SOCIAL CONTEXT OF GRAY WHALE *Eschrichtius robustus* SOUND ACTIVITY

A Thesis

by

SARAH MARIE CHARLES

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2011

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

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Committee Members,	Robert H. Benson
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ABSTRACT

Social Context of Gray Whale *Eschrichtius robustus* Sound Activity. (May 2011)
Sarah Marie Charles, B.S., Xavier University
Chair of Advisory Committee: Dr. Bernd G. Würsig

This thesis examines sound production of eastern gray whales (*Eschrichtius robustus*) in the wintering lagoons to determine whether sound use is a function of social context. Proportions of sounds used, parameters of each sound class, and rates of sounds were compared among social contexts. Data revealed the strong possibility of context-specific use for particular sound classes. Additionally, sound parameters and rates of production varied by social context. These results reflect similar variations in gray whale repertoire throughout their range that may be due to changes in social and behavioral contexts.

Gray whale sounds are classified into several classes based on aural and visual characteristics. This study verifies the classification system determined in previous studies, with the exception of class 8, and supports the division of class 1 into subclasses 1a and 1b. Class 1 appeared to be critical during sexual contexts and all highly social contexts, regardless of age and sex class. Although highly recognizable, its parameters exhibited much variation among social contexts; therefore class 1 may communicate graded emotional states in short-range interactions. Other classes of sounds may be utilized for long-distance communication, as startle responses, or “precursors” to the adult repertoire. Frequency-related parameters of all sound classes showed variation among social contexts, but duration demonstrated very little variation. Calf-containing contexts exhibited greatest and most varied frequencies; this is to be expected if gray whale’s sound mechanism is related to body and tracheal length. Variation also may indicate that physical maturity or learning play a role in the repertoire development. The lowest and least varied frequencies were observed in adult contexts. Sound production rates also varied by social context. Active adults produced sounds at high rates during short intervals; mixed/unknown contexts were often silent. Calf-containing contexts produced sounds at intermediate rates and were never silent. The correlations demonstrated here between social context and use of sounds will allow for acoustics to be an indicator of group composition, seasonal movements, and social patterns, thus relieving dependency on difficult visual observation. Additionally, such correlations provide preliminary information for determining sound functions.

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I. INTRODUCTION

In social animals, communication is necessary and can be accomplished by several sensory means (Halliday, 1983). Marine environments dictate the importance of acoustic communication for marine mammals; water does not always allow for significant visibility but does propagate sound well (Tyack, 2000). Additionally, the range and distribution of marine mammals and conspecifics can be great. The social context in which communication occurs may necessitate the use of different kinds of sounds, use of sound types in different proportions, or altering the characteristics of a general sound format (Clark, 1982; Clark, 1983; Ford, 1989; Caldwell *et al.*, 1990; Janik *et al.*, 1994; Oleson *et al.*, 2007).

Studies have shown that eastern gray whales (hereafter referred to as gray whales) vary the proportions of sounds used throughout their range. The "knocking" sound was predominant in both northern feeding grounds (79.5%) and southern calving lagoons (83.5%); on the migratory route it composed only 37.4% of sounds (Dahlheim *et al.*, 1984; Crane and Lashkari, 1996; Ollervides, 2001). Variation in vocalization use may reflect the variations in behaviors that occur geographically and temporally throughout the year.

While the gray whale sound repertoire is well documented, little is known about the functions or behavioral correlations of each sound or the purpose of variations within a class of sound (Dahlheim *et al.*, 1984; Ollervides, 2001). Correlations between social context and use of sounds will allow for acoustics to be an indicator of group composition, seasonal movements, and social patterns. This is important in the study of marine mammals, which are difficult to observe visually. The function of a sound will be elucidated if it can be determined who is producing a sound, when the sound is produced (i.e., behavioral context, annual cycle/seasons), and where (what part of their geographic range) it is produced.

This thesis follows the style Journal of the Acoustical Society of America.

The objective of this study is to determine whether sound use by gray whales is differentiated by social context while the population resides in its wintering lagoons in Baja California Sur, México. This study will examine differences in sound production by mother males, non-parturient females and immature whales who are feeding, courting and mating. This can be tested with three specific research questions 1) How does relative use of sound classes differ by social context? 2) How do acoustic parameters, such as frequency, repetition and duration, differ by social context? and 3) How do rates of sound production differ by social context?

The mysticete, or baleen whale, repertoire includes simple, low frequency moans, complex broadband pulsive sounds and clicks, knocks, and grunts (Thompson *et al.*, 1979; Clark, 1990). A few species use songs that are patterns and sequences of sound units (Payne and McVay, 1971; Winn and Winn, 1978; Clark and Johnson, 1984; Cummings and Holliday, 1987; Würsig and Clark, 1993; Fristrup *et al.*, 2003). Non-vocal sounds such as slaps, blows and breaches may have a communicative function, but it is believed that adventitious sounds such as baleen rattles and flatulence do not (Clark, 1990). Mysticetes share some vocal and communication trends, but each species also has unique characteristics. The repertoire of the migrating bowhead whale (*Balaena mysticetus*) is similar to that of the southern right whale (*Eubalaena australis*); both use simple moans and complex calls, although the bowhead's pulsed sounds have more variations (Clark and Johnson, 1984).

Determining sound function by social context

Classes/types of sounds

The extensive studies on the southern right whale point to a communication system in which particular sounds are consistently used for a particular function. Clark (1983) hypothesized that the function of a sound is best deduced by interpretation of the social context in which it was made and the changes in behavior that accompany it. Small, inactive groups and individuals of northern and southern right whales tended to be silent or make significantly fewer calls than other groups (Clark, 1983; Matthews *et al.*, 2001). Clark's (1983) study revealed that complexity of calls used by tight, active groups varied directly with the complexity of the social context, such as group size, number of males, and sexual activity. Groups of mixed sexes had higher rates of calling. Groups with highest activity levels always produced some kind of sound, and often at significantly higher rates than resting or swimming groups. Discrete frequency modulated up calls were used by resting and traveling whales while highly variable sounds were used by active whales (Clark, 1990). An up call by one whale may be returned with another up call from a whale several miles away; upon joining together, the calling will cease. As a result, Clark (1990) concluded that the discrete up call may be used for long-distance contact and cohesion; traveling groups and individuals used up calls almost exclusively and significantly more than resting or active groups.

Clark (1983) concluded that loud, harsh blow sounds may be produced by disturbed whales. These were produced by resting whales when joined by porpoises, sea lions (*Otaria byronia*) or whales that approached without vocalizing. Harsh blows were also produced by females in sexually active groups and mothers who have been separated from their calves. Individual mother whales also produced growl sounds when a calf was several hundred meters away and when joined by a third whale (Clark, 1983). On these occasions of separation, the calf either quickly returned to the mother or the mother retrieved the calf.

Parameter variations

Variations in acoustic parameters may indicate the sex, age class, size and motivational state of the producer. Moreover, information may be conveyed to receivers by variations in a graded communication system or call type. Mysticetes, most notably humpback whales (*Megaptera novaeangliae*), demonstrate temporal and geographic parameter variations; some changes even indicate cultural transmission (Cerchio *et al.*, 2001). Humpback song also varies in response to environmental circumstances (i.e., in response to Navy SURTASS LFA (Fristrup *et al.*, 2003)). Different oceanic populations of blue whales may have vocalizations distinguished by frequency, duration and repetition interval (Mellinger and Clark, 2003). Amazonian manatee (*Trichechus inungius*) vocalizations showed significant variations in several acoustic variables based on sex and age class (Sousa-Lima *et al.*, 2002). Adult vocalizations had longer duration and narrower range of fundamental frequencies. Females had greater values of mean, maximum and minimum fundamental frequencies, interval duration (between notes), and fundamental range. Males had significantly greater note duration. Moreover, individual recognition within an age class is possible based on these acoustic variables (Sousa-Lima *et al.*, 2002). Bottlenose dolphins (*Tursiops truncates*) also varied signature whistle parameters in relation to context (Janik *et al.*, 1994). Frequency and time domain distinctions were significant between an isolation context and an experimental discrimination task.

Rate of sound production

Rate of sound production is an additional variable that may be influenced by social context. Behavior patterns and group size may affect the whistle rate of bottlenose dolphins (Quick and Janik, 2008). Travelling animals had lower individual whistle rates than socializing or non-polarized (milling) animals, but all rates decreased when groups were larger than 10 animals. Thus, call rates may be an indicator of increased information exchange or means to maintain contact, until an upper limit is approached in which information transfer is less successful. In a study of humpback whale sound production, Silber (1986) found that group rates increase with group size, but not individual rates. Large groups of humpbacks engage in high levels of surface activity, “such as breaching, flipper- and tail-slapping, and under-water bubbling” and likely include aggressive behaviors as males compete (Silber, 1986). It is during these encounters that social sounds may demonstrate aggression or agitation. Similarly, gray whales have been observed to first form pairs and trios; these groups then aggregate to form a large group (Norris *et al.*, 1983). The behaviors of these aggregations include much physical contact, rolling, throwing pectoral fins and swiping flukes. Finally, confirming that these groups have some courting or mating function, there have been observations of whales probing genital areas and extended penises. The similarities between humpback and gray whale social behavior may extend to sound production rates as well.

Characteristics of social context

Caller identity

Caller identity is an important factor of social context and thus also in determining a sound's function. Parks and Tyack (2005) determined which classes of animals produced certain calls in the surface active groups of North Atlantic right whales (*Eubalaena glacialis*). Using simultaneous acoustic and video recording as well as timing of vocalizations and breathing patterns, they determined that females produce scream calls, males produce gunshot calls and up calls, and warbles were attributed to only female calves (Parks and Tyack, 2005). Data also suggest that percentages of call types are associated with group size and composition (Parks and Tyack, 2005).

Group composition

Age and sex composition also define social context of a group and therefore also possibly the vocalization content. In a study of bowhead whales, Richardson *et al.* (1995) found that in areas populated by large subadults and adults without calves, observations included more socializing groups, more vigorous socializing, more sexual activity, and more time spent at the surface. The relative proportions of call types varied during bowhead whale spring migration, possibly in association with changing age/sex composition of migrating whales (Würsig and Clark, 1993). Group size influences complexity of chickadee call (Freeburg and Harvey, 2008). Significant differences are found in the vocal patterns of different sex and age classes of Amazonian manatees (*Trichechus inunguis*) as well (Sousa-Lima *et al.*, 2002). While studying the possible existence of manatee signature calls, Sousa-Lima *et al.* (2002) found evidence of intra-individual variation, which may be an expression of the sender's motivation, the context, or individuality. Possible gender-specific cues in manatee calls could indicate mate attraction or recognition or simply be a reproductive display, as seen in many birds and humpback whales (Halliday, 1983; Clark and Clapham, 2004).

Range

The range at which individuals can communicate and maintain acoustic contact with conspecifics is critical in defining social context and eventually delineating a sound's function. This can be determined by calculating the source level of a sound and the rates at which it will attenuate (Cummings and Holliday, 1987). As large vocal ranges are realized, we may have to reconsider how a social group is defined (Janik, 2000). Range and social group will vary with environmental conditions. Due to ice cover and shallow waters in their Arctic feeding grounds, propagation of bowhead whale sounds was limited (2.5 km–10.7 km) more than whale sounds in temperate, deep water oceans (Payne and Webb, 1971; Cummings and Holliday, 1987).

Products of determining social context and function of sounds

Previous studies have described social contexts in which sounds are used. If correlations between sound use and social context can be established (Ferrer-i-Cancho and McCowan, 2009), acoustics can be an indicator of presence of individuals or populations, movements, and social context. Acoustic monitoring is facilitated by the low frequency and simple frequency-modulated structure of many baleen whale vocalizations that propagate long distances (Cummings and Thompson, 1971b; Clark and Ellison, 2000). The use of acoustics as a survey tool is critical for cetacean studies, where the subjects are visible at the surface for relatively brief periods. Acoustic monitoring is especially important for studying wide-ranging pelagic species where visual surveying and population counts are difficult (Mellinger and Clark, 2003). In combination with visual surveys, acoustic monitoring has revealed new insights to cetacean behavior and ranges (Frankel *et al.*, 1995; Gedamke and Robinson, 2010). Additionally, acoustic monitoring can overcome harsh environments or seasons in which traditional field observations may often be dangerous or impossible (Würsig and Clark, 1993; Raftery and Zeh, 1998; George *et al.*, 2004; Moore *et al.*, 2006). Additionally, acoustic monitoring is often less invasive, requires less effort and financing, and has a greater duration than satellite tagging (Moore *et al.*, 2010). With proper equipment, filtering, and new analyses, acoustic localization and population estimates are improving in accuracy (Raftery and Zeh, 1998; McDonald and Fox, 1999; Clark and Ellison, 2000). Critically endangered North Pacific right whales (*Eubalaena japonica*) had not been sighted in Gulf of Alaska for decades; however, autonomous recorders have recently detected their calls (Moore *et al.*, 2006). Autonomous recorders also detected over-winter calls from bowhead whales in the Beaufort and Chukchi seas, thus providing important information about seasonal migration movements and population size and trends without expensive, dangerous and time-consuming visual surveys (Stafford *et al.*, 2007a).

Thorough knowledge of a species' repertoire will allow for identification of the sound's producer, possibly even its sex, and perhaps its motivational state. Such identification allows for locating, tracking, and describing seasonal movements and distributions. Scientists have accessed the Navy Sound Surveillance System (SOSUS) of fixed hydrophone arrays to localize and track blue whales (*Balaenoptera musculus*) in the North Atlantic. Mellinger and Clark (2003) used the sounds acquired from SOSUS to compare North Atlantic blue whale vocalizations with those of other ocean regions. Although there are shared characteristics, several variations, such as the frequency contours, number of parts in phrases, and rates of frequency modulation, may distinguish geographically separate populations and may also indicate seasonal distributions and movements (Mellinger and Clark, 2003). There is evidence of genetic divergence among fin whale (*Balaenoptera physalus*) populations (Bérubé *et al.*, 1998; Palsboll *et al.*, 2004). Studies of distinguishing acoustic characteristics in these populations are beginning to corroborate the results of genetic studies (Thompson *et al.*, 1992; Clark *et al.*, 2002; Delarue *et al.*, 2009).

Population distribution, behavior or repertoire use may change seasonally. Evidence suggests that the Gulf of California population of fin whales, as well as Pacific and Atlantic ocean stocks, produce 20-Hz vocalizations in higher rates from late summer through early spring, and lower rates in late spring and early summer (Thompson *et al.*, 1992). Minke whales (*Balaenoptera acutorostrata*) also demonstrated seasonal variations in repertoire use. While minke whale pulse trains were detected between February and November, detection rates were low during spring, and peaked in late summer; they were detected in more than 80% of all recordings during August and September (Risch, 2010).

It is increasingly possible to distinguish between populations with differing dialects, structure, sex ratios, and even individual dolphin's signature calls (Winn and Winn, 1978; Winn *et al.*, 1981; Caldwell *et al.*, 1990; Tyack, 2000; Croll *et al.*, 2002; McDonald *et al.*, 2006). The matrilineal group-specific dialects of killer whales (*Orcinus orca*) are well documented (Ford, 1989; Miller and Tyack, 1998). Familiarity with killer whale pods' stereotyped acoustic repertoires will facilitate studies of relationships, social structure, distribution and movement (Ford, 2010). The songs of humpback whales are distinct in separate oceans, each recognizable by its content and patterns; localized dialects may exist within the same oceanic population (Winn *et al.*, 1981; Payne and Guinee, 1983).

The correlation between sex of producer and use of a particular sound is a fundamental step to elucidating a sound's function. Croll *et al.* (2002) used the combination of acoustic localization and molecular techniques to verify that only males produced the 20-Hz vocalization, despite a 1:1 sex ratio in the area, which supports the hypotheses that these vocalizations are produced by males to attract females. Humpback whale songs are produced by lone males (Winn and Winn, 1978; Tyack and Whitehead, 1983; Darling and Bérubé, 2001), and this knowledge has been significant in the development of hypotheses of song function. Among several current hypotheses are those suggesting that songs function as male sexual display for social ordering or attracting females (Tyack, 2000; Darling and Bérubé, 2001).

We can better determine a sound's function when behavior and context are visually correlated with sound production (Boisseau, 2005; Diaz-López and Shirai, 2009; Graham and Noonan, 2010). Behavior and context serve as indirect measurements for meaning (Ferrer-i-Cancho and McCowan, 2009). Context may be defined as the immediate behaviors and states of the animals involved, the identity of the sound producer (sex, age class) and the extent to which it is used (individual or groups, all) (Ferrer-i-Cancho and McCowan, 2009). This accumulation of knowledge regarding the context of a sound enables us to deduce behavior from acoustic analysis. Recent evidence of male humpbacks singing for extended periods in their northern feeding grounds indicates that breeding may be occurring (Clark and Clapham, 2004). Along with aseasonal conceptions, this evidence implies that mating continues during and after spring migration, despite long-held beliefs that it was contained to wintering grounds in the tropics (Clark and Clapham, 2004). Ultimately, temporal, geographic, and social patterns of use will reveal function.

Gray whale natural history

Gray whales exist in the North Pacific as two geographically and genetically distinct populations (LeDuc *et al.*, 2002). Although the eastern (California-Chukchi) population has recovered well from commercial whaling, the western (Korean-Okhotsk) population remains highly depleted (Weller, 2002; Bradford *et al.*, 2008). To date, there are no published acoustic studies on western gray whales.

Eastern gray whales spend the summer months in the Chukotskoe (Chuchki) and Bering Seas (Moore and Ljungblad, 1984; Petrochenko *et al.*, 1991). Gray whales (hereafter referring to eastern gray whales) in their arctic summer grounds are generally solitary or in pairs (Bogoslovskaya *et al.*, 1981; Bogoslovskaya *et al.*, 1982), and their behaviors indicate feeding (Moore and Ljungblad, 1984; Würsig *et al.*, 1986). Socialization and group formation increase in September, possibly the precursor of the mating that likely occurs during southward migration (Würsig *et al.*, 1986). Surprisingly, some animals do not complete the southward migration, as recordings in the Beaufort Sea have detected the presence of gray whales during winter months as well (Stafford *et al.*, 2007a).

Migrating whales often travel individually or in groups of 2 or 3 animals (Reilly *et al.*, 1983; Crane and Lashkari, 1996). There is a distinct segregation by sex, age and reproductive status (Rice and Wolman, 1971). On southward migration, females carrying near-term fetuses are first to migrate, followed by the remainder of adults and lastly, sexually immature whales. Recently impregnated females are the first to begin the northward migration, followed by the remainder of adults and then immature whales; mothers and calves are the last to make the migration.

Eastern gray whales migrate annually to wintering lagoons on the Pacific coast of Baja California in México. In many of the lagoons there is a distinct spatial separation, similar to the segregation observed during migration. Males, non-parturient females, and sexually immature whales are generally observed in the lower lagoons and deeper lagoon entrances, while mothers and their newborn calves remain in the shallower inner estuaries of the lagoons (Norris *et al.*, 1977; Norris *et al.*, 1983; Jones and Swartz, 1984; Pérez-Cortés *et al.*, 2004). In addition to spatial separation, behavioral and social differences are evident. Mothers and their calves remain in discrete pairs for the first few months, and spend much time nursing (Norris *et al.*, 1983; Pérez-Cortés *et al.*, 2004). Late in the wintering season, mother-calf pairs begin to socialize with other pairs, generally lasting several minutes and including much physical interaction (Jones and Swartz, 2002). As single adults leave for the northbound migration, mother-calf pairs move from the upper lagoons to the lower lagoons, now unoccupied by adults (Wisdom, 2000). The infrequent encounters between mother–calf pairs and single whales involve chasing the female, attempting to mate and high-speed swimming (Norris *et al.*, 1983; Jones and Swartz, 1984).

The aggregations of males, non-parturient females, and immature whales at lagoon entrances vary their behavior as a function of the tides (Norris *et al.*, 1983). During slack low or high tide when current velocities are lower, Norris *et al.* (1983) observed irregular diving and courting and mating behaviors of rolling, throwing pectoral fins and flukes, and probing of genital areas. Pairs of whales form until 7 or 8 groups have concentrated within several 100 meters. It is believed that not many conceptions occur during these social aggregations. The majority of conceptions occur in late November and early December, intromission is rarely seen in these aggregations, and sexually immature whales comprise part of these socially and sexually active groups (Rice and Wolman, 1971; Norris *et al.*, 1983; Swartz *et al.*, 2006). Such seemingly functionless behavior may be exploratory or serve other purposes (Norris *et al.*, 1983). When current velocities increase due to tidal changes, social and sexual behaviors diminish (Norris *et al.*, 1983). Diving becomes regular and often oriented into the current. Norris *et al.* (1983) suggest that feeding into high velocity currents could aid in concentrating food.

Few whales are found in the areas between the aggregations of mother-calf pairs and feeding/socializing singles (Norris *et al.*, 1983; Jones and Swartz, 1984). Feeding aggregations may find highest densities of food at lagoon entrances or need deeper water for mobility during social activities.

Gray whale sound repertoire

Gray whales produce simple sounds that may be described as clicks, knocks, grunts, or rumbles, in the frequency range of 20 Hz to 2 kHz (Dahlheim *et al.*, 1984; Crane and Lashkari, 1996). According to Clark (1990), there are no records of gray whale complex calls, described as broadband pulsive sounds with mixtures of amplitude modulation and frequency-modulated fundamentals, or songs, defined as highly patterned sequences of sounds. Sounds are sufficiently distinct to allow categorization, but variations within a category do exist (Dahlheim *et al.*, 1984). Such variations may be a result of individual differences, varying responses due to behavioral context, or conveying additional information.

A numerical classification system (1-6) of gray whale sounds was created based on visual (spectral) and aural comparisons of recordings in Laguna San Ignacio (Dahlheim *et al.*, 1984). This system was extended to other parts of the gray whale's range by Moore and Ljungblad (1984), Crane and Lashkari (1996), and Ollervides (1997, 2001) with new prefixes that indicate location: at northern feeding grounds (N), during migration route (M), and at the southern wintering lagoon of Bahía Magdalena Complex (BMC). Earlier studies of gray whale sounds were opportunistic recordings and sounds were described subjectively using onomatopoetic terms resulting in confusion and inconsistency in the literature (Cummings *et al.*, 1968; Fish *et al.*, 1974).

Additional studies of gray whale sounds in their wintering lagoons have supplemented the vocal repertoire recorded by Dahlheim *et al.* (1984). In addition to recording sounds that corresponded to Dahlheim's original 6 classes, S1-S6, Ollervides (2001) recorded sounds in Bahía Magdalena Complex (BMC) that he believed required new categories, and thus classified them as BMC 7-11. However, Ollervides (2001) acknowledged that these new categories may be caused by differences in recording, local environment, or subjectivity in classification. A baleen rattle similar to BMC 11 had also been described by Petrochenko *et al.* (1991) when recording in the arctic. Hereafter, gray whale sounds will simply be referred to as class 1-11.

Class 1 sounds are series of knocks or bongs with frequency modulation within the series. Wisdom (Wisdom, 2000) determined statistically distinct subclasses within class 1, termed 1a and 1b. Norris *et al.* (1977) also observed clicks with parameters distinct from those observed by Fish *et al.* (1974); this likely foreshadowed the distinction between subclasses 1a and 1b. According to Wisdom (2000) subclass 1b has fewer knocks within a series, longer individual knock duration, and greater inter-pulse interval. Class 2 is described as a low frequency upsweep (Dahlheim *et al.*, 1984; Ollervides, 2001). Class 3 is an amplitude-modulated, low frequency moan (Dahlheim *et al.*, 1984; Ollervides, 2001). Class 4 consists of pulse modulated, often “grunt-like” series (Ollervides, 2001). Class 5 sounds are distinct as large amounts of air released underwater, or bubble blasts, and class 6 sounds are longer trailing subsurface exhalations, occasionally with a sonorous quality (Dahlheim *et al.*, 1984; Ollervides, 2001). Classes 5 and 6 are likely the only sounds produced by physical processes in the elements surrounding the whale (Crane and Lashkari, 1996). Class 7 sounds are highly pulsive or complex tonal growls (Ollervides, 2001). Class 8 are described as “ugg” sounds, or short knocks (Ollervides, 2001). Class 9 sounds are described as complex roars (Ollervides, 2001). Class 10 is also grunt-like, but additionally described as similar to a creaking door and has broader bandwidth than class 4 (Ollervides, 2001). Class 11 is described as a “rattle,” also with large bandwidth. This sound is associated with skim feeding whales, and resembled the sound of fingers running down the teeth of a comb as water and krill strain past the baleen (Ollervides, 2001).

Because several classes are likely produced by non-vocal organs (i.e., baleen rattles), physical processes in the water (i.e., bubble blasts), or interactions between the whale’s body and water (e.g., fin or fluke slapping), the term *sound* is used rather than *vocalization*. Furthermore, the use of *vocalization* or even *signal* would indicate assumption of communication purposes. At this time, it is not certain that all classes of sounds actually have communicative functions. Behaviors have not been well correlated with most call types. Only classes 5 and 6 have been correlated with particular behaviors (bubble blasts and subsurface exhalations, respectively); however, even their function remains unclear. However, Dahlheim *et al.* (1984) observed increased sound production in circumstances of increased activity, such as higher concentration of whales, singles pursuing mother-calf pairs, presence of dolphins, increased non-biological noise, and when a whale was on intersecting paths with either another whale or boat.

From several brief studies in the northern feeding grounds, it appears that gray whales produce sounds, but use a less varied repertoire than has been recorded in the southern wintering lagoons. Moore and Ljunblad (1984) determined that the repertoire consisted of classes 1, 3, and 4, and Dahlheim (1987) recorded four types of sounds: classes 1, 3, 4, and 6. While it was previously believed that all gray whales migrated southward from the Alaskan Arctic waters, gray whale knocks have recently been detected on a weekly basis throughout winter months (Stafford *et al.*, 2007b).

In an early study on the migration route, just off San Diego's coast, Cummings *et al.* (1968) detected four classes of gray whale sounds: knocks, moans, bubble blasts and surface exhalations. More recently, Crane and Lashkari (1996) found that migrating gray whales produced fewer sounds in deep water than in shallow water, but in general produced sounds more frequently than previously believed. Recorded sounds corresponded to four of the categories established by Dahlheim *et al.* (1984). The most prevalent sound was class 3 (46.6%), but it was less than half of all sounds produced (Crane and Lashkari, 1996). During limited recordings in Washington State of four juvenile gray whales, some of which appeared to be feeding, there were no sounds recorded that could be attributed to the whales (Dahlheim, 1987).

Both studies in southern wintering lagoons found that class 1 sounds were used more often (79.5%, (Dahlheim *et al.*, 1984); 83.5%, (Ollervides, 2001)) than Crane and

Lashkari (1996) recorded on the migration route, where class 1 was 37.4% of the entire repertoire. Increased use of variable sound classes may indicate increased social activity; Clark (1982, 1983) observed that less active southern right whales produce mainly simple sounds while a whale in an active group may produce rapid sequences of more complex calls. The greater use of the variable and graded class 1 sound in the southern lagoons may be a result of the increased social activity and smaller inter-individual distance there (Dahlheim *et al.*, 1984; Crane and Lashkari, 1996; Ollervides, 2001). The greater use of class 1 sounds in social situations, in addition to variations in repetition, may indicate that class 1 sounds are signature vocalizations (Ollervides, 2001). Class 3 sound was proportionally much more prevalent during migration than in the southern lagoons. These simple, low frequency tonal sounds may be more important on the migration route where distances between individuals will be greater than in the lagoons (Richardson *et al.*, 1995; Crane and Lashkari, 1996).

The social contexts throughout the gray whale's range are distinct, depending on location and season. Additionally, there are social distinctions within the wintering lagoons. In this study, I hypothesize that variations in repertoire use throughout the gray whale's range (i.e., northern feeding grounds, migration route, southern wintering grounds) will be reflected in the varying repertoire use among distinct social contexts within the wintering lagoons. It may be likely that differences in sound use at various locations are due to the distinct social contexts.

II. METHODS

Bahía Magdalena Complex (BMC) in Baja California Sur, México, is one of several lagoons on the west coast of Baja California that is populated by gray whales from January to April (Figure 1). Bahía Magdalena Complex is the southernmost of these lagoons, only 275 kilometers north of Cabo San Lucas. The main central region is 31 km long and 22 km wide and mean depth is 30 m (Norris *et al.*, 1983; Ollervides, 2001). Most of the BMC is situated between 24^{o}20'N - 25^{o}20'N, and 111^{o}30' W – 112^{o}10'W (Amante and Eakins, 2009). Several recording sessions were conducted in the northern portion of the bay, an estuary referred to as Santo Domingo Channel; these sessions occurred near 25^{o}03'N, 112^{o}09'W. Mothers and newborn calves concentrate in the narrow, shallow estuary of Santo Domingo Channel (Pérez-Cortés *et al.*, 2004). Males, non-parturient females and immature whales aggregate near the mouth of the complex, a deeper 6 km wide entrance known as Boca La Entrada (BLE) (Norris *et al.*, 1983). Portions of the large, central region are locally known as El Bajo, "the shallows." This region was used by both adults and mother/calf pairs. This study did not include the southern portion of BMC, Bahía Almejas, due to distance from launch site and time restrictions.

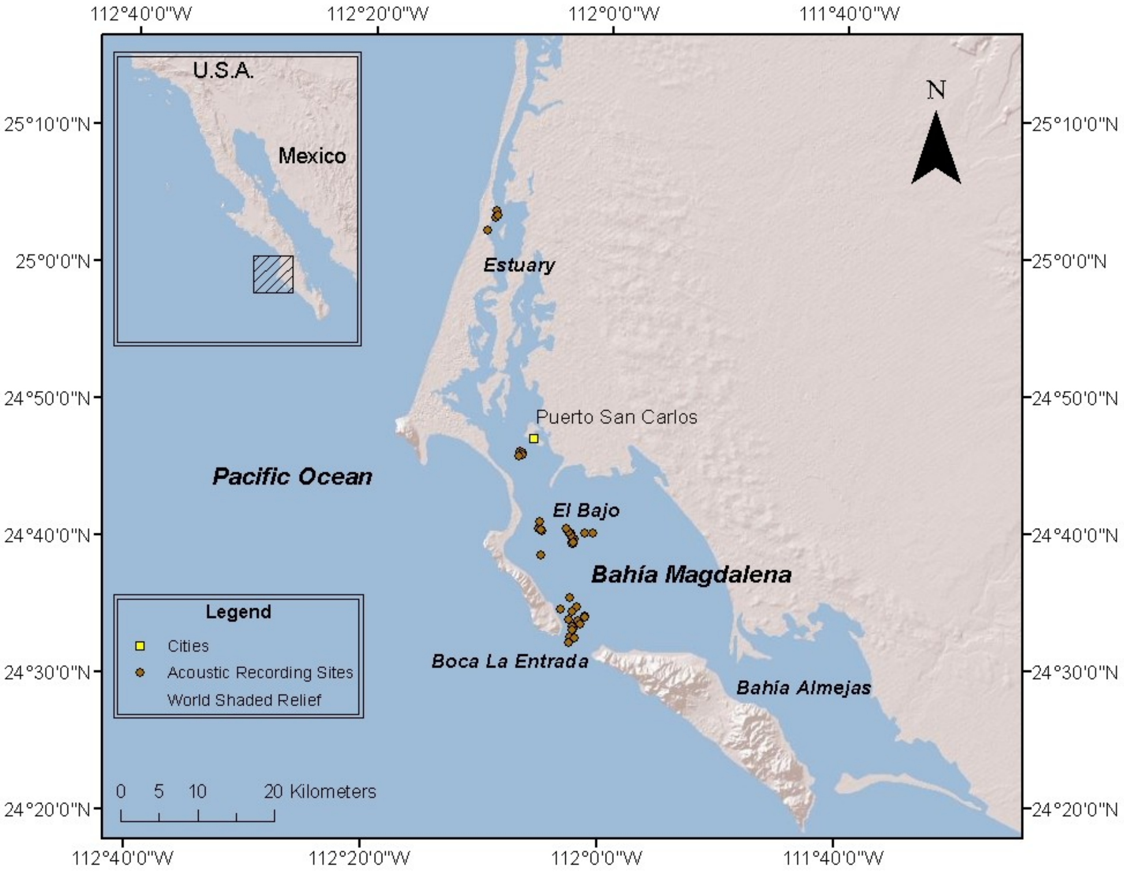

Figure 1. Map of study area of Bahía Magdalena Complex in Baja California Sur, México and sites of gray whale recording sessions in 2006 and 2007.

Simultaneous acoustic recording and behavior observations were acquired during two study periods between February – April, 2006 and 2007. Due to the concentration of whales in relatively small, well-known and distinct areas, recording sessions were opportunistic, as a whale group was encountered. Boat engine was turned off at a minimum distance of 50 m from whales. Sessions were at least 15 minutes when possible; due to whale movement, some sessions were slightly shorter. Concurrent with acoustic recording, one minute summaries of visual observations included: number and age class of whales, behavioral states (resting, traveling, socializing), behavioral events (flipper swish, fluke up dive, etc), and distance. Whales beyond "8 whale lengths" or approximately 100 m (8 x 13 m = 104 m) were observed as well as possible, but were noted as "out of range." At this distance, it was likely that sounds were recorded (Norris *et al.*, 1977), but visual observations (number and age class of whales, behavior states and events) may be lacking in detail or accuracy. Although determining caller identity would provide more information about a sound's function, this requires extensive effort and knowledge, both in the field and in analysis. Due to these challenges, it was not an objective of this study to attempt to identify individual sound producers. Therefore, social context is the best "substitute" or indirect measurement of the circumstances in which sounds are produced.

Observation platform was a 7 m fiberglass vessel with a 75-horsepower outboard engine, locally referred to as a "panga." The recording system consisted of a Reson TC4033-10M hydrophone, Reson Bandpass Filter and Pre-Amplifier VP2000 and Marantz PMD-670 digital recorder. Although "usable frequency range" was 1kHz to 140kHz, the Reson hydrophone had a receiving sensitivity of -203dB $\pm$ 2dB re 1V/uPa at 250Hz 21.69^{o} C. Recording occurred while boat was stationary, at 48 kHz sampling and hydrophone depth between 5 m and 10 m.

Behavior analysis

Whale encounters were grouped into three social contexts: calf present, adults, and unknown/mixed. Social context was assigned to an entire encounter, hereafter referred to as session, based on the types of whales and behaviors observed in a majority (60%) of minutes in the session. This assignment is conservative, as Quick and Janik (2008) assigned group behavior when 50% of animals were engaged in a particular behavior. Calf-containing groups were determined solely on the presence of at least one calf, as determined by size (4.5 – 6 m). Adults were recognized primarily by body length of 13 – 14 m (Jones and Swartz, 2002). Adults were observed in social/sexual aggregations which included highly active behaviors (rolling, fluke and flipper swishing) and in other behaviors (singles, groups traveling, resting). Unknown (out of range, could not identify as calf or adult, could not determine behaviors at distance) and any session in which there was no majority of social context was assigned as unknown/mixed. All minutes recorded, even those in which whales were "out of range," must be considered, as sounds were still detected; such minutes were also considered unknown.

Acoustic analysis

Whale sounds were detected by combination of aural and spectral review in Adobe Audition (Adobe Systems Incorporated, © 2003) which handled large recording files well and facilitated the marking and identifying of possible sounds. Spectrograms were analyzed with Hamming windows, a resolution of 1040 bands, and a window width of 60%. Spectrograms were viewed in 5 – 10 second increments and with a vertical axis of 0 – 2000 Hertz. The recordings were stereo and both channels were viewed simultaneously. Using aural quality and spectral features, sounds were then classified according to the established system in Ollervides (2001). Additionally, Wisdom (2000) further distinguished between subclasses 1a and 1b.

The classifiable sounds were then isolated into individual files and opened in Raven 1.2 software (Charif *et al.*, 2004). Raven provided the unique opportunity to measure several parameters and then copy into Microsoft Excel for further analysis. Because of the small sample size (n=432 sounds) and large number of independent variables (11 or 12 sound classes), sound classes were also collapsed into three simplified types: pulsed, tonal, and complex (Diaz-López and Shirai, 2009; VanOpzeeland *et al.*, 2009). This technique of simplifying categories based on structure may also have the effect of eliminating discrepancies due to human subjectivity and errors in judgment. Complex types include unique sounds that are a mixture of amplitude and frequency modulation or of a "hybrid" nature, i.e., tonal segues into pulse. However, complex type as defined here for gray whales is only relative to their repertoire and should not be considered equivalent to those complex calls as produced by bowhead, humpback and right whales (Clark, 1990). Although some classes were regularly re-classified into the same type (e.g., type 1 was always pulsed), some varied depending on the individual sound (e.g., although most class 3 sounds were tonal, some were complex).

In addition to classifying sounds, several parameters were measured in Raven 1.2 software (Charif *et al.,* 2004). The following five parameters were measured for sounds of all classes: low frequency (the lower boundary; minimum frequency of a sound), high frequency (the highest boundary; greatest frequency of a sound), maximum frequency (frequency at which greatest intensity occurred), bandwidth (delta frequency; frequency range), and duration. Because of the pulsive nature of class 1 sounds (knocks and croaks), the following parameters were also measured: number of pulses, individual pulse duration, pulse rate (pulses/second) individual pulse low, high and maximum frequencies; bandwidth and inter-pulse interval (Dahlheim *et al.*, 1984; Wisdom, 2000; Ollervides, 2001).

Statistical analysis

Data were log-transformed or square-root transformed (maximum frequency and number of pulses), but most residuals had values of $p < 0.010$ on the Kolmogorov-Smirnov goodness-of-fit test. However, sample size was relatively large and the log-transformed residual curves approximated normal distribution curves. Therefore, according to the Central Limit Theorem, modest deviations from normality in the residuals should not affect the validity of the models.

In order to statistically confirm significant parameter differences by class, linear regression tested for significant differences among classes. The purpose of this test was to validate the current classification system and highlight important acoustic features of each class. Likewise, the use of linear regression models of class 1 subclasses tested the validity of this additional classification level.

The relative use of each kind of sound by different social contexts was tested with logistic regression in SAS 9.2 software (SAS Institute Inc). Models were created with three social contexts (all adults, calf-containing, unknown/mixed). Additionally, models were created first with sounds classified in the 11 categories described by Ollervides (Ollervides, 2001). Secondly, models were analyzed according to the simplified “types” of pulsed, tonal, and complex sounds. Because sounds within one recording session were not independent, the model specified each session as a “cluster.”

To test variations in parameters, linear regression in SAS 9.2 (SAS Institute Inc.) software was used. Models were created with three social contexts (all adults, calf-containing, unknown/mixed). Models were created first with sounds classified in the 11 categories described by Ollervides (Ollervides, 2001). Secondly, models were analyzed according to the simplified "types" of pulse, tonal, and complex sounds. Because sounds within one recording session are not independent, the model specified each session as a "cluster."

Sound production rates were calculated and linear regression was conducted to determine if rates of sound production are dependent on social context. Calculations assessed individual rate (sounds/minute/whale) as well as group rate (sounds/minute). The former calculation assumes all whales contribute equally, which is unlikely. However, this will still be valuable when analyzing groups as a unit, providing a standardized quantity of vocalizations in each social context while incorporating whale density.

Some class 1 sounds were not readily sorted into subclasses 1a or 1b. A nearest-neighbor (k=15) non-parametric discriminant analysis was utilized. This supervised classification technique discriminated those not classified by initial review, using the originally classified 1a and 1b as the training set. This analysis also confirmed or re-classified original 1a and 1b. Because discriminant analysis classified based upon both entire series (e.g., entire duration) and individual pulse (e.g., individual pulse duration) parameters, there were cases in which some pulses in a series were classified as 1a and others classified as 1b (i.e., there was not complete agreement of pulses within a sound). If there was a majority, and this majority agreed with original classification, new classification was confirmed. Occurrences in which there was no majority (50%/50%) were decided by original classification and aural review. Finally, all classifiable sounds were subjected to linear regression to test parameter differences between 1a and 1b. Parameters modeled included: high frequency, low frequency, maximum frequency, bandwidth (delta frequency), duration, number of pulses in a series, and pulse rate for each entire vocalization, as well as similar variables for each individual pulse (IP) within a series: IP high frequency, IP low frequency, IP maximum frequency, IP bandwidth (delta frequency) and IP duration. Most variables were log transformed except maximum frequency, IP maximum frequency, and number of pulses, which were square root transformed. Histogram curves of residuals were approximately normal.

III. RESULTS

A total of 36 usable recording sessions were collected over 15 days during the two study periods. Total usable recording time was 10:14 hr:min with an mean 16:56 min:sec in each session. Recording time was not equal across social contexts: 232.5 minutes were recorded in presence of adults, 218.5 minutes in mixed/unknown groups and 163 minutes in presence of calf-containing groups. From these recordings, 432 gray whale sounds were detected and classified. Representative spectrograms were produced in Raven (Charif *et al.*, 2004) with Hamming windows, a resolution of 1040 samples, a 3dB filter bandwidth of 60 Hz, time grid overlap of 60%, and generally in segments of 2 – 4 seconds.

Classes of sounds and their parameters

Descriptive statistics provide the general characteristics of the gray whale repertoire (Table 1, Table 2). The sounds were very brief; most averaged less than 2.0 seconds. These sounds were produced in a very low frequency range; the highest frequency mean for any class was 2409.59 Hz (class 10), and the greatest maximum frequency was 445.30 (class 11).

Table 1. Descriptive parameter medians (± IQR) of gray whale sound classes recorded in Bahía Magdalena Complex, Baja California Sur, México, 2006 and 2007.

Class	n=	Relative %	Low Frequency (Hz)	High Frequency (Hz)	Maximum Frequency (Hz)	Bandwidth (Hz)	Duration (sec)	# Pulses	Pulse Rate
1	251	58.1	61.5	1330.0	351.6	1257.0	0.88	4.0	4.7
			(38.1, 89.8)	(1068.5, 1683.6)	(140.6, 492.2)	(954.0, 1621.9)	(0.50, 1.63)	(3.0, 7.0)	(3.9, 6.0)
1a*	*88*	*20.37*	65.2	1084.5**	375.0	1007.1**	0.78	4.5	5.3**
			(39.8, 87.3)	(864.5, 1372.9)	(234.4, 527.4)	(787.7, 1304.7)	(0.51, 1.37)	(3.0, 7.0)	(4.4, 6.5)
1b*	*163*	*37.96*	57.5	1442.3**	328.1	1391.8**	0.95	4.0	4.5**
			(34.1, 94.4)	(1187.2, 1817.5)	(117.2, 468.8)	(1080.1, 1752.4)	(0.47, 1.72)	(2.0, 7.0)	(3.8, 5.4)
2	26	6.02	45.9	256.9	93.8	208.6	0.94		
			(30.0, 58.7)	(218.9, 316.6)	(70.3, 140.6)	(183.3, 284.0)	(0.44, 1.31)		
3	40	9.26	55.5	207.5	105.5	150.9	1.07		
			(39.7, 85.2)	(175.7, 296.2)	(70.3, 164.1)	(122.5, 214.3)	(0.77, 1.32)		
4	60	13.89	63.2	561.8	187.5	477.2	0.68		
			(40.2, 89.8)	(325.7, 850.1)	(105.5, 281.2)	(261.9, 719.7)	(0.44, 0.97)		
5	17	3.94	70.1	410.0	187.5	371.0	1.34		
			(45.9, 90.0)	(323.6, 594.9)	(140.6, 257.8)	(300, 493.9)	(0.75, 2.27)		
6	11	2.55	64.7	903.5	257.8	811.9	3.01		
			(31.4, 91.7)	(692.5, 1013.5)	(175.8, 351.6)	(546.7, 982.1)	(1.59, 4.30)		
7	14	3.4	39.9	206.9	76.2	171.6	1.28		
			(32.0, 55.4)	(159.7, 283.7)	(70.3, 117.2)	(125.5, 228.3)	(0.97, 1.59)		
8	0	0							
9	5	1.16	66.0	554.5	164.1	488.5	1.08		
			(27.7, 74.4)	(506.2, 767.3)	(140.6, 316.4)	(431.8, 680.6)	(0.62, 1.53)		
10	6	1.39	90.3	2361.1	246.1	2230.2	0.53		
			(63.5, 112.2)	(1784.4, 2769.8)	(140.6, 539.1)	(1784.4, 2706.3)	(0.27, 0.73)		
11	2	0.46	288.0	1477.2	445.3	1189.3	0.91		
			(127, 449)	(1254, 1700.4)	(281.2, 609.4)	(1127, 1251.5)	(0.46, 1.35)		
Total	432								

**Not included in total*

***Indicates statistically significant difference at p<0.05(linear regression)*

Table 2. Individual pulse (IP) descriptive parameter medians (± IQR) for class 1 and its subclasses recorded in Bahía Magdalena Complex, Baja California Sur, México, 2006 and 2007.

Class	**n=**	**IP Low Frequency (Hz)**	**IP High Frequency (Hz)**	**IP Maximum Frequency (Hz)**	**IP Bandwidth (Hz)**	**IP Duration (sec)**	**Inter-pulse Interval (sec)**
1	1240	81.1	986.3	328.1	822.7	0.082	0.15[a]
		(55.3, 174.3)	(681.35, 1268.1)	(140.6, 492.2)	(541.7, 1151.8)	(0.063, 0.101)	(0.103, 0.217)
1a	453	87.3	768.8**	328.1	628.6**	0.082	0.12**[b]
		(56.1, 162.7)	(527.8, 1038.8)	(164.1, 468.8)	(392.8, 886.7)	(0.062, 0.102)	(0.075, 0.177)
1b	787	78.6	1091.2**	328.1	948.4**	0.082	0.168**[c]
		(50.5, 180.7)	(841.8, 1366.7)	(140.6, 515.6)	(666.7, 1279.5)	(0.065, 0.101)	(0.122, 0.234)

***Indicates statistically significant difference at $p<0.05$(linear regression)*

[a]: n = 989 intervals

[b]: n = 362 intervals

[c]: n = 627 intervals

Class 1 may be described as a series of pulses, knocks or bongs with frequency modulation among pulses. Class 1 had a very high mean high frequency (x= 1417.26 Hz), as well as a high maximum frequency (x=354.69 Hz) and wide bandwidth (x=1335.60 Hz). Subclass 1a (Figure 2) had shorter duration (entire sound) and smaller inter-pulse interval than 1b (Figure 3). Subclass 1b had higher frequencies and larger inter-pulse interval than 1a.

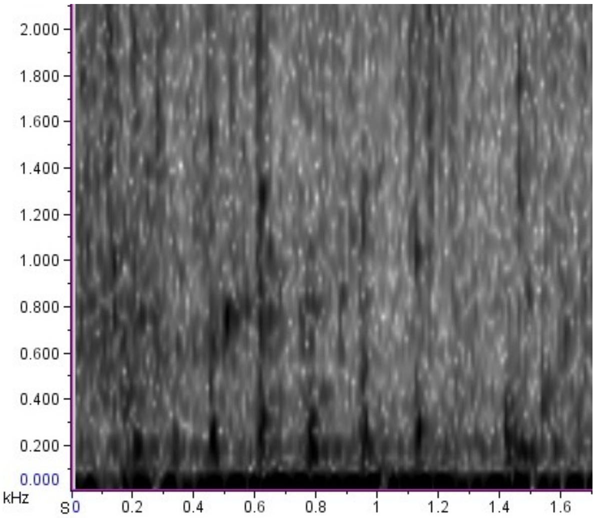

Figure 2. Spectrogram of gray whale sound class 1a.

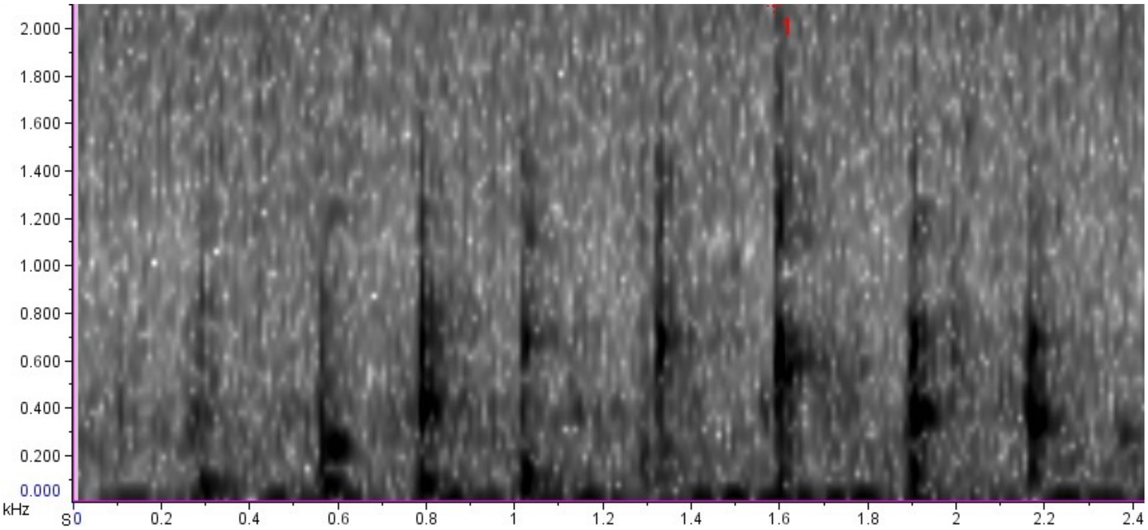

Figure 3. Spectrogram of gray whale sound class 1b.

Class 2 may be described as a frequency modulated upsweep (Figure 4). Class 2, although not the lowest of all sounds, had the second lowest mean high frequency (x=284.08 Hz) and second smallest mean bandwidth (x=232.18 Hz). Only class 3 had lower mean high frequency and smaller mean bandwidth.

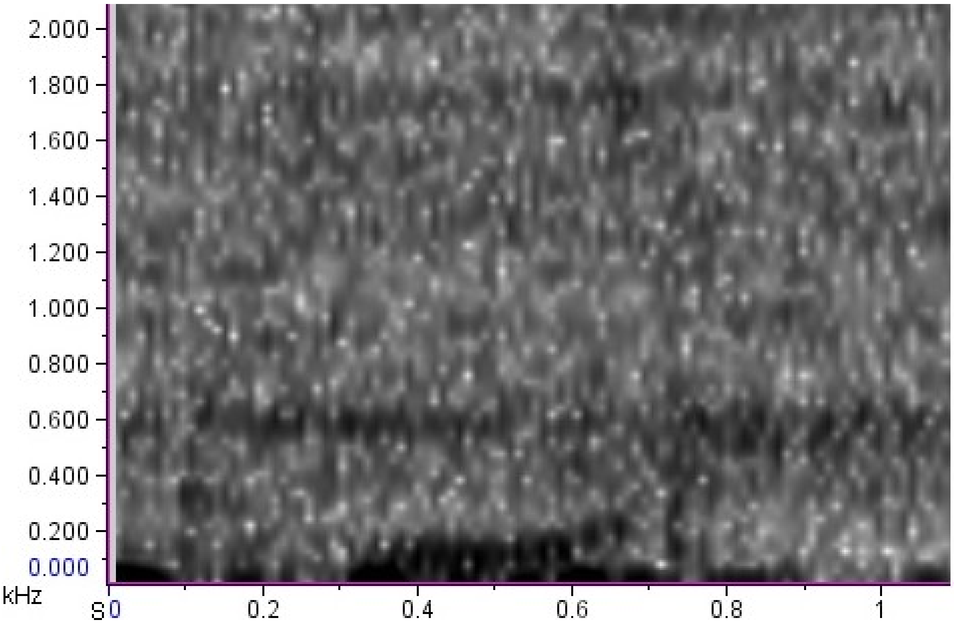

Figure 4. Spectrogram of gray whale sound class 2.

Class 3 was characterized as a low-frequency moan, generally with little frequency modulation (Figure 5). Class 3 had the lowest high frequency (x=269.67 Hz) as well as the smallest bandwidth (x=177.30 Hz).

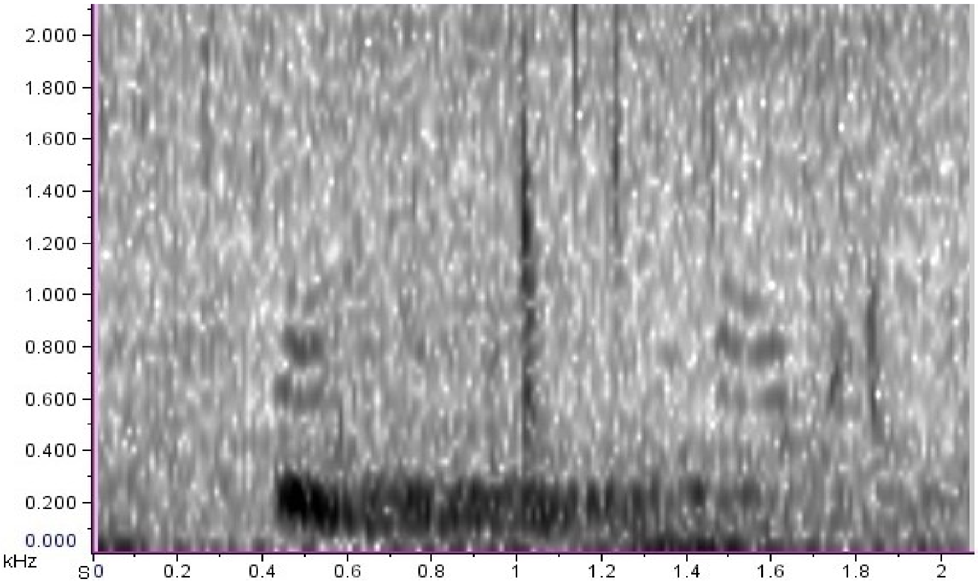

Figure 5. Spectrogram of gray whale sound class 3.

Class 4 was characterized as a series of frequency modulated grunts or pulses (Figure 6). Their rate is often rapid and may be the primary feature distinguishing class 4 from class 1. As a result of this high pulse rate, they aurally may be referred to as rumbles or zipper-like. Class 4 had the second shortest mean duration; only class 10 had shorter mean duration. Other mean parameters were unremarkable, showing no extremes.

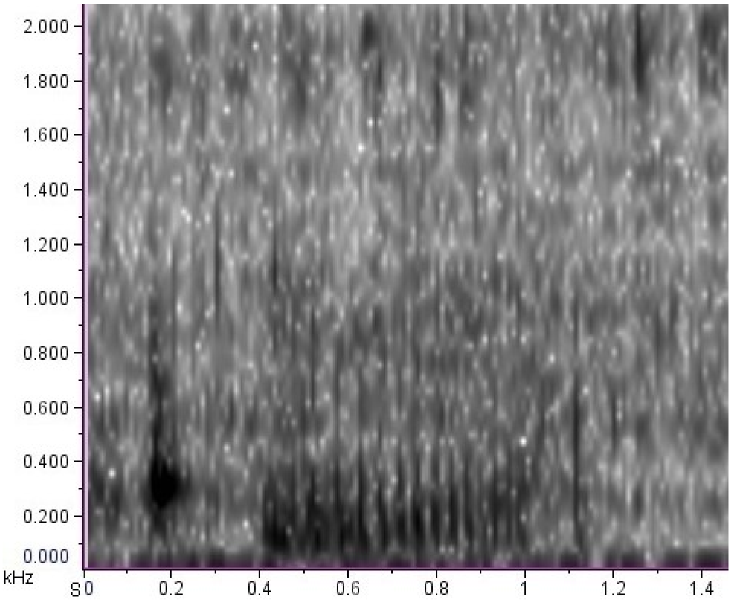

Figure 6. Spectrogram of class 4.

Class 5 has been described as a "bubble blast" for both its physical production and sound quality (Dahlheim *et al.*, 1984) (Figure 7). It may be aurally described as rumbling or gurgling, as would be expected when large amounts of air are released under water. Class 5 averaged long durations.

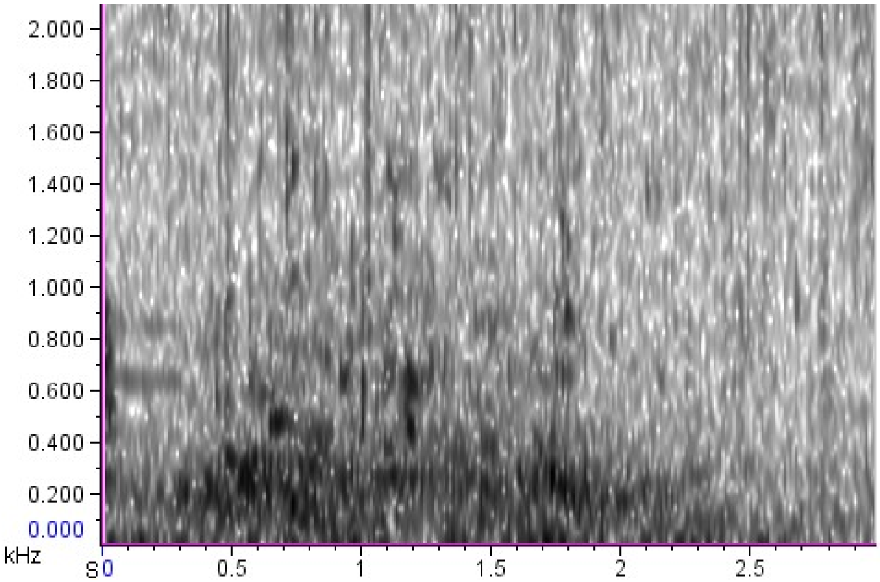

Figure 7. Spectrogram of gray whale sound class 5.

Class 6 may be aurally described as air exhaled at subsurface in a "sonorous" manner, perhaps produced by flatulence or a trail of bubbles (Dahlheim *et al.*, 1984; Ollervides, 2001) (Figure 8). Intensity of sound tends to "trail off" or decrease near end of sound. Class 6 exhibited the longest duration (x=3.29 sec) as well as a fairly large bandwidth (x=796.81 Hz). This mean duration, twice as long as any other sound class, was a parameter distinguishing class 6 from class 5. Additionally, although the mean low frequency was only slightly higher than that of class 5, the high frequency was much higher, and thus bandwidth was also greater.

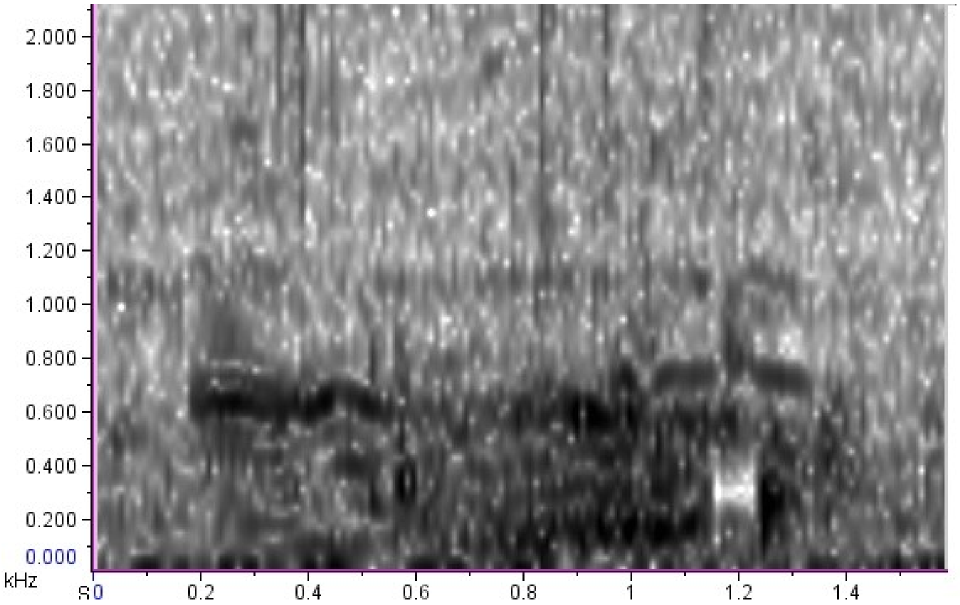

Figure 8. Spectrogram of gray whale sound class 6.

Class 7 may be aurally described as growls or roars that are almost always highly pulsive (Figure 9). Class 7 was notable for both the lowest mean low frequency (x=41.58 Hz) and the lowest mean maximum frequency (x=96.26 Hz). Only classes 2 and 3 had lower mean high frequencies and narrower bandwidths.

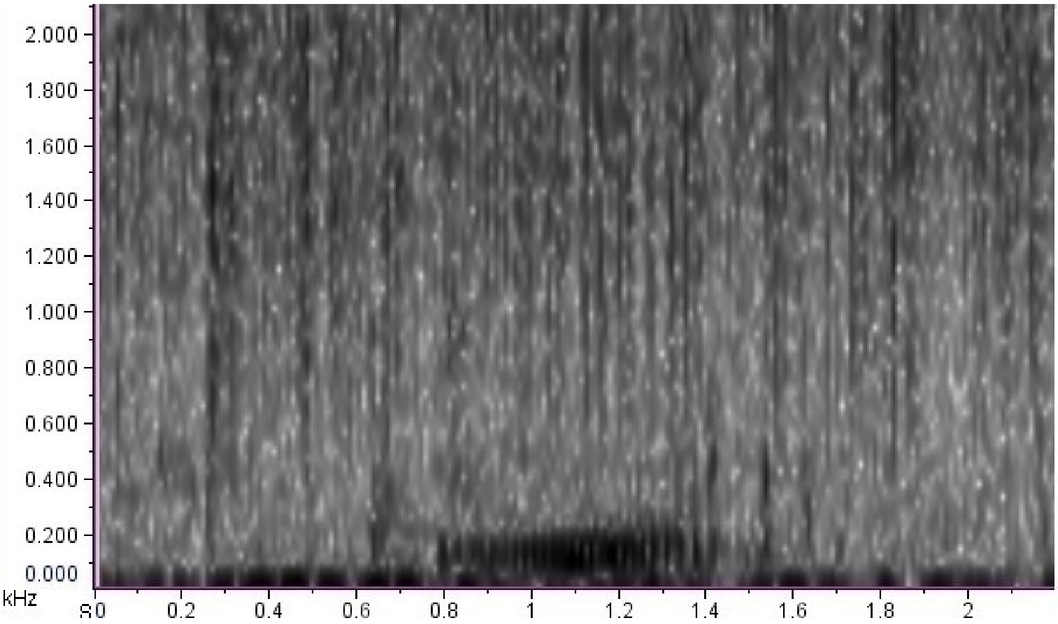

Figure 9. Spectrogram of gray whale sound class 7.

There were no occurrences of class 8 recorded in this study.

Class 9 resembled class 2, but may be differentiated aurally by its more complex and often pulsive quality "roar" (Figure 10). Although spectrally similar to class 2, four of five class 9 mean parameters (duration, high frequency, maximum frequency and bandwidth) were at least twice that of class 2. However, the actual differences are not likely this great, as class 9 contained one extreme outlier.

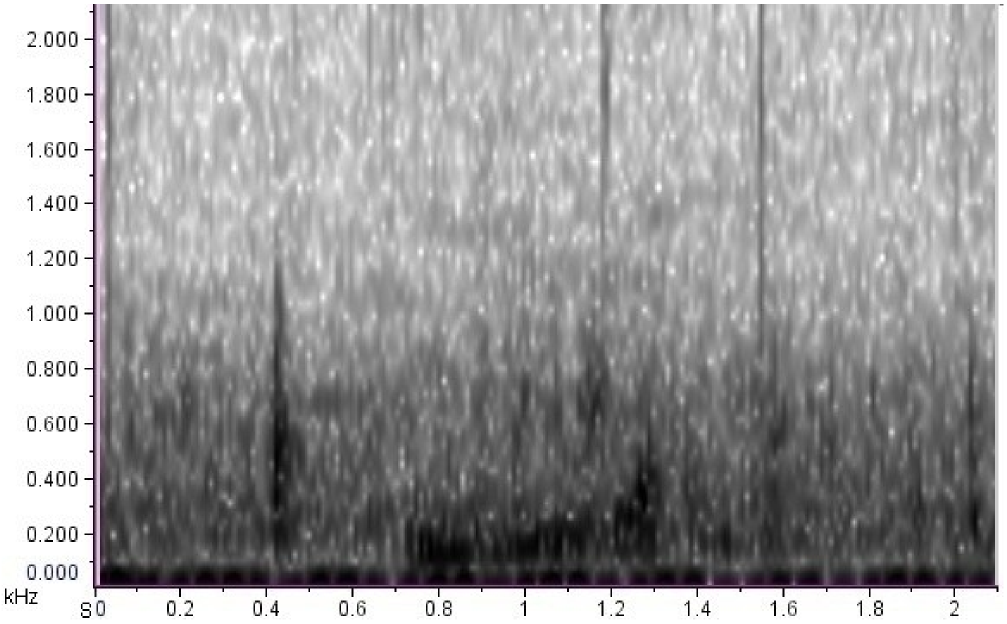

Figure 10. Spectrogram of gray whale sound class 9.

Class 10 was a grunt-like, highly pulsive, frequency modulated sound with an aural quality similar to a zipper (Figure 11). Class 10 was unique with the highest mean high frequency (x=2409.50 Hz), largest bandwidth (x=2327.28 Hz) and shortest mean duration (0.52 sec).

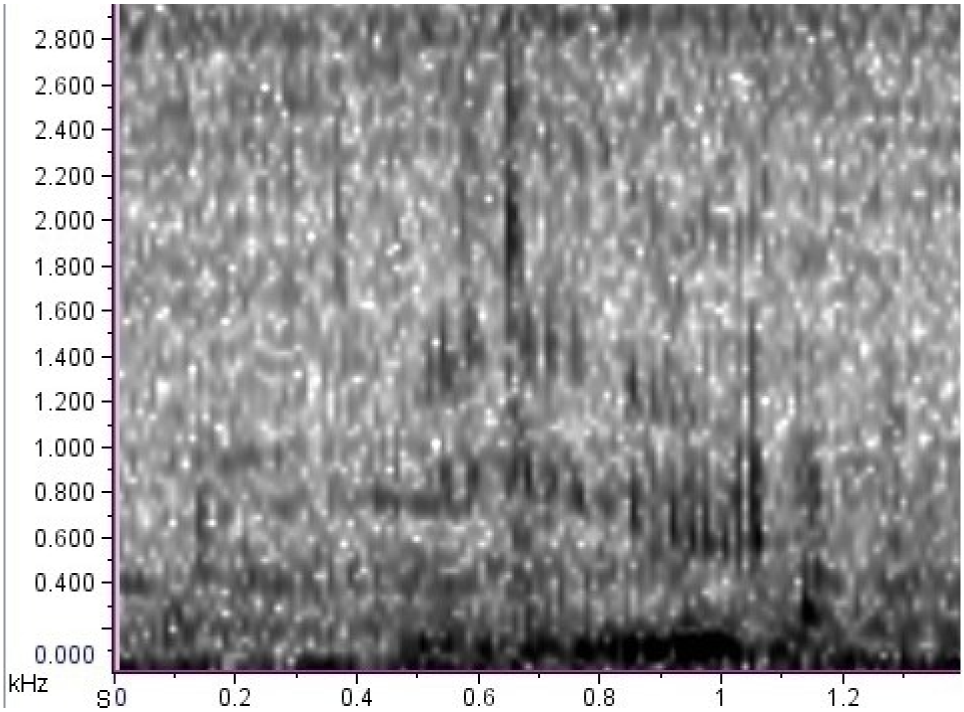

Figure 11. Spectrogram of gray whale sound class 10.

Class 11 was a highly pulsive, frequency modulated sound; it may be aurally described as similar to the sound of running fingers along the teeth of a comb (Figure 12). Class 11 exhibited the highest mean low frequency (x=288.00 Hz) and the highest maximum frequency (x=445.30 Hz).

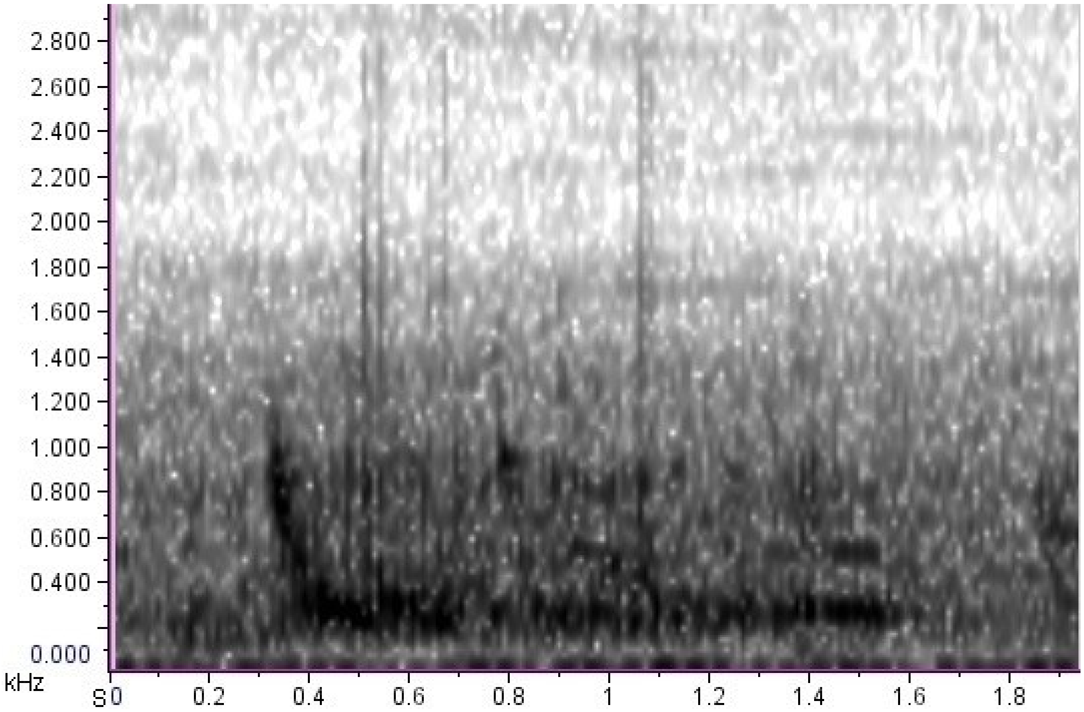

Figure 12. Spectrogram of gray whale sound class 11.

Parameter variations by class

Linear regression of parameters tested for significant differences among classes 1 - 11. All five parameters measured for sounds revealed significant inter-class variation. Class 11 had the greatest mean low frequency; class 7 had the lowest mean low frequency (F=20.27, p<0.0001) (Figure 13). Class 10 had the greatest mean high frequency; class 3 had the lowest mean high frequency (F=122.36, p<0.0001) (Figure

14). Class 11 had greatest mean maximum frequency; classes 7 and 2 had lowest mean maximum frequency (F=35.73, p<0.0001) (Figure 15). Class 10 had greatest mean bandwidth; class 7 had smallest mean bandwidth (F=129.56, p<0.0001) (Figure 16). Class 6 had greatest mean duration; class 10 had shortest mean duration (F=42.47, p<0.0001) (Figure 17).

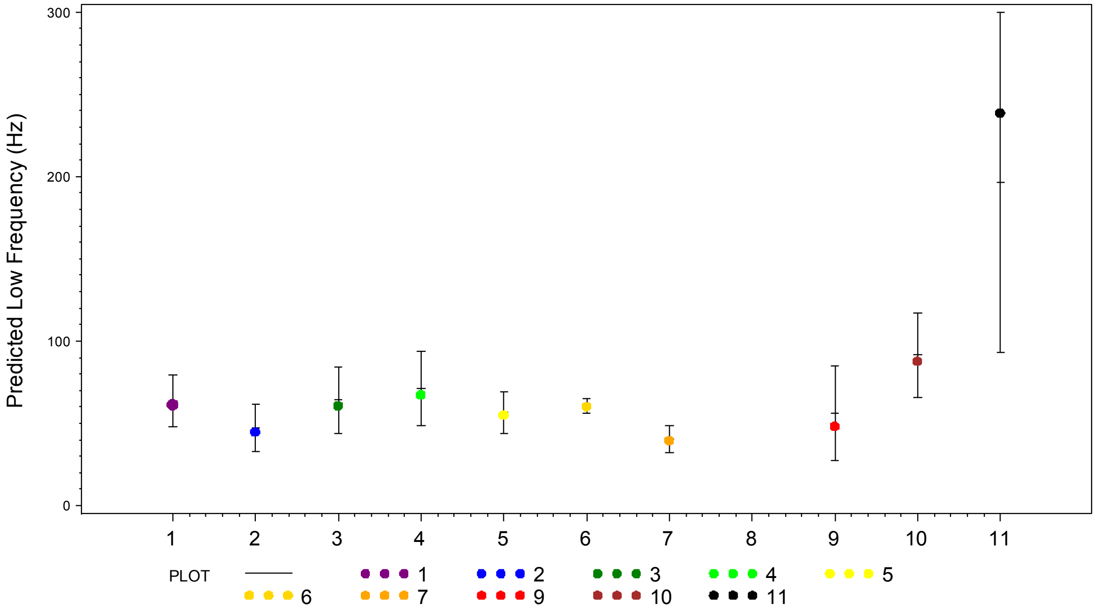

Figure 13. Plot of predicted low frequency by class. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

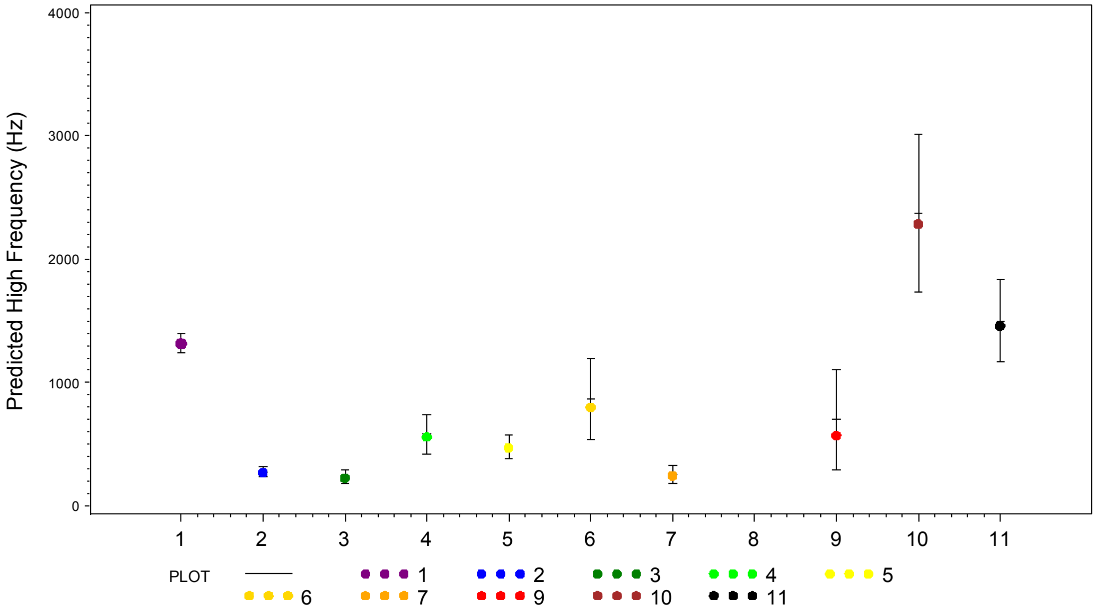

Figure 14. Plot of predicted high frequency by class. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

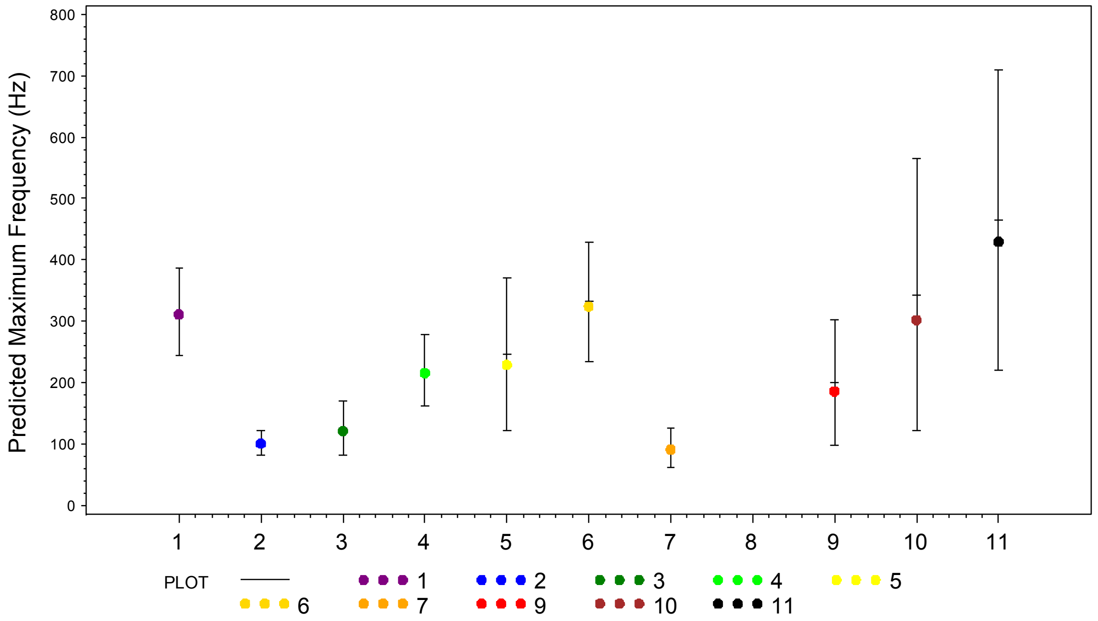

Figure 15. Plot of predicted maximum frequency by class. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

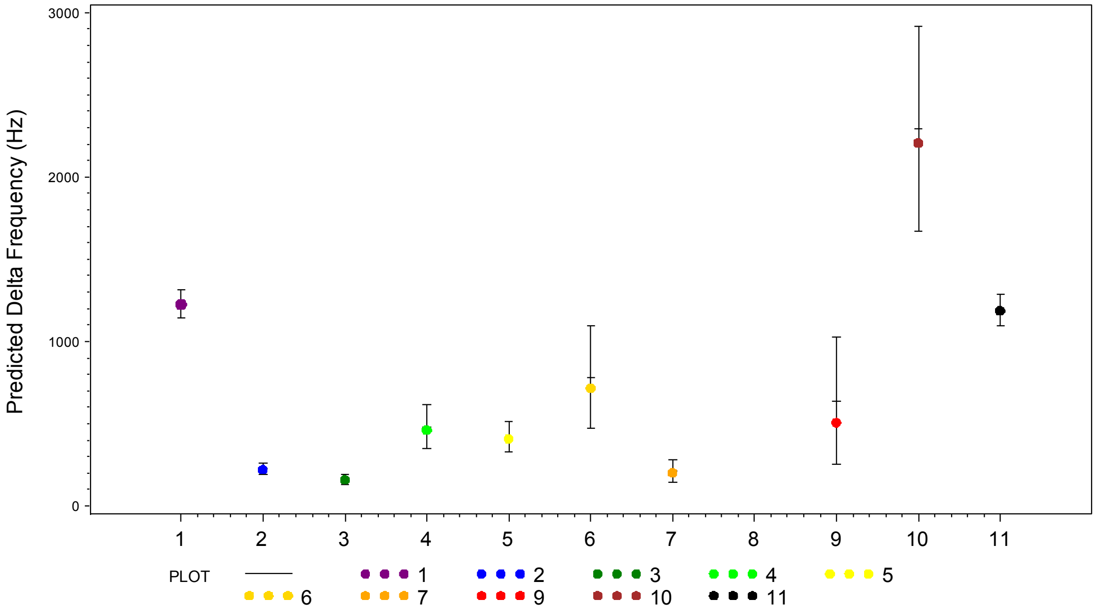

Figure 16. Plot of predicted bandwidth by class. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

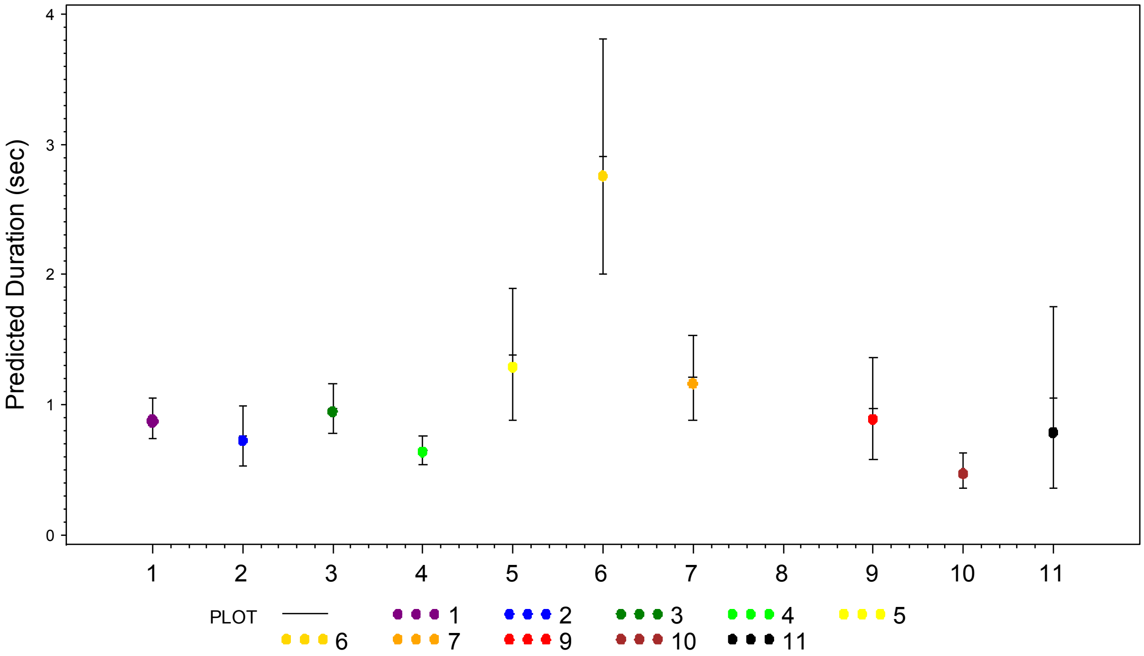

Figure 17. Plot of predicted duration by class. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Parameter variations between class 1 subclasses

Low frequency, maximum frequency, and number of pulses did not demonstrate significant differences between subclasses (see Appendix A). Number of pulses indicated a possible trend in which 1b may have greater number of pulses than 1a (p=0.0672) (see Appendix A).

Linear regression models determined that mean high frequency of subclass 1b was statistically greater than that of subclass 1a (F=19.12, p=0.0003) (Figure 18). Bandwidth of 1b was statistically greater than 1a (F=18.18, p=0.0004) (Figure 19). Pulse rate (pulses/second) of 1a was greater than 1b (F=20.61, p=0.0002) (Figure 20).

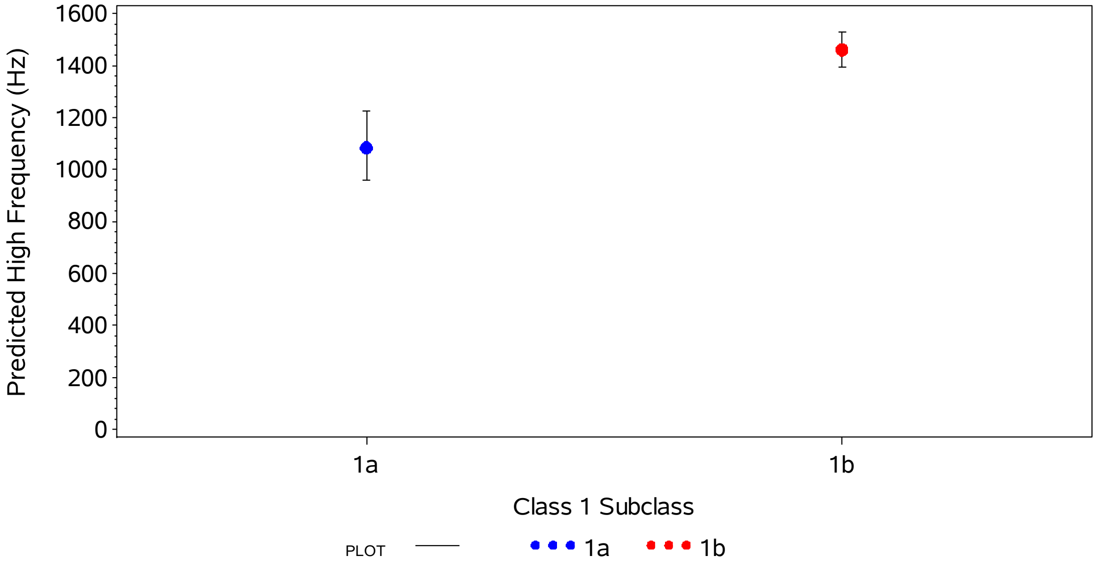

Figure 18. Plot of predicted high frequency by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

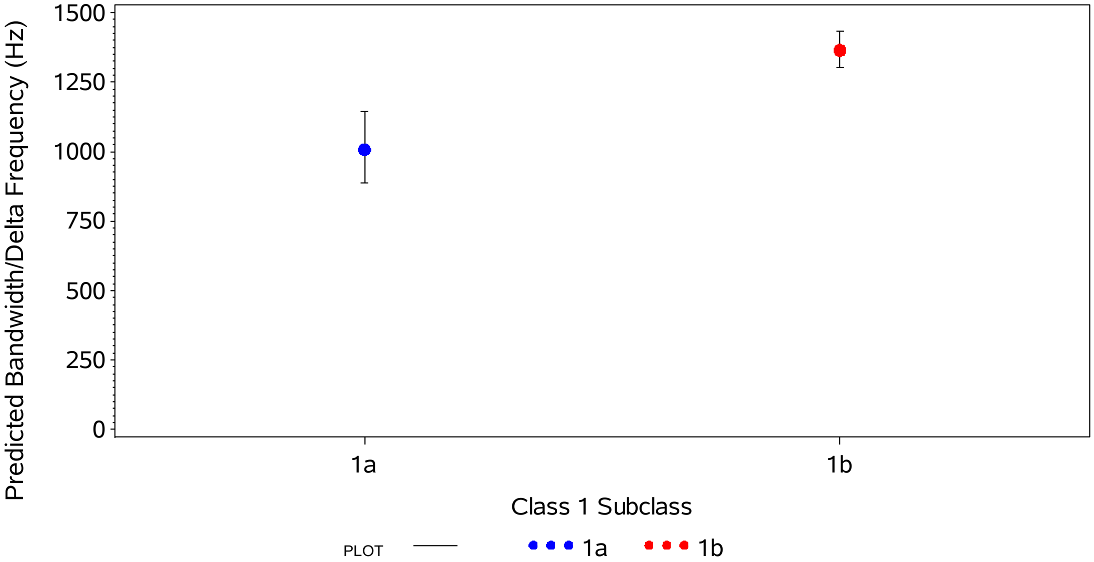

Figure 19. Plot of predicted bandwidth by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

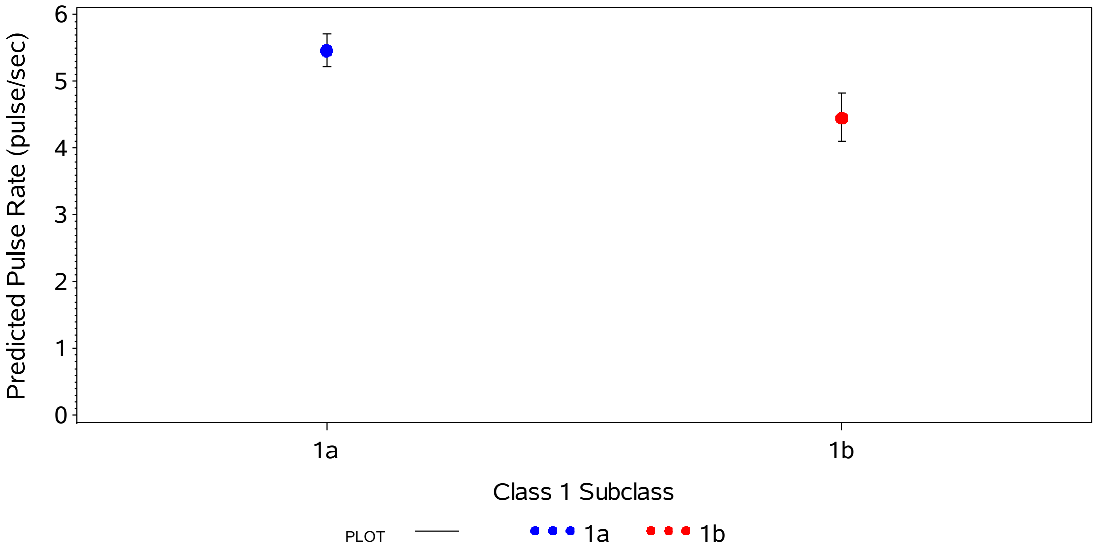

Figure 20. Plot of predicted pulse rate by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

When testing individual pulses, or knocks, within subclass series, individual pulse low frequency, individual pulse maximum frequency and individual pulse duration were not found to be significantly different between subclasses (see Appendix A).

Other parameters were found to be significantly different between subclasses. High frequency of individual pulses was significantly higher in 1b than 1a (F=12.10, p=0.0025) (Figure 21). Bandwidth of individual pulses of 1b was found to be significantly larger than 1a (F=13.40, p=0.0017) (Figure 22). Individual pulse interval (IPI) was significantly larger in 1b sounds than in 1a (F=68.03, p<0.0001) (Figure 23).

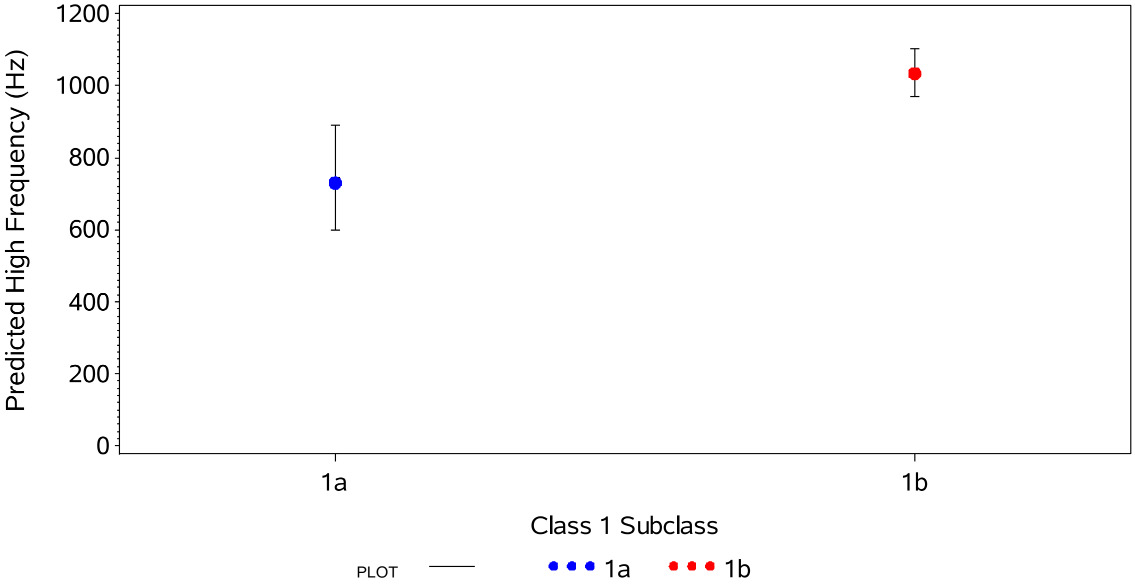

Figure 21. Plot of predicted individual pulse high frequency by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

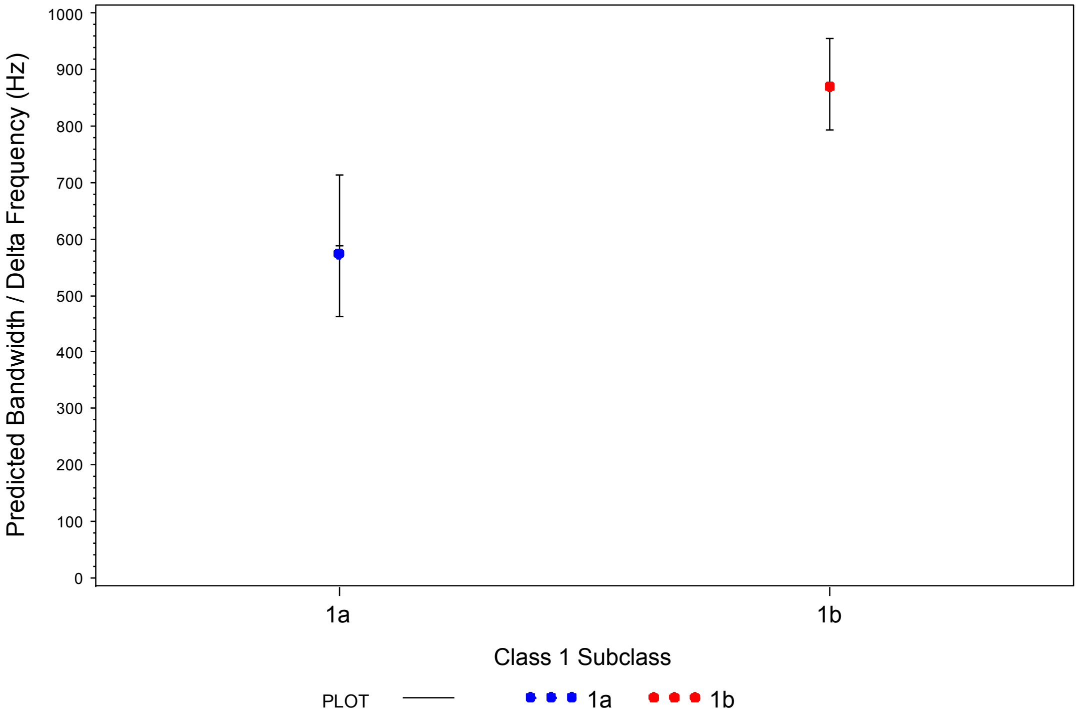

Figure 22. Plot of predicted individual pulse bandwidth by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

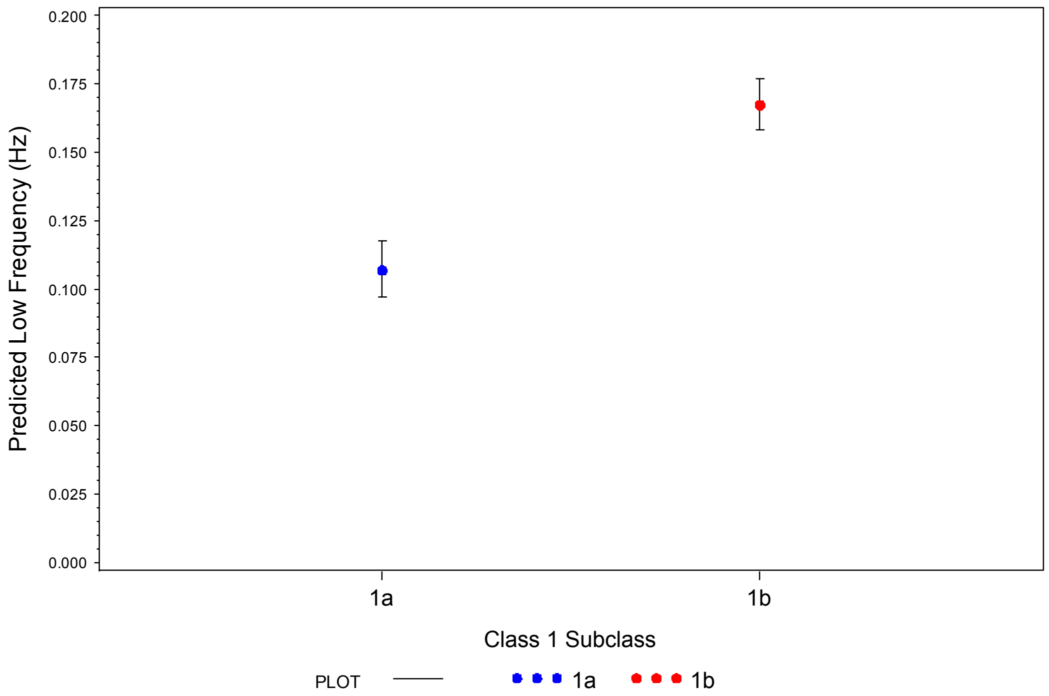

Figure 23. Plot of predicted inter-pulse interval by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Parameter variations by social context

Linear regression models found that low frequency varied significantly by both social context and class (F=26.89, p<0.0001) (Figure 24). Upon review of coefficients, most of the significance is due to differences between calf-containing groups and mixed/unknown groups (t=-11.21, p<0.0001). Adults had consistently similar low frequencies across classes. Unknown/mixed groups exhibited slightly more variation among classes, and calf-containing groups exhibit most varied and greatest range of low frequencies.

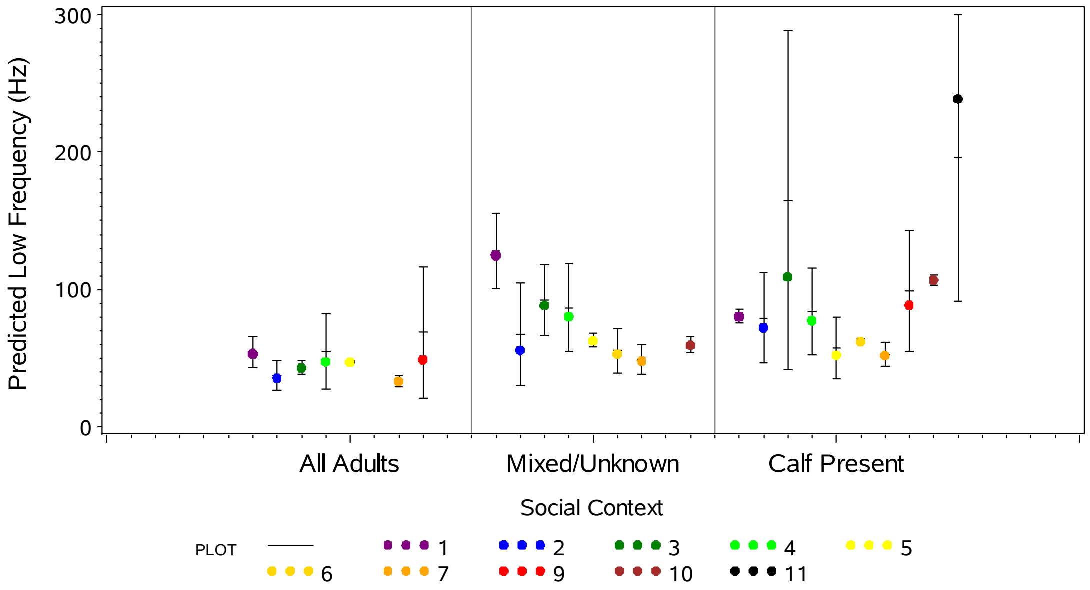

Figure 24. Plot of predicted low frequency by class and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

High frequency was significantly different by both social context and class (F=38.88, p<0.0001) (Figure 25). Calf-containing groups seemed to exhibit more varied and higher ranges of high frequencies. Class 1 was consistently higher than other classes in all social states. Only class 10 was higher than class 1.

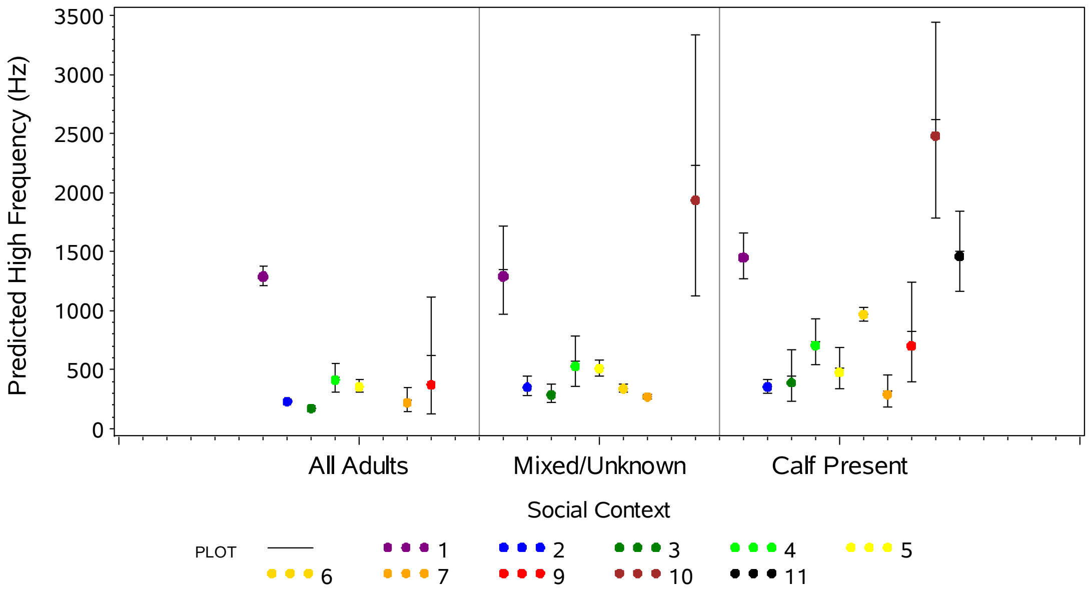

Figure 25. Plot of predicted high frequency by class and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Maximum frequency was significantly different by social context and class (F=27.59, p<0.0001) (Figure 26). Calf-containing groups exhibited higher and more varied maximum frequencies. As in high-frequency comparisons, class 1 had some of the greatest maximum frequencies across all social contexts.

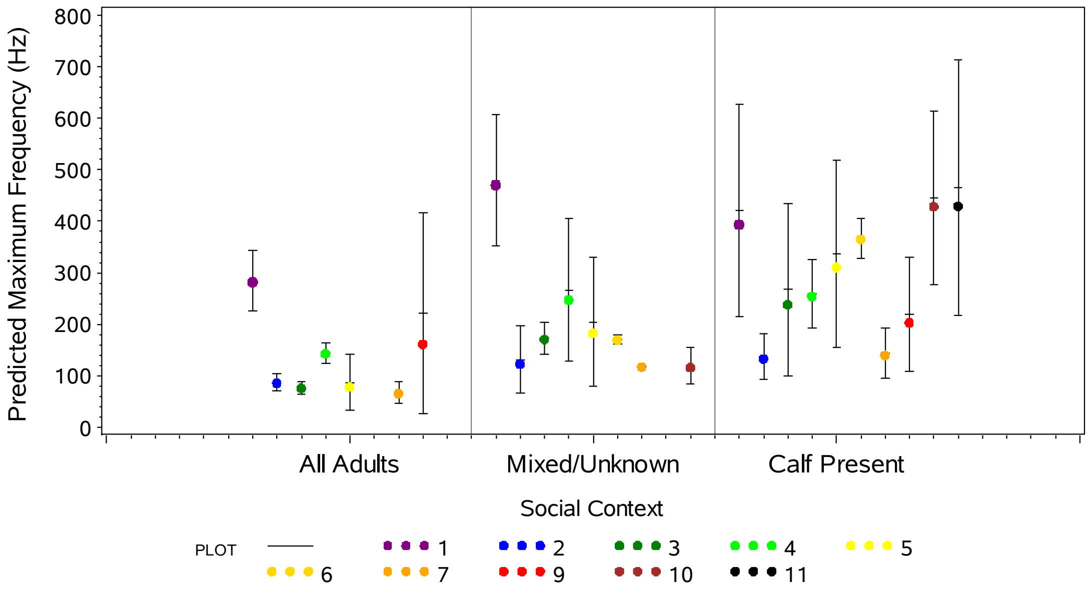

Figure 26. Plot of predicted maximum frequency by class and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Bandwidth was significantly different by both social context and class (F=26.48, p<0.0001) (Figure 27). Calf-containing groups exhibited larger and more varied bandwidths. Bandwidth had most significant differences among classes, regardless of social context. In other words, bandwidth exhibited the most variation among classes, regardless of social context. As seen in other parameters, class 1 had greatest bandwidth across social contexts. It was surpassed only by class 10 in unknown/mixed and calf-containing groups.

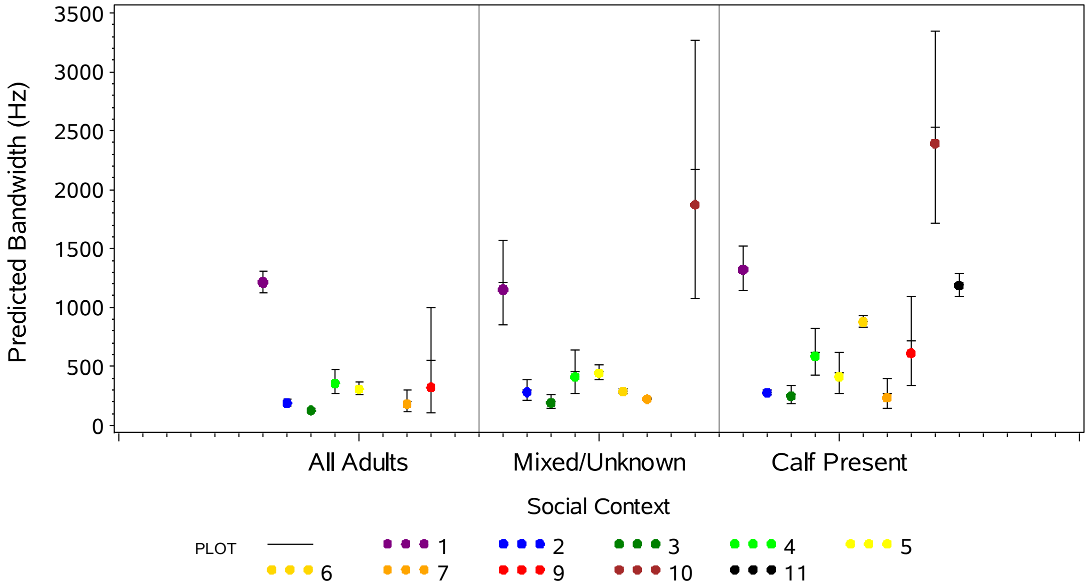

Figure 27. Plot of predicted bandwidth by class and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Duration of sound exhibited significant differences by both social context and class (F=16.90, p<0.0001) (Figure 28). Calf-containing groups exhibited only slightly longer and more varied durations. Duration is more uniform than other parameters across social contexts and classes.

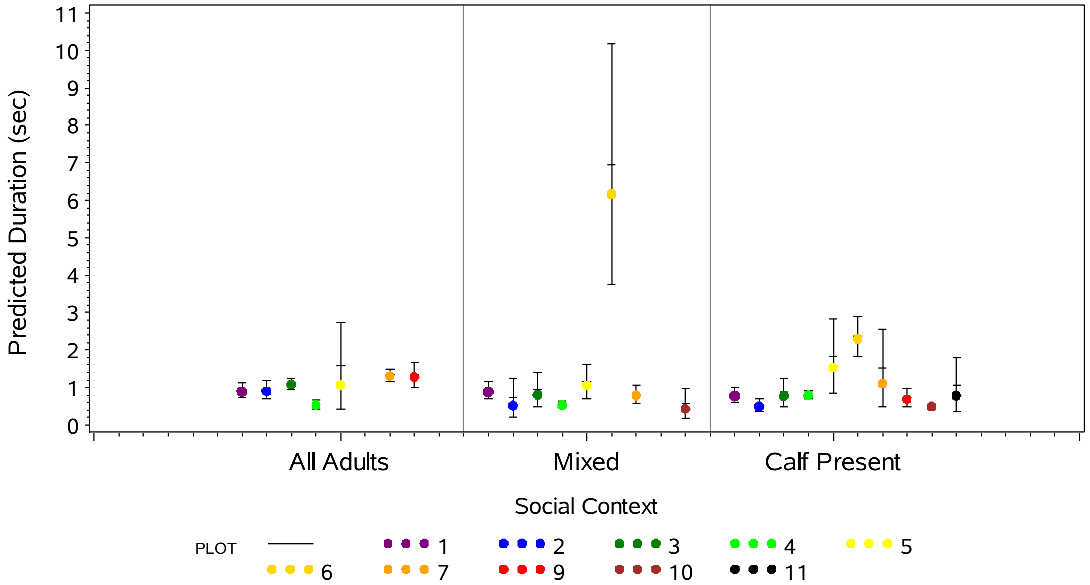

Figure 28. Plot of predicted duration by class and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Class 1 subclass parameter variations by social context

Linear regression models of type 1 subclass parameters by social contexts indicate that several parameters have significant differences; some in interaction of both social context and subclass, and some only in subclass (i.e., no significant difference among social contexts). Duration, individual pulse maximum frequency and individual pulse duration demonstrated no significant differences in logistic regression models (see Appendix B).

Low frequency of entire sound demonstrated significant difference among social contexts only (F=17.26, p<0.0001) (Figure 29); there was no significant difference between subclasses. Mixed/unknown groups had greatest mean low frequencies, followed by groups containing calves, and adults had the smallest mean low frequencies.

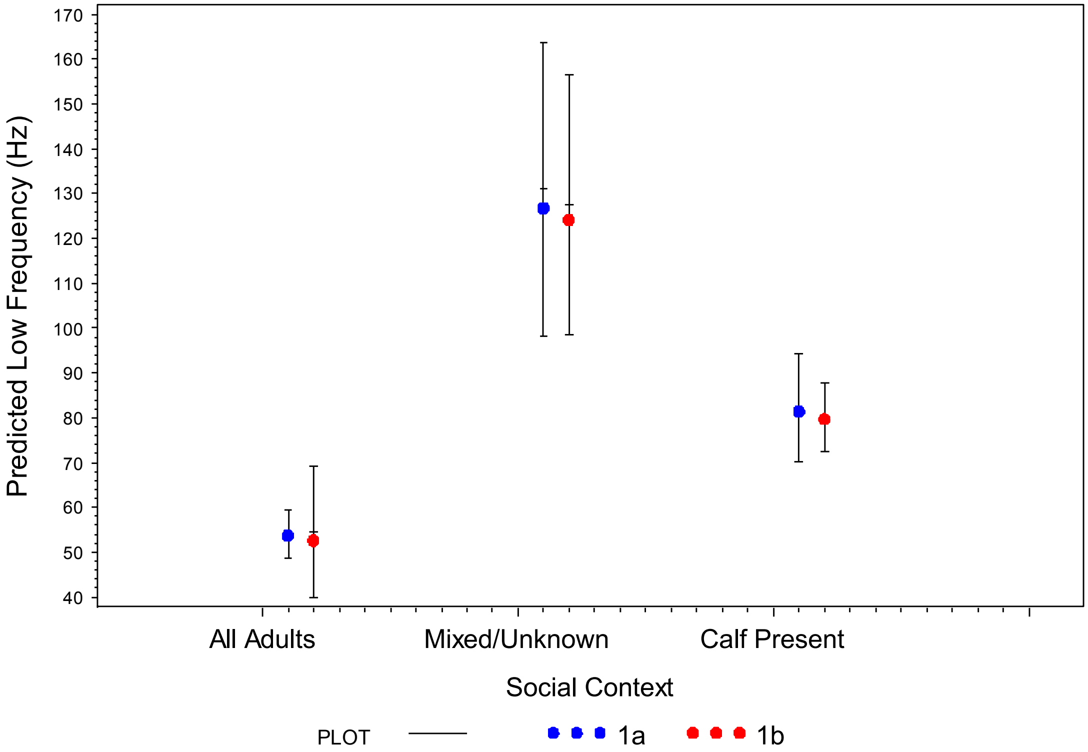

Figure 29. Plot of predicted low frequency by subclass and social context. Based on liner regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Mean high frequency was significantly different by the interaction model of social context and subclass (F=5.92, p=0.0101) and subclass alone (F=10.77, p=0.0039) (Figure 30). Calf-containing groups had slightly higher mean high frequencies, and subclass 1b had higher means than subclass 1a in all social contexts.

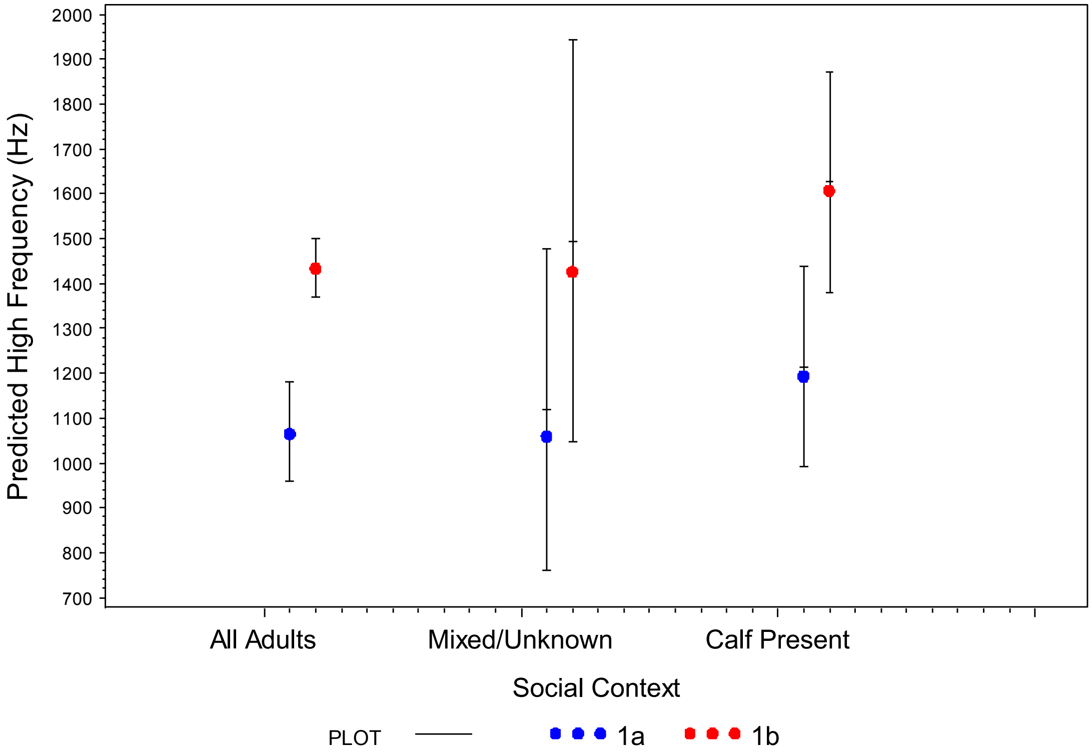

Figure 30. Plot of predicted high frequency by subclass and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Maximum frequency of subclass sounds also demonstrated significant differences by subclass and social context (F=12.66, p=0.0003) (Figure 31).

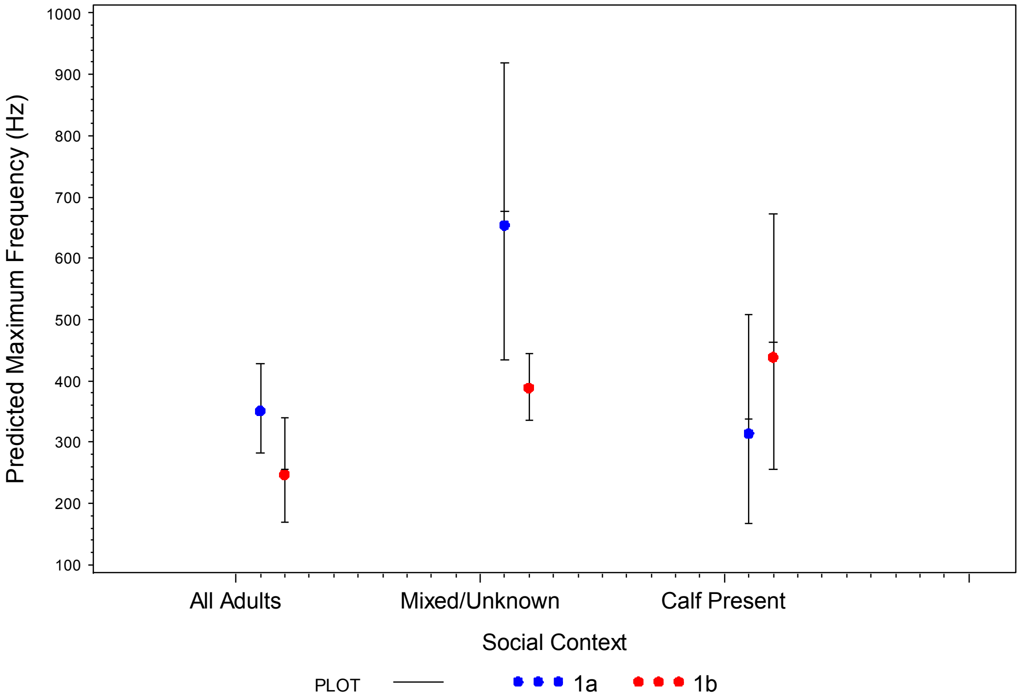

Figure 31. Plot of predicted maximum frequency by subclass and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Bandwidth, or delta frequency, was significantly different by social context and subclass (F=6.77, p=0.0060) (Figure 32). Interestingly, only in the adult groups were 1a and 1b significantly different from each other.

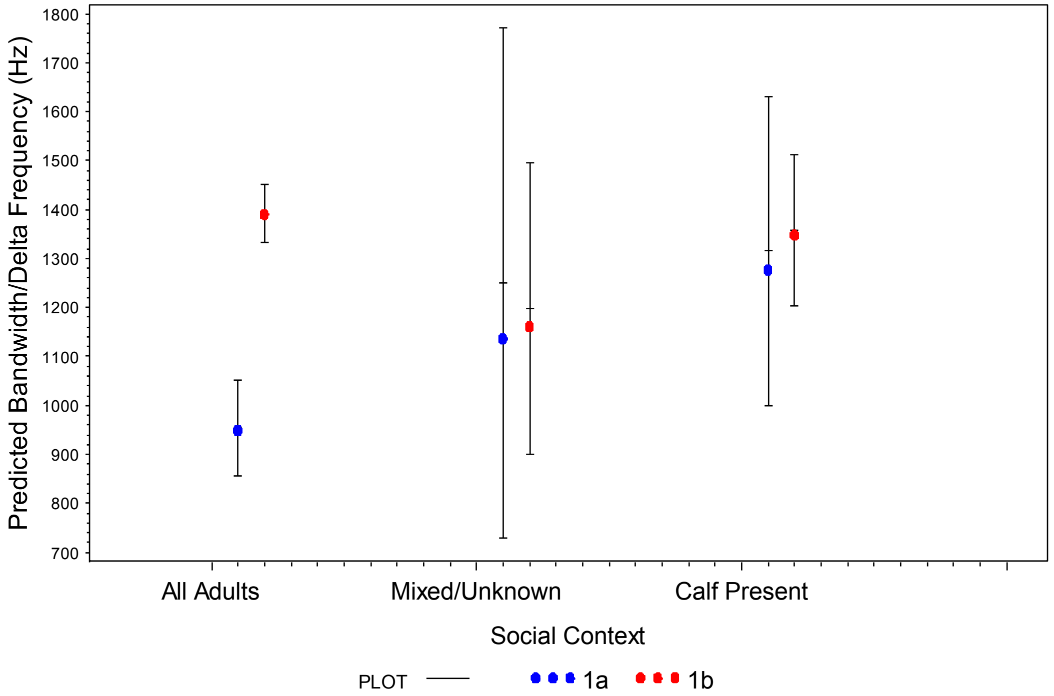

Figure 32. Plot of predicted bandwidth by subclass and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Number of pulses demonstrated significant differences in both social context and subclass (F=4.03, p=0.0116) (Figure 33).

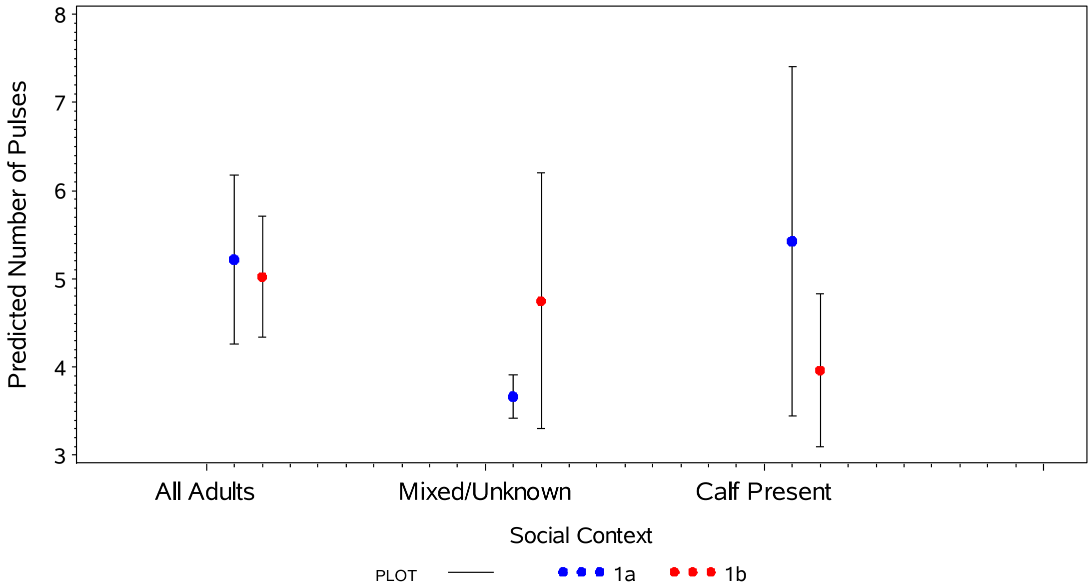

Figure 33. Plot of predicted number of pulses by subclass and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Pulse rate was significantly different by both social context and subclass (F=6.15, p=0.0087) (Figure 34). Pulse rate of 1a was significantly higher than 1b for both adults and calf-containing groups. Interestingly, pulse rates of 1a and 1b were very similar in mixed/unknown groups. Additionally, both subclasses in mixed/unknown social contexts had large ranges. Both of these characteristics may be due to small sample size. However, pulse rates of 1a sounds in calf-containing were higher than those of any other subclass or social context.

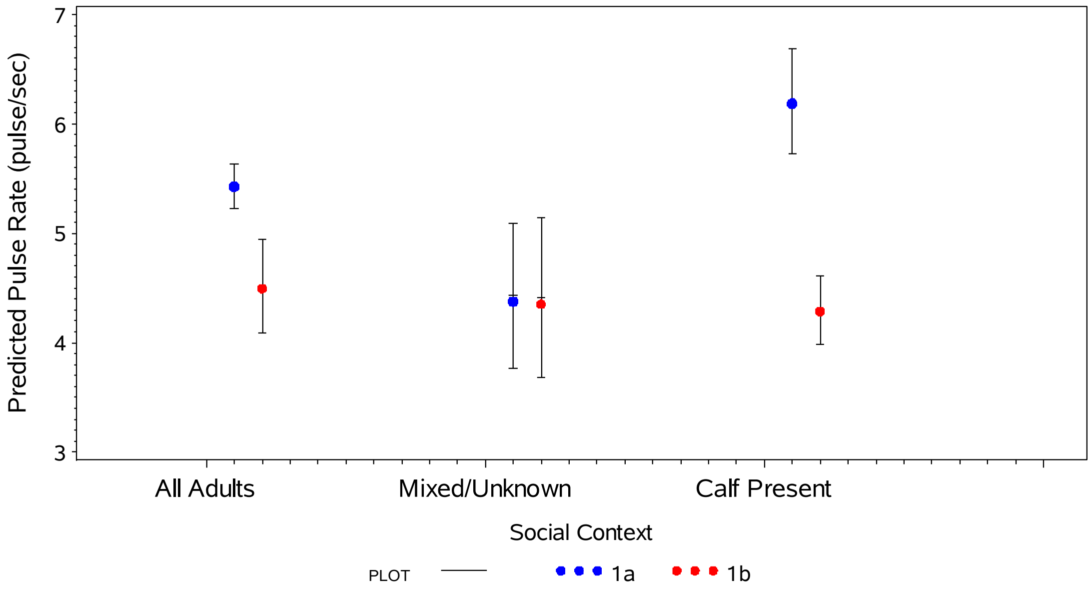

Figure 34. Plot of predicted pulse rate by subclass and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Class 1 subclasses were also tested by individual pulse (or knock) parameters for any significant differences among social classes.

Individual pulse low frequency was significantly different by both social context and subclass (F=5.43, p=0.0137) (Figure 35). It appears that greatest significant differences are exhibited among social context (F=8.46, p=0.0024) rather than between subclasses (F=0.01, p=0.9045). Mixed/unknown groups had highest mean low frequencies, followed by calf-containing groups; adults had lowest mean low frequencies.

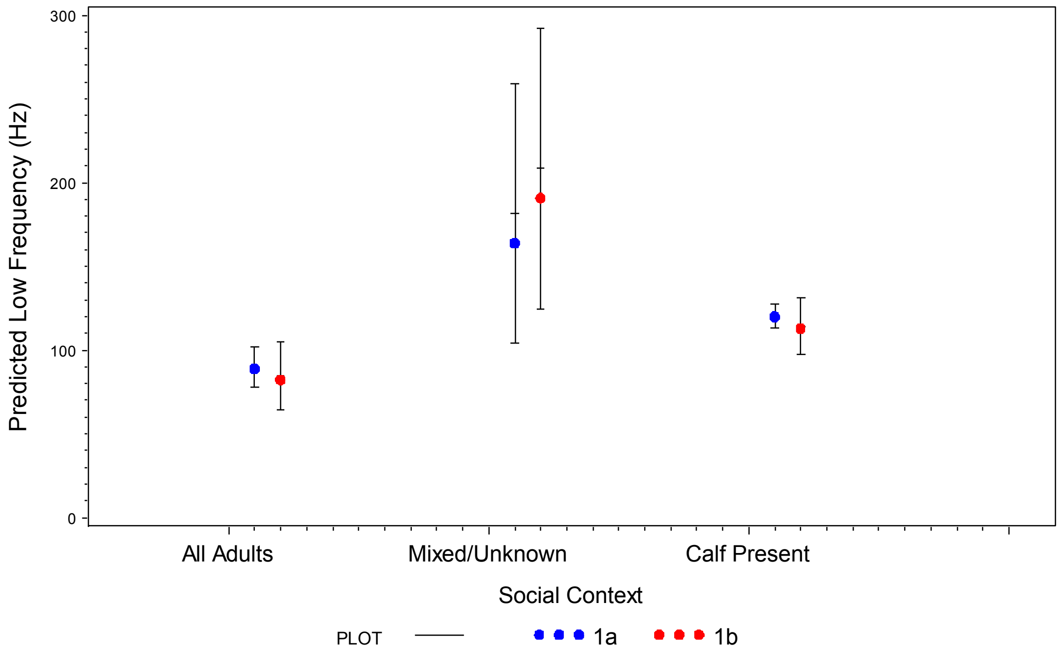

Figure 35. Plot of predicted individual pulse low frequency by subclass and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Individual pulse high frequency was not significantly different in interaction model, but was significantly different by both social context (F=6.31, p=0.0079) and subclass (F=14.27, p=0.0013) independently (Figure 36). Calf-containing groups had higher mean high frequency than adults (t=-3.55, p=0.0021). Additionally, subclass 1b was significantly higher than 1a in all social contexts (t=-3.78, p=0.0013).

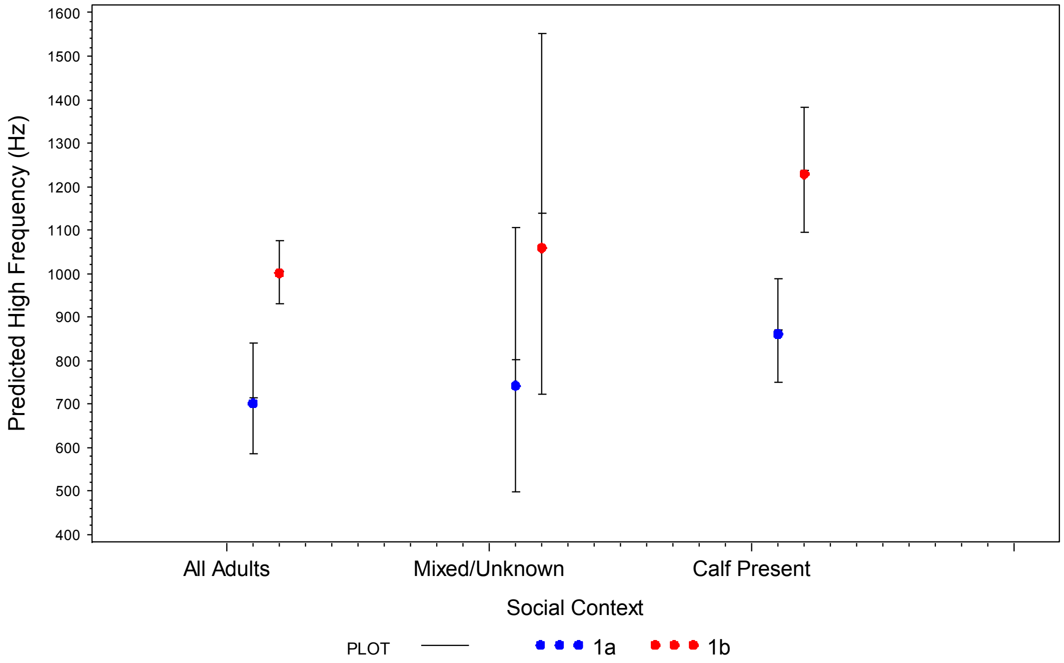

Figure 36. Plot of predicted individual pulse high frequency by subclass and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Individual pulse bandwidth was significantly different by subclass (F=15.44, p=0.0009) and by social context (F=3.71, p=0.0435) but not by interaction term (Figure 37). Bandwidth of 1b was greater than that of 1a across all social contexts (t=-3.93, p=0.0009). Calf-containing groups had significantly greater bandwidths (both subclasses) than adults (t=-2.68, p=0.0147).

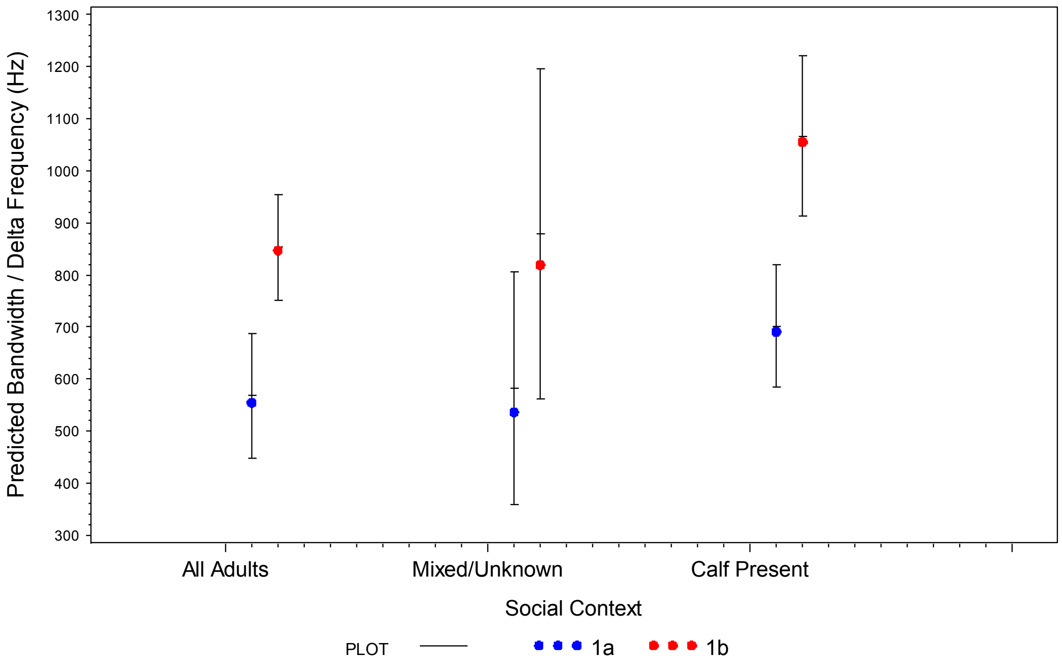

Figure 37. Plot of predicted individual pulse bandwidth by subclass and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Inter-pulse interval was tested, and interaction model was not significant. In regression model without interaction, inter-pulse interval was significantly different by subclass (F=60.34, p<0.0001) and social context (F=17.85, p=0.0001) (Figure 38). While not significant at p=0.05, inter-pulse interval of calf-containing groups were generally smaller than those of mixed/unknown groups (t=1.98, p=0.0623). Additionally, mixed/unknown groups had significantly larger inter-pulse intervals than adults (F=35.55, p<0.0001). Subclass 1b had significantly larger inter-pulse intervals across social contexts (F=60.34, p<0.0001).

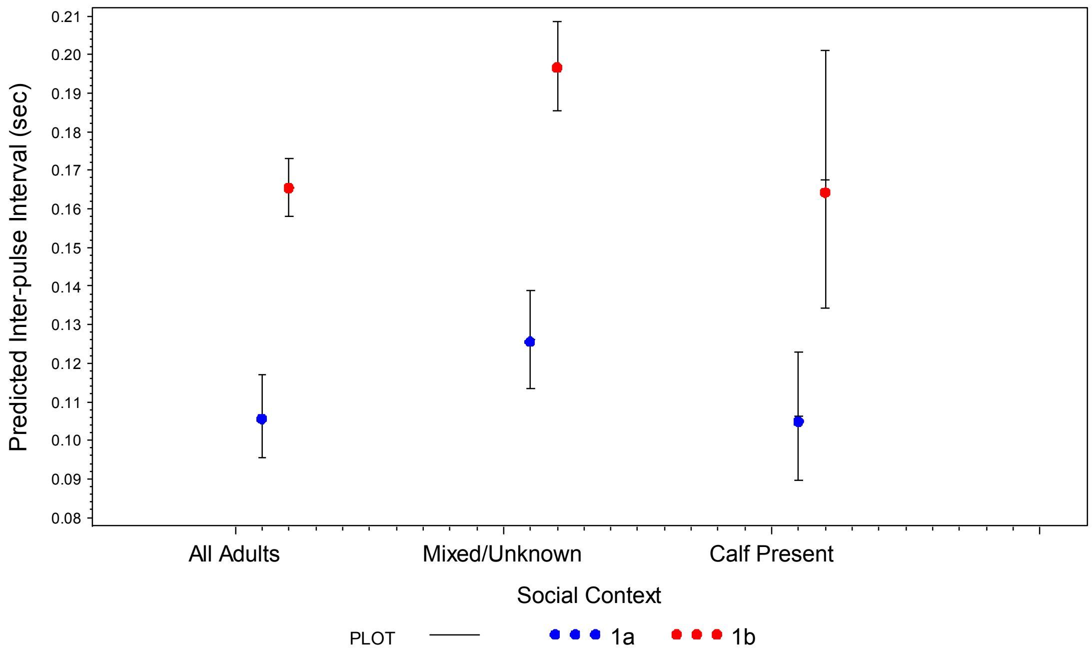

Figure 38. Plot of predicted inter-pulse interval by subclass and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Relative use of classes by social context

The relative use of sound classes provided unexpected results (Table 3). Only 58.1% of 432 classified sounds were class 1. Class 2 consisted of 6.02%, class 3 9.26%, class 4 13.89%, class 5 3.94%, class 6 2.55%, class 7 3.24%, class 9 1.16%, class 10 1.39% and 0.46% of the classified sounds were class 11. Note that there were no observations of class 8.

Adults produced 60% of all sounds produced; calf-containing groups produced about a quarter (26.2%) of all sounds and mixed/unknown groups produced 13.4% of all sounds observed.

Models indicate no significant differences in use of class 2, class 3, class 7, or tonal type of sounds (See Appendix C). Adults may have used subclass 1b slightly more than other social contexts (p=0.0733) (See Appendix C).

Adults had significantly greater probability of using class 1 than either unknown/mixed whales or calf-containing groups (Wald chi-square=13.73, p=0.0010) (Figure 39).

Unknown/mixed and calf-containing groups had significantly greater probabilities of using class 4 than adults (Wald chi-square=15.04, p=0.0005) (Figure 40). One session in which a calf engaged in very social behaviors, including swimming under the observation boat, produced 18% (11/60) of all class 4 sounds observed.

Table 3. Gray whale class use by social context in Bahía Magdalena Complex, Baja California Sur, México, 2006 and 2007. Individual class percentages (*italicized*) are proportion of sounds produced within that social context.

	Social Context							
Class	Adults		Mixed/Unknown		Mother/Calf		Total	% of repertoire
1	192	_73.6%_	18	_31.0%_	41	_36.3%_	251	58.10%
1a*	_68*_	_26.1%*_	_6*_	_10.3%*_	_14*_	_12.4%*_	_88*_	_20.37%*_
1b*	_124*_	_47.5%*_	_12*_	_20.7%*_	_27*_	_23.9%*_	_163*_	_37.96%*_
2	16	_6.1%_	4	_6.9%_	6	_5.3%_	26	6.02%
3	23	_8.8%_	9	_15.5%_	8	_7.1%_	40	9.26%
4	18	_6.9%_	15	_25.9%_	27	_23.9%_	60	13.89%
5	2	_0.8%_	6	_10.3%_	9	_8.0%_	17	3.94%
6	0	_0.0%_	2	_3.4%_	9	_8.0%_	11	2.55%
7	8	_3.1%_	2	_3.4%_	4	_3.5%_	14	3.24%
8	0	_0.0%_	0	_0.0%_	0	_0.0%_	0	0.00%
9	2	_0.8%_	0	_0.0%_	3	_2.7%_	5	1.16%
10	0	_0.0%_	2	_3.4%_	4	_3.5%_	6	1.39%
11	0	_0.0%_	0	_0.0%_	2	_1.8%_	2	0.46%
Total	261	_60.4%**_	58	_13.4%**_	113	_26.2%**_	432	100.00%

*Not included in totals

**Percentage of all sounds produced in all contexts

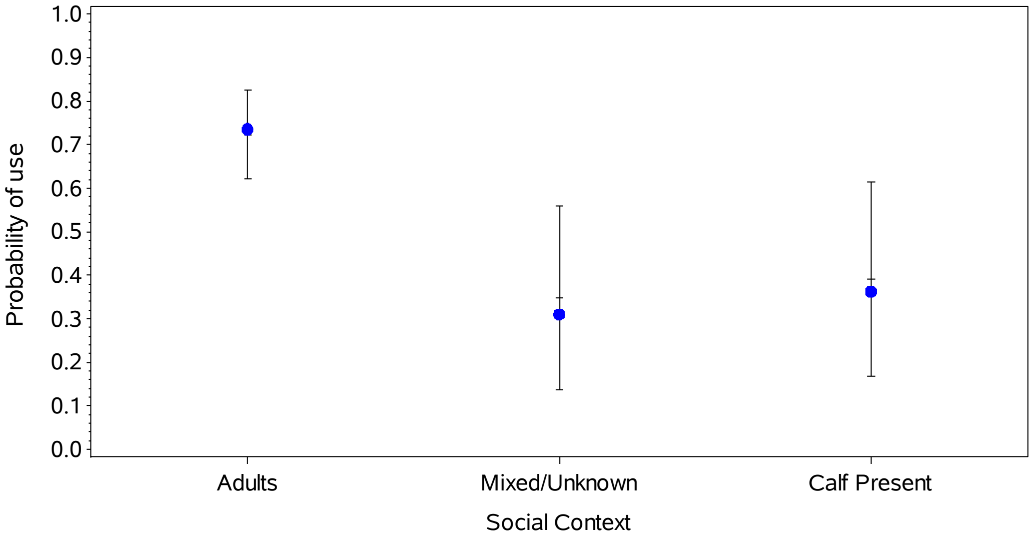

Figure 39. Plot of predicted use of class 1 by social context. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

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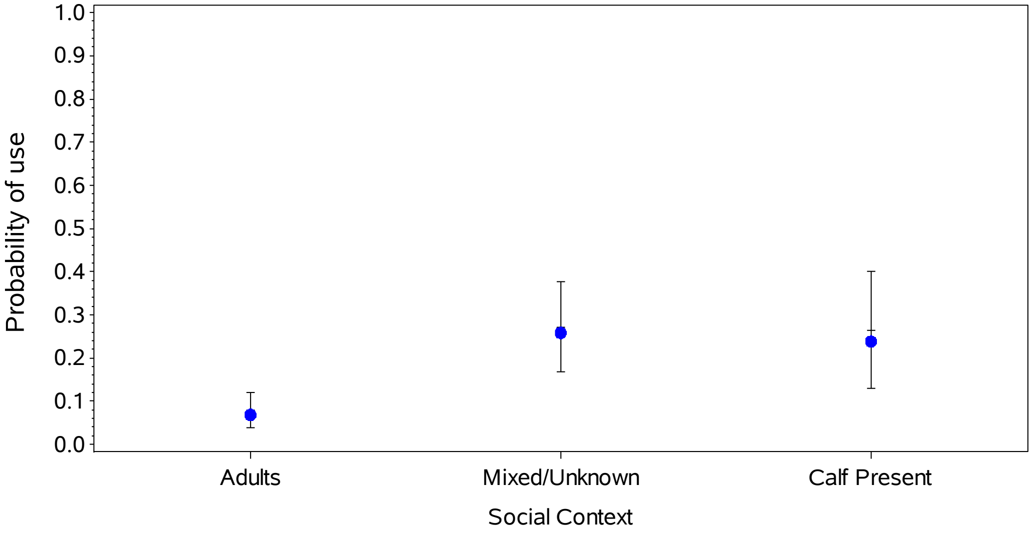

Figure 40. Plot of predicted use of class 4 by social context. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Social context had significant effect on use of class 5 sounds (Wald Chi-square=14.25, p=0.0008) (Figure 41). Both calf-containing (Wald Chi-square=14.08, p=0.0009) and unknown/mixed groups (contrast test Wald chi-square=7.76, p=0.0054) had greater probability of using class 5 than adults. Although not significantly different, it may be suggested that unknown/mixed groups have greater probability of using class 5 than calf-containing groups (Wald Chi-square=3.25, p=0.0715). One session observed 33% (5/15) of class 5 sounds. Although this session was defined as mixed/unknown, the only whales sighted were a mother and very young calf engaged in travelling and surfacing behaviors.

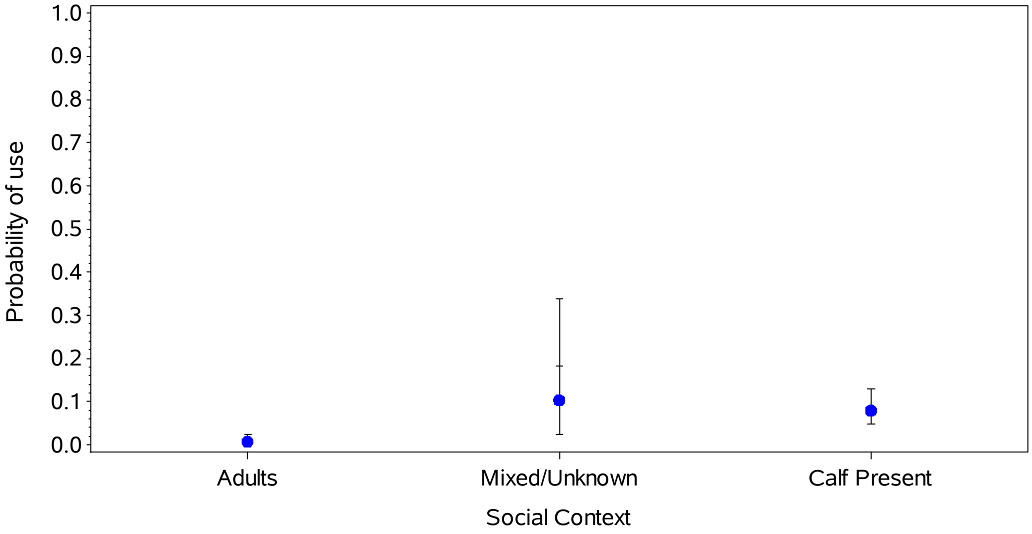

Figure 41. Plot of predicted use of class 5 by social context. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Classes 6, 9, 10 and 11 were excluded from logistic regression due to low rate of occurrence (small sample size). It is notable that there were no occurrences of class 6 or

10 in adult groups and there were no occurrences of class 9 in unknown/mixed groups. Finally, class 11 occurred only twice; both occurrences were in calf-containing groups.

An alternative solution to low sample size was to pool classes 5 through 11 (n=55). In addition to their small sample size as individual classes, more than half are complex (60%, 33/55), some are pulsed (36.4%, 20/55), but rarely are they tonal (3.6%, 2/55). Social context had a significant effect on use of these classes (Wald chi-square=21.29, $p<0.0001$) (Figure 42). This pooled type (classes 5-11) was 27.4% of the calf-containing repertoire; it was 20.7% of mixed/unknown repertoire and only 4.6% of the adult repertoire. Groups containing calves had significantly greater probability of producing than adults (Wald chi-square=21.15, $p<0.0001$). Unknown/mixed groups also had significantly greater probability of classes 5 through 11 occurring than did adults (Wald chi-square=11.33, $p=0.0008$).

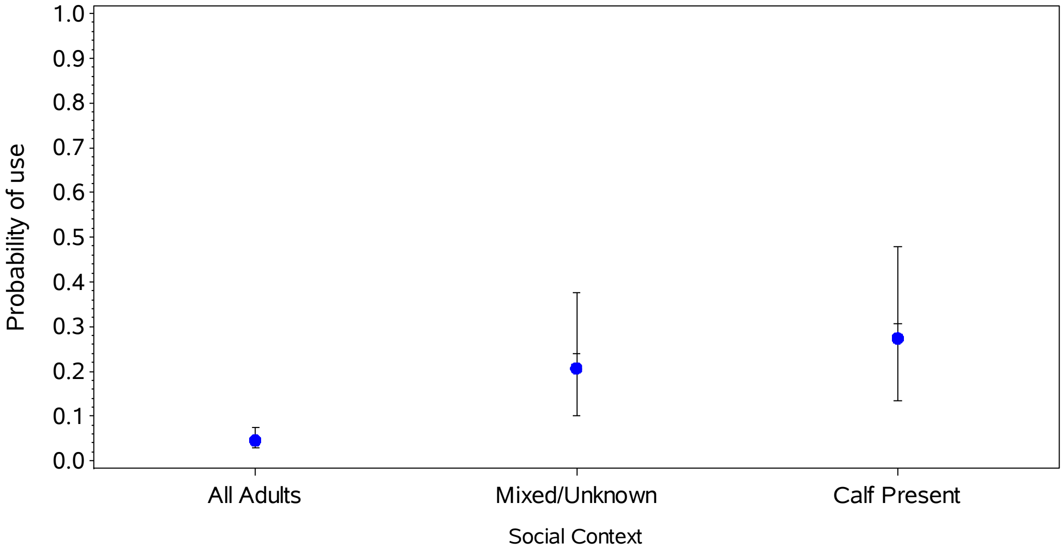

Figure 42. Plot of predicted use of classes 5-11 (pooled) by social context. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Relative use of class 1 subclasses

Use of subclass 1a was significantly different by social context (Wald chi-square=10.92, p=0.0043) (Figure 43). Adults had significantly greater probability of using subclass 1a than calf-containing groups (Wald chi-square=7.97, p=0.0048) and mixed/unknown groups (Wald chi-square=10.48, p=0.0012).

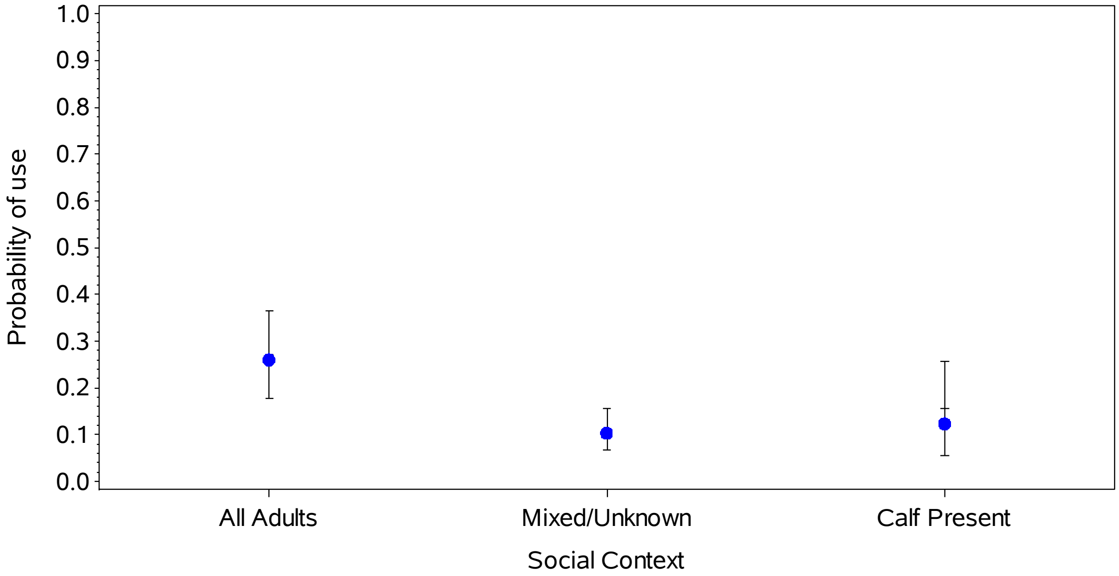

Figure 43. Plot of predicted use of subclass 1a by social context. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Subclass 1b was used more frequently than 1a by all social contexts (Table 3). Within each social context, 1b was used about twice as often as 1a. While adults use subclass 1b slightly more frequently than other groups, the overall model detected no significant differences among groups (Wald chi-square=5.22, p=0.0733).

More than half of all subclass 1a (48/88 = 54.5%) and most of subclass 1b (103/124 = 83.1%) sounds occurred during the same three sessions. Specifically, almost half of all subclass 1b (61/124 of all 1b = 49.2%) occurred during just one of these sessions. All three sessions were characterized by adult social behavior.

Relative use of types

Pulse, tonal, and complex types of sounds were also tested for difference in use by social contexts. This general categorization is based on the nature of the individual sound, regardless of original class. However, some classes were consistently assigned the same type (e.g., class 1 sounds were always pulsed).

Of the three sound types, pulsed sounds had the highest probabilities of occurrence in all three social contexts, and use was significantly different among social contexts (Wald chi-square=6.68, p=0.0354) (Figure 44). Adults had significantly greater probabilities of using pulsed sounds than calf-containing groups (Wald Chi-square=6.34, p=0.0118). Adults also had greater probabilities of using pulsed sounds than unknown/mixed groups (contrast test Wald chi-square=4.02, p=0.0450).

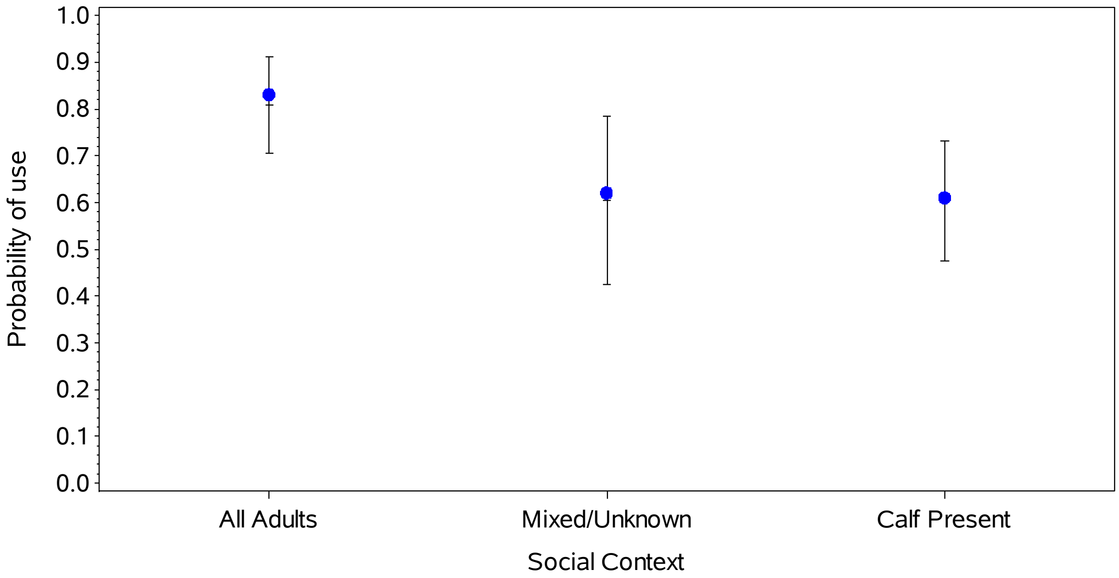

Figure 44. Plot of predicted use of pulsed sound type by social context. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Complex sounds included those of "mixed" or "hybrid" nature (i.e., both pulse and tonal within one sound), as well as unique sounds that are neither pulsed nor tonal. According to logistic regression models, social context had significant effect on use of complex sounds (Wald Chi-square=12.58, p=0.0019) (Figure 45). Adults had least probability of using complex sounds. Calf-containing groups had significantly greater probability of complex sounds occurring than did adults (Wald chi-square=12.58, p=0.0004). Unknown/mixed groups also had significantly greater probability of complex sounds occurring than adults (Wald chi-square=8.99, p=0.0027). There was not significant difference in probability of occurrence between calf-containing groups and unknown/mixed groups (Wald chi-square=2.95, p=0.08).

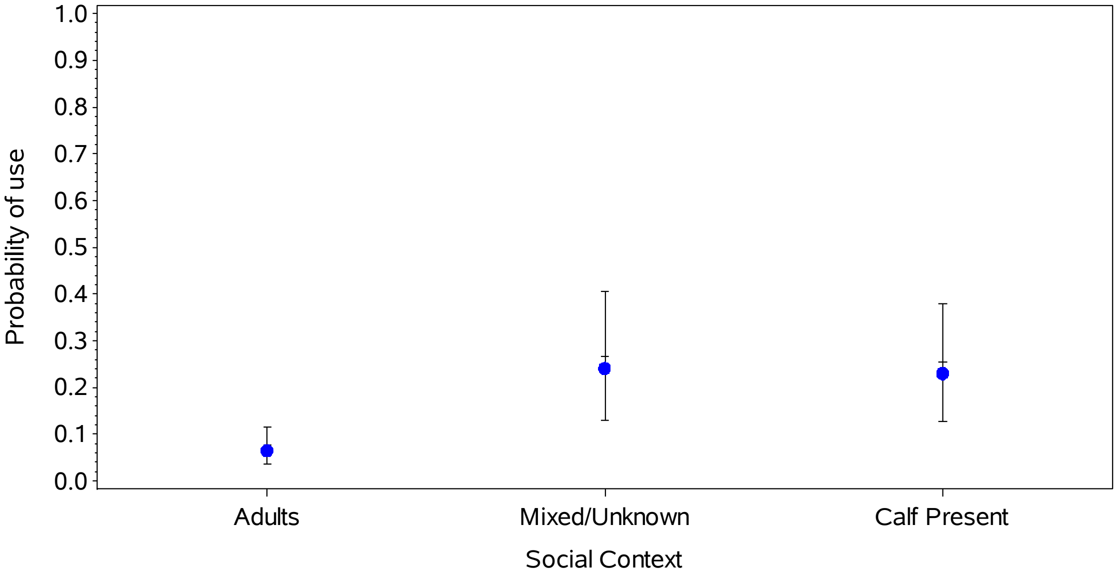

Figure 45. Plot of predicted use of complex sound type by social context. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Use of tonal type sounds was low for all social groups. There were no significant differences detected in probabilities of use among social groups (See Appendix C).

Rates of sound production

Median rates of sound production are likely more accurate than mean rates due to an outlier in mixed/unknown groups. When considering medians, adults and calf-containing groups produced sounds at rates almost ten times greater than mixed/unknown groups (Table 4). According to medians, individual rates of adults are greatest, followed by calf-containing groups; mixed/unknown had smallest individual rates of sound production. Calf-containing contexts always produced at least one sound per session.

Regression model found rates of individual sound production (sounds/minute/whale) were not significantly different across social context (F=2.32, p=0.1127) (Figure 46); rates were square root transformed (Kolmogorov-Smirnov, p>0.150). However, adults generally had higher rates of sound production than mixed/unknown groups (F=4.07, p=0.0512). Although not significant at p=0.05, it appears adults may have slightly higher rates of sound production than calves (t=1.79, p=0.0817).

Table 4. Rates of gray whale sound production (mean and *median*) by social context in Bahía Magdalena Complex, Baja California Sur, México, 2006 and 2007.

	Social Context			
	All whales	Adults	Mixed/ Unknown	Calf Present
# of sounds	432	261	58	113
Recording Duration (hours)	10.13	3.88	3.64	2.72
Recording Duration (min)	613.2	232.5	218.5	163.2
(Minimum) # of Whales	94	33	23	38
Sounds/min	0.705 *0.329*	1.123 *0.517*	0.265 *0.065*	0.692 *0.567*
Sounds/min/whale	0.013 *0.006*	0.020 *0.023*	0.010 *0.005*	0.009 *0.007*
Sounds/hour	42.270 *19.74*	67.355 *31.02*	15.927 *3.9*	41.544 *34.02*
Sounds/hour/whale	0.784 *0.383*	1.192 *1.406*	0.628 *0.273*	0.514 *0.446*

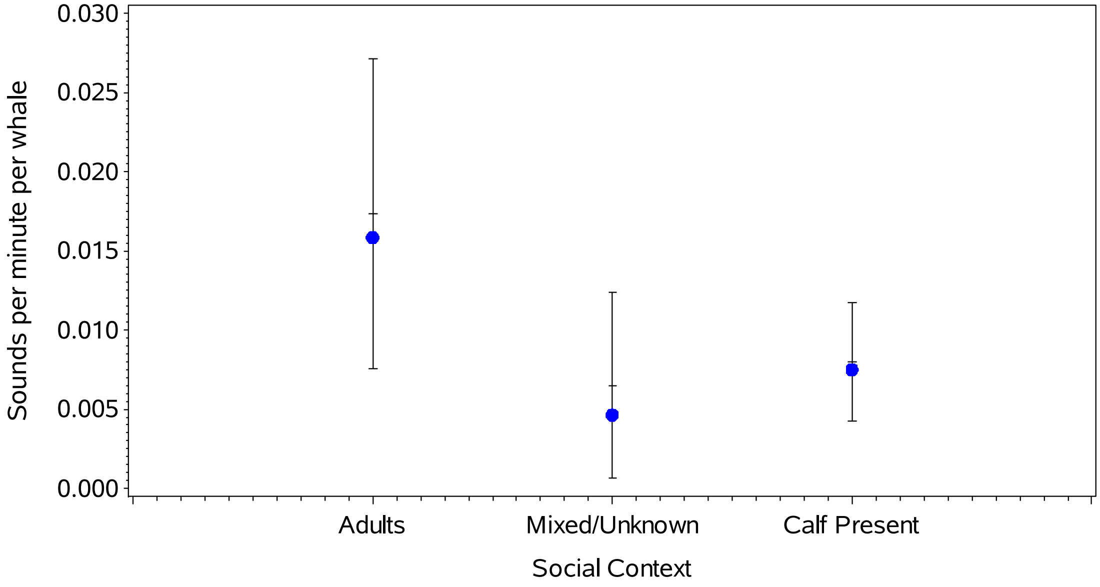

Figure 46. Plot of predicted rates of sound production by social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Social context had a significant effect on group rates (sounds/minute) of sound production (F=4.8, p=0.0143) (Figure 47). Specifically, both adult (F=7.15, p=0.0113) and calf-containing (F=-2.33, p=0.0258) groups produced more sounds as a group unit than did mixed/unknown groups. There was no significant difference found between adult and calf-containing groups. It is evident from the Figure 47 and Table 4 that calf-containing groups produced sounds at rates (sounds/minute and sounds/hour) at least twice that of mixed/unknown groups, although individual rates (sounds/minute/whale and sounds/hour/whale) of calf-containing groups were slightly lower than those of mixed/unknown groups.

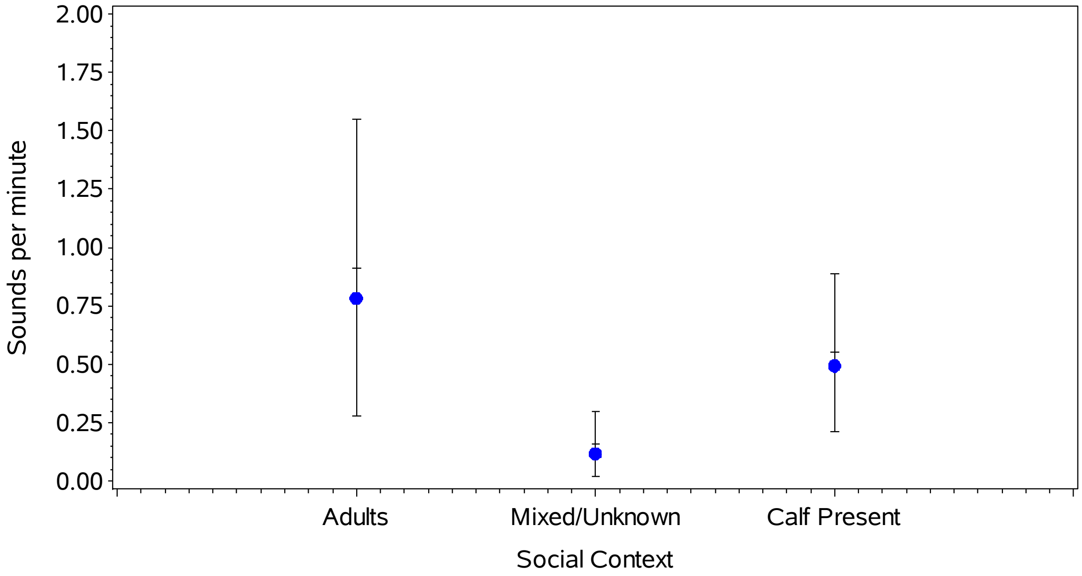

Figure 47. Plot of predicted group rates of sound production by social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Six of the seven sessions with the greatest mean rate (sounds/min/whale) were adult sessions. Three of these same adult sessions had the greatest mean group rates (sounds/min). In these three sessions, 50/58 (86%) minutes contained highly active adult behavior that is likely courtship or mating. However, because of the large number of whales present, individual rates (sounds/min/whale) were only slightly above average.

Active adult contexts demonstrated short-term (generally two to three minutes) group rates that range from 5.5 to 13 sounds per minute. The three minutes in which a penis was sighted had a rate of 7 sounds/min. In comparison, the most intense short-term period for a calf-containing session was 5.7 sounds/min. For mixed/unknown, peak was 2.3 sounds/minute. Additionally, 6 of 14 sessions of mixed/unknown groups produced no sounds. Only 1 of 12 adult sessions produced zero sounds. Calf-containing groups produced sounds in every session.

Use of four social contexts

Logistic regression models were tested with four social groups in which highly active and other adults were separated (i.e., highly active adults, other adults, calf present, unknown/mixed). Highly active adults produced 48% of all sounds observed; in contrast, other adults produced only 4% (Table 5). Calf-containing groups produced 26%, and mixed/unknown produced 21% of all sounds. Class 1 sounds produced by highly active adults were 38.9% of all sounds observed in this study.

Organization into four social contexts resulted in re-defining contexts for some sessions. This is due to majority changes (context with majority of minutes = context for that particular session). Therefore, some sessions that previously (in three social contexts) were considered adults may no longer have a majority (60%) of minutes characterized by adult context and may now be mixed/unknown. As a result, number of sounds produced in each context, most noticeably in mixed/unknown context, will not reflect those in analysis for three contexts.

Table 5. Gray whale class use by four social contexts in Bahía Magdalena Complex, Baja California Sur, México, 2006 and 2007.

	Social Context				
Class	Highly Active Adults	Other Adults	Mixed/Unknown	Calf Present	Total
1	168	11	31	41	251
1a*	*59*	*2*	*13*	*14*	*88*
1b*	*109*	*9*	*18*	*27*	*163*
2	9	2	9	6	26
3	9	5	18	8	40
4	14	1	18	27	60
5	1	0	7	9	17
6	0	0	2	9	11
7	7	0	3	4	14
8	0	0	0	0	0
9	1	0	1	3	5
10	0	0	2	4	6
11	0	0	0	2	2
Total	209	19	91	113	432

**Not included in totals*

Use of subclass 1a was significantly different across four social contexts (Wald chi-square=13.67, p=0.0034) (Figure 48). Specifically, highly active adults were significantly more likely to use 1a than other adults (contrast test, Wald chi-square=13.30, p=0.0003).

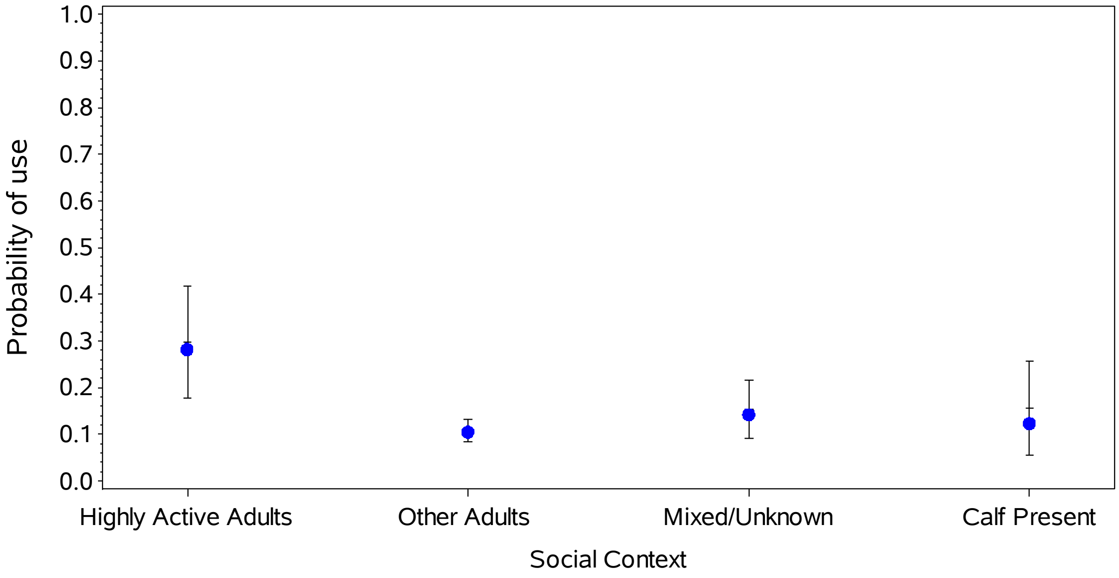

Figure 48. Plot of predicted use of subclass 1a by four social contexts. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Use of class 3 varied significantly by social context (Wald chi-square=24.18, p<0.0001) (Figure 49). Other adults used class 3 significantly more than highly active adults (Wald-chi square=5.75, p=0.0165).

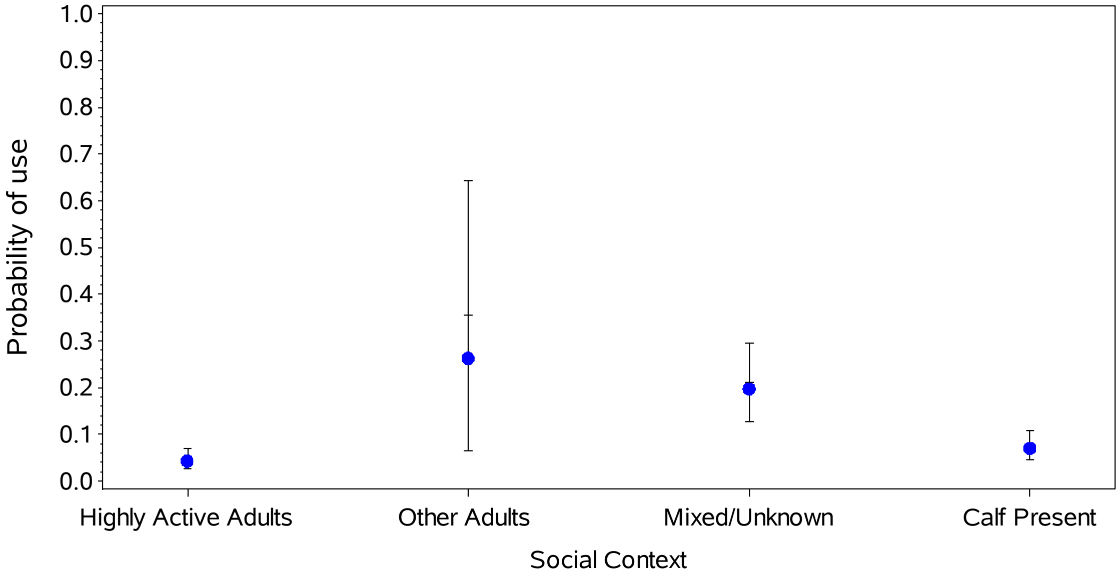

Figure 49. Plot of predicted use of class 3 by four social contexts. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Use of classes 5 through 11 (pooled to one "class"), was significantly different across social contexts (Wald chi-square 281.30, p<0.0001) (Figure 50). Although use by highly active adults was low, there was not a single observation of use by other adults, thus there is significantly different use between the two adult contexts (contrast test, Wald chi-square 203.86, p<0.0001).

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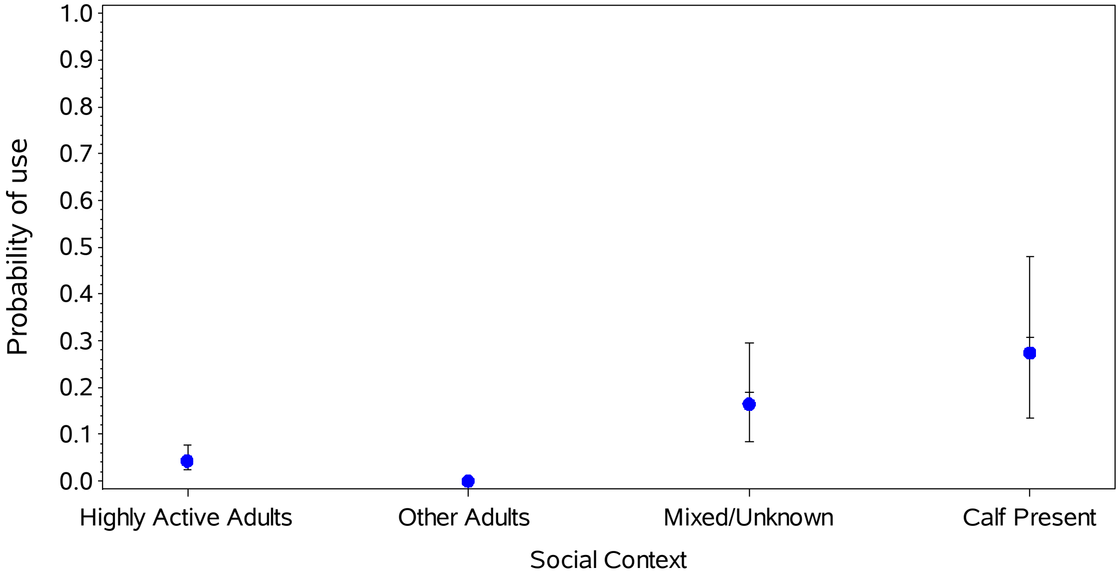

Figure 50. Plot of predicted use of classes 5-11 (pooled) by four social contexts. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Additionally, use of complex type sounds was significantly different (Wald chi-square=25.56, p<0.0001) (Figure 51). Although not significant at p=0.05, there is a trend of difference in use between the highly active adults and other adults (contrast test, Wald chi-square=3.43, p=0.0641).

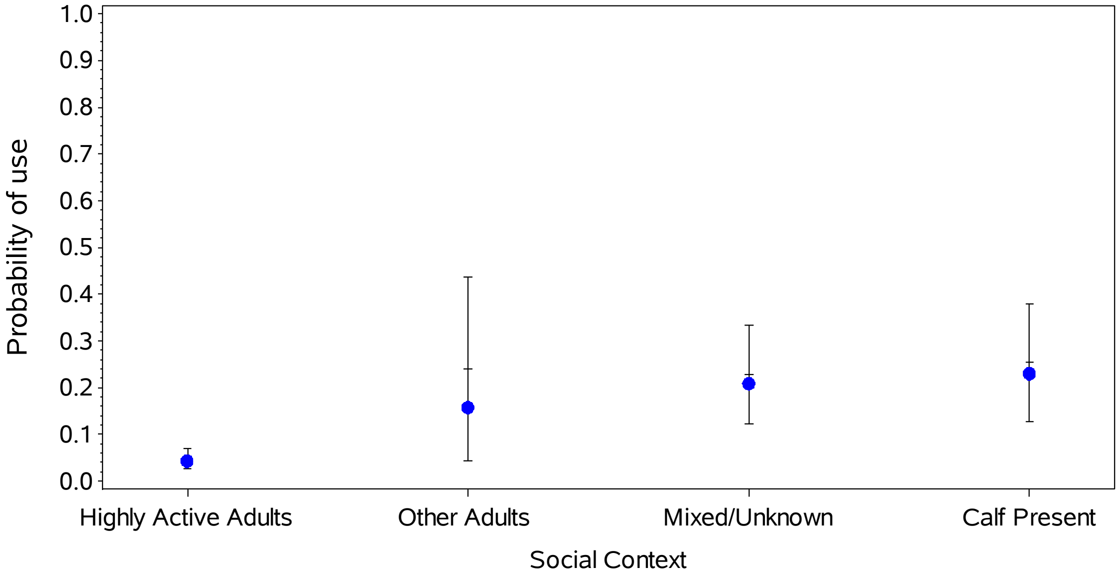

Figure 51. Plot of predicted use of complex sound type by four social contexts. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Analysis of individual rates (sounds/min/whale) by four social contexts found that rates varied significantly by social context (F=32.42, p<0.0001) (Figure 52). In contrast tests, highly active adult rates were significantly greater than those of calf-containing groups (F=48.71, p<0.0001). Individual rates (sounds/min/whale) of highly active adults were significantly lower than individual rates of other adults (F=5.92, p=0.0202). However, caution is warranted in drawing conclusions from this analysis; highly active adults had sample size of 4 sessions; other adults had sample size of only 2 sessions. This analysis indicates that there may be important differences between the two adult contexts; with a larger sample size, the difference in rates will be clearer. Of the six adult sessions with the highest means, four were of highly active adults.

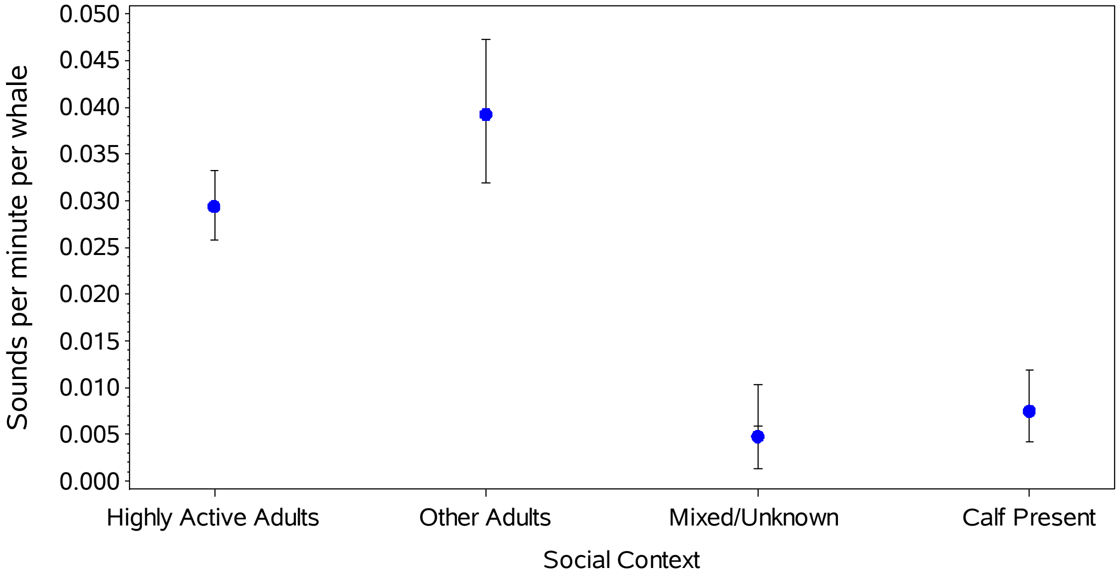

Figure 52. Plot of predicted rates of sound production by four social contexts. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Modeled by four social contexts, significant differences were found in group rates (sounds/minute) of sound production as well (F=12.72, p<0.0001) (Figure 53). Group rates of highly active adults were significantly greater than that of other adults (F=13.22, p=0.0009). Highly active adults had group rates significantly greater than calf-containing groups as well (F=12.53, p=0.0012). Calf-containing groups and other adults have similar group rates, but calf-containing groups had group rates significantly greater than mixed/unknown groups (F=5.23, p=0.0283).

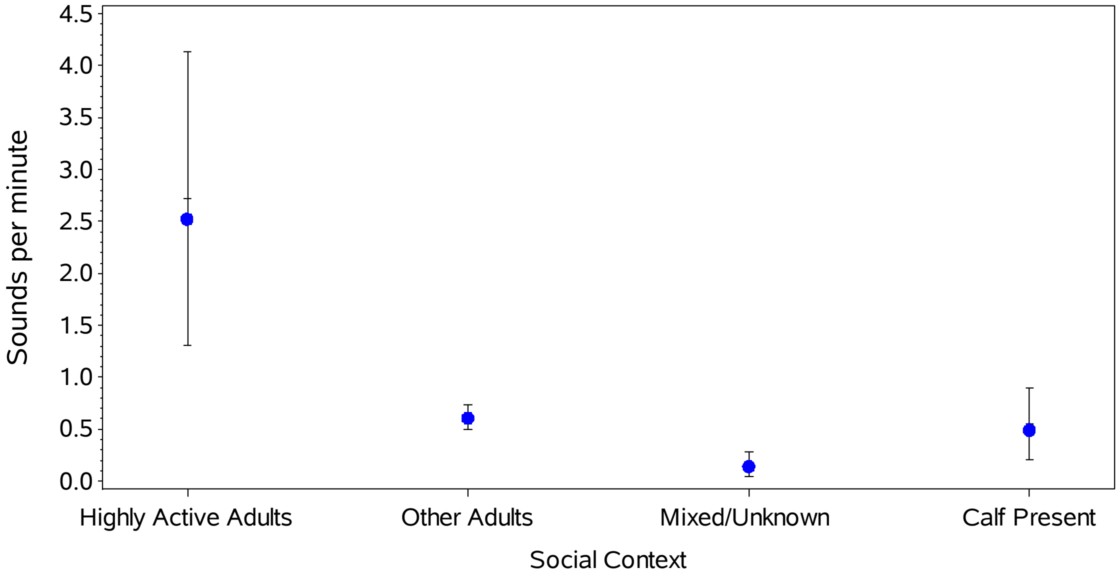

Figure 53. Plot of predicted group rates of sound production by four social contexts. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

IV. DISCUSSION

To interpret the function of gray whale sounds, this study observed use of classes, unique parameters and rates of sounds produced in particular social contexts. In an effort to investigate, confirm and streamline the gray whale repertoire, this study also examined classes of sounds produced and the acoustic parameters of each class. In general, frequency-related parameters of all sound classes showed variation among social contexts, but duration demonstrated very little variation among contexts. Class 1 appears to be critical during sexual contexts and all highly social contexts, regardless of age and sex class. Although highly recognizable, its parameters exhibited much variation among social contexts and therefore class 1 may communicate graded emotional and behavioral states in short-range contexts. Other classes of sounds may be utilized for long-distance communication, as startle responses, or "precursors" to the adult repertoire. Sound production rates also vary by social context. Adults produced sounds at high rates during short intervals; mixed/unknown groups were often silent. Calf-containing groups produced sounds at intermediate rates and were never silent.

This study found no new classes of sounds; it appears that the eastern gray whale repertoire has been well described. This study confirms that the gray whale repertoire consists of simple, short, low frequency sounds. Some classes are pulsed in nature (classes 1 and 4). A few sounds may be non-vocal in production (classes 5, 6, and 11). Classes previously described (Dahlheim *et al.*, 1984; Moore and Ljungblad, 1984; Clark, 1990; Crane and Lashkari, 1996; Wisdom, 2000; Ollervides, 2001) were observed in this study, with the exception of class 8. However, classification, although improving, has few structured guidelines and continues to be relatively subjective. Thus, classes continue to "evolve," as this study confirms the division of class 1 into subclasses 1a and 1b.

There are several challenges that must be overcome in classification. Gray whale sounds are of relatively low sound-to-noise ratio and low frequency ranges (Cummings *et al.*, 1968; Wisdom, 2000). Furthermore, sound types are not often stereotyped or may be graded intermediates, and it is difficult to establish well-defined parameters to use in classification; this appears to be a common phenomenon in mysticete repertoires (Chabot, 1988; Würsig and Clark, 1993) as well as odontocetes (Boisseau, 2005; Diaz-López and Shirai, 2009). Finally, the classification system is not firmly established, as it has been modified several times since its initial use (Wisdom, 2000; Ollervides, 2001). However, because this study confirmed all classes added by Ollervides (2001), except class 8, and this study did not add any other novel classes, the gray whale repertoire may be considered well described, but not necessarily easily classified.

Because gray whale sounds lack stereotypy and exhibit fluidity, we continue to have difficulties in establishing stable classification. Although the gray whale repertoire may be well described, these characteristics do not provide for simple, objective classification. Moore and Ljungblad (1984) observed classes 1, 3 and 4, but stated that "several miscellaneous sounds could not be so classified." Some classes seem to have observable or audible subclasses (class 1, class 4), but there is great deal of gradation in characteristics as well. During the course of communication with Dr. Sheyna Wisdom, we realized we each had independently come to the conclusion that perhaps these classes are better reorganized as a continuum from pulsed sounds to tonal sounds. In this study, there was considerable difficulty differentiating between class 1b (croak), class 4, and class 9, all of which are pulsed. The tonal sounds presented similar difficulties, in which classes 3, 4, and 5 are not easily discriminated. Additionally, some individual sounds may exhibit dual natures, or segue from one type to another. Thus, a particular sound may not fit into one class, but is rather a hybrid combination of two. Several studies of gray whale sounds have noted such challenges. Petrochenko *et al.* (1991) observed that gray whales rarely produce a single kind of sound, but more often in combinations. Fish *et al.* (1974) described one sound as a "long 'metallic-sounding pulse train' that merged into a low-frequency 'groan'." Likewise, Moore and Ljungblad (1984) also noted that class 4 sometimes occurred at end of class 1 burst.

It has already been suggested that the southern right whale (*Eubalaena australis*) and bowhead (*Balaena mysticetus*) repertoire are best described as existing on a continuum, with some types of sounds more common than others (Clark, 1982; Clark and Johnson, 1984). Difficulties in classifying sounds are often compounded by environmental effects on quality of calls, such as ambient noise, attenuation and degradation (Clark and Johnson, 1984). North Atlantic pilot whale (*Globicephala melaena*) whistles have been described as a continuum from simple to complex, with series of intermediates (Taruski, 1979). More recently, a study of long-finned pilot whale (*Globicephala melas*) pulsed calls observed "that there are no clear call types except for an apparent dichotomy based on the maximum frequency of the highest visible sideband;" such a division may indicate long- and short-range functions (Nemiroff and Whitehead, 2009). Killer whales also produced aberrant sounds that appeared to be highly modified or distorted from a more common click, whistle or pulsed call (Ford, 1989). Vocalizations of false killer whales (*Pseudorca crassidens*) have been described as a continuum from pulse trains to whistles, and some vocalizations demonstrated gradual modulation or rapid shifts between types (Murray *et al.*, 1998). If sounds exist in continuum rather than discrete types, their functions may not be discrete, but may rather indicate graded levels of arousal (Murray *et al.*, 1998). Murray *et al.* (1998) used "duty cycle" (i.e., proportion of time sound is "on" during entire duration) as one common, graded measurement to organize false killer whale vocalizations on a continuum.

Due to similar confounding factors, many sounds produced by gray whales are not easily classified. I have surveyed researchers experienced in classification of gray whale sounds. A small sample (n=29) of sounds, including other biological sounds (e.g., dolphins, sea lions, snapping shrimp) as well as non-biological sounds, was reviewed by two other gray whale researchers (F. Ollervides, N. Crane) and me. Agreement was mediocre to poor. More than 70% of the sounds had at least 2 reviewers agreeing upon the source (gray whale or other). However, only 24% of the sounds had agreement among all three observers as to the source (gray whale or other) of the sound. Of sounds agreed upon as produced by gray whale, only 25% (4/16) of these gray whale sounds were similarly classified by two reviewers. There was no instance of all three reviewers agreeing on classification of potential gray whale sounds.

At times, it is difficult to distinguish faint or subtle sounds as created by gray whales or the environment (ambient, biological, or even mechanical) (Dahlheim *et al.*, 1984). Crane and Lashkari (1996) as well as Wisdom (2000) also struggled to detect and analyze the gray whale's low level sounds in high ambient noise levels. Cummings *et al.* (1968) observed that underwater blow sounds were indistinct or completely masked by noise when more than 100 m from the hydrophone, with a mean source level of 112 dB re 0.0002 dyn cm^2. Such environmental noise may be a great hindrance to detecting some gray whale sounds, especially those of low frequency, and may have resulted in biases against some classes of sounds.

Due to poor agreement among researchers and lack of objective classification guidelines, I propose reconsideration of the current classification system. It may be more objective, complete and biologically accurate if these sounds are organized along a continuum. However, this does not necessarily disregard the current classes; rather, they may well exist as recognizable clusters or regions along a continuum. In addition to classifying into traditional classes, sounds in this study were also organized into simplified types of pulsed, tonal, and complex.

Class parameters

Descriptive statistics of sound parameters in this study support previous studies' observations on the characteristics of the gray whale repertoire. The sounds are very brief; most means were less than 2.0 seconds. These sounds are produced in a very low frequency range; the highest frequency mean for any class was 2409.59 Hz (class 10), and the greatest maximum frequency was 445.30 (class 11).

Statistical comparison of subclasses 1a and 1b supports the findings of the first study to distinguish these two subclasses (Wisdom, 2000); these are aurally and statistically distinct subclasses. In both studies, comparison of several parameters detected statistically significant differences. While sounds and their parameters were collected both from a captive gray whale calf, JJ, and wild mother-calf pairs in San Ignacio Lagoon, Wisdom (2000) used only JJ's parameter means for statistical tests. Wisdom (2000) found number of pulses, pulse duration, and inter-pulse interval to be statistically significant. Likewise, this study also found number of pulses and inter-pulse interval to be significantly different. In both studies, inter-pulse interval of 1b was greater than 1a. Additionally, this study found that mean high frequency and mean bandwidth were also significantly different. This study found that mean high frequency of 1b was greater than that of 1a. Likewise, bandwidth of 1b was greater than that of 1a by 300 Hz. Although these parameters were not found to be statistically significant for JJ's means, they exhibit similar trends. JJ's maximum frequency was not statistically tested, but the mean maximum frequency for 1b was very similar to that of this study. The maximum frequency of 1a did not share similar trends; Wisdom's (2000) study found 1a's maximum frequency to be lower than that of 1b; this study found 1a's maximum frequency to be slightly greater than 1b, but no significant difference was observed.

Although not tested for significant difference, the low (minimum) frequency of mother-calf pairs in Wisdom's (2000) study showed means very similar to this study; 1b had slightly higher low frequency means than 1a. Additionally, the mean low frequencies of class 1 determined by Dahlheim (1984) and Ollervides (2001) were very similar to the actual means of this study.

This study found that mean high frequency of 1b was statistically greater than that of 1a, with a difference of 300 Hz. Most studies, considering only class 1, had mean high frequency one to two times greater than this study's (Dahlheim *et al.*, 1984; Crane and Lashkari, 1996; Ollervides, 2001).

In the study of captive calf JJ, total duration of 1b was greater than 1a, but the difference was not statistically significant (Dahlheim *et al.*, 1984). This study also found that subclass 1b's greater duration was not statistically significant. In general, this study's mean duration of class 1 was very similar to those in other studies; some were slightly longer (Dahlheim *et al.*, 1984) and some were slightly shorter (Crane and Lashkari, 1996; Wisdom, 2000).

This study determined that the subclasses had similar number of pulses. The number of pulses in class 1 determined by this study was very similar to that found in Ollervides (2001) and Crane and Lashkari (1996). However, Wisdom's (2000) study found each subclass to have more pulses than its respective counterpart in this study. Additonally, Wisdom (2000) observed that subclass 1a had significantly more pulses in each sound than 1b. Subclass 1a had a pulse rate of 1 pulse/sec greater than subclass 1b.

Like Wisdom's (2000) study, this study also found inter-pulse interval of subclass 1b to be significantly greater than 1a. Similarly, Wisdom's (2000) study also found individual pulse duration of subclass 1b to be significantly greater than 1a. This study found the individual pulse duration of 1b to be greater, but detected no significant difference. Although both this study and Wisdom's (2000) found the inter-pulse interval of subclass 1b to be greater than 1a, this study's inter-pulse intervals were two to three times greater than their counterparts in Wisdom's study. Future studies should consider parameter changes with age, which may be either maturation or learning.

Interestingly, JJ's mean low and high frequencies were consistently two to four times greater than those of mother-calf pairs both in Wisdom's (2000) study and the means determined in this study. This may be an artifact of the man-made recording environment in contrast to natural lagoons. Nevertheless, JJ's mean durations of each signal were also noticeably shorter than the respective mean durations of wild mother-calf pairs (Wisdom, 2000). This difference may not be so easily explained by the man-made environment in which JJ was raised and observed. Therefore, as will be discussed later, this may introduce the hypothesis that calves produce signals of higher frequencies and possibly shorter durations, until growth and social learning develop the adult repertoire characterized by lower frequencies and longer durations (Wallschläger, 1980; Caldwell *et al.*, 1990; Tubaro and Mahler, 1998; Sousa-Lima *et al.*, 2002). This difference is compounded because JJ lacked the social circumstances in which a gray whale calf may need to learn and develop use of appropriate parameters.

Class 2 had a mean high frequency very similar to the mean determined by Dahlheim *et al.* (1984), but mean low frequency, bandwidth and maximum frequency observed in this study were much lower. In Dahlheim's (1984) study, class 2 had the shortest mean duration. In this study, there were two classes with shorter mean duration.

Class 3 had consistently low mean low, high and maximum frequencies both in this and Wisdom's (2000) study. It also had narrow mean bandwidth in both studies. However, JJ's mean frequencies, although lower than those in other classes, were consistently two to three times greater than those produced by mother-calf pairs in Wisdom's (2000) and in this study. Another notable difference was duration; this study's mean duration was twice as great as JJ's (Wisdom, 2000). Crane and Lashkari (1996) observed mean bandwidth, maximum frequency and duration very similar to those of this study. Dahlheim *et al.* (1984) calculated mean high frequencies much greater than this study, and therefore had a greater bandwidth as well. Mean duration in Dahlheim's (1984) study was almost twice as great as this study's mean duration. Ollervides (2001) observed means very similar to Dahlheim's study, except duration which tended reflect the short duration observed in Wisdom (2000).

The structure of low frequency sounds with little frequency modulation, such as class 2 and 3, appears to indicate their use as long distance communication sounds. Frequency ranges of ambient noise appear to influence optimal frequencies for transmission of bird song, thus allowing long distance communication (Brenowitz, 1982a; Brenowitz, 1982b). Also, emphasized frequencies vary by habitat, and songs in each habitat often fall within relatively quiet spectral regions, thus reflecting use of a particular "frequency window" (Morton, 1975; Ryan and Brenowitz, 1985). Morton (1975) proposed that producing sounds with a narrow frequency range permits greater source amplitude at that frequency. Dahlheim (1987) also observed that emphasized frequencies of gray whale sounds occur where biological and physical sea noise has less energy. These narrowband sounds may also travel more efficiently over wide-band ambient noise (Morton, 1975; Brenowitz, 1982b). Terrestrial noise may be rain or wind through the leaves; in marine environments, however, ambient noise may be waves and other marine life. Brenowitz (1982b) also hypothesized that these low frequencies are critical to species-specific recognition in long-distance communication; other frequencies that attenuate rapidly over long distances may be useful for individual recognition in short-range communication. Although red wing black birds (*Agelaius phoeniceus*) may use long-distance communication for purposes of territory protection or mate attraction (Brenowitz, 1982b), it is more likely that these low frequency sounds with little frequency modulation function as a contact call, similar to the southern right whale's up call (Clark, 1983). Gray whales may utilize class 3 and possibly class 2 for long-distance communication on the migration route to maintain contact between groups (Crane and Lashkari, 1996).

Class 4 demonstrated a fairly low mean low frequency; mean high frequency, maximum frequency, and bandwidth fell in the middle ground of all classes. This study, Crane and Lashkari (1996), and sounds produced by mother-calf pairs in Wisdom (2000), all shared very similar high frequency and bandwidth means. Dahlheim's (1984) mean high frequency and bandwidth were twice those previously discussed. Additionally, the captive calf JJ observed by Wisdom (2000) demonstrated a much briefer duration, and a very high mean high frequency and therefore a large bandwidth as well. Ollervides (2000) demonstrated a lower mean high frequency and therefore smaller bandwidth than all studies discussed. Duration was fairly short.

Both class 5, bubble blasts, and 6, sonorous bubble exhalations, have parameter means more similar to Dahlheim (1984) than Ollervides (2001). Crane and Lashkari (1996) describe class 5 as "stochastic" in nature, and this is an appropriate description for both classes as observed in this study. Ollervides (2001) found that class 6 had a narrower bandwidth, lower center frequency and longer duration than class 5. In this study as well, class 6 had longer mean duration; however, class 6 also had a wider bandwidth and higher center frequency. These results are similar to those of Dahlheim *et al.* (1984), in which class 6 had a higher low frequency, higher maximum frequency and slightly longer duration than class 5. Crane and Lashkari (1996) describe class 5 as "subsurface exhalations and bubble blasts (rapid release of air underwater)"; their study observed no occurrences of class 6. It is likely that upon closer analysis, some of these may be distinguished as class 6. Class 5 and class 6 appear to be the only sounds produced in the water, rather than mechanisms within or on the whale's body. Additionally, these are the only classes directly attributed to a specific behavior (Crane and Lashkari, 1996). Würsig and Clark (1993) describe typical blow sounds (exhalation and inhalation above water surface) of bowhead whales as "noisy with unstructured, broadband energy mostly between 100 and 400 Hz and durations of 1-2 sec." Distinct from the normal blow was an underwater blow, described as "similar to the exhalation noise from a SCUBA respirator: a sustained 2-4 sec, high-frequency, broadband noise mixed with a chorus of lower-frequency, short-duration broadband gurgles" (Würsig and Clark, 1993). Würsig and Clark (1993) proposed that longer duration of subsurface exhalation is due to the time required for bubbles to reach the surface. It is possible that class 6 is distinguishable from class 5 only by length of duration due to slower release of exhalation, which may be controlled by the whale for some purpose.

Wisdom (2000) described a rumble that had not been included previously in the gray whale repertoire. Ollervides (2001) soon thereafter expanded the repertoire with several new classes. Based on acoustic parameters described by Wisdom (2000), the rumble may be best represented by class 7. In this study, class 7 had a mean low frequency very similar to that of Ollervides (2001). The mean high frequency in this study was a bit lower than that observed by Ollervides (2001), and therefore mean bandwidth of this study was also a bit smaller. Mean maximum frequency observed in this study was also a bit lower than that of Ollervides (2001). Mean duration observed in this study was slightly longer than that of Ollervides (2001).

There were no observations of class 8.

Class 9 was very similar to all parameter means observed by Ollervides (2001). It is very similar to classes 4 and 5 in frequency ranges, but had a higher maximum frequency. It also shared the same duration as class 5; only class 6 had a longer mean duration.

Classes 10 and 11 combined have four of the most extreme mean parameters. Class 10 had highest mean high frequency and greatest mean bandwidth; class 11 had highest mean low and maximum frequencies. Six out of the eight occurrences of these classes were in the presence of calves. The remaining two occurrences were assigned "unknown/mixed" as social context; however, at least one session had calves present for a portion of the time. Such extreme parameters are an indication that the complex or rare sounds may be produced by calves, either as anomalous sounds while learning, or necessary for the mother/calf relationship.

Although actual mean parameters of class 11 were not as extreme as those observed in Ollervides (2001), the relative relationship to other classes in this study was similar to that in Ollervides (2001). The mean high and maximum frequencies, as well as bandwidth, were greater in Ollervides (2001) than in this study. Although not nearly as high as those in Ollervides (2001), this study observed class 11 to have the highest mean maximum and low frequencies of all classes. Furthermore, this class had a relatively large bandwidth and mean high frequency when compared to other classes in this study.

Class parameters by social context

Frequency-related parameters showed much more variation among context than duration. Duration is unlikely to reflect emotional states or indicate a sound's function, as it demonstrated very little variation among contexts. Because social context as defined in this study may to some degree reflect age class, frequency parameters may not only vary with emotional state, but also with physical growth and learning. Variability of parameters within a class of sound, and gradations between classes, may indicate ability to alter parameters and convey information about behavioral state or status, as is suggested for pilot whales (Nemiroff and Whitehead, 2009) and false killer whales (Murray *et al.*, 1998).

Calf-containing groups generally exhibited greatest means and most varied values of low, high and maximum frequencies. Mixed/unknown groups demonstrated slightly lower and less varied frequencies, with the exception of class 1, in which mixed/unknown had the greatest mean low frequency. The lowest and least varied values of low, high and maximum frequencies were observed in adult groups. These differences were most readily observed in classes 1, 2, and 3. Additionally, classes 10 and 11 often had the highest frequency values; moreover, these classes were never observed in adult groups. These results may indicate that physical maturity or learning play a role in the repertoire development. As young gray whales grow and mature, frequencies may become lower and repertoire is honed; the highly variable sounds (class 10, 11, and possibly 7 and 9) may then disappear as the smaller and more stereotyped adult repertoire is learned.

Most significantly, calves may produce generally higher frequencies due to smaller body size if sound production mechanisms are related to anatomical factors such as tracheal length resonance capacity (Wallschläger, 1980; Tubaro and Mahler, 1998). Ryan and Brenowitz (1985) confirmed that there is a negative correlation between body size and emphasized frequencies of bird song. Additionally, low-frequency yodels produced by common loons (*Gavia immer*) indicated larger body mass (Mager *et al.*, 2006). This is largely due to mass of vibrating structure responsible for sound production (Wallschläger, 1980). These results may be analogous to this study's observations, but there is currently limited knowledge about the possible sound-producing organ(s) in gray whales and mysticetes in general. Recent studies may have discovered a vocal fold homolog in mysticetes, which may produce vibrations; the laryngeal sac may serve as a resonant space (Reidenberg and Laitman, 2007). Future studies may determine if the size of these anatomical features co-vary with frequencies. Matthews *et al.* (1999) analyzed tonal calls of many cetacean species, and found an inverse relation between body size and tonal call frequency, although the correlation was stronger in odontocetes than in mysticetes. It appears this study used a mean length for each species (Matthews *et al.*, 1999); there may be a stronger negative correlation between body size and call frequency when further analyzed by individuals and across age classes.

Dahlheim (1987) found that during experimental exposure to engine and oil drilling noises, gray whale sounds exhibited increased sound levels, frequency modulation, pulses per series and repetition rate. However, sound duration, frequency range, and emphasized frequency bands were not significantly different from controls. This indicates that the frequency differences (high, low, max and bandwidth) found among social contexts in this study may be due to physiological restraints, rather than behavior modifications in various contexts.

Duration varied less among social contexts than other parameters. Calf-containing contexts produced calls with only slightly greater duration than adults and mixed/unknown contexts. In particular, classes 6 and 9 had longest durations; these sounds were only observed in mixed/unknown and calf-containing groups. In a study of manatee (*Trichechus inungius*) sounds, there were no detected differences in duration between sexes of manatees, while all other measured parameters differed significantly (Sousa-Lima *et al.*, 2002). However, manatee calves had smaller mean duration than adults and subadults (Sousa-Lima *et al.*, 2002). Additionally, younger Atlantic bottlenose dolphins (*Tursiops truncatus*) produced whistles of shorter duration than adults (Caldwell *et al.*, 1990). While the results of this study seem to be contradictory to those of other cetacean studies, it cannot be certain that the sounds of long duration are produced by the calves in calf-containing groups. It is possible that the mothers in these groups are producing sounds of greater duration, thus negating or masking (i.e., influencing the mean) any sounds of shorter duration produced by calves.

Although not considered in this study, one would not necessarily expect parameter differences between gray whale sexes, at least not based on size/morphology. Sexes are very similar in size; female length averages less than 1 meter more than males (Jones and Swartz, 2002). Therefore adult sounds many not demonstrate differences in parameters due to size, e.g., frequency. In contrast, the gray tree frog (*Hyla versicolor*) exhibits sexual dimorphism in its laryngeal morphology, thus there is a physiological source of sex-specific differences in sound production by gray tree frogs (Marsh and Taigen, 1987).

For future studies, it may be advisable to measure and compare more acoustic variables, such as start and end frequency and frequency contours (Miller and Bain, 2000). Moreover, three-dB bandwidth, *Q* ratio and harmonic/sideband interval are believed to be more robust and accurate measurements of a sound's characteristics in high ambient sound levels (Crane and Lashkari, 1996). Alternative analyses may be principal components analysis or other multivariate techniques to determine which variables contribute most to variability (Clark, 1982; Dunlop *et al.*, 2007; Nemiroff and Whitehead, 2009).

Frequency parameters exhibited more variation among classes and context. It is possible that varying frequencies may convey different information. Furthermore, some of these differences to be due to physical growth or repertoire learning. Duration showed much less variation; it is less likely to convey information, reflect physical maturation or repertoire learning. Future studies may further clarify the function of parameter variations if individuals producing sounds can be isolated. Additionally, other contexts that may be investigated include sex and aggression levels.

Class 1 subclass parameter variations by social context

Generally, calf-containing contexts exhibited the highest parameter means. However, mixed/unknown contexts had significantly higher mean low frequencies and inter-pulse intervals for both subclasses. Small sample size of class 1 subclasses from mixed/unknown contexts may have contributed to this anomaly; it was less than half the sample size of calf-containing contexts. Alternatively, higher means may be valid and represent the possible presence of immature whales in the mixed/unknown contexts. This unexpected difference may be heightened if the means of calf-containing contexts are lower than calves alone would produce, due to the presence of adult mothers. If calf sounds could be isolated, their mean low frequency may be greater than mixed/unknown contexts, as would be expected if smaller bodies produce higher frequencies (Wallschläger, 1980; Tubaro and Mahler, 1998).

Similarly, greater inter-pulse interval means may be observed in future studies if calf-produced sounds can be isolated. Learning or maturation may be critical to controlled use of this acoustic element; this will be revealed if sounds produced by calves could be isolated. This phenomenon may also explain why there was no distinction in pulse rates (# pulses/second in series) between the two subclasses in mixed/unknown contexts; in adult and calf-containing contexts, subclass 1a had greater pulse rates than subclass 1b. The similar rates found in mixed/unknown contexts may be due to the possible presence of immature whales, which may still be learning the repertoire and have yet to develop and control the rates distinctive to each subclass. The pulse rates exhibited in calf-containing contexts, which were distinct between subclasses, may be more similar to the subclass difference observed in adult contexts due to the presence of mother whales in calf-containing contexts. Had the sounds of calves been isolated, perhaps the pulse rates of subclasses would not exhibit this distinction. Juvenile killer whales did not produce regular call sequences, as adults did; this is currently attributed to inability to correctly convey their motivational state (Rehn *et al.*, 2007). Odontocetes can vary pulse rate, often inversely with target distance (Simard *et al.*, 2010). Although gray whales are likely not echolocating, class 1 is the most frequently used sound class, and contains much variation in number of pulses and pulse rate. Gray whales may vary pulse rates to convey information.

A less likely possibility when reviewing subclass parameters is that the variations are due to drift, directional change, or progressive structural changes in a population, similar to that of the humpback song (Winn and Winn, 1978; Cerchio *et al.*, 2001; Eriksen *et al.*, 2005). There is other evidence in gray whale sounds that parameters vary across years. Gray whales in their northern feeding grounds produced class 1 sounds that varied in parameters at two sites in two successive years; while duration remained constant, frequency of maximum energy and inter-pulse interval were significantly different (Moore and Ljungblad, 1984).

Relative use of classes

In contrast to other studies, this study found less use of class 1 in general and greater use of the remaining classes (Table 6). The proportions of sounds observed and classified in this study are surprising when compared to the results of other studies. Previous studies in the southern wintering lagoons found that almost 70% or more of all sounds were class 1 (Dahlheim *et al.*, 1984; Wisdom, 2000; Ollervides, 2001). On the migration route, less than 40% were class 1, but almost half were class 3 (Crane and Lashkari, 1996). The proportion of class 1 in this study is an intermediate between other studies in the wintering lagoons and the migration study (Table 6). However, the relative use of type 3 in this study is much less than the migration study (Crane and Lashkari, 1996).

The differences in relative use of repertoire may be the result of subjective and difficult classification. Although both visual and aural methods are used, the human eye and ear are still subjectively deciding classes that are vaguely defined. It was my objective and hope that this study has to some degree improved an imperfect classification. Additionally, the original objective of this study was to classify all classes of sounds; extra effort was required to classify difficult, complex, and more variable classes. It is possible that I put forth more effort and time when discriminating among classes, therefore had more diverse repertoire. Class 1, although it has graded characteristics, is very distinctive; in other studies, less identifiable sounds may have

Table 6. Comparison of gray whale repertoire use throughout its range.

	Southern Wintering Lagoons (México)				**Migration (California)**		**Northern Feeding Grounds (Alaska)**			**Captive Calf**
Class of Sound	This study 2009	Ollervides 2001	Wisdom 2000	Dahlheim et al 1984	Cummings et al 1968	Crane & Lashkari 1996	Moore & Ljungblad 1984	Dahlheim 1987	Petrochenko et al 1991	Wisdom 2000
1	58.1%	83.5%	69.7%	79.5%	4.8%	37.6%	92.0%	26.4%	59.0%	66.7%
1a*	*20.37%*		1.8%							50.0%
1b*	*37.96%*		67.9%							16.7%
2	6.0%	2.8%		4.2%						
3	9.3%	1.6%	2.9%	5.6%	87.4%	46.5%	3.7%	5.7%		17.2%
4	13.9%	4.2%	21.9%	4.2%		4.3%	4.3%	11.3%		16.1%
5	3.9%	1.4%		4.2%	2.2%	11.6%			21.0%	
6	2.6%	0.2%		2.1%	5.6%			56.6%		
7	3.2%	2.7%								
8	0.0%	1.8%								
9	1.2%	0.4%								
10	1.4%	0.4%								
11	0.5%	0.9%							8.0%	
Other			5.5%						12.0%	
Total (n)	432	976**	489	708	231	258	438	53	100	366

**Percentage of total repertoire*

***Personal communication (via email 6/17/2010)* been overlooked. Quieter vocalizations, those with smaller sound-to-noise ratio, are more easily and likely to be masked by ambient noise; if sounds are not entirely audible, they may not be classifiable or their parameters not measureable (Miksis-Olds and Tyack, 2009). Finally, the use of various recording systems in different environments, with variable ambient noise levels, will produce different "filters" through which sounds must be recognized. For example, if hydrophone used in this study was more sensitive, it would therefore pick up more sounds with better sound-to-noise ratio.

However, a difference in repertoire use could be a result of this study's very small sample size (n= 10:09 hrs:min) compared to other studies. Other studies ranged from 23.8 recording hours with isolated mother-calf pairs (Wisdom, 2000) to almost 600 hours of recordings (Dahlheim, 1987). Furthermore, our sampling began several weeks after the whales arrived at Bahía Magdalena. It has been documented that the composition of whales and their use of the bay changes over the weeks and months (Jones and Swartz, 1984; Pérez-Cortés *et al.*, 2004). Specifically, single whales leave the bay several weeks earlier than mother/calf pairs (Jones and Swartz, 1984) and are observed approximately one month earlier on the northward migration (Herzing and Mate, 1984). Norris *et al.* (1983) observed a possible peak of adult whales in entrance aggregations in January, but Jones and Swartz (1984) observed a peak of single adult whales in mid-February. The earliest recordings in this study (mid-February) may have been directly coinciding with or after the peak of adult social and sexual aggregations. Therefore, this study is clearly not representative of the entire season in the southern lagoons. While Dahlheim (Dahlheim *et al.*, 1984; Dahlheim, 1987) recorded many more hours, the duration of several of her field seasons in Laguna San Ignacio were later in the season and/or of shorter duration than this study. Additionally, while some studies recorded for 24 hours continuously (Dahlheim, 1987), this study was limited in its resources and recording times always occurred between 9 a.m. and noon local time (0900 and 1200). If there is any diel variation in gray whale sound production, such a limited window of observation is providing a small slice of the entire picture and may skew actual use of gray whale repertoire. However, this is not expected, as neither Dahlheim (1987) nor Wisdom (2000) observed any periodicity in sound production.

Finally, lower relative use of class 1 may have been a product of this study's objectives to observe several social contexts. There may have been increased effort to record mother-calf pairs, relative to other studies.

Class 1 is the most frequently used sound in the gray whale repertoire, and it is used in all contexts. Law of word meaning, in which a more frequently used word has more meanings (Ferrer-i-Cancho and McCowan, 2009), may apply to class 1. Therefore, it may have many meanings, some of which may be distinguished by use of class 1 subclasses, varying parameters, as well as visual and tactile communication. In this study, there were several parameters that varied significantly across social contexts. Moore and Ljungblad (1984) also found class 1 to be the most variable sound in the gray whale repertoire while in their summer feeding grounds. There is a similar correlation supporting this hypothesis for dolphin whistles, in which "more frequent whistle types tend to be associated to more behavior contexts," thus it may have more meanings (Ferrer-i-Cancho and McCowan, 2009).

It is still not completely clear if gray whales vary repertoire or sound parameters by season or geography. Only class 3 clearly appears to be associated with a particular environment. Class 3 was significant on the migration route (Cummings *et al.*, 1968; Crane and Lashkari, 1996), and has consistently low use both in southern wintering lagoons (Dahlheim *et al.*, 1984; Wisdom, 2000; Ollervides, 2001) and northern feeding grounds (Moore and Ljungblad, 1984; Dahlheim, 1987). Other baleen whales have demonstrated seasonality in sound production. Minke whale vocal activity was strongly seasonal; although pulse trains were detected between February and November, rates were very low during spring, but peaked in late summer when they were detected in more than 80% of all recordings during August and September (Risch, 2010).

Other classes are not so readily delineated by geography or seasonality. While Moore and Ljungblad (1984) observed very high relative use of class 1 (92%) in northern feeding grounds, similar to several studies in Baja (Dahlheim *et al.*, 1984; Ollervides, 2001), their sample size was extremely small (n=2 hours). This is unlikely to be representative of the sound repertoire on the northern feeding grounds. Additionally, it is not clear when the recordings were collected. It is possible that recordings collected late in the season encountered whales in increasing levels of social activity (Würsig *et al.*, 1986). Therefore, use of class 1 in documented by Moore and Ljungblad (1984) may have been unusually high. Rates of sound production observed by Moore and Ljungblad (1984) were also unusually high, especially when compared to other studies in the northern feeding ranges (Dahlheim, 1987; Petrochenko *et al.*, 1991). More studies with appropriate samples sizes are needed to fully understand how gray whale sound repertoire varies throughout their range and seasons. Classes 5 and 6 appear to have consistently low use in all locations. The remainder of the classes have only recently been described and therefore comparisons cannot be made; earlier studies often referred to several miscellaneous sounds that could not be classified (Moore and Ljungblad, 1984).

Relative use of classes by social context

The class 1 sound (subclass 1b and less frequently 1a) was the sound class used most frequently in all contexts. Adults most frequently used class 1; 73% of all adults sounds were class 1. Although mixed/unknown and calf-containing contexts also used class 1 more frequently than others classes, it was not such a large proportion of their repertoire (31% and 36% respectively).

These results indicate that class 1 appears to be a critical sound during highly social and sexual contexts. While class 1 is highly recognizable, it is not as stereotyped as tonal sound classes 2 or 3. In this study, class 1 subclasses exhibited significant variations in mean high frequency, bandwidth, individual pulse interval, and pulse rate. Several parameters also varied significantly across social contexts. Dahlheim (1987) noted considerable variation in “metallic sounding” character of class 1.

Mammalian repertoires may consists of discrete (distinct, highly stereotyped) and graded calls (Marler, 1967; Ford, 1989). It may be possible and advisable to organize variable sounds, such as class 1, into a continuum demonstrating its graded characteristics in a series of intermediates (Fischer and Hammerschmidt, 2002).

Discrete stereotyped calls may generally be used for long-distance communication (Marler, 1977; Waser and Waser, 1977). In the killer whale repertoire, such calls often have greater source levels and larger active space (Miller, 2006). Thus, they propagate well when communicating with group members out of visual range, and likely allow for localization and coordination of movements (Miller *et al.*, 2004). In the gray whale repertoire, classes 2 and 3 best reflect this structure and function; they are somewhat similar in structure and function to the southern right whale up call (Clark, 1982; Clark, 1983).

Highly variable sounds, like classes 1 and 4, are most likely associated with close-range social contexts. Killer whales produced significantly more variable calls and whistles with higher pitch and more complexity during excited, close-range socializing and beach-rubbing contexts than in foraging or travelling (Ford, 1989; Thomsen *et al.*, 2002). Graded, highly variable sounds appear to be used in close-range circumstances; it is in such contexts where subtleties in sound structure can reflect gradual changes in motivation or emotion, supplemented with visual and physical contact (Marler, 1977; Ford, 1989; Rehn *et al.*, 2007). That graded sounds are more often used in close-range communication is also documented in canines, felines and primates (Marler, 1977; Peters and Tonkin-Leyhausen, 1999; Robbins, 2000; Fischer and Hammerschmidt, 2002). Hybrid and pulsive calls together were the majority of sounds produced in sexually active southern right whale groups; these groups did not produce any simple tonal calls (Clark, 1983). In this study, gray whale adult sounds generally had lowest frequency values, but class 1 consistently had high values of high and maximum mean frequencies in all social contexts. Class 1 was used frequently by socializing and courting adults; such relatively high frequencies and variability (i.e., number of pulses, pulse rates, inter-pulse interval) may convey important motivational information in these close-range interactions.

Additionally, the use of variable and aberrant calls by killer whales is often in direct proportion with the level of activity (Ford, 1989). Further analysis of this study's data and future studies may reveal if this is also observed in gray whales. The use of subclass 1a by a captive gray whale calf was associated with high activity states (Wisdom *et al.*, 2001).

With confirmation of this study's results, subclasses 1a and 1b should be considered established as statistically distinct (Wisdom *et al.*, 2001). It would be expected that these subclasses may function differently. Subclass 1a occurred in all contexts. However, adults in this study used 1a significantly more than other contexts. It is notable that more than half (54.5%) of all observations of subclass 1a occurred in three highly social adult sessions. One session was also one of four sessions in which breaches were observed. Additionally, whales exhibited rolling, head raises, fluke or flipper swishes and a lateral lunge. A second session was the only session in which adult social behaviors characterized every single minute, indicating high levels of activity for the duration of the session. Furthermore, this is the only session in which a penis was observed. Finally, a third session observed an extremely high number of whales for its entire duration. Ten or more whales were detected for more than half of the session, and six or more whales for 95% (19/20 minutes) of session. Thus the mean number of whales sighted per minute in this session was 8.45, three times greater than the mean of 2.58 whales/minute for all sessions. Wisdom *et al.* (2001) also found that type 1a was associated with the captive calf's high activity states.

Subclass 1b was also used in all contexts. However, 1b was used twice as often as 1a; this trend is consistent in all three contexts. Three sessions that contain the majority of subclass 1b and 1a occurrences were characterized by exceptionally social adult behaviors (see previous paragraph). Therefore, to some degree, 1a and 1b are used together in highly social adult contexts. At this time, it is difficult to distinguish functions for subclasses 1a and 1b. However, because it is used twice as often as 1a, it is possible that subclass 1b has a more general function in high activity states. It is likely that identifying producers of these sounds will provide clarification. Further analysis may reveal a particular sex or age class as producers.

Captive gray whale calf JJ varied use of subclasses 1a and 1b over time; initially 1a was majority, then 1b became majority (Wisdom, 2000). In fact, class 1b was not recorded in JJ's repertoire until 7 months of age (Wisdom 2000). Wisdom believes that the occurrence of 1b was due to lack of reinforcement rather than necessity of vocal maturation or learning. This study can neither support nor oppose this suggestion that delayed use is a natural progression, as individual producers were not identified.

Norris *et al.* (1977) observed stranded gray whale calves producing "low resonant pulses" and "sharp clicks." On these occasions, the sounds were produced while stranded, continued after release, and ceased upon reuniting with their mothers (Norris *et al.*, 1977). These observations strongly suggest that some classes of sound, possibly class 1, 2, and/or 3 (or their related 'precursor' sounds), function as contact calls.

As already mentioned, a critical next step for future studies is to determine who is producing particular sound classes. This will further clarify function when it can be determined which age or sex classes are producing particular sounds. Observations support the hypothesis that focal females in southern right whales surface active groups produce scream calls (Clark, 1983), while there are indications that North Atlantic right whale males produce gunshot calls (Parks and Tyack, 2005). Once age or sex class can be determined, we can better understand the motivational state that is being conveyed with a class of sound. For example, in highly active adult contexts, it would be revealing to clarify if class 1 sounds are produced by aggressive males or alternatively, by distressed females.

Class 2 has been described as an "up/down sweep" by Dahlheim (1987); Ollervides (2001) only described as "upsweep 'whoop'." This study did not observe any downsweeps. Wisdom (2000) did not detect any occurrences of class 2 while recording captive calf JJ or wild mother-calf pairs in Baja. Additionally, there were no observations of class 2 by Crane and Lashkari (1996) on migration route or by Moore and Ljungblad (1984) at northern feeding grounds. However, Crane and Lashkari (1996) indicated there may be subclasses within class 3; some had amplitude modulation while others had frequency modulation. Therefore this sound has been observed only in several Baja lagoons.

The first of several possible explanations for this occasional use is that class 2 may have a very specific function and is not frequently used. Secondly, class 2 sounds have very low mean frequencies and very brief duration. It is possible other studies simply overlooked them or it was difficult to distinguish from ambient noise. Finally, the irregularity of its occurrence, as well as Crane and Lashkari's (1996) suggestion of subclasses within class 3, may indicate that classes 2 and 3 have been combined in some studies. Perhaps those studies that observed no occurrences of class 2 were actually including a broader range of sounds in class 3, and thus there may appear to be more diversity within that class. When reviewing and classifying, various time/frequency resolutions and authors' preferences will affect contour of sounds. An author's subjective opinion of contour will be dependent upon the zoom of vertical (frequency) axis used; i.e., upsweep may be overlooked if not viewed with appropriately zoomed vertical axis. If these are classification inconsistencies, there must be more definition of classes and precision in classification.

Regarding function of class 2, Wisdom (2000) stated that Dahlheim (via personal communication to Wisdom, 2000) observed type 2 to possibly be a "startle" response. In this study, boats (other than the research vessel) were present during the minute class 2 occurred or the preceding minute in 81% (21/26) occurrences. Additionally, boat observations were not consistently recorded in the second season; it is possible there were even more occurrences of boats. Moreover, it was observed rarely, but occurred in all three contexts. Brief analysis of this study's data supports the suggestion that class 2 may be a response to boat presence. Future studies may utilize playback experiments to confirm this hypothesis.

Class 3 was the most common sound on the migration route (Cummings *et al.*, 1968; Crane and Lashkari, 1996), and therefore it may function in general as a long-distance contact or cohesion call. In both the northern feeding grounds and southern lagoon studies, its proportion in the repertoire is relatively minor, always less than 6% of entire repertoire (Dahlheim *et al.*, 1984; Moore and Ljungblad, 1984; Dahlheim, 1987; Wisdom, 2000; Ollervides, 2001).

The structure of discrete calls may reflect their function. Studies on primates observed that the mangabey's (*Cercocebus albigena*) 'whoopgobble' was best suited for long-distance communication due to its structure, rather than its source intensity; low attenuation losses were attributed to energy concentration at low frequencies (Waser and Waser, 1977). Southern right whales appear to use discrete calls in a similar manner; discrete calls were often used to maintain contact and appeared to have little function in close-range social contexts (Clark 1982, 1983). Up calls were 68% (34/50) of sounds produced by swimming right whales and were used in significantly greater rates in swimming contexts than any other context (Clark, 1982; Clark, 1983). Sexually active groups did not produce any simple tonal calls; rather, hybrid and pulsive calls together were the majority of sounds produced in sexually active groups (Clark, 1982).

Killer whales tended to repeat discrete calls when individuals were out of visual range and more widely dispersed, e.g., while foraging and traveling (Ford, 1989). While discrete calls were a majority of killer whale's repertoire in all contexts, the proportion was greatest in foraging and traveling (Ford, 1989). In contrast, variable and aberrant calls were a very small portion of the repertoire in these contexts, and were observed when socializing activities occurred during predominantly foraging or travelling behavior (Ford, 1989). The killer whale N2 sound is the most stereotyped sound across killer whale matrilineal units and was used more often during meetings between pods than any other context, although it had average use during all other contexts (e.g., foraging, traveling, socializing) (Miller and Bain, 2000). This sound, which appears critical during pod meetings, but also necessary in other contexts, may communicate group size, spatial distribution, as well as emotional state to other pods and individuals (Ford, 1989; Miller and Bain, 2000). Although gray whale social structure is not organized into pods, it is likely there may be some exchange of similar information that is required in all or many social encounters. It is therefore hypothesized that structurally discrete sounds, such as class 3, are used for establishing contact and maintaining cohesion when conspecifics are out of tactile and visual range (Marler, 1977; Waser and Waser, 1977; Ford, 1989).

Although class 3 may be most useful during migration, it may continue to function as a contact call in the lagoons, but to a lesser extent. In general, it appears that low use in all studies at southern wintering lagoons (Dahlheim *et al.*, 1984; Wisdom, 2000; Ollervides, 2001) indicates that class 3 occurs in circumstances that rarely exist here. Although class 3 was a greater proportion of repertoire in mixed/unknown contexts, there was no significant difference among contexts. Mixed/unknown contexts may have been the most spatially dispersed of all social contexts in this study, and their traveling and milling behaviors in Bahía Magdalena may most closely reflect those during migration. Therefore it would be expected that the class 3 sound, which appears to be critical during migration, would be most useful during this context. Likewise, analysis by four social contexts revealed that other adults use class 3 significantly more than highly active adults; other adults are much more likely to be traveling, resting or feeding, and did not exhibit social behaviors. Highly active adults engage in close contact during highly social and sexual contexts, and thus may have little need for this call. Calf-containing contexts used class 3, but nearly constant physical contact between mother and calf (Norris *et al.*, 1977) may not necessitate the use of frequent vocal contact.

Wisdom *et al.* (2001) recorded 86% of captive calf JJ's class 3 (total n=63) sounds in two days. After this brief period, use of this call decreased until it disappeared from repertoire completely; in the entirety of the study, it was almost 18% of the calf's repertoire. This observation suggests that reinforcement, and possibly social context as well, are critical. As a captive calf without an adult model, JJ may have been in production or contextual learning stage (Locke, 1990; Janik and Slater, 1997; Janik and Slater, 2000; Wisdom *et al.*, 2001). This may be analogous to human infant "babble" (Kent and Bauer, 1985). Without reinforcement, the calf no longer used this sound. Wisdom (2000) observed that mother-calf pairs used class 3 about 2% relative to other sounds. Similarly, use of class 3 by calf-containing contexts was low in this study (7% of all sounds produced by calf-containing contexts).

Class 4 was second only to class 1 in proportion of repertoire. Although only 13% of all recorded sounds in this study, class 4 was approximately one quarter of mixed/unknown (26%) and calf-containing group (24%) repertoires; only 7% of adult repertoire was class 4 sounds. Calf-containing contexts used class 4 significantly more than adults. Wisdom (2000) observed that class 4 made up 18% of mother-calf repertoire and similarly, 16.1% of JJ's repertoire. However, it appears that captive gray whale calf JJ used class 4 preferentially in the first month of recording. During this first month (7% of all recorded hours), at approximately one or two months of age, JJ produced 30% (18/59) of all class 4 sounds recorded, and quickly tapered off during the following months. Because this study and others observed this sound in the presence of calves (Dahlheim *et al.*, 1984; Wisdom, 2000; Ollervides, 2001), but is observed less frequently in presence of adults, it may be unique to young whales. Although it was observed in this study in the presence of mixed/unknown whales, it may be produced by the immature individuals in these groups.

Moore and Ljungblad (1984) noted that class 4 occasionally occurred at the end of N1 bursts, but class 4 sounds were rarely recorded in presence of feeding whales. Class 4 and class 1 share a pulsed structure, and this study also observed occasions in which a sound type "merged" into class 4. Due to similar structure, examples of "merging" class 1 and class 4, and its use by calf JJ, there is ample evidence to propose that class 4 sounds are a precursor to class 1. It may be produced by young animals developing and learning the repertoire of adults. Occasions of merging sounds may occur during a "babbling" stage or production learning (Janik and Slater, 2000). Immature sounds may or may not initially resemble sounds from adult repertoire, but with time are gradually "molded" into correct structure (Locke, 1990; Doupe and Kuhl, 1999). Such stages have been well demonstrated by human infants and passerine songbirds (Doupe and Kuhl, 1999) and likely exist in bottlenose dolphins (McCowan and Reiss, 1997).

A review of other studies may illuminate a possible function of classes 5 and 6. Würsig and Clark (1993) documented possible association of underwater blow sounds with feeding and socializing bowhead whales and found that surface blow sounds were usually associated with socializing, perhaps due to increased physical activity. Groups of fully active and sexually active southern right whales used short, loud blows, unlike the less intense blows of swimming whales (Clark, 1983). Additionally, harsh blows were used by a mother separated from her calf, by resting whales joined by porpoises or sea lions and also by single resting whales joined by a silent whale (Clark, 1983). Furthermore, underwater blow sounds and loud exhalations in active groups of humpbacks may function as threat displays (Tyack and Whitehead, 1983). These circumstances indicate a function of communicating disturbance or threat, although it may also simply be more pronounced breathing due to increased exertion (Clark, 1983).

Similarly, this study's results provide further evidence that such exhalations and bubble blasts are sounds indicating disturbance or stress. A majority (22/23 occurrences in which boat data were taken) of class 5 and 6 sounds occurred in the presence of boats (other than the research vessel), or in the subsequent minute. Playback experiments and autonomous recorders (i.e., without presence of research vessel) will reveal if this hypothesis can be supported. Some classes of killer whales sounds occurred only in aggressive chase contexts (Graham and Noonan, 2010). As a result, these calls unique to chase contexts, along with parameter variations in more common calls, may readily identify this aggressive context by acoustic observation alone. If such a sound communicates stress or disturbance, conservation management and boaters should use classes 5 and 6 as indicators of a stressed group; restrictions should then be modified to better protect the whales.

Class 7 was used infrequently, but occurred in all social contexts. No unique circumstances provide insight into the function of this sound. In addition to occurring in all social contexts, class 7 occurred during highly social periods, as well as traveling and resting circumstances. Moreover, it occurred in both the presence and absence of boats. Perhaps localization of the producing animal, as well as playback experiments, will begin to clarify its function.

It is not surprising that this study found no occurrence of class 8. It is only described in Ollervides (2001), and in that study occurred rarely, at the same time and location, and in the presence of a calf. The sound recorded by Ollervides (2001) was similar in structure and parameters to class 1 or class 4 pulses. It was likely produced by a calf; therefore it may have been an “anomaly” sound that should have been included in an existing class, rather than creating a new class. As this study suggests, some of the infrequent and unusual sounds may be a demonstration of calf learning (Locke, 1990; Doupe and Kuhl, 1999). This class should be carefully reconsidered, as it may be redundant.

Class 9 was observed in both adult and calf-containing contexts; there were no occurrences in mixed/unknown contexts. Because of small sample size, it is difficult to draw conclusions regarding function. It may be more appropriate to draw conclusions when analyzed as pooled classes (classes 5 – 11), as discussed below. However, at least 3/5 occurrences were in presence of boats, and 4/5 occurred with highly active behaviors, such as fluke or flipper swishing, bubble blasts, head raises or rolling. With the exception of its pulsed nature, it shares an upsweep structure and some parameter features with class 2. This may be a variant of class 2.

As proposed by Ollervides (2001), class 10 may be considered a disturbance sound. Furthermore, data in this study suggest that it may be produced by calves or is at least unique to mother-calf contexts. All observances of class 10 sounds occurred in presence of boats; additionally, 5/6 occurrences were in the presence of at least one calf. One session in particular contained half (3/6) of class 10 sounds observed in this study. In addition to several boats present in close-range for several minutes, at least one juvenile or adult whale was present with the two mother-calf pairs; this also may add stress for mother/calf pairs (Norris *et al.*, 1977).

Class 11 sound was observed only twice; both occurrences were in the presence of calf-containing contexts. The groups observed not only included at least one calf, but also other adults and one unknown whale (unidentifiable as either adult or calf, perhaps due to distance) in each. Additionally, boats were present during both occurrences. In the only other study to observe this sound, it was attributed to whales skimming with baleen (Ollervides, 2001); but this study had no observations of surface-feeding whales. Therefore, neither production nor function of class 11 is clear. Bowhead whales were observed to produce an unusual pair of noisy, broadband sounds, termed "cr-unch," as if produced by two objects rubbed together; however, no surface behavior was observed (Würsig and Clark, 1993).

In an attempt to interpret the function of infrequent sounds, classes 5 through 11 were pooled and analyzed as one. These classes shared similar complex/mixed structures and lack of stereotype. Structure and use of these pooled classes provide possible evidence that these sounds are either specific to mother/calf relationship or "precursor" vocalizations produced by calves that are still developing and honing their repertoire. Human babies produce immature "babbling" and young songbirds produce subsong, but neither of these could be mistaken for adult speech or mature birdsong (Doupe and Kuhl, 1999). Bottlenose dolphin whistle is present at birth, but infants do not produce whistles with a multiloop structure; nor do newborns produce stereotyped whistles, but rather "tremulous and quavery" whistles (Caldwell and Caldwell, 1979).

Aberrant killer whale calls and whistles, which appear to be a distortion of more common sounds (Ford, 1989), may be attributed to maturation or production learning through mimicry (Yurk *et al.*, 2002).

This study did not localize the individual producer of each sound, so it cannot be determined whether mother or calf was producing these mixed/complex sounds. Some unique sounds may be reserved for very specific contexts, and are not applicable to any other circumstances. Such may be the case for some or all of these classes (5—11); these sounds may be unique to mother/calf communication or development of repertoire by calf. For future research, localization is critical to determine if these classes are unique to mother/calf contexts or evidence of learning in young calves. If produced only by calves, such data would indicate learning or maturation. If produced by both or only mother, it is more likely that these sounds are intentional and appropriate in mother/calf context. Northern right whale “warble” appears to be produced only by calves in surface active groups (SAG’s); this sound also has higher pitch and longer duration than adult “screams” and is often characterized by “stuttering pauses” (Parks and Tyack, 2005). These characteristics, like other “precursor” sounds proposed in this study, may indicate that the right whale “warble” is evidence of calves learning the repertoire; it is possibly produced only by female calves, “practicing” SAG behavior (Parks and Tyack, 2005).

There is some indication that unknown/mixed contexts may contain immature individuals without a fully developed repertoire. When modeled as four social states (i.e., unknown/mixed, other adults, active adults, and containing calves), both unknown/mixed contexts and calf-containing contexts had significantly higher probability of using complex type sounds.

Relative use of type

Of the three general types (i.e., tonal, pulsed, complex), pulsed sounds were used most frequently in all three contexts. This complements other studies that propose that sounds with subtle or graded structure variations are used in close-range interactions (Marler, 1977; Clark, 1983; Ford, 1989; Peters and Tonkin-Leyhausen, 1999; Rehn *et* *al.*, 2007). It is likely that gray whales are most gregarious in the southern wintering lagoons. These sites contain the unique contexts of the mother-calf relationship as well as lagoon aggregations (Norris *et al.*, 1983). Complex sounds were used more often in calf-containing and mixed/unknown contexts; use in adult contexts was low. Tonal sounds were used infrequently in all social contexts. The simple structure and low frequency of tonal sounds would be most important in long-range communication. This is confirmed by its greater use on the migration route (Crane and Lashkari, 1996). Bowhead whales were also found to increase use of tonal sounds, and thus relative use of pulsed sounds decreased, as social activities declined during the course of spring migration (Würsig and Clark, 1993).

While this appears to be the first study to simplify the gray whale repertoire, other mysticete repertoires have been described in a similar manner. Bowhead sounds were categorized as simple (frequency-modulated), complex (amplitude-modulated) and song notes (Tervo *et al.*, 2009). Some bowhead sounds could not accurately be described as pulsed or burst, due to broadband nature; rather, a “staccatolike” quality was produced that may be similar to the gray whale sounds this study termed ‘complex’ (Clark and Johnson, 1984). Principal components analysis organized the graded characteristics of the right whale repertoire into a continuum of sounds with varying tonality, pulsiveness, or degrees of frequency modulation; those most common or recognizable along the continuum were given names (Clark, 1983). The most distinct subdivisions in the southern right whale repertoire are the discrete up calls and the remaining variable and graded calls (Clark, 1982; Clark, 1983).

Although baleen whales share many similarities in their repertoire, there are a few distinctions. Clark and Johnson (1984) defined four bowhead calls: tonal frequency-modulated (“simple moans” were most common), pulsed, tonal amplitude-modulated, and complex (i.e., “lion’s roar,” complex moans, complex pulsive calls, and hybrid combinations). In this study, gray whales were not recorded producing any tonal amplitude-modulated (AM) calls. More recently, bowhead whale vocal calls were organized into two general groups: low frequency-modulated (FM) calls and complex calls (Würsig and Clark, 1993). Simple FM calls were further differentiated by their contours; complex calls were further classified as high, pulsed tonal, pulsive, growls and trumpets (Würsig and Clark, 1993). It appears that the bowhead repertoire contains several sounds with more complex structure than gray whale sounds. Gray whales in this study did not produce the harmonically-rich "pulsed tone" call with purr-like quality or the pulsive trumpet call with its mixture of "broadband pulses, FM undertones, and amplitude modulations" (Clark and Johnson, 1984; Würsig and Clark, 1993). However, neither grays nor bowheads exhibited stereotypy in the complex calls, thus creating difficulties in classification and inconsistencies among studies (Clark and Johnson, 1984). Additionally, gray whales in this study had higher probabilities of using pulsed sounds; the majority of sounds used by migrating bowheads were simple FM moans (Clark and Johnson, 1984). Finally, gray whales have not been found to produce long patterned repetition of calls, such as the bowhead's song (Stafford *et al.*, 2008).

Relative use of type by social context

Pulsed sounds were used significantly more by adults; in the southern wintering lagoons, adults are exceptionally social, when compared to other portions of their range. This again confirms hypotheses in other studies that varied, pulsed sounds are likely important in close-range, complex social contexts (Marler, 1977; Ford, 1989; Rehn *et al.*, 2007). Use of highly variable and graded calls by southern right whales is associated with groups of active whales, and therefore may be an indicator of the level and complexity of activity (Clark, 1982). Fully active groups of southern right whales had higher rates of using hybrid calls (mixture of FM sweeps and amplitude modulation) than fully active pairs of animals (Clark, 1983). Additionally, groups of mixed sex southern right whales used hybrid calls at greater rates than either same-sex groups (Clark, 1983). Carolina chickadees (*Poecile carolinensis*) also demonstrated a significant relationship between larger group size and increasingly varied and diverse calls (Freeburg and Harvey, 2008).

Low use of complex sounds by adult gray whales in this study, and greater use in calf-containing and mixed/unknown contexts indicates that these may be precursor sounds to the adult repertoire. Complex sounds, as defined and classified in this study, were often hybrid forms of tonal and pulse sounds, or broadband, but generally lacked stereotyped structure.

Rates of sound production

There appears to be evidence that social/sexual adults may vocalize more, despite results from this study's statistical analysis indicating that there was no significant difference in use among social contexts. It is likely that the statistical tests may misconstrue interpretation of the data, due to small sample size and a major outlier. The session with the highest mean rate of individual sound production was the previously discussed outlier in mixed/unknown context, and therefore may be misleading. It may be more revealing to note that six of the seven sessions with the greatest mean individual rates (sounds/minute/whale) were adult sessions. Three of these adult sessions also had the greatest mean group rates (sounds/minute). In these three sessions, 50/58 (86%) minutes contained highly active adult behavior that was likely courtship or mating. Additionally, three adult sessions with high group rates over short periods were the same three sessions in which class 1 was used frequently. Notably, these sessions displayed behaviors indicating courtship or mating, as these sessions were characterized by large groups of whales exhibiting many social behaviors, often for many consecutive minutes. Additionally, one session included the only observation of a penis in the entire study. However, because of the large number of whales present, individual rates (sounds/min/whale) during these three sessions were only slightly above average.

The short-term peak rates in each social context are also revealing. Both adult (13 sounds/minute) and calf-containing (5.7 sounds/minute) contexts had peaks more than twice that of mixed/unknown (2.3 sounds/minute). Adults vocalized at rates two to three times greater than unknown/mixed contexts and mother/calf contexts.

The number of sessions that were entirely silent is also revealing. Almost half (6 of 14) of mixed/unknown sessions produced no sounds, whereas only 1 of 12 adult sessions were silent. Although calf-containing contexts were occasionally silent for minutes at a time, every calf-containing session produced some sounds; this was the only context to do so. In southern right whales, rates of sounds production had a similar relationship to activity level and context. More than half of resting and swimming groups were silent, whereas all fully and sexually active groups produced sounds (Clark, 1983).

Wisdom (2000) found that isolated mother/calf pairs vocalized at rates of 19.4 calls/hour (Table 7). Captive calf JJ varied rate of production of subclass 1a from 4.5 calls/minute during extremely high activity states to only 0.0001 calls/minute during normal and low activity states (Wisdom 2000). This study found that calf-containing contexts vocalized at 41.91 calls/hour. The higher mean rates of this study are likely due to the presence of additional whales, including other mother/calf pairs or other single whales. This study's sample size was also much smaller.

For geographic and social context comparison, migrating gray whales vocalized at rates of 0.050 sounds/hour/whale in shallow water and 0.012 sounds/hour/whale in deep water (Crane and Lashkari, 1996). Rates of sound production during migration are much lower, perhaps due to increased risk of predation and fewer social behaviors (Table 7).

In a study comparing rates at several locations along the migration route, Dahlheim (1987) determined rates for each month. Although excluding classes 5 and 6 in calculations, whales at northern feeding grounds produced sounds at a rate of 0.013 sounds/hour/whale. Surprisingly enough, there were no sounds recorded that could be attributed to four feeding juvenile whales in Washington State (Table 7). In a southern wintering lagoon, Dahlheim (1987) observed rates ranging from 0.25 sounds/hour/whale to 0.33 sounds/hour/whale, which are clearly two to three times greater than the rates observed in summer feeding grounds. It is not stated which social contexts were

Table 7. Comparison of gray whale sound production rates throughout its range.

	Southern Wintering Lagoons (México)				**Migration (California)**		**Northern Feeding Grounds (Alaska)**			**Captive Calf**
	This Study: All whales	This Study: m/ca	Wisdom 2000 m/ca	Dahlheim Baja 1987	Crane Lashkari shallow water	Crane Lashkari deep water	Dahlheim 1987 North	Dahlheim 1987 Wash St	Petrochenko 1991	Wisdom 2000
# of sounds	432	113	489	*	220	38	53	0	269	366
Recording Duration (hours)	10.13	2.72	23.78	565	37.8	32	40	5	6	248
Recording Duration (min)	607.8	163.2	1426.8	33900	2268	1920	2400	300	360	14880
# of whales	93.41	38	72	195-258	110	96	100	4	*	1
Sounds/min	0.717	0.699	0.343	0.83 - 1.4	0.097	0.020	0.022	0.000	0.747	0.0001 - 4.5
Sounds/min/whale	0.013	0.009	0.005	0.0042 - 0.0055	0.001	0.000	0.0002	0.000	*	0.0001 - 4.5
Sounds/hour	43.023	41.912	19.4	50 - 84	5.820	1.188	1.325	0.000	44.833	0.006 - 270
Sounds/hour/whale	0.784	0.514	0.286	0.25 - 0.33	0.050	0.012	0.013	0.000	*	0.006 – 270

**Not provided.*

observed by Dahlheim (1987) in this wintering lagoon. As suggested in this study, Dahlheim (1987) also suggested that high rates of sound production in southern wintering lagoons are due to increased social activity that occurs there. Likewise, Parks (2003) observed that there are behavioral and possibly acoustic similarities among courting and mating groups of coastal baleen whales. This is most evident when low calling rates of individual animals at summer feeding grounds are compared to higher rates during more social contexts. Like gray whales on their northern feeding grounds that produce low sound rates (Dahlheim, 1987), humpback whales in Alaskan waters produce very few sounds when feeding individually (D'Vincent *et al.*, 1985). However, while in Hawaiian waters during winter, humpbacks used social sounds at high rates only in large groups demonstrating high levels of activity; lone singers and mother-calf groups were never recorded using social sounds (Silber, 1986).

An increase in sound production rates in social contexts is a phenomenon exhibited in other cetaceans. Diaz López and Shirai (2009) observed a positive relationship between group size and sound rates in bottlenose dolphins, thus confirming that these sounds have a communicative function, particularly in social contexts. Groups of cavorting and milling manatees, which exhibited high levels of excitement and social interaction, vocalized at greater rates than those feeding, swimming and resting (Bengtson and Fitzgerald, 1985). Graham and Noonan (2010) observed that captive killer whales produced sounds at rates three times greater during aggressive periods than during non-aggressive periods. Gray whale social and sexual contexts may also be aggressive or at least competitive in nature (i.e., males chasing females; males competing).

While group rates may increase with high surface activity, particularly in adult contexts, individual rates do not follow the same trend. This is indicated by the lower rate of sound production when calculated per whale. In humpbacks, vocalizations per group increased with group size while vocalization rate per individual did not vary significantly (Silber, 1986). This unequal production may be explained by determining the producer of the vocalizations, which should be a goal of future studies. To interpret a sound's function, it must be determined if the sound is produced by the focal female, or primary or secondary male aggressors.

Examples from other mammals demonstrate the importance of determining rates, particularly from specific age and sex classes. Furthermore, specific behavior events may be observed in conjunction with the use of specific sounds. White-faced capuchin monkey (*Cebus capucinus*) infants produced the majority of trills, at significantly higher rates than adult females (Gros-Louis, 2002). Trills were most frequently used by infants when approaching another individual, often followed by affiliative behavior. Territorial male Galápagos sea lions (*Zalophus wollebaeki*) vocalized at higher rates than non-territorial males; additionally, rates when establishing a territory were higher than at the end of territory tenure (Kunc and Wolf, 2008). Rates of vocalizing for sheep ewes (*Ovis aries*) and their lambs were highest prior to nursing (Sebe *et al.*, 2008).

More trends may be revealed by utilizing other analysis methods. Alternate methods to calculate and analyze rates were used by Quick and Janik (2008), in which they calculated individual rates by dividing average whistle rate per 2-minute section "by the median group size for each analyzed section." Such a method would allow for analysis of subtleties within a session, such as rapid changes that occur within a session. It will allow for recognition of extreme peaks and lows contained within one session that would otherwise be obscured when calculating means. Gray whales seem to have a short 'attention span': there was much variation within a session, as contexts could change during these short sessions (15 minutes). As a result, a session was analyzed as one context, but was not truly represented by only one context. Therefore, the use of mixed/unknown as a context has likely created some misleading results. Analysis on a smaller scale, such as the 2-minute units described above, may more clearly reveal how contexts affect sound use.

Use of four social contexts

Despite small sample size, these data provide strong suggestions that highly active adults (likely courting/sexual behaviors) may be distinct in sound production and rates from other adults, who were likely travelling or resting. Some models with four social contexts (i.e., highly active adults, other adults, mixed/unknown, calf-containing) were significant, and others indicated trends near significance. This was likely due to small sample size.

Use of subclass 1a by highly active adults was significantly greater than use by other adults. In general, it is notable that 38% of all sounds were class 1 produced in highly active adult contexts. Class 3 was more often produced by unknown/mixed contexts and other adults. While individual rates of sound production may not be an accurate measure of sound activity, group rates have proven to be revealing. When modeled by four social contexts, highly active adults produced rates significantly greater than any other context, including other adults. However, this is not evident when analyzed by three social contexts, in which the combination of highly active adults and other adults does not allow this difference to be revealed. Further studies with four social contexts should be pursued, especially with larger sample size.

V. CONCLUSIONS

This study confirms the sounds classified in previous studies (Dahlheim *et al.*, 1984; Wisdom, 2000; Ollervides, 2001) with the exception of class 8. Class 8 (Ollervides, 2001) should be reconsidered, as it may be a variation of another class. This study also supports the creation of class 1 subclasses, 1a and 1b, as visually and aurally recognizable and statistically significant. Although the remaining classes have been confirmed, objective and standardized definitions are still not distinct. Future revision of repertoire classification may replace classes with a continuum of "type," ranging from tonal to pulsed (Clark, 1982). Allowing for gradations between these types eliminates subjective classification leading to inconsistencies among studies. "Complex" signals, as defined for this study's purposes, were often mixed "hybrid" forms or simply lacking stereotype. These signals, generally classes 5 through 11, were more likely to be used in contexts that include a calf. Such signals may be "anomaly" or "precursor" sounds produced by calves; further study will reveal if this is evidence of learning or maturation (Locke, 1990; McCowan and Reiss, 1997; Doupe and Kuhl, 1999; Janik and Slater, 2000).

Differences in repertoire of baleen whales may be a result of species-specific adaptations to their particular social and sexual systems; specifically, complexity of repertoire may be a direct reflection of social and sexual complexity. Gray whales do not appear to demonstrate the social complexity of humpbacks (Jones and Swartz, 2002); nor does the gray whale repertoire demonstrate the complexity of the humpback's repertoire. Most notably, the gray whale repertoire lacks songs. The degree of complexity exhibited by humpbacks during the mating season (Clapham, 1996; Smith *et al.*, 2008) has not been observed in gray whale aggregations. Similarly, the long, complicated, predictably patterned, and stereotyped songs (Payne and McVay, 1971; Winn and Winn, 1978) of the humpback have no match in the gray whale repertoire. Gray whales demonstrate a promiscuous mating system, and it is likely that sperm competition occurs (Ralls and Brownell, 1988; Jones and Swartz, 2002), therefore not requiring complex and aggressive male-to-male interactions. It then follows that the gray whale repertoire would not demonstrate the complexity of sounds and songs exhibited by humpbacks. Additionally, their repertoire does not include sounds that parallel or reflect the complexity of some sounds described for the right whales or bowheads, i.e., the gunshot sound (Clark, 1990). Although a type of sound was termed "complex" for the purposes of this study, this is only relative to other classes of simpler sounds in the gray whale repertoire; these "complex" sounds still do not appear to reflect the complexity of some recorded in the mysticete species mentioned above. As a result, acoustic repertoire may be a reflection of social complexity. Environmental differences also affect differences in repertoire. Gray whales do not inhabit the thick ice that bowheads do; it has been proposed that bowheads use their low-frequency calls and echoes to navigate through ice and around deeply-keeled ice floes (George *et al.*, 1989; Würsig and Clark, 1993).

This study has revealed the strong possibility of context-specific use for particular sound classes; additionally, sound parameters and rates of production varied by social context. This supports the author's hypothesis that variations in gray whale repertoire throughout their range reflect changes in social and behavioral contexts. The nature and parameters of each sound class have been outlined, including variations that occur within specific contexts.

Classes 1 through 4, described as croaks and pops, upsweeps, moans and zipper grunts, were most frequently used; they were 87% of the entire repertoire. In contrast, classes 5 – 11, which were mostly complex type and lacked stereotype, were only 13% of repertoire. Class 1 and all pulsed sounds may be essential to highly social contexts in general, and were used frequently during adult socialization and mating. Class 1 was also distinctive, with its frequencies generally higher than other sounds commonly used by adults, such as classes 2, 3, and 4. Its pulsed and variable nature, high frequencies, and frequent use during social contexts support conclusions in other studies that variable signals contain subtle or emotional information relevant to close range contexts (Marler, 1977; Ford, 1989; Thomsen *et al.*, 2002; Rehn *et al.*, 2007).

Class 2 was a low, simple tonal sound, occasionally with an up-sweep contour. Data in this study suggest it may be a startle response. Class 3 was also a low, simple tonal sound, generally stereotyped and discrete. Its structure and low use in most contexts studied here, contrasting with much higher use on the migration route (Crane and Lashkari, 1996), indicate it may be a long-distance contact call. Class 4 may be a precursor to class 1. Class 4 shared a similar pulsed nature with class 1 and there were observations of "hybrid" occurrences of these two classes in this study and another (Moore and Ljungblad, 1984). Further, captive calf JJ used class 4 preferentially at a very young age (Wisdom, 2000). Class 5 and 6 are underwater blows and bubble blasts. Class 6 may be distinguished by its longer duration, greater high frequency and greater bandwidth. Class 5 and 6 may both be pronounced breathing due to exertion, or a disturbance response to boats, as observed in this study, or other threats, as observed in other mysticetes (Clark, 1983; Tyack and Whitehead, 1983; Würsig *et al.*, 1993). The few recordings of class 7 provide little indication of its function. It occurred in all social contexts and in both the presence and absence of boats. A larger sample size and localization of sound producer will likely clarify the function of this sound. There were no recordings of class 8. It may have been a variant of an existing class, and its classification should be reconsidered (Ollervides, 2001). There were very few recordings of class 9, but its structure and parameters suggest it may be a variant of class 2. Data strongly suggest that class 10 is a disturbance signal, possibly produced by calves. All occurrences included at least one calf in the presence of boats. Likewise, class 11 may also be a disturbance response by calves; this study's observations cannot support the suggestion that this is related to baleen-skimming (Ollervides, 2001).

More studies with greater sample size should be pursued, but there are indications that adult sound rates were twice those of calf-containing contexts and mixed/unknown contexts. This is not surprising, given the elevated levels of social behavior that adult aggregations exhibit in the southern wintering lagoons. In contrast, animals that are milling or feeding or alone, as well as mother and calf groups, have less need to communicate acoustically. This is not only supported by other gray whale studies (Dahlheim, 1987; Crane and Lashkari, 1996), but also studies of other marine mammals (Bengtson and Fitzgerald, 1985; D'Vincent *et al.*, 1985; Silber, 1986; Diaz-López and Shirai, 2009).

Acoustic parameters of each class provide some classification guidelines. Subclasses 1a and 1b have been distinguished as statistically distinct. Both this study and Wisdom's (2000) found subclass 1b to have greater inter-pulse interval than 1a. Additionally, there are indications that 1b may have fewer pulses per series, higher frequencies and greater bandwidth. Classes 10 and 11 were notable; they had several of the greatest mean frequencies. In general, calf-containing contexts produced sounds at higher frequencies than adults; this is to be expected if the gray whale sound mechanism is related to body and tracheal length (Wallschläger, 1980; Ryan and Brenowitz, 1985; Tubaro and Mahler, 1998). Localization will be necessary to determine if calves alone are producing sounds at higher frequencies. While frequency variations appear to be related to body size, increased sound levels, frequency modulation, pulses per series and repetition rate may be used to convey emotional states and other information (Dahlheim, 1987).

Although this study has taken a step toward determining the functions of gray whale sounds, there are many more tools to utilize. First, alternative statistical analyses may produce more revealing results. Requiring 60% of minutes to define the social context of a session was conservative and may have neglected subtle and frequently changing social contexts. Analyses that can be more sensitive to shorter durations of contexts are recommended; Quick and Janik (2008) assigned social context to 2-minute sections, as determined by the activity of at least half the group. Such a method may be less likely to marginalize short-term contexts.

Secondly, there are several alternative techniques that may facilitate more objective classification of sounds. Use of multiple uninformed observers has been successful in creating similar classes (Janik, 1999). Other analyses that may be successful are the use of other acoustic variables (Crane and Lashkari, 1996) and spectrographic cross-correlation (Boisseau, 2005). Multivariate techniques such as principal components analysis (PCA) and discriminant function analysis (DFA) could determine which parameters contribute to call variability (Clark, 1982; Boisseau, 2005; Nemiroff and Whitehead, 2009). Finally, automatic classification methods such as hierarchal average linkage clustering may prove moderately useful for gray whale sounds (Janik, 1999; Nemiroff and Whitehead, 2009).

Perhaps most important, a major leap in the study of gray whale repertoire will be provided by localization of sound producers, as already suggested by Wisdom (2000). Localization requires more equipment and effort, but identifying producers of sound classes will allow for a more accurate prediction of function. Focal females likely produce screams in SAGs of North Atlantic right whales (Parks and Tyack, 2005). In social and sexual aggregations of gray whales, it would be advantageous to determine if aggressive males or the pursued females produce knocks. Additionally, in this study it is proposed that rarer sounds of classes 5-11 may be precursors to adult repertoire or specific to mother/calf relationship; this uncertainty will be resolved when it is determined who is producing which sounds. There will be more clarity in repertoire use and better interpretation of function when studies can localize and identify individuals, or at least age and sex classes.

Autonomous recorders, such as sonobuoys and bottom-mounted recorders, provide continuous recordings for much greater durations than boat-based field work (Moore *et al.*, 2010). Further, autonomous recorders are a non-invasive method for detection and monitoring of a population. Automatic detection methods may facilitate handling large quantities of data (Mouy *et al.*, 2009). While automatic detection is possible for gray whale sounds, such techniques may be limited to class 1 and possibly classes 2 and 3. Automatic detection is generally successful with repetitive pulsed sounds and stereotyped, loud tonal sounds (Mellinger and Clark, 1997). The remaining gray whale classes may exhibit too much variation in parameters.

Playback experimentation is another tool that could produce revealing results about sound use. Playback experiments revealed that southern right whales respond preferentially to sounds of conspecifics (Clark and Clark, 1980). Humpback whales in various social contexts were observed to have significantly different responses to song or social sounds of conspecifics (Tyack, 1983). To date, playback experiments with gray whales have been limited to the use of killer whale calls to observe the response of migrating animals (Cummings and Thompson, 1971a). If classes of gray whale sounds have distinct functions, it would be expected that each sound class would produce distinct responses, as observed in humpbacks.

Although radio tracking has provided some limited insight into movements of gray whales (Norris *et al.*, 1977), a new generation of tags allows researchers to understand the environment from an animal's perspective, and has more recently been a powerful tool to associate behaviors and movements with sound production (Oleson *et al.*, 2007; Johnson *et al.*, 2009).

There is also a need for more studies in other parts of the gray whale range, especially migration route and northern feeding grounds. It may be advantageous to conduct a comprehensive study that extends throughout the range with consistent recording and analysis methods. Such a study would provide confirmation of repertoire and allow for clear comparison of repertoire use on temporal and geographic scales. Most needed, however, is a thorough acoustic study of the western gray whale population, which has not yet been conducted. An evaluation of both western and eastern population repertoires may reveal regional differences. These populations have been determined to be genetically differentiated (LeDuc *et al.*, 2002), and therefore population dialects may be observed. Blue whale songs have distinct types that vary by region (McDonald *et al.*, 2006), and humpbacks have regional dialects as well (Winn *et al.*, 1981; Payne and Guinee, 1983).

The various recommended methodologies for future studies will further elucidate the functions of gray whale sounds. Obtaining similar results, despite diverse methods and analyses, reinforces the validity of these conclusions. Such metareplication will reduce biases and errors may cancel each other out (Johnson, 2002).

The intent of this study was to investigate gray whale sound production in various social contexts. It is evident that improvements in the classification system of the gray whale sounds should be utilized. The results of this study also indicate that sound use is differentiated by social context. Correlations between various social contexts and use of sound classes, parameter variations, and rates of sound production will allow acoustics to be an indicator of presence of particular social groups, seasonal movements, and social patterns. Additionally, this study has taken a preliminary step in elucidating functions of sounds. Improved understanding of the sound production of marine mammals is necessary for human co-existence with and protection of marine mammals. This is especially critical for gray whales, which are the most coastal of baleen whales. As a result, human activities such as commercial and recreational boating, whale watching, and industries such as salt works, are frequently present in the gray whale's range. It is highly recommended that future studies determine if anthropogenic noise mask or interfere with gray whale sounds that are important to their communication.

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APPENDIX A

PARAMETER VARIATIONS BETWEEN CLASS 1 SUBCLASSES

Although not significant at p=0.05, duration (of entire sound) of 1b tended to be greater than that of 1a (F=3.77, p=0.0672) (Figure A-1). Low frequency (Figure A-2), maximum frequency (Figure A-3) and number of pulses (Figure A-4) did not vary significantly.

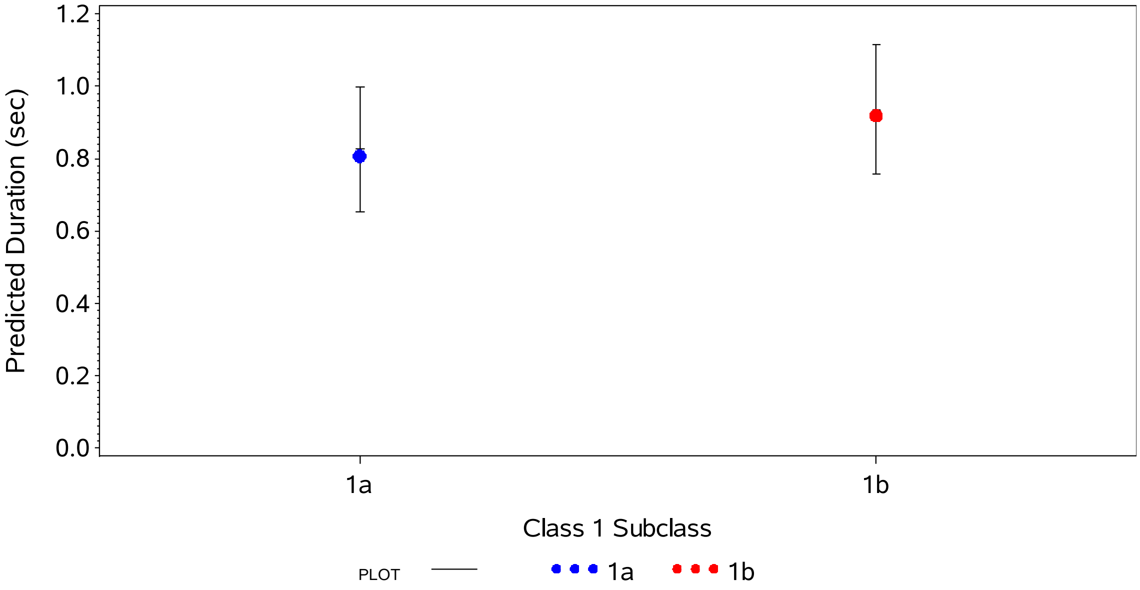

Figure A-1. Plot of predicted duration by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

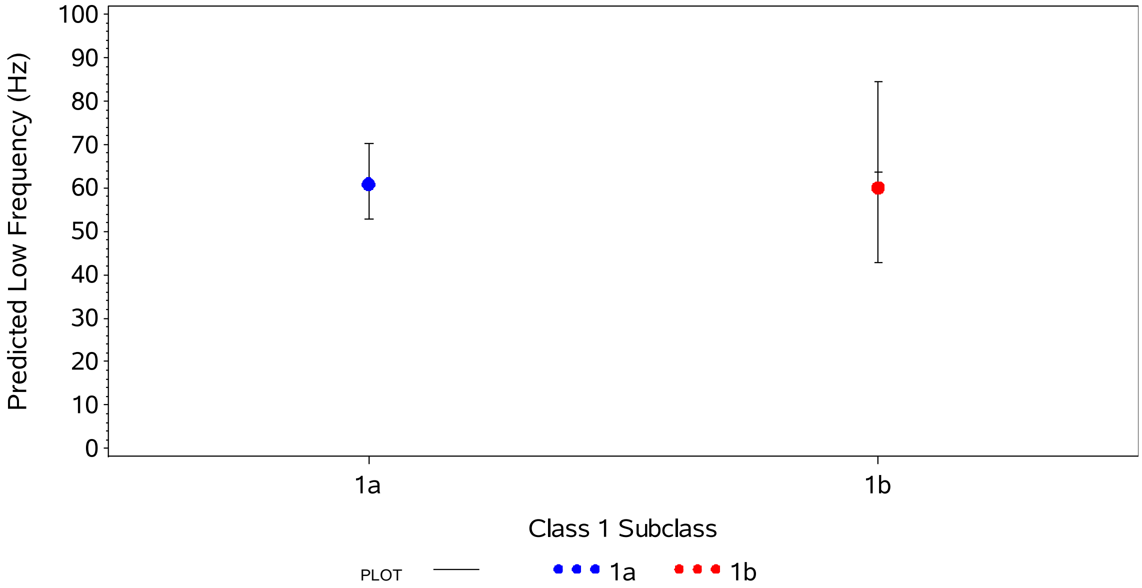

Figure A-2. Plot of predicted low frequency by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

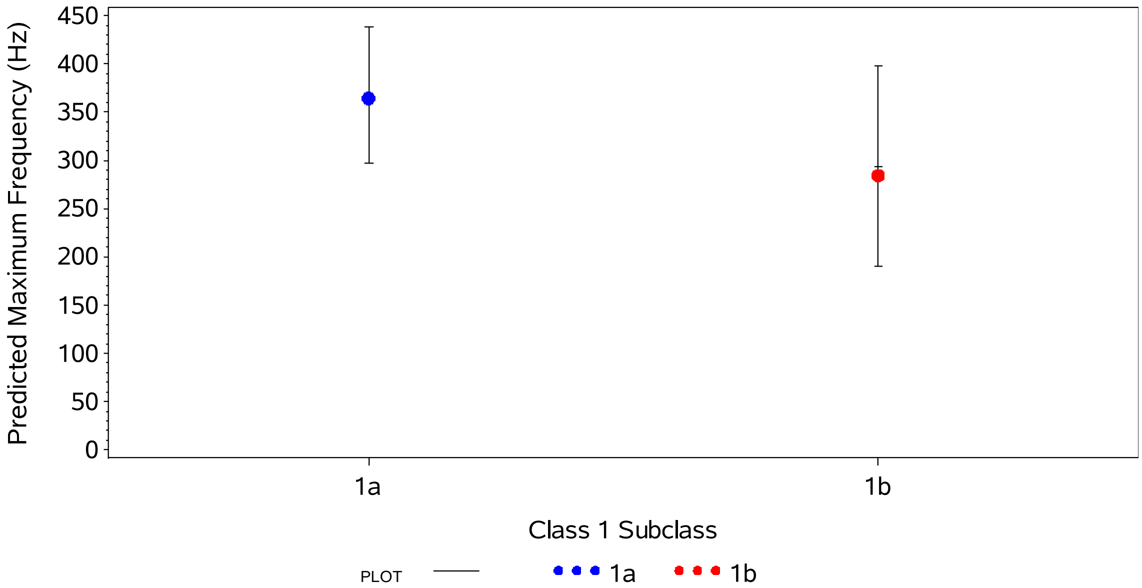

Figure A-3. Plot of predicted maximum frequency by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

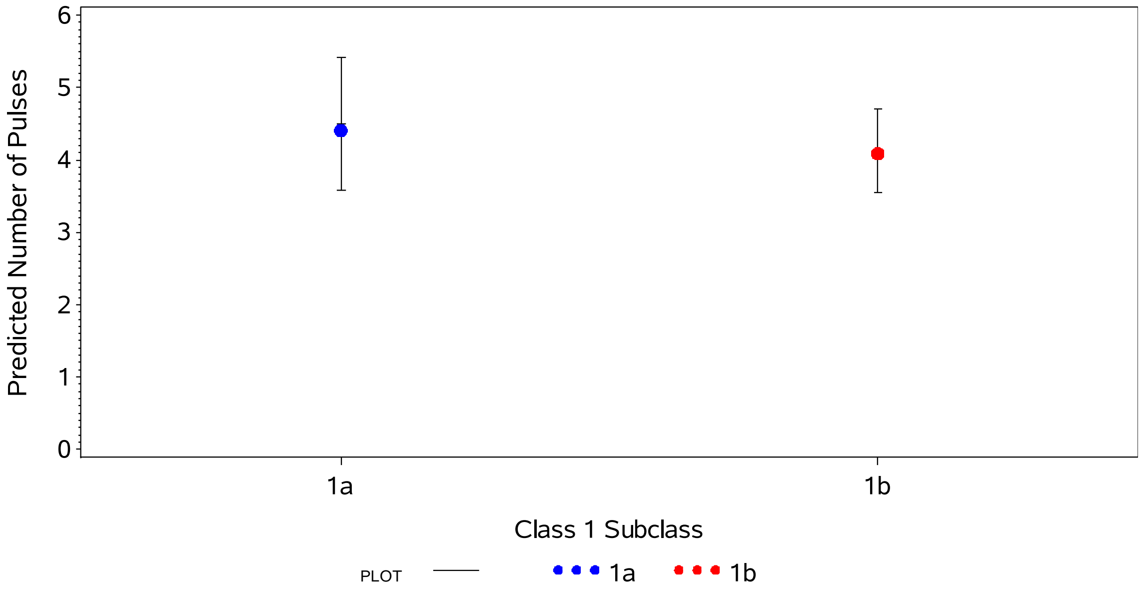

Figure A-4. Plot of predicted number of pulses by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Individual pulse low frequency (Figure A-5), maximum frequency (Figure A-6) and duration (Figure A-7) were not found to be significantly different between the two subclasses.

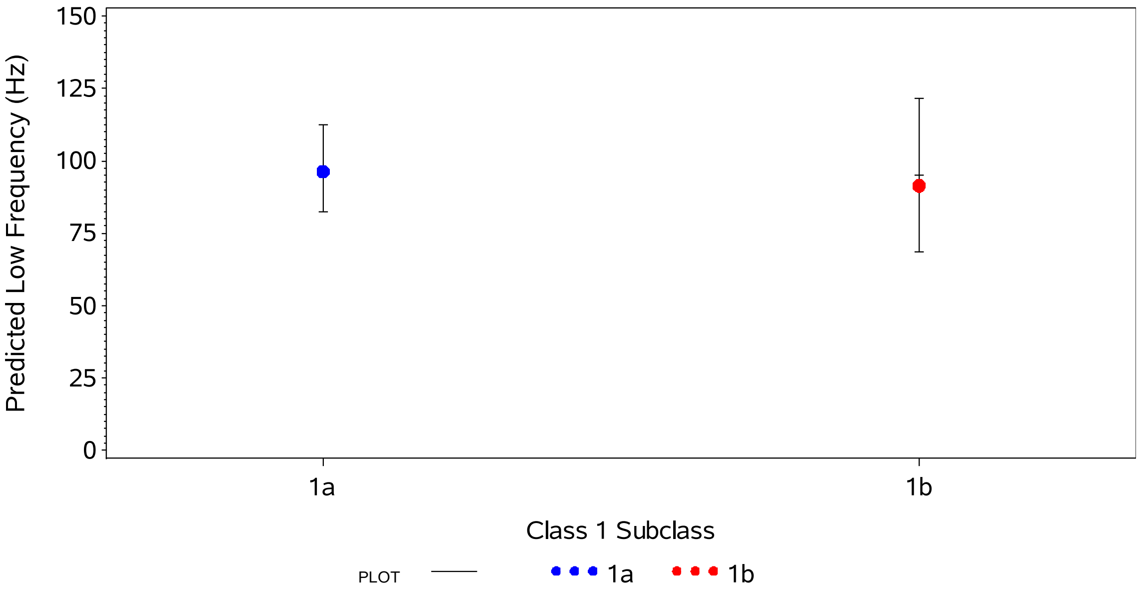

Figure A-5. Plot of predicted individual pulse low frequency by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

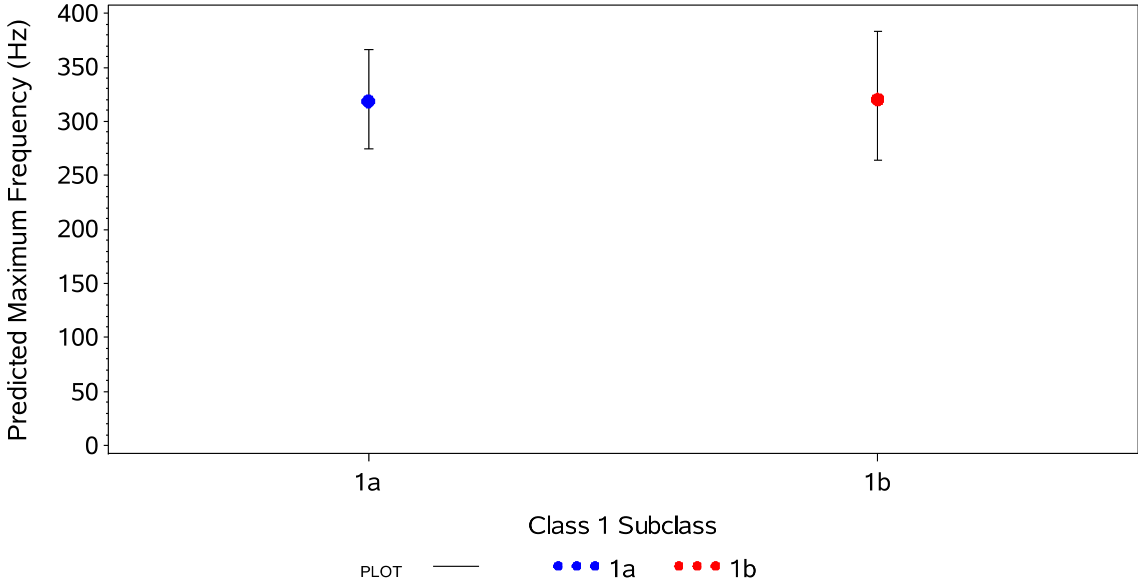

Figure A-6. Plot of predicted individual pulse maximum frequency by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

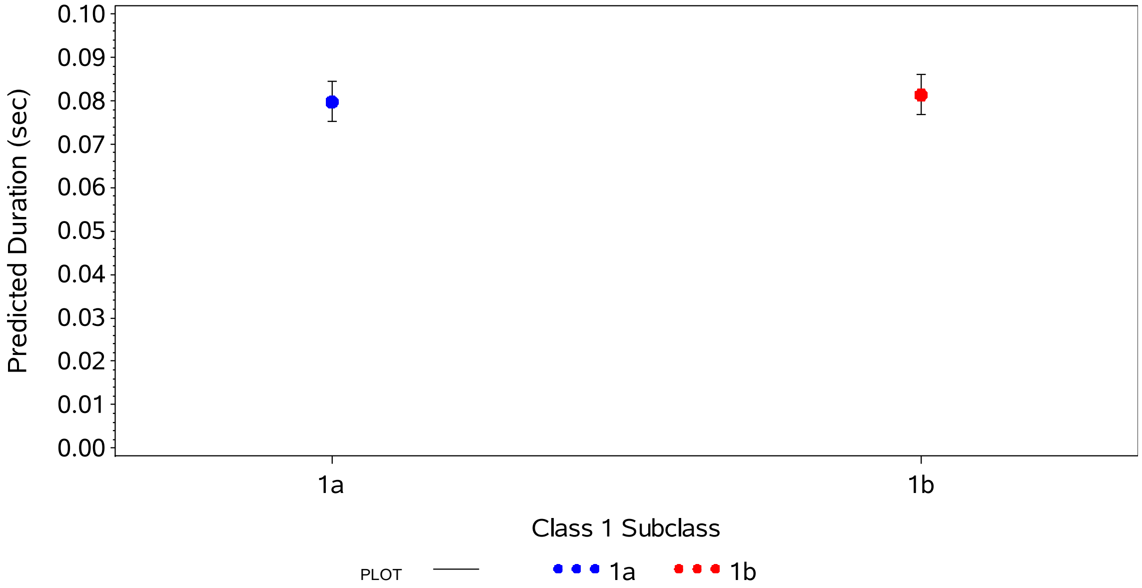

Figure A-7. Plot of predicted individual pulse duration by class 1 subclass. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

APPENDIX B

CLASS 1 SUBCLASS VARIATIONS BY SOCIAL CLASS

There were no significant differences found in duration between class 1 subclasses or social context (Figure B-1).

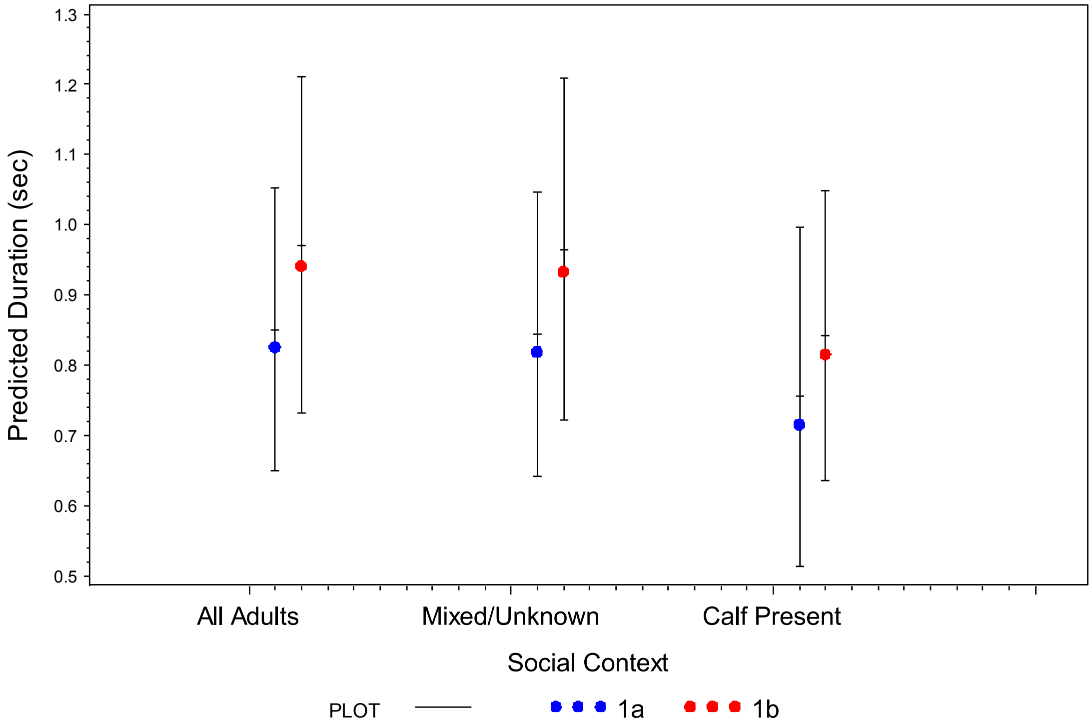

Figure B-1. Plot of predicted duration by subclass and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

While not significant at p=0.05, the interaction term (F=3.45, p=0.0526) and social context (F=3.02, p=0.0724) of individual pulse maximum frequency did exhibit trends towards significant differences (Figure B-2). In regression contrast test, means indicate trend towards mixed/unknown groups having a greater mean maximum frequency than adults (F=3.73, p=0.0685). There were not significant differences in subclasses. Individual pulse maximum frequencies were square root transformed.

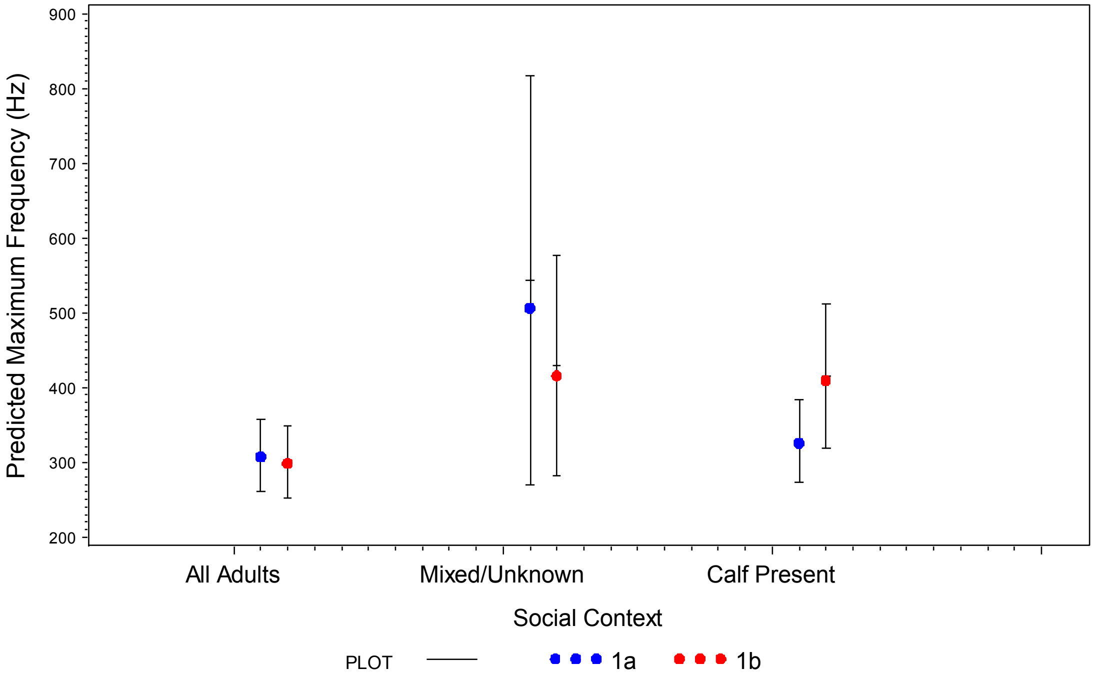

Figure B-2. Plot of predicted individual pulse maximum frequency by subclass and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Individual pulse duration was not significantly different in interaction, social context or subclass (Figure B-3). Although not significant at p=0.05, a trend indicates adults may have greater durations of both subclasses than those of mixed/unknown groups (F=3.62, p=0.0725).

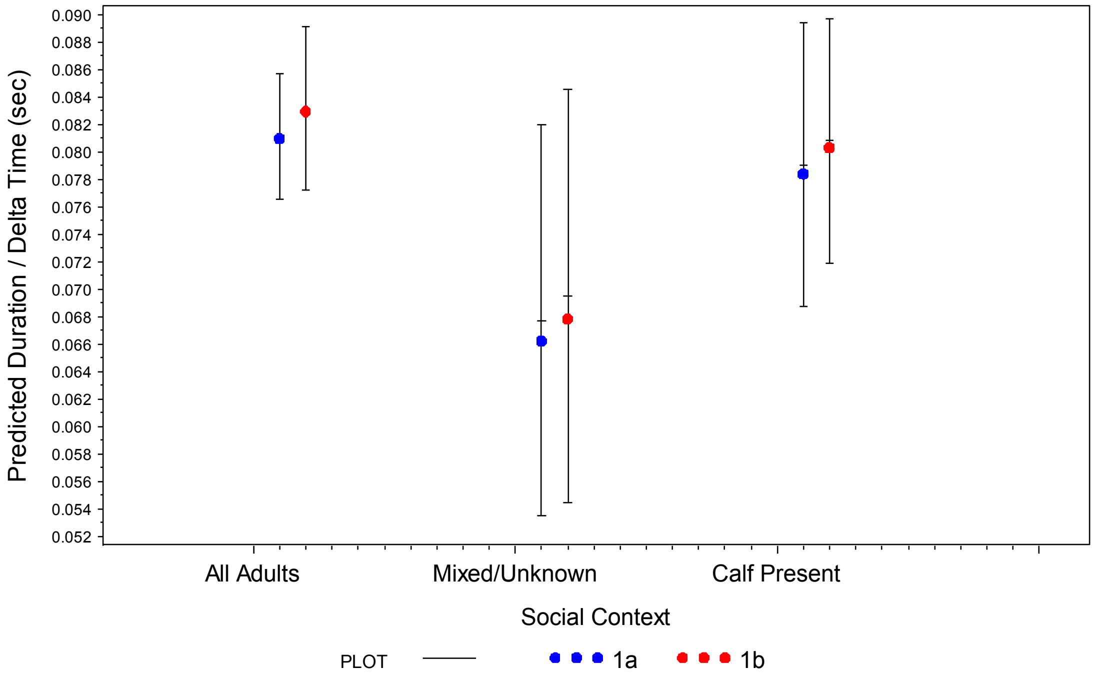

Figure B-3. Plot of predicted individual pulse duration by subclass and social context. Based on linear regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

APPENDIX C
RELATIVE USE OF CLASSES

There were no significant differences in use of class 2 by three social groups (Figure C-1). Probability of use for all groups was low.

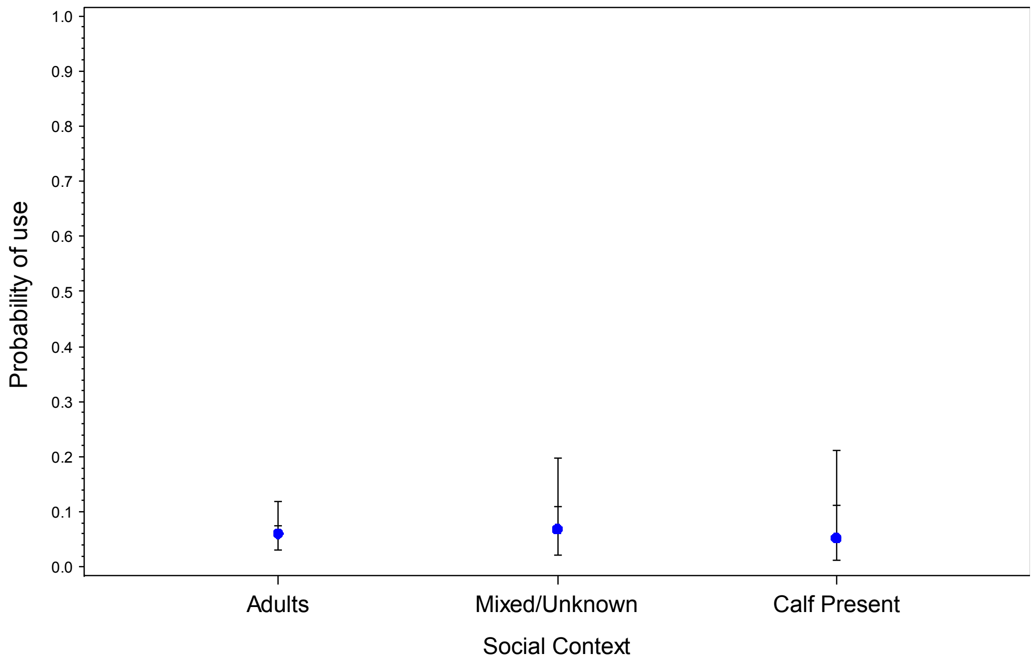

Figure C-1. Plot of predicted use of class 2 by social context. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Unknown/mixed groups had slightly greater probabilities of using class 3, but there were no significant differences (Figure C-2).

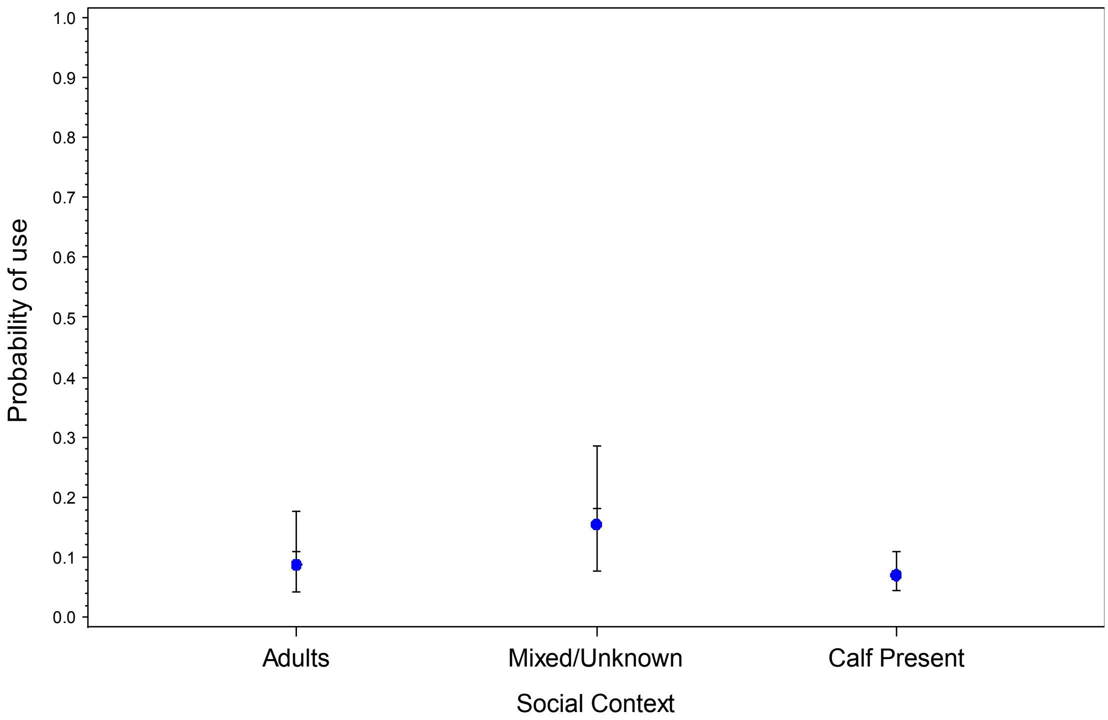

Figure C-2. Plot of predicted use of class 3 by social context. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

There were no significant differences in probability use of class 7 (n=14) among social groups (Figure C-3). Probability of use was low for all social groups. There were eight occurrences of class 7 in adult groups; there were only four occurrences in calf-containing groups and two occurrences in mixed groups.

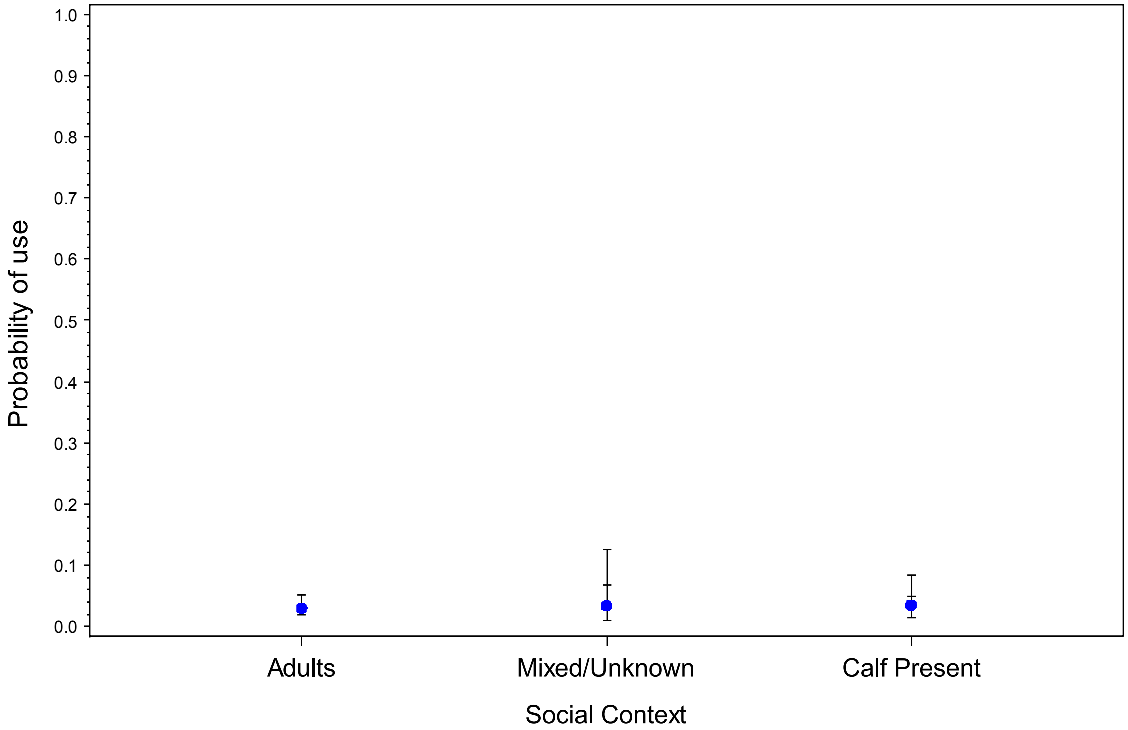

Figure C-3. Plot of predicted use of class 7 by social context. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

While adults used subclass 1b slightly more frequently than other groups, the overall model detected no significant differences among groups (Wald chi-square=5.22, p=0.0733) (Figure C-4). However, adults had significantly greater probability of using subclass 1b than calf-containing groups (Wald chi-square=5.22, p=0.0223). Additionally, although not significant at p=0.05, it appears adults may use 1b more often than mixed/unknown groups (Wald-chi square=3.46, p=0.0627).

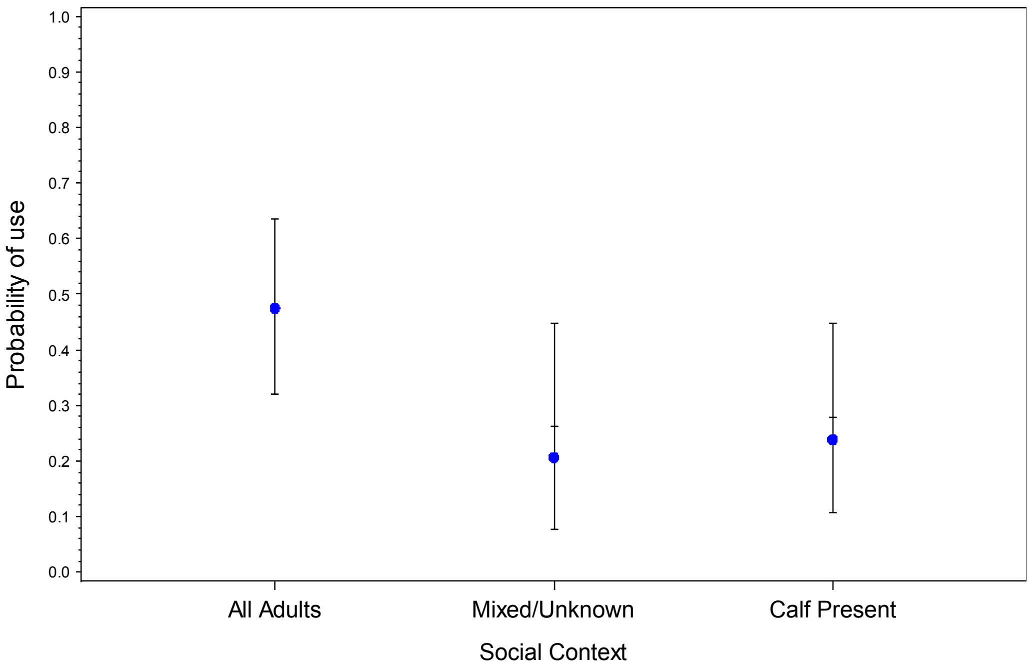

Figure C-4. Plot of predicted use of subclass 1b by social context. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

Use of tonal type sounds was low for all social groups (Figure C-5). There were no significant differences detected in probabilities of use among social groups.

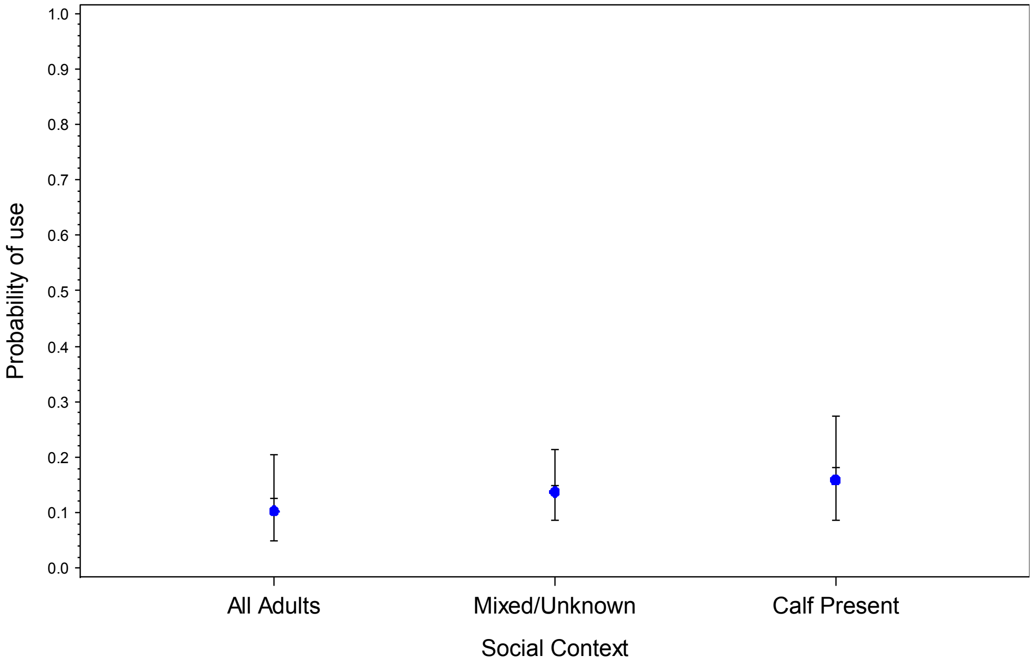

Figure C-5. Plot of predicted use of tonal sound type by social context. Based on logistic regression; central line (-) represents median, dot represents predicted mean; whiskers include 95% confidence limit.

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