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**Sound localization and auditory response capabilities
in the round goby (*Neogobius melanostomus*).**

By

Audrey Katharina Rollo

A Thesis

Submitted to the Faculty of Graduate Studies and Research
through the Department of Biological Sciences
in Partial Fulfillment of the Requirements for
the Degree of Master in Science at the University of Windsor

Windsor, Ontario, Canada
2005

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Abstract:

A fundamental role of vertebrate auditory systems is determining the direction of a sound source. While fish show directional responses to sound, sound localization remains in dispute. Determining directionality is the ability to distinguish between the left or right side, while localization is being able to determine where in space the origin is. The species used in the current study, *Neogobius melanostomus* (round goby) uses sound in reproductive contexts, with both male and female gobies showing directed movement towards a calling male. A two-choice laboratory experiment was used (active versus quiet speaker) to analyze behaviour of gobies in response to sound stimuli. When conspecific male spawning sounds were played, gobies moved in a direct path to the active speaker, suggesting true localization to sound. Of the animals that responded to conspecific sounds, 85% of the females and 66% of the males moved directly to the sound source. Auditory playback of natural and synthetic sounds showed differential behavioural specificity. Of gobies that responded, 89% were attracted to the speaker playing Italian goby (*Padogobius martensii*) sounds, 87% to a 100 Hz tone burst, 62% to white noise, and 56% to black goby (*Gobius niger*) sounds. During the round goby call, swimming speed to the playing speaker was doubled, and the angle standard deviation was two times more direct than during any other sound playback. Results suggest a strong localization of the round goby to a sound source, with some differential sound specificity. This research is the first to explicitly quantify the ability of a fish to localize a sound source.

Acknowledgements

Thanks most of all to my Mom, Dad, and Rob for all of your love and support.

Dennis – I am very honoured to be the first out of what will be a long list of graduate students to come out of your lab. I wanted to dedicate this thesis to you, because of your encouragement I decided to go to grad school. You are the best advisor a grad student could ask for, and a good friend. Thanks for all of your positive words, and your unwavering help. You are the smartest person I know....

Higgs Lab.....what can I say, the unofficial motto fits ☺Gotta love an all female lab (somehow you fit in there Rumi). Andrea, best of luck for finishing school quick and I can't wait to see the new baby. Thanks for being a good friend, I will miss the serenades. Kristen....I definitely see lots of papers coming out from you. Keep up all your hard work and don't let things get to you. Kirsten, good luck with the upcoming school year...if anyone can get first year into shape it's you! Eva, thanks for taking care of the lab and keeping us on our toes! Rumi.....the best one was the kids and the guy at the window...raggae style, also the kid on the street with the dog. Maria, to sum it up; ...Scottish accents, obscenities at the Detroit Science Center, and Vancouver craziness.

Misun...great times! What am I going to do without you!! You are a wonderful person and I am sure I will see you again...shyness. Christine, if anything good came out of TA'ing first year; it was meeting you....slices, cuties, casino, cuties, dancing, cuties. Thanks for always listening. Camilo, you made me want to be better, thanks for inspiring me. Carla, you've always being there for me – you are a great friend! Chelsey and Yakuta, we are the graduate sisters. It was nice to go through the last crazy month with you two...and then the celebrationssssss. ☺ I am so glad I met everyone here...I will miss you all very much!!

Sarah and Tori....you two are such good friends. You kept me sane through a lot of madness; I will always cherish our long, late night phone calls. I am so thankful that the boyz brought us together.

Thanks to all the graduate students from Bio, GLIER, and Earth Sciences, and all of the faculty and staff at the University, Nancy your the best.

Last but not least, puppy and Jade for your unconditional cuteness.

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Chapter One Introduction

Communication through Sound

The ability to communicate, through sounds or body language, is essential to pass along information to other individuals. Sounds can be produced in a variety of ways in animals. The most recognized way to produce sound is through vocal cords (like in many vertebrates), but sound can also be generated by using other parts of the body. Feral horses, *Equus caballus*, will stomp their foot to show aggression (Cameron et al 2003), while some birds, such as neotropical manakins (*Aves: Pipridae*), produce sounds by rubbing their wings or tail feathers together to attract a mate (Prum 1998). Underwater sound is essential for relaying messages to others when water visibility is limited. Hence the variability in sound producing mechanisms in aquatic animals is quite large. Snapping shrimp (*Synalpheus parneomeris*) are the largest source of sound in the coastal ocean, producing very loud broadband sounds by snapping their claws and cavitating water (Au and Banks 1998). One of the effects of the snapping is to stun or kill prey animals. When startled or frightened, Asian redbelly catfish (*Hemibagrus wyckioides*) emit a loud squeak by pressing out air from their gill slits (Heyd and Pfeiffer 2000). Sound-producing mechanisms in male cichlids (*Tramitichromis intermedius*) involve sound generation by the pharyngeal mill, amplified by the swim bladder (Lobel 2001). Adult croaking gouramis (*Trichopsis vittatus*) generate sounds by beating their pectoral fins against their body (Henglmüller and Ladich 1999). Even though the variation in sound producing mechanisms is vast, the type of functions for which

sound is used is more conserved. Several species are known to produce apparent warning, alarm, or escape sounds when prodded or attacked (Heyd 2000; Amorim 2004). In the study by Heyd (2000), 1000 - 4000 Hz sounds (frequencies above the hearing range of most fish) were produced from catfish when taken out of the water by predaceous fishing mammals and birds, which are able to detect these high frequencies. These sounds are thought to be made to warn the predator that the food they just caught will not be an easy meal (the pectoral and dorsal spines on the catfish are erected simultaneously, with locking mechanisms, when the fish is removed from the water). These warning sounds are very similar to the chat of rattlesnakes which caution nearby animals of its poisonous bite. Sound is also produced during territorial defence (Myrberg 1997; Johnson 2000). Kenyon (1994) showed male bicour damselfish, *Pomacentrus partitus*, exhibiting courtship sounds, a 'chirp' and a grunt. The chirp occurs at the beginning of courting and the 'grunt' just prior to spawning. Male competitors would travel towards spawning sounds only during the grunt phase. The intentions of the competitor damselfish would likely be to interfere with the imminent spawning or to gain a possible spawning partner. Pupfish, *Cyprinodon bifasciatus*, have territorial boundaries which they patrol. Calls are produced by males during pursuits of nearby fish, while the pupfish follows a female, as well as just after spawning (Johnson 2000). Amorim et al (2004) showed grey gurnard (*Eutrigla gurnardus*) produce sounds during competitive feeding. These grunts warn of the forager's presence to nearby competitors, deterring other fish from gaining access to disputed food items. The ability of a fish to communicate

effectively within its environment, regardless of the variability in the sound producing methods, is essential for survival.

Sound in Reproduction

Acoustic displays are not only important as a warning or alarm sound, but in a reproductive context as well. Mate competition and choice are two phases of the reproductive process in which fish can use sound to demonstrate their physical condition. Sound can indicate if the fish is suitable for reproduction, an attractant for the opposite sex, or if the fish is primed to copulate. Differences in sound amplitude and pulse rate could reveal a fish's body size (Ladich 1988; Lindström 1992; Malavasi et al 2003), which could be important for mate recognition and choice. Lindström (1992) studied male sand gobies (*Pomatoschistus minutes*) and found that body size often correlated with sound pressure levels, since acoustic pulses are generated by specialised sonic muscles (Demski et al. 1973), and the mass of these muscles increases with increasing body size (Lindström 1992). It can then be assumed that the larger the sonic muscle the bigger the fish, resulting in a deeper sound emitted from larger sand gobies. Rowe and Hutchings (2004) also looked at the sonic muscles, but in Atlantic cod (*Gadus morhua*). This study found that males had drumming muscles that were larger than females, which increased in mass prior to spawning and declined subsequently. Drumming muscle mass of spawning males was also positively associated with body size, condition, and fertilization potential, suggesting that sound production may be an indicator of the size of the signaller and may reveal information about individual quality. The cavity-nesting darters

Etheostoma nigripinne and *Etheostoma crossopeterum* also produce sounds associated with reproduction (Johnston and Johnson 2000). Males produce sounds during aggressive encounters and courtship activities, categorized as drums, knocks, and purrs. Sounds associated with aggressive encounters could indicate to a female that the fish is a strong defender of its territory, and would be more of a quality mate. Sound production indicating size of a mate during the spawning season has fitness benefits, perhaps through a role in mate competition.

Sound can also indicate, to potential mates, if another fish is ready to mate. Sound production rate has been shown to increase with reproduction, especially in fish that form spawning aggregations (Saucier and Baltz 1993; Finstad 2004). This relationship is largely due to increases in courtship calling rather than production of specific spawning sounds. Hawkins (2000) studied the haddock (*Melanogrammus aeglefinus*) and showed male fish produce a series of 'knocking' sounds during the spawning season. The male initially produces a short series of slowly repeated 'knocks' until the sounds becomes longer and faster (coinciding with an increase in arousal of the male). It is suggested that these sounds play a role in synchronising the reproductive behaviour of the male and female (Hawkins 2000). Some sounds are thought to attract the female to the spawning area (McKibben and Bass 1998). Lugli et al. (1995) found the freshwater Italian goby (*Padogobius martensii*) emits 'drumming' sounds to lure females into the nest.

Sound used to demonstrate viability as a mate, as well as an attractant to reproduce, is also used to synchronize copulation. *Hypoplectrus unicolor*, a coral reef fish,

produces sound prior to, or simultaneously with, gamete release into the water (Lobel 1992). This could be an acoustic signal to its mate to ensure synchronous gamete release. In the East African Rift Lake cichlid fish, *Tramitichromis intermedius*, only the male emits sound during courtship (Ripley and Lobel 2004). Sound is intentionally used to communicate that the male cichlid is ready to spawn, with the first sound emission coinciding with the first courtship activity (quivering), and spawning occurring just days later. Thus the ability to produce sound and perform quiver behaviour simultaneously could also be a measure of mate quality. Primed for reproduction, weakly electric mormyrid fish (*Pollimyrus isidori*) migrate from tributaries into shallow (2-3 m) flood plains during the flooding season (Crawford et al 1997). Male sound production is stimulated by the presence of the females, comprised of grunts and moans during the night. Fishes' ability to recognize a sound pattern is necessary to pick up cues when and with whom to mate, ensuring the survival of a community of fish.

Sound Detection in Fish

Producing sound would have no context if the organism was not capable of receiving the information. Thus, hearing is an integral part of understanding the environment, and consequently propagating a species. There are two physical properties of sound, particle motion and sound pressure. Sound can generate particle motion and sound pressure in the near field, but as the sound wave travels, the motion dissipates more quickly in the far field displaying only pressure (Braun and Coombs 2000). The near field is defined as the region of space close to a sound source, whereas far field is the

region where the radial distance from the sound source is much greater than a wavelength (Rogers and Cox 1988). Lateral line neuromasts (cupular organs) respond to near field effects with frequencies up to about 200 Hz (Braun and Coombs 2000). Fish should be able to determine the direction of a sound source in the near field by comparing responses of different cupular organs. Sound pressure effects are dominant at higher frequencies and at increasing distance from the fish. Detection of near-field vibrations can thus occur using both the ear and the lateral lines, but only in close proximity to the sound source. Far-field waves travel long distances in water, the inner ears of fish detect these sound waves.

Like other vertebrates, fish have inner ears located near the brain enabling the fish to hear (Figure 1). However, unlike mammals, the cochlea and the tympanic membrane (eardrum) are not present, and the ear does not open to the outside of the body. Instead, the sensory hair cells, located inside the ear, are stimulated by otoliths (tiny calcareous structures) and detect sound (Figure 2). There are six otoliths, each within the three sets of auditory organs; the saccule, lagena, and utricle. In most fishes, the saccule is thought to be primarily an auditory organ, playing important roles in directional hearing and frequency responses (Lu and Xu 2002). The lagena is still unknown as to its role in hearing (although in the goldfish the lagena responds with great sensitivity to acoustical particle motion) (Fay 1995). Traditionally the utricle has been considered a vestibular organ, however Lu et al (2004) has shown that the utricle in the sleeper goby (*Dormitator latifrons*) plays an auditory role in azimuth (horizontal) directionality and that the directional hearing response dynamic range is

Figure 1: Location of the ear and brain in a fish head. Labelled parts of the ear; saccule, lagena, and utricle. Weberian ossicles not found in all fish. Figure modified from Fay and Feng 1987.

Figure 2: Schematic drawing of the otolith above the hair cells. Depending on the direction of the sound source (indicated by arrows), the macula will move relative to the otolith, causing the hair cells to bend. This displacement is relayed to the brain, indicating the direction of the sound. Figure modified from Lu and Popper 2000.

extended by the utricular organ. Sound detection occurs when acoustic vibrations in the water are conducted through the skeleton of the head to the inner ears, causing a stimulation of the hair cells relative to the lagging otolith. Hair cells are extended epithelial cells with a ciliary bundle located apically (Figure 3). The ciliary bundle is composed of stereocilia, graded in size with the longest next to a single kinocilium. An acoustical wave passes through the flesh of a fish undisturbed (since it has the same density as the surrounding water) until it reaches the more dense otolith, this causes the hair cells (attached to the otolith) to bend in that direction. If the hair cell movement is in the direction of the kinocilium, the hair cell membrane potential will result in a depolarization (Schellart and Popper 1992). Displacement, or movement, of the stereocilia in the opposite direction of the kinocilium causes hyperpolarization. Thus, the cells' response is determined by the amplitude of stereociliary deflection along a single axis. This sends a signal to the brain with information about the sound source.

In addition to the ears in a fish, sound is also detected through the lateral line system (Figure 4). The mechanosensory lateral line system of fish is used to detect water motion (relative to the surface of the animal) and mediates such varied behaviours as prey detection, predator avoidance, hydrodynamic imaging, rheotaxis, schooling, and courtship communication (Coombs and Montgomery 1999). The lateral line system, which runs along the sides of the head and body, contains mechanoreceptors that detect movement by a mechanism similar to the function of those in the inner ear. In most fish, the lateral line system has two types of receptors: canal neuromasts and superficial neuromasts. Canal neuromasts lie within canals located beneath the skin

Figure 3: Schematic drawing of sensory hair cells with the ciliary bundle showing the stereocilia and kinocilia at the apical surface.

Figure 4: Drawing of the lateral line canal system on a generalized fish body and head.

surface, filled with a fluid slightly more viscous than the surrounding water. Small pores from the canals allow any disturbances in the water around the fish to be transferred to the canal fluid, past mechanoreceptors which are all along the tube. These receptors (neuromasts) each have a cluster of hair cells, with the sensory hairs embedded in a gelatinous cap (cupula) sensitive to water acceleration (Figure 5) (Denton and Gray 1982). As the displacement of the moving water bends the cupula, the hair cells transduce the energy into action potentials that are transmitted to the brain. Canal hair cell orientations are typically in opposite direction of each other so one of them will respond best to water flow in one direction in the canal, where the other to water flow in the opposite direction (Coombs et al 1995). In comparison, superficial, or free, neuromasts are found on the skin surface, usually in several specific locations and typically aligned in rows on the body and head (Figure 6). In superficial neuromasts, the cupula responds largely to the velocity of water flowing past it (Denton and Gray 1982). Water sliding past the cupula generates drag causing the cupula to bend. Thus the degree of bending is directly related to water velocity. The lateral line greatly expands the tactile area of perception, by allowing the fish to interpret its environment without actually touching an object.

Sound is also detected through the air-filled chambers (e.g. the swim bladder) in fish. The chambers vibrate, translating pressure of the sound wave into displacement information which is then transmitted to the inner ear. In some fish, sound pressure sensitivity is high and the fish is able to detect a broad range of frequencies due to the presence of hearing specializations creating an indirect pathway to the ears. Fish with

Figure 5: Schematic drawing of the cupula located in the lateral line canal. As water moves past the neuromasts (located in the cupula) information is sent through the lateral line nerve to the brain regarding displacement direction. Brassy sea chub (*Kyphosus vaigiensis*) photo modified from Richard Field. Drawing modified from Dijkgraaf 1962.

Figure 6: Superficial neuromasts (white dots in picture) located on the body and head of a zebrafish (*Danio rerio*), demonstrates general spatial distribution of neuromasts in fish. Neuromasts were stained with the fluorescent dye DASPEI, which selectively stains highly active cells. Fish total length (for scaling purposes) is approximately 10 cm.

these adaptations are termed “hearing specialists” (Popper and Coombs 1982; Ramcharitar et al 2004). Catfish and minnows have a series of bones called Weberian ossicles connecting the swim bladder to the inner ear directly (Von Frisch, 1938; Chardon and Vandewalle 1997) (Figure 7). These bones enable the fish to hear higher frequencies than non-specialists. *Carassius auratus* (goldfish) are the most studied hearing specialists and can detect sound up to 5000 Hz (Kenyon et al. 1998). Other specialists, such as the squirrelfish *Myripristis kuntzei* has the swim bladder directly contacting the ear (Popper 1977). Another type of hearing specialist adaptation is found in the mormyrids, with an auxiliary air bubble attached to the sacculus (Stepetic 1939). In at least two groups of teleosts the utricle is associated with specializations for hearing (Popper and Tavolga 1981; Higgs et al 2004). For example, the marine catfish (*Arius felis*) is an otophysan species with an acute hearing at ~200 Hz, where other otophysans hear best from 500 to 1000 Hz. This is due to the fact that *Arius* has an enlarged utricle with hair cells only along the striolar region (Popper and Tavolga, 1981). Clupeomorph fishes have an air-filled auditory bulla associated with the utricle (Denton and Gray, 1979; Best and Gray, 1980). This specialization in the utricle and associated structures may be the reason why clupeids in the subfamily Alosinae can detect ultrasound up to 180 kHz (Mann et al 1997, 1998, Higgs et al 2004). Fish that have narrower frequency ranges with higher auditory thresholds (and no auditory specializations) are termed “hearing generalists”. Hearing generalists do not detect frequencies above 800 Hz and tend to have higher auditory thresholds. Hearing generalists, such as the oscar (*Astronotus ocellatus*), can hear frequencies between 100 Hz and 2000 Hz (Lu et al 1996). Smith et al (2004)

Figure 7: Orientation of the Weberian ossicles in a zebrafish, linking the swim bladder and ear. Weberian ossicles (indicated by the arrow) are stained using standard cleaning and staining techniques (see Higgs 2003).

showed that tilapia (*Oreochromis niloticus*), a hearing generalist, was less susceptible to noise sound pressure levels than goldfish, a hearing specialist. This lower susceptibility was due to the tilapia's higher auditory threshold levels, where the goldfish was more sensitive to the higher frequencies. This shift in linear threshold relationship shows the divergence in susceptibility between hearing specialist and generalist fishes.

Directionality in Fish

Aquatic sound detection presents certain problems not normally encountered by terrestrial organisms. Humans and other land animals can perceive spatial localization which is the ability to discern azimuth or horizontal (left-right) directionality and zenith or vertical (up-down) directionality (Sabin et al 2005). This directionality can be perceived using localization cues such as Interaural Time Difference (ITD) (Hancock and Delgutte 2004) and Interaural Intensity Difference (IID) (Oswald et al 1999). The Interaural Time Difference (ITD) is the difference in arrival time of a sound to each ear, sounds coming from the left or right will arrive at the corresponding ear first. Although the delay time differences are slight, the brain can extract precise directional information from this data. The head, as well as shoulders and upper torso, form a barrier to a sound's arrival at one ear or the other. This creates an acoustical shadow and an effect called the Interaural Intensity Difference (IID) (Schleich et al 2004). The effect of the shadow is frequency dependent; high frequency sounds are more attenuated than low frequency sounds because low frequencies can bend around obstructions and are not as easily blocked.

For example, this is the reason high frequency information in a complex waveform is more readily perceived at the incident ear--this relative difference in resonance is yet another cue used to determine directionality. Given that sound speed in water is about five times higher than that in air, and the distances between the two ears in fish are generally no more than a few centimetres, fish cannot use interaural time, phase, and intensity differences of sound pressure to localize a sound source (Fay and Feng 1987). Current models of fish hearing assume fish determine the direction of incident sound through otolith motion along the direction of the acoustic wave (de Vries 1950; Fay 1984; Lu et al. 1996). The complex geometry of fish otoliths may help to distinguish flow patterns for sound from different directions (Popper and Coombs 1982).

The ears of fishes are stimulated by otolith motion, either directly (from the water medium to tissue and bone) or indirectly (by sound pressure from the swim bladder or other gas bubble near the ears). When sound energy is transmitted to the ears directly, the body of the fish takes up the sound's acoustic particle motion, and hair cell stimulation occurs due to the difference in inertia between the hair cells and their overlying otoliths. When the sound pathway to the ears is indirect, the swim bladder or gas bubble near the ears expands and contracts in volume in response to sound pressure fluctuations, and this motion may be transmitted to the otoliths. Fishes tend to respond to and encode the directionality of pressure gradients using both the ears and lateral line (Fay 1984; Lu and Popper 1997). Sensory hair cells are morphologically and physiologically polarized so that their response to hair bundle movement is proportional to a cosine function of the direction of stimulation relative

Figure 8: Directional sensitivity of a hair cell. The membrane potential varies with the cosine of the angle between the direction of maximum sensitivity and the applied displacement.

to the most sensitive axis of the cell (Hudspeth and Corey 1977) (Figure 8). This axis is defined as a line from the center of the hair bundle through the kinocilium. Since hair cell groups on the epithelia are oriented in different directions as well as having complex patterns, they may function in directional hearing (Figure 9). Many sensory epithelia have a complex curvature, increasing the range of stimulus directions possible. Plus, each end organ in an ear, as well as corresponding organs of the two ears, orient on nonparallel planes. So fish can potentially obtain a good deal of directional information by comparing separate hair cell inputs from both ears, as well as from all of the end organs (Wubbles et al. 1993). Localization acuity could be ascertained in two kinds of experiments; 180 degree discrimination (where the fish would choose in which direction to orient) or a measure of the smallest angle between the two sources (allowing the animal to discriminate between them). Schuijf (1975) showed cod's (*Gadus morhua*) ability to orient towards a sound source under free field conditions. Cod can also discriminate between sources separated by 10 – 20 degrees in azimuth (with a high signal level), as well as sources from opposing directions (180° apart) in both the horizontal and vertical planes (Schuijf and Buwalda 1975).

Round Goby

The species used in the current studies was the round goby (*Neogobius melanostomus*) (Figure 10). Round gobies are demersal and prefer shallow, brackish waters, but can also be found in freshwater and marine habitats with a depth range of 0 – 30m. They are eurythermal, tolerating temperature ranges of 0 to 30°C, but mainly thrive in

Figure 9: Schematic drawings of various hair cell orientations in fish. ** These patterns represent the majority of fish that have been studied. The arrows indicate the orientation of the hair cells (with respect to the location of the kinocilium) in each epithelial region. Figure from Popper and Fay 1999.

Figure 10: Round goby (*Neogobius melanostomus*). Photo from Dave Jude, Michigan Sea Grant.

warm temperate waters (Kottelat 1997). Round gobies are aggressive, voracious feeders with the ability to forage in total darkness (Dubs and Corkum 1996). Distribution originated in Europe (Sea of Azov, Black Sea and Caspian basins), however several countries (such as Canada and the United States) have reported an introduction of round gobies (via contaminated ballast water of transoceanic ships) with adverse ecological impact resulting (Vanderploeg et al 2002). The round goby is considered a pest in the Great Lakes Basin because they take over prime spawning and habitat sites traditionally used by native species, such as lake trout, *Salvelinus namaycush* (Chotkowski & Marsden 1999), lake sturgeon, *Acipenser fulvescens* (Nichols et al. 2003), and smallmouth bass, *Micropterus dolomieu* (Steinhart et al. 2004). Native fish recruitment is also affected due to the round gobies multiple spawning habits (up to six times a year), and high fecundity (Corkum et al 2004). Round gobies are even thought to reduce the quality of the water, by transferring energy and contaminants from the benthos to higher trophic levels (Morrison et al. 2000). Even though the mechanism for sound production in round gobies has not been studied, other gobies emit sound by expelling pressurized water out of their gills and snapping their jaw (Lugli et al 2004). Round gobies are known to produce several vocalizations, emitted by the male either attracting a female to the nest site or intimidates other males from entering their territory (Protasov et al. 1965). Sound detection in the round goby results from otolith displacement and through the lateral line, since they do not have a swim bladder. Even though round gobies lack a trunk canal, superficial neuromasts are on their body and head, with additional canal neuromasts in the head canals (Jude and DeBoe 1996). The presence of superficial

neuromasts on the body may enable the round goby to detect prey with more sensitivity than species where the body neuromasts lie within a canal.

The round goby was chosen for the current studies due to its sexually dimorphic behaviour, as well as for its abundance and easy collection. Sexual dimorphism can be seen in fish in a variety of attributes which can include behaviour and external morphology. External morphological features can consist of coloration, size differences, and sexual organs, whereas sexually dimorphic behaviour is expressed as different behaviours in opposite sexes of the same species. Corkum (2004) has shown the round goby respond aggressively in the presence of conspecific odours. When an odour is presented in an established male tank, the male reacts strongly and aggressively to the site where the odour was emitted. It has also been shown that the introduction of a large round goby to a weaker or smaller gobies shelter will induce a flight reaction in the smaller goby (Stammmler & Corkum 2005). Although sexually dimorphic behaviour to acoustical sounds has not been investigated in the round goby, studies have successfully shown Gobiidae species (as well as other fish species) react to auditory cues. Male sand gobies (*Pomatoschistus minutus*) produce sounds (consisting of a repeated train of pulses) when a female enters a nest before spawning (Lindström and Lugli 2000). The acoustic parameters of sand gobies indicate a possible role of sound in mate choice. Frillfin gobies (*Bathygobius saporator*) exhibit sexually dimorphic behaviour, with body movement and a change in appearance (Tavolga 1956).

The current thesis project focuses on the localization abilities of round gobies to conspecific spawning cues and the possible sound specificity gobies have to other sound sources. Auditory playback of natural and synthetic sounds showed differential behavioural specificity. Results suggest a strong localization of the round goby to a sound source, with some differential sound specificity.

Thesis Overview and Significance

This study quantifies sound localization in fish and their specificity to sound (including conspecific, heterospecific, and computer generated sounds). Behavioural analysis of the round goby to sound is beneficial in implementing possible capture methods of the fish as well as comprehending basic auditory processing in fish. This invasive, voracious fish threatens the ecosystem of the Great Lakes, through its consumption of larval native fish, out competing adult native fish spawning sites and food resources, and may ultimately cause a large monetary loss. The round gobies ability to localize sound could prove valuable in designing lure traps enticing them with a conspecific spawning sound. The ability of fish to localize sound is still highly debated in science; this research study is the first to explicitly quantify the ability of a fish to localize a sound source.

Chapter Two Introduction

The ability to use sound for communication is essential to pass along information to other individuals. The ability to localize that sound is probably one of the most functional aspects of the auditory system. Determining the direction of a sound could aid in, to name only a few; prey detection, predator or object avoidance, locating a potential mate. Like other vertebrates, fish have inner ears located near the brain enabling the fish to hear. However, unlike mammals, the cochlea and the tympanic membrane (eardrum) are not present, and the ear does not open to the outside of the body. Terrestrial vertebrates perform localization through a combination of interaural time and intensity differences (Hancock and Delgutte 2004, Oswald et al 1999). Although the delay time differences are slight, the brain can extract precise directional information from this data. Given that sound speed in water is about five times higher than that in air, and the distances between the two ears in fish are generally no more than a few centimetres, fish cannot use interaural time, phase, and intensity differences of sound pressure to localize a sound source (Fay and Feng 1987). These facts fuel the debates regarding the ability of fish to localize a sound source. One could argue that directional hearing underwater would be impossible because of the physical properties of a wavelength and the lack of interaural time between the two ears and yet some studies have shown fish can find sound sources readily (Schuijf 1975; McKibben and Bass 1998; Tolimieri et al. 2000).

Current models of fish hearing assume fish determine the direction of incident sound through otolith motion along the direction of the acoustic wave (de Vries 1950; Fay

1984; Lu et al. 1996). The complex geometry of fish otoliths may help to distinguish sound flow patterns from different directions (Popper and Coombs 1982).

Behavioural research studies, such as Schuijf (1975), show cod (*Gadus morhua*) have the ability to orient towards a sound source under free field conditions. Cod can also discriminate between sources separated by 10 – 20 degrees in azimuth (with a high signal level), as well as sources from opposing directions (180° apart) in both the horizontal and vertical planes (Schuijf and Buwalda 1975). Field studies have shown fish are able to localize sound. Tolimieri et al (2000) found higher concentrations of fish larvae in light traps with sound sources than light traps with out sound. Lu and Popper (2001) show fish localize sound from the morphological polarity of hair cells that otolithic afferent neurons innervate. This enables fish to encode directional information about a sound source (predominantly in elevation). McKibben and Bass (1998) show female midshipman fish (*Porichthys notatus*) respond selectively to audible sounds and are capable of differentiating between acoustic signals (duration, frequency, amplitude, and spectral/temporal content).

The current project focuses on the localization abilities of round gobies to conspecific spawning cues and the possible sound specificity gobies have to other sound sources. Prior hypotheses on sound localization in fish have suggested localization is accomplished by the phase difference between particle motion detected by the hair cells directly and sound pressure reradiated from the swim bladder (Schuif, 1975). The species used in the current study, round goby (*Neogobius melanostomus*) has no swim bladder or other obvious hearing specializations and yet it uses sound for reproductive communication (Protasov et al. 1965). Thus sound detection results

from otolith displacement and through the lateral line. The round goby was also selected due to its possible sexually dimorphic behaviour, as well as for its abundance and easy collection. Although sexually dimorphic behaviour to acoustical sounds has not been investigated in the round goby, studies have successfully shown Gobiidae species (as well as other fish species) react to auditory cues (Tavolga 1956, Lindström and Lugli 2000). The current study used playback of natural sounds (round goby, black goby ((*Gobius niger*)), and Italian goby ((*Padogobius martensii*)) spawning sounds) and synthetic sounds (100hz and white noise), to examine differential behavioural specificity and acoustic localization in free-swimming round gobies.

Materials and Methods

Housing Conditions

Fish used in these experiments were collected by angling at different shoreline sites from the Detroit River and Lake Erie. At collection, the goby was unhooked and placed into a large bucket filled with water from the area. After angling 10 to 20 gobies (time frame 30 to 60 minutes), the bucket containing the gobies was transported to the lab, approximately 15 - 30 minutes away. In the laboratory, the gobies were housed temporarily in the transport container equipped with an air-stone, until transferred to the experiment tank. Temporary housing conditions follow University of Windsor Animal Care procedures.

Experimental Set-up

Behavioural experiments were conducted in a 1020 litre rectangle tank with dechlorinated tap water (water depth = 33 cm). At one end of the tank were two underwater speakers (UW-30, Universal Sound Inc), connected to an amplifier (Alesis RA300), which was in turn connected to a Toshiba laptop computer. One speaker was designated the "active" speaker (playing the experimental sounds) and one the "quiet" speaker (no sound being played). The order of presentation alternated between the two speakers and the speakers were 25.5 cm apart. The tank was bisected by a mesh net, 107 cm from the speakers to allow placement of the goby at a defined distance from the speaker while reducing reflections off the back of the tank. To begin an experiment, one goby was placed into the experimental tank, along the mesh partition (Figure 11). The experimental sound started immediately afterward. No acclimation period was given because gobies were only responsive for a limited time (about 2 hours) once brought into the laboratory. The decibel level of the sound stimulus (as measured by a precalibrated hydrophone, Interocean Inc) in the experimental tank varied slightly dependent on sound stimulus presented, specific ranges are below. When a response was observed from the goby, or ten minutes had expired, the experiment ended. The goby was then removed and placed into an aquarium with a filter and air-stone. Sex was ascertained by examination of the urogenital papillae at the end of the trial (Figure 12). The female urogenital papillae are broad and blunt, 0.3-0.5 mm long and 0.2-0.4 mm wide (Miller 1984). The male papillae are somewhat longer, with a length of 0.3-0.6 mm and a terminal slit. Gobies were used only once during the experiment.

Figure 11: Experimental tank set-up. Goby is placed next to net (bottom of picture) in the center of the tank. Sound was played from one of the speakers at the top of the tank. Distance between the net and the speaker is 107 cm.

Figure 12: Urogenital papillae of male and female round goby (modified from Charlebois *et al.* 1997).

Two sets of experiments were performed, in which behaviour, swimming speed, and approach angle were measured in both. Gobies in the first set of experiments (experiment 1) were exposed to a male round goby spawning sound. The sound was recorded in a natural environment by John Janssen and Greg Androsso. A total of 137 round gobies were collected, during the months of July to September, 2004. Of the 137 fish tested 79 were males and 58 were females. The second experiment (experiment 2) had five sounds individually played during different trials. The sounds included vocalizations of round goby, black goby (*Gobius niger*), and Italian goby (*Padogobius martensii*), as well as computer generated 100 Hz tone bursts and white noise. Sound levels played were 138-141 dB re 1 μ Pa for the round goby, 132-140 dB re 1 μ Pa black goby, 138-140 dB re 1 μ Pa for the Italian goby, 144 dB re 1 μ Pa for the 100 Hz tone, and 136 dB re 1 μ Pa for white noise (136 dB re 1 μ Pa). Tank acoustics gradually decreased in dB from speaker to net (Appendix F). Control experiments had no sound. Experimental sounds were also played with a geophone (Geospace LP, sensitivity 19 mV per mm) positioned at the location of goby release in the tank to examine the amount of substrate vibration during playback. At no point did the geophone detect vibrations above background levels (1.5 dB re 1 μ Pa). Italian goby courtship sounds were provided by Marco Lugli (University of Parma, Italy) and black goby calls were obtained from fishbase (www.fishbase.org). The 100 Hz tone burst is similar to the fundamental frequency of the round goby call (168 Hz) whereas white noise encompasses all of the frequencies in the spectrum. Control experiments were run with the goby in a quiet tank (no speaker playing sounds). For the control trials, the amplifier was unplugged from the speakers to eliminate any

possibility of static or buzzing noise. A total of 120 round gobies were used for experiment two, 20 gobies per sound. No goby was used for more than one trial.

Measurements

Trials were recorded with a Sony Digital Handycam camcorder (model DCR-TRV27), then digitized and analyzed using Peak Motus Version 7.0 software. The camcorder was positioned on a tripod over the tank and recorded the behavioural responses of the goby to the sound stimuli. Reaction to the experimental conditions was quantified in terms of the percent of gobies that responded to each sound, which speaker the goby approached, how close to the speaker the goby came, and the speed, average angle, and path deviation at which an approaching goby moved. For percent responding, a goby was recorded as "responding" if it made any movement during the sound presentation. This behaviour was further subdivided into movement to the active speaker, movement to the quiet speaker, or non-directed movement in the tank. Of those fish that showed directed movement to the playing speaker, the nearest approach distance was recorded and subsequently grouped as movement within 10 cm of the active speaker, or stopping 10-13 cm away from the playing speaker, 13-18 cm away from the playing speaker, and 18-30 cm away from the playing speaker. Captured images were digitized and analyzed by Peak Motus Version 7.0. For those fish that responded, velocity, mean path angle to the speaker, and the standard deviation in path angle were recorded. For mean path angle, the angle determined by the Peak Motus program had to be manually corrected for fish position at the start of a trial. A mean corrected angle of 90° indicated a direct heading toward the active speaker. For simplicities sake, when referring to particular sounds, the notation in the

parenthesis will be used. The sounds used in experiment two were; black goby *Gobius niger* (B), Italian goby *Padogobius martensii* (I), round goby *Neogobius melanostomus* (R), 100 Hz tone (T), white noise (W), silent tank/absence of sound (S).

Statistical Analysis

All raw data (sex, sound, and activity), plus data from Peak Motus, were imputed into Microsoft Excel and Systat 10. Data in Excel calculated averages between velocity, angle, and sex of gobies, plus standard deviation of angles and velocity. A two sampled t-test (assuming equal variances) was used to compare sexes to find if there was any variation between them. A Chi square test was performed on the movement to sound between sexes, determining if there was significance in activity within a sex. Systat performed a two-way analysis of variance (ANOVA), between sex and sound type, independent variables, with speed and angle, the dependent variables. If the ANOVA results were significant, Tukey tests compared all the sounds individually and determined which sound was statistically significant.

Results

Experiment One

When the male round goby spawning sound was played in experiment one 37% of the males moved in the tank and 51% of the females moved in the tank (Figure 13). No significant difference ($P = 0.63$) was found in the percent of fish responding to sound between sexes. Of the fish that responded during the trials, three behaviours were

observed: fish that moved toward the playing speaker, fish that moved toward the silent speaker, or fish that moved to neither one of the speakers. When the gobies moved during the trial, 85% of the females, and 66% of the males, moved towards the playing speaker (Figure 14). When movement was observed to the silent speaker, 9% of the responding fish were females and 31% males. Non-directed movement was also observed, with 6% and 3% (female and males respectively), defined as moving less than 30 cm from the starting position.

The average angle to the playing speaker for the round goby in experiment 1 was 89.2° (with a straight path defined as 90°). Females traveled on average 87.4° to the playing speaker, with males moving 90.7° towards the speaker (Figure 15). There was no significant difference between average angle in females and males ($P = 0.60$).

Refer to Appendix A for individual average angles. The standard deviation in approach angle for the round goby females was 7.4° , males 12.0° . There was no significant difference between average angle in females and males ($P = 0.25$). Refer to Appendix A for individual standard deviation angles. When speed was averaged for females and males, females traveled 13.1 cm/sec to the playing speaker, whereas males traveled 19.5 cm/sec (Figure 16). A significant difference was found between sexes ($P = 0.04$), with males traveling much faster to the playing speaker than females. Appendix B has the itemized listing of speed. There was no significant difference in standard deviation of speed for males versus females ($P = 0.12$).

Females had a variation standard deviation of 5.7 cm/sec, males 8.6 cm/sec.

Figure 13: Movement of the round goby during experiment one in response to the male round goby spawning sound. Out of the 137 round gobies, 79 were male and 58 were female. Chi square showed no significant difference between sex and activity in the tank ($P < 0.05$).

Figure 14: Responses of male and female round gobies in experiment one in response to male round goby spawning sounds. Movements include; less than 30 cm of movement into the tank (minimal movement), movement to the silent speaker, or movement to the speaker playing the sound.

Figure 15: Average angle (± 1 s.d.) of approach to the playing speaker of the round goby during experiment one. Out of the 137 round gobies, 79 were male and 58 were female. T-tests showed no significant difference between average angle and sex ($P = 0.60$, $t = 0.91$).

Figure 16: Swimming speed (± 1 s.d.) of male and female round gobies in experiment one in response to male round goby spawning sounds. Out of the 137 round gobies, 79 were male and 58 were female. T-tests showed significant difference between sex and velocity ($P = 0.04$, $t = 2.20$).

Experiment Two

During the round goby call and the white noise trials, t-test found significant differences in size between sexes ($P = .00$ for round goby call and $P = .01$ for white noise). These significant differences indicate male gobies were larger than females for those trials. During the round goby call, 72% of the round gobies moved to the playing speaker, 6% moved to the silent speaker, and 6% moved to neither of the speakers (Figure 17). When the black goby call was played, 38% of the round gobies traveled to the playing speaker, 17% traveled to the silent speaker, and 33% moved to neither of the speakers. All of the round gobies moved to the playing speaker when the Italian goby call was played. During the playback of the 100 Hz tone burst, when the gobies moved during the experiment they either went to the playing speaker, 67%, or to the silent speaker, 17%. When white noise was played 56% of the gobies went to the playing speaker, 11% went to the silent speaker, and 6% moved in the tank (but to neither of the speakers).

When moving towards the playing speaker, all of the round gobies traveled within 10 cm of the speaker in response to the round goby call (Figure 18). During the black goby call, 15% moved within 13-18 cm from the playing speaker, and 23% came within 18-30 cm. For the Italian goby call, 85% moved within 10 cm of the playing speaker, 38% traveled 10-13 cm away from the playing speaker, and 8% of the round gobies moved 13-18 cm, another 8% 18-30 cm away. When the 100 Hz tone was played, 62% of the gobies moved within 10 cm of the playing speaker, while 15% moved 10-13 cm, with an additional 15% 13-18 cm away. During the white noise

Figure 17: Behavioural responses of round gobies movement in response to male spawning sounds from the round goby ($n = 15$), black goby (Niger) ($n = 14$), Italian goby ($n = 18$), 100 Hz tone bursts (tone) ($n = 15$), and white noise ($n = 14$). Movements include; less than 30 cm of movement into the tank (minimal movement), movement to the silent speaker, or movement to the speaker playing the sound.

Figure 18: Proximity to the playing speaker of the round goby at cessation of movement during experiment two for spawning sounds from: round goby (n = 13), black goby (Niger) (n = 5), Italian goby (n = 18), 100 Hz tone bursts (tone) (n = 12), and white noise (n = 10). Category groupings according to distance traveled by goby to the speaker playing the sound stimulus; within 10 cm of the speaker or goby movement up to 10-30 cm away from the playing speaker.

experiment, 46% of the fish moved within 10 cm of the playing speaker, 15% come within 10-13 cm, 8% 13-18 cm, and another 8% 18-30 cm away from the playing speaker. Refer to Appendix C for individual activity.

The average speed of the round goby, from the net to the speaker playing the sound, was 10.8 cm/sec for (B), 11.5 cm/sec for (I), 20.8 cm/sec for (R), 13.3 cm/sec for (T), 14.7 cm/sec for (W), and 9.9 cm/sec for (S) (Figure 19). There was a significant difference in average velocity between males and females; males would travel at a faster speed to the playing speaker than females ($P = .03$). The standard error for average velocity data was 1.6 cm/sec for (B), 1.1 cm/sec (I), 2.6 cm/sec (R), 1.4 cm/sec (T), 1.9 cm/sec (W), and 2.0 cm/sec (S). No significant differences in velocity between sexes. Refer to Appendix D for individual velocity. The standard deviation for velocity data was 2.23^0 for (B), 2.19^0 (I), 7.78^0 (R), 3.95^0 (T), 1.98^0 (W), and 5.96^0 (S) (Figure 20). Velocity standard deviation had no significant difference for sound ($P = .36$) and sex ($P = .18$). Refer to Appendix D for individual standard deviations in velocity. The average angle from start point of the round goby to the speaker playing the sound was 113.2^0 for (B), 97.2^0 for (I), 90.8^0 for (R), 107.8^0 for (T), 102.6^0 for (W), and 104.2^0 for (S) (Figure 21). No significant difference was found between average angle and sound ($P = .66$) and sex ($P = .15$). Refer to Appendix F for individual average angles. There was a significant difference ($P = 0.01$) in the standard deviation of mean angle (Figure 22), with the smallest angle deviation found in response to round goby calls. Thus fish made the most direct path to the speaker when the round goby call was being played. There was no affect of sex

Figure 19: Average swimming speed ($\pm$ s.e.) of round goby in experiment two in response to six different stimuli. Silent refers to the control in the experiment (a quiet tank). ANOVA tests showed significant difference between sound and the velocity of the fish to the speaker playing the male round goby spawning sound ($P = .03$, $F = 2.69$). Data points with different superscripts denote significant differences found in Tukey posthoc test.

Figure 20: The standard deviation in swimming speed of round goby during movement to the playing speaker (experiment two). ANOVA test showed velocity standard deviation had no significant difference for sound ($P = 0.36$; $F = 1.12$) or sex ($P = 0.18$; $F = 1.85$).

Figure 21: The average angle ($\pm$ s.e.) of approach to the playing speaker of round gobies in experiment two. ANOVA test showed no significant difference between average angle and sound ($P = 0.66$; $F = 0.27$) and sex ($P = 0.15$; $F = 1.70$).

Figure 22: The standard deviation in approach angle of round gobies during movement to the playing speaker (experiment two). ANOVA test showed a significant difference between the male round goby spawning sound and angle standard deviation ($P = 0.01$; $F = 5.90$). Data points with different superscripts denote significant differences found in Tukey posthoc test.

on responses nor was there a significant sound and sex interaction. Refer to Appendix G for individual standard deviations in angles.

Discussion

The current study shows a clear behavioural attraction of both male and female round gobies to male sounds. The motivation for this response remains unclear however. Sound can indicate if the fish is suitable for reproduction, an attractant for the opposite sex, if the fish is primed to copulate, or if it can defend its spawning habitat. Females could travel towards the speaker playing the sound for reproductive intentions. Hawkins (2000) studied the haddock (*Melanogrammus aeglefinus*) and showed male fish produce a series of 'knocking' sounds during the spawning season. The male initially produces a short series of slowly repeated 'knocks' until the sounds becomes longer and faster (coinciding with an increase in arousal of the male). These sounds attract the female to the nest, synchronising the reproductive behaviour of the male and female. Female midshipman show directed movements in response to male reproductive calls (McKibben and Bass 1998) and Lugli et al. (1995) found that freshwater Italian gobies emit 'drumming' sounds to lure females into the nest. Thus the sounds in the current experiment could be enticing the female round goby to find a potential mate. Males might swim towards the playing speaker to investigate a potential competitor with the objective of vacating the reproductive male from the area. Stammer and Corkum (2005) showed larger round gobies displacing smaller gobies in their nest without a fight (purely based on size). This would stand to reason, since the gobies in this experiment (newly found in a foreign environment)

might be more interested in investigating a potentially new home, with the chance of being the larger fish. Finally, some fish species employ competitive mating strategies in which extra-pair copulations is common (reviewed in Taborsky 2001). Male round gobies may be attracted to conspecific male sounds to employ a “sneaker male” strategy as seen in midshipman (e.g. Bass and McKibben 2003).

The current study also clearly shows that round gobies show specificity for conspecific sounds. In both experiments, the round goby consistently traveled to the playing speaker (more than any other movement in the tank), as well as traveled within the closest proximity to the playing speaker than during any other sound. Effect of intraspecific sound communication has been shown in other species as well, mainly during mating (sunfishes, Gerald, 1971; damselfishes, Myrberg et al., 1986; toadfishes, McKibben and Bass, 1998) and during agonistic interactions (Ladich, 1997). All of the sounds in this experiment varied, with differences in temporal structure, although the fundamental frequencies were similar. Since males show specificity for conspecific spawning sounds, future experiments could alter the spectral content of sound, by altering the number of pulses or adjusting the frequency to a higher or lower octave (or both, McKibben and Bass, 1998). This could determine which characteristic of the round goby call is of interest to them. Spawning sounds from other species comparable to the round goby spawning sound could also be used to determine if there is a similarity in behaviour response.

Significant findings were found in velocity, with males moving twice as fast to the playing speaker than females. Since males were significantly larger than the females,

the difference in response velocity between sexes could be due to effects of size.

Ware (1978) found that sockeye salmon (*Oncorhynchus nerka*) had swimming speeds proportional to their body length. In pink salmon (*Oncorhynchus gorbuscha*) both sex and reproductive status can affect swimming speed (Williams and Bell 1987). Males swim twice as fast as females during upstream movement and speed decreases as spawning progresses. In the round goby, the males were also twice as fast to swim towards the sound source. Since the experiment was conducted during the spawning season, and swimming speed might be influenced by reproductive behaviour, future experiments could look at the round gobies localization abilities outside of this season.

Sound plays an important role in spawning by indicating to fish the position of a possible mate or a potential competitor (Johnston and Johnson 2000). Determining the direction of that sound is essential in becoming the first to initiate spawning. The current study shows that not only is the round goby most attracted to conspecific spawning sounds, they are able to get to the sound source using a direct path and at faster speeds than any of the other sounds presented in this study. Although not conclusive, these findings suggest that the round goby shows a high specificity towards conspecific spawning cues. These findings are currently being used in our laboratory in an attempt to devise a selective trap for this invasive species.

When looking into the behavioural aspects of sound recognition, significant results occurred with standard deviation in angle, where the round goby had the most direct path to the round goby call than any other sound played. This minimal standard

deviation in angle of approach to a sound source indicates the fish's ability to localize where in space the sound is originating rather than just sampling sounds in different locations in the tank. If a fish could not localize a sound source, its path would not be as direct, showing a zigzag pattern, deciphering where the sound is coming from. While moths are well known to be able to find odour cues from a distance, they do not show true directionality; instead they zigzag across the odour plum until honing in on the source's location (Willis and Baker 1994). Localization requires a straight line path from a distance to the source of interest, as is shown in the current study. This is one of the first studies to demonstrate this ability in fish in such a quantified manner.

The mechanism through which round gobies determine sound source location still remains obscure. Fish can detect sound directly through particle displacement of auditory hair cells, via reradiating sound from a swim bladder (when available), and/or via stimulation of the mechanosensory hair cells of the lateral line system (if the sound is of low enough frequency) (Popper and Platt 1993). Much of the theoretical work on directional hearing in fish has concerned differential phase analysis of species with swim bladders (e.g. Schuif 1975, Rogers and Cox, 1988). Round gobies have no swim bladder but can still clearly localize a sound source, therefore the mechanism of this localization must be found in the auditory and/or mechanosensory hair cells. In the current behavioural trials, fish started well within the near field of the fundamental frequency of the goby call (near field/far field boundary = 140 cm assuming a monopole source). Thus particle displacement should predominate in the sound field, making it likely that both the ear and neuromasts are involved in the behavioural response seen. Future experiments that selectively ablate

the neuromasts (e.g. Baker and Montgomery, 1999) might be able to separate the roles of these two systems in goby localization but it seems clear that round gobies can indeed directly localize a sound source.

Appendix A: Standard deviation and average angles of individual round gobies in experiment one.

Date (2004)	Trial #	Sex	Size (cm)	Min Angle	Max Angle	Average Angle	Angle std dev
03-Aug	4	F	8.89	138.493	106.289	109.7	8.07
07-Aug	2	F	8.89	93.012	72.718	87.4	3.978
07-Aug	4	F	6.35	77.002	35.041	58.4	10.693
09-Aug	1	F	11.43	123.142	46.228	93	15.479
09-Aug	2	F	10.16	128.19	73.822	101.5	16.133
09-Aug	3	F	8.89	109.615	62.823	92.1	11.724
21-Aug	4	F	10.16	93.801	55.956	73	9.331
25-Aug	1	F	10.16	94.566	63.595	88.3	7.327
25-Aug	2	F	10.16	118.337	79.26	98.9	11.17
26-Aug	1	F	7.62	93.21	56.449	76.9	11.421
26-Aug	2	F	6.35	70.382	21.103	45.7	40.772
30-Aug	3	F	7.62	156.706	63.224	109.1	26.379
30-Aug	5	F	8.89	93.012	72.718	86.7	3.978
31-Aug	1	F	8.89	99.306	73.247	85.3	6.167
31-Aug	4	F	7.62	125.868	86.355	105	9.609
03-Aug	1	M	10.16	124.445	82.72	95.1	11.521
03-Aug	2	M	8.89	143.08	80.104	126	13.873
03-Aug	3	M	7.62	84.647	31.91	59.6	11.965
07-Aug	1	M	13.97	120.431	16.808	77.9	27.31
07-Aug	3	M	5.08	92.473	36.249	68.4	14.037
21-Aug	1	M	10.16	99.273	43.095	78.2	20.234
21-Aug	2	M	12.7	127.826	86.427	101.1	9.119
21-Aug	3	M	12.7	102.955	78.828	91.8	5.666
30-Aug	1	M	12.7	173.731	100.804	116	14.884
30-Aug	2	M	12.7	104.655	63.175	80.1	10.571
30-Aug	4	M	10.16	128.806	75.557	96	11.501
30-Aug	6	M	8.89	146.188	96.739	109.6	15.364
30-Aug	7	M	12.7	90.311	59.565	77.4	7.958
31-Aug	2	M	11.43	122.473	93.812	104.1	7.677
31-Aug	3	M	12.7	124.07	85.004	102.6	8.665
12-Sep	1	M	6.985	101.417	67.888	88.1	7.537
12-Sep	2	M	12.7	142.343	65.284	98.5	14.862
12-Sep	3	M	12.7	84.189	34.608	62.2	10.77
12-Sep	4	M	12.7	152.083	50.224	90.6	29.086
Total							
Avg F			8.805	107.64	64.589	87.4	7.379
Avg M			10.929	119.23	65.726	90.7	12.035

Appendix B: Standard deviation and average velocity of individual round gobies to the playing speaker in experiment one.

<u>Date</u> <u>(2004)</u>	<u>Trial</u> <u>#</u>	<u>Sex</u>	<u>Size</u> <u>(cm)</u>	<u>Min</u> <u>Velocity</u>	<u>Max</u> <u>Velocity</u>	<u>Average</u> <u>Velocity</u>	<u>Velocity std</u> <u>dev</u>
03-Aug	4	F	8.89	0.137	16.019	6.73	5.538
07-Aug	2	F	8.89	13.589	36.074	21.83	5.133
07-Aug	4	F	6.35	0.059	23.208	8.469	7.674
09-Aug	1	F	11.43	0.032	13.609	4.149	4.702
09-Aug	2	F	10.16	6.117	20.85	14.48	3.031
09-Aug	3	F	8.89	0.358	45.124	19.276	7.804
21-Aug	4	F	10.16	3.625	28.231	16.071	5.601
25-Aug	1	F	10.16	0.037	20.459	8.078	6.761
25-Aug	2	F	10.16	6.236	32.864	18.048	6.778
26-Aug	1	F	7.62	0.106	21.501	9.015	6.519
26-Aug	2	F	6.35	0.024	16.905	4.629	5.181
30-Aug	3	F	7.62	0.245	31.314	17.192	7.959
30-Aug	5	F	8.89	13.589	36.074	21.83	5.133
31-Aug	1	F	8.89	0.074	18.455	12.048	4.052
31-Aug	4	F	7.62	7.761	20.757	14.705	3.009
03-Aug	1	M	10.16	0.067	31.057	10.955	9.905
03-Aug	2	M	8.89	0.016	19.212	5.422	6.358
03-Aug	3	M	7.62	0.085	16.357	8.392	6.029
07-Aug	1	M	13.97	0.118	44.669	14.669	11.069
07-Aug	3	M	5.08	0.1	14.625	5.611	4.725
21-Aug	1	M	10.16	11.886	37.381	23.477	7.483
21-Aug	2	M	12.7	13.654	34.433	21.639	4.237
21-Aug	3	M	12.7	6.39	32.319	19.949	7.001
30-Aug	1	M	12.7	9.801	152.075	46.733	32.186
30-Aug	2	M	12.7	4.405	76.306	28.329	19.229
30-Aug	4	M	10.16	12.964	28.455	19.649	3.942
30-Aug	6	M	8.89	9.759	27.141	16.551	4.175
30-Aug	7	M	12.7	9.783	77.324	33.531	13.838
31-Aug	2	M	11.43	4.062	21.379	16.643	3.416
31-Aug	3	M	12.7	9.065	26.574	17.879	4.211
12-Sep	1	M	6.985	8.83	22.24	16.03	3.327
12-Sep	2	M	12.7	11.694	39.788	24.218	7.942
12-Sep	3	M	12.7	15.014	51.593	24.893	6.129
12-Sep	4	M	12.7	0.06	28.404	15.44	8.806
Total							
Avg F			8.805	3.466	25.43	13.10	5.658
Avg M			10.929	6.724	41.12	19.47	8.63

Appendix C: Activity of individual round gobies during experiment two.

<u>Sound</u>	<u>Date</u>	<u>Trial #</u>	<u>Sex</u>	<u>Size (cm)</u>	<u>Activity</u>
Black Goby	27-Sep	1	F	8.89	Silent
Black Goby	27-Sep	4	F	7.62	Minimal Movement
Black Goby	27-Sep	5	F	7.62	Minimal Movement
Black Goby	27-Sep	6	F	6.35	Minimal Movement
Black Goby	27-Sep	8	F	10.16	Silent up to 27.94 cm
Black Goby	27-Sep	9	F	7.62	Playing up to 27.94 cm
Black Goby	05-Oct	4	F	7.62	Silent
Black Goby	27-Sep	2	M	7.62	Minimal Movement
Black Goby	27-Sep	3	M	7.62	Minimal Movement
Black Goby	27-Sep	7	M	7.62	Playing up to 20.32 cm
Black Goby	05-Oct	1	M	7.62	Playing up to 15.24 cm
Black Goby	05-Oct	2	M	8.89	Playing up to 20.32 cm
Black Goby	05-Oct	3	M	7.62	Playing up to 15.24 cm
Black Goby	05-Oct	5	M	11.43	Minimal Movement
Italian Goby	15-Oct	3	F	7.62	Playing up to 10.16 cm
Italian Goby	15-Oct	4	F	7.62	Playing
Italian Goby	15-Oct	5	F	7.62	Drive by Playing up to 12.7 cm
Italian Goby	15-Oct	6	F	10.16	Playing up to 22.86 cm
Italian Goby	15-Oct	7	F	8.86	Playing
Italian Goby	15-Oct	8	F	10.16	Playing
Italian Goby	23-Oct	3	F	7.62	Playing
Italian Goby	23-Oct	4	F	7.62	Playing
Italian Goby	23-Oct	5	F	7.62	Playing up to 15.24 cm
Italian Goby	23-Oct	6	F	7.62	Playing
Italian Goby	23-Oct	7	F	10.16	Playing up to 12.7 cm
Italian Goby	23-Oct	8	F	8.89	Playing
Italian Goby	15-Oct	1	M	7.62	Playing
Italian Goby	15-Oct	2	M	7.62	Drive by Playing up to 12.7 cm
Italian Goby	15-Oct	9	M	10.16	Drive by Playing up to 12.7 cm
Italian Goby	23-Oct	1	M	8.89	Playing
Italian Goby	23-Oct	2	M	7.62	Hid Playing
Italian Goby	23-Oct	9	M	7.62	Hid Playing
Round Goby	26-Aug	1	F	7.62	Playing
Round Goby	26-Aug	2	F	6.35	Playing
Round Goby	30-Aug	3	F	7.62	Playing
Round Goby	30-Aug	5	F	8.89	Playing
Round Goby	30-Aug	1	M	12.7	Playing
Round Goby	30-Aug	2	M	12.7	Playing
Round Goby	30-Aug	4	M	10.16	Playing
Round Goby	30-Aug	6	M	8.89	Playing
Round Goby	30-Aug	7	M	12.7	Playing
Round Goby	31-Aug	2	M	11.43	Playing
Round Goby	31-Aug	3	M	12.7	Playing
Round Goby	12-Sep	1	M	6.985	Playing
Round Goby	12-Sep	2	M	12.7	Silent
Round Goby	12-Sep	3	M	12.7	Playing

Appendix C (continued): Activity of individual round gobies, experiment two.

<u>Sound</u>	<u>Date</u>	<u>Trial #</u>	<u>Sex</u>	<u>Size (cm)</u>	<u>Activity</u>
Round Goby	12-Sep	4	M	12.7	Minimal Movement
Silent	05-Oct	2	F	7.62	Jagged Movement
Silent	05-Oct	3	F	7.62	Jagged Movement
Silent	05-Oct	5	F	10.16	Jagged Movement
Silent	05-Oct	6	F	6.35	Minimal Movement to Corner
Silent	18-Oct	1	F	7.62	No Movement
Silent	05-Oct	1	M	7.62	Minimal Movement to Corner
Silent	05-Oct	4	M	8.89	Minimal Movement to Corner
Silent	05-Oct	7	M	7.62	Jagged Movement
Tone	20-Sep	1	F	8.89	Playing
Tone	20-Sep	2	F	10.16	Playing
Tone	20-Sep	3	F	10.16	Playing
Tone	20-Sep	6	F	7.62	Drive by Playing up to 12.7 cm
Tone	20-Sep	7	F	7.62	Playing
Tone	20-Sep	8	F	7.62	Playing
Tone	05-Oct	2	F	7.62	Silent to 10.16 cm
Tone	05-Oct	4	F	7.62	Playing
Tone	05-Oct	5	F	8.89	Silent
Tone	05-Oct	6	F	7.62	Drive by Playing up to 15.24 cm
Tone	05-Oct	7	F	7.62	Hid Playing
Tone	20-Sep	4	M	7.62	Playing
Tone	20-Sep	5	M	7.62	Playing up to 15.24 cm
Tone	05-Oct	1	M	7.62	Drive by Playing up to 12.7cm
Tone	05-Oct	3	M	10.16	Silent
White Noise	04-Oct	1	F	7.62	Playing up to 25.4 cm
White Noise	04-Oct	3	F	7.62	Playing up to 10.16 cm
White Noise	04-Oct	4	F	7.62	Playing
White Noise	04-Oct	7	F	7.62	Silent to 12.7cm
White Noise	04-Oct	8	F	7.62	Playing
White Noise	23-Oct	1	F	7.62	Playing up to 20.32 cm
White Noise	23-Oct	2	F	7.62	Hid Playing
White Noise	23-Oct	5	F	6.35	Playing
White Noise	04-Oct	2	M	7.62	Silent
White Noise	04-Oct	5	M	10.16	Playing
White Noise	04-Oct	6	M	8.89	Drive by Playing up to 17.78 cm
White Noise	04-Oct	9	M	10.16	Hid Playing
White Noise	23-Oct	3	M	11.43	Playing up to 12.7 cm
White Noise	23-Oct	4	M	7.62	Minimal Movement

Appendix D: Standard deviation and average velocity of the round goby during experiment two.

<u>Sound</u>	<u>Date</u> <u>(2004)</u>	<u>Trial</u> <u>#</u>	<u>Sex</u>	<u>Size</u> <u>(cm)</u>	<u>Min</u>	<u>Max</u>	<u>Average</u>	<u>std dev</u>
Black Goby	27-Sep	1	F	8.89	9.33	66.775	21.894	11.902
Black Goby	27-Sep	4	F	7.62	0.123	19.576	5.66	4.508
Black Goby	27-Sep	5	F	7.62	0.035	15.205	4.115	3.686
Black Goby	27-Sep	6	F	6.35	10.897	24.573	18.592	3.763
Black Goby	27-Sep	8	F	10.16	11.272	23.493	16.591	2.639
Black Goby	27-Sep	9	F	7.62	0.076	21.483	9.208	5.384
Black Goby	05-Oct	4	F	7.62	0.694	21.208	9.028	6.03
Black Goby	27-Sep	2	M	7.62	0.299	14.413	5.416	3.941
Black Goby	27-Sep	3	M	7.62	0.097	17.734	6.05	4.671
Black Goby	27-Sep	7	M	7.62	3.071	25.946	11.855	6.992
Black Goby	05-Oct	1	M	7.62	0.531	24.639	14.524	6.682
Black Goby	05-Oct	2	M	8.89	1.135	21.304	14.93	6.146
Black Goby	05-Oct	3	M	7.62	0.411	21.314	9.516	6.507
Black Goby	05-Oct	5	M	11.43	0.013	23.703	3.167	5.701
Italian Goby	15-Oct	3	F	7.62	2.215	22.119	13.884	7.752
Italian Goby	15-Oct	4	F	7.62	0.119	18.344	7.854	5.77
Italian Goby	15-Oct	5	F	7.62	2.42	25.488	10.015	6.812
Italian Goby	15-Oct	6	F	10.16	2.726	28.2	11.633	7.854
Italian Goby	15-Oct	7	F	8.86	0.825	45.053	19.96	11.749
Italian Goby	15-Oct	8	F	10.16	1.493	31.365	19.557	9.989
Italian Goby	23-Oct	3	F	7.62	0.009	19.379	7.278	7.278
Italian Goby	23-Oct	4	F	7.62	0.494	22.509	7.735	6.017
Italian Goby	23-Oct	5	F	7.62	1.281	25.278	15.979	7.279
Italian Goby	23-Oct	6	F	7.62	0.099	17.777	5.807	5.528
Italian Goby	23-Oct	7	F	10.16	0.242	21.267	8.931	5.57
Italian Goby	23-Oct	8	F	8.89	1.788	23.992	9.428	7.108
Italian Goby	15-Oct	1	M	7.62	0.101	14.036	6.678	4.639
Italian Goby	15-Oct	2	M	7.62	1.105	20.736	12.783	7.072
Italian Goby	15-Oct	9	M	10.16	17.75	22.347	20.468	1.241
Italian Goby	23-Oct	1	M	8.89	0.109	22.883	11.488	6.688
Italian Goby	23-Oct	2	M	7.62	1.071	16.923	6.73	4.839
Italian Goby	23-Oct	9	M	7.62	2.919	32.5	11.523	7.234
Round Goby	26-Aug	1	F	7.62	0.106	21.501	9.015	6.519
Round Goby	26-Aug	2	F	6.35	0.024	16.905	4.629	5.181
Round Goby	30-Aug	3	F	7.62	0.245	31.314	17.192	7.959
Round Goby	30-Aug	5	F	8.89	13.589	36.074	21.83	5.133
Round Goby	30-Aug	1	M	12.7	9.801	152.075	46.733	32.186
Round Goby	30-Aug	2	M	12.7	4.405	76.306	28.329	19.229
Round Goby	30-Aug	4	M	10.16	12.964	28.455	19.649	3.942
Round Goby	30-Aug	6	M	8.89	9.759	27.141	16.551	4.175
Round Goby	30-Aug	7	M	12.7	9.783	77.324	33.531	13.838
Round Goby	31-Aug	2	M	11.43	4.062	21.379	16.643	3.416
Round Goby	31-Aug	3	M	12.7	9.065	26.574	17.879	4.211
Round Goby	12-Sep	1	M	6.985	8.83	22.24	16.03	3.327
Round Goby	12-Sep	2	M	12.7	11.694	39.788	24.218	7.942

Appendix D (continued): Standard deviation and average velocity of the round goby during experiment two.

<u>Sound</u>	<u>Date</u> <u>(2004)</u>	<u>Trial</u> <u>#</u>	<u>Sex</u>	<u>Size</u> <u>(cm)</u>	<u>Min</u>	<u>Max</u>	<u>Average</u>	<u>std dev</u>
Round Goby	12-Sep	3	M	12.7	15.014	51.593	24.893	6.129
Round Goby	12-Sep	4	M	12.7	0.06	28.404	15.44	8.806
Silent	05-Oct	2	F	7.62	0.085	23.639	8.893	6.928
Silent	05-Oct	3	F	7.62	0.414	104.917	19.901	17.847
Silent	05-Oct	5	F	10.16	0.337	22.003	12.966	6.161
Silent	05-Oct	6	F	6.35	0.058	18.721	6.933	5.624
Silent	18-Oct	1	F	7.62	0.059	0.129	0.097	0.021
Silent	05-Oct	1	M	7.62	0.272	47.334	13.354	15.201
Silent	05-Oct	4	M	8.89	0.011	45.665	9.831	12.666
Silent	05-Oct	7	M	7.62	0.017	21.674	7.136	5.163
Tone	20-Sep	1	F	8.89	8.281	24.495	16.016	3.48
Tone	20-Sep	2	F	10.16	6.328	26.408	17.583	4.168
Tone	20-Sep	3	F	10.16	13.65	28.915	20.773	3.665
Tone	20-Sep	6	F	7.62	0.199	42.096	16.916	9.645
Tone	20-Sep	7	F	7.62	0.367	22.753	12.198	4.981
Tone	20-Sep	8	F	7.62	4.159	29.83	14.809	5.881
Tone	05-Oct	2	F	7.62	0.192	23.376	7.826	6.407
Tone	05-Oct	4	F	7.62	0.425	21.385	8.583	5.612
Tone	05-Oct	5	F	8.89	0.507	62.015	18.083	15.972
Tone	05-Oct	6	F	7.62	16.079	26.678	22.95	3.194
Tone	05-Oct	7	F	7.62	0.815	17.471	7.014	5.122
Tone	20-Sep	4	M	7.62	0.077	21.814	6.902	5.446
Tone	20-Sep	5	M	7.62	0.056	15.72	4.432	4.264
Tone	05-Oct	1	M	7.62	0.745	45.433	12.91	14.357
Tone	05-Oct	3	M	10.16	0.297	43.961	12.312	10.19
White Noise	04-Oct	1	F	7.62	0.492	21.595	11.879	7.102
White Noise	04-Oct	3	F	7.62	9.789	30.574	21.901	5.429
White Noise	04-Oct	4	F	7.62	17.343	36.066	25.454	4.865
White Noise	04-Oct	7	F	7.62	14.164	25.791	19.899	2.759
White Noise	04-Oct	8	F	7.62	0.067	20.097	12.497	6.806
White Noise	23-Oct	1	F	7.62	0.092	19.887	2.655	3.837
White Noise	23-Oct	2	F	7.62	0.059	20.879	5.233	5.295
White Noise	23-Oct	5	F	6.35	0.023	19.75	4.462	4.715
White Noise	04-Oct	2	M	7.62	10.315	23.758	17.039	3.5
White Noise	04-Oct	5	M	10.16	14.165	27.909	19.763	3.924
White Noise	04-Oct	6	M	8.89	16.331	26.233	19.814	2.897
White Noise	04-Oct	9	M	10.16	11.257	36.034	22.985	8.083
White Noise	23-Oct	3	M	11.43	0.103	28.959	9.612	7.773
White Noise	23-Oct	4	M	7.62	0.168	37.096	12.411	8.718

Appendix E: Standard deviation and average angle of the round goby during experiment two.

<u>Sound</u>	<u>Date</u> <u>(2004)</u>	<u>Trial</u> <u>#</u>	<u>Sex</u>	<u>Size</u> <u>(cm)</u>	<u>Min</u>	<u>Max</u>	<u>Average</u>	<u>std dev</u>
Black Goby	27-Sep	1	F	8.89	91.462	38.112	44.6	13.974
Black Goby	27-Sep	4	F	7.62	52.959	48.829	2.76	29.096
Black Goby	27-Sep	5	F	7.62	72.935	42.766	2.21	31.177
Black Goby	27-Sep	6	F	6.35	156.119	54.976	97.5	31.819
Black Goby	27-Sep	8	F	10.16	154.9	34.796	116.5	27.394
Black Goby	27-Sep	9	F	7.62	283.765	109.006	205	60.815
Black Goby	05-Oct	4	F	7.62	270.692	34.194	119.2	68.782
Black Goby	27-Sep	2	M	7.62	273.305	101.807	186.1	53.679
Black Goby	27-Sep	3	M	7.62	344.255	83.895	202.5	75.794
Black Goby	27-Sep	7	M	7.62	317.417	81.539	191.9	73.798
Black Goby	05-Oct	1	M	7.62	273.911	60.12	138.4	56.137
Black Goby	05-Oct	2	M	8.89	217.867	29.057	113.1	57.328
Black Goby	05-Oct	3	M	7.62	259.366	39.168	129.8	56.192
Black Goby	05-Oct	5	M	11.43	53.597	89.296	34.6	47.066
Italian Goby	15-Oct	3	F	7.62	182.385	77.288	120.6	34.983
Italian Goby	15-Oct	4	F	7.62	119.827	80.253	45.4	60.441
Italian Goby	15-Oct	5	F	7.62	142.994	8.946	125.9	33.02
Italian Goby	15-Oct	6	F	10.16	91.199	67.112	11.5	44.736
Italian Goby	15-Oct	7	F	8.86	80.957	48.555	23.4	39.056
Italian Goby	15-Oct	8	F	10.16	211.41	81.099	135.3	27.517
Italian Goby	23-Oct	3	F	7.62	145.018	41.252	79.8	25.87
Italian Goby	23-Oct	4	F	7.62	160.209	14.623	69.5	38.615
Italian Goby	23-Oct	5	F	7.62	183.597	79.259	135.8	37.025
Italian Goby	23-Oct	6	F	7.62	142.121	41.113	95	26.551
Italian Goby	23-Oct	7	F	10.16	403.015	34.291	142.7	97.58
Italian Goby	23-Oct	8	F	8.89	214.801	79.449	108	27.05
Italian Goby	15-Oct	1	M	7.62	157.298	30.848	95.6	40.362
Italian Goby	15-Oct	2	M	7.62	135.281	19.465	61.9	34.451
Italian Goby	15-Oct	9	M	10.16	183.375	73.33	126.7	31.613
Italian Goby	23-Oct	1	M	8.89	178.509	12.741	107	45.827
Italian Goby	23-Oct	2	M	7.62	189.31	78.557	143.4	28.831
Italian Goby	23-Oct	9	M	7.62	176.758	80.091	122.6	30.321
Round Goby	26-Aug	1	F	7.62	93.21	56.449	69.9	11.421
Round Goby	26-Aug	2	F	6.35	70.382	21.103	35.8	-40.772
Round Goby	30-Aug	3	F	7.62	156.706	63.224	112.1	26.379
Round Goby	30-Aug	5	F	8.89	93.012	72.718	77.7	3.978
Round Goby	30-Aug	1	M	12.7	173.731	100.804	126	14.884
Round Goby	30-Aug	2	M	12.7	104.655	63.175	84.1	10.571
Round Goby	30-Aug	4	M	10.16	128.806	75.557	102	11.501
Round Goby	30-Aug	6	M	8.89	146.188	96.739	117.6	15.364
Round Goby	30-Aug	7	M	12.7	90.311	59.565	71.4	7.958
Round Goby	31-Aug	2	M	11.43	122.473	93.812	114.1	7.677
Round Goby	31-Aug	3	M	12.7	124.07	85.004	112.6	8.665
Round Goby	12-Sep	1	M	6.985	101.417	67.888	83.1	7.537
Round Goby	12-Sep	2	M	12.7	142.343	65.284	107.5	14.862

Appendix E (continued): Standard deviation and average angle of the round goby during experiment two.

<u>Sound</u>	<u>Date</u> <u>(2004)</u>	<u>Trial</u> <u>#</u>	<u>Sex</u>	<u>Size</u> <u>(cm)</u>	<u>Min</u>	<u>Max</u>	<u>Average</u>	<u>std dev</u>
Round Goby	12-Sep	3	M	12.7	84.189	34.608	49.2	10.77
Round Goby	12-Sep	4	M	12.7	152.083	50.224	98.6	29.086
Silent	05-Oct	2	F	7.62	158.588	181.325	21.8	123.511
Silent	05-Oct	3	F	7.62	330.049	46.574	156.2	57.558
Silent	05-Oct	5	F	10.16	272.179	2.577	123.5	72.626
Silent	05-Oct	6	F	6.35	184.685	96.454	148.3	24.675
Silent	18-Oct	1	F	7.62	121.953	93.692	108.1	8.155
Silent	05-Oct	1	M	7.62	93.782	4.083	45.3	32.75
Silent	05-Oct	4	M	8.89	142.008	102.546	129.2	9.664
Silent	05-Oct	7	M	7.62	167.022	46.293	101.1	35.66
Tone	20-Sep	1	F	8.89	115.048	84.571	99.6	8.002
Tone	20-Sep	2	F	10.16	130.51	93.155	113.2	7.561
Tone	20-Sep	3	F	10.16	123.098	90.458	107.6	8.438
Tone	20-Sep	6	F	7.62	150.651	51.22	110.7	31.401
Tone	20-Sep	7	F	7.62	103.826	62.519	89.6	9.713
Tone	20-Sep	8	F	7.62	102.279	76.316	96.4	7.002
Tone	05-Oct	2	F	7.62	167.332	170.023	29.1	112.11
Tone	05-Oct	4	F	7.62	252.951	81.51	158.7	66.86
Tone	05-Oct	5	F	8.89	143.392	91.814	123	13.525
Tone	05-Oct	6	F	7.62	154.563	74.219	114.5	21.545
Tone	05-Oct	7	F	7.62	174.219	77.174	108.5	29.131
Tone	20-Sep	4	M	7.62	136.116	90.637	117.6	11.975
Tone	20-Sep	5	M	7.62	151.442	84.511	126.4	16.04
Tone	05-Oct	1	M	7.62	121.524	78.685	62.5	55.819
Tone	05-Oct	3	M	10.16	247.475	62.34	158.9	45.613
White Noise	04-Oct	1	F	7.62	161.633	78.951	128.7	30.082
White Noise	04-Oct	3	F	7.62	142.385	80.759	105.3	18.738
White Noise	04-Oct	4	F	7.62	130.765	80.719	108.5	15.576
White Noise	04-Oct	7	F	7.62	174.492	111.961	135.2	13.418
White Noise	04-Oct	8	F	7.62	109.481	0.239	69.4	34.928
White Noise	23-Oct	1	F	7.62	93.783	110.447	71.3	30.221
White Noise	23-Oct	2	F	7.62	23.12	126.355	80.8	23.401
White Noise	23-Oct	5	F	6.35	38.926	198.18	137.9	42.66
White Noise	04-Oct	2	M	7.62	165.84	82.271	113	26.597
White Noise	04-Oct	5	M	10.16	122.094	90.332	112.8	10.305
White Noise	04-Oct	6	M	8.89	141.506	73.575	96.6	17.741
White Noise	04-Oct	9	M	10.16	129.07	87.45	108.6	9.533
White Noise	23-Oct	3	M	11.43	83.827	180.685	134.4	33.11
White Noise	23-Oct	4	M	7.62	91.363	32.205	34.1	47.739

Appendix F: Experimental tank acoustics. Sound travels from the left side (speaker) to the right side (net).

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