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Response of round gobies, *Neogobius melanostomus*, to conspecific sounds

By

Lisa Isabella-Valenzi

A Thesis
Submitted to the Faculty of Graduate Studies
through Biological Sciences
in Partial Fulfillment of the Requirements for
the Degree of Master of Biological Sciences
at the University of Windsor

Windsor, Ontario, Canada

2012

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by

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ABSTRACT

A useful model group to examine reproductive plasticity in acoustic responsiveness is the family Gobiidae. Male round gobies *Neogobius melanostomus* emit calls and females respond to these calls with high specificity. The current study investigates differential attraction between reproductive morphologies of the goby to conspecific calls and explores the use of calls to develop a bioacoustic trap. Behavioural responsiveness to conspecific calls was tested using playback experiments in the lab and field. Females showed a strong attraction to the grunt call in both the lab and field, while nonreproductive and sneaker males preferred the drum call in the lab, but favoured the grunt call in the field. By determining the relationship between reproductive state and auditory responsiveness to conspecific calls, I am further elucidating the function of acoustic communication in the round goby and may be essential when creating control strategies to prevent the spread of the invasive species.

DEDICATION

To Mom and Dad for their continuing love and support.

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To Dennis Higgs for his great supervision and help these last two years. Thanks for always being patient with my constant questions, helping with any issues I was having out in the field and advice throughout the duration of my thesis.

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GENERAL INTRODUCTION

Introduction

Fish, like many other taxa use signals in a variety of ways to communicate with conspecifics, with acoustic communication working best from a distance (Amorim 2003). Fish use acoustic communication in a number of ways, including mate attraction (Raffinger and Ladich 2009), courtship (Smith 1992), territorial defense (Amorim and Hawkins 2000), and in some cases, exploit sounds via eavesdropping (Myrberg 1981). The characteristics of these sounds between conspecifics and heterospecifics have been found to differ in ways that allow for not only species recognition, but also mate recognition, to prevent costs such as wasted energy and reduced reproductive success (Kihslinger and Klimley 2002). The manner in which fish produce sounds varies from one species to the next which can encompass the use of the swim bladder (associated with sonic muscles) and the rubbing and knocking of hard structures, such as bones, together to generate sounds (Kasumyan 2008). Furthermore, the manner in which fish detect sound can differ between species as well. For example, some fishes use their swim bladder in association with specialized structures to detect the pressure component of sound from farther distances, which allows for the detection of higher frequency sounds (Popper and Fay 1993, 1999). In contrast, fishes that do not possess these hearing specializations are usually restricted to low frequency hearing**.** In addition, fishes with hearing specializations in association with the swimbladder have also been found to lower the hearing threshold of fish, which is frequency dependent (Popper and Fay 1993, 1999)**.** While all fish use their ears to detect sounds in some shape or form, those without a swimbladder must depend on other mechanosensory mechanisms (Popper and Fay 1993, Popper and Schilt 2008). Despite communication modalities playing a large role in the life of organisms, in order for any modality to work efficiently and relay information accurately, signal types must be able to transmit through the environment properly. As a result, due to constraints that exist in some habitats, certain forms of communication are better suited to one habitat type more so than others, and therefore modalities that prove advantageous should be used accordingly (Roger and Cox 1988). In regard to aquatic environments, the modality that proves most useful is acoustic communication as sound is able to maintain the signal's integrity in both in the speed of transmission and maintaining information within the sound itself, through a variety of novel situations, including over varying distances (long and short), depths (shallow and deep), light intensity, and turbidity, allowing organisms to interact with their environment and with one another (Rogers and Cox 1988). However, while acoustic communication is more suitably utilized in aquatic environments, transmission of sound in water is not without its problems. The transmission of sound can be affected by fluctuating environmental characteristics such as temperature, salinity, and water pressure that changes with depth that can alter the ability of the water medium to transmit sounds accurately and thereby affecting propagation and attenuation of acoustic signals (Popper and Fay 2011).

Acoustic communication is very complex in function, production, and interaction between conspecifics and heterospecifics. The following review will examine the mechanisms used by fishes to produce sounds, what aspects of sound matter to fishes, sound propagation in water and how fish hear, uses of acoustic communication in fishes, and provide an overview of my study species, the round goby, *Neogobius melanostomus*, its known background and behaviour, and the objectives of my study .

Mechanisms of Sound Production in Fishes

Swimbladder and Sonic Muscles

Fish possess different organs and mechanisms for sound production, and one of the best studied mechanisms in fish (and the most commonly used to produce sounds) is the swimbladder (Tavolga, 1960). The swimbladder is a gas-filled sac (also known as the gasbladder) that's function is typically to assist with maintaining a fish's buoyancy within the water column (Kasumyan 2008). However, the swimbladder can have a secondary function when associated with an anatomical striated structure called sonic muscles, used to produce sound in some fishes (Kasumyan 2008). Sonic muscles, when contracting, causes vibrations in the swimbladder to occur, that in turn, generates sonic vibrations, described as drumming sound similar to the beating of a drum (Tavolga 1960). Sonic muscles have been found to be attached to the swimbladder, either directly or indirectly (Kasumyan 2008). Sonic muscles connected directly to the swimbladder wall laterally have been observed in the grey gurnards, *Eutrigla gurnarrdus*, and in the family, Mormyridae (Amorim et al 2004, Crawford et al. 1986). When these muscles contract, sounds are generated by resonation of the swimbladder itself (Tavolga 1971). In other species, such as the pigfish, *Congiopodus leucopaecilus*, striated muscles run between the vertebral intercentra and the back border of the pectoral girdle, resulting in a drum-like sound through the swimbladder when the muscles contract (Packard, 1960), similar to plainfin midshipman, *Porichthys notatus*. Indirect connections are associated with the bony elements of the axial skeleton, connecting with the swimbladder by means of ligament attachments, such as catfish of the Mochokidae family, where the sonic muscle first inserts onto a thin, bony plate (elastic spring) and extends to the swimbladder, where rapid contractions of the sonic muscles cause the elastic spring and the swimbladder to vibrate (Ladich and Bass 1996, 1998).

There is some controversy on how the swimbladder produces sound when the sonic muscles contract as it is believed that the size and shape of the swimbladder affects sound production in fish (Zelick et al. 1999, Kasumyan 2008, Amorim 2006). In many species, the swimbladder possesses protrusions and diaphragms or membranes (Zelick et al. 1999, Kasumyan 2008, Amorim 2006). These diaphragms break up the swimbladder into a number of chambers, where a small opening surrounded by non-striated muscle, allows for gas to move from one chamber to another. Though not experimentally tested, it is believed that sounds in fish are produced when gas moves from one chamber to another when the sonic muscles are contracting, causing swimbladder volume to change rapidly, within a chamber (Green 1924). The more generally accepted idea for sound production, instead, deals with vibrations or oscillations of the swimbladder wall when the sonic muscles contract (Kasumyan 2008). The sound is seen to increase as a result of a resonance that occurs when the frequency of the oscillations produced by the sonic muscles and the swimbladder are in tune (Alexander 1966, Demski 1973). Though interestingly, upon removal of the gas from the swimbladder of the freshwater goby, *Padogobius martensii*, the amplitude of the sounds produced by this species is greatly reduced, while maintaining other sound characteristics, indicating that the gas in the swimbladder plays somewhat of a role in how sounds are produced (Lugli et al. 2003).

Rubbing and Knocking of Bones

The rubbing and knocking of bones to produce sounds is a commonly used specialization for acoustic communication by teleost fish (Kasumyan 2008). The process of producing sounds by rubbing and knocking of bones is known as stridulation, which can consist of rubbing the teeth, bones of the skull, fin rays, and many more (Kasumyan 2008). Some examples include rubbing of the first spine (that is ribbed) of the pectoral fin, in the sockets of the shoulder girdle as seen in the family Siluriforidae (Brosseau 1978). Sounds are produced when sliding the ribbed surface of the ray along the rough surface of the spinal fossa. Contact between each bony protrusion off the spine results in a distinct pulse of sound (Brosseau 1978). Another example of sounds produced by stridulation, can be seen in seahorses of the genus *Hippocampus*, where sounds are produced during the movement of two unpaired bones, the supraoccipital and coronet, against one another with the assistance of a bony hinge that lies between the two bones (Colson et al. 1998). The movement of the two unpaired bones tends to occur during agonistic interactions between males when fighting over a female, producing a cracking sound (Masonjones and Lewis 1996). Upon removal of the bony hinge, the sound is no longer produced (Colson et al. 1998). Currently, the meaning of the signal is unclear.

Sounds produced in this manner are often short, wide-band pulses or burst-like sounds and can generate higher dominant frequencies than sounds that are produced by the swimbladder (Ladich 1999). Sounds that are produced by rubbing teeth together usually occur during feeding and chewing of food (Kasumyan 2008). These sounds occur involuntarily and therefore are considered unspecialized sounds, however, fishes who feed predominantly on hard-shelled organism, such as molluscs, posses a specialized structure known as pharyngeal teeth, that exists deep in the oral cavity along both the dorsal and ventral surfaces of the pharynx (Burkenroad 1930). Pharyngeal teeth have also been found to be used to generate sound for conspecific communication (Burkenroad 1930). Pharyngeal teeth are composed of bony plates, that when ground together, produce a burst-like sound in nature, often associated with grunts; short, broadband repeated pulses. Sounds produced by pharyngeal teeth are lower in energy than sounds produced by the swimbladder (Burkenroad 1930).

Attenuation and Propagation Underwater

Reflection

Reflection of sound refers to the phenomenon where sound waves following emission from a sender, rebound off a surface interface, seafloor, or some other solid object, as the signal is travelling towards the intended receiver (Rogers and Cox 1988). Reflection during transmission of an acoustic signal can pose a problem as it can distort and alter the information within the signal produced by the sender, thereby giving the receiver incorrect information of the location of the sender itself. However, there are some boundaries and objects that can conduct sound waves better than others, causing sound waves to be reflected all the more. The surface interface situated at the air-water boundary is such a reflector, where sound absorption is smallest, making it an effective reflector for long distance transmission. In regard to bottom substrates, however, more sound waves are absorbed rather than reflected, and as a result, substrates are better suited for propagating sounds over short distances (Rogers and Cox 1988).

Scattering

Scattering, as the name suggests, occurs when sound waves are disrupted during transmission, propelling the sound waves into several different directions, causing sound to travel in a direction that was not originally intended (Rogers and Cox 1988). Scattering usually occurs when sound waves come into contact with objects such as aquatic organisms, man-made structures, or disturbances in the water that are generated by ships (Richardson et al. 1995). Different substrates, ranging from silt to bedrock, can also cause sound waves to scatter, therefore presenting an issue for fishes that depend on sound to communicate with conspecifics (Rogers and Cox 1988). To limit the scattering effect of substrates, senders, when emitting a vocalization, should reduce the distance between themselves and the seabed as much as possible (Mann 2006).

Refraction

Refraction refers to the direction sound waves are bent when entering a medium that differs in speed of sound. The direction in which the sound wave will be bent is dependent on the speed of sound of the medium that the waves are passing through (Rogers and Cox 1988). For instance, sound waves are bent back towards the original medium and refracted in the direction of the interface when the second medium has a faster speed of sound. In contrast, if the second medium has a slower transmission rate, than the signal will bend away from the interface and move further into the second medium (Rogers and Cox 1988).

Environmental Effects on Sound Propagation

The speed of a wave propagating through a medium is not a constant in non-homogeneous media (Rogers and Cox 1988). In relation to aquatic environments, factors such as temperature, salinity, and water pressure can alter the speed of sound of a medium and therefore, the distance over which a sound can propagate. As pressure increases with depth, the speed of sound also increases (Mann 2006). Conversely, in regard to temperature, the opposite trend is apparent, where depth increases, water temperatures decline, causing the speed of sound to decrease. For salinity, as it increases, the speed of sound also increases, and *vice versa*. However, salinity varies very little with depth, but stronger variations can occur near areas where a high inflow (or outflow) of freshwater can alter water salinity (alters the ratio between the amount salt particles dissolved in water and the amount of freshwater), such as river estuaries or melting ice (Mann 2006). Interestingly, at a depth of approximately 1000 m, there exists a horizontal layer of water in the ocean known as the Sound Fixing and Ranging channel (SOFAR). The SOFAR channel is where the speed of sound is at its minimum because parameters such as temperature, pressure, and salinity are in balance, allowing for sound to propagate in a single direction (Rogers and Cox 1988).

Sound Detection in Fish

Nearfield and Farfield

Sound is defined as vibrations that travel through a medium. For water, sound is composed of two physically linked components: scalar pressure waves and directional particle (water) motion, which can differ in the manner required to reach the inner ear of a fish (Fay and Popper 1975). The pressure component refers to the true sound where movement of the particle velocity is only due to fluid compression by the source itself

(Mann 2006). The particle motion component, on the other hand, refers to the flow where the particle velocity of sound can be felt by the receiver. However, the manner in which a fish hears a sound is highly dependent on particle motion because hair cells in the fish ear can only respond to direct movement, on its own. For fish to hear sound pressure, first, the sound pressure must be converted from a pressure wave into particle motion. What aspects of sound a fish can hear is highly dependent on distance from the sound source, known as the nearfield and the farfield. The nearfield is composed of two parts that consists of both the pressure and particle motion components. In contrast, the farfield consists only of the pressure wave component. In regard to fish hearing, the distinction between the two different fields is of importance as the pressure component of sound can only be detected indirectly by some fishes via the development of adaptive specialized structures (Mann 2006). These adaptive specialized structures allow for the pressure wave to be converted into particle motion, to stimulate the hair cells in the inner ear (Mann 2006).

Inner Ear

All fish ears are internal, consisting of two inner ears with no direct fluid connection to their environment (Fay and Popper 1975). Each inner ear is comprised of three endolymph-filled semicircular canals and three sound receptive epithelium known as the saccule, urticle, and lagena, where the sound receptors are located (Popper and Fay 1999). The sound receptors that are responsible for hearing in fish are known as hair cells, comprised of many stereocillia and a single kinocilium, similar in structure to the cells found in the human ear (Fay and Popper 1975). During sound detection, these projections off the hair cells are bent during sound detection, opening ion channels and generating an action potential, allowing the recipient to hear the sound (Fay and Popper 1975). However, sound detection is not as simple underwater as on land and therefore poses a problem for fish due to the environment in which they live (Popper and Fay 1973). For fish, because their body is about the same density as its surroundings, when sound vibrations pass through the water, the fish moves along with it, preventing the hair cell from being stimulated. To counteract the similarity in densities between the recipient and its environment, the fish ear contains a structure known as the otolith, a small, hard structure that is situated atop the cilia that makes up the hair cell, which assists fish with detecting sound vibrations. The otolith, being heavier and thusly, different in density than water, lags behind the motion of water generated by sound vibrations, causing the hair cells to bend and the fish to hear (Popper and Fay 1973).

Several studies have shown that fish can determine the range and direction of sound underwater however the manner in which a fish can directionalize a sound is complicated (Popper and Fay 1993, Bleckmann 1993, Mann 2006, Popper and Schilt 2008). Humans and other terrestrial organisms directionalize sound using interaural timing and intensity differences between the two ears (Popper and Fay 2011). However, since sound travels five times faster in water than it does on land, the distance between a the inner ears of a fish, due to their small head size, is no more than a few centimeters, therefore interaural timing and intensity differences are not available for fish to directionalize sound and must depend on a different mechanism to do so. In some fishes, the mechanism that is thought to be used to directionalize sound is the lateral line (Coombs and Conley 1997, Fay 2005). However, some fish are believed to detect the direction of particle motion and localize the sound source using a hearing specialization involving the inner ear's hair cell orientation and the swimbladder; this is known as the phase model. The phase model states that when detection of particle motion between the hair cells and the swimbladder are in phase, this allows the individual to determine that the sound source is situated behind them (Popper and Fay 2008). However, when the two structures are out of phase, this indicates that the source is in front of them (Kasumyan 2008, Popper and Fay 2011), allowing a fish to travel along the axis of particle motion and localize the sound source (Fay 2005).

In some fish species, the detection of sound pressure has been made possible by modification of the swimbladder and it is thought that the use of the swimbladder in fish allows for the detection of sound along the horizontal plane; in front or behind (Popper and Fay 2011). All fish can detect particle motion however those species that are able to detect sound pressure use the gas within the swimbladder as a means to convert pressure waves into vibrations that can be translated by the otolith for the inner ear to detect (Popper and Fay 2011). In order for the inner ear to detect the sound, a connection must occur between the swimbladder itself and the inner ear. Many different types of structures exist that allow communication between swimbladder and the inner ear however they vary between fish species but work more or less in the same manner (Popper and Schilt 2008). For example, direct bony connections between the swimbladder and the ear such as Weberian ossicles (a modified vertebrate), the use of auditory bullae (small bubbles connected directly attached to the swimbladder and ear), simple swimbladder extensions (similar in structure to the swimbladder in the shape of a horn), and branchial bubbles (bubbles in the mouth of a fish), have all been found to be used by fishes as a means of detecting sound pressure in the environment (Popper and Schilt 2008).

Lateral Line

The lateral line is a mechanosensory system that consists of sensory receptors that are known as neuromasts that are composed of a number of hair cells and the orientation of the lateral line of a fish can differ in location depending on the species (Bleckmann 1993). Neuromasts, like inner ear hair cells, respond to water motion. Neuromasts, similar to the inner ear hair cell, suffers the same concern in regard to density, and as a result, each cluster of hair cells has an attached hardened, gelatinous structure known as the cupula that acts to offset the density difference between the recipient and its environment. The cupula, similar to the otolith of the inner ear, lags behind the motion of the water, bending and thereby stimulating the hair cell, allowing the recipient to detect the surrounding particle motion. Depending on how the hair cell bends, different signals are sent to the brain and used to interpret the direction and orientation of the disruptions within the water column. In fish, there are two types of neuromasts, superficial and canal. Superfical neuromasts, as the name suggests, are neuromasts that are situated along a fish's body, exposed to the environment (Popper et al. 2003). Superficial neuromasts are sensitive to low frequency sounds (up to 10 Hz), and primarily function as a means for rheotaxis. Canal neuromasts, in contrast, are similar in structure to those exposed on the body's surface, but are embedded within the depressive pores situated within a canal pathway within the lateral line itself. Canal neuromasts differ from superficial in that they can detect higher frequencies (up to 100 Hz) and detect particle gradients from one pore to the next (Popper et al. 2003). Although the orientation and position of the lateral line varies between species, in some fishes that lack hearing specializations, neuromasts, both superficial and canal, can be used to detect disruptions in particle motion and determine the direction in which the sound source is located (Popper et al. 2003). Therefore, sound detection in most fish, is comprised of a combination of both the ears itself and the lateral line (Bleckmann 1993, Popper et al. 2003, Fay 2005).

Function of Acoustic Communication in Fishes

Mate Attraction and Territorial Defense

Fish emit sounds in a variety of situations, usually in conjunction with diverse behaviours, performed during agonistic interactions, courtship and spawning in regard to mate attraction and territorial defense (Ladich, 1997, Kasumyan 2009). Vocalizations performed to attract females are often unique between species and have been found to occur during advertisement, courtship, pre-spawning, and spawning phases (Kasumyan 2009). However, the structure of these sounds can differ depending on the time in which these vocalizations are performed. For instance, advertisement calls are sounds that are meant to attract females to their nesting site from a distance, and as a result, these calls should be long in duration, and repeated; these are known as call trains (Kasumyan 2009). The humming vocalization of the plainfin midshipman is a prime example of a long duration and loud vocalization that draws females from a distance (McKibben and Bass 1998, Sisneros and Bass 2003, Sisneros 2009). Continuously performed vocalizations are ideal during the breeding season, as fish often spawn in groups where males procure nesting sites in relatively close proximity to one another (Fay 2005). As a result, in order for a female to locate the sound source, a continuously performed signal is often ideal as it allows the female to concentrate on the male that originally drew her interest (Fay 2005).

Courtship sounds are often performed by males during the time that they are alone in the nest and are used to convey to females that they are ready to mate (Amorim and Neves 2007, Malvasi et al. 2009, McKibben and Bass 1998). Interestingly, courtships sounds have been found to change once a female has moved into the male's territory. In male haddock, *Melanogrammus aeglefinus*, males at first will perform a slow interpulse duration knocking vocalization when alone, but will alter the call rate of this same call to that of rapidly repeated knocks once the female is in close proximity to the vocalizing male (Casaretto and Hawkins 2002). Pre-spawning sounds, however, are performed before the actual spawning phase once the female has localized the position of the male, and are usually performed in conjunction with visual displays (Kasumyan 2009). In Hawaiian dascyllus, *Dascyllus albisella*, males perform rapid up and down migrations to and from the water column, known as signal dips and jumps, while vocalizing, once a female has approached (Mann and Lobel 1997). In contrast, male green damselfish, *Abudefduf abdominalis*, upon the arrival of a female, will swim looping or zigzagging patterns as a means to maintain the female within his territory. If the female responds, males will emit long sounds in response, and continue to do so once the female has entered the nest (Maruska et al. 1997). Spawning acoustic signals, interestingly, are often used to assist with the synchronization of the release of gametes between the male and female, commonly performed by broadcast spawners, as seen in Atlantic Cod, *Gadus morhua*. Male cod will perform muffled grunting sounds that signals the female to move upward in the water column where spawning occurs (Hutchings et al. 1999)

Aggressive sounds, in contrast, are implemented in the function of territorial defense to maintain spatial relations between conspecifics and can be performed as warning signals to indicate that a site is occupied or during agonistic interactions, usually between males, during competitions, or to assert dominance within a hierarchy (Ladich 1997). Commonly, aggressive sounds that are used for territorial defense are often performed during the reproductive season, as a means for males to maintain nesting sites from competitors (Ladich 1997). Valinski and Rigley (1981) demonstrated the importance of performing sounds to maintain nesting sites; when male skunk loaches, *Botia horae*, are made mute they were unable to protect their territory from other conspecifics despite performing aggressive displays. Similarly, in bicolour damselfish, removal of the defending fish from a site would result in rapid occupation by other conspecifics. Playing recordings of a defending male in the absence of the owner at that same site causes other males to take a sufficiently longer time to approach the nest and make it their own (Myrberg and Riggio 1985, Myrberg et al. 1997). Interestingly, some fishes such as the plainfin midshipman and toadfish, *Opsanus tau* and *Halobatrachus didactylus,* have been found to perform aggressive grunts when being handled and is thought to be performed in fear (Amorim 2006).

Interspecific Differences for Mate Attraction Calls

A simple difference between interspecific mate attraction calls in fish is the way they sound to the human ear (Kasumyan 2009). For example, in the plainfin midshipman, toadfish, and damselfish, each species has its own unique calls that are used during the breeding season known as hums, boatwhistles, and chirps that are used to attract females (Amorim 2006). For the plainfin midshipman, hums, are long in duration, harmonic in structure, reaching up to 700 Hz and have a fundamental frequency lying between 90-100 Hz, depending on the individual performing the sound and can last up to an hour in some cases (Sisneros 2009). As a result, the sound is believed to be a mate attraction call that is commonly performed in the plainfin midshipman (McKibben and Bass 1998). In regard to the toadfish, males perform a sound known as a boatwhistle that lures females to the nest to spawn (Amorim et al. 2006). In comparison to the hum call emitted by midshipman, the boatwhistle is shorter (500 ms) in duration (Dos Santos et al. 2000). The boatwhistle is a multi-harmonic call, reaching a fundamental frequency of 130 Hz, and is composed of two segments (Dos Santos et al. 2000). The first segment is composed of a signal grunt while the second component is comprised a multi-harmonic hoot (Tavolga 1960). Finally, damselfish perform a brief, multi-pulse broadband vocalization known as a chirp during courtship, which consists of three pulses that are emitted in conjunction with visual displays (Myrberg and Spires 1972).

Primarily, in relation to mate attraction and recognition by females, there are differences in the components that make up these sounds that allow for fish to distinguish one call from another (Kihslinger and Klimley 2002). The same can be said when differentiating between vocalizations that are emitted by nearby conspecifics and heterospecifics. These differences are primarily temporal in nature and include the length of a call (call duration), intercall duration, pulse duration, and interpulse duration. Furthermore, fish calls differ in being either pulse or tonal and further differences can include being broadband can vary with frequencies (Kihslinger and Klimley, 2002).

In relation to call structures and distinguishing between conspecific and heterospecifics calls, the most telling and best understood aspects of fish vocalizations are components in relation to pulse characteristics. Pulse number refers to the amount of pulses that occur within a call (Kihslinger and Klimley 2002) and varies between call types within a species as well as between species (Myrberg et al 1978). Pulse rate within a call is described by the number of pulses that are performed per second, where each pulse individually can vary in length and pulse duration refers to the time at which a pulse begins and ends (Kihslinger and Klimey 2002). Interestingly, it has been suggested that the silence that elapses from one pulse to another contains the most information when distinguishing between different species calls (Myrberg et al. 1978). Furthermore, it has been speculated that since these pulse characteristics vary between species, that pulse rate provides a means of species recognition and mate choice in fish (Myrberg et al. 1978), which has been thoroughly investigated with the use of playback experiments (Myrberg et al. 1978, 1986, 1993, Crawford et al. 1997, McKibben and Bass 2001). The importance of temporal characteristics as a function of species recognition as well as mate recognition is better facilitated by examining the response of fish to conspecific sounds in contrast to heterospecific sounds in playback experiments found that while fish approach conspecific sounds more readily and vigorously (Myrberg and Spires 1972, Rollo and Higgs 2008). Furthermore, in relation to recognition of mate attraction sounds, this is best shown in playback experiments examined for toadfish and midshipman where, upon examining the response of different reproductive morphs to the suspected mate attraction call, gravid females approach the speaker play this vocalization more frequently than nonreproductive females and other males (Winn 1972, McKibben and Bass 1998).

In relation to mate attraction recognition by females, frequency also plays a role in mate recognition, although not as fundamental as temporal characteristics (Kihslinger and Klimley 2002). In relation to frequency of a call, many characteristics can be used when describing a fish vocalization. Frequency consists of the dominant frequency, frequency modulation, fundamental frequency and the frequency range (Kihslinger and Klimey 2002). Dominant frequencies refer to the frequency that occurs most often in a fish vocalization, while frequency modulation and fundamental frequency refer to the changes in frequencies within a call and the natural frequency, respectively (Kihslinger and Klimley 2002). The frequency at which a fish performs is often associated with body size and provides a means of individual recognition for conspecifics (Amorim and Vasconcelos 2008, Amorim et al 2008). While frequency may indicate the size of the individual performing the sound, this pattern does not apply to all fish species. However, in regard to reproduction, frequency may act as a function of honest signalling in some fishes, as females could assess male size as an indicator of quality (Malavasi et al. 2003, Colleye et al. 2009). Foraging abilities, territory, and nest guarding have all been found to be associated with male body size that could indicate parental and fitness qualities to females. Furthermore, in some fish species, females prefer larger males and are more attracted to conspecific males performing low frequency vocalizations rather than high frequency sounds (Malavasi et al. 2003, Colleye et al. 2009). However, while frequency may track fish size, females would only be able to assess male size using frequency characteristics from a vocalization, but not the species of the individual performing the sound (Crawford et al. 1997). Fish vary in their ability to detect frequencies since fish do not possess any known frequency filtering structure, such as the cochlea in mammals (Hawkins 1993), but interestingly, evidence of neurons that are specialized to detect fine temporal components of a sound have been found, such as in the family Mormyridae (Crawford et al. 1997).

Of interest in playback experiments when examining species-specific responses to conspecific sounds is when temporal characteristics are altered and how the behavioural responses of fish change when presented with these new sounds. For example, in a series of studies examining response to a number of different damselfish species to altered conspecific calls, Myrberg et al (1978, 1986, 1993) found that when altering the number of pulses in a conspecific call, fish responded more discriminately to the sounds that were similar to the normal number of pulses that exist within the wild version of the sound. However, when conspecific sounds were standardized to each having only four pulses, the difference in interpulse interval was used as a means to differentiate between sounds. However, when differences in the "off-time" between pulses were eliminated, fish were no longer able to differentiate between conspecific and heterospecific vocalizations. The same responses were seen displayed by both male and female damselfish in relation to the chirp vocalization, as males have been found to intercept other male vocalizations used in mate attraction (Myrberg et al. 1978, 1986, 1993).

In plainfin midshipman, alteration of the temporal envelope modulation of their vocalizations was found to be a means of examining vocal recognition (McKibben and Bass 2001). Temporal envelope modulation is thought to be important in differentiating between different call types within a species, such as the grunt and the hum of the midshipman (McKibben and Bass 2001). For instance, continuous tones, such as the hum, are much more effective in attracting gravid females than simple pulsed sounds, such as the grunt, during playback (Bass and McKibben 2003). Interestingly, the hum of the midshipman does not contain any means of amplitude fluctuations and therefore lacks any means of temporal envelope modulation. However, hums have been found to be adjusted when vocalizing near other performing male and create beats due to interference between two sounds that differ slightly in fundamental frequency, generating an amplitude and phase modulation (McKibben and Bass 2001). As a result, it is thought that females distinguish between frequencies and use that component to recognize the sound; when gravid females were presented with the choice between a pulsed or tonal vocalization, it was the reduction in beat modulations was the most important characteristic in facilitating female response as they were highly sensitive to slight increases in beat frequency (McKibben and Bass 2001). An interesting model in the investigation of acoustic communication of fishes in regard to both hearing and behaviour is the invasive round goby, *Neogobius melanostomus*, as past studies have found that gobies are able to differentiate between conspecific and heterospecific sounds (Rollo and Higgs 2008) as well as the ability to localize sound sources (Rollo et al. 2006, Rollo and Higgs 2008) despite not having any known hearing specializations. In addition, the function of acoustic communication in the round goby is unknown and requires further investigation that could be useful in the control of the invasive species.

The Round Goby

The round goby is a small, bottom-dwelling teleost fish that is believed to have first entered the St. Lawrence River by transportation in ballast water of commercial ships originating from the Ponto-Caspian region (Vanderploeg et al. 2002). Since its establishment in 1990, the round goby has moved into all five Great Lakes (Charlesbois et al. 2001). Due to its highly aggressive and competitive nature, round gobies have begun to negatively impact the freshwater ecosystems of North America (Jude et al.

1992). By outcompeting native species for shelter and food, the round goby has successfully increased their population size to an enormous number in a decade after being reported (Charlesbois et al. 2001). The rapid population growth portrayed by the invasive species is primarily due to the goby's ability to spawn multiple times in a single breeding season, allowing for the rapid population growth of the fish (MacInnis and Corkum 2000). Since then, the populations of numerous native species, such as mottled sculpins, *Cottus bairdii,* and logperch, *Percina caprodes*, have suffered a decline (Charlesbois et al. 1997).

In an attempt to control and prevent the expansion of the round goby into other freshwater systems and alleviate the extensive damage the invader has caused in the Great Lakes, current research has been lead in the direction of understanding the reproductive behaviour of the round goby. A popular paradigm of research when investigating the goby's reproductive behaviour is often in association with communication modalities that are used in mate attraction, where one modality in particular has received the most attention; chemical communication. Chemical communication is believed to be used in mate attraction in the round goby due to the circumstances of the environment in which they live (Charlesbois et al. 1997). Since round gobies live in turbid waters, visual communication would be impracticable. In contrast, past studies have found that males are suspected of releasing pheromones in their urine as a sex attractant to lure gravid females to their nest to spawn as a much more effective means of sending signals between conspecifics (Corkum et al. 2006). Females spend more time near synthesized steroids that are representative of compounds that have been isolated from reproductive male round goby testes and believed to be released in their urine (Corkum et al. 2008). In addition, female gobies have been found to spend more time near washings of RMs than non-reproductive males (Gammon et al. 2005). Finally, male round gobies also were found to increase gill ventilation rates when exposed to either gonadal extracts of gravid females or estrone (Belanger et al. 2006). Currently, investigation of steroids that comprise male pheromones that is responsible for attracting gravid females is on-going, following the discovery of female preference towards conjugated steroids blends (etiocholanolone glucuronide, etiocholanolone sulfate, 11-oxo-etiocholanolone glucuronide, and 11-oxo-etiocholanolone sulfate) and avoidance of free steroids (11β-hydroxy-androstenedione, and 11-ketotestosterone) (Corkum et al. 2008). Research efforts are now intensifying in an attempt to isolate the steroid that facilitates the strongest attraction as well as discovering other sex attractants that are likely responsible for initiating courtship and spawning behaviours in females.

Though lackluster in comparison to the attention that has been directed to chemical communication research for the round goby, the use of acoustic communication for mate attraction in the species has also undergone investigation. While investigation of round goby hearing has shown poor hearing sensitivity(Belanger et al. 2010) , long distance auditory communication is not required since round gobies are colonial and live in relatively close proximity to one another (Charlesbois et al. 1997). The very first investigation and description of acoustic communication behaviour of the round goby was by Protasov et al. (1965), where it was stated that round goby males, to attract females to the nest, emit sounds resembling croaking or squeaks, that is than followed by the male lashing its tail near the incoming female in an attempt to lead her into the nest to spawn. In addition, Protasov et al (1965) was also the first to investigate female response to conspecific male calls using playback experiments, and found that these sounds have an attractive effect. Further examination of round goby response to conspecific acoustic signals remained stagnant until recently (Rollo et al. 2006, Rollo and Higgs 2008). In the field, round gobies show significantly strong phonotactic attraction to the playing speaker emitting the conspecific call in contrast to the nearby silent speaker however, due to the limitations of field dynamics, quantification of sex could not be determined (Rollo et al. 2006). Lab playback experiment revealed that while both male and female round gobies responded to the conspecific call, females were found to be much more responsive to the conspecific call than males were, providing evidence that the vocalization that had been recorded from the field could potentially be a mate attraction call (Rollo et al. 2006). To further evaluate the specificity and attraction to the same conspecific call implemented in Rollo et al. (2006), the response of male and female round gobies to both conspecific and heterospecific calls were examined in Rollo and Higgs (2008), where they found that both sexes responded to the conspecific call much more vigorously and with a higher specificity than to the heterospecific sounds. However, the conspecific sounds again were found to elicit the strongest phonotactic response from females, further supporting that the call examined had some function in mate attraction (Rollo and Higgs 2008). More recently, Kasurak et al. (2012) examined the multimodal response of gravid female round gobies to both conspecific odours and sounds. While odours and sounds alone do elicit an attractive response, the two elements together elicited a significantly stronger attraction to the source itself, thereby supporting the idea that mate attraction behaviour of the round goby encompasses both chemical and acoustic communication, rather than implementing just the one modality. While it has been found that both male and female gobies respond to the conspecific sound, the importance of the reproductive status of the fish has not been taken into account, behaviourally. By doing so, it can help clarify which gobies are attracted to these calls as well as which call is more efficient for mate attraction and implement these findings in design of an acoustic trap to use in the control of the round goby population.

Invasive Species

With the constant transport of invasive species by anthropogenic technologies, such as commercial ships, and pleasure crafts, the concern to impede the transport of these unwanted species outside their native range has come to a head (Mills et al. 1993). Invasive species can include both flora and fauna which, more often than not, are deleterious when introduced to environments outside their natal range, as they are able to out-compete native species for resources with ease (Mills et al. 1993). The competitive edge that many invasive species possess is usually in part due to a number of traits, such as fast growth, rapid reproduction, high dispersal ability, robust ecological competence, and phenotypic plasticity (Lovell et al. 2006, Olson 2006, Lockwood et al. 2007). As a result, because an invasive species' natural predators are not present to otherwise control its rapid expansion and growth, the invaders development in new areas goes unchecked and excessive damage to the environment and food webs occur (Lovell et al. 2006, Olson 2006, Lockwood et al. 2007). Common examples of invasive species that have caused excessive damage to environments both ecologically and commercially are the brown tree snake, *Boiga irregularis,* sea lamprey, *Petromyzan marinus*, and Kudzu, *Pueraria lobata*, that have led to the reduction or eradication of native species populations in a number of areas, such as Guam, the Laurentian Great Lakes, and North America as a whole (Lovell et al. 2006, Olson 2006, Lockwood et al. 2007)**.** As a result, invasive species, not only impact native flora and fauna directly, but can also indirectly negatively affect native food webs extensively and thereby broadens the range in which a invasive species does damage.

While most invasive species are brought into new regions unintentionally, very few tried and true strategies have been developed that would otherwise prevent this phenomenon from occurring, though attempts have been made (Daunys et al. 2006, Madenjian et al. 2008). For example, commercial ships that transport invasive species with the intake and release of ballast water from port to port are now required by law, upon moving from one body freshwater system to another, to intake a percentage of saltwater when crossing the ocean, in the hopes of upsetting the osmotic balance of freshwater species within the ballast water, and thereby eradicating any potential invaders before being released at port (Daunys et al. 2006, Madenjian et al. 2008). In addition, strict rules exist for transporting non-native wood across borders to prevent invasive insects from being introduced (Simberloff and Stiling 2006). However, even with these preventative attempts, invasive species still manage to get across either due to human ignorance or the refusal to take the necessary precautions to prevent an invasive introduction from occurring (Daunys et al. 2006, Madenjian et al. 2008). As a result, invasion of non-native species still can occur, albeit not as frequently as it has occurred in the past (Lovell et al. 2006, Olson 2006, Lockwood et al. 2007). Since eradication of invasive species, in most cases, is impossible, regulation of the spread and size of these species is often performed. For example, to reduce the impact of sea lamprey on native fishes, the use of lampricide, a reproductive inhibitor that targets lamprey larvae, assists with keeping lamprey numbers low and thereby alleviating stress on prey species (Coble et al. 1999, Stokstad 2003). Similarly, for invasive brown tree snakes and kudzu, similar strategies have been implemented for control purposes, where the use of capturing methods (use of mice-baited traps and acetaminophen to increase mortality) and herbicides have been constructed to reduce damage on native species that have been affected by these invaders presence (Lovell et al. 2006, Olson 2006). However, while strategies have been put to use in controlling a number of invasive species, there are still those that exist in areas that are far more deleterious than those already mentioned, that have gone unchecked for decades (Lovell et al. 2006, Olson 2006); one being the round goby (Charlesbois et al. 1997).

Thesis Objectives

The first objective of the current study was to examine the response of round gobies to two suspected mate attraction calls recorded from conspecific males, dubbed the “grunt” and the “drum”, in relation to reproductive state and sex. While past studies have examined the response of male and female gobies to conspecific calls (Rollo et al. 2006, Rollo and Higgs 2008, and Kasurak et al. 2012), the important of the reproductive state of the individual has yet to be investigated, behaviourally. By investigating both reproductive state and sex differences to conspecific calls, it can be better understood and more accurately stated what the function of these conspecific sounds are in the round goby’s behaviour. Playback choice experiments were used in the lab to determine the response of gobies of both sexes to recordings of two conspecific calls suspected to play a role in mate attraction, a grunt and a drum, in relation to reproductive status of responding fish. I hypothesized that since these calls are suspected to play a function in mate attraction, reproductive females (RFs) should show the strongest response as that is its function (high initial response, high number of approaches, and largest time spent at a conspecific call). In contrast, reproductive males (RMs) were hypothesized to show the lowest response to the conspecific calls, as in nature it is deleterious for a male to leave his nest just to investigate another male calling as he exposes his nest to egg predation or loss of the male's nesting site. For nonreproductive males (NRMs), nonreproductive females (NRFs) and sneaker males (SMs), it was hypothesized that if these morphs did show a positive response to the conspecific calls, then they could potentially be acting as eavesdroppers, but for different reasons. Yavno and Corkum (2010) have found that the odour of conspecific eggs attract nonreproductive fish significantly, indicating that they do in fact use chemical cues to locate conspecific eggs, but the dispersal of chemical signals is directionally limited (i.e.: current), making it difficult to locate a nest from a distance. Nonreproductive fish could also eavesdrop on calls produced by nest guarding males that are trying to attract females to his nest. Since females tend to spawn with males that have eggs (Wickett and Corkum 1998), nest-guarding males should continue to call when eggs are already in the nest. As a result, nonreproductive fish should eavesdrop on these calls and use them as a means to locate the nesting site and use odours to determine if eggs are present. As a result, SMs were predicted to perform a similar behaviour as NRMs and NRFs, but instead attempt to sneak fertilizations upon determining the location of the nest rather than eat the eggs that are present. Results from the lab study would later be incorporated into examination of round goby response to conspecific calls in the field and facilitate the construction of a bioacoustic trap (objective

2) that could be used in population control of the round goby in the Great Lakes by using a conspecific call as a lure.

The second objective of the current study was to design a bioacoustic trap that would implement the use of round goby calls as a lure, capturing them in large numbers, and be used to regulate the population size of the invasive species. Playback experiments using three pairs of traps were used in the field to determine the response of gobies of both sexes to recordings of two conspecific calls suspected to play a role in mate attraction, a grunt and drum, in relation to reproductive status of responding fish. Though it is impossible to eliminate the round goby from the Great Lakes completely, reducing their numbers may be a plausible solution. Bergstrom and Mensinger (2009*)* found that native species are able to persist in areas where the population size of the goby is low. This indicates that the impact of the round goby is not due to its mere presence, but rather their overwhelming number that native species cannot contend with. Therefore, if I develop a way to construct a technique that could lower their numbers, the result would be the reduction of competitive stress on native species. Using sound as a lure has such advantages as species-specific calls will reduce capture of non-target species. Most importantly, gravid females may be the most responsive to the call, whose capture and removal would greatly reduce the reproductive success of the species. This is because round gobies have an extensive breeding season that extends from early May to late August and spawn multiple times within a single season, while native species only spawn once per year (MacInnis and Corkum 2000). This results in a large population size and is responsible for their success as an invasive species. In relation to behavioural responses, I quantified the number of individuals captured by treatment, reproductive state, and month. I predicted that since the round gobies reproductive season peaks in May and declines continuously into late August, a majority of gobies would be captured in May and capture rate would decline progressively by month. Based on previous findings from our playback experiment performed in the lab, I predicted that the grunt call would be the most effective in attracting round gobies, especially in regard to reproductive females (RF), while the drum call would attract the least. In contrast, reproductive males (RMs) were predicted to show the lowest response to the conspecific calls, as it is deleterious for a male to leave his nest to investigate another male calling as he exposes his nest to egg predation or loss of nesting sites to potential competitors in the area. In regard to nonreproductive males (NRMs) and sneaker males (SMs), I predicted that these morphs would respond the most to the drum call as eavesdroppers, as displayed under lab conditions. As for nonreproductive females (NRFs), despite lab results, I predicted that if this morph did show a positive response to the conspecific calls in the field, then they could potentially be acting as eavesdroppers.

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CHAPTER 2:

STATE-DEPENDANT ATTRACTION OF ROUND GOBIES, *NEOGOBIUS MELANOSTOMUS*, TO CONSPECIFIC CALLS

Introduction

Fish emit sounds in a variety of ways and the sounds are often associated with distinct behaviours (Amorim 2006). Sounds can be expressed during agonistic interactions (Raffinger and Ladich 2009), in the presence of predators (Smith 1992), when feeding (Amorin and Hawkins 2000), and during courtship (Lobel and Kerr 1999). One of the most common purposes of auditory communication is for mate attraction (Kasumyan 2008). Usually males of a species call not only to indicate their location but also to advertise to females (Amorim 2006). Acoustic signals have been found to play an important role in the mating and reproductive behaviour of freshwater fishes (Kasumyan 2009, Ladich 2004). For example, in the plainfin midshipman *Porichthys notatus,* during the breeding season, Type I males guard nests and emit long duration hums and short grunts in the presence of a female, attracting females to the nest to spawn (Brantley and Bass 1994; Sisneros 2009; Zeddies et al 2010). Similar behavioural responses of have been observed in the Lusitanian toadfish *Halobatrachus didactylus*, where males are believed to perform boatwhistles that are exploited by females for individual recognition when selecting a mate (Amorim and Vasconcelos 2008), and male haddock *Melanogrammus aeglefinus* that are known to produce calls described as short repeated knocks to indicate location to a female. Furthermore, male haddock are known to alter their call to a long series of repeated knocks as the female comes closer to synchronize spawning (Hawkins and Amorim 2000). While many studies have examined acoustic communication in association with mate attraction and have determined what types of conspecific calls females show favourable response to (Gray and Winn 1961, Myrberg and Spires 1972, Myrberg et al. 1986, McKibben and Bass 1998), seldom investigated how internal physiological cues, such as hormones, drive female mate choice decisions and behaviour.

Although, female auditory sensitivity has been shown to increase in response to male calls during the spawning season in some species (McFadden 1998, Sisneros et al. 2004), the mechanism that drives this shift in behavioural preference between the breeding and non-breeding season remains largely uninvestigated in fishes**.** Hormones are well known to initiate sexual maturation and the development of secondary sexual characteristics in fish (Fostier et al. 1983) however they may also play a role in female mate choice behaviour (Nelson et al. 1990, Munakata et al. 2010). For instance, gravid female cichlids, *Astatotilapia burtoni* prefer associating with territorial (reproductive) males over non-territorial (non-reproductive) males while non-gravid females show no preference (Clement et al. 2004). Similarly, gravid female plainfin midshipmen perform robust phonotactic responses to male advertisement calls while spent females never approach a speaker playing these calls (McKibben and Bass 1998). Summer (reproductive) female midshipman also show strong temporal encoding to acoustic signals up to 340Hz while winter females only display temporal encoding up to 100Hz, corresponding to enhanced detection of the higher harmonic components of conspecific mate attraction calls (Sisneros and Bass 2003). As a result, these studies provide behavioural and physiological evidence that responses can differ between reproductive females and females that are no longer within their reproductive cycle.

A useful model group to examine reproductive plasticity in acoustic responsiveness is the teleost family Gobiidae. Male gobies often display elaborate vocalizations performed during the breeding season (Malavasi et al. 2008) and construct a nest from which they vocalize grunt-like sounds to attract females (Kasumyan 2009). Reproductive male Arno gobies, *Padogobius nigricans,* vocalize almost pure tones during the pre-spawning phase of the breeding cycle to lure a female towards his nest (Lugli et al 1996). As the distance between the sender and receiver outside of the nest decreases, the male responds by increasing the repetition and intensity of the signal, suggesting that males enhance their call rate to advertise to the female (Lugli et al 1996). Similarly, male black-spotted gobies, *Pomatoschistus canestrinii,* perform a combination of vocal and visual displays when a female is present outside of the nest (Malavasi et al. 2009). Once the female enters the nest, males continue to vocalize and are thought to signal their value as a mate and readiness to spawn, rather than for female stimulation (Kasumyan 2009). While the family Gobiidae has been a focal interest of research in regard to behaviour and sound generation (Tavolga 1954, 1956, 1958, Lugli et al. 2004, Amorim and Neves 2007, Malavasi et al. 2008), state-dependant responses has so far been overlooked.

The focus of the current study is to investigate the response frequency of various reproductive morphs of the round goby, *Neogobius melanostomus*, to conspecific calls suspected to be used for mate attraction and how reproductive state affects behaviour. The round goby *Neogobius melanostomus* is a small, bottom-dwelling teleost fish that first entered the St. Lawrence River in 1990 (Vanderploeg et al. 2002) and since then have invaded all five Great Lakes in little over a decade (Charlesbois et al. 2001). Due to its highly aggressive and competitive nature, round gobies negatively impact the freshwater ecosystems of North America (Jude et al. 1992) by outcompeting native species for shelter and food due to their large population size (Charlesbois et al. 2001), causing native species such as sculpins *Cottus bairdii* and logperch *Percina caprodes*, populations to suffer a decline (Charlesbois et al. 1997). However, recent studies have shown that round gobies have become prey for some native piscivorous fish, leading to an increased growth rate in these predator species (King et al. 2006). Since round gobies live in turbid waters, visual communication would be impracticable except at extremely close distances. Therefore, auditory communication may be an alternative means for the species to interact in their environment. Male round gobies have been found to produce calls during mate attraction (Rollo et al. 2006) and female round gobies respond to these calls with high specificity (Rollo and Higgs 2008). In addition, round gobies approach both heterospecific and conspecific calls, but respond to conspecific sounds more vigorously and seem to be able to localize the source more readily (Rollo and Higgs 2008). It has been suggested that these calls serve a reproductive function (Rollo et al. 2006, Rollo and Higgs 2008) but both males and females respond to acoustic cues, leaving the precise function largely unresolved.

The goal of the current study was to examine differential attraction and state-dependent response between reproductive morphologies to a range of conspecific call types in the round goby. Playback choice experiments were used in the lab to determine the response of gobies of both sexes to recordings of two conspecific calls suspected to play a role in mate attraction, a grunt and a drum, in relation to reproductive status of responding fish. In relation to behavioural responses, I measured the percent of individuals who first responded to a playing speaker (initial response), number of approaches, time spent, and path angle deviation in accordance to relative distance travelled and time elapsed when travelling to a speaker for the different sound types examined. I predicted that since these calls are suspected to play a function in mate attraction, reproductive females (RFs) should show the strongest response. In contrast, reproductive males (RMs) were predicted to show the lowest response to the conspecific calls, as it is deleterious for a male to leave his nest to investigate another male calling as he exposes his nest to egg predation or loss of nesting sites to potential competitors in the area (Corkum et al. 1998). In regard to nonreproductive males (NRMs), nonreproductive females (NRFs) and sneaker males (SMs), it was predicted that if these morphs did show a positive response to the conspecific calls, then they could potentially be acting as eavesdroppers.

Materials and Methods

Animal Housing

Round gobies were collected by angling from the Canadian shore of the Detroit River at Windsor, ON [42^{o}20′N, 82^{o}56′W] during the morning from early May to mid-August; when the reproductive season peaks for the species (Charlesbois et al . 2001). Fish were kept at the University Animal Quarters in accordance with the University of Windsor Animal Care Guidelines. Upon arrival to the laboratory, gobies were housed in 37.8 litre glass tanks (50.8 cm x 25.4 cm x 30.4 cm) that were aerated and using a filtration system. Individual tank bottoms were lined with gravel and water was held at a temperature of 18^{o}C (± 2^{o}C) and a photoperiod of 16h:8h light:dark cycle during the experimental period. Gobies were fed Big Al’s Staple Fish Flakes (Big Al’s Aquarium

Services Co, Woodridge, ON, Canada) 5 times a week and were tested within a week of capture to prevent domestication.

Gobies that were tested consisted of all possible reproductive morphs that develop during their spawning season: reproductive males (RM), reproductive females (RF), non-reproductive males (NRM), non-reproductive females (NRF), and sneaker males (SM). Male and female round gobies were identified based on shape differences of their urogenital papillae (Charlesbois et al. 1997). Reproductive males were distinguished from NRMs by possessing secondary sexual characteristics such as being dark in colouration (usually jet black), having swollen cheeks and a developed papilla, as well as slime production (Marentette et al 2009). Reproductive females, in contrast, were identified from NRFs by possessing a swollen papilla (larger and yellow) and belly (Corkum et al 2008). Finally, SMs were identified as being small in size and mottled colouration resembling a female, but possessing a long, developed papilla (Marentette et al 2009). Reproductive status was confirmed following a trial by euthanizing the fish with clove oil and calculating Gonadal Somatic Index (GSI): GSI = total gonad mass (testes + seminal vesicles/ovarian eggs)/total body bass *100 (Schreck and Moyle, 1990). Males that were found to have a GSI measurement of $\geq 1.3\%$ and any female with a measurement of $\geq 8.0\%$ were considered to be reproductive (Belanger et al. 2004). If any males or females were found to have a GSI of $< 1.3\%$ and $< 8.0\%$ respectively, they were considered non-reproductive. Suspected RFs that were found to have a GSI $< 8.0\%$, were not included in the analysis to avoid confounding results for NRFs. For SMs, if the GSI was found to be $\geq 4.0\%$, then the individual was considered a reproductive sneaker male (spawning potential), any SMs that had a GSI $< 4.0\%$ were not considered reproductive. (Marentette et al 2009). In regard to nonreproductive fish (both NRM and NRF) following GSI, no developed gonads were present (quantified as having a GSI value of zero) assuring the individuals were not sexually mature when tested and therefore not affecting their response to sounds (Table 2.6).

Behavioural Trials

Lab experiments occurred in a 1020 liter rectangular (243.8 cm x 91.4 cm x 91.4 cm) fibreglass tank that was filled to a depth of 33 cm with dechlorinated water, held at 18^{o}C (±1^{o}C), to match holding conditions. Two underwater speakers (UW-30, Lubell Labs, Columbus, OH, U.S.A) were placed on opposite ends of the tank at a distance of 243.8 cm from one another (Fig. 2.1). To reduce reverberations generated when the speaker was playing, the speakers were set on acoustic foam to muffle vibrations. In addition, speakers were placed inside of a small barrier enclosed around all sides, to prevent gobies from hiding underneath the speaker and using it as a shelter (Fig. 2.2A). The starting area where individual gobies were released was situated at the centre of the tank and at a distance of 100.6 cm away from the speakers on either end. The starting area was enclosed by a barrier composed of PVC pipe and plastic grating that stood at a height of 74.9 cm (Fig. 2.2B). To allow the individual to leave the starting area, opened slots were created at the base of each barrier wall at a fixed distance, causing the individual to search to locate the exits (Fig. 2.2A). No particular individual was seen to have difficulty finding the exits that would cause it to turn from one barrier wall and try to escape from the opposite end. Therefore, the barrier design does ensure that the speaker the subject first approaches is preserved as the initial response. Prior to performing a trial and during resting periods, the individual was held in 3.8 L tank prior to exposure to a new treatment period for acclimation and to relieve any stress that may result from handling, using water from the experimental tank to maintain similar water chemistry and temperature. Each trial was recorded using a security camera (EverSecure, Model SX-800-HR) positioned directly above the tank, providing a full view of the experimental area.

For behavioural measurements, an approach to a speaker of choice by a fish was considered a true approach only if the individual was in relatively close proximity to the actual speaker itself. All behavioural responses measured were quantified within a single, 10-minute treatment per trial, per fish. For first approach to a speaker upon initial exposure to a treatment (initial response), a goby approaching the playing speaker was considered a positive response (weighted a value of 1) and an approach to a silent speaker or remaining in the starting area was considered a negative/no response to a treatment (weighted a value of 0). For total number of approaches, a single approach to either the playing or silent speaker was quantified as being close in proximity to the speaker itself and then returning to the starting area. Time spent at a speaker was quantified from the time the subject reached the speaker of choice and ended when the individual returned to the starting area. Mean time elapsed when travelling towards a speaker was quantified from the time an individual would leave the starting area and ended upon reaching the speaker of choice. For mean relative distance travelled, the distance ratio for the fish's swimming path was used to determine how straight the individual's path to the speaker was. This ratio was calculated as:

$$\text{Distance ratio} = \frac{\text{Actual Distance Travelled(cm)}}{\text{Straight line distance to speaker (cm)}} \qquad \text{(Speares 2007)}$$

The actual distance travelled was the sum of the distance traveled each second by the fish (as measured by Ethovision XT), from when the fish first left the starting area until they stopped in front of the speaker of choice. The straight line distance to a speaker was always 100.58 cm, which was the measured distance from one barrier wall to the speaker on either side of the tank. A straight path was quantified as being a low ratio value (equal to 1) for distance travelled indicating a direct path to the speaker and meandering for higher ratio values (greater than 1), displaying an indirect path when travelling towards a speaker (Speares 2007).

The conspecific call, the grunt, was recorded in Lake Michigan from a nest-guarding male (RM) in the field, via the use of a geophone recorder and corresponds to the “Round Goby” call in Rollo et al. (2006). The nest-guarding male was described as having eggs present in his nest during the time that the male was vocalizing. The grunt call was characterized as being a long, broadband pulse train consisting of 7-8 pulses on average (Rollo et al. 2006). The call fundamental frequency was 180Hz, with most of the energy falling under 400 Hz. Pulse train duration averaged 0.07 s and the interpulse interval was approximately 0.25s. The drum call, recorded in the Higgs lab (University of Windsor) from a nest-guarding male in response to a playback recording of another male vocalization, was measured to have a fundamental frequency of 160 Hz, with most of the energy below 350 Hz, consisting on average of 10-11 pulses. The drum was also characterized to be a broadband pulse train but having a pulse train duration and interpulse interval shorter than that found in the grunt call (Fig. 2.3).

A single goby of a particular reproductive status and sex was released into the starting area and then exposed to each of four treatments in a randomized order. Each treatment was ten minutes in duration, separated by ten minutes of acclimation, to alleviate any stress due to handling before exposing the individual to the next treatment. The four treatments were: the grunt call, the drum call, white noise, and a silent control. To prevent bias, the speaker that was chosen to be playing was selected at random initially and then the ‘playing speaker’ was alternated for each progressive treatment. Sounds were played at a continuous rate and at an intensity of 140 decibels (dB re 1μPa) at the starting area, which is within the range of the natural calling thresholds of most the family Gobiidae (Lugli and Torricelli 1999, Linstrom and Lugli 2000). Sound intensity at the sound source was measured to be ~150 dB re 1μPa and ~130 dB re 1μPa at the silent speaker. Prior to performing a trial, gobies were allowed to acclimate to the trial room in a small holding tank filled with dechlorinated water from the experimental tank for one hour. Sound treatments were tested on 30 females (16 RF, 14 NRF) and 36 males (15 RM, 8 SM, 13 NRM) and each individual was only tested once per trial.

Hormone Assays

Reproductive and nonreproductive males and females, following a playback trial, were anaesthetized with clove oil (~60 mg L^{-1}) to measure hormone levels in the individual’s bloodstream and determine if the concentration of sex-related hormones affected behavioural responses to conspecific sounds (Zeyl, submitted). Sneaker males were not included in hormonal assays as the amount of blood drawn was insufficient to perform proper analysis, due to their small size. Males were tested for 11-ketotestoterone (11-KT) and testosterone (T) levels, while females were examined for 17β-estradiol (E2) and testosterone. Blood was collected from individuals via the use of heparinised capillary tubes following removal of the caudal peduncle to allow blood to be drawn from the caudal vein; total volume of plasma collected for fish varied from 5-40 μL. Plasma was typically collected in the afternoon between 13:00 and 18:00 h to maintain consistent hormone sampling from one fish to the next, as hormone levels can fluctuate depending on spawning behaviour of a species. Blood was spun at 14,500 rpm (Micro-Hematocrit Centrifuge LWS-M24, LW Scientific, and Lawrenceville, GA, USA) for ten minutes and then stored at -80^{o}C and assayed at a later time.

Diethyl ether was used to extract steroids once prior to assay and samples were run in triplicate using enzyme-linked immunosorbent assays (Cayman Chemical, Ann Arbour, MI, USA) with individuals randomly assigned to plates. Plasma 17β-estradiol and T was assayed from 25 females (16 RF, 9 NRF) while 11-KT and T was assayed from 26 males (13 RM, 13 NRM). Extraction recoveries were determined separately for each reproductive morph as a result of limited plasma volumes collected from a single fish. Therefore, cold spike recoveries on plasma pools consisted of equal volumes from at least ten individuals (Bowley et al., 2010). Testosterone extractions for both males and females were poor and varied between the reproductive morphs; however, similar recoveries for 11-KT and T were collected in regard to male plasma pools, despite different dilution and spike amounts.

Statistical Analysis

All data were analyzed using the statistical software, SPSS (IBM SPSS Statistics, v. 19.0). Responses to treatments were analyzed in relation to percent response to a playing speaker (initial response), number of approaches, time spent at a playing speaker per approach (in seconds), relative distance travelled to a speaker, and time elapsed traveling to a speaker. Mean distance travelled to a speaker (path angle deviation) was analyzed in Ethovision XT (Noldus Information Technology, v. 15.0) prior to data analysis. Data failed to be normal following transformations so nonparametric tests were used to analyze the response of fish for between-morph comparisons. For initial response, data were quantified dichotomously as yes or no responses (1 = approach to the playing speaker and 0 = no response or approaching the silent speaker) and were analyzed using logistic regression, where the least responsive reproductive morph was used as a comparison. For number of approaches, time spent at a playing speaker, and time elapsed, data were analyzed using Kruskal-Wallis one way analysis and Mann-Whitney U-Test post-hoc. For within-morph comparisons, Friedman's two-way analysis and Wilcoxon signed rank post-hoc was used when examining RF responses for number of approaches, time spent, time elapsed, and relative distance travelled. Bonferroni corrections were applied following all post-hoc tests to avoid inaccurately detecting significance when performing comparisons. Finally, hormone data were log-transformed for normality and was analyzed using simple regression when quantifying correlations between responses and hormones levels by reproductive morph and sex.

Results

Reproductive Morph Choice Playback Experiment

Logistic regression analysis revealed that RFs initially responded to the grunt call (Fig. 2.4A) significantly more often than NRMs (Wald = 4.529, P = 0.033, d.f. = 1, Table 2.1) and SMs initially responded to the drum call (Fig. 2.4B) significantly more often than RMs (Wald = 5.113, P = 0.024, d.f. = 1, Table 2.2). There was no significance difference between RFs and NRFs for either call type (Wald = 2.257, P = 0.133, d.f. = 1, Table 2.3). No significance differences were detected between morphs for either white noise (Wald = 3.623; P = 0.459; d.f. = 4; Fig. 2.4C; Table 2.4) or the control (Wald = 3.623; P = 0.459; d.f. = 4; Fig. 2.4D; Table 2.5). In regard to RFs, the grunt call elicited 56.3% response rate in contrast to NRMs that only had a 15.4% response rate and NRFs that had a 28.6% response rate. Similarly, SMs displayed a 62.5% response rate to the drum call as opposed to RMs that only responded to the drum call 26.6% of the time. Interestingly, RFs had a 0% response rate upon initial exposure to the drum call.

There was a significant difference between reproductive morphs in the mean number of approaches to a playing speaker in regard to the grunt call ($X^2_{4,\,66} = 11.597$; P = 0.021; Fig. 2.5A). No significance differences were detected between morphs for either the drum call ($X^2_{4,\,66} = 4.371$; P = 0.358; Fig. 2.5B), white noise ($X^2_{4,\,66} = 4.334$; P = 0.363; Fig. 2.5C) or the control ($X^2_{4,\,66} = 4.375$; P = 0.358; Fig. 2.5D). Reproductive females approached the grunt call significantly more than RMs ($U_{1,\,31} = 64.50$; Z = -2.432; P = 0.015) and NRFs ($U_{1,\,30} = 49.0$; Z = -2.938; P = 0.003), after calculating for Bonferroni correction (P = 0.016). An average of 0.9 approaches to the grunt call speaker was displayed by RFs in contrast to RMs (μ = 0.4 approaches) and NRFs (μ = 0.2 approaches).

For mean time spent at the playing speaker, there was a significant difference between morphs for the drum call ($X^2_{4,30} = 15.516$; P = 0.004, Fig. 2.6B) and white noise ($X^2_{4,30} = 14.966$; P = 0.005, Fig. 2.6C), but not for the grunt ($X^2_{4,30} = 7.677$; P = 0.104, Fig 2.6A) or the control ($X^2_{4,30} = 6.495$; P = 0.165; Fig. 2.6D) Post-hoc tests revealed that for the drum call, RFs spent significantly less time at the playing speaker than SMs ($U_{1,\,24} = 0.000$; Z = -3.496; P < 0.01) and NRMs ($U_{1,\,29} = 4.500$; Z = -3.011; P = 0.003). Similarly, RFs spent significantly less time at white noise than NRFs ($U_{1,\,30} = 0.000$; Z = -

3.286; $P = 0.001$) and NRMs ($U_{1, 29} = 1.00$; $Z = -2.984$; $P = 0.003$) and approached significance relative to RMs ($U_{1, 31} = 6.00$; $Z = -2.349$; $P = 0.019$), following Bonferroni correction ($P = 0.016$). The RFs spent an average of 0 s at the drum call playing speaker, while SMs and NRMs spent an average of 70.2s and 502.75s, respectively. In comparison, RFs spent an average of 6.5 s at the white noise playing speaker followed by RMs (188.4s), NRMs (201.6s), and NRFs (273.5s).

There was no significant difference between morphs for mean time spent at the grunt playing speaker, but RFs were observed to have spent the most time at the grunt call than any other morph and were examined as a within-morph analysis. The RFs spent significantly more time at the grunt call playing speaker than at the drum call silent speaker ($Z = -2.66$; $P = 0.008$), drum call playing speaker ($Z = -2.66$; $P = 0.008$), grunt call silent speaker ($Z = -2.66$; $P = 0.008$), and white noise playing speaker ($Z = -2.66$; $P = 0.008$), following Bonferroni correction ($P = 0.0125$). The RFs spent an average of 234.6s at the grunt playing speaker (Fig. 2.7) as compared to the drum silent speaker (42.9s), drum playing speaker (0s), grunt silent speaker (29.8s), and white noise playing speaker (6.6s).

With respect to path angle deviation in accordance to relative distance moved when travelling towards a speaker, there was no significance difference between morphs, but examining within-morphs showed an overall significance for RFs ($X^2_{7,9} = 22.081$; $P = 0.002$; $X^2_{7,9} = 31.365$; $P < 0.01$ respectfully). For relative distance moved, RFs had a significantly straighter path when travelling to the speaker playing the grunt call than when travelling towards the drum call playing speaker ($Z = -2.66$; $P = 0.008$). In addition, RFs also displayed a significantly straighter path when travelling towards the drum call silent speaker in contrast to the speaker playing the drum call (Z = -2.366; P = 0.018), following Bonferroni correction (P = 0.025). The RFs travelled a relative distance of 2.3 towards the grunt call playing speaker (Fig. 2.8) relative to the drum playing speaker. In addition, RFs also travelled a relative distance of 7.0 towards the drum silent speaker relative to the drum playing speaker.

The RFs moved significantly slower when travelling towards the grunt call playing speaker than when travelling towards the white noise playing speaker (Z = -2.549; P = 0.011; Fig. 2.9), the left silent control speaker (Z = -2.547; P = 0.011), and approaching significance in regard to the right silent control speaker (Z = -2.371; P = 0.018), following Bonferroni correction (P = 0.0125). For RFs, 64.2 seconds elapsed when travelling towards the grunt call playing speaker more so than when travelling towards the white noise playing (7.1s), and the left silent control speaker (9.6s).

For hormone assays, there were no significant correlations between male and female hormones levels and behaviour parameters measured, but a positive pattern was seen in regard to E2 levels and mean time spent at the grunt call in regard to RFs (P =0.328; R = 0.398; R^2 = 0.159; AR^2 = 0.018; Fig. 2.10A) and pooled female data (P = 0.609; R = 0.174; R^2 = 0.030; AR^2 = -0.078; Fig. 2.10B), largely due to the influence of the one female with the largest E2 level. No pattern was detected for T levels and mean time spent at the grunt call for RFs (P = 0.777; R = 0.111; R^2 = 0.012; AR^2 = -0.129; Fig. 2.11A) and pooled females (P = 0.542; R = 0.196; R^2 = 0.038; AR^2 = -0.058; Fig. 2.11B).

Discussion

State-dependant responses to acoustic signals are rarely investigated in freshwater fishes in association with behaviour and tend to focus on male or female response alone.

The underlying issue with male- or female-focused studies on behavioural responses to acoustic signals is that the effect of acoustic communication within a species' community is only partly investigated. For instance, differentiating the response between a reproductive and nonreproductive female to playback of a male call, may only determine that the call has some function in mate attraction if gravid females show favor towards it, leaving males, nonreproductive fish, and alternative reproductive tactics if they exist within the target species, out of the investigation entirely. To think of any form of communication as being a simple one to one relationship (a single sender and receiver), is unrealistic as the signal is still audible to conspecific individuals, and therefore can be understood, allowing a non-target to respond. Interception, more commonly known as eavesdropping, was first proposed by Myrberg (1981) whereby conspecific receivers that are the unintended target of the sender's signal, detect the signal and respond to it. If the response is beneficial to the non-target receiver, then eavesdropping should evolve in that species' population, and trigger the response when detecting the signal (Earley 2010). Such examples of beneficial eavesdropping are seen in the bicolour damselfish, *Pomacentrus partitus*, whereby males intercept grunt calls (indicates the presence of a female) emitted by other males as a means to interfere with courtship and gain a possible spawning partner (Kenyon 1994). In contrast, Siamese fighting fish, *Betta splendens*, females have been found to eavesdrop on male-male displays as a means to assess male mate quality (Doutrelant and McGregor 2000). Failure to investigate the full-scope of responses to conspecific signals within a species, may lead to undocumented behaviours and the effects those behaviours may have on senders beyond simple predictions observed at the surface. The current study provides evidence that may indicate a relationship between reproductive state and auditory responsiveness to conspecific calls in the round goby and provides a model of how reproductive state can affect phonotactic response between the sexes. Furthermore, results may also provide some insight on function of the conspecific calls examined.

Courtship signals are believed to have evolved in relation to female preference that triggers a sensory bias coded in the female's behaviour and that once heard elicits a robust response to the signal upon recognition (Ryan and Hector 1992). In the current study, RFs displayed a significantly strong attraction to the grunt call in a number of behavioural measures examined, including strong initial response to the grunt call which may indicate recognition, attraction, and an attempt to locate the male that is producing the call. Similarly, in the plainfin midshipman, gravid females display the most robust and consistent phonotaxis in response to male courtship hums upon initial exposure to the sound in contrast to spent females (McKibben and Bass 1998). In bicolour damselfish, *Pomacentrus partitus*, females display a highly attracted response to male chirps and are thought to assess male quality via the signal itself (Myrberg et al 1986). Therefore, RFs may be displaying a triggered response elicited by characteristics in the male's call given its sensitive and robust phonotactic response to the grunt call.

The RFs were also found to approach the grunt call significantly more often than NRFs and RMs (Fig. 2.4A), though rarely did a RF approach the sound source more than twice (Fig. 2.5A). It seems the initial exposure to the sound elicits the strongest response, and failure to locate the male results in fewer responses from RFs. While it has not been documented in the round goby, other members of the family Gobiidae, often use acoustic communication as a means of drawing the female to the nesting site, which is then followed by a visual display. For example, the painted goby, *Pomatoschistus pictus,* following vocalization, will display erect fins and perform a quivering motion towards the female in front of the nest (Amorim and Neves 2007). Similarly, *Padogobius martensii*, when the female is in the nest, will perform head raising and covering the opercula of the spawning partner (Lugli et al. 1995). It is speculated that females assess male quality based on these visual displays. Round goby males have been observed to perform a head shaking, moving in and out the nest, and undulating fins following vocalizations usually within vicinity of females (personal observation). Interestingly, nest-guarding males, while in their nuptial colouration (jet black), have prominent white bands along the edge of the dorsal, pectoral, and caudal fins and may be an ornament that female's assess as part of a visual display (personal observation). Furthermore, RFs spending a large amount of time at the grunt call (Fig. 2.7) may indicate possible searching behaviour. For example, after locating the sound source, RFs may be examining the vicinity of the speaker area to locate the male, but after following failure to do so, the RF loses interest and eventually leaves. Similarly, responding female plainfin midshipman spend only a short period of time (an average of 30 seconds) at the sound source emitting a male call upon investigation, indicating that the sound alone is not enough to maintain the female's interest and requires the male's physical presence (McKibben and Bass 1998). Within-morph responses for mean time spent were examined for RFs which were found to spend the largest amount of time at the grunt call upon first exposure to a sound treatment (Fig. 2.6A, Fig. 2.7). These results show that RFs display the highest level of attraction to the grunt call and may be a mate attraction call. These results are consistent with findings from Rollo et al. (2006) where both male and female gobies responded to the conspecific call, the grunt more vigorously, but females were significantly more attracted to the playing speaker than were males. Thus, the RFs in the current study may be approaching the speaker in response to the acoustic cue but then leaving when not getting the visual reinforcement of a calling male.

The RFs were found to show no initial response to the alternative conspecific call, the drum (Fig. 2.4B). Reproductive females instead were found to either avoid the sound stimuli by moving towards the silent speaker on the opposite side of the tank or remain in the starting area. The RFs lack of interest in the drum call may indicate that this call is unattractive, as a spawn-ready female would be more likely to seek out the male upon initial recognition of the sound. Instead, RFs display the opposite response to the drum call (ignore or avoid), providing some evidence that the drum call has no function in mate attraction as previously thought. Given the context in which the drum call was recorded, it is possible that the drum call is for territorial defense given that it performed in response to another male call. For example, red-finned loaches, *Yasuhikotakia modesta*, during agonistic encounters, perform two kinds of vocalizations during aggressive encounters, which consist of butting sounds during physical contact with an intruder and clicking sounds for long distance communication (Raffinger and Ladich 2009). Similarly, in oyster toadfish, *Halobatrachus didactylus*, parental males emit mostly boatwhistles along with other sounds when conspecific male intruders are present near their nesting sites, often joined by additional threatening behaviours (Vasconcelos et al. 2009). Thus, RFs may be displaying avoidance behaviour when presented with the drum call as it may be a means to ward away intruders.

Generally, fish without hearing specializations or a swimbladder are thought to be unable to localize the sound source properly and must depend on other means of detecting particle motion (Popper and Schilt 2008). Despite the lack of hearing specializations or swimbladder, round gobies, both male and female, have been found to localize the sound source quickly and with minimal meandering when travelling towards the sound source (Rollo et al. 2006, Rollo and Higgs 2008). Our data showed RFs travelled the straightest path when moving towards the grunt playing speaker (Fig. 2.8) but travelled the slowest when approaching the grunt call (Fig. 2.9). The RFs displayed a stop and go motion of travel when moving towards the playing speaker. Fish that do not possess hearing specializations or a swimbladder are thought to localize a sound source by sampling different points within the soundscape and determining location by differentiating where the sound was loudest using the lateral line (Sand and Bleckman 2008). For example, mottled sculpins, *Cottus bairdii*, a species that also does not possess a swimbladder, when approaching a dipole source, approaches the sound source indirectly (described as a zigzag pattern) and were speculated to be sampling the sound environment via the use of their lateral line to assist with orientation (Coombs and Conley 1997). In contrast, the plainfin midshipman, were found to perform a fairly direct and straight path when travelling towards a sound source via the assistance of their swimbladder and ears (Zeddies et al. 2010). While not the zigzagging pattern displayed by sculpins, the stop and go motion of movement displayed by RFs, may be a means to sample the soundscape using their lateral line to differentiate where the sound is the loudest to assist with localization. Sampling the soundscape may be the reason why RFs display a slower paced movement when in response to the grunt call, despite other measures indicating a positive phonotactic attraction. Differences in my results from Rollo and Higgs (2008) in regard to time elapsed when travelling to the playing speaker may be due to experimental design. In Rollo and Higgs (2008), the playing and silent speakers were both on the same side of the experimental arena as opposed to my design where each speaker was situated on opposite ends from one another (Fig. 2.1). My design may have been more difficult for individuals to locate the sound source as they must determine if the sound is loudest from the left or right side as opposed to a single option, resulting in slower paced movement to better assess the location of the sound source.

In midshipman, summer females, in association with hormones levels, are better suited to detect the higher harmonics of a male's call than non-gravid females, and therefore are more sensitive to mate attraction calls (Sisneros and Bass 2003). Hormone assays in the current study, however, did not show such a relationship between E2 levels (Fig. 2.10) or T levels (Fig. 2.11) for either RFs or pooled female data. A recent study (Maruska et al. 2012) examined the response of African cichlid females, *Astatotilapia burtoni*, where only sexually mature females were found to significantly prefer courtship calls over brown noise. Given that, RFs spent the least amount of time at an alternate sound type (Fig. 2.7) in the current study indicates that RFs are not just responding to sound in general and are displaying a higher specificity in their response to conspecific calls, at least for the grunt call, which may be facilitated by naturally circulating steroids in the blood.

Sneaker male preference to the drum call (Fig. 2.4B) may be a means of eavesdropping that allows SMs to intercept a male's call and locate the nesting site. Round gobies are colonial living in large groups within rocky and turbid substrates, providing a difficult task for SMs to locate a male's nest (Young et al 2009). In addition, parental males heavily guard the nest entrance from all intruders (excluding gravid females), making it difficult for a SM to fertilize the eggs, undetected (Wickett and Corkum 1998). Since spawning events are relatively short-lived, approximately 30 minutes (Meunier at al. 2009), localizing a nesting site must occur quickly. As a result, SMs would need to depend on cues emitted during spawning, such as auditory signals as sounds travel faster and farther from its sound source than chemical cues from eggs odours, allowing for rapid localization (Tavolga 1971). Interestingly, Meunier et al (2009) recorded "barking calls", reported as a pulse series, being emitted from a nest-guarding male before, after, and during the spawning process. Therefore, SMs may be able exploit sexual signals produced by parental males as a means of pinpointing the nest and sneak fertilizations once located; a common behaviour displayed by males that utilizes alternative reproductive tactics in other species (Brantley and Bass 1994, McKibben and Bass 1998, Alonzo and Warner 1999, Bass and McKibben 2003). Round goby SMs may attempt to intercept spawning events by eavesdropping on male calls as a means of fertilizing eggs. While no physical evidence of a round goby performing sneaking behaviours has been recorded, physiological evidence has been found that indicates that sneaking tactics may exist in the species. Marentette (2009) examined the physiological difference between a dark male vs. a light morph males (commonly referred to as RMs and SMs) and found that dark males invested more in larger body size, accessory glands, and higher concentrations of 11-ketotestoterone in the blood, while light morphs invest more in testes mass and a greater volume of sperm per ejaculate than dark males. These findings are indicative of alternative reproductive tactics and sperm competition theory (Parker 1970), supporting the potential existence of sneaking males in the round goby.

Similarly to SMs, NRMs may also be performing eavesdropping behaviour when responding to the drum call (Fig. 2.6B), but for another purpose. Round gobies are aggressive egg predators of both heterospecific and conspecific fishes (Charlesbois et al. 1997), and it has been found that nonreproductive gobies are highly attracted to egg odours (Yavno and Corkum 2011). Given that round gobies live in large aggregations and in turbid conditions (Young et al 2009), locating a nest visually would not be an easy task for any reproductive morph. As a result, they must depend on other modalities, such as chemical or auditory signals to locate the nest-guarding male, but the dispersal of chemical signals is directionally limited and can be difficult to use for locating a nest from long distances (Bossert and Wilson 1963). Nonreproductive fish could also eavesdrop on calls produced by nest guarding males that are trying to attract females to his nest. Since females tend to spawn with males that have eggs (Wickett and Corkum 1998), nest-guarding males should continue to call when eggs are already in the nest. As a result, non-reproductive fish could eavesdrop on calls and use them as a means to locate the nest site from a distance and then use chemical cues to determine if eggs are present, which my results may indicate in regard to the drum call.

As to the reduced response of RMs to conspecific sounds (Fig. 2.4A-B, 2.5A-B, 2.6A-B) two different possibilities exist. It may be that hearing in RMs is poorer than the other morphs. The hearing ability of RMs has recently been shown to have the worst hearing than any other morph examined and may be an evolutionary deterrent to prevent triggering agonistic behaviours upon recognition of conspecific calls (Zeyl, submitted).

Alternatively, it may be deleterious for a male to leave his nest to investigate another male calling as he exposes his nest to egg predation or may lose the nesting site to a potential competitor. In the field, round gobies are colonial and live in close proximity to one another even during the breeding season, whereby parental males will build nests right next to one another, increasing the probability of agonistic interactions (Wickett and Corkum 1998). Despite living in close proximity to one another, parental males were rarely seen to leave the nest or interact with neighbours (Wickett and Corkum 1998), indicative of the dear-enemy effect that facilitates to reduce aggression between familiar conspecific neighbours (Temeles 1994). As a result, the low phonotactic response of RMs to conspecific calls (Fig. 2.4A-B, 2.5A-B, 2.6A-B) may be a result of poor hearing sensitivity, and therefore investigative or territorial behaviour is triggered infrequently.

While NRMs and SMs displayed positive phonotaxis to the drum call and RFs performed the opposite response (Fig. 2.4B, 2.6B), the function of the drum call still remains unclear. Given the context that the drum call was recorded under (see methods), it could play a role in territorial defense, which would initially confound SM and NRM results for this study. Why would an RM perform the drum call if it is supposedly deleterious? Round gobies live in large colonial aggregations and in close proximity to nesting sites during the breeding season (Charlesbois et al. 1997). The overlying issue that SMs and NRMs face when attempting fertilizations or egg predation is the size of a nest-guarding male. Nest-guarding males are two to three times the size of SMs and NRMs (Charlesbois et al. 1997, Marentette 2009) and an attack on a male's nest by a single goby is rarely successful (Wickett and Corkum 1998). In nature, when a male's nest is successfully attacked, it is the result of a large number of gobies working together as the nest-guarding male becomes overwhelmed, exhausted, and most importantly, distracted (Wickett and Corkum 1998). While a single performance of the drum call may deter conspecifics away from the nest, constant performance, as this study presented, of the sound may indicate stress and failure to frighten intruders. Consequently, NRMs and SMs may cue in on the male's stress and investigate the sound, and may present an opportunity that is not always readily available to these morphs. Future studies should investigate eavesdropping behaviour on acoustic signals in the round goby more extensively in relation to egg predation and sneaking behaviour. Juvenile round gobies are attracted to conspecific egg odours (Yavno and Corkum 2011), but chemical communication is restricted to short distances as odour disperse slowly from its source. By incorporating long distance signals (acoustic communication) in conjunction with egg odours it can be determined that egg predators (and potentially sneaking behaviour) use sound to pin-point the location of a nest, and then uses chemical cues to confirm if eggs are present. In addition, group effects and call rate can be incorporated in SM eavesdropping studies to better establish if indicators of nest-guarding male stress and distraction plays a role in facilitating eavesdropping behaviour.

The initial response may be more indicative of round goby behavior since RFs were seen to investigate the sound source only once and rarely approached the speaker a second time. The tendency for RFs to investigate the sound source once may be the result of RFs spending more time at the grunt call playing speaker, indicating possible searching behaviour. Therefore, RFs are more likely to ignore the sound following initial investigation as they may be aware that no male is actually present at the sound source. Another variable that is useful in describing goby behaviour is mean relative distance travelled as it reiterates that gobies can in fact directionalize and localize the sound source. However, since gobies have no apparent hearing specializations, they may use their lateral line to sample the sound source, since females were found to travel the slowest when approaching the grunt call sound source, facilitated by a stop and go travelling pattern. In conclusion, initial response and mean distance travelled behavioural measurements examined in the current study should be considered the most useful when describing round goby behaviour.

The current study provides new evidence of state-dependent response to conspecific calls as a model and in the round goby, as well as provides some insight into the function of the calls examined. The results show that RFs display the strongest phonotactic response to the grunt call (Fig. 2.4A, 2.5A, 2.7, 2.8, 2.9) supporting that the call plays a function in mate attraction, which is consistent with Rollo et al (2006) and Rollo and Higgs (2008). Furthermore, hormone assays revealed seasonal plasticity may be playing somewhat of a role in affecting the behaviour of RFs in their response to the grunt call, similar to plainfin midshipman (Sisneros and Bass 2003) and to an extent, *Astatotilapia burtoni* cichlids (Maruska et al 2012). Reproductive males, on the other hand, showed a low response to either conspecific calls (as was predicted) given that in nature, it would be deleterious to investigate conspecific calls as it exposes a nest to predation and theft by other males. In contrast, RFs showed poor phonotactic response to the alternative conspecific call, the drum (Fig. 2.4B, 2.7), disproving my prediction of having a function in mate attraction. However, SMs and NRMs exhibited a robust attraction to the drum call (Fig. 2.4B, 2.6B) and may be intercepting these signals as a means of locating a nest to feed on eggs and sneak fertilizations.

Finally, to further understand female response to conspecific acoustic signals, call rates should be examined as different call rates can have various meanings depending on the species (Seyfarth and Cheney 2006), which is currently unknown in the round goby. In addition, behavioural response to different sound intensities should also be examined as intensity threshold for the round goby has yet to be investigated, at least behaviourally. In conclusion, the current study provides new insight into state-dependent responses to acoustic signals as well as provides a model for other fishes in relation to both behaviour and physiology. While few and far between, previous studies have found that seasonal plasticity plays a role in driving reproductive behaviour of female plainfin midshipman and cichlids in response to sexual signals facilitated by differences seen between gravid and non-gravid females during the breeding season (Brantley and Bass 1994, McKibben and Bass 1998, Bass and McKibben 2003, Sisneros and Bass 2003, Maruska et al 2012) and should be investigated more thoroughly in other fish species. Moreover, these findings provide further understanding of acoustic communication in the round goby and some insight into call function of the sounds examined as well as supports that acoustic communication can be used for mate attraction in the species. By understanding the behavioural responses and function of acoustic communication, I can determine how gobies interact in nature. Using this knowledge, I can create new ways and techniques in controlling the number and spread of the round goby in the freshwater systems of North America.

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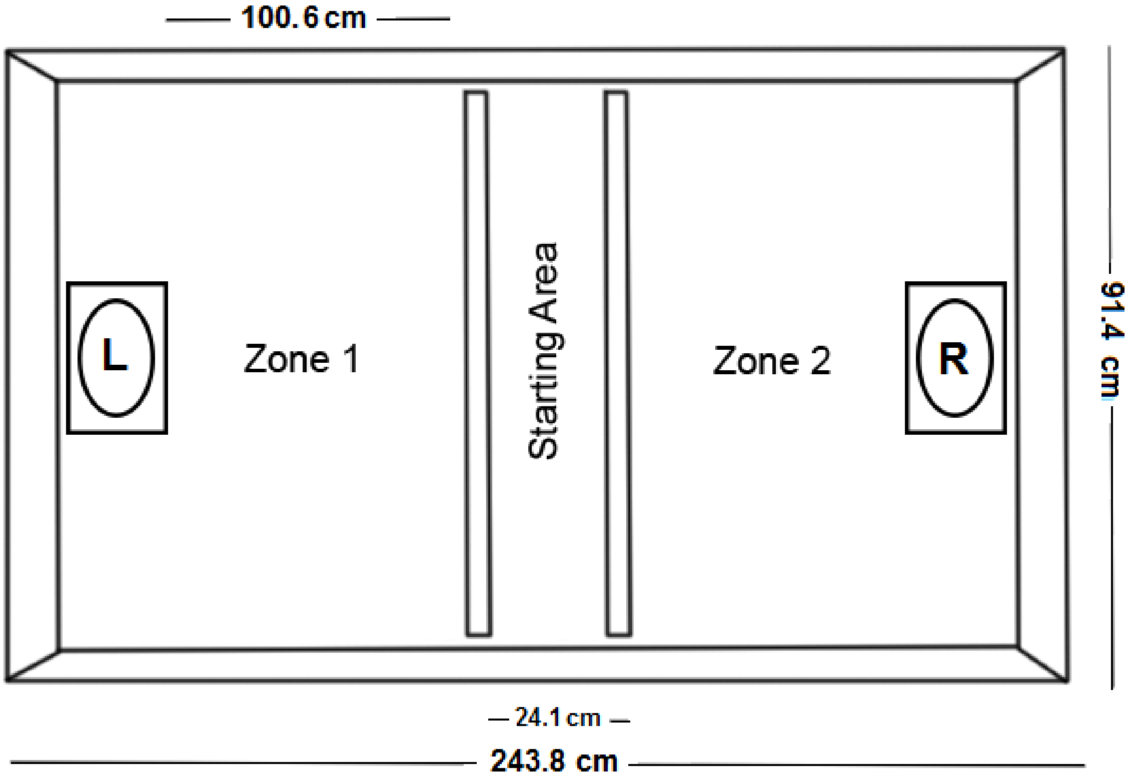

Figure 2.1: Depiction of trial set-up. A single tank (1020 litres; 243.8 cm x 91.4 cm x 91.4 cm) with two underwater speakers placed on opposite sides of the tank. Two barrier walls are placed at the centre of the tank acting as the starting area. A single camera was suspended above the tank to allow full-view recording of all goby activity within the experimental area.

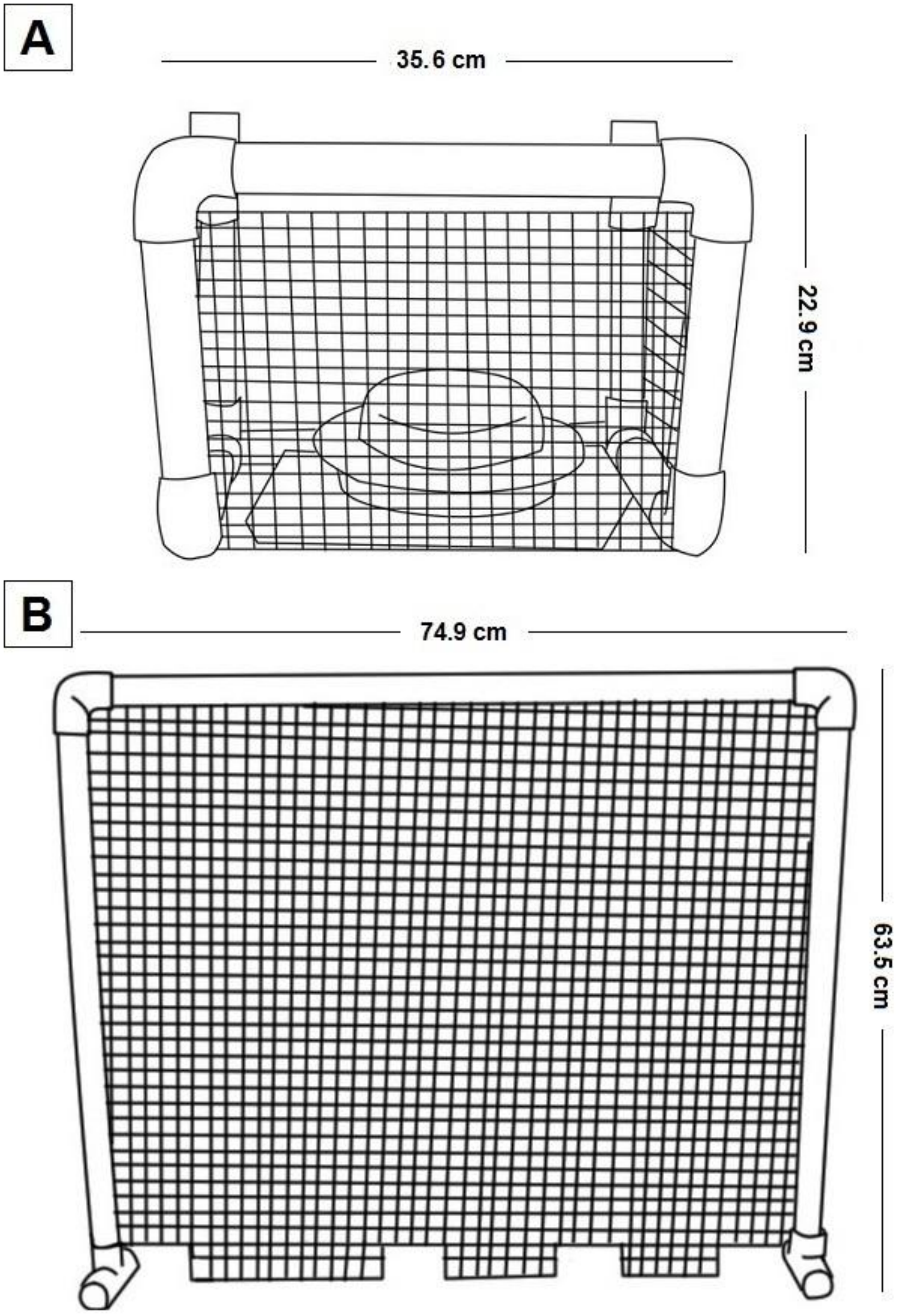

Figure 2.2: A) Depictions of barrier wall used to delineate the starting area (74.9 cm x 12.7 cm x 63.5 cm) constructed from PCV piping and plastic grating. **B)** Depiction of speaker barricade (35.6 cm x 24.3 cm x 22.9 cm), constructed from PCV piping and plastic grating.

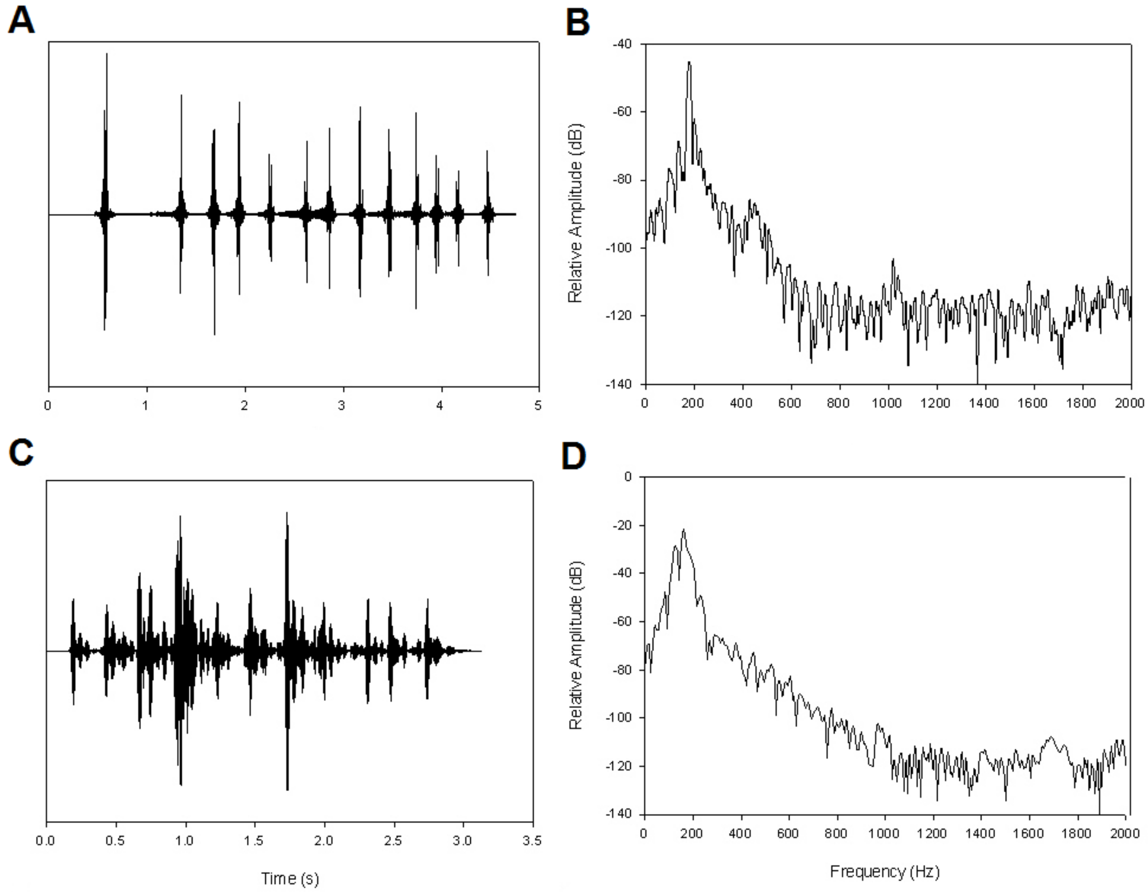

Figure 2.3: Oscillograms (left) and power spectra (right) of the Grunt (A-B), and Drum (C-D) sounds produced by male round gobies. Grunt call received from John Janssen (University of Wisconsin).

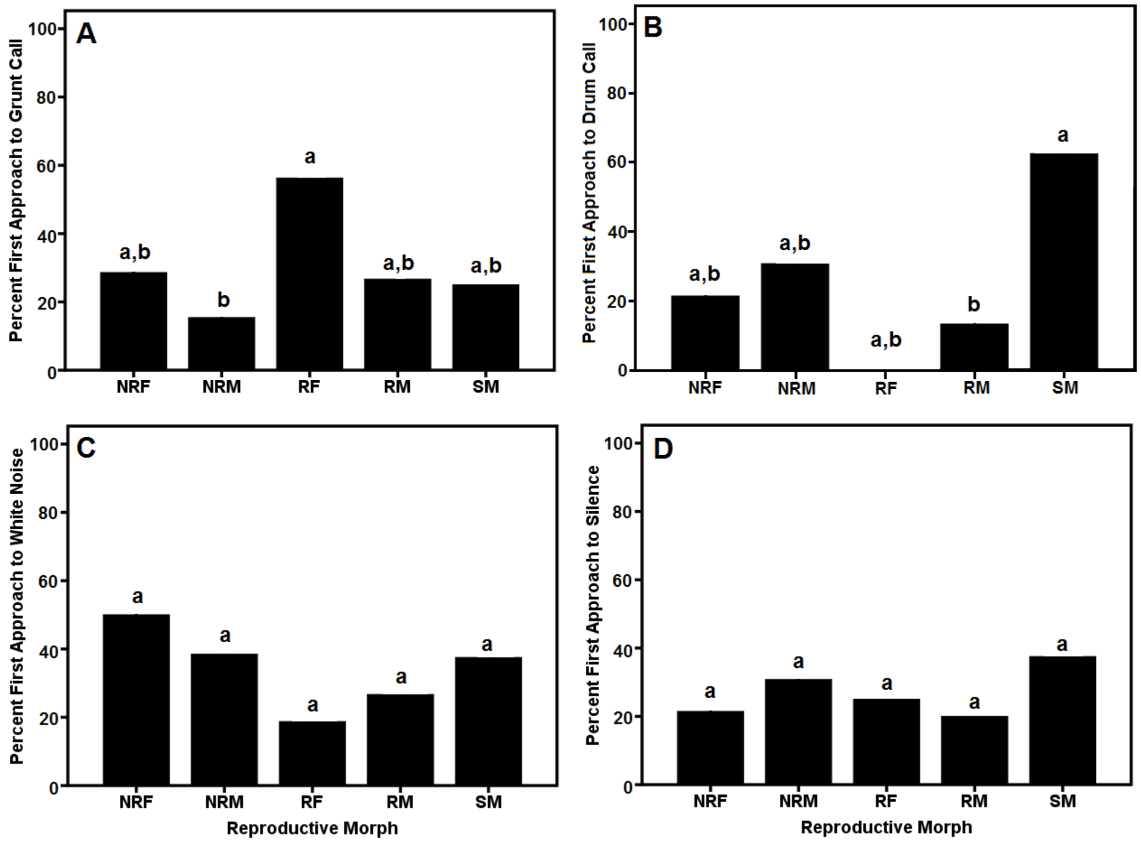

Figure 2.4: Percent (± S.E.) first approach response rate of reproductive and nonreproductive males (15 RM, 13 NRM), females (16 RF, 14 NRF), and sneaker male (8 SM) round gobies to: **A)** Grunt Call, **B)** Drum Call, **C)** White Noise, **D)** Silence. Gobies approaching the playing speaker were considered a positive response (weighted a value of 1) and the silent speaker or remaining in the barrier was considered a negative/no response (weighted a value of 0), over a 10-minute treatment period. Reproductive females initially responded to the grunt call significantly more so than NRMs (p = 0.033) while SMs initially responded to the drum call significantly more so than RMs (p = 0.024). Letters denote significant differences.

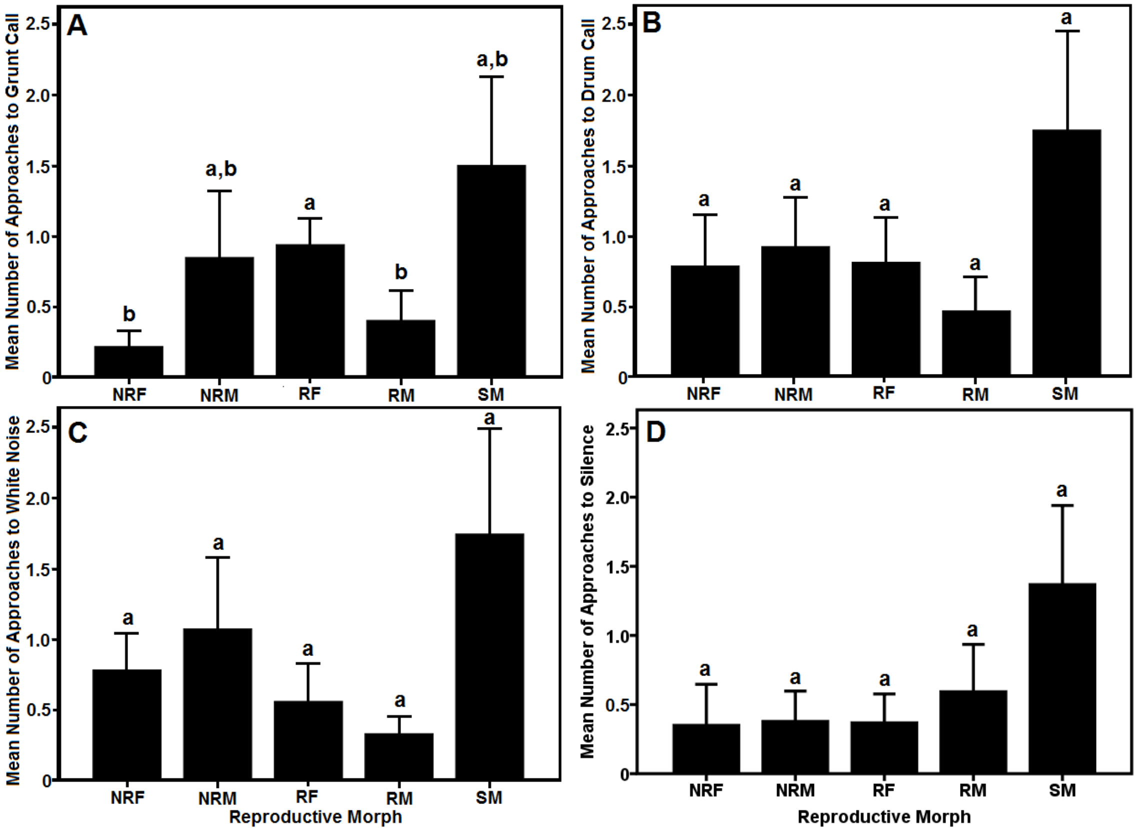

Figure 2.5: Mean (± S.E.) number of approaches to a playing speaker of reproductive and nonreproductive male (15 RM, 13 NRM), female (16 RF, 14 NRF), and sneaker male (8 SM) round gobies to: **A)** Grunt Call, **B)** Drum Call, **C)** White Noise, **D)** Silence. A single approach to either the playing was quantified as being in relatively close proximity to the speaker itself and returning to the starting area, over a 10-minute treatment period. Reproductive females approached the grunt call playing speaker significantly more often than RMs (p = 0.015) and NRFs (p = 0.003). Letters denote significant differences.

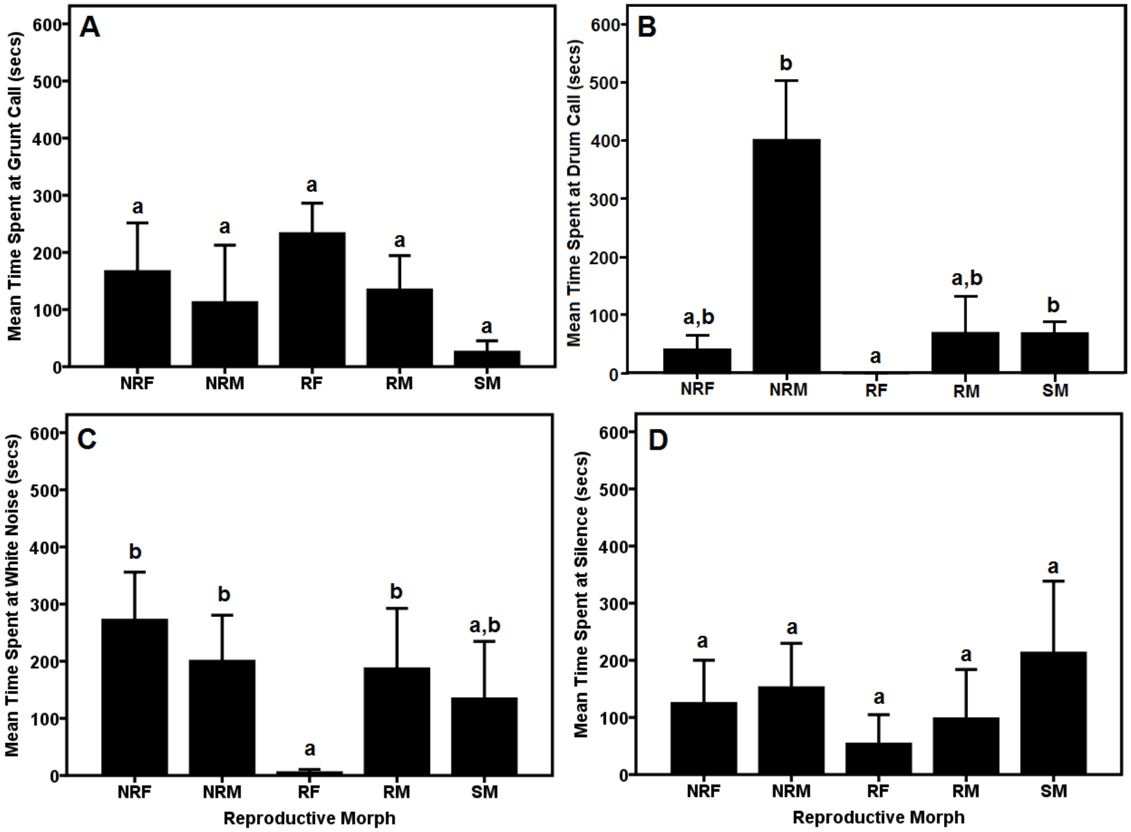

Figure 2.6: Mean (±S.E.) total time (seconds) spent by reproductive and nonreproductive male (5 RM, 5 NRM), female (9 RF, 6 NRF), and sneaker male (5 SM) round gobies to: **A)** Grunt Call, **B)** Drum Call, **C)** White Noise, **D)** Silence. Time spent was quantified from the time the subject reached a speaker to and returned to the starting area, over a 10-minute treatment period. Reproductive females spent significantly less time at the drum call playing speaker than SMs ($p < 0.01$) and NRMs ($p = 0.003$). In addition, RFs were found to spend significantly less time at white noise than NRFs and approaching significance for RMs. Letters denote significant differences.

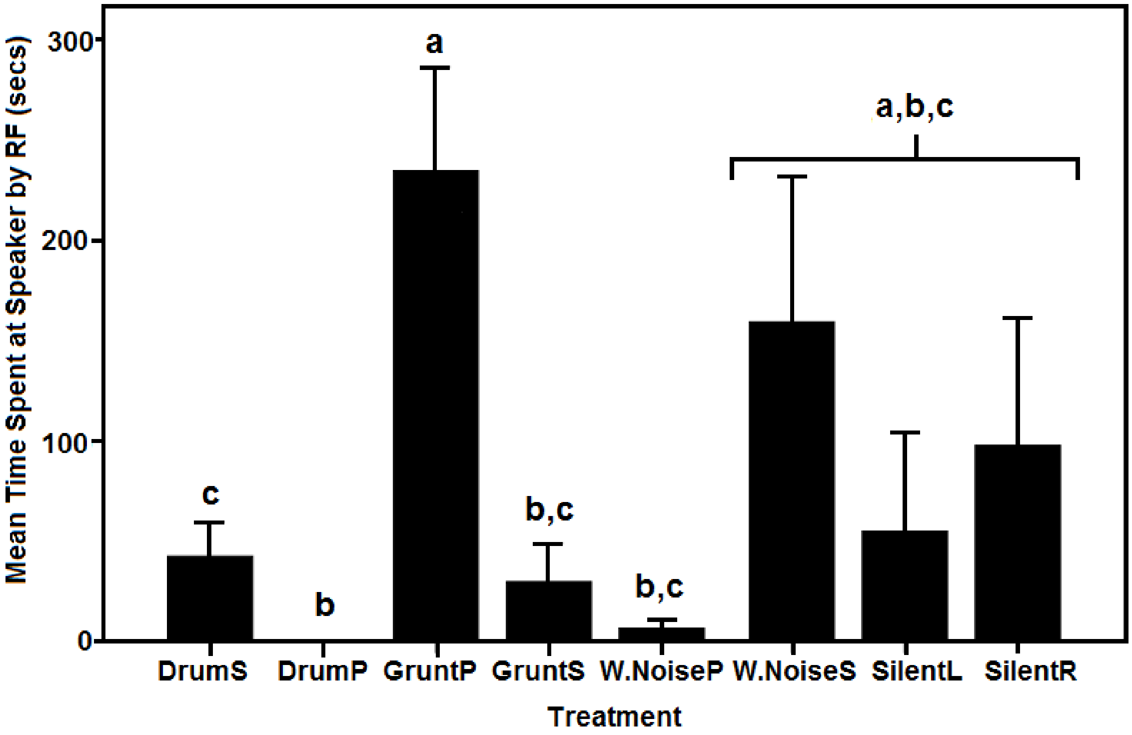

Figure 2.7: Mean (±S.E.) total time (seconds) spent by reproductive females (9 RF) for a single treatment for all possible approaches: grunt call playing speaker (GruntP), grunt call silent speaker (GruntS), drum call playing speaker (DrumP), drum call silent speaker (DrumS), white noise playing speaker (W.NoiseP), white noise silent speaker (W.NoiseS), and left (SilentL) and right silent (SilentR) speakers for the control. Time spent was quantified from the time the subject reached a speaker to and returned to the starting area, over a 10-minute treatment period. Reproductive females spent significantly more time at the grunt call playing speaker than at the drum call silent speaker ($p = 0.008$), drum call playing speaker ($p = 0.008$), grunt call silent speaker ($p = 0.008$), and white noise playing speaker ($p = 0.008$). Letters denote significant differences.

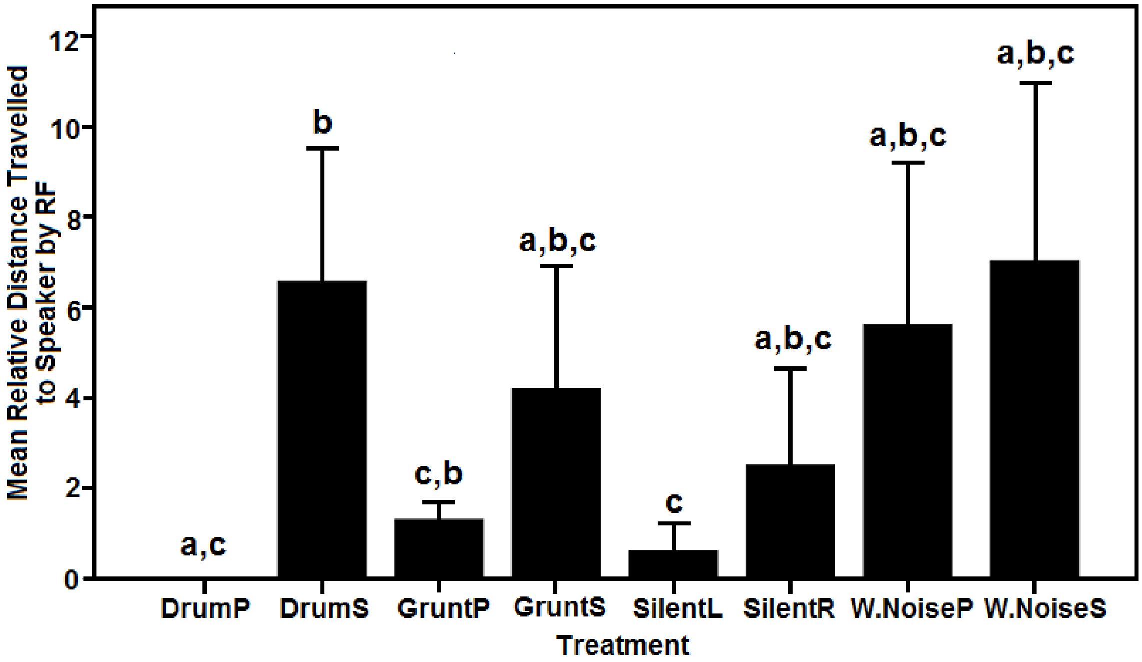

Figure 2.8: Mean (±S.E.) relative distance (cm) travelled to a speaker (first approach only) by reproductive females (9 RF) for a single treatment for all possible approaches: grunt call playing speaker (GruntP), grunt call silent speaker (GruntS), drum call playing speaker (DrumP), drum call silent speaker (DrumS), white noise playing speaker (W.NoiseP), white noise silent speaker (W.NoiseS), and left (SilentL) and right silent (SilentR) speakers for the control, per trial over during a 10-minute treatment. A straight path was quantified as being low in value for distance travelled and meandering for high values. Reproductive females were found to have a significantly straighter path when travelling towards the grunt call playing speaker than when travelling towards the drum call playing speaker (p = 0.008). Furthermore, RFs displayed a significantly straighter path when travelling towards the drum call silent speaker in contrast to the drum call playing speaker (p = 0.018). Letters denote significant differences.

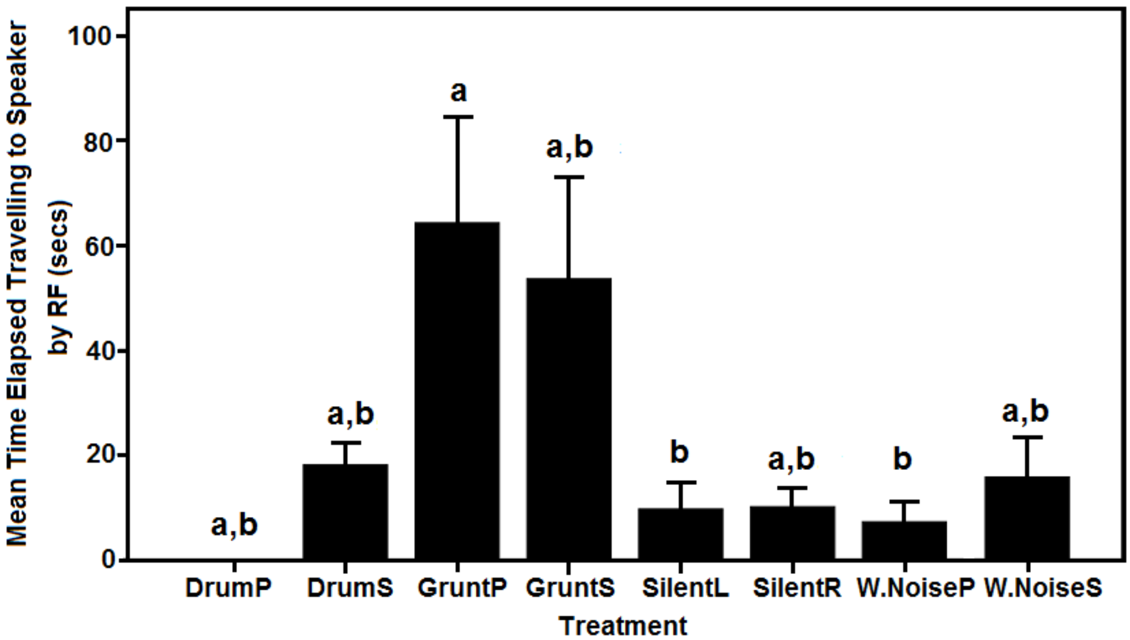

Figure 2.9: Mean (±S.E.) time elapsed (seconds) for first approach when travelling to a speaker by reproductive females (9 RF) for all possible approaches: grunt call playing speaker (GruntP), grunt call silent speaker (GruntS), drum call playing speaker (DrumP), drum call silent speaker (Drums), white noise playing speaker (W.NoiseP), white noise silent speaker (W.NoiseS), and left (SilentL) and right silent (SilentR) speakers for the control, per trial over during a 10-minute treatment. Time elapsed when travelling towards a speaker was quantified from the time an individual would leave the starting area until reaching the speaker. Reproductive females travelled significantly slower when travelling towards the white noise playing (p = 0.011) and the left silent control speaker (p = 0.011). Letters denote significant differences.

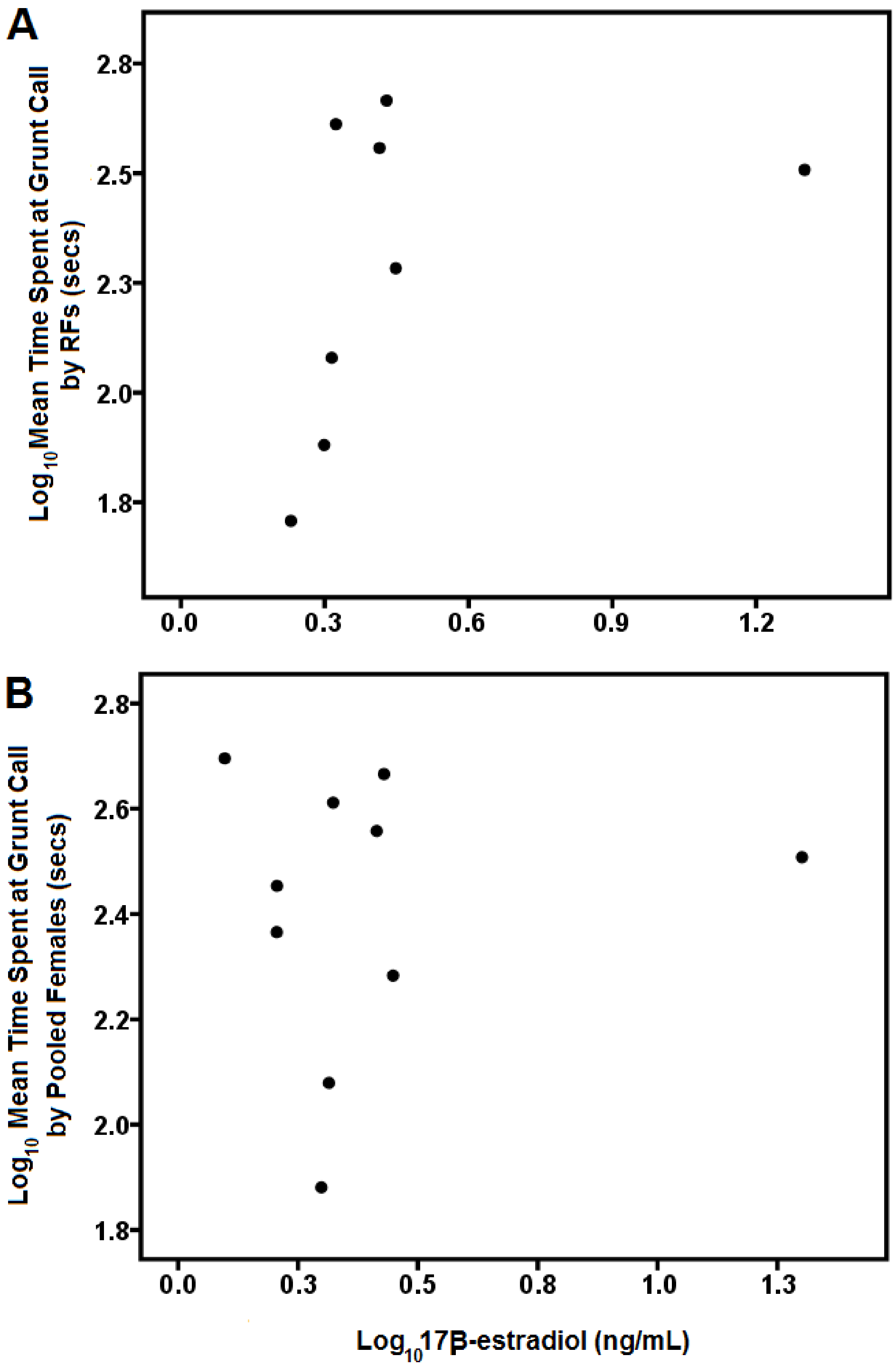

Figure 2.10: Linear regressions of mean time spent in seconds (first approach only) at the grunt call for 17β-estradiol on **A)** reproductive females (9 RF) **B)** pooled females (9 RF, 3 NRF). Each data point represents a single individual.

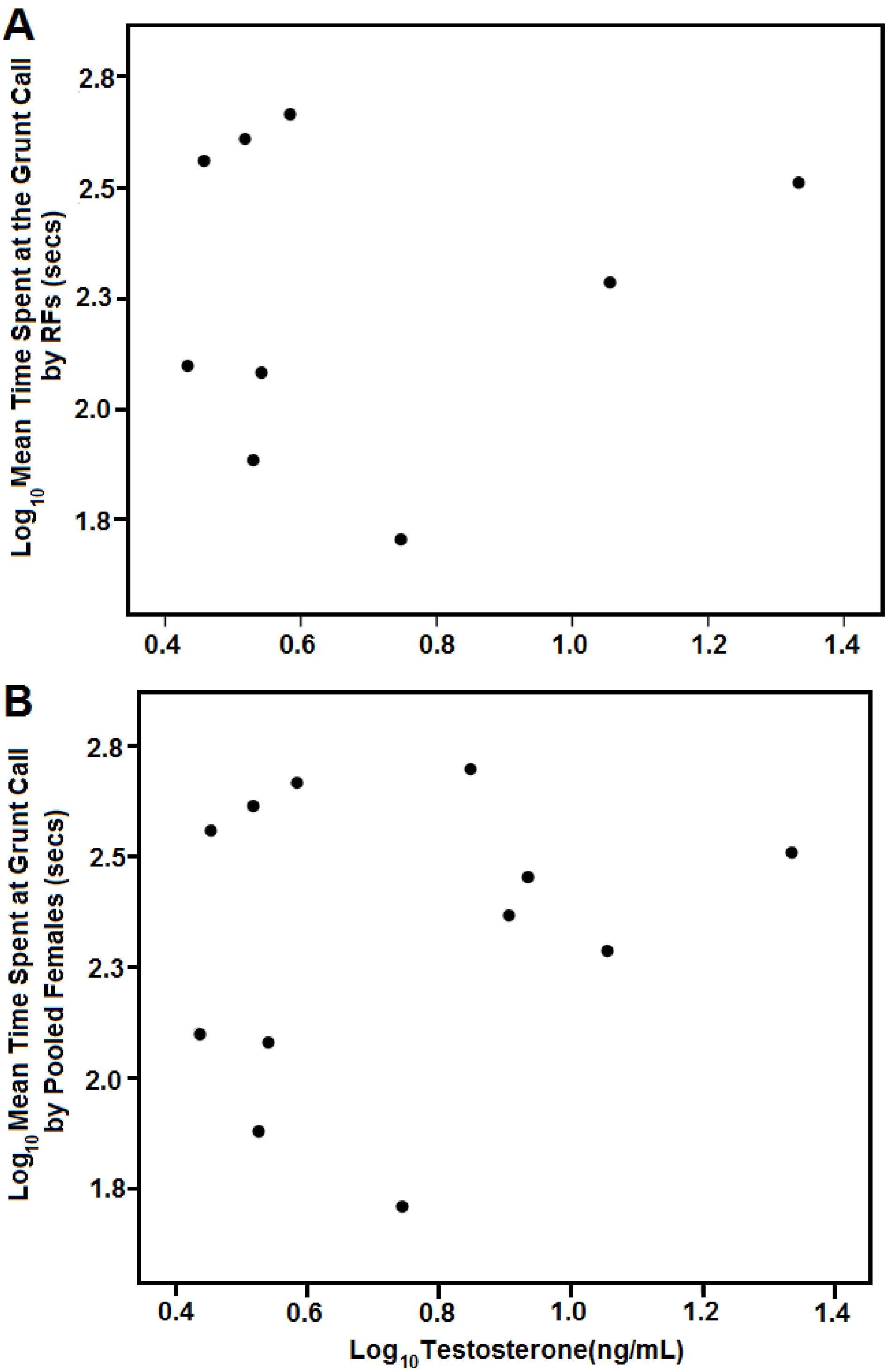

Figure 2.11: Linear regressions of mean time spent in seconds (first approach only) at the grunt call for testosterone on **A)** reproductive females (9 RF), **B)** pooled females (9 RF, 3 NRF). Each data point represents a single individual.

Table 2.1: Percentage of RMs, RFs, NRFs, and SM round gobies that elicited a positive response during the grunt call sound treatment when compared to response rate of NRMs for percent first approach to a playing speaker. Positive responses were denoted when a goby swam into Zone 1. B – *b* coefficient ; S.E – standard error; Wald – Wald statistic; d.f. - degrees of freedom; Exp(B) – odds ratio.

Reproductive Morph	**B**	**S.E.**	**Wald**	**d.f.**	**Sig.**	**Exp(B)**
NRM			5.928	4	.205	
RM	.693	.965	.516	1	.473	2.000
RF	1.956	.919	4.529	1	.033	7.071
SM	.606	1.121	.292	1	.589	1.833
NRF	.788	.970	.661	1	.416	2.200
Constant	-1.705	.769	4.918	1	.027	.182

Table 2.2: Percentage of RFs, NRMs, NRFs, and SM round gobies that elicited a positive response during the grunt call sound treatment when compared to response rate of RMs for percent first approach to a playing speaker. Positive responses were denoted when a goby swam into Zone 1. B – *b* coefficient; S.E – standard error; Wald – Wald statistic; d.f. - degrees of freedom; Exp(B) – odds ratio.

Reproductive Morph	**B**	**S.E.**	**Wald**	**d.f.**	**Sig.**	**Exp(B)**
RM			5.759	4	.218	
NRM	1.061	.969	1.200	1	.273	2.889
RF	-19.331	10048.243	.000	1	.998	.000
SM	2.383	1.054	5.113	1	.024	10.833
NRM	.573	1.001	.327	1	.567	1.773
Constant	-1.872	.760	6.073	1	.014	.154

Table 2.3: Percentage of RFs, NRMs, RMs, and SM round gobies that elicited a positive response during the grunt call sound treatment when compared to response rate of NRFs for percent first approach to a playing speaker. Positive responses were denoted when a goby swam into Zone 1. B – *b* coefficient; S.E – standard error; Wald – Wald statistic; d.f. - degrees of freedom; Exp(B) – odds ratio.

Reproductive Morph	B	S.E.	Wald	d.f.	Sig.	Exp(B)
NRF			5.928	4	.205	
RM	-.095	.831	.013	1	.909	.909
RF	1.168	.777	2.257	1	.133	3.214
SM	-.182	1.008	.033	1	.857	.833
NRM	-.788	.970	.661	1	.416	.455
Constant	-.916	.592	2.399	1	.121	.400

Table 2.4: Percentage of NRFs, NRMs, RMs, and SM round gobies that elicited a positive response during the white noise sound treatment when compared to response rate of RFs for percent first approach to a playing speaker. Positive responses were denoted when a goby swam into Zone 1. B – *b* coefficient; S.E – standard error; Wald – Wald statistic; d.f. - degrees of freedom; Exp(B) – odds ratio.

Reproductive Morph	B	S.E.	Wald	d.f.	Sig.	Exp(B)
RF			3.623	4	.459	
RM	.455	.867	.275	1	.600	1.576
NRM	.996	.857	1.350	1	.245	2.708
SM	.956	.971	.968	1	.325	2.600
NRF	1.466	.834	3.089	1	.079	4.333
Constant	-1.466	.641	5.241	1	.022	.231

Table 2.5: Percentage of NRFs, NRMs, RFs, and SM round gobies that elicited a positive response during the control when compared to response rate of RMs for percent first approach to a playing speaker. Positive responses were denoted when a goby swam into Zone 1. B – *b* coefficient; S.E – standard error; Wald – Wald statistic; d.f. - degrees of freedom; Exp(B) – odds ratio.

Reproductive Status	**B**	**S.E.**	**Wald**	**d.f.**	**Sig.**	**Exp(B)**
RM			3.623	4	.459	
RF	-.455	.867	.275	1	.600	.635
NRM	.542	.816	.440	1	.507	1.719
SM	.501	.935	.287	1	.592	1.650
NRF	1.012	.792	1.633	1	.201	2.750
Constant	-1.012	.584	3.002	1	.083	.364

Table 2.6: Tablulation of gonadsomatic index (GSI) measurements taken from round goby morphs used in behavioural trials, including reproductive males (RM) and females (RF), sneaker males (SM) nonreproductive males (NRM) and females (NRF). Males with a GSI of ≥ 1.3% and females with a GSI of ≥ 8.0% were reproductive. Nonreproductive fish (NRMs, NRFs) were included in the analysis if and only if gonads were absent. For SMs, if the GSI was ≥ 4.0%, then the individual was a reproductive sneaker male.

Reproductive Morph (Males)	GSI (%)	Reproductive Morph (Females)	GSI (%)
RM	1.39	RF	8.16
RM	1.35	RF	9.81
RM	1.46	RF	10.13
RM	1.53	RF	10.84
RM	1.63	RF	12.29
RM	1.72	RF	12.90
RM	1.79	RF	13.28
RM	1.91	RF	13.45
RM	1.93	RF	13.48
RM	1.97	RF	13.60
RM	2.24	RF	13.79
RM	2.46	RF	13.88
RM	2.56	RF	14.98
RM	2.66	RF	16.73
SM	4.05	RF	17.46
SM	4.23	RF	17.80
SM	4.29	NRF	0.00
SM	4.66	NRF	0.00
SM	4.68	NRF	0.00
SM	6.01	NRF	0.00
SM	6.51	NRF	0.00
SM	6.69	NRF	0.00
NRM	0.00	NRF	0.00
NRM	0.00	NRF	0.00
NRM	0.00	NRF	0.00
NRM	0.00	NRF	0.00
NRM	0.00	NRF	0.00
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CHAPTER 3:

ATTRACTION OF ROUND GOBIES, *NEOGOBIUS MELANOSTOMUS*, TO CONSPECIFIC SOUNDS IN THE FIELD

Introduction

The role of invasive species in ecosystem disruption is of increasing concern as species are transported from one region to another (Mills et al. 1993). The movement of individuals is often the result of anthropogenic actions, especially where commerce is concerned (Mills et al. 1993). Under normal circumstances, natural barriers exist that prevent or impede the migration of species to non-native areas (Lovell et al. 2006, Olson 2006, Lockwood et al. 2007) as these barriers cannot readily be crossed by organisms unassisted due to either physically or chemically restrictions (Mills et al. 1993). For example, to cross an ocean successfully, an organism must be physically able to travel over long distances and even for a bird, traveling over a vast body of water would be difficult as they require a place to rest when travelling over long distances, otherwise fatigue and drops in altitude will occur (Bruderer and Liechti 1998). However, aquatic species face a more prominent concern. Migration of fishes is limited by the chemical characteristics of water (Marshall and Grosell 2006). Many freshwater species cannot move into salt water and vice versa as their osmotic balance would be offset, causing cell damage and ultimately death (Marshall and Grosell 2006). With increasing commerce and technology that allows for humans to conduct business with neighbouring countries and even with those that are overseas, these barriers are often eliminated (Koler and Lodge 2001), providing an outlet for invasive species to sidestep natural barriers and span areas with relative ease (Mills et al. 1993), often having profound negative impacts on the native environment and community; an ever-growing concern for environmental biologists (Lovell et al. 2006, Olson 2006, Lockwood et al. 2007).

A major problem with invasive species is they are often the root cause of widespread disturbance in native species populations that both affect natural ecosystems and give rise to concerns for commercial industries (Lovell et al. 2006, Olson 2006, Lockwood et al. 2007). Invasive species have been shown to adversely affect aquatic populations and caused significant economic damage to commercial fisheries in the Laurentian Great Lakes (Scholesser et al. 2006, Daunys et al. 2006, Coble et al 1999, Madenjian et al. 2008). With the overlaying issue of invasive species problems persisting in the Laurentian Great Lakes basin, means of eliminating or controlling the spread and population size of the invaders are of great interest. Many mechanisms of invasive species management are currently in effect and range from the use of natural, chemical, and mechanical control (Simberloff and Stiling 1996, Allendorf and Lundquist 2003), with the two latter methods being most commonly applied. For example, in relation to chemical control, the use of lampricide, a chemical designed to target the larvae of invasive sea lamprey, *Petromyzan marinus*, in river systems before their recruitment as parasitic adults, effectively reduces their population size (Christie et al. 2003). In regard to mechanical control, the use of electric barriers is applied as a means to prevent the spread of Asian carp of the genus *Hypophthalmichthys,* into new Great Lakes habitats (Stokstad 2003). For the most part, mechanical and chemical control are typically well-suited methods in controlling the spread and size of invasive species populations, however, these methods are not without their faults. Lampricides have been found to produce problems for amphibians, such as mudpuppies, *Necturus maculosus*, and fishes such a sturgeon, *Acipenser fulvescens*, (the latter an endangered species), which often share the same habitats (Boogaard et al. 2003)**.** In addition, lampricide, specifically of the TFM variety (3-trifluoromethyl-4-nitrophenol), has been found to drop pH levels wherever released, greatly affecting fish populations that are sensitive to pH changes, thereby harming non-target native species (Bills and Johnson 1992). In regard to electric barrier in the use of preventing the further spread of Asian carp, while it is successful in preventing the species from moving into new bodies of water, it also impedes the movement of migratory fish species from doing the same (Pimental 2005). Furthermore, electric barriers can be prone to failure in that a simple power outage would provide Asian carp the opportunity to cross the barrier unharmed (Stokstad 2003). As a result, mechanical and chemical control methods can be unreliable and most importantly, unpredictable, leading to the development of natural control techniques for invasive species management.

For natural control methods sensory modalities may be exploited, with the use of species-specific pheromones most often being implemented as a means of attracting the appropriate sex, capturing them in large numbers, and actively removing them (El-Sayed et al. 2006). The use of naturally occurring chemical signals (isolated pheromones) as bait lures to traps have seen success when controlling invasive insects (Witzgall et al. 2008) terrestrially. Similarly, intraspecific chemical communication methods have been implemented in aquatic system traps, especially for sea lampreys that possess male-released pheromones that are synthesized and implemented in traps as a means of collecting receptive females, and by doing so, reducing the number of females available for males to spawn with and reducing recruitment into the population (Johnson et al.

2008). Despite the success of the synthetic pheromones, this method has its shortcomings, especially in aquatic systems, as the process can be time-consuming and a lengthy process at best, due to financial, logistical, or ethical reasons. Of potential greater utility is the use of bioacoustics but this important modality has been largely ignored for invasive control. Bioacoustics refers to the sounds organisms use to communicate with one another, and the most common use of acoustic communication in fishes is mate attraction, often produced by males (Myrberg 1980). Past studies have found that females are highly attracted to conspecific mate attraction calls and are able to localize the sound source in an effort to locate the males (McKibben and Bass 1998, Fine 1978, Rollo et al. 2006, Rollo and Higgs 2008). Despite evidence of attractive localization to conspecific sounds, fish sounds have not been used in the control and capture of invasive species, although artificial sounds have been used as barrier deterrents (Nestler et al. 1992, Ross et al. 1993, Ross et al. 1996, Maes et al. 2004). The overlying issue with deterrent methods for invasive species control is that eventually, fish may habituate to these unnatural sounds and does not eliminate or deplete an already established population; it merely slows down spread. The advantage of bioacoustics is that they are species-specific and naturally occurring, so no adverse effect should occur on freshwater ecosystems and non-target native species. By implementing acoustic communication into invasive species programs, one could use naturally occurring sounds as a lure to attract conspecifics to the sound source, trap them within that area, and actively remove them; a strategy that the current study discusses in regard to one of the most successful and deleterious invaders to the Great Lakes, the round goby, *Neogobius melanostomus*.

The round goby is a small, bottom-dwelling teleost fish that is believed to have first entered the St. Lawrence River by transportation in ballast water of commercial ships originating from the Ponto-Caspian region (Vanderploeg et al. 2002). Since its establishment in 1990, the round goby has moved into all five Great Lakes and has begun to travel into the Mississippi basin (Charlesbois et al. 2001). Due to its highly aggressive and competitive nature, round gobies have begun to negatively impact the freshwater ecosystems of North America (Jude et al. 1992). By outcompeting native species for shelter and food, the round goby has successfully increased their population size to an enormous number in a decade after being reported (Charlesbois et al. 2001). This is primarily due to the goby having multiple spawning periods in a single breeding season, allowing for the rapid population growth of the fish (MacInnis and Corkum 2000). Since then, the populations of numerous native species, such as mottled sculpins *Cottus bairdii* and logperch *Percina caprodes*, have suffered a decline (Charlesbois et al. 1997). However, recent studies have shown that round gobies have become prey for some native piscivorous fish, leading to an increased growth rate in these predator species (King et al. 2006). Since round gobies live in turbid waters, visual communication is limited and auditory communication may be an alternative means for the species to interact in their environment. Male gobies have been found to produce calls during mate attraction (Rollo et al. 2006) and female gobies respond to these calls with high specificity (Rollo and Higgs 2008). In addition, round gobies approach both heterospecific and conspecific calls, but respond to conspecific sounds more vigorously and are able to localize the source more readily (Rollo and Higgs 2008).

The goal of the current study was to design an acoustic trap that would implement the use of round goby calls as a lure, capturing them in large numbers, and potentially using this strategy to regulate the population size of the invasive species. Playback experiments using three pairs of traps were used in the field to determine the response of gobies of both sexes to recordings of two conspecific calls suspected to play a role in mate attraction, a grunt and drum, in relation to reproductive status of responding fish. In relation to behavioural responses, I quantified the number of individuals captured by treatment, reproductive state, and month. I predicted that since the round goby reproductive season peaks in May and declines continuously into late August (Charlesbois et al. 1997, Corkum et al. 1998), a majority of gobies would be captured in May and capture rate would decline progressively by month. Based on previous findings from my playback experiment performed in the lab that examined the response of round gobies to these same conspecific calls (see chapter 2), I predicted that the grunt call would be the most effective in attracting round gobies, especially in regard to reproductive females (RF), while the drum call would attract the least. In contrast, reproductive males (RMs) were predicted to show the lowest response to the conspecific calls, as it is deleterious for a male to leave his nest to investigate another male calling as he exposes his nest to egg predation or loss of nesting sites to potential competitors in the area. In regard to nonreproductive males (NRMs) and sneaker males (SMs), I predicted that these morphs would respond the most to the drum call as eavesdroppers, as displayed under lab conditions. As for nonreproductive females (NRFs), despite lab results, I predicted that if this morph did show a positive response to the conspecific calls in the field, then they could potentially be acting as eavesdroppers.

Methods and Materials

Field Site and Goby Identification

Field experiments consisted of deploying six acoustic traps (see below) overnight at Detroit River (McKee Park) at Windsor, ON [42^{o}20′N, 82^{o}56′W] during the morning from early May to late June; when the reproductive season peaks for the species (Charlesbois et al. 1997). Traps were collected the following morning after a period of 20 hours and any gobies that had been trapped were collected and quantified in regard to date captured, water temperature of day captured, total number of individuals caught, sex, and reproductive status using secondary sexual characteristics as visual cues (Charlesbois et al. 2001). Fish were kept at the University Animal Quarters in accordance with the University of Windsor Animal Care Guidelines, kept for behavioural experiments (chapter 2).

Gobies that were captured consisted of all possible reproductive morphs that develop during their spawning season, which were reproductive males (RM), reproductive females (RF), non-reproductive males (NRM), non-reproductive females (NRF), and sneaker males (SM). Male and female round gobies were identified by examining the shape of their urogenital papillae where males are identified as having a pointed urogenital papilla, while the females' are blunt and rounded (Charlesbois et al. 1997). Reproductive males can be distinguished from NRMs by possessing secondary sexual characteristics such as being dark in colouration (usually jet black), having swollen cheeks and a developed papilla, as well as slime production (Marentette et al 2009). Reproductive females, in contrast, were identified from NRFs by possessing a swollen papilla (larger and yellow) and belly (Corkum et al 2008). Finally, SMs can be identified as being small in size and mottled colouration resembling a female, but possessing a long, developed papilla (Marentette et al 2009).

Field Setup

Acoustic traps were composed of a steel, rectangular framework (62.2 cm x 44.7 cm x 20.8 cm) and enclosed by plastic mesh netting, mimicking a standard fish box trap using funnel entrances (Fig. 3.1). Each trap retained 2.5 cm of steel lining at its base to allow the structure to sink into the silt and lock in place, reducing any movement following deployment and prevent gobies from hiding underneath the trap. A total of six funnel entrances were situated throughout the perimeter of the trap near its base, to allow gobies to easily find and swim into the entrances and also reduce capture of non-target species. Funnel openings were designed to be positioned low near the base of the trap and large in diameter for entry, but to be elevated and smaller in diameter at the end leading into the trap. As a result, when a fish swam into the funnel to enter the trap, the weight of the fish acted to displace the funnel's position, thereby lowering it downwards. Once the fish entered the trap, the funnel returned back to it elevated state, trapping the fish and making escape difficult. Each trap had a single underwater speaker (UW-30, Lubell Labs, Columbus, OH, U.S.A) situated at its center, suspended by steel cables at a fixed height of 3 cm to prevent the speaker from making contact with the bottom of the trap, thereby reducing vibrations that may deter gobies from approaching. Underwater speakers were powered by an electronic rig (held within a waterproof container) situated on shore that consisted of 12V-7.2AH/20HR sealed lead acid battery (Leoch LP-12, Leoch Battery Co. Ltd. Shenzhen ,China), 300-watt stereo amplifier (Scosche SA-300, Scosche Industries, Oxnard, CA, U.S.A), and an mp3 player (Sony Digital Media Player NWZ-E464, Sony Entertainment Network, Los Angeles, CA, U.S.A).

A single trial was composed of three trap pairs placed in three different inlets along a rock island that were sheltered from the main river channel (Fig. 3.2). Two pairs of traps acted as treatments, composed of a playing trap and a silent trap. Additionally, the third pair of traps was treated as a true control consisting of two silent traps, to assure that gobies were actively responding to the sound and not using the trap as a shelter. Conspecific sounds, the grunt and drum call, were used to test the attractive response of round gobies in the field and to determine if results differed from that seen in the lab. Sound, control, and trap trial locations as well as the trap types (the grunt treatment, drum treatment, or control) were selected randomly by alternating inlet deployment by treatment from day to day and dropping traps within the inlets by using a tossing method (while maintaining a fixed distance between the playing and silent traps per treatment) to prevent sampling bias. Background noise levels in the field varied between 120 and 130 dB re 1µPa, depending on boat or wave activity, therefore conspecific sounds were played at 140 dB re 1µPa (mimicking lab settings) to assure that sounds always played above the background noise and are within the range of natural calling thresholds within the family Gobiidae (Lugli and Torricelli 1999, Lindstrom and Lugli 2000). Sounds were played continuously to also mimic methodology used in lab trials.

Data from playing and silent traps per treatment (control being two silent traps) were added together to represent the total number of gobies trapped in a given inlet, as the sound may have attracted gobies to the silent trap in the pair. Population assessment sampling per inlet at the field site was attempted using multiple methods (angling, umbrella net, and seine net) in the morning and during the day but failed due to a number of difficulties ranging from inconsistent sampling attempts between inlets, awkward sampling conditions of the waterbed and environment, and seine net tangling; as a result, attempts were abandoned. I speculated that the sound was attracting gobies into the inlet during overnight trials, but due to poor propagation and background noise, gobies are unable to localize the sound source properly and enter the silent trap for a sound treatment incorrectly (discussed more below).

Presently, sound production of the round goby is poorly studied and as a result, the peak of male calling activity during their spawning season is unknown. Since most freshwater species of fish have been found to perform vocalizations ranging between late evening and early morning (Kasumyan 2009), overnight deployments were chosen to allow trials to cover the full range of potential calling periods and to mimic a nest guarding male emitting vocalizations more naturally. Furthermore, overnight trials were performed to reduce the amount of background noise generated by boat traffic and wave action during trials, assuring that goby calls could be heard from a distance. A hydrophone (Interocean Inc., San Diego, CA, U.S.A) was used to determine the appropriate distance a silent trap should be placed away from the sound trap in a single location to prevent sounds from interacting with the silent trap. Sounds were found to propagate less than 182.8 cm away from sound trap, measuring below 120 dB and becoming indistinguishable from background noise when quantified with a hydrophone. As a result, treatment traps were initially placed 182.8 cm or farther away from the silent trap in a single location to prevent confounding results as it put the sound pressure well below the background noise. Control traps were placed at a similar distance from one another to maintain trial consistency in conjunction to treatment traps.

Sound Types

The conspecific call, the grunt, was recorded in Lake Michigan by John Janssen at the University of Wisconsin from a nest-guarding male (RM) in the field, via the use of a geophone recorder. The nest-guarding male was described as having eggs present in his nest during the time that the male was vocalizing. The grunt call was characterized as being a long, broadband pulse train consisting of 7-8 pulses on average (Rollo et al. 2006). Its fundamental frequency was 180Hz, with most of the energy falling under 400 Hz. Pulse train duration was an average of 0.07 s and the interpulse interval approximately 0.25s. The drum call, was recorded in the Higgs lab (University of Windsor) from a nest-guarding male (RM) in response to a playback recording of another male vocalization. The drum call had a fundamental frequency of 160 Hz, where most of the energy was below 350 Hz, consisting on average of 10-11 pulses. The drum call was also characterized to be a broadband pulse train but having a pulse train duration and interpulse interval shorter than that found in the grunt call (Fig. 3.3).

Statistical Analysis

All data were analyzed using the statistical software, SPSS (IBM SPSS Statistics, v. 19.0). Responses to sound treatments (grunt and drum call traps) and the control (silent traps) were analyzed in relation to total number of gobies captured regardless of sex or morph and total of number of gobies captured in relation to sex and morph. Data from each pair of traps for a treatment was quantified as a sum of gobies captured within an inlet per trial. In regard to data analyzed in relation to total of number of gobies captured regardless of sex or morph, data were analyzed by total number of gobies that were captured and accumulated in three months by trap type, total number of gobies that captured in the months of May, June, and July per trap type, and total number of gobies captured in the month of May only for the grunt call trap. For total number of gobies captured, data were transformed using the square root function to normalize data, and analyzed with a two-way ANOVA for total of gobies captured in all months by trap type, one-way ANOVA for both total number of gobies captured in the month of May, June, and July by trap type and capture in the grunt call trap only by month. Tukey post-hoc was applied for each analysis. For total number of gobies captured in relation to sex and morph, data were analyzed in two different ways: within-morph and between-morph for sound and control traps. For within morph comparisons, data were analyzed in relation to the number of each morph captured by month for the grunt trap. For between morph analysis, data were examined in relation to number of morphs captured in each trap type for the month of May. Data failed to be normal following transformations so Kruskal-Wallis nonparametric tests and Mann-Whitney U-test post hoc were used to analyze the response of fish for between-morph and within-morph analysis. Bonferroni corrections were applied following all post-hoc tests to avoid inaccurately detecting significance when performing comparisons.

Results

Total Number of Gobies Captured

There was no significant difference in the total number of gobies captured by treatment ($F_{2, 60} = 2.554$; $P = 0.088$) or by month ($F_{2, 60} = 2.230$; $P = 0.118$) alone for the grunt, drum, and control traps, but there was a significant interaction between treatment and month ($F_{4, 120} = 2.581$; $P = 0.048$), where the effect by treatment was found to be dependent on the month the traps were deployed for total number of gobies captured**.**

Due to the significant interaction term, treatment and month effects were analysed independently. When examined by treatment, there was a significant effect of month on capture in the grunt call treatment ($F_{2, 22} = 7.025$; $P = 0.005$; Fig. 3.4A), with significantly more gobies captured in May than in June ($P = 0.013$; Fig. 3.4B) and July ($P = 0.009$; Fig. 3.4A), but not between June and July ($P = 0.963$; Fig. 3.4A). There was no significant month effect for the drum call treatment ($F_{2, 19} = 0.935$; $P = 0.413$; Fig. 3.4B) or the control ($F_{2, 19} = 0.248$; $P = 0.783$; Fig. 3.4C)**.** For the grunt call (Table 3.1), an average of 23 (±2.6 SE) gobies was caught in May in contrast to June during which an average of 10.5 (± 2.4 SE) gobies were captured, and July during which an average of 10 (± 2.9 SE) gobies were captured in total.

For capture rate for treatment effect by month, an overall significant difference was detected for the month of May ($F_{2, 15} = 8.369$; $P = 0.005$), where significantly more gobies were captured in the grunt call traps than in the drum call trap ($P = 0.006$; Fig. 3.4B) or the control ($P = 0.049$; Fig. 3.4C), but no difference was found between the drum call trap and the control ($P = 0.567$; Fig. 3.4D). No overall significant differences were detected for June by treatment ($F_{2, 22} = 0.069$; $P = 0.993$) or July by treatment ($F_{2, 23} = 0.072$; $P = 0.930$), following Bonferroni correction ($P = 0.025$). For the month of May, the grunt call (Table 3.1) captured an average total of 23 (±2.6 SE) gobies in contrast to the drum call (Table 3.2) that captured an average of 7.6 (±2.3 SE) gobies and the control (Table 3.3) that captured an average 11.8 (± 3.5 SE) gobies.

Within-Morph Captured

Examining only morphs captured in the grunt call trap there was an overall significant difference between months for RFs ($X^2_{2, 22} = 10.712$; $P = 0.005$; Fig. 3.5A) and SMs ($X^2_{2, 22} = 15.257$; $P < 0.01$; Fig. 3.8B), and RMs ($X^2_{2, 22} = 6.286$; $P = 0.043$; Fig. 3.5C), but not for NRMs ($X^2_{2, 22} = 4.300$; $P = 0.116$; Fig. 3.5D), or NRFs ($X^2_{2, 22} = 0.212$; $P = 0.900$; Fig. 3.5E). For RFs, significantly more RFs were captured in May (5 ± 1.6 SE; Table 3.1) than in June (0.8 ± 0.4 SE; Table 3.1; $U_{1, 15} = 7.50$; $Z = - 2.443$; $P = 0.015$; Fig. 3.5A) and July ($U_{1, 14} = 2.00$; $Z = -2.978$; $P = 0.003$; Fig. 3.5A), but not between June and July (0.3 ± 0.2 SE; Table 3.1; $U_{1, 15} = 22.5$; $Z = -0.763$; $P = 0.446$; Fig. 3.5A), following Bonferroni correction ($P = 0.016$). For SMs, significantly more SMs were captured in May (2 ± 0.4 SE; Table 3.1) than in June (0.4 ± 0.2 SE; Table 3.1; $U_{1, 14} = 0.00$; $Z = -3.377$; $P = 0.001$; Fig. 3.5B) or July (0 males; Table 3.1; $U_{1, 15} = 4.50$; $Z = - 2.875$; $P = 0.004$; Fig. 3.5B), but not between June and July ($U_{1, 15} = 17.50$; $Z = -1.750$; $P = 0.08$; Fig. 3.5B), following Bonferroni correction ($P = 0.016$). For RMs, significantly more RMs were captured in May (2.1 ± 1.2 SE; Table 3.1) than July (0 males; Table 3.1; $U_{1, 14} = 10.5$; $Z = -2.241$; $P = 0.025$, Fig. 3.5C), but following Bonferroni correction ($P = 0.016$), the difference was no longer significant. There was no significant difference between May and June (0.3 ± 0.2 SE; Table 3.1; $U_{1, 15} = 16.0$; $Z = - 1.574$; $P = 0.116$; Fig. 3.5C) or June and July ($U_{1, 15} = 21.0$; $Z = - 1.373$; $P = 0.170$; Fig. 3.5C) for RMs.

Between-Morph Captured

Kruskal-Wallis one-way analysis for the number of morphs captured for all treatments per month revealed that for May, an overall significant difference was found for the grunt call trap ($X^2_{2, 21}$ = 10.789; P = 0.005; Fig. 3.6A) and the control ($X^2_{2, 12}$ = 7.853; P = 0.020; Fig. 3.6B), but not for the drum call trap ($X^2_{2, 12}$ = 5.308; P = 0.07; Fig. 3.6C). For the grunt call, NRMs were captured significantly more than RMs ($U_{1, 14}$ = 4.5; Z = - 2.581; P = 0.010; Fig. 3.6A) and SMs ($U_{1, 14}$ = 1.50; Z = - 2.989; P = 0.003; Fig. 3.6A). For the control, the differences between morphs was no long truly significant, following Bonferroni correction (P = 0.016). For the grunt call, an average of 8.4 (±1.6 SE) NRMs was captured in May in contrast to an average of 2.1 (±1.2 SE) RMs and an average of 2 (± 0.4 SE) SMs captured.

Non-targets Captured

For the number of non-target organisms captured in all trap types, there was no overall significant difference in the number of nontargets captured for month ($X^2_{2, 60}$ = 0.471; P = 0.790; Fig. 3.7A; Table 3.1, 3.2, 3.3) or treatment ($X^2_{2, 60}$ = 0.986; P = 0.611; Fig. 3.7B; Table 3.1, 3.2, 3.3). The most commonly captured non-targets consisted of aquatic species such as rock bass, *Ambloplites rupestris,* yellow perch, *Perca flavescens*, common mudpuppy, ***Necturus maculosus*,** and signal crayfish, *Pacifastacus leniusculus* (Table 3.4).

Discussion

The current study, to my knowledge, is the first application of conspecific acoustic signals as a lure to attract an invasive fish species. Interestingly, recent work on invasive amphibians have successfully used conspecific calls as a lure and implemented these sounds in traps as a population control strategy (Schwarzkopf and Alford 2007). Particularly in May, the trap playing the grunt call captured significantly more gobies than the other two traps (Fig. 3.3), showing positive phonotaxis and a selective trapping mechanism. The success in May, particularly of reproductive individuals such as RMs, SMs, and RFs (Fig. 3.4, 3.5A), is most likely due to preferred water temperatures for breeding in this species (Charlesbois et al. 1997) and further indicates the selective utility of this trap. The grunt call, long suspected to have a function in mate attraction, (Rollo et al. 2006, Rollo and Higgs 2008, and chapter 2), could be used to lure females to a sound source, capture them, and actively remove them from key areas where goby populations have a large impact on native fishes. However, while the trapping mechanism used in the current study did capture a frequent number of RFs in May when using the grunt call as a lure (Fig. 3.3A), the sound was also successful in capturing a large total number of gobies (both reproductive and nonreproductive) in contrast to the drum call (Fig. 3.3B) and the control (Fig. 3.3C). In addition, a similar number of RFs and NRFs were captured in the grunt call in May, indicating that the grunt call can be used to capture all females (Fig. 3.5A). Therefore, this strategy could be used as a means to capture and reduce the number of gobies at key areas, such as shared spawning beds where native species also reside. In addition, due to the minimal capture of non-target species (Fig, 3.6), the use of conspecific signals is a practical tactic in capturing invasive species without harming native species.

Successful capture of all gobies by treatment was found to be highly dependent on the month in which the traps were deployed (Fig, 3.3), indicating a potential relationship between time of spawning season and effective response to conspecific sounds. Interestingly, the month of May (Fig. 3.3D) was found to be more successful in capturing gobies than June or July (Fig, 3.3A). The round goby spawning season locally is between early May and late August (Charlesbois et al. 2001), but the time at which the goby's breeding season begins and ends can fluctuate with water temperature (Charlesbois et al. 1997) and varies depending on geographic location (Miller 1986). It seems that round gobies are more responsive to conspecific acoustic signals early in the spawning season and declines over the progression of the summer months, further supported by results seen in chapter 2. The onset of May brings about warmer water temperatures and it is speculated that once water temperatures reach 10 degrees Celsius, the onset of the round gobies' reproductive cycle is triggered (Charlesbois et al. 1997). However, since round gobies typically spawn in shallow waters (MacInnis and Corkum 2000), water temperatures increase as the summer progressives, causing shallow bodies of water to be too warm for the round goby to spawn in comfortably and they are believed to move to deeper waters where it is cooler (Charlesbois et al. 1997, Corkum et al. 1998), due to a shift in spawning site preference as a result of rising temperature. In the current study, trials were restricted to shallow water along a rock island where water temperature increased substantially in the months of June and July (May, $\mu = 16^{o}C$; June, $\mu = 21^{o}C$; July, $\mu = 22^{o}C$; Table 3.1, 3.2, 3.3), which may have caused gobies to leave the field site and move into deeper and cooler waters. Past studies have shown a trade-off exists between optimal reproduction and temperature preference in temperate area fish, leading to a reduction in reproductive output in both disruptions of gonad development and egg quality (Sandstrom et al. 1997, Davies and Bromage 2002, Vlaming 2006, Van der Kraak and Pankhurst 1997). A study has yet to be performed that provides evidence of rising temperature conflicting with the round goby's reproductive output, however, since round gobies spawn throughout the entire summer, raising temperature may have some adverse effect on gonad development and egg quality as it has been found to disrupt the reproductive cycle of other species, and therefore may cause goby's to move into deeper and cooler waters. Gobies have been found to spawn in a wide range of temperatures from 9^{o}C to 26^{o}C (Charlesbois et al. 1997, MacInnis and Corkum 2000), however, while gobies may be able to spawn in higher temperatures, the frequency of spawning events with rising temperatures has not been taken into account, thusly it may be possible that while gobies spawn in very warm water, the number of gobies spawning declines as others move to preferable cooler, temperature waters. Kulikova (1985) found that over a progressing spawning season, the number of gravid females near its start is highly abundant at a site, but as the summer progresses, a rapid decline is observed and by July, gravid females all but disappear. Furthermore, Young et al. (2009) found that round goby abundance in shallow areas was related to temperature with the highest capture rate was seen at water temperatures between 15 and 17^{o}C during the breeding season. Therefore, it may be possible that the decline in gravid females in my study, could explain the decline in the number of reproductive gobies that were captured in June and July, regardless of being initially high in the month of May (Fig. 3.4).

Another reason as to why a decline in capture rate was observed from May to July is that while the round goby is known to spawn multiple times throughout a single breeding season, the number of times an individual spawns in a single summer before reproductive reception decreases is poorly understood. In other words, as the reproductive season progresses from one month to the next, the number of receptive gobies present later in the season may change as conditions change. Under most circumstances, ideal conditions for breeding is earlier in the season when water temperatures, food availability, and spawning sites are stable and then decline as the summer progresses as habitat changes and resources are depleted (Lee and Johnson 2005). While a majority of fishes spawn once during a single breeding season, indeterminate multiple spawning native species, will only spawn multiple times when the productivity of a stream is high and optimal abundance of food sources are available (Fox 1978, Mann et al. 1984, McEvoy and McEvoy 1992). Therefore, a change in productivity in the spawning site with altering habitat may cause gobies to leave the present spawning site as a result of suboptimal abundances of food sources and/or possible presence of predators in the area. At the field site where the current study was performed, in May, the surrounding habitat consisted of a silt bed with rocks scattered about the river floor. However, as the summer progressed, vegetation began to grow and altered the habitat (pers. obs.). Ideally, gobies prefer living and spawning in areas that are composed of hard, rocky substrates, where substantial food sources, such as molluscs, would be more likely to thrive (Charlesbois et al. 1997, MacInnis and Corkum 2000). An increase in vegetation and alteration of habitat may have not been ideal for adult, sexually mature gobies to remain in high abundance, resulting in lower densities of gobies present at shallower sites. In addition, an increase in vegetation for the habitat may have attracted more predator species, such as largemouth bass, *Micropterus salmoides,* and smallmouth bass, *Micropterus dolomieu*, that feed on round gobies (Belanger and Corkum 2003), as the round goby has been observed to decline from a site, usually at night, when piscivorous predators are in abundance (Ray and Corkum 2001). In addition, since round gobies are colonial and spawn in large groups, food resources, such as molluscs could have declined to an extent that could no longer sustain a large group of fish in a single area; as it has been found with rising water temperature (up to 26^{o}C), the food consumption rate of gobies increases (Lee and Johnson 2005). In the round goby, these ideal conditions are present usually in May (when water temperatures reach 10 degrees Celsius) and decline substantially with upcoming months locally (Charlesbois et al. 1997). Peak spawning activity in May can be further understood when examining the capture rate of gobies in relation to reproductive morph observed in the current study.

The very first and only examination of round goby response to conspecific sounds in the field was performed by Rollo et al. (2006), where gobies were found to be highly attracted to conspecific calls. Unfortunately, neither reproductive state nor sex could be quantified in the field, causing female preference to be later determined in the lab (Rollo and Higgs 2008). In the current study, the use of acoustic traps allowed for the quantification of reproductive state and sex (henceforth referred to as reproductive morph), in response to two conspecific sounds, known as the grunt and the drum call, suspected to play a role in mate attraction. Furthermore, the grunt call used in the current study is the “Round Goby” call referred to and tested in Rollo et al. (2006) and Rollo and Higgs (2008). When examining May captures for reproductive state, the number of RFs captured were higher than SMs and RMs, but more NRFs and NRMs were captured overall (Fig. 3.5; Table 3.1, 3.2, 3.3). Further examination of reproductive morph captures in the month of May revealed that the most successful trap type at catching reproductive individuals was the grunt call (Fig. 3.3D). As stated earlier, the grunt call is suspected to be for mate attraction as females display robust phonotactic response when presented with the call (Rollo et al. 2006, Rollo and Higgs 2008, see chapter 2 results). A similar behaviour has been found to be displayed by female plainfin midshipman, *Porichthys notatus,* where both under lab and field conditions, gravid females display robust phonotactic response when presented with humming vocalizations performed by Type I males (Brantley and Bass 1994; Sisneros 2009; Zeddies et al 2010). It seems that females display a strong phonotactic response to the grunt call also in the field, but declines progressively from June to July (Fig. 3.4A). It was observed when capturing gobies and quantifying their reproductive state from trap to trap, that all RFs were substantially gravid, however, as the months progressed, this level of gravidity in RFs declined as well (pers. obs.). Interestingly, with the onset of June, RFs were absent for the first two weeks of that month, and then returned the last two weeks of June (Table 3.1, 3.2, 3.3). However, by July, RFs completely disappeared (Table 3.1, 3.2, 3.3). Female round gobies have a quick turnover of eggs once their reproductive season is over (Kulikova 1985), with the percentage of gravid females present dropping to substantially low numbers by the end of July in local waters (MacInnis and Corkum 2000), and therefore response to conspecific calls may drop substantially as the summer progresses simply because there are fewer gravid females that are not present in high numbers, therefore reducing the probability of capture. Similar to the changes in responsiveness with reproductive state in midshipman to conspecific sounds (McKibben and Bass 1998, Sisneros and Bass 2003), peak gravidity in females should facilitate a stronger phonotactic response to male signals as females would warrant deposition of eggs upon reaching full maturation, providing a potential explanation for the significantly large number of females captured in May and the decline into June and July as a result of declining female presence. Furthermore, with declining availability of gravid females to spawn with at a given site, this may have also caused the reduction in the number of reproductive gobies (RMs and SMs) in that same area and could be another possible explanation as to why capture rates of reproductive fish were high in May, but then suffer a decline from June to July in the current study.

The SMs and NRMs were also captured in the grunt call trap significantly in the month of May (Fig. 3.4B, 3.5A), and may be performing eavesdropping behaviour, but for different reasons. In regard to SMs, it has been suggested that intercepting mate attraction calls produced by nest-guarding males provides a means for a localization of a spawning event by males who practice alternative reproductive tactics (Myrberg 1981). In plainfin midshipman, Type II males (sneaker males) have been found to respond to the hum call (mate attraction call), and display behaviours that are indicative of sneaking activity, indicating that Type II males may intercept sexual signals to locate spawning events and sneak fertilizations (McKibben and Bass 1998). In the round goby, spawning events are short in duration (30-minutes) (Meunier et al. 2009) and require quick localization by sneaker males to perform fertilizations. To locate a spawning event quickly, SMs would need to depend on cues emitted during spawning, such as auditory signals as sound travels faster and farther from its source than chemical cues from eggs odours (Tavolga 1971). Nest-guarding males have been described to perform “barking calls”, reported as a pulse series, before, after, and during the spawning process (Meunier et al. 2009) therefore SMs may locate a nest by exploiting sexual signals, providing an opportunity to sneak fertilizations. The exploitation and interception of sexual signals in fish is a common behaviour displayed by males that utilize alternative reproductive tactics in other species (Brantley and Bass 1994, McKibben and Bass 1998, Bass and McKibben 2003, Alonzo and Warner 1999). Presently, no physical evidence of actual sneaking behaviour performed on spawning events has been recorded for the round goby, however, evidence that indicate sperm competition theory (Parker 1970) and alternative reproductive tactics has been found (Marentette et al. 2009). The NRMs may also be performing eavesdropping behaviour, but with an ulterior purpose which is egg predation. Round gobies are known egg predators of both conspecifics and heterospecifics (Charlesbois et al. 1997) and nonreproductive gobies are highly attracted to conspecific egg odours (Yavno and Corkum 2011). Nonreproductive fish could eavesdrop on male calls as a means to locate a nest with eggs, since males have been found to emit calls and attract females when eggs are already present in the nest (Wickett and Corkum 1998). Since chemical cues from eggs are slow to disperse and therefore are restricted to short distances, nonreproductive fish could eavesdrop on calls and use them as a means to locate the nest site from a distance, and then depend on chemical cues to determine if eggs are present in the nest. Interestingly, though contradictory to results seen in the lab (see chapter 2), SMs and NRMs did not show a strong phonotactic response to the drum call in the field (Fig. 3.5C, Table 3.2). It is difficult to determine why the contrast in phonotactic attraction exists between the lab and the field other than the conspecific sounds was presented to the SMs under a more natural setting, and therefore more indicative of natural behavioural responses. In addition, multimodal cues from conspecifics in the trap, such as odours, may have facilitated a stronger phonotactic response to the grunt call that was not present in lab trials (see chapter 2).

For RMs, the successful capture of this morph to a suspected mate attraction call (Fig. 3.5A) was not expected. In most cases, a male that has acquired a nest should not be seeking out the sound source as it may be deleterious for a male to abandon their nest to investigate another male calling, as it exposes the nest to egg predation and theft (Charlesbois et al. 1997). Unfortunately, whether the RMs had a nesting site prior to investigating the grunt call trap is unknown, so it is possible the RMs that were captured may have been potential floaters (adult males who had yet procured a nesting site) and used the trap as a shelter, given that the number of RMs captured in May was very low. It is currently not known whether male calling frequency alters with size in the round goby, but some evidence suggests that with larger body size, males produce lower frequency sounds (Speares 2007); therefore floater RMs may have investigated the sound source in relation to frequency: size differences. For example, bicolour damselfish, *Stegastus partitus*, and Lusitanian toadfish, *Halotrachus didactylus*, females prefer courtship chirps of lower frequency that indicate a larger male body size and male condition (Myrberg et al. 1986, Myberg et al. 1993), and males of bicolour damselfish are known to intercept the following grunt call that is emitted by males during actual courtship of the female (Kenyon 1994). While the size of the male that produced the grunt call used in the current study is also unknown, it is possible that the frequency of the grunt call provided size information to floater males that indicated that the male performing the call was smaller than themselves and therefore would be able to commandeer the nesting site from the "performing male". In addition, the capture of RMs may have been random as an unexpected large quantity of RMs were captured in a single trap one day when traps were retrieved, and may have been the result of new RMs moving into the field site, and procuring the trap as a nesting site.

To prevent confounding results between the playing and silent trap for a treatment, traps were placed at fixed distance that put the sound pressure well below the background noise. However, the hydrophone is not an accurate representation of the components of sound that a fish can detect and as the hydrophone only measures sound pressure, which the goby is not likely to detect. The round goby, as far as I know, has no hearing specializations that allow the species to detect sound pressure and is mostly likely detecting particle motion, which the hydrophone cannot quantify. Therefore, it is possible that particle motion that was generated by playing sounds were still available for gobies to detect from a distance using the lateral line similar to other fishes (Sand and Bleckman 2008). Furthermore, the sounds may have been distorted by the background noise and made finding the location of the sound source difficult, resulting in incorrect localization of the sound source by gobies and error when entering the silent trap for a treatment. Since the control trap did not show the same level of success in either capture of gobies by total number or morph captured, I can say with certainty that higher capture in the grunt call trap was due to the attraction to the sound alone and individuals were not attracted to trap as a shelter. In contrast, the drum call attracted the least gobies both in total and by morph in May and seemed to deter gobies from approaching it. Given the manner in which the drum call was recorded (see methods), it is possible that the call plays a role in territorial defence, thereby explaining the low capture rate in the drum call trap for May (Fig. 3.3D). For example, in red-finned loaches, *Yasuhikotakia modesta*, during agonistic encounters, two kinds of vocalizations are performed during aggressive encounters, which consist of butting sounds during physical contact with an intruder and clicking sounds for long distance communication (Raffinger and Ladich 2009). Similarly, in the painted gobies, *Pomatoschistus pictus,* parental males emit drumming vocalizations, joined by threatening visual displays, when intruders are near their nest (Amorim and Neves 2008). While the current study suggests using acoustic signals to capture round gobies as a population control strategy, the trap design can be modified to implement any type of lure (whether be conspecific odours, food, etc), for control of other invasive species. The only modification that would be required in relation to capture of other invasive species would be altering the height of the funnel entrances as they are situated for benthic species to enter the trap more easily. The trap design itself may provide an alternative and safer technique to deleterious methods of controlling invasive species, such as reproductive disruptors (Bills and Johnson 1992, Boogaard et al. 2003) or poison (Zavaleta et al. 2001).

Due to the turbidity of water at the field site where the current study was conducted, video recording of overnight trials could not be performed and therefore I was unable to quantify the number of gobies that approached the trap in contrast to the number of gobies that were captured. While the trap was designed to make it easier for round gobies to find the entrances upon localizing the sound source, there may still be unforeseen difficulties in locating the funnel entrances, since they are spaced out to maintain volume in the trap and prevent the funnels from blocking one another. Li et al. (2006) examined the catch efficiency of a commercial trap used for the capture arabesque greenling, *Pleurogrammus azonus*, and found a relationship between funnel angle/length and capture efficiency. Li et al. (2006) suggested that commercial traps used to capture greenlings, should be modified so that the inclination angle of traps were less steep and to keep funnel length short (but slightly longer than funnels were presently), to maximize catch efficiencies. As a result, it is possible that unforeseen design flaws may be present in my trap design, despite high capture rate of gobies in May. Furthermore, while overnight trials were chosen to cover all possible calling activity of the round goby as it has yet to be investigated, I was unable to determine the time of day capture and approaches to the trap mostly occurred. On average, most vocalizing fish tend to perform at twilight (Kasumyan 2009) however it is currently unknown when males of the round goby vocalize. Future studies could implement the use of underwater cameras in areas with higher water clarity to determine if traps are designed sufficiently to maximize goby capture as well as determine when peak response to the conspecific sounds occur to better determine when to deploy the trap and when to play the sound.

While the trap was successful in capturing gobies, the strategy of using acoustic traps as a means of controlling round goby populations is not without its flaws. The overlying issue with using an acoustic trap or any baited traps is that while sound does travel farther and faster in water than odours and on land (Kasumyan 2009), the range of the round goby's call is restrictive. Sound propagation in the field was measured using a hydrophone, where it was found that the sound usually did not travel farther than six feet away from the sound source, due to the shallow water environment in which the trials were conducted. The overlaying issue with shallow water habitats is that they restrict the distance that an acoustic signal can travel due to the numerous reflections off the substrate and rocks situated in a habitat (Rogers and Cox 1988, Thorne 1998). For the round goby, the short distance propagation of acoustic signals is not detrimental as the species is colonial and therefore live in close proximity to one another (Wickett and

Corkum 1998), therefore sounds do not necessarily need to travel far for an individual to hear the sound. In addition, trials conducted in shallow water were unavoidable since round gobies typically spawn in that type of habitat, as long as water temperatures remain low (Charlesbois et al. 1997). The inability for sound to propagate over long distances and the manifestation of acoustic noise within shallow water is further elaborated when comparing capture rates of round gobies between a playing and silent trap released in the same inlet. Oddly, gobies tended to be captured in the silent trap more often when paired with a playing trap, regardless of the sound being played, but when combining the number of gobies captured in each pair of traps by treatments (grunt, drum, control), an obvious difference in quantity captured was apparent. Given that more gobies were captured in the grunt call trap in the month of May, but no difference was seen for the control, it seems that the sound lures the gobies into the inlet, but they are unable to localize the sound source properly and error when entering the trap. The hearing sensitivity of the round goby is poor in comparison to other species that use acoustic communication (Belanger et al. 2010) since they do not possess a swimbladder or any form of hearing specializations that we are aware of (Charlesbois et al. 2001). Gobies may use a combination of their ears and the lateral line to detect intensity differences within the near field soundscape, to localize the sound source. Similarly, mottled sculpins, *Cottus bairdii*, a species that also does not possess a swimbladder, when approaching a dipole source, were speculated to use their lateral line as a means to sample the sound environment to assist with localizing the sound source, made apparent when fish approached the speaker indirectly, described as a zigzag pattern (Coombs and Conley 1997). As a result, the round goby may use their lateral line as a means to sample the soundscape to localize a sound source. Nevertheless, round gobies may be able to hear the sound from a distance and locate the inlet where the traps are located, but because shallow water restricts acoustic communication and results in overlapping acoustic noise, gobies are unable to localize the sound source properly, and as a result, move into the wrong trap. Despite the inability of the round goby to localize the playing trap properly, it does not disregard the success of acoustic trap, but rather indicates that for acoustic traps to be successful, traps must be deployed in pairs, one playing while the other is silent, to maximize capture rate. In addition, because the sound only propagates over a short distance as a result of habitat, field sites where goby densities are high must be located prior to deployment in order for the trap to work efficiently.

Although the trapping mechanism using acoustic signals as a lure requires further investigation in the field, a potential strategy that could be used when deploying these traps along a spawning bed can be suggested. Before trap deployment can take place, the location of the nesting sites of RMs needs to be assessed at a spawning bed. Locating the nesting sites will reveal the position of the goby colony since RMs move into the shallow waters first with females and other gobies preceding them (Charlesbois et al. 1995, Corkum et al. 1998). Round gobies, females in particular, are thought to remain in the deeper waters to avoid predation and move into the shallow water only when ready to spawn (Kulikova 1985). Given that the conspecific sounds only propagate over a short distance (six feet as determined by the current study), traps must be deployed close enough to the spawning bed as sound propagation allows. Moreover, traps should be deployed lying between the shallow and deep water boundary where gobies are likely to cross when travelling to and from the spawning beds, to ensure that gobies will interact with the trap itself. As for the number of traps that would need to be deployed to have an effect on the goby population would depend on the numbers of gobies that reside in the location of interest. I suggest that for every 200 gobies, six traps should be present and deployed near the spawning bed. Furthermore, the number of traps should be adjusted relative to the size of the spawning area, so that complete coverage of the site itself can transpire. I suggest six traps per 200 gobies simply because the traps used in the current study have captured ~30 gobies per trap pair itself (Table 3.1, 3.2, 3.3), and therefore six traps should be reasonable to avoid carrying capacity of the traps and reduce the probability of diminishing capture. Furthermore, in the current study, the total number of gobies captured using two traps and the grunt call over three months captured ~300 gobies, therefore six traps should capture three times that number in a single summer (Table 3.1). The current study showed that round gobies are unable to differentiate between the playing and the silent trap, but are able to localize the sound source within an inlet. Therefore, I suggest that instead of using a single playing speaker per trap, use a single playing speaker situated at the center of a group of six traps that are spaced apart, as to lure gobies into an inlet where the traps are situated, thereby reducing deployment costs.

In conclusion, the current study provides the first application of conspecific acoustic signals as a lure for the capture and control of the round goby and also provides a trapping model that can be used for the control of other invasive species, implementing the use of other naturally occurring attractants. In addition, the current study provides additional insight for attractive phonotactic response to conspecific sounds by the round goby in the field, and provides further supporting evidence that the grunt call plays a role in mate attraction facilitated by a successful capture rate of female gobies. Finally, upon examination of the number and types of gobies captured through the summer, results show that maximum capture efficiency and phonotactic attraction to conspecific sounds occurs early in the spawning season of the round goby and declines as the summer progresses. By implementing the use of conspecific acoustic signals as a lure to attract and capture round gobies as well as applying a mate attraction call that attracts gravid females, may provide a strategy to capture and control round goby populations in key areas, that could be used as a means to reduce the impact of the round goby in freshwater systems of North America.

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Figures and Tables

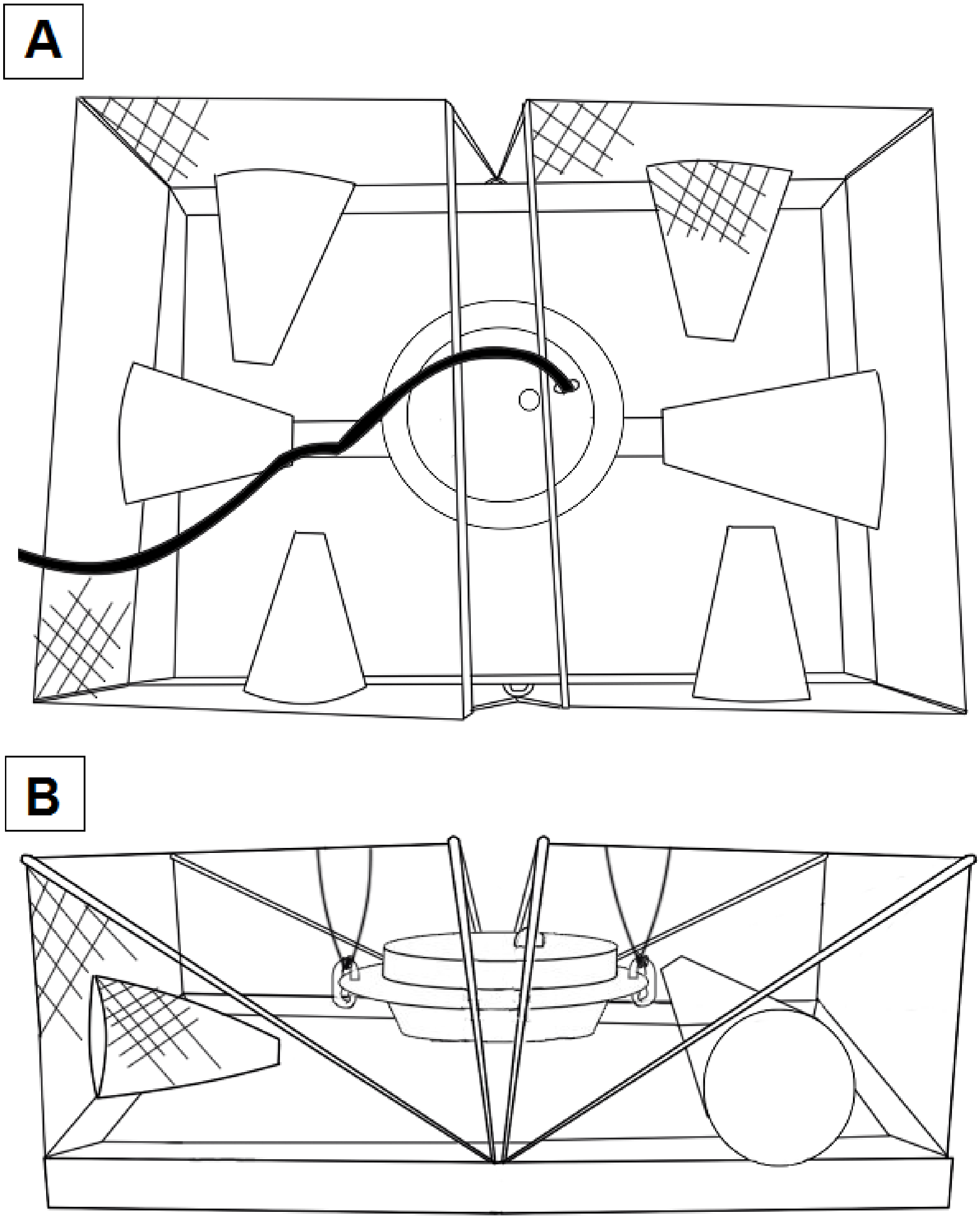

Figure 3.1: Depiction of trap design used in field experiment, displaying **A)** Top View, and **B)** Side View. Acoustic traps were composed of a stainless steel, rectangular framework (62.2 cm x 44.7 cm x 20.8 cm) and enclosed by plastic mesh netting, mimicking a standard fish box trap using funnel entrances.

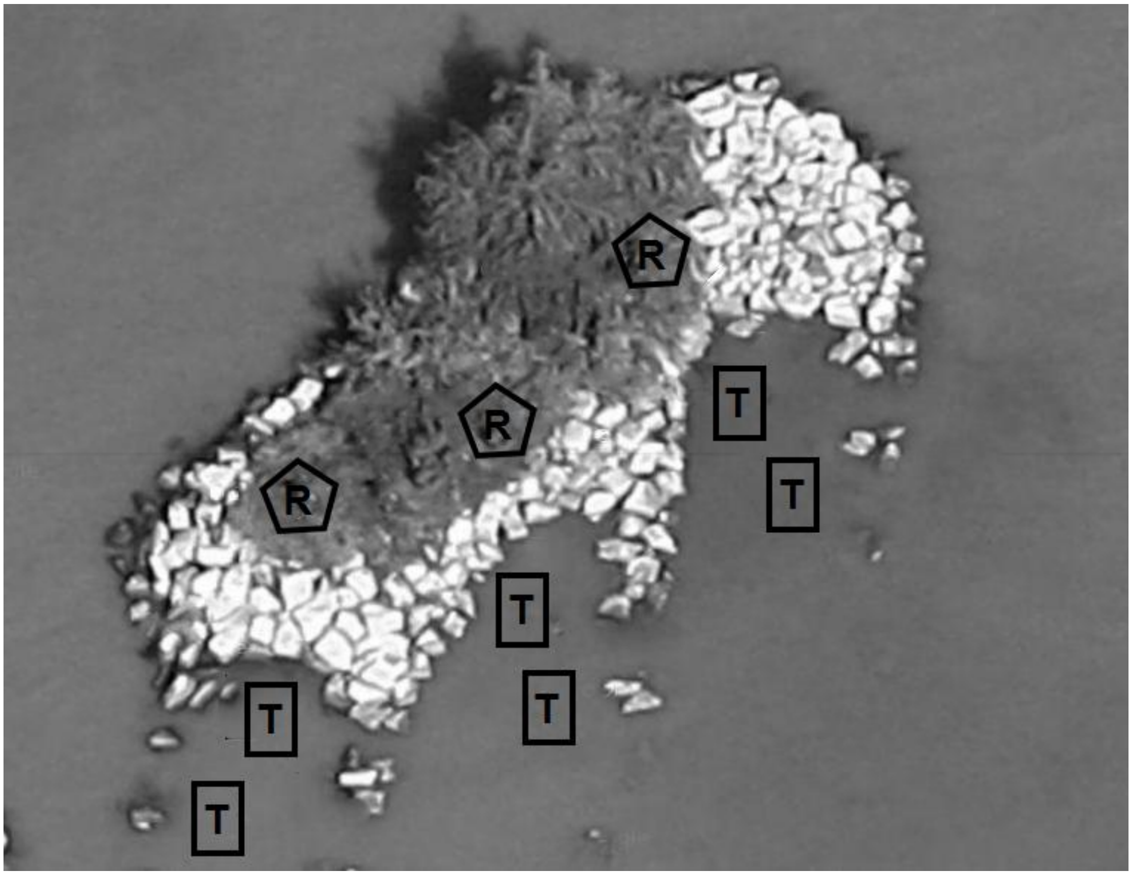

Figure 3.2: Depiction of field site (McKee Park), located on the Detroit River at Windsor, ON [42°20′N, 82°56′W]. Each trial consisted of three pairs of traps, which included two treatments (grunt and drum call) and a control (silence). Each treatment consisted of a playing trap and a silent trap, while the control consisted of two silent traps. Traps (T) were released randomly in one of each three inlets along the field site and electronic rig (R) containing equipment (12-V battery, car amp, mp3 player) was situated on the island itself, hidden from view. All trials were deployed at night and then picked the following morning, for a period of 20 hours.

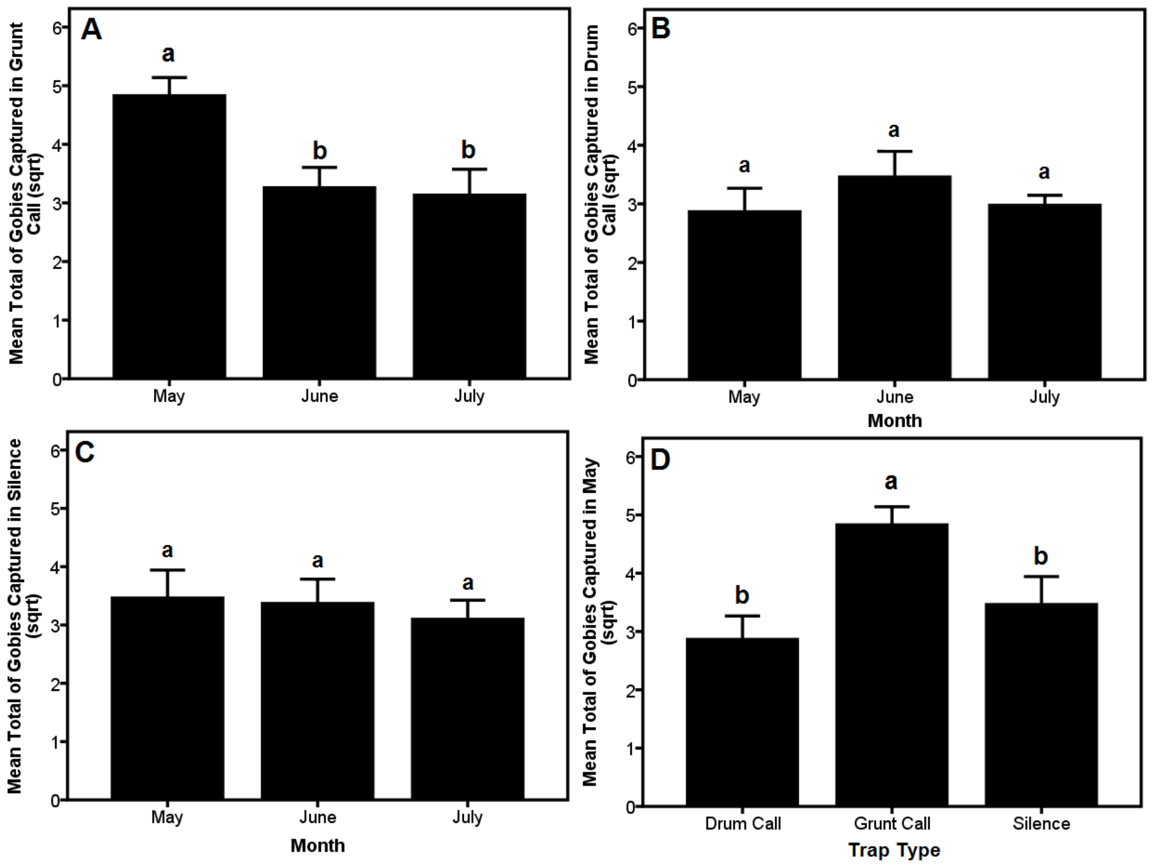

Figure 3.3: Mean (±S.E.) total number of gobies captured for all treatments per month for **A)** Grunt Call (n =22), **B)** Drum Call (n = 19), **C)** Control (n = 19), and total number of gobies captured in **D)** May (n = 15) for all trap types. For the grunt call, significantly more gobies were captured in May than in June (P = 0.013) and July (P = 0.009), but not between June and July (P = 0.963). No overall significant differences were found for the drum call treatment (P = 0.413) or the control (P = 0.783) by month**.** For the month of May, a significant number of gobies were captured more in the grunt call traps than in the drum call trap (P = 0.006) or the control (P = 0.049), but no difference was found between the drum call trap and the control (P = 0.567). Letters denote significant differences.

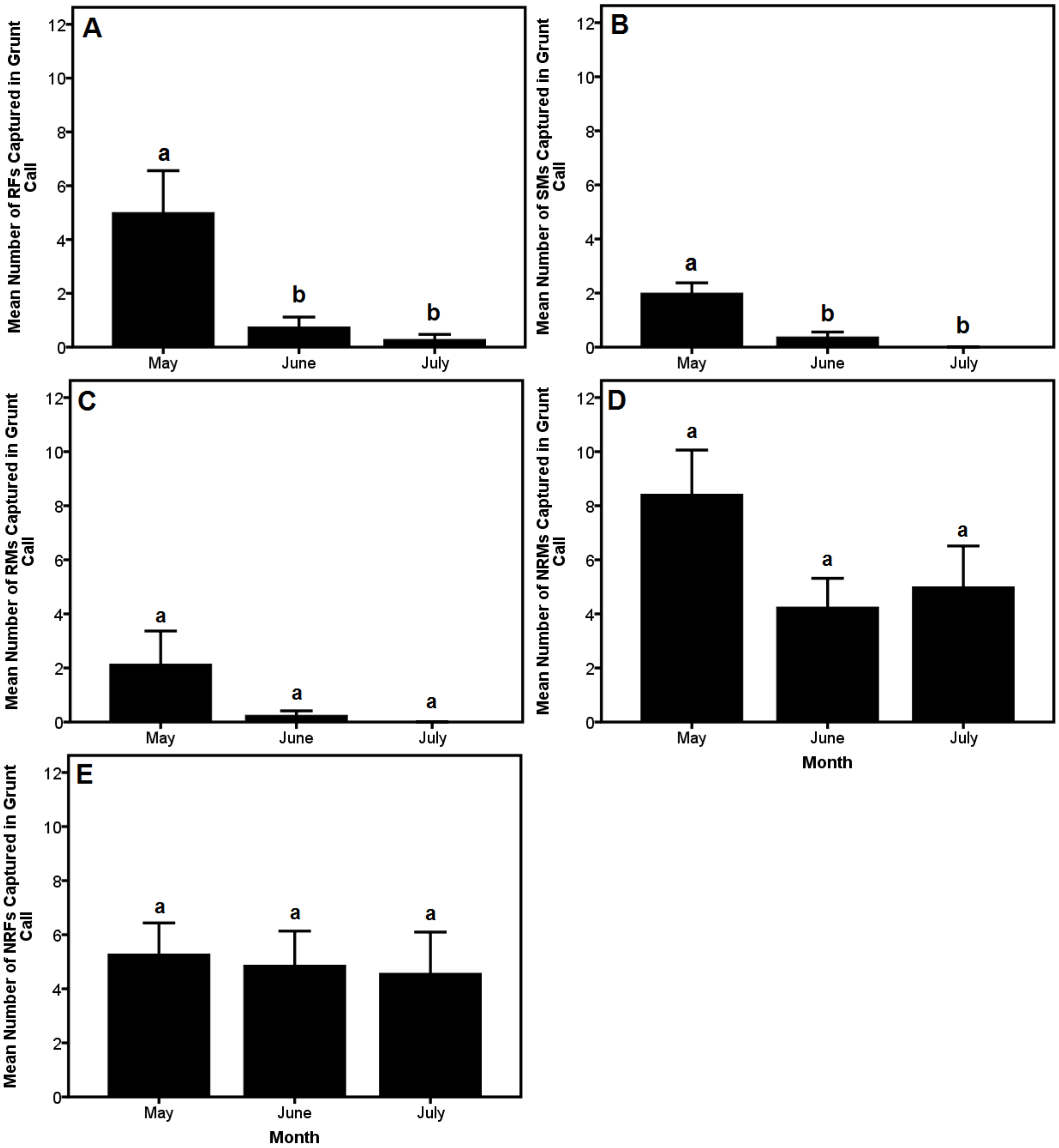

Figure 3.4: Mean (±S.E.) number of reproductive morphs captured in the grunt call trap over three months (n = 22) for **A)** Reproductive females (RFs), **B)** Sneaker males (SMs), **C)** Reproductive males (RMs), **D)** Nonreproductive males (NRMs), and **E)** Nonreproductive females (NRFs). Significantly more RFs were captured in May than in June (P = 0.015) and July (P = 0.003), but not between June and July (P = 0.446). Significantly more SMs were captured in May than in June (P = 0.001) or July (P = 0.004), but not between June and July (P = 0.08). Significantly more RMs were captured in May than July (P = 0.025). No significance was found between May and June (P = 0.116) or June and July (P = 0.170) for RMs. Letters denote significant differences.

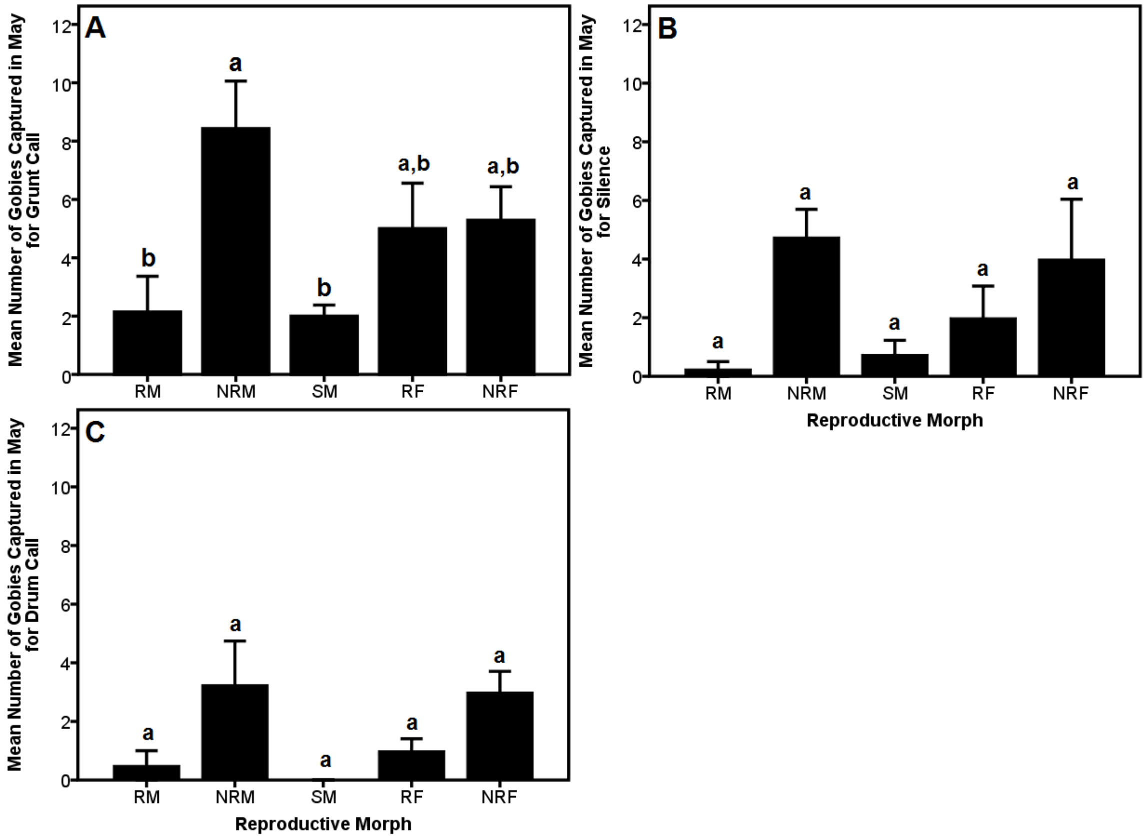

Figure 3.5: Mean (±S.E.) number of reproductive morphs captured in May (n = 12) for **A)** Grunt Call, **B)** Silence (control), and **C)** Drum Call. For the grunt call, NRMs were captured significantly more than RMs (P = 0.010) and SMs (P = 0.003). Letters denote significant differences.

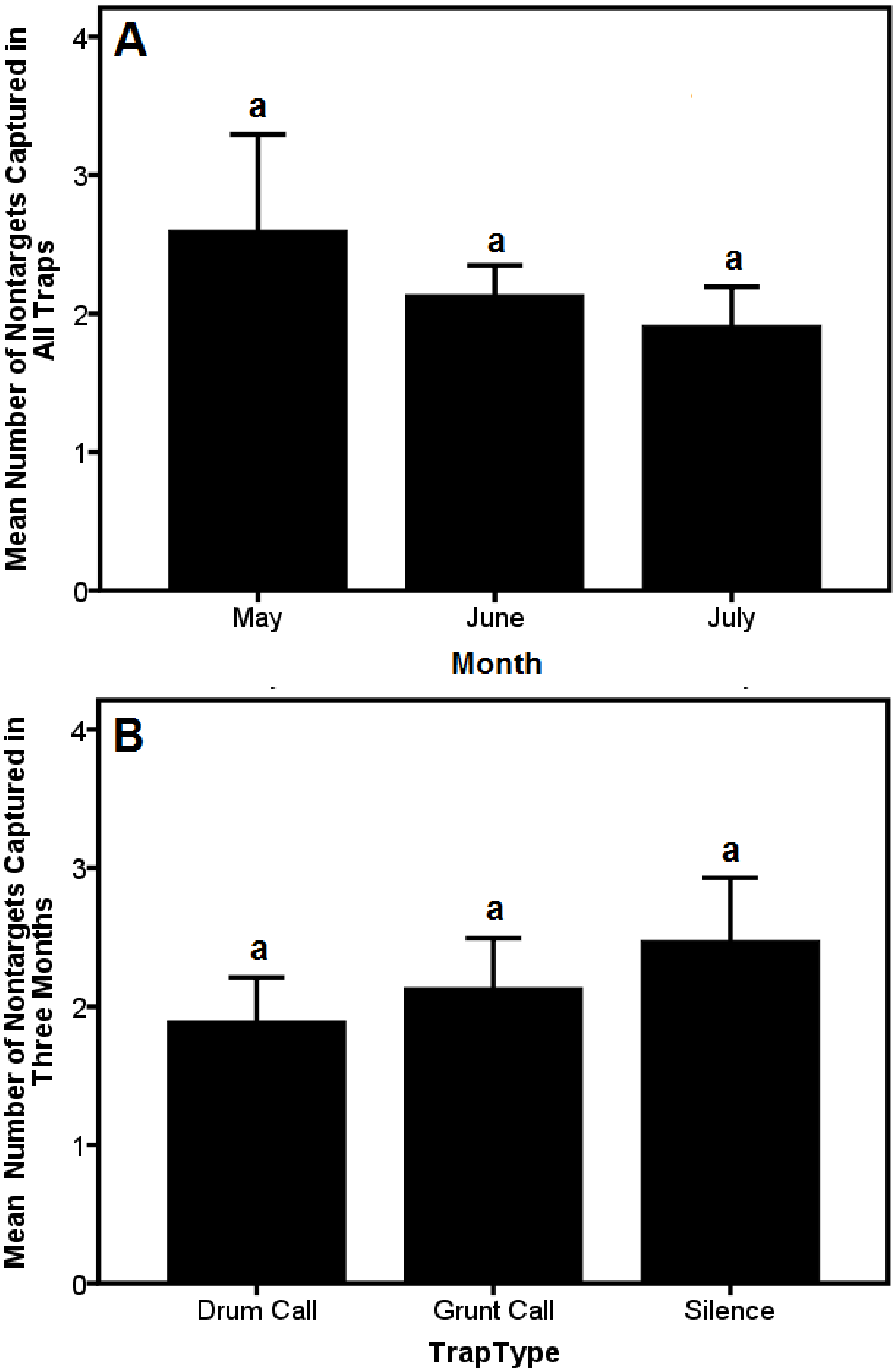

Figure 3.6: Mean (±S.E.) number of non-target organisms captured in all traps, in **A)** All traps per month (n = 60), and **B)** Three months per treatment (n = 60). Capture rate for all treatments per month, no overall significant differences were found for either May (P = 0.753), June (P = 0.875), or July (P = 0.329). For capture rate for all months per treatment, no overall significant differences were detected for either the grunt call (P = 0.668), drum call (P = 0.295), or the control (P = 0.809).

Table 3.1: Tabulation of all gobies captured in the field during the summer of 2012 for the grunt call displaying: capture by date deployed and retrieved, water temperature, reproductive morph captures, total gobies captured, and non-targets captured.

Date	Water Temp (°C)	RM	NRM	SM	RF	NRF	Total	Non-targets
May 8, 9	16	1	5	1	10	7	24	2
May 10, 11	16	3	16	1	9	1	30	8
May 16, 17	16	0	11	2	9	8	30	1
May 17, 18	17	2	9	3	1	9	25	0
May 28, 29	21	9	6	3	3	2	23	2
May 30, 31	17	0	9	3	1	6	19	2
May 31, June 1	17	0	3	1	2	4	10	1
June 4, 5	18	0	1	1	0	3	5	1
June 7, 8	20	0	1	0	0	8	9	2
June 11, 12	21	0	6	1	2	1	10	2
June 14, 15	21	1	5	0	0	3	9	0
June 18, 19	22	0	5	0	2	7	14	4
June 21,22	21	1	10	1	2	11	25	2
June 25, 26	21	0	2	0	0	1	3	3
June 28, 29	23	0	4	0	0	5	9	3
July 3, 4	21	0	13	0	1	11	25	2
July 9, 10	21	0	7	0	0	9	16	3
July 12, 13	23	0	5	0	0	2	7	2
July 16, 17	24	0	3	0	1	3	8	3
July 19, 20	19	0	3	0	0	5	8	2
July 24, 25	19	0	3	0	0	0	3	2
July 26, 27	19	0	1	0	0	2	3	0
Total	**N/A**	**17**	**128**	**17**	**43**	**108**	**315**	**47**

Table 3.2: Tabulation of all gobies captured in the field during the summer of 2012 for the drum call displaying: capture by date deployed and retrieved, water temperature, reproductive morph captures, total gobies captured, and non-targets captured.

Date	Water Temp (°C)	RM	NRM	SM	RF	NRF	Total	Non-targets
May 8, 9	16	0	2	0	1	1	4	5
May 10, 11	16	2	4	0	1	3	10	1
May 16, 17	16	0	7	0	2	4	13	2
May 31, June 1	17	0	0	0	0	4	4	1
June 7, 8	20	0	2	0	0	6	8	2
June 11, 12	21	1	1	0	0	0	2	3
June 14, 15	21	1	9	0	1	7	18	3
June 18, 19	22	0	3	0	0	2	5	2
June 21,22	21	1	8	0	1	3	13	3
June 25, 26	21	0	7	2	2	10	21	2
June 28, 29	23	0	11	0	1	6	18	1
July 3, 4	21	0	1	0	1	8	10	4
July 5, 6	22	0	7	0	0	4	11	0
July 9, 10	21	0	2	0	1	2	5	2
July 12, 13	23	0	3	0	0	3	6	1
July 16, 17	24	0	10	0	0	1	11	0
July 19, 20	17	0	5	0	0	0	5	0
July 24, 25	19	0	3	0	0	5	8	3
July 26, 27	19	0	3	0	0	6	9	1
Total	**N/A**	**5**	**88**	**2**	**10**	**150**	**181**	**36**

Table 3.3: Tabulation of all gobies captured in the field during the summer of 2012 for the control displaying: capture by date deployed and retrieved, water temperature, reproductive morph captures, total gobies captured, and non-targets captured.

Date	Water Temp (^{o}C)	RM	NRM	SM	RF	NRF	Total	Non-targets
May 17, 18	17	0	6	0	2	1	9	9
May 28, 29	21	1	6	0	5	10	22	3
May 30, 31	19	0	5	2	0	3	10	0
May 31, June 1	17	0	2	1	1	2	6	2
June 4, 5	18	2	6	1	0	6	15	1
June 7, 8	20	0	1	0	0	1	2	2
June 11, 12	21	0	6	0	0	6	12	1
June 18, 19	22	0	0	0	2	1	3	3
June 21, 22	21	0	10	1	2	4	17	1
June 25, 26	21	0	10	0	3	3	16	3
June 28, 29	23	0	5	2	0	8	15	3
July 3, 4	21	0	3	1	0	5	9	4
July 5, 6	22	0	4	0	0	3	7	2
July 9, 10,	22	0	12	0	1	7	20	4
July 12, 13	23	0	2	0	0	7	9	3
July 16, 17	24	0	0	0	0	1	1	2
July 19, 20	17	0	9	0	0	3	12	0
July 24, 25	19	0	1	1	0	6	8	3
July 26, 27	19	0	4	0	0	5	9	1
Total	**N/A**	**3**	**92**	**9**	**16**	**89**	**202**	**47**

Table 3.4: Tabulation of all non-targets captured in the field during the summer of 2012 for all three treatments (drum call, grunt call, and silence) for the four most commonly captured native species, being rock bass, yellow perch, common mudpuppy, and signal crayfish.

Date	**Trap Type**	**Rock Bass**	**Yellow Perch**	**Mudpuppy**	**Crayfish**
May 8, 9, 2012	*Drum Call*	4	0	1	0
May 10, 11, 2012		1	0	0	0
May 16, 17, 2012		1	0	0	1
May 31-June 1, 2012		1	0	0	0
June 7, 8, 2012		0	0	0	2
June 11, 12, 2012		2	0	1	0
June 14, 15, 2012		0	0	0	3
June 18, 19, 2012		0	0	0	2
June 21,22, 2012		2	1	0	0
June 25, 26, 2012		1	0	0	1
June 28, 29, 2012		0	1	0	0
July 3, 4, 2012		4	0	0	0
July 5, 6, 2012		0	0	0	0
July 9, 10, 2012		0	0	0	2
July 12, 13, 2012		0	0	0	1
July 16, 17, 2012		0	0	0	0
July 19, 20, 2012		0	0	0	0
July 24, 25, 2012		1	0	0	2
July 26, 27, 2012		1	0	0	0
Date	**Subtotal**	**18**	**2**	**2**	**14**
May 8, 9, 2012	*Grunt Call*	1	0	0	1
May 10, 11, 2012		7	0	1	0
May 16, 17, 2012		1	0	0	0
May 17, 18, 2012		0	0	0	0
May 28, 29, 2012		1	0	0	0
May 30, 31, 2012		1	0	1	0
May 31, June 1, 2012		1	0	0	0
June 4, 5, 2012		1	0	0	0
June 7, 8, 2012		0	0	1	1
June 11, 12, 2012		1	0	0	1
June 14, 15, 2012		0	0	0	0
June 18, 19, 2012		0	0	4	0
June 21,22, 2012		0	0	1	0
June 25, 26, 2012		2	0	0	1
June 28, 29, 2012		1	0	0	0
July 3, 4, 2012		0	0	0	2

July 9, 10, 2012		0	0	0	3
July 12, 13, 2012		0	0	0	2
July 16, 17, 2012		0	0	0	3
July 19, 20, 2012		1	0	0	1
July 24, 25, 2012		0	0	0	2
July 26, 27, 2012		0	0	0	0
Date	**Subtotal**	**18**	**0**	**8**	**17**
May 17, 18, 2012	*Silence*	4	2	1	2
May 28, 29, 2012		0	0	0	3
May 30, 31, 2012		0	0	0	0
May 31, June 1, 2012		0	0	0	1
June 4, 5, 2012		0	0	0	1
June 7, 8, 2012		1	0	0	0
June 11, 12, 2012		0	0	0	1
June 18, 19, 2012		0	0	1	2
June 21, 22, 2012		1	0	0	0
June 25, 26, 2012		1	0	0	2
June 28, 29, 2012		0	0	1	1
July 3, 4, 2012		0	0	0	4
July 5, 6, 2012		2	0	0	0
July 9, 10, 2012		0	0	0	3
July 12, 13, 2012		2	1	0	0
July 16, 17, 2012		1	0	0	1
July 19, 20, 2012		0	3	0	0
July 24, 25, 2012		0	0	0	1
July 26, 27, 2012	**Subtotal**	**12**	**6**	**3**	**22**
Overall Total		*48*	*8*	*13*	*53*

CHAPTER 4:

THESIS FINDINGS AND SIGNIFICANCE

Function of Acoustic Communication and State-Dependant Responses

The round goby, *Neogobius melanostomus*, as far back as the first assessment of goby acoustic behaviour by Protasov (1965), has been speculated to use acoustic communication as a function of mate attraction (Rollo et al. 2006, Rollo and Higgs 2008); a common occurrence in the teleost family Gobiidae (Lugli et al. 1995, Lindstrom and Lugli 2000, Lugli et al. 2004, Amorim and Neves 2007, Malavasi et al. 2009). Many sound types have been recorded from male round gobies and explored as to what information these signals contain that allow for gobies to communicate with each other. One such call that has been recorded and is thought to play a role in mate attraction is known as the grunt call given the context it had been recorded (see chapter 2 and 3 methods). While behavioural responses to the grunt call have been performed in the past via the use of playback experiments (Rollo et al. 2006, Rollo and Higgs 2008), the importance of differentiating behavioural responses by reproductive state had yet to be performed in regard to these sounds, and was merely speculation derived from female preference (including both reproductive and nonreproductive females; RFs and NRFs, respectively) seen in past studies. However, Chapter 2 showed RFs preferred the grunt call in a number of behavioural measures examined in contrast to NRFs who did not display a preference to any sounds, and no other reproductive morphs examined displayed the same preference for the grunt call. Furthermore, strong phonotactic attraction to the grunt call was also seen in the field by RFs in May, early in the goby's spawning season. Courtship signals are thought to have evolved in conjunction with female preference for particular male traits, and that upon recognition of a signal, elicit a robust response by triggering sensory bias coded in the female's behaviour (Ryan and Hector 1992). Similar behaviours have been seen in gravid females of other species in response to conspecific male mate attraction signals that trigger a robust phonotactic response when the sound is heard (McKibben and Bass 1998, Myrberg et al. 1986); with much reduced response by other conspecifics of differing reproductive state and sex. Therefore, RFs may be displaying a triggered response elicited by characteristics in the male's call due to its sensitive and robust phonotactic response to the grunt call. In contrast, RMs displayed no preference to any conspecific call and behavioural responses to sounds were found to be low (as was predicted) as in nature, it would be deleterious to investigate conspecific calls as it exposes a nest to predation and theft by other males. Given RFs preference for the grunt call and evidence found in past studies (Rollo et al. 2006, Rollo et al. 2008), it can be said with more certainty that the grunt call may play a role in mate attraction. Another round goby call that has been discovered and recorded recently, known as the drum call, was also suspected to play a role in mate attraction after preliminary investigation of the sound in the lab (Mancini 2010), however, in the current study, RFs were found to either ignore the sound altogether or avoid it, potentially disproving the claim that the drum call played a role in mate attraction, as the intended recipient did not appear to care for it.

The nonreproductive males (NRMs) and sneaker males (SMs) were found to display somewhat of an attraction to the drum call and was speculated that non-target receivers may intercept the sound as means of eavesdropping to locate a nest with eggs, as males have been found to vocalize to females while eggs are within the nest (Meunier et al. 2009, Wickett and Corkum 2008). Surprisingly, the same behaviour was not displayed towards the drum call in the field as NRMs and SMs seemed to intercept the grunt call instead. However, intercepting of the grunt call does not disregard the eavesdropping claim, as it as it still provides a means to localize the nesting site for egg predation and sneaking fertilizations (Brantley and Bass 1994, McKibben and Bass 1998, Alonzo and Warner 1999, Bass and McKibben 2003). The field results are probably more indicative of accurate behavioural responses to conspecific sounds since it's performed under a more natural setting. Interestingly, the drum call had the lowest capture rate of gobies in contrast to the other two traps types (see chapter 3). In Chapter 2, it was speculated that female avoidance of the drum call may indicate that the drum call plays a role in territorial defense due to the manner it was recorded (see chapter 2 and 3 methods). Using acoustic signals in territorial or aggressive displays is also a common occurrence in the family Gobiidae (Lugli 1997, Sebastianutto et al. 2008, Amorim and Neves 2008). In regard to NRMs and SMs, the fact that the drum call did not deter these morphs from approaching the sound source, however, the results in the lab and field may have differed simply due to the "environment"; water in the lab was clear while in the field, it was turbid. Potentially, after determining that no physical male was present at the sound source, NRMs and SMs approached the drum call regardless, while in the field, turbidity of the water prevented visual determination of the nest-guarding male's presence and chose to avoid the trap playing the drum call. The same cannot be said for RFs as they never attempted any investigative behaviour towards the drum call. With these results in mind, the current study provides some insight and clarity into the function of the two round goby calls, the grunt and the drum call, given responses seen both in the lab and the field.

Secondly, Chapter 2 provides new evidence of state-dependent response to conspecific calls as a model in the round goby, given the differential levels of phonotactic responses to conspecific sounds displayed in the lab and to a degree in the field. Evidence of state-dependent responses to acoustic signals is of interest as it is rarely investigated in freshwater fishes in association to behaviour (Sisneros and Bass 2003, Bass and McKibben 2003, Clement et al. 2004). Instead, behavioural responses to conspecific calls via playback studies tend to either be male or female focused. The problem with separating male and female behavioural responses to acoustic signals is that the full scope of the function of acoustic communication within a community is investigated haphazardly and only provides part of the story. For example, to truly determine if a male call is for mate attraction, the response between reproductive and nonreproductive females should be different, as the function of the call is to attract gravid females. As a result, mate attraction calls should facilitate a stronger phonotactic response due to hormones responsible for reproductive maturity circulating in the blood. However, by doing so, alternative reproductive morphs that exist within the goby population are disregarded from the investigation entirely, such as males, both reproductive and nonreproductive, and alternative reproductive tactics. To think of any form of communication as of occurring between a single sender and receiver is unrealistic in nature, as any vocalization performed by an individual is audible to any conspecific within range of hearing the sound, and therefore can be understood. Unintended recipients of the vocalization can then intercept these signals and respond to them.

Myrberg (1981) when first stating his idea on signal interception, also known as eavesdropping, speculated that males that practiced alternative reproductive tactics (sneaker males) should intercept sexual signals as it provides information on the location of a potential spawning event and therefore an opportunity for a male to sneak fertilizations; a claim while reasonable is rarely investigated due to male or female focused studies. Realistically, if responding to an acoustic signal is beneficial to the non-target recipient, eavesdropping should evolve, and therefore trigger the response when the sound is heard. Disregarding the investigation of responses to conspecific signals by all members within a species may lead to overlooked and undiscovered behaviours and the effect those behaviours may have on senders beyond predictions that are made at the surface. To further understand female response to conspecific sounds, call rates should be examined as different call rates can have various meanings (Seyfarth and Cheney 2006), which is currently unknown in the round goby. In addition, intensity threshold responses should be investigated to sounds played at different intensities, as it has yet to be investigated behaviourally in the round goby. The current study provides evidence that may indicate a relationship between reproductive state and auditory responsiveness to conspecific calls in the round goby and provides a model of how reproductive state can affect phonotactic response between the sexes. Furthermore, results may also provide some insight on function of the conspecific calls examined.

Population Control Strategy Using Acoustic Signals in a Trapping Mechanism

Chapter 3 examined the response of round gobies to conspecific calls in the field and examined the use of acoustics as a lure in a trapping system to be used in the control and capture of the invasive species. Since the 1990s, the round goby has been a prominent and deleterious invader in the Laurentian Great Lakes (Jude et al. 1992, Charlesbois et al. 2001), however, strategies to reduce the negative impact the species has had on freshwater ecosystems has yet to be fashioned. The current study, to my knowledge, is the first application of conspecific acoustic signals as a lure to attract and capture an invasive fish. The grunt call in May was found to capture significantly more gobies than the other two traps (drum call and the control), showing a positive phonotactic response and a selective trapping system. Successful capture of reproductive individuals, in particular RMs, SMs, and RFs in the grunt call trap, was most likely due to preferred water temperatures for spawning in this species and provides further evidence in the selective utility of this trap. While the goby is a voracious and aggressive competitor (Charlesbois et al. 2001), the true nature of its impact is not due its presence in the Great Lakes, but rather the number of individuals that are present in areas where native species thrive (Bergstrom et al. 2008). The round goby's extensive range and population size is a result of the species ability to spawn multiple times in a single breeding season, causing a high recruitment rate from one year to the next and outnumbering native fish populations that only spawn once per breeding season (Charlesbois et al. 1997). Bergstrom and Mensinger (2009) found that where density of the invasive species was low, native species were able to compete for limited resources and persist despite the round goby's presence, while in areas where goby density was high, native species were outcompeted and driven to extinction. Since complete removal of the round goby from freshwater systems in likely impossible, a means of reducing the round goby's population size may be a good strategy in reducing the species' impact on the Great Lakes. In regard to the round goby, the most successful method in controlling population size of a species that spawns multiple times in a single season is to reduce the number of gravid females available for nest-guarding males to spawn with. By reducing female availability, I could potentially reduce round goby impact in key sites and alleviate competitive stress on native fish. In the current study, while the trapping mechanism used did capture a large number of RFs in May when using the grunt call as a lure, the sound was also successful in capturing a large total number of gobies (both reproductive and nonreproductive) in contrast to the drum call and the control; therefore, using the grunt call as a lure is a good strategy as a means to capture and remove a large number of gobies of all reproductive morphs from key areas, thus alleviating competitive stress on native species and reducing the round goby's negative effect on freshwater ecosystems. Furthermore, non-target capture of species was found to be minimal when implementing this trapping design and is therefore a practical tactic in selectively capturing the round gobies without harming native species in the process. Furthermore, the trapping mechanism used in the current study could also be used in the control of other invasive species by implementing the use of natural occurring attractants. Future directions should focus on recording overnight trials to determine if the number of gobies attracted to the traps was higher than that what was captured and make modifications to increase capture efficiencies. In addition, underwater cameras could also be used to determine when peak response to conspecific sounds occurs in the field and deploy traps and play sounds appropriately, as the calling activity of the round goby is currently unknown.

The current study also provides additional insight of phonotactic response to conspecific sounds by the round goby in the field in relation to reproductive state, which is the first of its kind. Finally, when examining the amount of gobies captured both in regard to successful capture rate and by reproductive state, results show that maximum capture efficiency and phonotactic attraction to conspecific sounds occurs early on in the spawning season of the round goby and declines as the summer progresses. By implementing the use of acoustic signals as a lure to attract and capture round gobies as well as applying a mate attraction call that attracts gravid females and other reproductive morphs, I can reduce the number of females available for spawning and cause a decline in recruitment. In addition, by reducing the density of round gobies in key areas, I can alleviate competitive stress on native species and the impact of native species in freshwater systems of North America.

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