Gray Whale (*Eschrichtius robustus*) Sex, Reproductive Behavior, and Social Strategies

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ABSTRACT

Gray whale sexual behavior and copulation are observed throughout their range. The most prominent period for reproductive behavior is during the southward migration from summer feeding areas to wintering areas where some breeding occurs and calves of the year are reared. The seasonal migrations of gray whales are believed to function, in part, to bring together individuals that are otherwise widely distributed during the period of estrus to facilitate mating and reproduction. Sexual behaviors and sexual strategies for this species appear to align closely with those of balaenid (not rorqual) whales, although such comparisons need further investigation. Gray whales are polygynandrous (multi-mate) breeders. There does not to appear to be female choice of mates, as groups of numerous females and males aggregate, and multiple copulations occur. Female estrus begins in mid-November and continues to early December; females may undergo a second estrus, extending into February, if they fail to conceive during their first cycle. Male gray whales have large testes and concomitantly produce large volumes of sperm, so they are believed to be sperm competitors; that is, they rely on multiple copulations (and sperm volume) to produce offspring. Multiple copulations with different males during the female estrus period may increase the likelihood that the timing of conception results in the birth of a calf approximately 13 months near or in the wintering area(s). Mating bouts can last for minutes to hours, interspersed with surface active social-sexual behavior. Some all-male groups have been observed with erect penises engaged in socio-sexual behavior in the absence of any females. Instances of male aggression toward postpartum females with calves of the years, sometimes resulting in injury or death, have been reported. As a result of dedicated long-term research in the past several decades, the state of knowledge on gray whale reproduction has greatly expanded and updated information on this topic is summarized in this chapter.

Keywords: *gray whales, Eschrichtius robustus, western North Pacific population, eastern North Pacific population, polygynandrous (multi-mate) breeding, scramble competition, migration, sexual strategies, socio-sexual behavior, sperm competition, male aggression, acoustics.*

1.0 MIGRATION AND THE REPRODUCTIVE CYCLE

Gray whales occur along the margins of the eastern North Pacific (ENP) and western North Pacific (WNP), migrating annually from northern feeding areas to southern wintering areas that represent a round trip journey of 15,000 to 20,000 km that spans up to 55º latitude (Swartz 2018). Seasonally predictable sources of food have helped shape the life history of gray whales into two general periods that are linked by the annual migration: (a) summer feeding in the higher latitude waters where food is abundant and whales are widely dispersed across a large territory and (b) over wintering in lower latitude waters, where whales are more closely aggregated. The seasonal occurrence in southern wintering areas serves several hypothesized functions, including: (a) escape from inhospitable environmental conditions (e.g., sea ice, water temperature) in northern areas, (b) reduction of risk from killer whale predation during the period when calves are born (Corkeron and Connor 1999; Sumich 2014; Weller *et al*. 2018; Black *et al*. 2023) and to (c) benefit the successful rearing and survival of calves (Jones and Swartz 2009). The gray whale reproductive cycle is tightly synchronized with this migration and this relation is described below.

1.1 Migration and Reproductive Timing

The southward migration helps to concentrate whales spatially and temporally, thereby facilitating mating. By late November, most gray whales are moving south from summer feeding areas to wintering areas. This southern migration is segregated by age, sex and reproductive condition. The first pulse of migrants is led by: (a) near-term pregnant females, followed by (b) estrus females and mature males and then (c) immature animals of both sexes (Rice and Wolman 1971). The northward migration begins about mid-February and is also segregated according to age, sex and reproductive condition. The first phase of this northward migration includes: (a) newly pregnant females followed later by (b) adult males and anestrus females and then (c) immature whales of both sexes. The second phase of the northward migration consists mostly of mothers with calves. These pairs are observed on the migration route between March and May and they generally arrive to the summer feeding grounds between May and June (Jones and Swartz 1984b).

During summer and fall, most whales in the ENP feed in the Chukchi, Beaufort and northwestern Bering Seas. An exception to this generality is a relatively small number (roughly 200) of "Pacific Coast Feeding Group" (PCFG) whales that routinely return each summer and feed along the Pacific coast between southeast Alaska and northern California (Darling 1984; Calambokidis *et al*. 2002; Moore *et al*. 2007). Three primary wintering aggregation areas and lagoons in Baja California Sur, Mexico, are utilized, and some females are known to make repeated returns to specific lagoons (Jones 1990, Martínez-Aguilar *et al*. 2022b). In the WNP, gray whales feed off Far East Russia during summer and fall in the western Okhotsk Sea and southeastern Bering Sea (Weller *et al.* 1999, 2002; Tyurneva *et al.* 2010). Historical accounts (Andrews 1914; Nishiwaki and Kasuya 1970; Wang 1984) and contemporary data (Weller *et al*. 2008, 2016; Nakamura 2021) indicate that coastal waters off Asia were, and continue to be, part of a WNP migratory route and portions of the South China Sea are reputed wintering areas (Weller *et al*. 2002, 2013). Until about the mid-2000s, whales in the WNP were thought to be geographically isolated from whales in the ENP, however, satellite-tagging, photo-identification and genetic research has documented some whales identified during the summer in the WNP migrating to the ENP in the winter, including coastal waters off Canada, the U.S. and Mexico (Weller *et al*. 2012, 2016; Mate *et al*. 2015; Martínez-Aguilar *et al*. 2022a). These findings suggest that some whales summering in the WNP migrate to the ENP west coast of North America in winter, while others migrate south to waters off Japan and China (Weller *et al*. 2008, 2013, 2016).

Studies of gray whales summering in areas off the Pacific Northwest between southeastern Alaska and Northern California and off Sakhalin Island in Far East Russia have found intra- and inter-annual fidelity for many of the whales observed (Darling 1984; Weller *et al.* 1999; Calambokidis *et al.* 2002, 2017; Bröker *et al.* 2020). While this same pattern of seasonal site fidelity may exist in various areas in the Arctic feeding grounds, data from those areas does not exist at the level necessary to determine such.

1.2 Implications of Summer Feeding Location on Mating

With the above in mind, the location(s) of where whales feed in the summer has possible implications for mating. For instance, some information on the timing of migration has been gleaned from three whales satellite-tagged during 2010 and 2011 on the Sakhalin Island summer feeding area in the WNP. All three whales migrated east, with one (a 13 year-old male) remaining off Sakhalin until 10 December while the other two (both females, ages six and nine) remained there until 24 November before migrating to areas occupied by ENP gray whales (Mate *et al.* 2015). These data indicate that at least some, and perhaps all, animals making the winter migration from the WNP to the ENP are still far to the west, and therefore only in proximity to other whales migrating from the WNP, during the primary conception period that occurs between late November and early December (Rice and Wolman 1971). The plausibility of this possibility is consistent with the results of genetic analyses, in which significant nuclear genetic differences have been found between the whales that feed off Sakhalin Island in the WNP and gray whales in the ENP (Brüniche-Olsen *et al.* 2018, Lang *et al*. 2022). These differences indicate that whales feeding off Sakhalin Island are not mating at random with ENP gray whales, a finding that suggests assortative mating may be occurring as a result of location (*i.e.* summer area) and migratory timing (Lang *et al.* 2022).

Similarly, the above scenario for whales summering in the WNP may also apply to PCFG gray whales and other similar seasonal aggregations that may exist in the ENP. Over 50% of PCFG individuals have been sighted in areas off the Pacific Northwest in November and December despite a limited amount of effort. Satellite tagging research on PCFG gray whales revealed that 18 whales started their southward migrations between 3 December to 13 February (Lagerquist *et al.* 2019), a period of time that is later than the estimated period of conception between mid-November to early December (Rice and Wolman 1971). Although these factors could result in a higher likelihood of assortative mating among PCFG, genetic analyses do not support such a hypothesis; research has yet to detect significant nuclear DNA differences when PCFG whales are compared with ENP whales that feed in Arctic waters or those using the wintering aggregation areas and lagoons (Lang *et al.* 2014, D'Intino *et al.* 2013).

2.0 REPRODUCTIVE LIFE HISTORY

2.1 Estrus and Conception

Most gray whale conceptions occur each year during a 3-week period, overlapping the early portion of the southward migration, from mid-November to early December (Rice and Wolman 1971). In the ENP, studies have shown that sexual activity and copulatory behavior occur during migration (Norris *et al.* 1983; Swartz 1986) and continue once the whales have reached their wintering areas off Mexico. These observations seemingly support the suggestion that females that failed to conceive after their first ovulation may experience a second estrus cycle that is later, possibly extending into February, in the same breeding season (Rice and Wolman 1971). Newly pregnant females are the first to leave the Baja wintering areas in the spring, migrating to summer feeding areas to begin replenishing their metabolic "energy stores" that had been greatly depleted during the previous southward migration in combination with the nutritional demands related to the growth of their fetuses (Sumich 2014).

2.2 Age, Sexual Maturity and Sex Ratio

The oldest female gray whale killed during scientific whaling operations between 1959-1969 in the ENP was estimated to be 75 years old and was pregnant (Rice and Wolman 1971). Minimum age estimates for individual gray whales photo-identified off Mexico range from 45 to 53 years (Martínez-Aguilar 2022b).

Males and females attain sexual maturity between 5 to 11 years (average is 8 years for both sexes) (Rice and Wolman 1971; Bradford *et al*. 2010). Females generally produce one calf every two years, although longer inter-birth intervals of three or more years may occur (Rice and Wolman, 1971; Jones, 1990; Weller *et al*. 2008; Martinez *et al*. 2022b). Gray whale calves are born singly and the sex ratio has been reported to be 1:1 in the ENP (Rice and Wolman 1971). A recent study using genetic analysis found that 66.1% of whales first identified as calves on the WNP feeding area in the Okhotsk Sea were males (Weller *et al.* 2009, Lang 2010). It is not known what factors influence the proportion of male calves born per year, and the male bias found in the aforementioned study may simply reflect stochastic variation (Cooke *et al*. 2016).

2.3 Gestation, Size at Birth, Weaning

The gestation period for gray whales is estimated to be 11 to 13 months with births occurring from late December to early March (Jones and Swartz 1984b; Sumich 2014). The median birth date is 27 January when near-term pregnant females are migrating southward and in or near their wintering destinations. At birth, calves are 4.5-5.0 m in length and weigh approximately 1000 kg. Females have a close and protective bond with their calves and fight fiercely to defend them when threatened (Scammon 1874). Weaning occurs at 6 to 8 months, primarily in summer feeding areas, when calves are 7.6 to 8.5 m in length (Rice and Wolman 1971; Weller et al. 1999, Sychenko 2011). Post-weaning survival (survival from their first feeding season as calves to the following season) is estimated at 0.65 to 0.70 and varies annually (Bradford *et al.* 2006, Cooke *et al*. 2019).

2.4 Lactation and Female Resting Period

To nurse, a female gray whale swims slowly or rests motionless at the surface while her calf approaches from below and nudges the abdominal area of its mother as a cue, whereupon milk is pumped from the female's teat into the mouth of the calf. Calves consume about 189 liters of milk daily, which is 53% fat and 6% protein (Sumich 2014). Mothers and calves remain in the wintering areas off Mexico until April or May, allowing calves sufficient time to strengthen and rapidly increase in size before their first northward migration. After weaning their calves in July and August on the summer grounds, females then have a 3 to 4 month resting period to focus on feeding to fatten and replenish their "energy stores" in advance of their next estrus cycle that begins anew around November to December, thus completing the 2-year reproductive cycle (Swartz 1986; Jones 1990; Rice and Wolman 1971).

Studies in the WNP show that lactating females are commonly in poorer body condition than other whales (Bradford *et al*. 2012). Although their body condition typically improves somewhat through the feeding season, the probability that lactating females would have complete within-season recovery is generally low, indicating that post-parturient females are typically not able to fully replenish their energy stores before their next opportunity to breed. Calves are in consistently good body condition, resulting from high maternal investment during lactation, even after weaning.

3.0 GRAY WHALE REPRODUCTIVE STRATEGY

As mentioned above, female gray whales enter their first seasonal estrus at the onset of the southward migration and along the migratory route. The compressed breeding season of gray whales combined with the segregated and phased nature of the migration appears to have helped shape their mating system by precluding the monopolization of available females by males.

3.1 Polygynandrous Mating System

The mating system of gray whales is polygynandrous (multi-male and multi-female). Male defense of mates in 'harems' or other similar aggregations that give dominant males exclusive access to females, as seen in other polygynous mammals with compressed breeding seasons, does not appear to be the case with gray whales. When in estrus, females copulate with multiple mates to enhance the likelihood of conception. There does not to appear to be female-based pre-copulatory choice of mates, as mating groups vary in size, often with numerous females and males aggregated together. In these groups, multi-mate and multiple copulations occur. Social-sexual behavior is not limited solely to the wintering areas. Video capable suction cup tags have revealed that gray whales feeding off the Pacific Northwest coast in the spring engage in close physical contact both underwater and at the surface, rubbing against each other with their bodies and flippers, that is sometimes accompanied by males with erect penises (JC, pers. comm.). Sexually active all-male groups are also seen during migration as well as winter and summer areas (Darling 1977; Jones and Swartz 1984b, 2009; Youngson and Darling 2016; Fig. 1).

3.2 Operational Sex Ratio and Scramble Competition

The two-year breeding cycle reported for gray whales (Rice and Wolman, 1971) means that at the start of each breeding season 50% of the mature females are available (or unavailable) for mating. This proportion of available females skews the operational sex ratio to a 2:1 male bias. Thus, competition between males for mating opportunities would be expected (Emlen and Oring, 1977). Evidence for overt aggressive male-male competition for available females, however, has not been reported. Instead, gray whales appear to have evolved a more cooperative "scramble competition" mating strategy where males jostle to be in position next to an estrus female without being directly aggressive to each other (Clutton-Brock 2016). Such mating can occur in what are termed 'explosive breeding assemblages', where both sexes converge (*e.g.,* during migration) for a relatively short-lived, highly synchronized mating period. Sexual activity occurs during their migration and while the whales occupy the wintering aggregation areas and lagoons in the ENP (Gilmore, 1960; Rice and Wolman, 1971; Jones and Swartz, 1984a; Norris *et al*. 1983) suggesting that, rather than mating in one specific portion of their range or location, the timing of reproduction is more important. That is to say, a 'core time' rather than 'core area' is the factor that assures gray whales conceive within a limited period and, in turn, best ensures that calves will be born 11-13 months later in an optimal wintering location; one that increases their potential for growth, development and survival (Jones and Swartz 2009). This line of reasoning suggests that the long-time use of "breeding area" to describe the lagoons of Mexico in the ENP, and similar regions in the WNP, is not accurate and should be properly termed "wintering aggregation areas" where some mating occurs (as we have done in this chapter).

3.3 Testes-to-Body Weight Ratio and the Multi-Mate Breeding System

The lack of direct evidence for male-male competition in gray whales, such as pronounced sexual dimorphism, male territorial defense and communal displays, suggests that competition and sexual selection may occur at some level other than that of the individual. The testes-to-body-weight ratio in gray whales predicts a multi-male breeding system, which is consistent with the breeding behavior observed in this species. Brownell and Ralls (1986) reviewed the literature on baleen whale testes size, penis length, and mating system. They reasoned that in species with sperm competition, large testes that produce large amounts of sperm per ejaculation would serve to dilute and displace the sperm of rival males and that longer penises would deliver the sperm closer to the ova. Gray, right (*Eubalaena glacialis*) and bowhead (*Balaena mysticetus*) whales are species without obvious male-male competitive behavior and possess both large testes-to-body weights and penis-to-body lengths. Conversely, the humpback whale (*Megaptera novaeangliae*) with smaller testes, a shorter penis, and conspicuous interactions between breeding males, has been selected to compete to a greater extent by preventing rival males from mating rather than by sperm competition (Brownell and Ralls 1986).

4.0 REPRODUCTIVE BEHAVIOR IN THE EASTERN NORTH PACIFIC WINTERING LAGOONS

The scientific understanding of gray whale reproductive behavior during the winter, when calves of the year are nursing and breeding among single whales continues, comes almost strictly from studies conducted in the lagoons of Mexico.

4.1 Surface Active Behavior

Early reports of gray whale mating behavior that described "trios" consisting of a mating pair and a third individual or "helper" were oversimplifications (Gilmore 1976; Miller 1975; Samaras 1974). More recent observations have confirmed that mating groups range in size from pairs to several individuals of mixed age/sex (except calves) and may stay engaged in mating bouts that last for two or more hours with additional whales joining in the bouts as if stimulated by the sexual activity of the core group (Jones and Swartz 1984b, Figs. 2a-d). Mating bouts may also include high-speed chases, termed "freight train races", where group members (presumably males) appear to pursue a lead animal (presumably a female in estrus), with multiple individuals lunging through the water creating spectacular bow-waves, and sometimes cover 3 to 4 km before resuming a mating bout. As the winter season progresses and the northward migration begins, the occurrence of sexual activity becomes less frequent as the numbers of single adult whales in and near the lagoons decline.

4.2 Acoustic Behavior

While gray whales are acoustically active throughout their range, including during their migration (*e.g*., Guazzo *et al*. 2017, Burnham *et al.* 2018), and while feeding (*e.g.* Moore and Ljungblad *et al*. 1984), they appear to be most acoustically active in their wintering areas (Dalheim *et al*. 1984; Ollervides 2001), both in terms of the variety of sounds produced and the frequency of vocalizations. Acoustic calls attributed to gray whales in the wintering lagoons include "low frequency rumbles", "pulses, moans and whistles", "chirps", "clicks", "bongs", "knocks", "pulses", "snorts", "slamming" and "bubble bursts". There are over 14 distinct, mostly low frequency, sound types produced by gray whales reported in the scientific literature.

While gray whales have been reported to produce a variety of different calls, the "S1" call is common in the wintering lagoons (Dalheim *et al.* 1984; Ollervides 2001; Charles 2011), but relatively rare during fall and spring migrations (Guazzo et al 2017). The S1 is characterized by a sequence of knocks with the tonal texture of conga drums (Dahlheim, 1987; Fig. 3) and has a high source level, or volume, that makes it detectable over greater distances than other types of calls (Dahlheim 1987). The S1 call is thought to serve a communication function, with animals producing their own S1 call in response to hearing another animal's S1 call (Ponce *et al*. 2012). Field observations of gray whales found associations between the occurrence of the S1 call and social-sexual reproductive behavior (Charles 2011). The S1 call has also been reported during social-sexual interactions by feeding gray whales off British Columbia, Canada (Youngson and Darling 2016). In summary, the S1 call is a loud, common call that is used for two-way communication between individual whales of all demographics but is particularly common among individuals engaged in mating or social-sexual behavior.

4.3 Spatial Segregation and Behavioral Incompatibility

In January and February, females with calves and adult courting whales occupy the lagoons, and although female-calf pairs routinely travel the entire length of a lagoon, they actively avoid passing through areas with concentrations of courting adult whales. In broad terms, gray whales in the wintering lagoons behave as two separate segments: (a) social-sexual mating groups of single adult males and females in estrus and (b) post-parturient females with their newborn calves. Single breeding adults of both sexes engage primarily in social-sexual behavior, while females with new calves generally remain solitary, devoting their energies to nursing and nurturing their offspring (Jones and Swartz 1984b).

In one of the wintering lagoons (Laguna San Ignacio) courting groups composed of adult whales (males and females without calves) are found at highest densities in the "lower" one-third of the lagoon nearest the lagoon entrance and their density decreases with increasing distance from the entrance. In contrast, most females with newborn calves are concentrated in the inner two-thirds of the lagoon furthest from the entrance. These inner waters are often referred to as "nurseries", where mothers and their calves are mostly resting and nursing (Figs. 4-5). Few single whales visit these nursery areas, providing relative solitude for females following parturition and during early development of their calves (Jones and Swartz 1984b; Jones and Swartz 2009).

The average minimum length of stay for single adult whales (adult males and females without calves) is short (7.5 days) in comparison to the average length of stay for females with calves (32.2 days). These residency times reflect a high rate of turnover for single whales in the lagoons (Martínez-Aguilar 2022b). Further, photo-identification studies show that during the winter single adult whales circulate among the three primary breeding lagoons and the nearshore bay waters, presumably looking for mating opportunities, while females with calves spend longer periods within the lagoons (Martínez-Aguilar 2022b). Harassment by courting whales is a major factor driving female-calf pair avoidance of courting whales (Jones and Swartz 1984b). Members of courting groups (presumably males) pursue females with calves and attempt to mate with the females. Mating bouts are highly disruptive events and involve groups of multiple individuals thrashing at the surface, throwing their flukes and flippers, as they maneuver for mating position (Norris et al. 1983; Swartz 1986 ; Jones and Swartz 1984b, Figs 6-10). Calves may become separated from their mothers and/or can sustain injuries or even be killed in these circumstances. In one instance, a well-known female with her calf were relentlessly pursued and harassed by courting single adult whales, and the mother was separated from the calf. A few days later, this female was found dead, likely as the result of her injuries. The fate of her calf was never determined (S. Martínez-Aguilar. *Pers. Comm*).

4.4 Acoustic Crypsis

The levels of ambient biological noise in the inner lagoon areas, where females with young calves segregate themselves, can be high and thereby provide acoustic "crypsis", or the ability of mother-calf pairs to avoid observation or detection by other animals through the exploitation of sound. This ambient noise arises from snapping shrimp sounds, tidal flow across the ocean bottom, wind-generated waves on the surface, and to a lesser extent panga transits and fish chorusing (Seger *et al.* 2015). Sounds recorded from mainly mother-calf pairs, suggest a larger repertoire than previously reported possibly due to faint calls recorded only at close range (Frouin-Mouy *et al*. 2020). Thus, in the wintering lagoons, mothers and calves may take advantage of acoustic cryptic communication strategies (low-level sounds in high-noise areas) for maintaining contact in a low-visibility environment while simultaneously reducing a potential risk of eavesdropping by predators or courting whales. Acoustic crypsis strategies have also been proposed in North Atlantic right whales (Parks *et al.* 2019), southern right whales (Nielsen et al. 2019) and humpback whales (Videsen *et al.* 2017).

5.0 FUTURE DIRECTIONS FOR STUDYING GRAY WHALE REPRODUCTION

5.1 Paternity Research Although valuable information on female reproductive success can be obtained through visual observations of mothers associated with their calves, evaluating factors that influence male reproductive success is only feasible through genetic analyses of paternity. Such analyses provide the most information when a high proportion of animals in the population have been sampled, and the genetic results can be integrated with long-term sighting histories of individual whales. For example, in North Atlantic right whales, where ~63% of identified individuals were sampled, the combination of genetic analysis of paternity with 20 years of photo-identification records revealed that the age distribution of assigned fathers was biased toward older males, with the youngest assigned father being approximately twice the average age of first fertilization in females (Frasier *et al.* 2007). These results suggested that mate competition may prevent younger male right whales from reproducing. A similar approach in areas where a high proportion of whales have been genetically sampled (*e.g.* WNP, PCFG) and those samples are linked to long-term sighting histories of individuals, could provide insight into factors influencing male reproductive success in gray whales.

Another method that may increase understanding of gray whale reproduction is assessment of reproductive hormones. In other baleen whale species, reproductive hormone assays of blubber biopsies and fecal samples have been used to determine pregnancy rates (*e.g.,* Atkinson *et al.* 2020), better understand the physiological stress levels associated with different reproductive states (*e.g.*, Valenzuela-Molina *et al.* 2018), and infer patterns of male reproductive seasonality based on trends in testosterone levels over time (*e.g.,* Vu *et al.* 2015, Carone *et al.* 2019). Reproductive hormones have also been measured in whale blow samples (*e.g.,* Burgess *et al.* 2018). In addition, analysis of reproductive hormones in baleen, while only attainable from dead whales, provides the opportunity to track the recent reproductive histories of individuals, increasing understanding of calving intervals, age of sexual maturity, and timing of the breeding season (Hunt *et al.* 2016, 2022; Lowe *et al.* 2021). In gray whales, analysis of reproductive hormone concentrations in fecal samples and blubber biopsies have focused on evaluating how reproductive hormones vary with age, reproductive status, season, and life history stage (Lemos *et al.* 2020, Melica *et al.* 2021). Although analysis thus far have been limited to a single sample, Hunt *et al.* (2017) demonstrated that reproductive hormones can be detected in gray whale baleen. These studies highlight the potential utility of reproductive hormone assessments to provide insight into gray whale reproduction in the future.

5.2 Linking Reproductive and Acoustic Behavior

Bioacoustic tags, capable of collecting acoustic data as well as information on acceleration and depth, and Unmanned Aerial Vehicles (UAVs or drones) equipped with video, photographic and other sensors (*e.g.* thermal) are examples of rapidly-developing technologies that can further expand the understanding of reproductive behavior in gray whales. When paired together, underwater calls of gray whales that are linked to their behavior at the surface can be collected simultaneously, including data from breeding and other social-sexual groups. Alternatively, a recent study using two drones, one capable of landing on the water near whales to collect acoustic recordings and the other for obtaining aerial imagery of whale behavior, demonstrated the feasibility and utility of this research approach (Frouin-Mouy *et al.* 2020).

Acoustic communication plays a vital role in the social interactions of many marine mammal species, but gray whale acoustic behavior and vocalizations are just beginning to be evaluated. While the S1 call described in section 4.2 above seems associated with gray whale reproduction, its specific role has yet to be determined. The statistical approach taken by Ponce *et al.* (2012), could be designed to count the number of S1 calls detected, not only in relation to the total number of whales, but to the two demographic classes: single whales and female-calf pairs. If the S1 call is indeed a social contact call used mostly by single whales that are actively trying to breed, its presence should be correlated with the presence of single whales but uncorrelated with the presence of female-calf pairs, when observed across multiple seasons.

5.3 Role of Wintering Lagoon Entrance Aggregations in Reproduction

Whalers in the 19th century first reported aggregations of gray whales at the wintering lagoon entrances off Mexico, leading to the eventual discovery and exploitation of the high concentrations of whales inside of the lagoons proper. In recent decades, reports from scientists and observations of local fishers and eco-tourism operators confirm that gray whales actively enter and leave the winter lagoon interiors and form aggregations at the entrance points (Jones and Swartz, 1984b, 1990). These entrance point aggregations of whales are difficult to observe due to their distance from the shore and high surf where they occur, precluding detailed study and evaluation of the importance of these areas to gray whale reproductive behavior in the winter. A new generation of affordable "fixed-wing" and "hovering" drones have good potential to serve as effective and safe platforms to observe gray whale sexual and mating behavior in these portions of their winter range.

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Figures for Gray Whale Reproductive Behavior Chapter

Figure 1. *A group of three sexually aroused male gray whales. No female was identified in this group. While this "homosexual" behavior is observed throughout the gray whales' range, the utility or significance of this behavior remains unclear.* *Photo Credit: Fabian Rodríguez-González.*

Figures 2a-d. *A typical gray whale courting/mating group sequence photographed by drone in Laguna San Ignacio. Photo Credit: Fabian Rodríguez-González.*

Figure 2a*. Three gray whales (presumed males) investigating and stimulating an estrus female in advance of initiating a mating bout and copulation.*

Figure 2b. *Courting/mating bouts typically begin with male gray whales gathering and positioning themselves around the estrus female for attempts at copulation.*

Figure 2c. *Typical "hugging" position of male gray whales when attempting copulation with an estrus female.*

***Figure 2d**. While one male copulates with the estrus female, other males remain with the courting group and stand by for additional mating opportunities.*

Figure 3. *Spectrogram of a gray whale S1 call recorded on bottom mounted acoustic recorders in Laguna San Ignacio, Baja California Sur, Mexico: February 10, 2008 at 00:19:49 local time. Note the varying peak frequencies in each pulse, or 'note'.* *Photo Credit: Aaron Thode.*

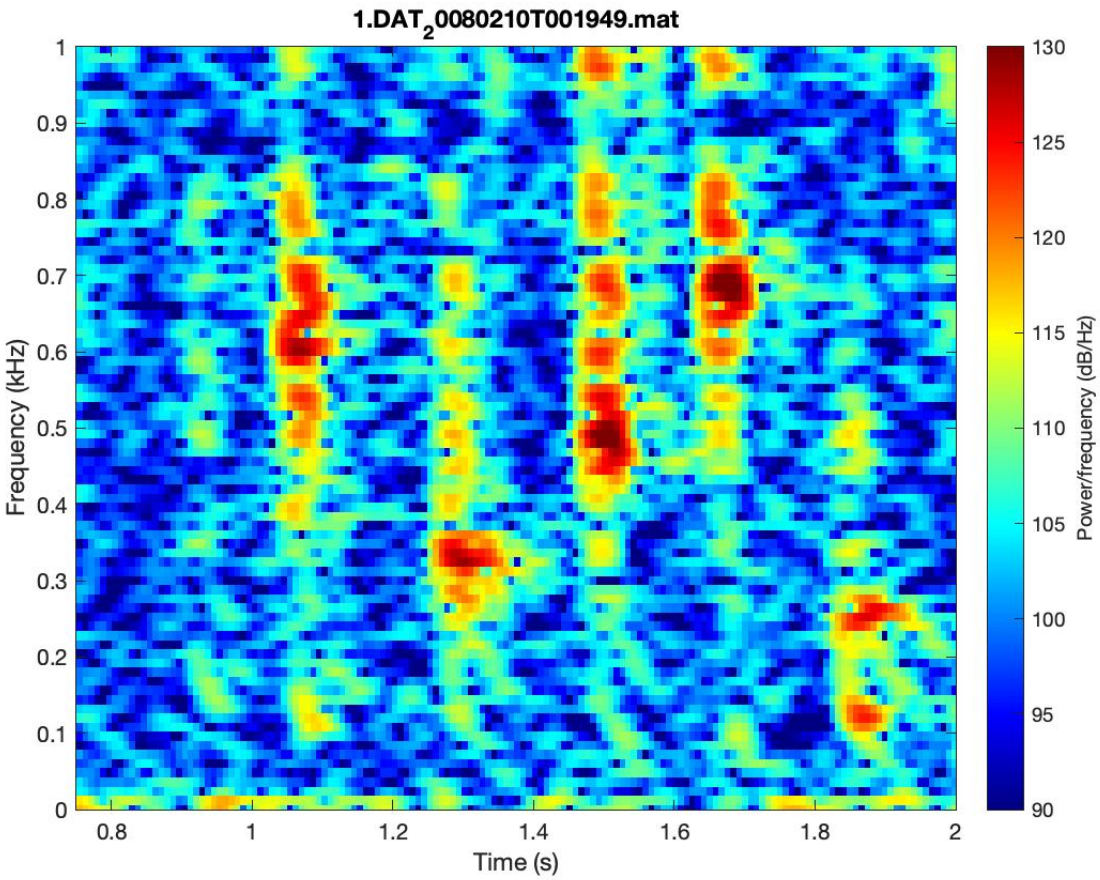

***Figure 4**. Female gray whale and her newborn calf in Laguna San Ignacio, Baja California Sur, Mexico. Female gray whales will often support their newborn calves by swimming underneath the calf and keeping it near to the water surface until the calf develops a regular swimming rhythm for surfacing to breathe. Photo Credit: Sergio Martínez-Aguilar.*

Figure 5*. When traveling the gray whale calf often positions itself close to and just behind the head of its mother where the "slipstreaming" effect of water passing around the mother's body will assist the calf's swimming by pulling it along.* *Photo Credit: Steven L. Swartz.*

***Figure 6**. A gray whale surface active socio-sexual courting/mating group of mixed sexes of individual adult whales in Laguna San Ignacio, Baja California Sur, Mexico. Photo Credit: Steven L. Swartz.*

Figure 7. *A gray whale male approaching and positioning itself at the side of a presumed female for a mating opportunity in Laguna San Ignacio, Baja California Sur, Mexico.* *Photo Credit: Steven L. Swartz.*

Figure 8. *A gray whale male (right) approaching and "hugging" a presumed female (left) with its flippers for a mating opportunity in Laguna San Ignacio, Baja California Sur, Mexico.* *Photo Credit: Steven L. Swartz.*

Figure 9. *Gray whale males in a courting/mating group approaching a presumed estrus female and positioning themselves for a mating opportunity in Laguna San Ignacio, Baja California Sur, Mexico. Photo Credit: Steven L. Swartz.*

Figure 10. *The erect penis of a male gray whale in Laguna San Ignacio, Baja California Sur, Mexico. The gray whale penis with its bifurcated tip appears to be "prehensile" and this capability may serve to assist the male in locating the entrance of the estrus female's vagina for intromission of semen.* *Photo Credit: Steven L. Swartz.*