A Review of Toadfish Boat Whistle Literature and Its' Regard for Anthropogenic Factors

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Toadfish Species and the Family *Batrachoididae*

The family *Batrachoididae* is composed of toadfish and midshipman. This group is well studied because of their vocal organ and unique acoustic behaviors. (Staaterman, Erica, et al, 2018). Animals in the family tend to be solitary and territorial, laying their deposited eggs on a surface which acts as a nest (Breder, 1941). According to Fishbase, there are currently 83 species in the family. In Panama, this includes the Bocon toadfish (*Amphicythys cryptocentrus*), Bearded toadfish (*Sanopus barbatus*), Boulenger's toadfish (*Batrachoides boulengeri*), Large-eye toadfish (*Batrachoides gilberti*), Pacific toadfish (*Batrachoides pacifici*), Pacuma toadfish (*Batrachoides surinamensis*), Walker's toadfish (*Batrachoides walkeri*), Dow's toadfish (*Daector dowi*), Reticulated toadfish (*Daector reticulata*), and Schmitt's toadfish (*Daector schmitti*) (*Fishbase*). Despite this great diversity within the family, only sounds from eight species have been described in detail (Mosharo and Lobel 2012; Rice and Bass 2009).

Most Studied Toadfish Species and their Contribution to Current Knowledge

Sounds from four toadfish species have been the most extensively studied. The first to be studied were the oyster toadfish (*Opsanus tau*) and the gulf toadfish (*Opsanus beta*). In 1958, Tavolga described the underwater sounds of these two species (Tavolga WN, 1958). They found differences in pitch, harmonic content, duration, and repetition rate across the "boat whistle" sounds produced by each species of toadfish. Their results showed that gulf toadfish 'hoots,' which later became known as 'boops,' were shorter and higher than that of the oyster toadfish (Tavolga WN, 1958). In this study, they also found that oyster toadfish from Florida called in lower pitches than those from Rhode Island for reasons unknown to the researchers. This was one of the first major studies to describe the actual structure of the toadfish boat whistle and its' components;. Tavolga described that there are "hoots" preceded by "grunts", and that the hoots are "clearly" harmonic (Tavolga WN, 1958). In a different study, Tavolga also demonstrated, in combination with visual stimuli, short grunts attracted females during reproduction (Tavolga, 1956).

A few years later, another study was conducted on the oyster toadfish, *Opsanus tau*, by Gray and Winn (Gray GA and Winn HE, 1961). This was the first study to systematically check nests throughout the reproductive season; because toadfish nest in shallow water, it made for easy observation. Their results show that reproduction and spawning of the oyster toadfish is heavily dependent on temperature, toadfish are polygamous, and males guarding eggs have greater stimulation to produce grunt calls (Gray GA and Winn HE, 1961). This stimulation can be assumed to be protection of the eggs, as the grunt class serves as a warning for others to stay away from the next. This was the first study to suggest that only males make the boat whistle calls; they state the boat whistle call is given off by males at nests ready to spawn, and that the call is an attractive stimulus for females ready to lay eggs (Gray GA and Winn HE, 1961).

A later study on plainfin midshipman, in the same family as toadfish, described the relationship between body mass with calling behavior (Brantley RK and Bass AH, 1994). In this, researchers described two types of males; type 1 males had much larger body mass and sonic muscles, maintain nests, and readily vocalized. These vocalizations consisted of long‐duration ‘hums’ and sequences of short‐duration ‘grunts’, which were found to attract females to nests to spawn, and then were left to protect the eggs alone. On the other hand, type II males were smaller in body mass, had larger testicles, had no acoustics or nest, and instead ‘satellite spawned’ at nests of Type I male. These males rarely made sounds, but when they did they resembled those of females.

Another commonly studied Batrachoididae is the Listuanian Toadfish. Vasconcelos et al., 2012, describe how the vocal behavior of these toadfish predict reproductive success (Vasconcelos RO et al., 2012). This relationship between acoustic signaling and reproductive success is important to understand, yet so understudied in fish. In this, researchers recorded nest-holding males and extracted data on calling rate, calling effort (% of time calling), and sound dominant frequency. All of these factors were found to be higher in males with clutches than males without clutches. They also found that sex steroids were not correlated with the clutches, so the main factor in determining if they had a clutch or not was based on calling effort (Vasconcelos RO et al., 2012). This study was important in contributing to the validity of how vocal behavior in vocal fish is a significant indicator of reproductive success with higher and constant rates of calling indicating male body size and body condition, and elevated motivation for reproduction.

Toadfish Call Type and Function

Call Structure

The earliest dates in literature in which the first record of acoustics in toadfish are noted are in 1884, by Sorensen, who worked on sound production in organ fishes. He declared that the air bladder of a toadfish was capable of producing sound by contraction and relaxation of the muscles of this bladder (Sorensen, 1884). Gill, in 1907, uses this data to compare the life history of toadfishes to others similar. In this article, Gill also cites a story by Captain Charles B. Hudson in which, potentially, the first human to hear the toadfish sound is reported. The Captain was in Key West making drawings of fishes. Frequently at work, he would hear a musical sound coming from under the pier, of which he could not identify; he described it as sounding like 'koong-koong,' and assumed it was produced by a fish. Only after he had caught a toadfish in a bucket or pan of water and heard that same sound in his hut where the toadfish was did he make the connection (Gill, 1907). After this, the discovery and research on the boat whistle was ignited.

Boat whistle sounds of the Batrichoididae family were first described in Oyster Toadfish in 1954 (Fish, 1954). They described grunts as a reaction to aggression or fear, possibly from other males. They also rightly presumed the boat whistle had to do with mating, and could indicate if a fish was mature enough for sex (Fish, 1954). Tavolga describes hoot-like sounds present during the breeding season, which are typically preceded by grunts. They describe the grunts as being non-harmonic, and discontinuous harmonics throughout the duration of hoots (Tavolga, 1958). In this same study, researchers also explained how hoots vary from species to species of toadfish. In this case, hoots of *Opsanus beta* are shorter, higher pitched, and frequently double that of *Opsanus tau.* This indicates that boat whistles may vary and be unique to each species of toadfish (Tavolga, 1958).

In 1972, a study examined Oyster toadfish and found they produced two distinctive sounds. First, they identified the "grunts" which they observed were made by both male and female toadfish, but more frequently by the males in aggressive encounters (Winn HE, 1972). This information is consistent with what we see today across species, in that the grunts typically increase around other male toadfish. They also identified the “boat whistle call,” which they found was only made by males in long spontaneous sequences at their nests, often at the beginning of mating seasons when males were ready to spawn. Within this boat whistle call, they note that grunts may be interspersed (Winn HE, 1972).

Following this study, most other research on toadfish assumed the “grunts” and “boops” were the main components of the call that we know today. Later studies classified the difference between full boat whistles and grunts alone, describing the grunt as a short-duration pulsatile call, while the boat whistle is a complex call typically consisting of zero to three introductory grunts, a long tonal boop note, and zero to three shorter boops (Thorson and Fine, “Acoustic,” 2002). This finding was compared in many species and in different studies. For example, in that same year researchers examined boat whistle advertisements of the gulf toadfish and found they consisted typically of an initial grunt (typically zero to three with a strong mode of one) followed by one to four long duration boops (Thorson and Fine, “Crepuscular,” 2002). It was found that the fundamental frequency of the tonal portion of the boop was almost constant with no significant modulation. Calling rate increased after sundown, with a peak of 34-131 calls in a half hour; coincident with this, the boop number and call duration significantly decreased. The concluded that the advertisement of the gulf toadfish is more complex than that of the oyster toadfish, with more introductory grunts and variable long-duration tonal notes that form a boat whistle. So, while still confirming that these certain structures of calling exist, they were able to explain slight differences in call structure across species of toadfish (Thorson and Fine, “Crepuscular,” 2002).

More recent studies on the call structure of toadfish boat whistles have focused on these differences, as well as variations due to a number of factors. Bocon toadfish were recorded in a seagrass habitat over six nights in Bocas del Toro, Panama (Staaterman, 2018). Data showed low between-individual variation in frequency of call components, however, they showed that individuals can be identified by call composition on call rate instead. This suggested a novel idea, that each toadfish has a signature “voice” that can differentiate itself from others, based on its’ components and call rate (Staaterman, 2018). Perhaps these results suggest the frequency is a critical component of the toadfish call in this species, and therefore, cannot be changed when differentiating individuals. This frequency change is the topic of current research .

Call Function - Reproduction

Understanding the relationship between acoustic communication and reproductive success in fish is critical in understanding the purpose of this evolved vocalization. That being said, there are more in-depth studies on the actual function of the calls produced by toadfish. The first, most obvious, noted function is for reproduction. In the beginning of literature on the toadfish and their boat whistles, many authors hypothesized or briefly acknowledged the role of calls in reproduction. However, it was not until later that researchers performed more in depth experiments on how these calls affected reproduction. The first mention I was able to find was from Tavolga in 1958, who demonstrated, in combination with visual stimuli, that short grunts attracted females during reproduction (Tavolga, 1958). A few years later, Gray and Winn conducted a study to further examine this relationship between sound production and behavior, noted that the boat whistle call is given off by male toadfish at a nest when they are ready to spawn. They explained that this call is an attractive stimulus to females that are ready to lay eggs. (Gray and Winn, 1961)

Later studies examined how an array of variables influenced this presumed mating call and what that could indicate about toadfish behavior. In 1978, the mating call of the oyster toadfish was compared throughout seasonal and geographic variations (Fine, 1978). They described this boat whistle as a single boop note with harmonics that lasts for several hundred milliseconds. During the off-season, they found, fewer boat whistles were emitted and they had a distinctly lower fundamental frequency. Additionally, the fundamental frequency varies with temperature and season, and call duration varies seasonally but not with temperature (Fine, 1978). This was one of the initial studies to show variation during on and off seasons of the mating call, and how the season and temperature of water is an indicator to the toadfish of whether it is on or off season. A few years later, the response of the mating call by the plainfin midshipman (in the same family as toadfish) was experimented for its' response to a variety of receiving individuals (Ibara et al., 1983). This call is described as a long, monotonous hum only heard at night. They found the hum from male stimulated male-searching behavior in gravid females, and served as a localization beacon to find males. Spent females, juveniles, and other males showed little response to these hums (Ibara et al., 1983). This study is a great example of showing the sexual and reproduction specific function of these boat whistle calls.

After these studies and ones similar to them, it became quite established that this boat whistle was a main factor on reproduction. Further studies focused on how the boat whistle influenced reproductive success in these males. Thorson and Fine describe how the introductory grunts at the beginning of a boat whistle most likely function to alert other fish that a boat whistle is imminent, increasing the likelihood that a call will be heard during a non peak time (Thorson and Fine, "Crepsecular," 2002). Even further, experiments show the relationship between frequency and clutch absence or presence (Vasconcelos, 2012). Calling rate, calling effort, and sound dominant frequency were all higher in males with clutches than those without clutches; this shows these behaviors give individuals an advantage in reproducing. These vocal variables also were correlated with male's total length, condition, and sonic muscle mass. This finding could prove to be incredibly useful on studies regarding phenotypic plasticity, as I hope to focus on in the future.

Call Function - Intrasexual Competition

First experimentally tested by Gray and Winn in 1961, the concept of intrasexual competition in regard to male oyster toadfish vocalization was examined. The researchers noticed that toadfish grunted whenever taken out of water, handled, or when a swimmer or other male toadfish came by a nest (Gray and Winn, 1961). After placing a number of different objects, from food to other toadfish individuals, in front other guarding male toadfish the behaviors were examined. Their results show that only toadfish, especially active males, were the only stimuli to elicit a grunt from guarding males. Males with eggs or young were more likely to grunt or attack than males without, indicating that males guarding eggs have greater stimulation to produce grunt calls as a warning for others to leave (Gray and Winn, 1961). Fine et al. later attribute this motivation for grunting behavior from the internal state of the animal, undoubtedly governed by hormones and external stimuli provided by other calling males and ripe females (Fine et al., 1977).

It was not until much later that other studied provided further support for this claim and expanded on current knowledge. In an article on the auditory sensitivity of Lusitanian toadfish, comparisons of audiograms and sound spectra within the same-sized fish revealed something rather fascinating (Vasconcelos and Friedrich, 2008). They showed that smaller juveniles would barely be able to detect agonositic grunts from other males, while the same grunts would clearly be perceived by larger fish. This demonstrates the development of a directed call for an incredibly specific reason - to reach other ripe males. Vocalizations as a territorial signal were later expanded on by the same researcher. They hypothesis the emission of whistles not during the breeding season indicate other contexts (Vasconcelos et al., 2010). As resident males defended their shelters from experimentally introduced males, parental males emitted these agonistic grunts and revealed higher aggression levels involving additional threats. This study actually compared the grunt of an agonistic interaction, to the grunts that typically precede a boat whistle. Agonistic grunts were similar in duration and harmonic structure to those in boat whistles, but varied in less amplitude modulation and lower dominant and fundamental frequency (Vasconcelos et al., 2010). These slight but apparent differences act to differentiate 'keep out' grunts from those meant to attract females.

In more recent studies, focus has shifted on new species of toadfish that had not been previously examined. The Bocon Toadfish, my toadfish species of interest, is one of these. Specifically, they used bocon toadfish calls to examine this idea that grunts act as a response signal to other males (Salas, Wilson, and Ryan, 2018). Using a null model, they found that grunts were in response to calls from neighboring males as opposed to being random, suggesting acoustic competition. Males typically responded to the second harmonic of neighbor's calls, and call and grunt rates increased when males were exposed to higher acoustic activity rates from neighboring fish (Salas, Wilson, and Ryan, 2018). These results demonstrate that the spatial landscapes of surrounding male toadfish has an impact on calling rates of others as well as the overall soundscape.

Impact of noise/boat traffic

In more recent years, the impact of anthropogenic factors on the call structure and activity of toadfish has been a topic of interest. Because boat whistle calls are so critical to toadfish reproductive success, as demonstrated by previous studies, it is important to understand how human activities may be impacting them. One of the first studies examining this focuses on Lusitanian toadfish in the Tagus River of Portugal, which is prone to noise pollution from shipping noises by ferry-boats (Vasconcelos, Amorim, and Ladich, 2007). They measured hearing sensitivities in a quiet lab setting, as well as in the river. Under ambient noise conditions, hearing was slightly masked at lower frequencies. However, in the presence of ship noise, auditory thresholds increased significantly (up to 36 dB), due to the ship noises being in the main sensitive hearing range of toadfish. Further analyses revealed that ship noise decreased the ability to detect conspecific acoustic signals, providing the first evidence of ship noises impairing fishes' auditory signaling (Vasconcelos, Amorim, and Ladich, 2007). This study paved the way for research on toadfish communities in other environments altered by human activity.

Years later, the findings of this study were supported by another long-term experiment on oyster toadfish in North Carolina (Lucszkovich et al., 2016). Long-term recorders were placed in a high vessel-noise set as well as a low vessel-noise site. These recording data showed that there were many fewer toadfish detections at the high vessel-noise site and calling rates were lower in the high-boat traffic area (Lucszkovich et al., 2016). This indicates that toadfish cannot call over loud vessel noise, thus reducing the overall calling rate. Rather, they may have to call more when vessels are absent. This study is indicative of one strategy to avoid noise masking, which is simply the avoidance of noise. Conversely, another potential strategy to avoid noise masking is vocal compensation. This was observed in another boat noise study of teleost fish, brown meagre (Picciulin et al., 2012). While not in the same family of toadfish, it does present the case that different species may respond to noise masking differently. In this case, brown meagre increased mean pulse rate with multiple boat passages, as a form of vocal compensation.

More often than not, however, in the toadfish we see noise avoidance across most environments. Further study on the lusitanian toadfish reveals a similar result as the oyster toadfish (Alves, Amorim, and Fonseca, 2016). The goal in this case was to compare the maximum distance a fish can perceive a conspecific boat whistle, before and after embedding the same acoustic signal in boat noise (two types were used, a ferryboat and small motorboat). As expected, noise from both the motorboat and the ferryboat significantly reduced communication range. A study that was published most recently in 2020, exposed ship engine sounds or conspecific vocalization to oyster toadfish and found that exposure to boat whistles had no effect on auditory sensitivity, but exposure to anthropogenic noise did for at least three days immediately following exposure. More and more evidence in recent years supports this idea that exposure to excess noise from human activity alters toadfish sensitivity to boat whistle calls, and poses a problem for how they can avoid this masking. Without avoiding this masking, it is not likely other individuals will hear their call, thus reducing reproductive fitness.

Gaps In Knowledge and Where to Go From Here

The "acoustic adaptation hypothesis" states that efficient communication in contexts of mate choice or attraction and territorial defense is predicted to enhance the Darwinian fitness of the individual making the call, despite potentially having adverse costs (Slater, P.J.B, 1983). Most studies to date have focused on birdsong and habitat structure (Boncoraglio et al., 2007), however, it is quite a novel situation with fish and boat traffic. Sound transmission in different habitats suggest that acoustic signal spanning long-distances are likely to be degraded by a number of environmental factors; human noises are no exception (Hansen, P., 1979). Natural selection will favor calls that are able to span those long distances despite degradation from factors. Masking, or threshold change in signal level from neighboring noise (Pollack I, 1975), describes how boat noises can degrade toadfish calls. We expect these changes to influence a greater survival rate, according to the acoustic adaptation hypothesis.

So far, it is clear that toadfish and other teleost fish are evolving ways in which they can avoid noise completely or alter their behavior to make their boat whistles more apparent to other individuals. However, a lot of information lacks in how, specifically, they are altering their call structure and call frequency behavior across the globe. There is also limited comparison of different species of toadfish and how they are similar or different in regard to the anthropogenic factors influencing them.

In current research, I am examining how boat traffic in Bocas del Toro, Panama, is influencing the call structure and characteristics of the Bocon Toadfish that inhabits many marine seagrass habitats there. Data suggests that toadfish are lowering the frequency and duration of their calls in order to avoid the noise masking as mentioned before. Based on this, there are many implications for evolution that can be studied in the future. In order to create a lower frequency sound, there is likely an associated increase in swim bladder size. In toadfish, they have a swim bladder which is a large pocket of air located in their abdomen; sound is produced through the drumming of the sonic muscle on the swim bladder, causing contraction and expansion at high rates ("How", 2019). Frogs and roadway traffic noise have been extensively studied; results from these studies show males used higher frequencies to avoid traffic masking, and were therefore, significantly smaller in size closer to the road (Hoskin, C.J., and Miriam, W.G., 2010). Similarly, because toadfish potentially lower their frequencies to avoid masking from ship noise, we could speculate individuals with greater swim bladder size, and therefore greater body size, to be present in boating areas.

Future studies could determine if the acoustic adaptation hypothesis holds true here, and describe a novel case of anthropogenic masking in fish. As anthropogenic modification in natural environments continues to increase, species have to adapt quickly in order to survive. Understanding this in toadfish gives insight as to how some communities are changing in response to one human factor; boat traffic and noise. Given the importance of toadfish as health indicators of marine communities these results are important as they indicate how humans are changing their calls and physiology.

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