveling waves at low frequencies, but also manipulation of pressure and velocity ratios and therefore represents a substantial improvement over the earlier design. For example, the active control system could be modified to produce pressure or velocity nodes or antinodes as well. In addition, it is not unreasonable to suggest that the current apparatus may be useful for behavioral studies, although the ambient noise levels would need to be reduced.

C. Experimental measurements

The experimental measurements required anesthetizing and tethering individual fish within a low-frequency sound field. Two experimental setups were used to cover the frequency range 12.5 to 3000 Hz. At the lower frequencies, the sound field was generated using two low frequency acoustic sources flanged to the acoustic waveguide. This system used an active control technique to achieve traveling wave conditions at frequencies down to 12.5 Hz. At higher frequencies, tests were conducted in a vinyl swimming pool with the fish located in the direct field of the acoustic source. In either case, as the fish was insonified by the low frequency source, the *in vivo* responses of the swimbladder, Weberian ossicles, and otolith organs were measured in 22 goldfish.
The displacement amplitude was measured in the medial-lateral direction only. The measurement system was theoretically capable of measuring displacement amplitudes on the order of 1.5 nm. However, in practice the ultrasonic carrier amplitude limited the dynamic range of the system; at low ultrasonic carrier amplitudes, the minimum detectable target motion was higher. Because the otoliths and Weberian ossicles are irregularly shaped and lie deep within the fish's body, it was often difficult to obtain sufficient carrier amplitudes. The accuracy of the measurement system was estimated by measuring the response of an acrylic post excited by an electromechanical shaker. The amplitude and phase measured with the ultrasonic system were compared to the "actual" amplitude and phase measured with a calibrated accelerometer. In terms of the normalized displacement and normalized velocity, the estimated amplitude accuracy was ±0.42 nm/Pa and ±2.6 (μm/s)/Pa at 1000 Hz, respectively. The accuracy of the phase measurement was estimated to be ±3.0°.

At low frequencies, the auditory organs moved with the same amplitude and phase as the rest of the fish's body (confirmed by measuring the motion of the tail and jawbone). The responses of the swimbladders, tripus, and otoliths were identical at these low frequencies. It therefore appears that, at low frequencies, the acoustic particle motion carries the entire fish along with it. At higher frequencies, the swimbladder response showed clear amplitude peaks at the resonance frequency of the bladder. The mean resonance frequencies for the anterior and posterior swimbladders were 900 and 1015 Hz, respectively, which are near the upper frequency range of hearing for the goldfish. Multiple amplitude peaks were often seen in the responses of the swimbladder chambers. The second bladder, which may be of different size and have a unique resonance frequency, is coupled to the first due to their close proximity. The multiple resonances thus represent the response of the second bladder appearing in that of the first.
The swimbladder resonance also appeared in the tripus and saccular otolith responses, though both showed lower amplitudes at the resonance. The tripus phase angle normally matched that of the anterior swimbladder; the saccular otolith (sagitta) phase angle normally followed that of the tripus at low frequencies (but sometimes lagged the tripus phase at high frequencies, sometimes by as much as 360°). The facts that the anterior swimbladder resonance appears in the tripus and sagitta responses and the motions are normally in-phase with the swimbladder indicate strong coupling between the swimbladder and the Weberian apparatus and sagitta. The normalized displacement amplitude of the sagitta was on the order of 1–10 nm/Pa. Motion of the lagenar otolith was only detected in a few tests; when the lagenar otolith was found to be moving, the amplitude was below that of the saccular otolith and the tripus. The utricular otolith was not moving with any measurable amplitude in any of the tests. The phase angle data from the saccular otoliths seem to indicate a complex pattern of motion, including rotation.

A surprising feature of the experiments was the large ultrasonic reflection from the outer body surface of the fish. Near the swimbladders, the body surface was found to move with the same phase as the bladder wall itself. This revelation may have implications on the interpretation of data from previous studies [e.g., Cox (1987) and Lewis (1994)], where the locations of the sample volumes were not specified. Also surprising was the length of time the fish could be kept anesthetized. Previous studies had been conducted in smaller volumes of water, where it was not impractical to add anesthetic directly to the water in the test apparatus. For this study, fish were deeply anesthetized by immersing in a 1:2500 solution of MS-222 for 2–2.5 h. This was normally sufficient to keep the animal anesthetized for several hours, even after immersion in fresh water.

The main drawback to the experimental method was the lack of motion information from all but the medial-lateral direction. The measurement system may be modified to provide information in the dorso-ventral direction, but it would be impossible to obtain any
motion data along the rostro-caudal axis. Dorso-ventral tests would likely be hindered by
the presence of the skull; it would probably require a larger input to the ultrasonic source in
order to receive a significant echo. Still, these tests would provide the most direct evidence
of the motion of the saccular otolith in the direction of the ciliary bundles.

The small size of the ultrasonic sample volume was intended to allow independent
measurements along the otoliths or Weberian ossicles. However, the small sample volume
made it very difficult to find the structures of interest. It seemed that the smaller fish were
somewhat easier to test because of the relative size between the sample volume and the
tripus or otoliths. Also, a larger sample volume would probably have made the system
more tolerable of low-frequency target motion (i.e., respiration); this has been reported by
Lewis (1994). It therefore appears that, for future work, increasing the sample volume
somewhat may lead to a more stable system and make it easier to locate the organs of
interest.

D. Auditory system model

Prior to this study, models of the auditory system have focused individually on the
swimbladder, otoliths, or hair cells. The goldfish peripheral auditory system model
developed in this research represents the first time that individual models for the
swimbladder, Weberian apparatus, and otoliths have been coupled and presented as a
complete system. The resulting system models the transduction of acoustic energy to hair
cell ciliary bundle shear within the saccule.

The model consists of three major subsystems which mathematically describe the
motion of the swimbladder, Weberian apparatus, and saccule. The goldfish swimbladder
chambers are modeled as a 2-DOF lumped mechanical system. The Weberian apparatus
model uses a lumped mechanical arrangement for the ossicles and a rigid-walled, lumped
cylindrical pipe network for the fluid canals. The coupling between the swimbladder and
Weberian ossicles is achieved through a phenomenological model for the swimbladder tunica externa. The saccule model features only a single degree of freedom, corresponding to translation of the otolith in the direction of hair cell orientation.

The responses predicted by the auditory system model generally agree with the experimentally measured response of the swimbladders and tripus. The model predicts the correct amplitude and phase relationships between the swimbladders and shows the coupling observed between the anterior swimbladder and tripus. The resonance frequencies for the individual ossicles are well above the auditory range, thus the Weberian apparatus acts essentially as a spring at audio frequencies and couples the swimbladder to the saccule. The model also predicts a high-pass filter effect due to the tunica externa compliance; however the model low frequency roll-off of 5 dB/decade is insufficient to prevent a change in depth from supplying a large amplitude input to the Weberian apparatus; another mechanism may exist to prevent changes in depth from affecting the Weberian apparatus performance.

For the sagitta, the model predicts that, at low frequencies, the sagitta moves in the same direction as the sensory epithelium. At higher frequencies, the sagitta moves in response to the fluid entering the saccule from the transverse canal. The model results for the relative displacement between the sagitta and the sensory epithelium show the saccule response to be analogous to that of a displacement sensor. The model results also agree with the data presented by Furukawa and Ishii (1967a) which shows that the relative motion between the sagitta and the sensory epithelium lags the acoustic pressure by 20–60° between 600 and 800 Hz. The model predicts a sagitta amplitude on the order of 10 nm/Pa.

If the relative displacement is broken down into components due to the direct, indirect, and Weberian paths, the Weberian path component dominates above 20 Hz and is roughly 40 dB larger than the others at frequencies above 100 Hz. This agrees with data showing a severe loss of hearing sensitivity after removal of the swimbladder or tripus.
(Poggendorf, 1952; Fay and Popper, 1974). The phase relationships between the direct component and the others change as the source is moved from the front to the back of the fish. Phase relationships such as this may influence directional hearing.

Because of the uncertainties present in the model parameters, the results are most useful in predicting general trends, rather than exact responses. The swimbladder shear moduli, loss factors, and the tunica externa compliance seem to have the largest impact on the model results. Varying the number or stiffness of hair cell ciliary bundles does not change the saccule model results.

The peripheral auditory system model suffers mainly from a lack of reliable material property data and the limited availability of morphological data. This is most obvious in the saccule model, where the manner of coupling between the otolith, otolithic membrane, ciliary bundles, and the saccular chamber is largely unknown. The first step to improve the model would be to use magnetic resonance imaging (MRI) techniques to obtain detailed information on the structure of the auditory system, and the sizes of and spatial relationships between the auditory organs. Direct experimental tests on the properties of the tunica externa and the Weberian ossicle ligaments may also improve the reliability of the model predictions.
APPENDIX A

WAVEGUIDE FABRICATION DRAWINGS
FIGURE A.1 Waveguide assembly drawing.
FIGURE A.2 Flange detail drawing.
FIGURE A.3 Gasket detail drawing.
FIGURE A.4 Support block assembly drawing.
TABLE B.1 Table of experimental test parameters. ASB – anterior swimbladder; PSB – posterior swimbladders; TR – tripus; LA – lagenar otolith; SA – saccular otolith; UT – utricular otolith; WG – waveguide; x – structure was located and data collected; † – no useful data was obtained; ‡ – data was collected from the outer body surface.
<table>
<thead>
<tr>
<th>Code</th>
<th>Date</th>
<th>Tag</th>
<th>in vivo?</th>
<th>ASB</th>
<th>PSB</th>
<th>TR</th>
<th>WB</th>
<th>LA</th>
<th>SA</th>
<th>UT</th>
<th>Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>GF0429</td>
<td>04-29-96</td>
<td>x01</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0430</td>
<td>04-30-96</td>
<td>x02</td>
<td>yes</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0501</td>
<td>05-01-96</td>
<td>x03</td>
<td>yes</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0528</td>
<td>05-28-96</td>
<td>x04</td>
<td>yes</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0612</td>
<td>06-12-96</td>
<td>x05</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0613</td>
<td>06-13-96</td>
<td>x06</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0627</td>
<td>06-27-96</td>
<td>x07</td>
<td>yes</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0702</td>
<td>07-02-96</td>
<td>x08</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0709</td>
<td>07-09-96</td>
<td>x09</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0711</td>
<td>07-11-96</td>
<td>x10</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0717</td>
<td>07-17-96</td>
<td>x11</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0718</td>
<td>07-18-96</td>
<td>x12</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0719</td>
<td>07-19-96</td>
<td>x13</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0725</td>
<td>07-25-96</td>
<td>x14</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0730</td>
<td>07-30-96</td>
<td>x15</td>
<td>yes</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0731</td>
<td>07-31-96</td>
<td>x16</td>
<td>yes</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0801a</td>
<td>08-01-96</td>
<td>758.1</td>
<td>yes</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0801b</td>
<td>08-01-96</td>
<td>755.1</td>
<td>yes</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0806</td>
<td>08-06-96</td>
<td>761.1</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0807</td>
<td>08-07-96</td>
<td>754.1</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0808</td>
<td>08-08-96</td>
<td>759.1</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0812</td>
<td>08-12-96</td>
<td>755.1</td>
<td>yes</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0814</td>
<td>08-14-96</td>
<td>757.1</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0815</td>
<td>08-15-96</td>
<td>760.1</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0820a</td>
<td>08-20-96</td>
<td>x17</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0820b</td>
<td>08-20-96</td>
<td>751.1</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0821</td>
<td>08-21-96</td>
<td>758.1</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0823a</td>
<td>08-23-96</td>
<td>758.2</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0823b</td>
<td>08-23-96</td>
<td>750.2</td>
<td>no</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
</tbody>
</table>

(continued)

290
## Figure B.1 (continued)

<table>
<thead>
<tr>
<th>Code</th>
<th>Date</th>
<th>Tag</th>
<th>in vivo?</th>
<th>ASB</th>
<th>PSB</th>
<th>TR</th>
<th>WB</th>
<th>LA</th>
<th>SA</th>
<th>UT</th>
<th>Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>GF0826</td>
<td>08-26-96</td>
<td>753.2 no</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0827a</td>
<td>08-27-96</td>
<td>757 yes</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0827b</td>
<td>08-27-96</td>
<td>761.2 no</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0827c</td>
<td>08-27-96</td>
<td>752.2 no</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0828</td>
<td>08-28-96</td>
<td>756.2 no</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0829</td>
<td>08-29-96</td>
<td>757 yes</td>
<td>x/‡</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0903</td>
<td>09-03-96</td>
<td>755.1 no</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>TANK*</td>
</tr>
<tr>
<td>GF0909</td>
<td>09-09-96</td>
<td>x18 no</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0911</td>
<td>09-11-96</td>
<td>754.3 no</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0912</td>
<td>09-12-96</td>
<td>006 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0913a</td>
<td>09-13-96</td>
<td>013 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0913b</td>
<td>09-13-96</td>
<td>001 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0913c</td>
<td>09-13-96</td>
<td>007 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0915</td>
<td>09-15-96</td>
<td>008 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0916</td>
<td>09-16-96</td>
<td>x19 no</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0917a</td>
<td>09-17-96</td>
<td>013 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0917b</td>
<td>09-17-96</td>
<td>004 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0918a</td>
<td>09-18-96</td>
<td>000 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0918b</td>
<td>09-18-96</td>
<td>001 yes</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0919</td>
<td>09-19-96</td>
<td>756 yes</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0920</td>
<td>09-20-96</td>
<td>008 yes</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0923</td>
<td>09-23-96</td>
<td>007 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0924a</td>
<td>09-24-96</td>
<td>003 yes</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0924b</td>
<td>09-24-96</td>
<td>013 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0926a</td>
<td>09-26-96</td>
<td>001 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0926b</td>
<td>09-26-96</td>
<td>006 yes</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0926c</td>
<td>09-26-96</td>
<td>008 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0927a</td>
<td>09-27-96</td>
<td>000 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0927b</td>
<td>09-27-96</td>
<td>756 yes</td>
<td>❌</td>
<td>❌</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
</tbody>
</table>
Figure B.1 (continued)

<table>
<thead>
<tr>
<th>Code</th>
<th>Date</th>
<th>Tag</th>
<th>in vivo?</th>
<th>ASB</th>
<th>PSB</th>
<th>TR</th>
<th>WB</th>
<th>LA</th>
<th>SA</th>
<th>UT</th>
<th>Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>GF0930</td>
<td>09-30-96</td>
<td>002</td>
<td>yes</td>
<td>‡</td>
<td>‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1001a</td>
<td>10-01-96</td>
<td>004</td>
<td>yes</td>
<td>‡</td>
<td>‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1001b</td>
<td>10-01-96</td>
<td>003</td>
<td>yes</td>
<td>‡</td>
<td>‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1002</td>
<td>10-02-96</td>
<td>006</td>
<td>yes</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1003</td>
<td>10-03-96</td>
<td>756</td>
<td>yes</td>
<td>‡</td>
<td>‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1007</td>
<td>10-07-96</td>
<td>008</td>
<td>yes</td>
<td>‡</td>
<td>‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1008</td>
<td>10-08-96</td>
<td>004</td>
<td>yes</td>
<td>‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1010</td>
<td>10-10-96</td>
<td>010</td>
<td>yes</td>
<td>‡</td>
<td>‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1011</td>
<td>10-11-96</td>
<td>756</td>
<td>yes</td>
<td>x/‡</td>
<td>‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1013</td>
<td>10-13-96</td>
<td>004</td>
<td>yes</td>
<td>‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1014</td>
<td>10-14-96</td>
<td>011</td>
<td>yes</td>
<td>‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1025</td>
<td>10-25-96</td>
<td>010</td>
<td>yes</td>
<td>x/‡</td>
<td>x/‡</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1027</td>
<td>10-27-96</td>
<td>016</td>
<td>yes</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1028a</td>
<td>10-28-96</td>
<td>003</td>
<td>yes</td>
<td>x/‡</td>
<td>x/‡</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1028b</td>
<td>10-28-96</td>
<td>006</td>
<td>yes</td>
<td>x/‡</td>
<td>x/‡</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1029a</td>
<td>10-29-96</td>
<td>024</td>
<td>yes</td>
<td>x/‡</td>
<td>x/‡</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1029b</td>
<td>10-29-96</td>
<td>002</td>
<td>yes</td>
<td>x/‡</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1029c</td>
<td>10-29-96</td>
<td>011</td>
<td>yes</td>
<td>x/‡</td>
<td>x/‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1031</td>
<td>10-31-96</td>
<td>016</td>
<td>yes</td>
<td>x/‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1101</td>
<td>11-01-96</td>
<td>013</td>
<td>yes</td>
<td>x/‡</td>
<td>x/‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1104a</td>
<td>11-04-96</td>
<td>756</td>
<td>yes</td>
<td>x/‡</td>
<td>x/‡</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1104b</td>
<td>11-04-96</td>
<td>000</td>
<td>yes</td>
<td>x/‡</td>
<td>x/‡</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1105a</td>
<td>11-05-96</td>
<td>001</td>
<td>yes</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1105b</td>
<td>11-05-96</td>
<td>024</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1106</td>
<td>11-06-96</td>
<td>010</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1107</td>
<td>11-07-96</td>
<td>017</td>
<td>yes</td>
<td>x/‡</td>
<td>x/‡</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1113</td>
<td>11-13-96</td>
<td>006</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1114a</td>
<td>11-14-96</td>
<td>756</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1114b</td>
<td>11-14-96</td>
<td>017</td>
<td>yes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td></td>
<td>POOL</td>
</tr>
</tbody>
</table>

(continued)

292
<table>
<thead>
<tr>
<th>Code</th>
<th>Date</th>
<th>Tag</th>
<th><em>in vivo?</em></th>
<th>ASB</th>
<th>PSB</th>
<th>TR</th>
<th>WB</th>
<th>LA</th>
<th>SA</th>
<th>UT</th>
<th>Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>GF1115</td>
<td>11-15-96</td>
<td>024</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1118a</td>
<td>11-18-96</td>
<td>010</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1118b</td>
<td>11-18-96</td>
<td>000</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1119</td>
<td>11-19-96</td>
<td>012</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1120</td>
<td>11-20-96</td>
<td>011</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1121</td>
<td>11-21-96</td>
<td>002</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1126</td>
<td>11-26-96</td>
<td>016</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1127</td>
<td>11-27-96</td>
<td>004</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1129</td>
<td>11-29-96</td>
<td>013</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF1214a</td>
<td>12-14-96</td>
<td>012</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1214b</td>
<td>12-14-96</td>
<td>002</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1215</td>
<td>12-15-96</td>
<td>000</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1216a</td>
<td>12-16-96</td>
<td>006</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1216b</td>
<td>12-16-96</td>
<td>006</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1217a</td>
<td>12-17-96</td>
<td>010</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF1218</td>
<td>12-18-96</td>
<td>024</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0102</td>
<td>01-02-97</td>
<td>016</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0105</td>
<td>01-05-97</td>
<td>017</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0106</td>
<td>01-06-97</td>
<td>001</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0107</td>
<td>01-07-97</td>
<td>018</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0108a</td>
<td>01-08-97</td>
<td>019</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0108b</td>
<td>01-08-97</td>
<td>006</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0109</td>
<td>01-09-97</td>
<td>012</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0110</td>
<td>01-10-97</td>
<td>002</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0111</td>
<td>01-11-97</td>
<td>010</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>WG</td>
</tr>
<tr>
<td>GF0124</td>
<td>01-24-97</td>
<td>024</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF0125</td>
<td>01-25-97</td>
<td>000</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF0127</td>
<td>01-27-97</td>
<td>016</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF0129</td>
<td>01-29-97</td>
<td>012</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
</tbody>
</table>

(continued)
TABLE B.1 Table of experimental test parameters. ASB – anterior swimbladder; PSB – posterior swimbladders; TR – tripus; LA – lagenar otolith; SA – saccular otolith; UT – utricular otolith; WG – waveguide; x – structure was located and data collected; † – no useful data was obtained; ‡ – data was collected from the outer body surface.

* Early high-frequency tests were conducted in a rectangular glass tank (1.2 x 0.3 x 0.45 m); however, no meaningful, in vivo data was obtained from the tank setup. All later tests at high frequency were conducted in the pool setup described in Chapter 4.

<table>
<thead>
<tr>
<th>Code</th>
<th>Date</th>
<th>Tag</th>
<th>in vivo?</th>
<th>ASB</th>
<th>PSB</th>
<th>TR</th>
<th>WB</th>
<th>LA</th>
<th>SA</th>
<th>UT</th>
<th>Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>GF0130</td>
<td>01-30-97</td>
<td>756</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF0131a</td>
<td>01-31-97</td>
<td>019</td>
<td>no</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>POOL</td>
</tr>
<tr>
<td>GF0201</td>
<td>02-01-97</td>
<td>000</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>POOL</td>
</tr>
<tr>
<td>GF0202</td>
<td>02-02-97</td>
<td>002</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>POOL</td>
</tr>
<tr>
<td>GF0203</td>
<td>02-03-97</td>
<td>012</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>POOL</td>
</tr>
<tr>
<td>GF0204</td>
<td>02-04-97</td>
<td>756</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF0205a</td>
<td>02-05-97</td>
<td>020</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>POOL</td>
</tr>
<tr>
<td>GF0205b</td>
<td>02-05-97</td>
<td>021</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF0206</td>
<td>02-06-97</td>
<td>020</td>
<td>yes</td>
<td>†</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF0207</td>
<td>02-08-97</td>
<td>022</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF0210a</td>
<td>02-10-97</td>
<td>022</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>POOL</td>
</tr>
<tr>
<td>GF0210b</td>
<td>02-10-97</td>
<td>023</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>POOL</td>
</tr>
<tr>
<td>GF0220</td>
<td>02-20-97</td>
<td>020</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>POOL</td>
</tr>
<tr>
<td>GF0221</td>
<td>02-21-97</td>
<td>022</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td>POOL</td>
</tr>
<tr>
<td>GF0223a</td>
<td>02-23-97</td>
<td>012</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>POOL</td>
</tr>
<tr>
<td>GF0223b</td>
<td>02-23-97</td>
<td>025</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>POOL</td>
</tr>
<tr>
<td>GF0223c</td>
<td>02-23-97</td>
<td>026</td>
<td>yes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>POOL</td>
</tr>
</tbody>
</table>
APPENDIX C

AUDITORY SYSTEM MODEL SOURCE CODE

main.m
% Model of the peripheral auditory system in the goldfish
% v2.0
% created 10-8-96 by Jim Finneran
% modified last 3-25-97, JF

clear
c1c;
disp('Goldish auditory system model')
disp('working...')
global j densityWater speedWater TRUE FALSE

% Global variables
j = sqrt(-1);
TRUE=1;
FALSE = 0;
densityWater = 1000; % density of water (kg/m^3)
speedWater = 1500; % sound speed in water (m/s)

if -strcmp(matlabVersion , 'S3.5')
    frequencyArray = ([logspace(1, 3, 75) 980 980 1000 linspace(1000,5000,50)]);
    Pa = 1*ones(size(frequencyArray));
else
    frequencyArray = ([logspace(1, 3, 5) linspace(1100,5000,5)]);
    Pa = 1*ones(frequencyArray);
end

w = 2*pi*frequencyArray; % array of w (rad/s);
s = j*w; % Laplace variable

% Fish parameters
massFish = 34.4; % g
lengthFish = 30.92e-3 * massFish ^ (1/3); % m

% Get dynamic parameters from swimbladder (swimbladder.m)
Msb = swimbladder(w, massFish);
Zsb1 = Msb(:,1); Zsb2 = Msb(:,2);
Z12 = Msb(:,3); Z21 = Msb(:,4);
Zle = Msb(:,6); ZL = Msb(:,5);
Gt = Msb(1,9); S1 = Msb(2,9); S2 = Msb(3,9);
R1 = Msb(4,9); R2 = Msb(5,9); d12 = Msb(6,9);
clear Msb;

% Get dynamic parameters from Weberian ossicles (webOssicles.m)
Mossicles = webOssicles(s, Zle, ZL, lengthFish);
Zle = Mossicles(:,1); Z3 = Mossicles(:,2); Zc = Mossicles(:,3);
Z4 = Mossicles(:,4); Zsc = Mossicles(:,5);
GL = Mossicles(1,6); Ad = Mossicles(2,6);
clear Mossicles;

% Get dynamic parameters from Weberian apparatus fluid canals (webCanals.m)
Mcanals = Webcanals(w, lengthFish);
Zfc = Mcanals(:,1); Ate = Mcanals(2,2);
clear Mcanals;

% Get locations of swimbladders, saccule in source coordinates
getCoordinates;

% Get acoustic parameters at SBs due to direct field (getDirectField.m)
Mdirect = getDirectField(w, Pa, r1_s, r1_s);
Vd = Mdirect(:,1:3); % velocity is v(y)
% calculate energy density using velocity y-component only
Ed = 0.5*densityWater*(abs(Vd).*abs(Pa)/densityWater/speedWater).^2;

% Setup 6x6 matrix of equations and solve for velocities and pressures
solveWebApparatus;

% Get indirect path particle velocity vector at the saccule
V = getIndirectField(w, rSac_1, rSac_2, r1_s, r2_s, V1, V2);

% Get direct path particle velocity vector at the saccule
Mdirect = getDirectField(w, Pa, rSac_s, r1_s);
Vd = Mdirect(:,1:3);
clear Mdirect

% Solve for sagitta motion, HC shear using 1-D sagitta model
Msaccule = saccule1D(w, lengthFish, massFish, Vd, Vi, Vsa);
VWeb = Msaccule(:,3); Xrel = Msaccule(:,4);
Xsg = Msaccule(:,5); Xse = Msaccule(:,6);
Hse = Msaccule(:,7); Hsa = Msaccule(:,8);
clear Msaccule R1 R2 d12 Vd Vi
clear r1_s r2_s rSac_1 rSac_2 rSac_s

% Enter specific plotting routines for each platform
if ~strcmp(matlabVersion,'S3.5')
    plot40
else
    plot35
end

% Clear unnecessary variables
clear RM1 RM2 RM3 Rmc RMsc RMsa RMdirect RMindirect RMweb Dsg Dse Drel
clear phase1 phase2 phase3 phaseSC phaseSA phaseDirect
    clear phaseIndirect phaseWeb phaseSG phaseSE phaseRel choice f

% Save results if desired
if matlabVersion == 'S3.5'
disp('');
disp('Directory contents.');
dir
filename = input('Enter save filename : ','s');
if filename ~= '0'
eval(['save ',filename]);
end
else
    [filename, pathname] = uiputfile('.*','Save as');
    if filename ~= 0
...
matlabVersion.m

function y = matlabVersion;
% This function returns a four character string
% which identifies the version of matlab
% that is running
% string = 'Student' means version = 'Student 4a', student version 4.0a
% string = 'S3.5' means version = 'S3.5', student version 3.5
% created 2-14-97 by Jim Finneran
% last modified 2-22-97, JF
x = version;
y = x(1:4);
return

cordinates.m

% Get the location of each organ in the source coordinates
% created 1-26-97 by Jim Finneran
% last modified 3-24-97, JF
% All coordinates specified in [mm], convert to [m] at the end
% Fish origin located at anterior sb center
% source location in fish coordinates
rSource_f = [-1000 0 0];
if rSource_f(1) < 0
    location = ['source in front (' num2str(abs(rSource_f(1)/1000)) ' m)'];
else
    location = ['source behind (' num2str(abs(rSource_f(1)/1000)) ' m)'];
end
% Define organ locations in fish coordinates
r1_f = [0 0 0];
r2_f = [d12*1000 0 0];
rSac_f = [-18 1 3];
r1_s = (r1_f - rSource_f)/1000;
r2_s = (r2_f - rSource_f)/1000;
rSac_s = (rSac_f - rSource_f)/1000;
rSac_1 = (rSac_f - r1_f)/1000;
rSac_2 = (rSac_f - r2_f)/1000;
clear r1_f r2_f rSac_f

directField.m

function QoutDirect = getDirectField(w, Pa, rp, r1)
% y = getDirectField(w, Pa, rp, r1)
% w = circular frequency (rad/s)
% rp = location of test point w.r.t source
% r1 = location of A-SB w.r.t. source (zero pressure phase location)
% Pa = acoustic pressure (Pa)
% Va = acoustic particle velocity (m/s)
% Va = [Vx Vy Vz], each is column vector of size(w)
% created 1-25-97 by Jim Finneran
% last modified 3-9-97, JF
if ~strcmp(matlabVersion , 'S3.5')
    eval('global j Pamb densityWater speedWater TRUE FALSE');
    end
end
k = w./speedWater;  % wave number m^-1
RP = sqrt(rp*rpf);  % rrp
R1 = sqrt(r1*r1);  % r11
va = (1-j.*k.*RP1)*R1*R1.*Pa./densityWater.*exp(-j.*k.*(RP-R1));
for n = 1:length(w),
    Va(n,1:3) = va(n)*rp/RP;
end
QoutDirect = [Va];

getindirectField.m
function QoutIndirect = getindirectField(w, rp1, rp2, R1, R2, V1, V2)
% Va = getindirectField(w, rp1, rp2, R1, R2, V1, V2)
% Get acoustic particle velocity vector sum due to contributions
% from anterior and posterior swimbladders
% w = vector of circular frequencies
% rp1 = vector location of test point w.r.t A-SB (m)
% rp2 = vector location of test point w.r.t. P-SB (m)
% R1 = A-SB radius (m)
% R2 = P-SB radius (m)
% V1 = A-SB radial velocity (m/s)
% V2 = P-SB radial velocity (m/s)
% created 1-25-97 by Jim Finneran
% last modified 3-24-97, JF
if ~strcmp(matlabVersion, 'S3.5')
    eval('global j Pamb densityWater speedWater TRUE FALSE');
end
k = w./speedWater;
RP1 = sqrt(rp1*rp1);
RP2 = sqrt(rp2*rp2);

% Calculate acoustic particle velocity from
% anterior swimbladder with radial velocity V1
% Use (-V1) since V1 is defined as positive radially inward
t1 = (1+j*k.*RP1);
t2 = (1+j.*k.*R1);
t3 = (R1/RP1)^2;
t4 = exp(-j.*k.*(RP1-R1));
va1 = t3*t1/t2.*(-V1).*t4;

% Calculate acoustic particle velocity from
% posterior swimbladder with radial velocity V2
% Use (-V2) since V2 is defined as positive radially inward
t1 = (1+j*k.*RP2);
t2 = (1+j.*k.*R2);
t3 = (R2/RP2)^2;
t4 = exp(-j.*k.*(RP2-R2));
va2 = t3*t1/t2.*(-V2).*t4;
for n = 1:length(w),
    Va1(n,1:3) = va1(n)*rp1/RP1;
    Va2(n,1:3) = va2(n)*rp2/RP2;
end
Va = Va1 + Va2;
QoutIndirect = [Va];
return
function Qoutsb = swimbladder(W, fishMass)
% This .m file calculates the mechanical impedances of the anterior and
% posterior swimbladders, including the tunica externa, in the goldfish
%
% The output is in the form of a [size(W), 9] matrix:
% [ Zab1 Zab2 Z12 Z11 ZL Za1 Za2 Constants ]
% where
% Constants(1) = Gt
% Constants(2) = S1 (anteriorSurfaceArea)
% Constants(3) = S2 (posteriorSurfaceArea)
% Constants(4) = anteriorRadius
% Constants(5) = posteriorRadius
% created 10-8-98 by Jim Finneran
% last modified 4-2-97, JF

if ~strcmp(matlabVersion, 'S3.5')
    eval(['global densityWater speedWater TRUE FALSE
          Constants = zeros(size(W));
          ONES = ones(size(W));
    '])
else
    Constants = zeros(W);
    ONES = ones(W);
end
s = sqrt(-1)*W;

% Environmental parameters
gammaAir = 1.4; % ratio of specific heats in air
Pamb = 1.013e5;

linearTE = FALSE; % Use linear model for te?
coupledSB = TRUE; % Swimbladders coupled?

anteriorRadius = 1.84e-3 * fishMass ^ (1/3);
bladderRatio = 0.83; % R2/R1
posteriorRadius = bladderRatio*anteriorRadius;
u1 = 1e+5; % N/m^2
n1 = 100 * W; % N/m
u2 = 5e+5; % N/m^2
n2 = 100 * W; % N/m^2

% Geometrical Properties of Goldfish Swimbladders - model as spherical shells
anteriorSurfaceArea = 4. * pi * anteriorRadius^2; % m^2
posteriorSurfaceArea = 4. * pi * posteriorRadius^2; % m^2
lossFactor1 = n1; %
lossFactor2 = n2; %
shearModulus1 = u1; % N/m
shearModulus2 = u2; % N/m

% **** Anterior swimbladder ***************
Pxs1_cmHg = 2.4; % excess pressure (cm Hg)
Pxs1 = Pxs1_cmHg * 1.013e5 / 760.0; % (Pa)
e1 = 0.90; % % kg
m1 = densityWater * anteriorRadius * anteriorSurfaceArea * e1;
gasStiffness1 = (3. * gammaAir * (Pamb + Pxs1)) / anteriorRadius * anteriorSurfaceArea; % N/m
tissueStiffness1 = anteriorSurfaceArea * 4 * shearModulus1 * (1-e1^3/anteriorRadius); % N/m
k1 = gasStiffness1 + tissueStiffness1; % N/m
tissueDamping1 = anteriorSurfaceArea * 4 * lossFactor1 * u1 * (1-e1^3/anteriorRadius); % Ns/m
b1 = tissueDamping1; % Ns/m
Zsb1 = m1 * s + b1 + k1 * s; % Ns/m
Za1 = b1 + k1 * s; % Ns/m
% *** Posterior swimbladder **************
Pxa2_cmHg = 2.4; % excess pressure (cm Hg)
Pxa2 = Pxa2_cmHg * 1.013e5 / 76.0; % (Pa)
e2 = 0.90; % R2/Ro2
m2 = densityWater * posteriorRadius * posteriorSurfaceArea * e2; % kg
gasStiffness2 = (3. * gammaAir * (Pamb + Pxs2)) / posteriorRadius * posteriorSurfaceArea; % N/m
tissueStiffness2 = posteriorSurfaceArea * 4 * shearModulus2 * (1 - e2^3) / posteriorRadius; % N/m
tissueStiffness2 = posteriorSurfaceArea * 4 * shearModulus2 * (1 - e2^3) / posteriorRadius; % N/m
k2 = gasStiffness2 + tissueStiffness2; % N/m
tissueDamping2 = posteriorSurfaceArea * 4 * shearModulus2 * (1 - e2^3) / posteriorRadius; % N/m
b2 = tissueDamping2; % N/m
Zsb2 = m2 * s + b2 + k2 * s; % N/s/m
Za2 = b2 + k2 * s; % N/s/m
% *** Coupling coefficients **************
h12 = 0.6e-3; % m
d12 = anteriorRadius + posteriorRadius + h12; % m
G12 = d12 * anteriorRadius / (d12^2 - anteriorRadius * posteriorRadius);
G21 = d12 * posteriorRadius / (d12^2 - anteriorRadius * posteriorRadius);
k12 = G12 * k2; % N/m
b12 = G12 * b2; % N/s/m
k21 = G21 * k1; % N/m
b21 = G21 * b1; % N/s/m
if (coupledSB == TRUE),
    Z12 = k12 * s + b12; % N/s/m
    Z21 = k21 * s + b21; % N/s/m
else
    Z12 = zeros(size(s)); % N/s/m
    Z21 = zeros(size(s)); % N/s/m
end
% *** Tunica extema properties **************
teRadius = anteriorRadius; % m
teThickness = 0.15e-3; % m
gapThickness = 0.1e-3; % m
gapViscosity = 0.1; % Ns/m*2
slitRadius = 0.2 * teRadius; % m
teComplianceConstant = 3e-6; % m^2/N
if (linearTE == TRUE)
    % Use linear system fit to data using Levy's method
    % Jte = Ate*(a(1)*s^4 + a(2)*s^3 + ... + a(5))./(b(1)*s^4 + b(2)*s^3 + ... + 1)
    % a = [2.73186-15 2.49686e-10 2.6207e-06 3.4629e-03 4.0725e-01];
    % b = [7.5967e-14 3.6953e-09 2.3188e-05 1.7195e-02 1.0000e+00];
    % teCompliance = teComplianceConstant*.freqs(a,b,W); % m^2/N
else
    % Use power function
    teCompliance = teComplianceConstant*gamma(teCompliancePower1).*s.^teCompliancePower;
end
% *** TE dynamic parameters **************
ZL = 2. * pi * teRadius^2 * gapViscosity / gapThickness*ONES; % N/s/m
Zte = 4. * pi * teRadius * teThickness * slitRadius / (4. * teRadius^2 - slitRadius^2) ./ (s.*teCompliance); % N/s/m
Gt = 4. * teRadius / slitRadius;
% *** Define variables to output **************
% Output matrix must be square, so put constants into a vector: [Constants] having the same length as [W]
webOssicles.m

function Qoutweb = webOssicles(s, Zte, ZL, lengthFish);

% Define mechanical impedances for Web ossicles
% created 10-8-96 by Jim Finneran
% last modified 3-22-97, JF

if ~strcmp(matlabVersion, 'v3.5')
    eval(['global j densityWater speedWater TRUE FALSE']);
    Constants = zeros(size(s));
else
    Constants = zeros(s);
end

% density of fish bone
densityFishBone = 1805; % kg/m^3

% ******** Tripus **************
% Define the Geometric and material properties of the Tripus
% Model tripus as rectangular (1) and quarter-elliptical plates (3)
% along with 3 negative regions (2,4,5)

rhoT = densityFishBone; % kg/m^3
LT = 0.060*lengthFish; % m (overall length)
a1 = 0.39*LT; b1 = 0.43*LT; % m (The following are
a2 = 0.27*LT; b2 = 0.37*LT; % m estimated from
b3 = 0.68*LT; z4 = 0.21*LT; % m Cyprinus carpio
b4 = 0.36*LT; b5 = 0.15*LT; % m and exp's on goldfish)
d4 = 0.19*LT; % m
Tt = 0.07*LT; % m (thickness of tripus)
% Jt is the mass moment of inertia for the tripus about pivot point [kgm^2]
% Includes a factor of 1.5 to account for effect of surrounding fluid
Jt = 1.5*rhoT*LT^2*(a1^2 b1/3(a1^2+b1^2)-a2^2 b2/12(a2^2+b2^2+b1^2)+pi*b4^3/16*sin^2(a1^2+b3^2)-
pi^2*a4^4/16*sin^2(a4^2+b4^2)+a5^4/16*(a4^2+b5^2+b6^2d4^2));

% Define lengths of effective lever arms for mechanical connections
l1 = 0.20 * LT; % m Ligament LI
l2 = 0.15 * LT; % m Ligament L2
l3 = 0.38 * LT; % m Ligament L3
ITE = 0.62 * LT; % m Insertion of Tunica Externa
G1 = l1 / l3;
G2 = l2 / l3;
GL = ITE / l3;

% ******** Intercalarium ************
% Define Geometric and material properties of Intercalarium
% Model intercalarium as 3 circular cylinders intersecting at common point
% Element #2 is the articulating process
% Element #3 is the ascending process

rhoI = densityFishBone; % kg/m^3
LI = 0.20*LT; % m
R1 = 0.025*LT; L1 = 0.19*LT; % m

301
\[ R_2 = 0.01 \text{LT}; \quad L_2 = 0.06 \text{LT}; \quad \text{m} \]

\[ R_3 = 0.01 \text{LT}; \quad L_3 = 0.08 \text{LT}; \quad \text{m} \]

\[ \theta_2 = \frac{\pi}{180}(-75); \quad \text{rad} \]

\[ \theta_3 = \frac{\pi}{180}32.5; \quad \text{rad} \]

\[ l_i = 0.20 \text{LT}; \quad \text{m} \]

\% Distances for transfer of axes

\[ d_{i1} = \text{abs}(L_1/L_2 - L_2^2 \cos(\theta_2) + j \sin(\theta_2)); \quad \text{m} \]

\[ d_{i2} = L_2/2; \quad \text{m} \]

\[ d_{i3} = \text{abs}(L_3/2 \cos(\theta_3) + j \sin(\theta_3) - L_2^2 \cos(\theta_2) + j \sin(\theta_2)); \quad \text{m} \]

\% Ji=Mass moment of inertia for intercalarium about pivot point [kgm^2]

\% Include factor of 1.5 to account for effect of surrounding fluid

\[ J_i = 1.5 \rho_i \pi \left( \frac{R_1 M^2 L_1 + R_2 M^2 L_2 + R_3 M^2 L_3}{4 \pi \rho_i^4 \times L_1^5} + \frac{R_2^2 L_2^3}{12} + \frac{R_3^2 L_3^3}{12} \right) \]

\% Define geometric and material properties of scaphium

\% Model scaphium as a half-ellipsoid (flat base covers Sinus Impar)

\[ \rho_S = \text{densityFishBone}; \quad \text{kgm}^3 \]

\[ l_s = 0.11 \text{LT}; \quad \text{m} \]

\[ a = 0.11 \text{LT}; \quad b = 0.11 \text{LT}; \quad \text{m} \]

\[ c = 0.04 \text{LT}; \quad \text{m} \]

\[ A_d = \pi a b; \]

\% Mass moment of inertia about pivot point

\% Include factor of 1.5 to account for effect of surrounding fluid

\[ J_S = 1.5 \rho_S \pi \left( a^2 b^2 c^2 (9b^2 + c^2) \right); \quad \text{kgm}^2 \]

\% Tripus/Intercalarium ligaments

\% Z1=mechanical impedance of ligament L1 (collagen)

\% Z2=mechanical impedance of ligament L2 (elastin)

\% Z3=mechanical impedance of ligament L3 (collagen+ichthyocol)

\% Z4=mechanical impedance of ligament L4 (collagen+ichthyocol)

\% Model L1, L2 as pure springs

\% Model L3, L4 as Voigt elements

\% K_L1 = 1.8e5; \quad Z_1 = K_L1 s; \quad \text{Nsec/m}

\% K_L2 = 108; \quad Z_2 = K_L2 s; \quad \text{Nsec/m}

\% K_L3 = K_L1; \quad Z_3 = K_L3 s + 0.01 Z_t e; \quad \text{Nsec/m}

\% K_L4 = K_L1; \quad Z_4 = K_L4 s + 0.01 Z_t e; \quad \text{Nsec/m}

\% Z_L=mechanical impedance of tripus

\% Z_i=mechanical impedance of intercalarium

\% Z_s=mechanical impedance of scaphium

\[ Z_i = J_i(s^2 + s G_1^2 L_1 + G_2^2 s L_2 + G_3^2 s L_3 + Z_3); \quad \text{Nsec/m} \]

\[ Z_i = J_i(s^2 + s Z_3 + Z_4); \quad \text{Nsec/m} \]

\[ Z_s = J_i(s^2 + s Z_3 + Z_4); \quad \text{Nsec/m} \]

\% Constants(1) = GL;

\% Constants(2) = Ad;

\% Qoutweb = [Z1 Z2 Z3 Z4 Z_s Constants];

\textbf{webCanals.m}

\textbf{function Qoutcanals = webCanals(w, lengthFish)}

\% created 10-8-96 by Jim Finneran

\% last modified 3-10-97, JF

\textbf{s} = sqrt(-1) \wedge w;

\textbf{if ~strcmp(matlabVersion, 'S3.5')}

\textbf{eval('global \_densityWater speedWater TRUE FALSE');}

\textbf{Constants = zeros(size(s));}

\textbf{else}

\textbf{Qoutcanals = webCanals(w, lengthFish)}

\textbf{end}
```matlab
else
    Constants = zeros(s);
end
s = sqrt(-1)*w;

% Model SI, SE, and TC in three circular, branching sections
% Define geometric and material properties for each section
% rho = density
% MB = Bulk modulus
% u = dynamic viscosity
% D = diameter
% L = length
% A = cross-sectional area

% Section 1
rho(1) = 1008;
D(1) = 0.022*lengthFish;  \quad \text{m}
L(1) = 0.028*lengthFish;  \quad \text{m}
A(1) = \pi*D(1)^2/4;  \quad \text{m}^2
u(1) = 0.76e-3;  \quad \text{Ns/m}^2

% Section 2
rho(2) = 1010;
D(2) = 0.01*lengthFish;  \quad \text{m}
L(2) = 0.059*lengthFish;  \quad \text{m}
A(2) = \pi*D(2)^2/4;  \quad \text{m}^2
u(2) = 1.20e-3;  \quad \text{Ns/m}^2

% Section 3
rho(3) = 1010;
D(3) = 0.044*lengthFish;  \quad \text{m}
L(3) = 0.077*lengthFish;  \quad \text{m}
A(3) = \pi*D(3)^2/4;  \quad \text{m}^2
u(3) = 1.20e-3;  \quad \text{Ns/m}^2

% release membrane
Rrm = 1.0e-3;  \quad \text{m}
k1 = 0.171;
E3 = 1.0e9;  \quad \text{Nm}^2
toverR = 0.24;

% inertance and resistance for each section depend on
% freq - dictates laminar or turbulent behavior
for m = 1:3
    w0 = u(m)*rho(m)/D(m)^2;
    M1 = 4./3.*rho(m)/A(m)*L(m);
    M2 = rho(m)/A(m)*L(m);
    R1 = 128*u(m)*A(m)*D(m)*L(m);
    R2 = 8*L(m)/D(m)*3*sqrt(2*rho(m)*u(m)*w);  \quad \text{Ns/m}^2
    R20 = 8*L(m)/D(m)*3*sqrt(2*rho(m)*u(m)*2*rho(m)*u(m)*w*7200);  \quad \text{Ns/m}^2
    for n = 1:length(w)
        if (w(n) < 32*w0)
            M(n,m) = M1;
            R(n,m) = R1;
        elseif (w(n) > 7200*w0)
            M(n,m) = M2;
            R(n,m) = R20;
        else
            M(n,m) = M1 + (M2-M1)/(7200*w0-32*w0)*(w(n)-32*w0);
            R(n,m) = R1 + (R20-R1)/(7200*w0-32*w0)*(w(n)-32*w0);
        end
    end
end
```
% Compliance of saccular chamber
C3 = 2/3*pi*k1*Rrm^3/E3/(toverR)^3; % m^3/Pa

% Mechanical impedances (PAQ) of each section
Z1 = M(:,1).*s + R(:,1); % Ns/m
Z2 = M(:,2).*s + R(:,2); % Ns/m
Z3 = M(:,3).*s + R(:,3) + (1./C3).*s; % Ns/m
Zfc = (2.*Z1 + 2.*Z2 + Z3); % Ns/m

Constants(1, 1) = A(1);
Constants(2, 1) = A(3);
Qoutcanals = [Zfc Constants];

solveWebApparatus.m
% This script sets up the 4x4 frequency matrix and solves
% for the velocities of the various structures
% created 1-25-97 by Jim Finneran
% last modified 3-26-97, JF

V1 = ((Zsb2+Z21)*S1+S2*Zl2)./((Zsb1+Z12).*Z12.*Z21);
V2 = ((Zsb1+Z12).*S2+Z1.*Z21)./((Zsb1+Z12).*Z21.*Z12);
D = (Z3/2).*(Zsc+Ac^2.*Zfc)-Zic.*Ztr.*Zsc.*Ac^2.*Zfc-2.*Ztr;
Vsc = (GL*Gt*Z3.*Zte.*Z4).*V1;
Vic = (GL*Gt*Z3.*Zte).*Zsc.*Ac^2.*Zfc.*Ztr.*Zfc+Z4.*2)./D;
V3 = -GL*Gt*Zte.*V1.*(-Zic.*Zsc-Ac^2.*Zic.*Zfc+Z4.*2)/D;
Psi = Ad*GL*Gt*Z3.*Zte.*V1.*Z4.*Zfc/D;
Vsa = Ad/Atc*Vsc;
Vt = -GL*V3;

clear a b Zsbl Zsb2 Z12 Z21 Zte Ztr Zic Z3 Z4 Zsc Zfc

daculate1D.m
function QoutSaccule1D = daculate1D(w, lengthRsh, massFish, Vd, Vi, Vsa)
% %
% created 1-26-97 by Jim Finneran
% last modified 3-11-97, JF

j = sqrt(-1);
s = j*w;

% Setup rotation matrix to convert velodies to saccule coordinates
Q = pi/6;
R = [-cos(Q) 0 sin(Q);0 -1 0;sin(Q) 0 cos(Q)];

% Find direct and indirect particle velocity in hair cell direction
for n = length(w),
    VdSac(1:3,n) = R*Vd(n,1:3);
    ViSac (1:3,n) = R*Vi(n,1:3);
end

% Endolymph properties
rhoE = 1010; % kg/m^3;
visE = 1.20e-3; % Ns/m^2

% Saccular otolith properties
ms = 0.0085e-6*massFish; % kg
Lsg = 0.034*lengthFish;  % sagitta length (m)
rhoS = 2390;   % kg/m^3
Vol = ms/rhoS;   % m^3
Vadd = Vol;   % m^3 (additional volume due to fluid)
me = rhoE*Vadd + ms;   % effective mass
Dsg = 1.0e-3;   % sagitta diameter (m)

% Single hair cell ciliary bundle properties
Ktotal = 1.35e-3;   % N/m
Kgs = 0.225*Ktotal;   % N/m
Ksp = 0.375*Ktotal;   % N/m
Ksof = 0.400*Ktotal;   % N/m
Bsof = 0.027e-6;   % N/m
Bcb = 6e-6;   % N/m
Zhc = Kgs*Bcb./(Bcb*s+Kgs)+Ksp./B+Ksof.^Bsof;

% Mech impedance for viscous drag on otolith
wO = w.*visEhoE/(Dsg/2)^2);
Zcyl = 2*pi*L^g*visP(1 + 2*sqrt(wO)+j*sqrt(wO).*(2+sqrt(wO))).

if -strcmpCmatlabVersion, '83.5')
    Zom = Inf * ones(size{w};
    Zsg = me.*(1+Zhc.^om).*s+Nhc*Zhc+Zcyl.*(1+Zhc./Zom);
else
    %Zom = Inf * ones(w;
    Zsg = me.*s+Nhc*Zhc+Zcyl;
end

% Mech impedance of input terms
Zm = ms.*(1-rhoEAtioS).*s;
Zf = rhoE*(Vol+Vadd)*s + Zcyl;

vDirect = -Zm./Zsg.*VdSac(3,:);
vindirect = -Zm./Zsg.*ViSac(3,:);
vWeb = -Zf./Zsg.*Vsa;

Xrel = (vDirect + vindirect + vWeb)./s;
Xse = (VdSac(3,:)+ViSac(3,:))./s;
Xsg = Xrel + Xse;
Hse = -Zm.^sg;
Hsa = -Zt./Zsg;
QoutSacculet D = [vDirect vindirect vWeb Xrel Xsg Xse Hse Hsa];
return

setupOutput.m
% setupOutput.m
% Setup relative motions and phase
% created 2-20-97 by Jim Finneran
% last modified 3-25-97, JF

f = frequencyArray;
RM1 = abs(V1).*sqrt(Ed / densityWater).*densityWater.*speedWater./1e-6;
RM2 = abs(V2).*sqrt(Ed / densityWater).*densityWater.*speedWater./1e-6;
RM3 = abs(V3).*sqrt(Ed / densityWater).*densityWater.*speedWater./1e-6;
RMT = \abs{V_t} \cdot \sqrt{Ed / \text{densityWater} \cdot \text{speedWater} \cdot 1e-6};
RMic = \abs{V_{ic}} \cdot \sqrt{Ed / \text{densityWater} \cdot \text{speedWater} \cdot 1e-6};
RMsc = \abs{V_{sc}} \cdot \sqrt{Ed / \text{densityWater} \cdot \text{speedWater} \cdot 1e-6};
RMsa = \abs{V_{sa}} \cdot \sqrt{Ed / \text{densityWater} \cdot \text{speedWater} \cdot 1e-6};

\text{phase1} = 180/\pi \cdot \text{unwrap(\angle(V_t))};
\text{phase2} = 180/\pi \cdot \text{unwrap(\angle(V_{ic}))};
\text{phase3} = 180/\pi \cdot \text{unwrap(\angle(V_{sc}))};
\text{phaseT} = 180/\pi \cdot \text{unwrap(\angle(V_t))};
\text{phaseIC} = 180/\pi \cdot \text{unwrap(\angle(V_{ic}))};
\text{phaseSC} = 180/\pi \cdot \text{unwrap(\angle(V_{sc}))};
\text{phaseSA} = 180/\pi \cdot \text{unwrap(\angle(V_{sa}))};

Ddirect = \abs{\text{vDirect}} \cdot \sqrt{Ed / \text{densityWater} \cdot \text{speedWater} \cdot 1e-6};
Dindirect = \abs{\text{vIndirect}} \cdot \sqrt{Ed / \text{densityWater} \cdot \text{speedWater} \cdot 1e-6};
Dweb = \abs{\text{vWeb}} \cdot \sqrt{Ed / \text{densityWater} \cdot \text{speedWater} \cdot 1e-6};

\text{phaseDirect} = 180/\pi \cdot \text{unwrap(\angle(Ddirect))};
\text{phaseIndirect} = 180/\pi \cdot \text{unwrap(\angle(Dindirect))};
\text{phaseWeb} = 180/\pi \cdot \text{unwrap(\angle(Dweb))};

\text{phaseSG} = 180/\pi \cdot \text{unwrap(\angle(Xsg))};
\text{phaseSE} = 180/\pi \cdot \text{unwrap(\angle(Xse))};
\text{phaseRel} = 180/\pi \cdot \text{unwrap(\angle(Xrel))};

\% Shift Xsg by 360° if necessary
if \abs{\text{phaseSG}(1) - \text{phaseSE}(1)} > 300
    \text{phaseSG} = \text{phaseSG} - 360;
end

plot35.m
\% Plot35 script
\% menu choices for plot styles for matlab v3.5
\% This script handles the output plotting under matlab v3.5
\% Since multiple figure windows do not exist, a simple menu
\% dialog is used to toggle between desired outputs
\% created 2-20-97 by Jim Finneran
\% last modified 3-23-97, JF

\% Define relative motions / phases
setupOutput

choice = 1;
while choice <= 4
    clf
    clg
    disp('Legend')
    if (choice == 1)
        subplot(211), semilogx(f, RM1, '-', 'f, RM2, --', 'f, RM3, -', 'f, RMic, x, f, RMsc, +')
xlabel('frequency (Hz)')
ylabel('mag [(um/s)/Pa]')
title('relative velocity - location')
    subplot(212), semilogx(f, phase1, '-', 'f, phase2, --', 'f, phase3, -
', 'f, phaseIC, x, f, phaseSC, +')
xlabel('frequency (Hz)')
ylabel('phase (deg)')
disp('RM1 -')
disp('RM2 --')
disp('RM3 -');
end

306
disp('RMic x');
disp('RMsc +');

elseif (choice == 2)
    subplot(211), loglog(f,RMdirect,'-',f,RMindirect,'-',f,RMweb,'-.');
xlabel('frequency (Hz)')
ylabel('mag (um/Hz)')
title('Relative velocity - ')
subplot(212),semilogx(f,phaseDirect,'-',f,phaseindirect,'-',f,phaseWeb,'-.');
xlabel('frequency (Hz)')
ylabel('phase (deg)')
disp('Direct -');
disp('Indirect --');
disp('Web .-');

elseif (choice == 3)
    subplot(211), loglog(f,Dsg,'-',f,Dse,'-',f,Drel,'-.')
xlabel('frequency (Hz)')
ylabel('mag (um/Pa)')
title('Displacements - ') subplot(212),semilogx(f,phaseSG,'-',f,phaseSE,'-',f,phaseRel,'-.',f,180/pi*angle(Pa));
xlabel('frequency (Hz)')
ylabel('phase (deg)')
disp('Xsg -');
disp('Xse --');
disp('Xrel .-');
disp('Pa .-');
else (choice == 4)
end
choice = menu('Select plot style','Swimbladders/Web Ossicles','HC shear','Saccule displacements','Quit');
end

plot40.m
% Plot40 script
% created 2-20-97 by Jim Finneran
% last modified 3-26-97, JF

% display normalized velocities?
plotVelocities = FALSE;
% display normalized displacements?
plotDisplacements = FALSE;
% display transfer functions?
plotTFs = TRUE;
% display titles?
showTitle = FALSE;
% display along with exp data?
showData = FALSE;

hstart = 50;
vstart = 50;
hsizex = 450;
vsizex = 525;
pos = [hstart vstart hsizex vsizex];
currentFig = 1;

% Define relative motions / phases
setupOutput

if (plotVelocities)
    f1 = figure(currentFig);
set(f1,'Position', pos);
subplot(2,1,1);
semilogx(f,RM1,'r-',f,RM2,'w--',f,RMT,'b:');
set(gca,'FontSize',[10]);
set(gca,'XTickLabels',[10 100 1000 10000]);
RMylim = get(gca,'YLim');
xlabel('frequency (Hz)');
ylabel('amplitude (μm/s)/Pa')
legend('r-','w--','b:',' atr','-1')
if (showTitle)
    title('normalized velocity - ' location)
end
subplot(2,1,2);
semilogx(f,phasel,'r-',f,phase2,'w-',f,phaseT,'b:');
set(gca,'FontSize',[10]);
set(gca,'YLim',[-360 360], 'YTick', [-360 -180 0 180 360]);
set(gca,'XTickLabels',[10 100 1000 10000]);
xlabel('frequency (Hz)');
ylabel('phase (deg)')
legend('r-','w-','b:',' atr','-1')
currentRg = currentRg +1;
end
if (plotDisplacements)
    f2 = figure(currentRg);
    set(f2,'Position', pos);
    f2a1 = subplot(2,1,1);
    loglog(f, Ddirect, 'r-', f, Dindirect, 'm--', f, Dweb, 'w-');
    set(gca,'FontSize',[10]);
    set(gca,'XTickLabels',[10 100 1000 10000]);
    xlabel('frequency (Hz)');
ylabel('amplitude (nm/Pa)')
legend('r-','m--','w-',' dir ',' ind ',' web','-1')
if (showTitle)
    title('normalized displacements - ' location)
end
f2a2 = subplot(2,1,2);
semilogx(f,phaseDirect,'r-',f,phaseIndirect,'m--',f,phaseWeb,'w-');
set(gca,'FontSize',[10]);
set(gca,'XTickLabels',[-360 360], 'YTick', [-360 -180 0 180 360]);
set(gca,'XTickLabels',[10 100 1000 10000]);
xlabel('frequency (Hz)')
ylabel('phase (deg)')
legend('r--', 'm-', 'w:', 'web', '-1')
currentFig = currentFig + 1;

f3 = figure(currentFig);
set(f3,'Position' , pos);
subplot(2,1,1), loglog(f,Dsg,'r-',f,Dse,'m-',f,Drel,'w:');
set(gca,'FontSize',[10])
set(gca,'XTickLabels',[10 100 1000 10000]);
xlabel('frequency (Hz)')
ylabel('amplitude (nm/Pa)')
legend('r--', 'Xsg ','m-',' Xse ','w:',' Xrel ','-1)
if (showTitle)
title(\"normalized displacements - ' location\")
end
subplot(2,1,2);
semilogx(f,phaseSG,'r-',f.phaseSE,'m-',f,phaseRel,'w:');
set(gca,'FontSize',[10])
set(gca,'YLim',[-540 360]);'YTick',[-540 -360 -180 0 180 360]);
set(gca,'XTickLabels',[10 100 1000 10000]);
xlabel('frequency (Hz)')
ylabel('phase (deg)')
legend('r--', 'Xsg ','m-',' Xse ','w:',' Xrel ','-1)
currentRg = currentRg +1 ;

f5 = figure(currentFig);
set(f5,'Position' , pos);
set(gca,'FontSize',[10])
set(gca,'XTickLabels',[10 100 1000 10000]);
xlabel('frequency (Hz)')
ylabel('amplitude ratio (dB)')
legend('r--', '1/20*log10(abs(V3/V1))','b--','20*log10(abs(V1/V3))','w:')

f7 = figure(currentFig);
set(f7,'Position' , pos);
set(gca,'FontSize',[10])
set(gca,'XTickLabels',[10 100 1000 10000]);
exlabel('frequency (Hz)')
ylabel('amplitude ratio (dB)')
legend('r--', '1/20*log10(abs(Hse))','b--','20*log10(abs(Hsa))','w:')

309
end
subplot(2,1,2);
semilogx(1,180/pi*unwrap(angle(Hse)),'r-',f,180/pi*unwrap(angle(Hsa)),'b-');
set(gca,'FontSize',[10])
set(gca,'YLim',[-360 360]),'YTick',[360 -180 0 180 360]);
set(gca,'XTickLabels',[10 10 100 1000 10000]);
xlabel('frequency (Hz)');
ylabel('phase (deg)');
legend('Hse','b--','Hsa','-1');
currentFig = currentFig +1;
end
if (showData)
  % load experimental data -> get w, mag(w), phase(w)
  if strcmp(matlabVersion, 'S3.5')
    disp('Directory contents:');
dir;
    filename = input('Enter data filename: ');'
  else
    [filename, pathname] = uigetfile('*.dat', 'Select data file');
    eval('cd ', pathname);
  end
  eval(['load ', filename]);
  dataMatrix = strtok(filename, '.');
  freq = dataMatrix(:, 1);
  mag = dataMatrix(:, 2);
  phase = dataMatrix(:, 3);
s = figure(currentFig);
set(s,'Position', pos);
topAxis = subplot(2,1,1);
semilogx(freq,mag,'bo',f, phase,'r-');
set(gca,'FontSize',[10])
set(gca,'YLim',[0 100]);
set(gca,'XTickLabels',[10 10 100 1000 10000]);
xlabel('frequency (Hz)');
ylabel('amplitude (m/s)/Pa');
botAxis = subplot(2,1,2);
semilogx(freq,phase,'bo',f,phase,'r-');
set(gca,'FontSize',[10])
set(gca,'YLim',[-360 360]),'YTick',[360 -180 0 180 360]);
set(gca,'XTickLabels',[10 10 100 1000 10000]);
xlabel('frequency (Hz)');
ylabel('phase (deg)');
currentFig = currentFig +1;
end
clear plotVelocities plotDisplacements plotTFs showTitle


Doebelin, E.O. (1972). System Dynamics: Modeling and Response (Ohio State University, Columbus, Ohio).


the cod," J. Comp. Physiol. 122, 1–8.

of the frog," Hearing Res. 23, 93–104.

adaptation in mechanoelectrical transduction by the bullfrog's saccular hair cell,"

Science 230, 745–752.

the response of vertebrate hair cells to controlled mechanical stimuli," Proc. Natl.
Acad. Sci. 74, 2407–2411.


NY).

Anim. Behav. 15, 324–335.


Jaramillo, F. and Hudspeth, A.J. (1993). "Displacement-clamp measurement of the forces
1334.

Am. J. Anat. 150, 605–630.


transduction in the frog vestibular sensory apparatus: I. The otolithic membrane,"
Hearing Res. 45, 179–190.


Tavolga, W.N., Editor. (1976). Sound Reception in Fishes. Benchmark papers in animal behavior, Vol. 7 (Dowden, Hutchinson & Ross, Stroudsburg, Pa.).


