Harbor Seal (Phoca vitulina) Reproductive Advertisement Behavior And The Effects Of Vessel Noise

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Abstract

Harbor seals (*Phoca vitulina*) are a widely distributed pinniped species that mate underwater. Similar to other aquatically mating pinnipeds, male harbor seals produce vocalizations during the breeding season that function in male-male interactions and possibly as an attractant for females. I investigated multiple aspects of these reproductive advertisement displays in a population of harbor seals in Glacier Bay National Park and Preserve, Alaska. First, I looked at vocal production as a function of environmental variables, including season, daylight, and tidal state. Vocalizations were highly seasonal and detection of these vocalizations peaked in June and July, which correspond with the estimated time of breeding. Vocalizations also varied with light, with the lowest probability of detection during the day and the highest probability of detection at night. The high probability of detection corresponded to when females are known to forage. These results are similar to the vocal behavior of previously studied populations. However, unlike previously studied populations, the detection of harbor seal breeding vocalizations did not vary with tidal state. This is likely due to the location of the hydrophone, as it was not near the haul out and depth was therefore not significantly influenced by changes in tidal height. I also investigated the source levels and call parameters of vocalizations, as well as call rate and territoriality. The average source level of harbor seal breeding vocalizations was 144 dB re 1 µPa at 1 m and measurements ranged from 129 to 149 dB re 1 µPa. Analysis of call parameters indicated that vocalizations of harbor seals in Glacier Bay were similar in duration to other populations, but were much lower in frequency. During the breeding season, there were two discrete calling areas that likely represent two individual males; the average call rate in these display areas was approximately 1 call per minute. The harbor seal breeding season also overlaps with peak tourism in Glacier Bay, and the majority of tourists visit
the park on a motorized vessel. Because of this overlap, I investigated the impacts of vessel noise on the vocal behavior of individual males. In the presence of vessel noise, male harbor seals increase the amplitude of their vocalizations, decrease the duration, and increase the minimum frequency. These vocal shifts are similar to studies of noise impacts on other species across taxa, but it is unknown how this could impact the reproductive success of male harbor seals. Finally, I looked at the role of female preference for male vocalizations. Using playbacks of male vocalizations to captive female harbor seals, I found that females have a higher response to vocalizations that correspond to dominant males. Females were less responsive to subordinate male vocalizations, which had a shorter duration and a higher frequency. Given that male harbor seals decrease the duration and increase the frequency of vocalizations in the presence of noise, it is possible that these vocalizations become less attractive in noise.
HARBOR SEAL (*PHOCA VITULINA*) REPRODUCTIVE ADVERTISEMENT BEHAVIOR
AND THE EFFECTS OF VESSEL NOISE

by

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B.S. Biology, Baylor University, 2011

DISSERTATION
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in Biology

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A brief introduction to aquatically mating pinnipeds and a summary of the

life history of harbor seals

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Introduction to Pinniped Mating Strategies

The pinnipeds are a group of semiaquatic marine mammals that includes the true seals (Phocidae), the sea lions and fur seals (Otariidae), and the walruses (Odobenidae). Reproductive behavior and mating strategies vary widely across these species and range from serial monogamy in pack-ice breeding seals, such as crabeater seals (*Lobodon carcinophagus*) (Siniff et al., 1979), to extreme polygyny in elephant seals (*Mirounga spp.*) and the otariids (e.g.: Le Boeuf, 1974; Campagna & Le Boeuf, 1988; Riedman, 1990; Fabiani et al., 2004). The type of mating system employed by each species depends on the abundance and distribution of females during the breeding season, with a higher environmental potential for polygamy (EPP) in species where females are clustered temporally and geographically (Emlen & Oring, 1977). A high EPP is typical for pinniped species that mate on land, as females often congregate on small islands during the breeding season; males can therefore monopolize large groups of females and sire multiple pups (e.g.: Le Boeuf, 1974; Campagna & Le Boeuf, 1988; Riedman, 1990; Fabiani et al., 2004).

Approximately 45% of all pinniped species (80% of the true seals) mate underwater (for a review, see Van Parijs, 2003). Given the three-dimensional space of underwater environments, females in these aquatically mating species are less clustered during the breeding season and there is a lower EPP (Stirling et al., 1983; Coltman et al., 1997, 1998a; Boness et al., 2006). Males of these aquatically mating species exhibit similar behaviors during the breeding season, mainly in the production of underwater vocalizations (Van Parijs, 2003). These vocalizations either function in male-male interactions, as attractants for females, or both.

Bearded seals (*Erignathus barbatus*) are an Arctic phocid species and during the breeding season, male bearded seals produce vocalizations, called “trills”, to advertise breeding condition
Males make series of stereotypical dives and surface intervals and produce an average of 1.5 trills per dive (Van Parijs et al., 2003). In this species, different males use different mating tactics: some males occupy small discrete territories (0.27-1.93 km²) and produce long trills (around 40 s), while other males patrol, or “roam,” a larger range (5.31-12.50 km²) and produce trills that are shorter in duration (around 11 s) (Van Parijs et al., 2003). It is thought that territorial males have a higher reproductive success and that trills of longer duration are a signal of male quality (Van Parijs et al., 2003).

Antarctic phocids also produce underwater displays during the breeding season (for a review, see Van Opzeeland et al., 2010). Weddell seals (Leptonychotes weddellii) are one of the most vocal phocids, with 12 call groups that are subdivided into 34 call types (Thomas and Kuechle, 1982). One call group, the “trill”, is only produced by males and functions in territory defense (Thomas & Kuechle, 1982; Terhune et al., 2008). Leopard seals (Hydruga leptonyx) exhibit cycles of vocalizing and breathing during the breeding season, which are also thought to be associated with territoriality (Stirling & Siniff, 1979). Their repertoire includes anywhere from 7 to 12 different call types (Van Parijs, 2003). Acoustic recordings have indicated that leopard seals produce vocalizations from October to January, which fully covers the breeding season (Van Opzeeland et al., 2010). It is possible that males are making these calls in search of mates or to defend territories that are important for reproduction (Stirling and Siniff, 1979; Rogers et al., 1996).

The Harbor Seal

Harbor seals (Phoca vitulina) (Figure 1.1) are one of the most well studied aquatically mating pinnipeds. They are found in a variety of habitats, including rocky coastlines, sandy
beaches, and glacial ice, and have a circumpolar distribution in the Northern hemisphere (Figure 1.2) (Bigg, 1981). There are five different subspecies of harbor seals found around the globe: *P. v. vitulina* (Eastern Atlantic), *P. v. concolor* (Western Atlantic), *P. v. richardii* (Eastern Pacific), *P. v. stejnegeri* (Western Pacific), and *P. v. mellonae* (inhabits a few freshwater lakes and rivers in Quebec, Canada) (Figure 1.2) (Lowry, 2016).

There is not extreme sexual dimorphism in harbor seals that is seen in other pinnipeds, such as elephant seals (*Mirounga spp.*) or grey seals (*Halichoerus grypus*) (Lindenfors et al., 2002). Adult males are 1.6-1.9 m long and can weight 70-150 kg, while females are only slightly smaller, measuring 1.5-1.7 m in length and weighing 60-110 kg (Lowry, 2016). Harbor seals can live to be up to 35 years old, with females living slightly longer than males (Lowry, 2016). Males become sexually mature around the age of 4-6, and females become sexually mature around the age of 3-5 (Lowry, 2016). They have a variable diet, depending on habitat and season, and eat many species of fish, cephalopods, and benthic invertebrates (Riedman, 1990). Predation on harbor seals also varies by habitat; known predators include great white sharks (*Carcharodon carcharias*), other marine mammals, including killer whales (*Orcinus orca*) and Stellar seal lions (*Eumetopias jubatus*), and terrestrial predators, such as eagles and coyotes (Riedman, 1990).

Harbor seal females, along with the majority of other pinnipeds, have a delayed implantation mechanism to allow annual scheduling of pupping and mating. In harbor seals, delayed implantation last for 1.5-3 months and gestation is around 9-11 months (Bigg & Fisher, 1975; Riedman, 1990; Temte, 1994). Pupping occurs generally at the same time every year and is influenced by photoperiod (Bigg & Fisher, 1975; Temte, 1994). This causes a latitudinal gradient for pupping phenology; for example, populations at lower latitudes in Baja California
pup as early as mid-March and populations at higher latitudes in northern Washington State pup in early June (Temte et al., 1991). More recent studies have also demonstrated that the timing of pupping can also be influenced by population age structure and the prey availability (Jemison and Kelly, 2001; Reijnders et al., 2010; Cordes & Thompson, 2013). After females give birth to pups, they nurse the pups for approximately 3-6 weeks (Bigg, 1981; Riedman, 1990). Toward the end of this lactation period, females leave their haul out sites during the day to forage (Boness et al., 1994; Bowen et al., 1994, 2001). It is during this time that mating takes place (Thompson, 1988).

Before the mating season, male harbor seals occupy large ranges, and then, during the mating season, males decrease the size of their range (Van Parijs et al., 1997). They also decrease the amount of time spent offshore (26% to 15% in Atlantic harbor seals) and increase the time spent near the haul outs (34% to 44%) during the mating period, compared to the before the onset of mating (Boness et al., 2006). This is likely to increase the potential for interactions with females.

Male harbor seals drastically decrease time spent foraging during the breeding season (Coltman et al., 1997; 1998b; Baechler et al., 2002). This results in a change in body composition, with males losing 0.47% of their initial mass for each day of the breeding season (Coltman et al., 1998b). Large males cease to forage altogether, as they have more energy available in stores compared to smaller males, who are forced to make opportunistic foraging trips during the breeding season (Coltman et al., 1997).

Males also alter their diving behavior during the mating season. Coltman et al. (1997) noted that Atlantic harbor seal males in Sable Island, Nova Scotia make deep dives (>20 m) early in the season and then switch to shallow dives (<20 m) during the peak of mating. The deep
dives occur primarily during the day, are uniform in shape, last 4.6 minutes, on average, and are associated with foraging (Coltman et al., 1997). The shallow dives serve a reproductive function, vary in shape, only last around 3 minutes, and occur at twilight and during the night (Coltman et al., 1997). By making these dives at night, it is thought that males can increase encounters with females who are returning to the haul out from foraging trips (Coltman et al., 1997). Male harbor seals in Scotland also make short dives during the mating season, and these dives are accompanied by vocal displays (Van Parijs et al., 1997).

During the breeding season, male harbor seals produce vocalizations known as “roars” (Figure 1.3) (Hanggi & Schusterman, 1994; Van Parijs et al., 1999). Previous work has shown that these vocalizations vary based on social status of the individual (Nicholson, 2000). In a population in Monterey Bay, CA, dominant males produce roars that are longer in duration and lower in frequency than subordinate males (Nicholson, 2000). Given this variation, it is likely that seals use vocalizations to assess competition among males or to attract females (Nicholson, 2000). Playback experiments by Hayes et al. (2004b) further confirmed the role of roar vocalizations in male-male interactions. This study showed an higher number of approaches to the playback speaker and increased aggressive behaviors, such as flipper slapping, during playbacks of other roar vocalizations (Hayes et al., 2004b). Only one individual responded to the playbacks in a given area, indicating that a single male occupied a defined area during the breeding season (Hayes et al., 2004b).

There have been multiple studies focused on the territorial nature of harbor seal males during the breeding season (Van Parijs et al., 1997; 2000; Hayes et al., 2004a). In a population of Atlantic harbor seals, there were two separate acoustic display areas that ranged from 40-135 m² (Van Parijs et al., 2000). These same areas were each occupied by only one individual for
three consecutive years, and it is possible that the same male returned to its display area for multiple years (Van Parijs et al., 2000). In California, Pacific harbor seals also establish non-overlapping territories (Hayes et al., 2004a). In this population, four males were seen occupying territories along a travel corridor in between the haul out and foraging locations, and these territories had an average size of 0.039 km$^2$ (Hayes et al., 2004a). Not all males establish territories; this behavior is restricted to areas in which there is a higher EPP, such as estuaries or narrow travel corridors (Hayes et al., 2004a). However, territoriality does not necessarily correspond to higher reproductive success for individual male harbor seals.

Paternity analysis has revealed that there is only slight polygyny among harbor seal populations (Coltman et al., 1998a; 1999; Hayes et al., 2006). Studies at Sable Island, Nova Scotia reveal that most males sire a single offspring, and successful males are often correlated with moderate body size, and behaviors such as being rarely sighted along, associating with many groups on shore, and hauling out infrequently (Coltman et al., 1998a; 1999). There are similar levels of polygyny seen for harbor seals in Elkhorn Slough, California (Hayes et al., 2006). Despite the similar levels of polygyny, there are differences in the male mating strategies. While the most successful males in Sable Island spent the majority of time offshore patrolling offshore, the most successful male in Elkhorn Slough, who sired five pups over four breeding seasons, held a territory in the travel corridor (Hayes et al., 2006).

**Glacier Bay National Park and Preserve, Alaska**

Glacier Bay National Park and Preserve (GBNPP) is a wilderness area in Southeast Alaska that is home to one of the largest regional aggregations of harbor seals during the breeding season (Figure 1.4) (Calambokidis et al., 1987). Harbor seals in GBNPP use either
terrestrial or glacial ice habitats for haul outs, and foraging behavior varies between the two harbor seal habitats in GBNPP. Glacial ice seals travel farther distances to forage, dive deeper distances, and dive for a longer duration, while terrestrial seals travel shorter distances and have shallower, shorter dives (Blundell et al., 2011; Womble et al., 2014). These differences in foraging behavior are directly correlated to prey availability. The prey in glacial sites is at deeper depths and the density is lower, however, the prey is of higher quality (Blundell et al., 2011; Womble et al., 2014). High quality prey allows for these longer, deeper foraging dives (Blundell et al., 2011; Womble et al., 2014). Alternatively, the prey at terrestrial sites occurs at shallower depths and at a much higher density (Womble et al., 2014).

From 1992 to 2008, there was an overall decline in the population of harbor seals of -11.5% per year (Womble et al., 2010). Counts of non-pup individuals in glacial ice habitats declined by an average of -7.7% per year in the pupping season (June) and by -8.2% in the molting season (August) (Womble et al., 2010). Terrestrial counts also decreased by -12.4% per year in the molting season (Womble et al., 2010). Updated trends (1992-2013) still indicate that there is an overall population decline at terrestrial sites (approximately -7% per year), but the more recent trend (2009-2013) is positive (+13% per year) (Womble et al., 2015). However, the number of harbor seals in GBNPP is not back to the levels before the decline began (Womble et al., 2015).

Reproductive behavior has not been studied in GBNPP to the extent that other populations have been studied, such as those in Sable Island, Scotland, and California. However, acoustic data from the area reveals the presence of harbor seal roar vocalizations during the breeding season (Temte et al., 1991; Mathews & Pendleton, 2006; McKenna et al., 2017). This dissertation aims to further investigate vocal behavior of harbor seal males during the breeding
season in GBNPP by assessing seasonality and diel trends of roar production, source levels, call rate and territoriality, and the effects of anthropogenic noise on acoustic behavior. This dissertation also examines the role of female preference for male roar vocalizations in harbor seals.
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**Figure 1.1:** Harbor seal (*Phoca vitulina*) in Glacier Bay National Park and Preserve, Alaska.
Figure 1.2: Distribution map of the five harbor seal subspecies (created using data from Lowry, 2016). *P. v. mellonae* is only found in a few freshwater lakes in Quebec, Canada and is therefore not shown on the map.
Figure 1.3: Spectrogram of a harbor seal roar vocalization.
**Figure 1.4:** Map of Glacier Bay National Park and Preserve with known harbor seal haul out and foraging locations for glacial and terrestrial harbor seals (created using data from Womble et al., 2010 & 2014).
The role of season, tide, and diel period in the presence of harbor seal (*Phoca vitulina*)

breeding vocalizations in Glacier Bay National Park and Preserve, Alaska

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Abstract

Glacier Bay National Park and Preserve is a marine protected area in southeastern Alaska that is home to some of the largest seasonal aggregations of harbor seals (*Phoca vitulina*) in the region. Harbor seals, like the majority of phocids, are an aquatically breeding pinniped species. During the breeding season, male harbor seals use acoustic signals to defend underwater territories from other males and possibly to attract females. We used a long-term passive acoustic dataset to examine the trends in harbor seal vocal behavior near a terrestrial haul out as a function of season, tides, and time of day. Seasonality analyses indicated a sharp increase in vocal activity during the months of June and July, which correlates with the estimated timing of the breeding at this location. Contrary to previous studies, there was no effect of tidal height on the documented calling behavior of harbor seals at this location, perhaps because the recordings were made farther from shore, within 10 km of the major haul-out area. Diel analyses showed that harbor seal males call throughout the day, but, similar to other populations, calling significantly increased at night when more seals are foraging. This analysis provides evidence that specific environmental parameters play a role in harbor seal acoustic behavior in Glacier Bay National Park and Preserve and allows for behavioral comparisons among different harbor seal populations across the globe to guide future research efforts working to protect harbor seals during the breeding season.
Introduction

Animals communicate using a variety of cues, including visual, acoustic, chemical, and tactile signals (Bradbury & Vehrencamp, 2011). Given the efficient propagation of sound underwater, acoustic communication is a primary signaling modality for marine mammals (Au & Hastings, 2008). These acoustic signals produced by marine mammals provide an opportunity for researchers to eavesdrop on acoustically active individuals, adding valuable insight into the behavioral ecology of species that are otherwise difficult to study. Passive acoustic monitoring (PAM) is a technique that employs autonomous recording systems to collect acoustic data in a given location and for an extended period of time, even when visual sampling is impractical, such as in remote locations or during inclement weather (Mellinger et al., 2007). Many marine mammal species use specific acoustic signals that are hypothesized to be for reproductive purposes (e.g.: Rogers et al., 1997; Parks et al., 2005). Investigating the timing and locations of the production of these reproductive signals using PAM fosters a better understanding of their role in the natural history of the species, provides information relevant to protection of these species, and allows for cross-comparison of separate breeding populations (Winn et al., 1981; Van Parijs et al., 2009).

Harbor seals (*Phoca vitulina*), like the majority of phocids, mate underwater (Van Parijs, 2003). The type of environment that harbor seal populations inhabit affects male mating strategies. For example, in a harbor seal population inhabiting an open-water area, females are widely distributed and the most successful males spend the majority of their time offshore (Coltman et al., 1999). In populations occupying enclosed estuaries, however, a few (n = 4) males have been shown to form territories along narrow travel corridors between haul outs and foraging locations where females are known to travel (Hayes et al., 2006). Paternity analysis in...
this population revealed that the most successful male, who sired five pups in four years, was a territory holder (Hayes et al., 2006). The level of polygyny does not appear to vary between these populations (Hayes et al., 2006), but the environment can be a determining factor in male behavior (territorial vs. non-territorial) during the breeding season.

Acoustic cues produced by territorial harbor seal males, referred to as roars, are important for male-male signaling in territory defense and may also play a role in female choice (Hanggi & Schusterman, 1994; Van Parijs et al., 1999; Hayes et al., 2004). The detection of roar vocalizations on PAM systems can be used to provide insight into the timing and duration of the harbor seal mating season. This is especially useful for harbor seal populations that are difficult to study, such as those in remote locations, for populations in which little is known about their behavior, or for comparing the behavior of harbor seal males between habitat areas (e.g.: Van Parijs et al., 1999).

In Elkhorn Slough, California, a narrow inlet in Monterey Bay, four male harbor seal individuals were identified that held territories and produced acoustic cues over multiple years (Hayes et al., 2004). In Atlantic harbor seals, two display areas in the Kessock channel in Scotland were each occupied by a single individual over a three-year period (Van Parijs et al., 2000). Males in Scotland vocalized in the summer months (July and August), consistent with the beginning of weaning (Van Parijs et al., 1999). Vocal behavior of seals in both Elkhorn Slough and the Atlantic varied as a function of tidal state (Van Parijs et al., 1999; Hayes et al., 2004).

The environmental characteristics of Glacier Bay National Park and Preserve, Alaska (GBNPP), including its many inlets and narrow corridors between islands, suggest that harbor seal males in this area likely establish underwater territories and are acoustically active during the breeding season, similar to harbor seal males in Elkhorn Slough. GBNPP is a glacial fjord
ecosystem that hosts one of the largest seasonal aggregations of harbor seals in southeastern Alaska (Calambokidis et al., 1987). Harbor seals in this area rest on either drifting ice from tidewater glaciers or on terrestrial sites (Mathews & Pendleton, 2006). Recent surveys have estimated over 2,500 seals in Johns Hopkins Inlet, a primary glacial haul out site, and up to 1,200 individuals in the terrestrial sites (Womble et al., 2010; Womble et al., 2015).

Pupping in GBNPP begins in mid to late May (Temte et al., 1991; Mathews & Pendleton, 2006) and is followed by 3-5 weeks of lactation (Blundell et al., 2011). If this population follows the pattern shown elsewhere, harbor seal males should begin vocalizing in June, when the pups are being weaned and the females begin to forage. Tides in GBNPP often reach heights that cover some of the terrestrial seal haul outs, and thus at high tides, more individuals of both sexes are in the water (Mathews & Pendleton, 2006; Womble et al., 2010). If males have a higher likelihood of encountering females at high tide, one would expect an increase in acoustic behavior, similar to observations from Elkhorn Slough (Hayes et al., 2004). Diel trends in vocal behavior, with an increase at night during the times that females are foraging have been documented in other harbor seal habitats (Coltman et al., 1997; Van Parijs et al., 1999) and would also be expected in GBNPP. Behavioral comparisons between harbor seal populations give further insight into the drivers of behavior and can inform conservation efforts during the breeding season.

Concerns about the effects of vessel traffic on wildlife, especially marine mammals, prompted the National Park Service (NPS) to begin long term passive acoustic monitoring of the underwater acoustic environment of GBNPP in May 2000 (Kipple & Gabriele, 2003). The goals of this NPS effort were to characterize the frequency, occurrence, and seasonality of biotic and abiotic sounds as well as vessel-generated ambient noise (McKenna et al., 2017). In this study,
existing data from this established PAM system was used to assess the seasonal, diel, and tidal variation in male harbor seal roar production near a terrestrial haul out site in GBNPP to give insight into the underwater behavior of harbor seals in this area as well as compare acoustic activity with previously studied populations. Identifying key periods of male breeding advertisement can shed light on the differences in behavior between populations across the globe. An improved understanding of how seals and other marine mammals use their acoustic habitat is essential for future studies that will assess potential effects of manmade noise on biologically essential acoustic behavior.

**Methods**

**Data Collection**

In May 2000, a cabled hydrophone was installed in the Bartlett Cove area of GBNPP (58.43501 N, 135.92297 W) and was bottom mounted in 30 m of water, approximately 1 m off the ocean floor (Figure 2.1). This location was within approximately 8 km of a terrestrial harbor seal haul out. The system consisted of a calibrated ITC type 8215A broadband omnidirectional hydrophone (nominal sensitivity -174 dB re 1 V/µPa) connected to a shore-based data system and made 30-second recordings once per hour for 24 hours a day (88 kHz sampling rate). The detection range of the hydrophone was calculated using the passive sonar equation, with an signal to noise ratio (SNR) value of 6 dB re 1 µPa, a source level of 144 dB re 1 µPa (Matthews, et al., 2017), a noise level of 84 dB re 1 µPa (Kipple & Gabriele, 2003), and a transmission loss of 15log(r) (Malme et al., 1982), with r being the maximum distance a call could be detected from the hydrophone. Male roar vocalizations could be detected within approximately 4 km of the cabled hydrophone. The recording system had a flat frequency response from 20 Hz to 20
kHz (± 2 dB), which fully covered the range of harbor seal roar vocalizations (primary frequency range: 40 to 500 Hz, Matthews et al., 2017) (Figure 2.2). For each acoustic sample, one-third octave (10 Hz to 31.5 kHz) and narrow band sound pressure levels were archived along with 30-second audio clips (.wav format). Each 30-second audio recording was visually analyzed for the presence of harbor seal roar vocalizations. Four years of data were analyzed: 2001, 2002, 2007, and 2008.

This 30-second sampling strategy took into account the goals of the original NPS study, the geography of the area, and the sound sources to be characterized. Hourly samples were made to acquire sufficient data to characterize the ambient noise environment, to keep the data analysis task manageable, and to economize on disk space. The 30-second sample duration created a snapshot of ambient noise, giving the analyst enough time for assessment, and with enough spectral data to characterize the sample and provide a sufficient number of averages to smooth the narrowband spectra (e.g. 30 averages for the 1000 Hz frequency range).

Seasonality Analysis

To investigate peaks in acoustic activity for harbor seal roars, the total number of hours per day in which roars were detected was tallied, with a maximum of 24 hours. Data from 2001 included all months of the year (346 days) and the 2002 data included the months of January through August (213 days). For 2007 and 2008, data were available roughly from May through September (107 and 123 days, respectively). A total of 789 days (18,936 acoustic samples) were available for this analysis.

Tidal Analysis
The peak months of harbor seal acoustic activity, based on the analysis of seasonality, were analyzed for the presence of tidal trends. Only days for which all 24 hourly samples were available were used in order to ensure similar sample sizes for each of the current directions. A total of 1,208 audio samples were available for the tidal analysis. The acoustic file from each hour was coded for either the presence (1) or absence (0) of harbor seal roars. Each 30-second audio file was marked with the corresponding tidal height for that date and time and the current direction (ebb or flood). Additionally, tidal heights were rounded to the nearest whole number and the presence and absence data were averaged to calculate an overall probability of detecting roar vocalizations for each tidal height.

Diel Analysis

The peak months of harbor seal acoustic activity were also analyzed for the presence of daily trends. The same data used for the tidal analysis was used for the diel analysis. Because the amount of daylight and night are not equal in the summer in southeastern Alaska, four non-overlapping two-hour time blocks were denoted for sunrise, day, sunset, and night. Sunset and sunrise times were determined using data from the United States Naval Observatory (United States Naval Observatory, 2016) and times were rounded to the nearest hour; the two-hour blocks for sunrise and sunset were centered on these times. The day and night blocks occurred at the midpoint between sunrise and sunset, and sunset and sunrise, respectively. These four time blocks were collectively used to assess the effects of light regime on calling presence. The probability of detecting harbor seal roar vocalizations during the four light regimes was calculated by averaging the presence and absence of roars for all hours in each of the four time periods.
**Statistical Analysis**

To investigate peaks in acoustic activity, monthly averages of the number of hours per day with harbor seal detections were calculated. A linear mixed effects model (lme4 package in R, Bates et al., 2014) compared the occurrence of harbor seal roars as a function of month, with year as a fixed effect. Following the model, pairwise comparisons using Tukey’s method were done among months and years to parse out seasonal differences in calling behavior (lsmeans package in R, Lenth, 2014). The presence of daily trends and tidal influences were analyzed using generalized linear mixed effects models with a logit regression for binomial data. Fixed effects included light regime, tidal height, and whether it was an ebb or flood tide as well as if it was a spring or neap tide. Tidal height was used as a continuous variable, while light regime, current direction (ebb vs. flood), and whether or not it was a spring or neap tide were used as categorical variables. The random effects were nested variables for year, month and day. Post-hoc pairwise comparisons using Tukey’s method were also done for statistically significant fixed effects to more accurately describe the differences in harbor seal acoustic behavior as a function of environmental parameters (lsmeans package in R, Lenth, 2014). All statistical analyses for the seasonality, diel, and tidal analyses were done in the statistical program *R v. 3.2.3* (R Core Team, 2013).

**Results**

Analyses of the acoustic activity during the year revealed peaks in the number of hours per day with male harbor seal roaring activity in June and July (Figure 2.3, Supplemental Table 2.1). For June, the mean number of hours per day in which harbor seals were acoustically
detected was 12.1 hours (SD = 8.0). For July, the mean was 18.1 hours (SD = 6.8). In comparison, the mean number of hours per day in which harbor seals were vocalizing during the months of May and August were 2.0 hours (SD = 3.1) and 3.0 hours (SD = 4.0), respectively. A linear mixed effects model indicated that in June and July, harbor seal roars were detected in significantly more hours per day than in other months (p < 0.0001 at \( \alpha = 0.05 \)). The mean number of calls in August and September (p = 0.0012) were also significantly different from each other. Pairwise comparisons between years indicated that there were no statistical differences in the mean number of hours per day that harbor seal calls were detected between sequential years (2001 and 2002, 2007 and 2008), but there were statistically significant differences between non-sequential year comparisons (Supplemental Table 2.2).

Roars were detected across all tidal heights (Figure 2.4). The minimum probability of detecting harbor seal roars was 60.4% (SD = 49.2%) and was observed at a tidal height group of 0 ft (n = 96). The maximum probability of roar detection was 90.0% (SD = 31.6%) and occurred at a tidal height group of 17 ft (n = 10). However, tidal heights this large were rare, as they occurred during spring tides only. There was no significant difference in the probability of detecting harbor seal roars during ebb versus flood tides (p = 0.63) or spring versus neap tides (p = 0.55). Results from the generalized linear mixed-effects model indicated that there was no significant difference in the presence of harbor seal roars across tidal heights (p = 0.42) (Supplemental Table 2.3).

During peak months of roar activity, harbor seal calls were detected throughout the day, with a minimum probability of detection during the daytime of 70.5% (SD = 45.7%). Calling probability increased to 84.8% (SD = 36.0%) at night. The probability of harbor seal calls during sunrise periods was 72.9% (SD = 44.6%) and during sunset was 76.5% (SD = 42.5%).
The generalized linear mixed effects model and subsequent pairwise contrasts demonstrated a statistically significant difference between the probabilities of detecting harbor seal roars during different light regimes, with a lower detection during the day and a higher detection at night (Supplemental Table 2.4). There was no difference between the sunrise and sunset periods.

Discussion

There was an overall trend in harbor seal roar production by males in GBNPP, with peaks in June and July. Around mid-June, there was a sharp increase in the number of hours per day in which harbor seal male roar vocalizations are detected. A few weeks after pupping, as the pups are weaned, female harbor seals begin to make foraging trips, and it is during this time that mating is thought to take place (Bones et al., 1994; Bowen et al., 1994, 2001). Similarly, male advertisement behavior in GBNPP begins a few weeks after the onset of pupping and likely indicates the onset of the mating season. Thus, these results are consistent with previous studies that indicate that in GBNPP, the harbor seal pupping season typically begins in late May (Temte et al., 1991; Mathews & Pendleton, 2006). Previous acoustic studies of other harbor seal populations also indicate an onset of acoustic displays that correspond to weaning (Van Parijs et al., 1999). Additionally, these results demonstrate that the period of male advertisement in GBNPP lasts into late July and male acoustic displays stop before the molting period in August (Calambokidis et al., 1987). Due to the missing data, it is not possible to completely rule out that male harbor seals might vocalize during other times of the year. However, given the lack of vocalizations during off-peak months in the year round data from 2001 and the consistency of available months for other years, we speculate that these roar vocalizations are restricted to the breeding period.
Although there were positive acoustic detections of male harbor seal roars in May and August, these months were not significantly different than the majority of other months sampled (excluding June and July). The increase in acoustic detections compared to April and September potentially indicates a ramp-up and cool-down phase in roar production. We speculate that male harbor seals may establish territories by roaring before the mating season begins and may hold territories until after the mating season has concluded. This would account for the statistical difference seen between August and September. Satellite telemetry studies have indicated that the female harbor seals typically depart Glacier Bay after the breeding season in September (Womble & Gende, 2013). The percentage of tagged seals returning back to GBNPP increases in late April and early May, prior to the breeding season (Womble & Gende, 2013). The timing of departure and arrival of female harbor seals from GBNPP mirrors the pattern of acoustic detections of male harbor seal roar vocalizations. It has been shown in other pinniped species, such as Atlantic walruses (*Odobenus rosmarus rosmarus*) (Freitas et al., 2009), that males arrive at the breeding grounds and begin to establish dominance a few weeks before the onset of mating before females arrive to the breeding grounds. Therefore we would anticipate male advertisement to start in late April or early May in this population, which is consistent with the data presented here.

Although there were statistical differences in the seasonality between non-sequential years, this is likely attributed to the missing data, as the peak in vocal activity in begins in June of each year and drops off in August (Figure 2.2). Since harbor seal annual pupping has been shown to generally correspond to photoperiod (Bigg & Fisher, 1975; Temte, 1994) it would be expected that there would be no difference between years. The photoperiod response, paired with a 1.5-3 month delayed implantation and a 9-11 month gestation, accounts for inter-annual
stability (Bigg & Fisher, 1975; Temte, 1994). However, there have been documented shifts in the timing of pupping in Alaska (Jemison & Kelly, 2001) and Atlantic populations (Reijnders et al., 2010; Cordes & Thompson, 2013), which are believed to correspond to changes in the population’s age structure or the quality and availability of prey. Shifts in the age structure may influence pupping because older females give birth earlier than younger females (Reiter et al., 1981; Lunn & Boyd, 1993). Additionally, prey quality and availability can affect maternal body condition (Jemison & Kelly, 2001). It is also possible that prey availability is affecting male body condition, and therefore the differences in the mean number of hours per day that male harbor seal roars were detected may reflect differences in foraging and reproductive ecology between non-contiguous years of the study.

In contrast to studies elsewhere, there was no significant difference in the presence or absence of roars relative to tidal height in GBNPP. The vocalizing males in the Elkhorn Slough population exhibited higher vocalization rates during higher tides, when more females were present in the water due to inundation of haul out sites (Hayes et al., 2004). In the Atlantic, roars were highly dependent on tides in both study areas, with peak vocal activity during high tides (Van Parijs et al., 1999). In GBNPP, aerial survey counts have confirmed that there are more individuals in the water at high tide compared to low tide (Mathews & Pendleton, 2006; Womble et al., 2010). However, the presence/absence data for roars from the 30-second audio clips indicated that harbor seal roars were detectable across all tidal levels. One possible explanation for this result is the distance of the hydrophone to the haul out. Male harbor seals defending territories closer to the haul out might be more influenced by tidal state in GBNPP. Further investigation into the spatial distribution of males near the hydrophone will help clarify if there is a tidal influence on the number of calls detected or the number of individuals calling.
Harbor seals called significantly more at night, when compared to other times of day. During the breeding season, female harbor seals in GBNPP typically make deep dives from 0500 to 2000 (daylight) and shallower dives from 2100-0400 (night) (Womble et al., 2014). These shallow dives are thought to be driven by vertically migrating prey moving toward the surface at night (Womble et al., 2014). Therefore, if foraging dives are predominantly occurring at night, it is likely that male harbor seals would have a larger audience at that time. Although it is unknown if male harbor seals are altering their dive behavior in GBNPP, the acoustic data indicated a behavioral shift that is consistent with the idea that males are attempting to increase encounters with females. Similarly, Atlantic harbor seals in the U.K. also have been shown to increase their vocal behavior at night (Van Parijs et al., 1999). Before the onset of mating, male harbor seals in Nova Scotia were documented making deep daytime dives associated with foraging, but during the breeding season they switch to shallower dives during twilight and at night, believed to increase their chances of encountering females (Coltman et al., 1997).

Additionally, female harbor seals have been observed foraging near the hydrophone in Bartlett Cove used in this study (Womble et al., 2014), adding strength to the argument that males are likely defending underwater territories in this area. It is also possible that male harbor seals are calling more at night to avoid vessel-generated noise, which is more prevalent during the day (McKenna et al., 2017), or the calls are more detectable at night in quiet conditions. Future studies will investigate the impacts of vessel noise on the calling behavior of male harbor seals in GBNPP.

Although PAM is a powerful tool, there are a few limitations associated with studying harbor seal acoustics with data from a single fixed hydrophone. The primary limitation is a relatively small detection range for vocalizations and the inability to localize calling individuals,
potentially limiting the samples to a few males. In this study, the detection range of the hydrophone did not include the water directly adjacent to the closest haul out, but did include areas in which harbor seals have been observed foraging. Additional hydrophones closer to the haul out might detect additional male callers. It is also not possible to determine whether the increase in the detection of vocalizations in the summer months and at night is due to an increase in calling behavior by individuals or due to an increased number of males calling in the area at those times. Evidence from visual spectrogram analysis indicated up to five individuals in the same 30-second audio clip, so although the area of detection was small, there were still multiple males calling at the same time. Further, while males do show site fidelity (Van Parijs et al., 2000) and the same males may be present in multiple years (2001-2002 & 2007-2008), it is likely that turn over in specific individuals in this location occurred between 2002 and 2007. A multi-element hydrophone array covering a larger area could help in resolving these limitations and allow for localization of callers.

This study provides data from the longest acoustic data set used to monitor harbor seal roar vocalization published to date. It provides further evidence that passive acoustic monitoring is a useful tool for determining the length of the breeding season of harbor seal populations. Additionally, these data complement previous studies on the seasonal and diel trends in harbor seal acoustic advertisement during the breeding season. Further investigation is needed to understand the variation in acoustic trends between populations as a function of tidal cycles.

Acoustic monitoring is a powerful approach to studying harbor seal breeding behavior and habitat use and allows for the monitoring of behavior in relation to a changing environment. As new technologies advance, future studies may enlighten understanding of social interactions and the role of different habitats in pinnipeds that cannot be studied by visual methods alone.
Comparing PAM results from multiple harbor seal populations can also indicate acoustic differences in populations and add insight into how the addition of manmade noise may affect these reproductive signals.
Acknowledgements

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References


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**Figure 2.1:** Map of Glacier Bay National Park and Preserve with the location of the cabled hydrophone system (star) and the closest harbor seal haul out (circle) (Geographic Coordinate System: North American Datum 1983).
**Figure 2.2:** Spectrogram of a harbor seal roar vocalization recorded near Bartlett Cove in Glacier Bay National Park and Preserve (spectrogram parameters: Hann window, 50% overlap, discrete Fourier transform (DFT) size = 4096).
**Figure 2.3:** Numbers of hours per day from January – December that harbor seal roar vocalizations were detected from acoustic data. Grey areas indicate missing data. The bottom panel shows the combined data for all four years.
**Figure 2.4:** Plot indicating the average probability of harbor seal call detection across all observed tidal heights. The numbers below each bar indicate the sample sizes for each of the tidal height groups.
**Supplemental Table 2.1:** The pairwise comparisons of the hours per day in which harbor seal roar vocalizations were detected in different months indicate that June and July are significantly different than all other months. There was also a significant comparison between August and September, likely due to the “cool down” phase of vocalizations after the breeding season.

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Supplemental Table 2.2: The pairwise comparisons of different years indicate that non-sequential years are significantly different.

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**Supplemental Table 2.3:** Results from the generalized linear mixed effects model for the tidal and diel analysis show significance during different light regimes at $\alpha = 0.05$.

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**Supplemental Table 2.4:** The pairwise comparisons of different light regimes indicate that day and night were significantly different than sunrise and sunset.

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Source levels and call parameters of harbor seal breeding vocalizations near a terrestrial haulout site in Glacier Bay National Park and Preserve

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Abstract

Source levels of harbor seal breeding vocalizations were estimated using a three-element planar hydrophone array near the Beardslee Islands in Glacier Bay National Park and Preserve, Alaska. The average source level for these calls was 144 dB$_{RMS}$ re 1 µPa at 1 m in the 40-500 Hz frequency band. Source level estimates ranged from 129 to 149 dB$_{RMS}$ re 1 µPa. Four call parameters, including minimum frequency, peak frequency, total duration, and pulse duration, were also measured. These measurements indicated that breeding vocalizations of harbor seals near the Beardslee Islands of Glacier Bay National Park are similar in duration (average total duration: 4.8 s, average pulse duration: 3.0 s) to previously reported values from other populations, but 170 – 220 Hz lower in average minimum frequency (78 Hz).
Introduction

Harbor seals (*Phoca vitulina*) are the most widely distributed pinniped in the northern hemisphere and occupy a variety of habitats including rocky reefs, islands, and glacier ice (Bigg, 1981). Although harbor seals may range widely during the post-breeding season (Lowry et al., 2001; Peterson et al., 2012; Womble and Gende, 2013), they typically exhibit a high degree of fidelity to pupping areas during the breeding season (Blundell et al., 2011).

Harbor seals, along with the majority of other phocid species, mate underwater (Van Parijs, 2003). During the breeding season, male harbor seals establish underwater territories and use breeding vocalizations, known as roars, to defend these areas against other males and possibly to attract females (Hanggi & Schusterman, 1994; Hayes et al., 2004a). Previous studies indicate that Pacific harbor seals in California (*Phoca vitulina richardii*) produce roars that are 2-10 seconds long and occupy the 300-1,100 Hz band (Hanggi & Schusterman, 1994). Roars from Atlantic harbor seals (*Phoca vitulina vitulina*) have an average duration of approximately 5 seconds, and range in frequency from 250-1,300 Hz (Van Parijs et al., 2000).

The one breeding vocalization source level reported for a single captive harbor seal is 145 dB\(_{\text{RMS re } 1 \mu \text{Pa at } 1 \text{ m}}\) (Casey et al., 2016). Investigating the variability in source levels of harbor seal roars from multiple individuals in different habitats is important for estimating the intensity and detection range of these biologically important signals. Herein we present results of a study that measured the frequency characteristics and source levels of harbor seal roars in a wild population.

Methods

*Acoustic Data Collection*
Four calibrated autonomous underwater hydrophones (AUHs) were deployed in Glacier Bay National Park and Preserve (GBNPP) near the Beardslee Islands adjacent to the Spider Island Reef complex, the largest terrestrial harbor seal pupping site in GBNPP. The number of harbor seals at Spider Reef typically peaks during the pupping period in June (215 seals ± 96 (SD), max = 453, years: 2004-2014) and the molting period in late July through August (308 seals ± 196 (SD), max = 723, years: 2004-2014) (Womble et al., 2010). AUHs were deployed in a diamond shaped planar array, at depths of 65-81 m, with a baseline of approximately 1 km between units. The array recorded continuously from May 27 to October 29, 2015 in the 15 Hz to 4 kHz range (hydrophone model ITC1032, 10 kHz sampling rate, low pass filter at 4 kHz, 16 bit resolution), which fully covers the frequency range of harbor seal breeding vocalizations (Hanggi & Schusterman, 1994; Van Parijs et al., 2000). Hydrophones were attached to aluminum moorings and acoustic recovery systems. Each AUH was outfitted with a highly precise clock (Q-Tech model number QT-2001, error of approximately 1 second per year) to allow for time-synchronization of the four channels and subsequent acoustic localization of vocalizing seals. Files from the AUHs were converted from .dat to .wav files using a custom written Matlab script. The eastern-most hydrophone could not be time-aligned due to an erroneous clock and was therefore excluded from this analysis.

Acoustic data were subsampled over the duration of the harbor seal breeding season by randomly selecting one day for each week of peak vocal activity (June 1 – July 31, L. Matthews & GBNPP, unpublished data). Within each sample day, four hours were selected that represented four non-overlapping light regimes based on angle of the sun – sunrise (June 1 – July 20: 0200 – 0600 hours, July 21 – July 31: 0300 – 0700 hours), day (June 1 – July 20: 0600 – 2000 hours, July 21 – July 31: 0700 – 2000 hours), sunset (June 1 – July 31: 2000 – 0000 hours),
and night (June 1 – July 20: 0000 – 0200 hours, July 21 – July 31: 0000 - 0300) (United States Naval Observatory, 2016). Overall, a total of 36 hours of acoustic data were selected from nine recording days that spanned a two-month period. Spectrograms for each hour of multi-channel acoustic data were visually analyzed for the presence of harbor seal roar vocalizations. There were no other species present in the area that produce calls similar to harbor seal roars, allowing for accurate identification of these breeding vocalizations.

**Call Parameter Analysis**

Previous studies describe four acoustic parameters that are most useful for comparative analyses of harbor seal roar vocalizations (Van Parijs et al., 2000): total duration (duration from the start to end of the roar), pulse duration (duration of the broadband component, which begins 1-2 seconds after the onset of the roar), minimum frequency, and peak frequency, where peak frequency is frequency component with the greatest amplitude (Figure 3.1). These parameters were measured for roars that were detected in the acoustic data in which all four parameters were visible and the signal to noise ratio (SNR) exceeded 10 dB (spectrogram parameters: Hann window, discrete Fourier transform (DFT) size = 1024, analysis resolution = 9.7 Hz and 0.05 s, 50% overlap). Call parameters were measured using Raven 1.5 (Bioacoustics Research Program, 2014). The frequency parameters were used to determine the appropriate frequency band for source level estimates.

**Acoustic Localization**

Harbor seal breeding vocalizations were localized using Raven 2.0 (Bioacoustics Research Program, 2016). Localization used near-field beamforming search for the set of time
of arrival delays that gave maximum power from the beamformer output (Hawthorne, 2016). A
simulated annealing algorithm was used to find the point in space that generated maximum
power. Each localized roar was assigned a latitude and longitude position. A sound speed of
1472 m/s was used based on the results of Malme et al. (1982). A follow-up CTD cast done by
the National Park Service in the study area in 2015 revealed no significant changes in the sound
speed. The measured differences fell well within the accuracy range of the instrument.
Bartlett’s formula was used to estimate the variance of the energy output from the beamformer
and resulted in error values for the northern and eastern bearings for each call. We used a
maximum error of 100 m in either direction as a first quality control measure for the data and
discarded locations with errors above this threshold.

Calculating Source Levels

The source level of a vocalization recorded at ranges greater than 1 m can be estimated
by adding the received level of the call detected at the hydrophone (RL) to the estimated
transmission loss between the call’s origin and the hydrophone (TL) (Equation 1), where both
RL and TL are in dB. Absorption is negligible at the frequencies of harbor seal roar
vocalizations (Francois & Garrison, 1982) and was therefore not considered in source level
calculations.

\[ SL = RL + TL \]  

(1)

Source levels for harbor seal breeding vocalizations were calculated by (1) determining the
distance to the roar’s origin, (2) calculating the transmission loss of the roar, (3) calibrating the
acoustic system and measuring the received level of the roar, and (4) determining the source
level for each roar in dB_{RMS} re 1 \mu Pa at 1 m.
2D-distances between localized roars and hydrophones were calculated using the `earth.dist` function from the ‘fossil’ package in R (Vavrek, 2011). Transmission loss has previously been described for the area, and was determined to be $15\log(r)$, where $r$ is the distance between the calling animal and the hydrophone (Figure 29 in Malme et al., 1982). We used this equation and the previously calculated distances to estimate transmission loss for each localized roar.

Received levels were measured using Raven 1.5 (Bioacoustics Research Program, 2014) as follows. Individual selection tables were created for each acoustic file that contained the start and end times for each localization and a standardized bandwidth of 40 Hz to 500 Hz to fully encompass the frequency range of harbor seal breeding vocalizations in GBNPP. Spectrograms were calibrated using the hydrophone sensitivity and pre-amplifier gain, and the “inband power” measurement in Raven was used to determine received levels. There is no evidence to support that harbor seal roars are directional, therefore directionality effects on source level estimates were assumed to be negligible.

Three source level estimates in dB re 1 µPa at 1m were made for each roar (one for each hydrophone used in analysis) using Equation 1. These three source level estimates in dB were converted to voltages, averaged, and then reconverted to dB to produce a single source level estimate for each localized breeding vocalization.

Background noise level in the 40-500 Hz band was measured for each of the localized roars for the two-second period preceding the call. A corresponding signal-to-noise ratio (SNR) was then calculated. Of these localized calls, we chose roars with an SNR $\geq$ 10 dB on all channels as a second measure to ensure that only high quality calls were used in source level
estimates. As an additional quality control measure for the data, we removed all roars located outside of the array to ensure there was no effect of distance on the source level estimates.

The number of calling individuals was estimated for each hour of acoustic data in order to ensure that acoustic data was collected from multiple animals. Locations of calling animals were plotted and the number of acoustic hotspots – areas of high roar density – was counted as a proxy for the number of callers. Areas of high roar density were defined as geographic clusters of two or more calls that were separated by at least 100 m. Hayes et al. (2004b) estimated that male harbor seals defended underwater territories with an average area size of 0.04 km$^2$ ($n = 4$). Given this territorial nature of harbor seal males, the authors believe the number of acoustic hotspots is an appropriate estimator for the minimum number of calling individuals (Hayes et al., 2004b).

Results and Discussion

A total of 6,477 harbor seal breeding vocalizations (Figure 3.1) were visually detected over the 36 hours of acoustic data; call parameters were measured for 484 calls that met the SNR criteria. The average minimum frequency was 78 Hz ± 10 Hz (SD) and measurements ranged from 50 to 104 Hz. The average peak frequency was 119 ± 8 Hz (SD) and ranged from 98 to 147 Hz. The average total duration and pulse durations were 4.8 ± 1.1 s (SD) and 3.0 ± 1.0 s (SD) and ranged from 2.0 to 9.1 s and 0.9 to 7.1 s, respectively. Overall, harbor seal roars in GBNPP are similar in duration to other populations. However, the minimum frequency of roars in this location are approximately 170 Hz lower than Atlantic populations (Van Parijs et al., 2000) and approximately 220 Hz lower than previously reported values for Pacific populations (Hanggi and Schusterman, 1994).
Approximately 18% (n = 1,155) of the visually detected roars were successfully localized. Reasons for unsuccessful localizations included the roars being too faint or undetectable on one or more channels, high localization error, and noise from the moorings or biological sounds such as killer whales or other harbor seals. Figure 3.2 illustrates the range of SNR values for all the localized roars; 554 of these roars had an SNR ≥ 10 dB for all three channels. There were 539 roars localized within the interior dimensions of the array (Figure 3.3). These roars were used for the final source level estimates. The average source level for harbor seal breeding vocalizations was 144 dB\text{RMS} re 1 µPa at 1 m and the median source level was 144 dB\text{RMS} re 1 µPa at 1 m (40-500 Hz bandwidth, n = 539, 95% CI: 143.61, 143.95 dB\text{RMS} re 1 µPa). Source level measurements ranged from 129 to 149 dB\text{RMS} re 1 µPa (Figure 3.4). On average, the range of source level values for one roar from the three hydrophones was 8 dB\text{RMS} re 1 µPa. The average errors associated with the localization in the eastern and northern bearings were 34.2 m and 18.6 m, respectively. There were 23 hours, out of 36 hours that were analyzed, in which harbor seal breeding vocalizations were detected. The estimated number of callers in each file varied from one to six, with an average of 2.3 ± 1.4 (SD). Given this result, we surmise that the source level estimates presented here represent a minimum of 6 different individuals.

This is the first study to report source levels for roars from a wild population of harbor seals. The average source level is 1 dB lower than the previously reported value estimated from a solitary captive male, but the previously reported value does fall within the range of measurements seen in this study (Casey et al., 2016). The source levels reported here are similar to harp seal underwater vocalizations that are thought to function for breeding purposes (103 to 180 dB re 1 µPa at 1 m), but are lower than pinniped breeding vocalizations from Antarctic seals, including Weddell seals (148 to 193 dB re 1 µPa at 1 m) and leopard seals (153 to 177 dB re 1
μPa at 1 m) (Thomas & Kuechle, 1982; Rossong & Terhune, 2009; Rogers, 2014). It is possible that the differences between species is due to body size, as male harbor seals and male harp seals are similar in body length and weight, while Weddell and leopard seals are much larger.

Future studies should investigate the potential variation in acoustic parameters, including source levels, of harbor seal breeding vocalizations produced by males in glacier ice habitats in tidewater glacier fjords, which host some of the largest seasonal aggregations of harbor seals in Alaska (Calambokidis et al. 1987). The Spider Reef complex likely accounts for <15% of harbor seals in GBNPP; the majority of seals occur in glacier ice habitat Johns Hopkins Inlet in GBNPP (Mathews & Pendleton 2006; Womble et al. 2010). Given the management concern regarding acoustic disturbance of marine mammals in Alaska, future studies will also investigate the effects of vessel noise on harbor seal acoustic behavior.
Acknowledgements

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References


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the Acoustical Society of America, 136, 1495–1498. doi:10.1121/1.4895685


Figure 3.1: Spectrogram of a harbor seal roar recorded in the Beardslee Entrance of Glacier Bay National Park and Preserve with measured call parameters. Call parameters are based on those reported in Van Parijs et al., 2000. (Spectrogram parameters: Hann window, discrete Fourier transform (DFT) size = 1024, analysis resolution = 9.7 Hz and 0.05 s, 50% overlap).
Figure 3.2: Distribution of the signal-to-noise ratios for localized calls. Black indicates calls that were removed from analysis, while the grey bars represent calls with an SNR $\geq 10$ dB.
Figure 3.3: Map of hydrophone array in the Beardslee Entrance and acoustic localizations used in the source level analysis (n = 554). Light grey points indicate roars that were removed from analysis based on their position outside of the array. Stars represent locations of hydrophones (North AUH: 58.51648°N, 135.97198°W, South AUH: 58.50585°N, 135.97225°W, East AUH: 58.51106°N, 135.96348°W, West AUH: 58.51186°N, 135.98110°W). The easternmost hydrophone, represented by the light grey star, was not used to localize harbor seal breeding vocalizations.
Figure 3.4: Histogram representing the range of calculated source levels for all calls used in analysis (n = 539).
Call rates and territorial behavior of male harbor seals during the breeding season in
Glacier Bay National Park and Preserve, Alaska

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3Cooperative Institute for Marine Resources Studies, Oregon State University and NOAA Pacific Marine Environmental Laboratory, Newport, OR, 97365
4Humpback Whale Monitoring Program, Glacier Bay National Park and Preserve, P.O. Box 140, Gustavus, AK 99826
5Glacier Bay Field Station, National Park Service, Juneau, AK 99801

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Abstract

In some populations of harbor seals, select males establish and defend underwater territories during the breeding season. Males then vocalize from these areas as either a male-male interaction or an attractant for females. This study explores the characteristics of male harbor seal underwater territories in Glacier Bay National Park and Preserve, Alaska and the associated call rates. Localized calls from one year of acoustic data collection show two distinct territories that are occupied during the breeding season. The average call rate for harbor seal breeding vocalizations in these areas was 1.02 calls per minute. Territories in Glacier Bay were established in habitats that were deeper and subject to stronger currents compared to previously described populations. We suggest two explanations for the differences in harbor seal territory habitat in Glacier Bay compared to other populations.
Introduction

Within mammalian mating systems, males often use mate-guarding techniques to ensure paternity or to increase their number of mating attempts with receptive females (Clutton-Brock, 1989). Males in some species guard individual females after copulation, while males in other species defend larger groups of females and deter other males (Clutton-Brock, 1989). Alternatively, instead of guarding the females, males have been shown to defend geographic areas, or territories, within the females’ range (Clutton-Brock, 1989). Within the pinnipeds, males of different species use different tactics, depending on the environment in which they mate. In terrestrial mating pinnipeds, females are often clustered on beaches or small islands during the breeding season, and large dominant males can defend these groups; this is evident in species such as elephant seals (Mirounga angustirostris) and sea lions (Le Boeuf, 1972, 1974; Riedman, 1990). In ice seals, such as hooded seals (Cystophora cristata), females tend to be solitary and are therefore easily guarded by individual males (McRae & Kovacs, 1994).

Aquatically mating pinnipeds are faced with a different challenge in that females are widely distributed in the three-dimensional underwater environment. Males of these species do not guard females, but rather, some males have been shown to defend underwater territories and produce underwater vocalizations where females are likely to be (Van Parijs, 2003). For example, male bearded seals (Erignathus barbatus) vocalize in specific areas (270,000-1,930,000 m$^2$), and it is hypothesized that these territorial individuals have a higher reproductive success than non-territorial males (Van Parijs et al., 2003). Male Mediterranean monk seals (Monachus monachus) defend territories that are strategically located at the mouths of caves inhabited by females and juveniles to increase the number of encounters with females (Pastor et al., 2011). It is also hypothesized that male Antarctic seals, including Weddell seals
Leptonychotes weddellii) and leopard seals (Hydrurga leptonyx) establish underwater territories and acoustic display areas during the breeding season (Stirling & Siniff, 1979; Harcourt et al., 1998). The most well studied phocid, in regards to territoriality during the breeding season, is the harbor seal (Phoca vitulina).

Harbor seals are a commonly occurring phocid species that mate underwater and, during the breeding season, some male harbor seals produce underwater vocalizations called “roars” (Hanggi & Schusterman, 1994; Van Parijs et al., 1997). Vocalizing males can be found near the pupping haul outs, on offshore foraging grounds, or in travel corridors that link the two habitats (Van Parijs et al., 1997; Hayes et al., 2004). There is slight polygyny within harbor seal populations, and the behavior of the most successful males depends on the topography of the area; successful males in open water areas patrolled offshore, while the most successful male in a narrow estuary held a territory (Coltman et al., 1998; 1999; Hayes et al., 2006).

In Miquelon, an island south of Newfoundland, Canada, male western Atlantic harbor seals (P. v. concolor) defend large adjacent underwater territories, ranging from 1,600 to 30,000 m² (Perry, 1993, size estimated from figures Hayes et al., 2004). Eastern Atlantic harbor seal (P. v. vitulina) males in Scotland have also been shown to vocalize in discrete areas (40-135 m²) (Van Parijs et al., 2000). These same areas were occupied over multiple consecutive years by single animals, with evidence to support the idea that the same males return to the same areas (Van Parijs et al., 2000). Similarly, male eastern Pacific harbor seals (P. v. richardii) in Elkhorn Slough, CA occupy non-overlapping territories along a travel corridor between the haul out and foraging ground (Hayes et al., 2004). Acoustic display areas in Elkhorn Slough averaged 4,228 m² and were encompassed by larger territories with a mean size of 39,571 m² (Hayes et al., 2004).
This study explores the territorial nature of harbor seal males in Glacier Bay National Park and Preserve, a large wilderness area in southeastern Alaska. Male harbor seals in this area are known to vocalize (McKenna et al., 2017), but it is unknown from where individuals are calling (whether it is near the haul out, the foraging grounds, or in between) or how often individuals call in these areas. Understanding the locations of critical habitat areas for harbor seals within the Park is important for park managers as they work to balance tourism and protection of the species.

**Methods**

A hydrophone array was deployed near the Spider Island Reef Complex in the Beardslee Islands, a large terrestrial harbor seal pupping area, in Glacier Bay National Park and Preserve, Alaska. The array consisted of four autonomous underwater hydrophones (AUHs) that recorded from May 2015 to October 2015 in the 15 Hz to 4 kHz range (hydrophone model ITC1032, 10 kHz sampling rate, low pass filter at 4 kHz, 16 bit resolution). AUHs were deployed in a diamond shape with a 1 km baseline at a range of depths of 65-81 m. Highly precise clocks installed on each of the units allowed for the acoustic files to be accurately time-synchronized. There was a clock malfunction on the east hydrophone, which prevented synchronization, and therefore the data from this AUH was not included in analysis.

Twelve hours of acoustic data from the peak months of harbor seal vocal activity (June – July) (L. Matthews, unpublished data) were selected for analysis. Three hours were selected from each of four different light regimes based on the position of the sun – sunrise, day, sunset, and night (L. Matthews, unpublished data) – which covered all times of day and tidal heights. All harbor seal roar vocalizations in these files were localized using Raven 2.0 (Bioacoustics
Research Program, 2016). Vocalizations from each hour of recordings were mapped and assigned to individual animals based on their location. Groups of localized calls were assumed to originate from a single caller, based on previous studies of harbor seal territoriality during the breeding season (Perry, 1993; Van Parijs et al., 2000; Hayes et al., 2004).

A 95% minimum convex polygon (MCP) was calculated for each cluster that contained more than 20 calls in each hour of recordings using the adehabitatHR package (Calenge, 2006) in R v. 3.2.3 (R Core Team, 2013). Call rate was also calculated for each cluster of calls by summing the number of calls in each cluster and dividing by the time spent calling. Time spent calling was determined by taking the start time of the first call and the end time of the last call, rounding to the nearest five minute mark, and summing the number of minutes in between these two time points.

**Results**

Out of the 12 hours of recordings, 11 hours had localized clusters of calls that met the minimum cutoff of 20 calls. A total of 677 calls were localized in the 11 hours of recordings. Within these files, there was a maximum of two callers observed in a given hour (n = 2) and there was a single caller for all other files (n = 9). Overall, the mean 95% MCP for all the call clusters was 565.77 m$^2$ (n = 13; SD = 482.01 m$^2$). A map of the MCPs revealed two non-adjacent calling areas that were separated by approximately 500 m (Figure 4.1). The mean 95% MCP size for calling area 1 was 924.71 m$^2$ (n = 3; SD = 878.03 m$^2$) and the mean 95% MCP size for calling area 2 was 458.09 m$^2$ (n = 10; SD = 247.79 m$^2$).

The overall mean call rate was 1.02 calls per minute (n = 13; SD = 0.22 calls per minute). The mean call rate for calling area 1 was 0.76 calls per minute (n = 3; SD = 0.30 calls per
minute) and the mean call rate for calling area 2 was 1.10 calls per minute ($n = 10; SD = 0.12$ calls per minute). A summary of the results is available in Table 4.1.

**Discussion**

These results indicate that a small number of harbor seal males are maintaining acoustic display areas during the breeding season in GBNPP. Previous studies on harbor seal territoriality indicate that a single male occupies a defined area in a given season, and likely for consecutive years (Van Parijs et al., 2000; Hayes et al., 2004). It is therefore probable that the two calling areas defined here represent two individual males. It is also possible that there are more males vocalizing and maintaining display areas in the vicinity, but they could not be localized using the array. These acoustic display areas were in the south-southwest portion of the array and near the border; more males may by occupying display areas outside of the array to the south or the southwest.

Harbor seal males in GBNPP behave similarly to previously studied populations in that they occupy non-overlapping display areas (Van Parijs et al., 2000; Hayes et al., 2004). Display areas in GBNPP described here were separated by approximately 500 m, while eastern Atlantic harbor seals were shown to be separated by 200-250 m and Pacific harbor seals in California were separated by 100-300 m (Van Parijs et al., 2000; Hayes et al., 2004). The larger separation of acoustic display areas in GBNPP is likely due to the fact that GBNPP is larger in size than the habitats occupied by previously studied populations. The channel in which males establish display areas in GBNPP is over 2 km in width, while Pacific harbor seals in Elkhorn Slough, CA and Atlantic harbor seals in Scotland occupy channels that are 100-300 m wide and 500 m wide, respectively (Van Parijs et al., 2000; Hayes et al., 2004). Additionally, the display area size seen
in this study is within the range of previous reported values (40-135 m² for a population in Scotland, and an average of 4,228 m² for a population in California) (Van Parijs et al., 2000; Hayes et al., 2004).

In both Scotland and California, harbor seal males vocalize and occupy defined acoustic display areas in narrow travel corridors that link the haul out sites to foraging grounds (Van Parijs et al., 2000; Hayes et al., 2004). Males set up their acoustic display areas in shallow water: display area depths ranged from 5-15 m in Scotland, and the maximum depth in Elkhorn Slough, California is approximately 12 m (Van Parijs et al., 2000; Hayes et al., 2004). In Scotland, the display areas are outside of a strong current area (20-40 m deep) that runs through the middle of the channel (Van Parijs et al., 2000). In this study however, male harbor seals set up display areas in much deeper water that is subject to strong currents.

The display areas in GBNPP are located near the south hydrophone, which was deployed at a depth of 70 m, and the west hydrophone, which was deployed at a depth of 81 m. Harbor seal males may not be using the entire water column to display, but it is of interest that they are choosing to display in an area much deeper than areas of previously studied populations. It is possible that this is driven by acoustic propagation in the area, with a deeper channel allowing sound to travel further with less attenuation. Future work will investigate the depth at which male harbor seals vocalize and whether or not there is an acoustic advantage to advertising at this depth.

The acoustic display areas also have fairly strong currents. Modeling of this region indicates that the area to the west of the hydrophone array is much more calm (Figure 9.8 in Hill, 2007). This calm and shallow area also contains the nearest breeding haul out to the array. However, dip hydrophone recordings made during the breeding season do not show that males
are utilizing this area to vocalize, as no breeding vocalizations were detected in that area (L. Matthews, unpublished data).

Similar to previously studied populations, males in GBNPP are displaying in areas that are in between the breeding haul out and foraging areas (Womble et al., 2010; 2014). As stated above, however, these areas are much deeper and have stronger currents than areas utilized by other populations. Males in other populations also vocalize near the haul out or on the foraging grounds (Van Parijs et al., 1997). It is of interest that males in GBNPP are choosing to display in the travel channel, as there is much more calm and shallow water surrounding the breeding haul out. There are two possible explanations for this choice. First, it is possible that female harbor seals are putting a selective pressure on vocalizing males in GBNPP by choosing individuals that can hold and defend acoustic display areas in suboptimal environments, thereby selecting for males of high quality. Studies of female choice in other species, such as red deer (Cervus elaphus), indicate that females often prefer traits that are honest indicators of male quality (Clutton-Brock & Albon, 1979; Charlton et al., 2007). Secondly, GBNPP, unlike the habitats of previously studied harbor seal populations, is home to a large population of humpback whales. Humpback whales have been shown to use the area near the harbor seal haul out, which is calmer and more shallow, to forage during the summer (L. Williams & M. Fournet, unpublished data). It is possible that the presence of humpback whales influences habitat selection for territories in GBNPP.

This study does not rule out the possibility that male harbor seals in GBNPP are using alternative mating tactics to copulate with females and sire pups. The number of breeding males in this population, similar to other populations, is likely much higher than the number of males occupying acoustic display areas. Alternative mating strategies have been documented in other
aquatically mating pinnipeds species (Van Parijs et al., 2003; Harcourt et al., 2008). In Weddell seals, some males have been observed spending the majority of time near the surface, while others make deep dives and a third group alternate between diving and staying near the surface (Harcourt et al., 2008). All three of these strategies were successful for siring pups (Harcourt et al., 2008). Male bearded seals also employ various tactics, with a portion of males maintaining small underwater territories and other males “roaming” throughout much larger areas (Van Parijs et al., 2003). In harbor seals, the evidence supporting alternative mating tactics is not conclusive (Van Parijs et al., 2000; Hayes et al., 2004; Boness et al., 2006). However, the presence of alternative mating strategies could explain the low levels of polygyny in harbor seal populations (Coltman et al., 1998; 1999; Hayes et al., 2006). There are only a few males that occupy acoustic display areas and they only sire 1-2 pups per year (Hayes et al., 2006). Other pups are likely sired by males that are patrolling elsewhere in the females’ range (Hayes et al., 2006). Tagging efforts in GBNPP could help elucidate the variability in male behavior during the breeding season and determine if males are using strategies other than holding territories.

This study focused on harbor seals in GBNPP that inhabit terrestrial haul out sites. However, in GBNPP, the majority of harbor seals haul out on glacial ice floes (Calambokidis et al., 1987; Mathews and Pendleton, 2006; Womble et al., 2010). The breeding behavior of male harbor seals in these glacial ice habitats is unknown, but it is likely that select males are establishing acoustic display areas along the fjord between haul outs and foraging grounds. However, these habitats are unique given the variable nature of an ice substrate. Multi-year studies on the behavior of males in these areas would help clarify how individuals alter their behavior in different environments of GBNPP.
Acknowledgements

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References


Table 4.1: Summary of results of the MCP and call rate analysis.

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<thead>
<tr>
<th>Date</th>
<th>Light</th>
<th>Calling Area</th>
<th>Number of Calls</th>
<th>95% MCP (m²)</th>
<th>Call Rate (calls/min)</th>
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</thead>
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<td>20150606</td>
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<td>57</td>
<td>509.46</td>
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<tr>
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<td>1.13</td>
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<tr>
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<td>62</td>
<td>622.01</td>
<td>1.03</td>
</tr>
<tr>
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<td>37</td>
<td>101.77</td>
<td>0.96</td>
</tr>
<tr>
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<td>105.71</td>
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</tr>
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Figure 4.1: Map with results of the 95% MCP analysis and the locations of calling area 1 and 2. Red starts represent the locations of the hydrophone array (light red star represents the east hydrophone, which was not used in analysis). Black circles indicate the locations of the two primary calling areas, which are expanded in the larger map to show the boundaries of the calculated 95% MCPs. Colors of the polygons indicate different times of day.
Vessel noise affects the reproductive advertisement behavior of an aquatically breeding pinniped

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Abstract

The impacts of anthropogenic noise on marine mammals have been a major research focus for many years. However, little attention has been given to the potential for underwater noise to disrupt the mating behavior of pinnipeds. The majority pinniped species, including harbor seals, mate underwater and can be exposed to noise during this critical time. During the harbor seal breeding season, some males establish underwater territories and use vocalizations to defend these areas against intruder males and possibly to attract females. This study used passive acoustic monitoring to examine the vocal behavior of harbor seal males in Glacier Bay National Park and Preserve, Alaska and determine whether anthropogenic noise, specifically from passing vessels, affects breeding vocalizations. Vocalizations of individual males were examined before, during, and after vessel passages to assess changes in the source level, several call parameters (minimum frequency, peak frequency, total duration, and pulse duration), and call rate. In the presence of vessel noise, the source level and the minimum frequency of vocalizations increased. The total duration and pulse duration of vocalizations decreased during vessel passages and the calling rate was lower after vessel passages than before. We suggest that these changes in vocal behavior in the presence of vessel noise may alter the ability of males to hold underwater territories or attract females.
Introduction

Successful acoustic communication requires a signal to be recognized by a receiver. Noise, whether biotic, abiotic, or anthropogenic, poses limitations on signal detection (Wiley & Richards, 1978). The increase in human activities has produced novel acoustic environments to which individuals must adapt their signals. In the presence of noise, individuals must either increase their signal amplitude or shift their vocalizations either temporally or spectrally to avoid acoustic masking (Brumm & Slabbekoorn, 2005). These acoustic behavioral changes are widely apparent across taxa (e.g.: Richardson et al., 1995; Brumm & Slabbekoorn, 2005; Patricelli & Blickley, 2006; Weilgart, 2007; Ortega, 2012; Hotchkin & Parks, 2013; Shannon et al., 2016).

One way to increase call detection in the presence of noise is to increase the amount of information being sent to the receiver. This can be accomplished by increasing the call rate or the call duration (Patricelli & Blickley, 2006). Increased call rate in the presence of noise has been demonstrated in a variety of species, including birds (e.g.: Potash, 1972; Lengagne et al., 1999), anurans (e.g.: Sun & Narins, 2005; Kaiser & Hammers, 2009), and marine mammals (e.g.: Buckstaff, 2004; Di Iorio & Clark, 2010). Increased call duration is also evident in a range of species (e.g.: Brumm et al., 2004; Foote et al., 2004).

Another tactic for successful communication in noise is increasing the amplitude of the vocalization. This phenomenon, often referred to as the Lombard effect, was first noted in humans (Lombard, 1911), but has since been applied to many different species. A review by Brumm and Slabbekoorn (Brumm & Slabbekoorn, 2005) indicated that the Lombard effect is widespread across bird species. Many mammals including bats (Hage et al., 2013) and various whales (Scheifele et al., 2005; Holt et al., 2009; Parks et al., 2011) also increase the amplitude of their vocalizations in the presence of noise (Hotchkin & Parks, 2013).
Individuals can also alter the frequency of their calls in the presence of noise in order to mitigate masking. This is especially evident in species that are exposed to low frequencies typical of anthropogenic noise, and they respond with vocalizations that have a higher frequency (e.g.: Lesage et al., 1999; Slabbekoorn & Peet, 2003; Wood & Yezerinac, 2006; Parks et al., 2009). All of these alterations in vocal behavior are surmised to increase the likelihood of call detection by conspecifics during noisy periods (Patricelli & Blickley, 2006) but the overall fitness costs and benefits of these modifications are not well understood (Slabbekoorn, 2013).

Masking from anthropogenic noise is a particular problem for species that have sexually selected acoustic advertisement displays. These acoustic displays are often associated with mate quality and are the basis for female choice or male-male competition (Clutton-Brock & Albon, 1979; Ryan, 1980; McComb, 1991). Vocal modifications to reduce masking effects can impact the response of conspecifics to these signals. For instance, increasing the frequency of a vocalization to avoid acoustic masking has also been shown to decrease the response by both females (Halfwerk et al., 2011) and males (Luther & Magnotti, 2014). Additionally, these acoustic displays are often long-range signals, and increased noise can decrease the potential audience by decreasing the communication range of the individual (Jensen et al. 2009, Hatch et al. 2012).

Marine mammals rely heavily on acoustic communication for many aspects of their life history, including reproduction (Au & Hastings, 2008). Unlike terrestrial species, marine mammals are limited to using acoustic signals for long-range communication, as other signal modalities, such as visual and chemical communication, are not effective in the underwater environment (Tyack, 2008). Additionally, the physics of underwater sound propagation allows low frequency anthropogenic noise to travel quickly and for great distances in deep water.
Anthropogenic noise in the ocean is therefore a major hindrance to successful communication of many marine species.

Anthropogenic noise in the marine environment is dominated by noise from commercial shipping in many parts of the world (Hildebrand, 2009). Shipping noise is low in frequency, ranging from 10 Hz to 5 kHz with peak energy between 350 and 1200 Hz (Hildebrand, 2009). There are also ultrasonic components of ship noise, but these frequencies do not transmit because of absorption (Hermannsen et al., 2014). This low frequency noise can drastically decrease the detection range of a marine mammal with vocalizations in this same frequency band. It is estimated that some species suffer a reduction in communication range by 50-70% in the presence of certain types of vessels (Jensen et al., 2009; Hatch et al., 2012).

The majority of the current literature on the effects of anthropogenic noise on marine mammals focuses primarily on cetaceans (whales and dolphins) (Richardson et al., 1995; Nowacek et al., 2007; Clark et al., 2009). Relatively few articles address the pinnipeds (seals, sea lions, and walruses) (Bohne et al., 1986; Myrberg, 1990). Even fewer address aquatically mating species (Cummings & Holliday, 1984), despite the fact that 45% of all pinnipeds (80% of true seals) mate underwater (Van Parijs, 2003). This is a sizeable gap in research related to marine mammal reproductive biology and the impacts of noise. This study addresses this gap by investigating the impacts of noise on male advertisement behaviors of an aquatically breeding pinniped species, the harbor seal.

Harbor seals (*Phoca vitulina*) are a widespread and numerous pinniped in the northern hemisphere, with a circumpolar distribution and a worldwide abundance near 500,000 individuals in numerous subpopulations (Thompson & Harkonen, 2008). This large range allows harbor seals to inhabit a variety of different environments, including rocky shores, sandy
beaches, narrow inlets, and icebergs in tidewater glacier fjords (Riedman, 1990). Harbor seals are aquatically breeding, with mate choice and copulation occurring in the three dimensional marine environment, rather than on land. In the marine environment, harbor seal males have limited ability to control resources and monopolize potential mates (Coltman et al., 1998a).

Males in populations inhabiting enclosed estuaries have been observed to use acoustic signals for territory establishment during the breeding season (Hanggi & Schusterman, 1994; Van Parijs et al., 1997). Territories are established along narrow corridors where females travel between haul-out sites and feeding grounds. These vocalizations, known as roars, are low frequency signals (primarily 100-1100 Hz) that range in duration from 2-10 seconds (Hanggi and Schusterman, 1994). Roars are thought to function both for male-male and male-female interactions (Hayes et al., 2004b). Harbor seal roar vocalizations occupy a frequency band that directly overlaps with the low frequency noise produced by vessels, highlighting that these coastally breeding seals are likely to experience acoustic masking in the presence of vessel traffic.

This study focuses on harbor seals in Glacier Bay National Park and Preserve (GBNPP). GBNPP is a glacial fjord system and wilderness area in southeastern Alaska and is home to one of the largest seasonal aggregations of harbor seals in the region (Calambokidis et al., 1987; Womble et al., 2010). In GBNPP, there is extensive tourism-related motor vessel traffic during the harbor seal breeding season, including cruise ships, charter fishing boats, and personal-use recreational vessels (McKenna et al., 2017). This motor vessel traffic introduces significant acoustic energy into the environment (Kipple & Gabriele, 2003) and overlaps in frequency with the roars produced by male harbor seals. We hypothesize that male harbor seals will modify
their calling behavior to reduce the effects of masking in the presence of noise from passing vessels.

**Methods**

A four-element hydrophone array was deployed near a terrestrial pupping site in Glacier Bay National Park and Preserve in May 2015. The array recorded continuously until October 2015 and fully covered the timing of the harbor seal breeding season when males are acoustically active (June – July) (L. Matthews, unpublished data). The hydrophones were arranged in a diamond planar array with approximately 1 km between units; the depths of the units ranged from 65-81 m. The array recorded from 15 Hz to 4 kHz (hydrophone model ITC1032, 10 kHz sampling rate, low pass filter at 4 kHz, 16 bit resolution), which includes the range of harbor seal breeding vocalizations in GBNPP (Matthews et al., 2017). Each hydrophone was equipped with a precise clock for time-synchronization and acoustic localization of roar vocalizations. However, the clock on the eastern-most hydrophone malfunctioned and the acoustic data from that hydrophone were therefore excluded from the analysis.

Vessel passages during the harbor seal breeding season were randomly selected and analyzed for the presence of harbor seal roar vocalizations. Only vessel passages for which one or two individuals were calling were used in the final analysis; this allowed the roar vocalizations to be more accurately localized. In some instances, vessel passages could not be used because there were too many individuals calling and roar vocalizations could not be localized. A total of ten vessel passages were available for analysis. All of the calls that occurred in the presence of vessel noise were measured for source level, a suite of call parameters, and call rate. All calls within the 15 minutes before and after vessel noise were also
measured. In some instances, the before and after periods were less than 15 minutes because the individual ceased calling.

Calls were localized using Raven 2.0 (Bioacoustics Research Program, 2016) and source levels were measured following the methods detailed in Matthews et al. (Matthews et al., in press). Measured call parameters included total duration, pulse duration, minimum start frequency, and peak frequency (Figure 5.1). Total duration refers to the length of time between the start and end of the roar vocalization, while pulse duration refers to the length of the broadband component of the vocalization, which occurs towards the end of the roar (Matthews et al., 2017). The minimum start frequency is the lowest frequency at the onset of the call and the peak frequency is the frequency with the greatest amplitude. These call parameters have been previously shown to be important for comparative analyses of roar vocalizations (Van Parijs et al., 2000). Call parameters were measured in Raven 1.5 (Bioacoustics Research Program, 2014) (spectrogram parameters: Hann window, discrete Fourier transform (DFT) size = 1024, 50% overlap, analysis resolution = 9.7 Hz and 0.05 s.).

Harbor seal calls detected from each vessel passage were mapped and ascribed to individual animals based on geographic acoustic hotspots. Acoustic hotspots were defined as areas of high call densities that were separated by at least 100 m. A separation distance of 100 m was selected based on the results of Hayes et al. (Hayes et al., 2004a), which indicated acoustic display areas that were separated by 100-300 m. Call rate was then calculated for each individual in each before, during, and after period by summing the number of calls and dividing by the number of minutes in each period.

All statistical analyses were done in R v. 3.2.3 (R Core Team, 2013). Linear mixed effects models were used to assess the effects of vessel noise on the source levels, call
parameters, and call rates of roar vocalizations using the nlme package (Bates et al., 2014; Pinheiro et al., 2017). The mixed-effects models accounted for potential pseudoreplication, non-normality within the data, and unbalanced samples sizes (Cnaan et al., 1997). All models for source levels and call parameters were run with individual and vessel passage as a random effect interaction to account for variation. The model for call rate did not have a large enough sample size to account for the interaction, so individual and vessel passage were accounted for in the model as separate random effects. Pairwise comparisons were done for significant measurements using the glht function in the multcomp package (Hothorn et al., 2008).

Results

(a) Source Levels

Source levels of vocalizations were significantly different when comparing the before, during, and after vessel noise periods (p <0.001). Roar vocalizations were significantly louder during vessel passages compared to both before (p = 0.016) and after (p = 0.025), but there was no difference between the before and after periods (p = 1.00) (Table 5.1, Figure 5.2A).

(b) Call Parameters

There were significant differences for three of the four call parameters (Table 5.1): total duration (p <0.001), pulse duration (p <0.001), and minimum frequency (p < 0.0001). The total duration and pulse duration of roar vocalizations were significantly shorter during vessel passages compared to the before (total duration: p = 0.0011; pulse duration: p <0.001) and after (total duration: p <0.001; pulse duration: p <0.001) periods (Figures 5.2B and 5.2C). The minimum frequency was higher during vessel passages compared to before (p <0.001) and after
(p <0.001) (Figure 5.2D). In all of the statistically significant call parameters, the before and after periods were not statistically different (total duration: p = 1.00; pulse duration: p = 1.00, minimum frequency: p = 1.00). There was no significant difference in the peak frequency for the before, during, and after vessel noise periods (p = 0.065) (Figure 5.2E).

(c) Call Rate

There was overall statistical significance for call rate in the before, during, and after vessel noise periods (p = 0.0087) (Table 5.1, Figure 5.2F). Call rate during vessel noise was slightly lower than the before period, but was not significant (p = 0.055). Similarly, call rate after vessel noise was not significant compared to during vessel passages (p = 0.96). However, call rate did change significantly between the before and after periods (p = 0.0024). Results from all measured parameters can be found in Table 5.1.

Discussion

The results of this study demonstrate that vessel noise affects multiple aspects of the underwater reproductive acoustic displays of harbor seal males. When faced with noise from passing vessels, male harbor seals adjust the amplitude, duration, and frequency of roar vocalizations, which are consistent with adjustments observed in other species (Richardson et al., 1995; Brumm & Slabbe koorn, 2005; Patricelli & Blickley, 2006). Calling at a louder amplitude in the presence of noise is a common tactic across taxa (e.g.: Brumm & Slabbe koorn, 2005; Scheifele et al., 2005; Holt et al., 2009; Parks et al., 2011; Hage et al., 2013; Hotchkin & Parks, 2013). Vocalizing male harbor seals in GBNPP increase the amplitude of their calls during vessel passages and then decrease back to pre-exposure levels once the vessel has passed. It has
been demonstrated in bottlenose dolphins (*Tursiops truncatus*) that there is an increased energetic cost associated with calling at a higher amplitude (Holt et al., 2015). There is likely a similar cost for harbor seals. The acoustic displays made by male harbor seals during the breeding season are extremely costly, as they forgo foraging in order to spend more time advertising (Coltman et al., 1997; 1998b; Baechler et al., 2002). Previous work has indicated that male harbor seals lose 0.47% of their initial body weight during each day of the breeding season (Coltman et al., 1998b). Calling at a higher amplitude for extended periods of time during high noise periods might be even more costly than regular acoustic displays, and could potentially have survival impacts on individuals.

Both the total duration and pulse duration measurements were shorter in the presence of vessel noise. Signal detection theory predicts than an increase in call duration will increase the probability of successful communication in the presence of noise (Brumm & Slabbekoorn, 2005), and prior studies have shown that several species do increase the duration of their vocalizations when exposed to noise (Brumm et al., 2004; Foote et al., 2004). However, this might only be beneficial for species with short-duration calls that are below a few hundred milliseconds (Brumm & Slabbekoorn, 2005). Additionally, the parameters of the noise may influence the way in which an animal adjusts their vocalization. In the presence of continuous masking sources, such as noise from vessels, it would not be beneficial for an individual to increase their call duration, as the masking source would still be present throughout the length of the vocalization. By decreasing the duration, males may shift energy expenditure to more advantageous vocal adjustments, such as altering the frequency or the amplitude of roars.

There was also an upward shift in the minimum frequency of roars in the presence of vessel noise. This is consistent with previous research that assessed the impacts of low
frequency noise on acoustic communication (Lesage et al., 1999; Slabbekoorn and Peet, 2003; Wood & Yezerinac, 2006; Parks et al., 2009;). Conversely, it has been shown that southern right whales (*Eubalaena australis*) shift their vocalizations down in frequency in the presence of higher frequency noise from fish chorusing (Parks et al., 2016). Shifting the frequency of vocalizations either up or down in the presence of noise likely functions to decrease the effects of masking by shifting the call frequency out of the noise band. This subsequently aids in the ability of conspecífics to detect calls over a wider range in noise or maintain communication space.

The shifts in duration and minimum frequency may have negative implications for the reproductive success of individual males. In playback experiments to captive female harbor seals under quiet conditions, there was a higher response to long duration, low frequency roar vocalizations than to short duration, high frequency calls (L. Matthews, unpublished data). It is unknown, however, whether masking from vessel noise would impact female harbor seal preference for signals. Previous work with canaries (*Serinus canaria*) by des Aunay et al. (2014) demonstrated that although low frequency male calls were preferred in a silent environment, this preference was absent in the presence of urban noise. Responses to higher frequency male calls did not decrease in noise (Aunay et al., 2014). Similar results have been seen in treefrogs (*Hyla ebraccata*), with females decreasing their response to lower frequency vocalizations in the presence of noise (Wollerman & Wiley, 2002). Future studies should aim to investigate these unanswered questions on reproductive behavior of harbor seals.

Some species, when exposed to noise, increase their call rate (Buckstaff, 2004; Foote et al., 2004; Di Iorio & Clark, 2010), most likely to increase the likelihood of call detection by the intended recipient. However, we show that there is a significant decrease in harbor seal call rate
after vessel passages compared to before. There was also a decrease in calling rate during vessel passages, compared to before, although this comparison was not statistically significant. This decrease reduces the time available for advertisement and communication. A decrease in calling in the presence of noise has also been seen in other species, such as beluga whales and right whales, and various anurans (Lesage et al., 1999; Sun & Narins, 2005; Parks et al., 2007). In these studies, decreases in call rate are hypothesized to be caused by the frequency overlap of the signal and the background noise (Lesage et al., 1999) or the trade-off associated with calling at a higher amplitude (Parks et al., 2007). Results of Sun & Narins (2005) indicate that males wait for quieter periods of time to vocalize. These are all possible explanations for the results seen in this study. The frequency of vessel noise directly overlaps with harbor seal roar vocalizations and, given the increased amplitude of calls produced during vessel passages, it is possible that harbor seal males are decreasing how often they call in order to call at a higher amplitude. Additionally, because males defend territories continuously and call throughout the day, it is possible that they are postponing vocal displays for a more ideal, or quiet, acoustic environment.

Although the potential costs of this vocal delay may be relatively low for each vessel-passing incident, the total percentage of communication time lost may have drastic implications on the reproductive success of individuals. The majority of visitors to GBNPP travel via motorized vessel, and the peak tourist season (May-September) overlaps with harbor seal breeding season (June-July) (McKenna et al., 2017; L. Matthews & GBNPP, unpublished data). GBNPP has enacted various measures to mitigate underwater noise, such as vessel quotas, speed restrictions, and the designation of biologically important areas as non-motorized (McKenna et al., 2017). These measures have been effective in regulating underwater noise (McKenna et al., 2017), but noise from vessels is still apparent biologically important areas, such as those used by
males for acoustic advertisement during the breeding season, and is altering the behavior of individual animals on a short time scale. Up to two cruise ships enter and exit GBNPP on a given day during the breeding season. Future work should investigate the cumulative effects of repeated vessel noise exposure on the behaviors of harbor seal males.

In Alaska, including GBNPP, some of the largest breeding aggregations of harbor seals occur in tidewater glacier fjords (Mathews & Pendleton, 2006). Harbor seals, glacier ice, and tidewater glacier fjords are all highly sought after viewing opportunities for Alaska tourists, yet are often only accessible via vessel. Given this overlap in timing, it is likely that a large proportion of ice-inhabiting harbor seals are also experiencing high levels of vessel noise during peak breeding season when they are acoustically active. Comparisons of the vocal behavior of harbor seals near terrestrial sites (discussed in this study) and harbor seals near glacial sites will give insight into the best management practices for these drastically different habitat types.

The current understanding of harbor seal roar vocalizations is that they play an important role in male-male interactions and possibly in male-female interactions during the breeding season. It is unknown, however, how vessel noise impacts the reproductive success of individuals. More research is necessary before we can fully understand the influence of vessel noise and anthropogenic sound on marine species.
Acknowledgements

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Shannon, G., McKenna, M. F., Angeloni, L. M., Crooks, K. R., Fristrup, K. M., Brown, E.,


Table 5.1: Results of mixed effects models and pairwise comparisons for all measured call properties. The * indicates statistical significance at $\alpha = 0.05$. 

113
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|                      | Estimate | Std. Error | z-value | Pr(>|z|) |
|----------------------|----------|------------|---------|---------|
| Before – During      | 898720   | 323021     | 2.782   | 0.016   | *      |
| During – After       | 915479   | 346187     | 2.644   | 0.025   | *      |
| Before – After       | 16760    | 335928     | 0.050   | 1.00    |        |

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|                      | Estimate | Std. Error | z-value | Pr(>|z|) |
|----------------------|----------|------------|---------|---------|
| Before – During      | -0.378   | 0.103      | -3.663  | <0.001  | *      |
| During – After       | -0.395   | 0.111      | -3.557  | 0.0011  | *      |
| Before – After       | -0.016   | 0.108      | -0.151  | 1.00    |        |

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|                      | Estimate | Std. Error | z-value | Pr(>|z|) |
|----------------------|----------|------------|---------|---------|
| Before – During      | -0.349   | 0.081      | -4.311  | <0.001  | *      |
|                          | Estimate | Std. Error | z-value | Pr(>|z|) |
|--------------------------|----------|------------|---------|---------|
| Before – During          | 8.456    | 0.820      | 10.317  | <0.001  |
| During – After           | 8.042    | 0.876      | 9.184   | <0.001  |
| Before – After           | -0.414   | 0.851      | -0.487  | 1.00    |

### Minimum Frequency

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### Call Rate

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|                          | Estimate | Std. Error | z-value | Pr(>|z|) |
|--------------------------|----------|------------|---------|---------|
| Before – During          | -0.204   | 0.086      | -2.362  | 0.055   |
| During – After           | 0.086    | 0.086      | 0.993   | 0.96    |
| Before – After           | 0.290    | 0.086      | 3.355   | 0.0024  |
Figure 5.1: Spectrogram of harbor seal roar vocalization with measured call parameters
(spectrogram parameters: Hann window, discrete Fourier transform (DFT) size = 1024, 50% overlap, analysis resolution = 9.7 Hz and 0.05 s).
**Figure 5.2:** Line graphs illustrating the effect of vessel noise on source level, call parameters, and call rate of harbor seal roar vocalizations. Colored lines represent different individuals and ship passages.
Female harbor seal (*Phoca vitulina*) behavioral response to playbacks of underwater male acoustic advertisement displays

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Abstract

During the breeding season, harbor seal (*Phoca vitulina*) males make underwater acoustic displays using vocalizations known as roars. These roars function in territory establishment and have been hypothesized to be important for female choice. This study used a series of playback experiments to captive female harbor seals to determine if females respond differently to different categories of roars. Categories included roars from dominant males (long duration, low frequency), subordinate males (short duration, high frequency), combinations of call parameters from dominant and subordinate males (long duration, high frequency and short duration, low frequency), and control playbacks. Results indicate that females have a higher level of response to playbacks that imitate dominant males when compared to control playbacks. Investigating female preference for male harbor seal vocalizations is a critical step in understanding the harbor seal mating system and environmental factors that may impact female behavior, such as the effects of anthropogenic noise.
**Introduction**

Acoustic communication is a critical component for reproductive success in a wide range of species: males use reproductive signals to attract females or defend territories against other males (Andersson, 1994). Acoustic reproductive displays have several advantages over visual signals in low visibility habitats, such as areas of dense foliage, underwater, or under low light conditions at night. Signalers can use acoustic signals to rapidly transmit a high volume of information to potential receivers, and the animals do not have to see each other in order to communicate (Endler, 1993).

Female preference for acoustic signals plays an important role in sexual selection (Andersson, 1994). Females of some species have been shown to prefer signal traits that reflect honest indicators of male size, dominance status, or energetic reserves. For example, female red deer (*Cervus elaphus*) prefer calls with a lower frequency, which corresponds to males of larger size (Charlton et al., 2007). Female tungara frogs (*Physalaemus pustulosus*) also prefer calls with a lower frequency (Ryan, 1980). Female Hermann’s tortoises (*Testudo hermanni*) prefer fast-rate acoustic displays, which are related to hematocrit levels in males and represent high quality mates (Galeotti et al., 2005).

Females have also been shown to prefer males who demonstrate a higher rate of signal output. In red deer, females show preference for higher calling rates, which possibly correspond to male quality (McComb, 1991). Likewise, female grey mouse lemurs (*Microcebus murinus*) prefer higher calling activity, which corresponds to the relative dominance status of the male (Craul et al., 2004). Females of some species show preference for calls that have a longer duration, such as female gray tree frogs (*Hyla versicolor*) (Gerhardt et al., 2000) and Gulf Coast toads (*Bufo valliceps*) (Wagner & Sullivan, 1995).
The physics of the underwater environment, specifically the incompressible nature of water compared to air, allows for extremely efficient sound propagation. Therefore, species that spend the all or most of their lives underwater, such as marine mammals like cetaceans and pinnipeds, have evolved to rely on acoustic communication for many behaviors, including reproductive advertisement displays.

Harbor seals are a commonly occurring pinniped species that breed underwater. During the breeding season, harbor seal males produce underwater acoustic cues, known as roars. These signals are low in frequency (250-1,300 Hz) and can be up to 10 seconds in duration (Hanggi & Schusterman, 1994; Van Parijs et al., 2000). Nicholson (Nicholson, 2000) studied male-male interactions of harbor seals in Monterey Bay, CA from various age groups and determined that subordinate males generally have roars that are shorter in duration and higher in frequency, while dominant males have roars with longer duration and lower frequency. These observations of harbor seals are similar to other mammalian species with older, dominant males producing longer, and lower frequency signals (e.g. Vannoni & McElligott, 2008; Wyman et al., 2012).

A previous study demonstrated that roars were important for underwater territory establishment by males (Hayes et al., 2004). In this study, wild male harbor seals in Elkhorn Slough, CA were exposed to three acoustic stimuli: long duration and low frequency roars (dominant male signals), short duration and high frequency roars (subordinate male signals), and ambient water noise (control) (Hayes et al., 2004). Male harbor seals responded most aggressively to stimuli representing signals produced by subordinate male roar vocalizations (Hayes et al. 2004). There were no observed responses by females to any of the stimuli presented in the study, however it is hypothesized that the roars may also influence female
preference for potential mates (Hayes et al., 2004). It is possible that females can distinguish between male vocalizations and have a preference for specific varieties of acoustic cues.

A common approach for studying female preference for acoustic cues is via playbacks (e.g.: Ryan, 1980; Hedrick, 1986; Searcy & Andersson, 1986; Catchpole, 1987; McComb, 1991). Previous playback experiments have investigated call function in a variety of marine mammal species. In the first playback to marine mammals in the field, Watkins & Schevill (1968) played back recorded Weddell seal (*Leptonychotes weddellii*) calls to male Weddell seals in order to test the call function of various vocalizations. Other playbacks to cetaceans, including humpback whales (*Megaptera novaeangliae*) (Tyack, 1983; Mobley et al., 1988), southern right whales (*Eubalaena australis*) (Clark & Clark, 1980), and North Atlantic right whales (*Eubalaena glacialis*) (Parks, 2003), have tested reactions to conspecific calls and artificial calls. There have also been additional playbacks to various pinnipeds, such as subantarctic fur seals (*Arctocephalus tropicalis*), Australian sea lions (*Neophoca cinerea*), and northern fur seals (*Callorhinus ursinus*) that have investigated caller recognition (Insley, 2001; Charrier et al., 2003, 2009). These studies indicate that playbacks are a powerful tool for studying marine mammal behavior. Studying female responses to male acoustic signals in captivity is an excellent way to add further insight into the underwater behavior of marine mammals.

The experiments described in this paper use playback experiments with captive individuals to investigate the presence of female response to breeding vocalizations in harbor seals. We tested multiple combinations of male call parameters (duration and frequency) to determine which was most attractive to females, with the hypothesis that females will be most attracted to calls with long duration and low frequency, representing signals of dominant male harbor seals.
Methods

Two years of playback experiments (2015 and 2016) were conducted at the Oregon Coast Aquarium in Newport, OR. Five female harbor seals were used for the first year of trials and four female harbor seals were used for the second year. The individuals were all reproductively mature, demonstrating signs of estrous in previous years, and ranged in age from 6 to 30 years (Table 6.1). Experiments were conducted while the individuals were in estrous, with the exception of three individuals during the 2015 season, who were tested after the molting period, which occurs after estrous.

Playback Preparation

Acoustic recordings of male harbor seal roars were collected in Elkhorn Slough, CA during May 2015. Recordings were made in close proximity to a single individual to obtain a series of high quality recordings. The recordings were divided into segments that each contained five roars. The duration and frequency of the roars were adjusted in Adobe Audition to create signals for the playback experiments. A total of 200 roars were modified as test signals.

Signals were created to test combinations of male call parameters. Two groups of playbacks represented calls found in nature: one for subordinate male roars (short duration, high frequency), and the other for dominant male roars (long duration, low frequency). These signals mimicked those used in the playback experiments of Hayes et al. (2004). The “subordinate” playbacks consisted of roars that were less than 2.5 s (mean ± SD: 2.10 ± 0.05 s) and had a minimum frequency of greater than 220 Hz (mean ± SD: 247.30 ± 8.80 Hz) (Nicholson, 2000; Hayes et al., 2004). The “dominant” roars were greater than 3.0 seconds in length (mean ± SD:
3.33 ± 0.09 s) and a minimum frequency of less than 200 Hz (mean ± SD: 178.19 ± 8.63 Hz) (Nicholson, 2000; Hayes et al., 2004). The other two groups of playbacks represented combinations of the call parameters found in subordinate and dominant roars – short duration, low frequency (mean ± SD: 2.14 ± 0.66 s and 156.27 ± 45.45 Hz) and long duration, high frequency (mean ± SD: 3.54 ± 1.08 s and 264.70 ± 62.61 Hz). These playbacks were used to tease out the acoustic characteristics to which females respond.

A total of five playback files were made for each group. Each playback consisted of 1-2 minutes of active playback that contained five roars that were based on the natural roar timing of the recorded individual, and 1 minute of silence, when no roars were present. The call intervals varied slightly between playbacks, with an average interval of 12.15 ± 8.95 seconds (SD). This series was repeated eight times for a total of approximately 20 minutes.

Two additional groups of playback files were created as controls. The first control consisted of only water noise recorded in Elkhorn Slough and contained no biologically significant sounds. The secondary control consisted of water noise with an occasional synthetic tonal sound that was similar in frequency and duration to harbor seal roars. This tonal sound contained no biologically significant information and was used to ensure that female harbor seals were responding to the roar vocalizations in the experimental trials, rather than the occurrence of novel sounds. The secondary control was only used in the second year of playback experiments.

**Experimental Design**

Each individual was exposed to one playback per day for three to four consecutive days, depending on the year. Three playbacks stimuli were used in the first year of experiments (dominant, subordinate, and the water noise control) and four stimuli were used during the
second year (two playbacks of call parameter combinations and both controls). Playbacks were arranged in a randomized block design, with three or four treatments (i.e., playbacks) and four or five blocks (i.e., individuals), depending on the year, and each subject was exposed to a unique series of playbacks to avoid pseudoreplication. All trials were conducted in the same enclosure. The individual was allowed in to the testing pool prior to the start of the playback and playbacks began after the individual had been swimming for a few minutes.

Playback Experiments

An underwater speaker (Lubell Labs LL916) was lowered approximately 1.5 m into the pool directly next to the wall. The speaker was housed in a PVC cage and was positioned in the same place for every trial. The speaker was connected to an amplifier (Dual XPA2100), and the amplifier was connected to an iPod, which was pre-loaded with the playback files. Received levels were measured throughout the pool at multiple depths to ensure that the playbacks were approximately equal in loudness to those found in nature (155 dB re 1 µPa, C. Reichmuth, personal communication). Measured levels ranged from 149 to 156 dB re 1 µPa. A GoPro camera (HERO4 Silver) was used to record all of the trials. The camera was placed on an overlook above the enclosure, which allowed for full coverage of the playback pool, and the location of the camera was the same for all the trials.

Video Analysis

Behavioral sequencing was done for the videos of the playback experiments. The number of approaches to the playback speaker was counted as a proxy for female response. Approaches were defined as a deliberate investigation of the speaker. This included any
touching of the speaker with the vibrissae or curious examination of the PVC apparatus. The amount of time spent at the speaker for each approach was also measured. The number of approaches to the playback speaker was compared using a nonparametric Friedman’s test to account for differences between individuals. Post hoc comparisons using the Wilcoxon-Nemenyi-McDonald-Thompson test were used to further investigate significant comparisons (Hollander et al., 2013). The two years of playbacks were analyzed separately because the individuals tested varied between years. A second set of Friedman’s tests was used to compare the amount of time spent at the speaker. Statistical analyses were done in R v. 3.2.3 (R Core Team, 2013).

**Results**

There was a significant difference in the number of approaches made to the playback speaker for the first year of playback experiments (Figure 6.1a, \( p = 0.028 \) at \( \alpha < 0.05 \)). Female harbor seals approached the playback speaker significantly more during the dominant male playback when compared to the control (\( p = 0.021 \) at \( \alpha < 0.05 \)). The maximum number of approaches during dominant male playbacks was 4, which was noted for two of the five individuals, and the minimum number was 1 approach. No individuals approached the speaker during the control playback. There was no statistical difference between the number of approaches during the subordinate and dominant male playbacks (\( p = 0.377 \) at \( \alpha < 0.05 \)) or the subordinate and control playbacks (\( p = 0.367 \) at \( \alpha < 0.05 \)). For the second year of playbacks, there was no difference in the number of approaches to the speaker for any of the stimuli (Figure 6.1b, \( p = 0.732 \) at \( \alpha < 0.05 \)), with overall low numbers of approaches to all stimuli.
The results of the Friedman’s tests for the amount of time spent at the speaker were identical to the approach results. In the first year of playbacks, approaches ranged from 1 – 13 total seconds, with the longest approach times occurring during dominant male playbacks. In the second year, approaches lasted from 4 – 10 seconds. A summary of the time spent at the speaker during each approach is available in Table 6.2.

**Discussion**

This study is the first to specifically investigate female preference for male breeding vocalizations in harbor seals. The results indicate that females respond more frequently, and for longer durations, to dominant male roars compared to the control. A previous study on male harbor seal response to playbacks in the wild did not note any behavioral shifts in females (Hayes et al., 2004), but the responses made by females in our experiments were fairly brief and were only detectable because there was a clear view to the bottom of the pool. It is possible that females did approach the playback speaker in the previous study, but the approaches were undetectable to the researchers due to turbidity of the water.

These results also show that there was no significant difference in response when comparing the call parameter combination playbacks and the controls. Both a low frequency and a long duration or a high frequency and short duration are necessary for females to respond to vocalizations; the non-natural combinations elicited no response. It is possible that females are using these acoustic cues to make decisions on mate preference when other modalities, such as sight and smell, are limited and are selecting males of a higher status. Females from other species have also been shown to prefer vocalizations that are honest advertisements and denote a
higher dominance rank (e.g.: Clutton-Brock & Albon, 1979; McComb, 1991; Craul et al., 2004; Galeotti et al., 2005; Puechmaille et al., 2014).

In the first year of trials, only two individuals were confirmed to be in estrous during the playback experiments. However, similar trends – an increase in the number of approaches during the dominant male playback compared to the subordinate and control playbacks – were observed between estrous and non-estrous individuals, with the exception of one individual. One female, Pinky approached the speaker three times during the subordinate male playback and only two times during the dominant male playback. This could be due to a variety of factors. It’s possible that she was unmotivated due to lack of estrous and the approaches were purely based on curiosity. Additionally, Pinky was the oldest of the test subjects and might not have as great an ability to discriminate acoustic signals as younger individuals.

Future studies should investigate other factors that might impact female responses to male harbor seal breeding vocalizations, such as the presence of noise. Anthropogenic noise, from sources such as vessels, may alter female response by causing individuals to either decrease their response rate or prefer vocalizations that can better be heard in noise. It is possible that low frequency ship noise causes male harbor seals to increase the frequency of their vocalizations to avoid acoustic masking, and females might shift their preference to match this shift in male behavior.
Acknowledgements

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doi:10.1016/j.anbehav.2003.06.019


doi:http://dx.doi.org/10.1016/j.anbehav.2012.08.037
Table 6.1: Individuals used in playback experiments, their approximate dates of birth, and whether or not they were in estrous during the playbacks for either year of experiments. Boots was not included in the 2016 experiments.

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<td>August 1991</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Tater</td>
<td>March 1994</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Tazzy</td>
<td>2009</td>
<td>Yes</td>
<td>Yes</td>
</tr>
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</table>
Table 6.2: The average time spent investigating the speaker during each approach and the range of times observed for approaches for each trial during both years of playback experiments. The NA values in the range column correspond to trials for which there was only one approach.

<table>
<thead>
<tr>
<th>Year</th>
<th>Dominant</th>
<th></th>
<th></th>
<th>Subordinate</th>
<th></th>
<th></th>
<th>Control 1</th>
<th></th>
<th></th>
<th>Control 2</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Individual</td>
<td>Avg. (s)</td>
<td>Range (s)</td>
<td>Avg. (s)</td>
<td>Range (s)</td>
<td>Avg. (s)</td>
<td>Range (s)</td>
<td>Avg. (s)</td>
<td>Range (s)</td>
<td>Avg. (s)</td>
</tr>
<tr>
<td>2015</td>
<td>Boots</td>
<td>3.25</td>
<td>2 – 5</td>
<td>2.33</td>
<td>2 – 3</td>
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<td>0.00</td>
<td>0.00</td>
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<tr>
<td></td>
<td>Pinky</td>
<td>3.50</td>
<td>1 – 6</td>
<td>3.67</td>
<td>2 – 6</td>
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<td>0.00</td>
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</tr>
<tr>
<td></td>
<td>Swap</td>
<td>1.33</td>
<td>1 – 2</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
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<tr>
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<td>Tater</td>
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<td>NA</td>
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<td>0.00</td>
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<td>LF/Short</td>
<td>Avg. (s)</td>
<td>Range (s)</td>
<td>Avg. (s)</td>
<td>Range (s)</td>
<td>Avg. (s)</td>
<td>Range (s)</td>
<td>Avg. (s)</td>
<td>Range (s)</td>
<td>Avg. (s)</td>
</tr>
<tr>
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<td>3 – 4</td>
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<tr>
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</tr>
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<td>NA</td>
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<td>0.00</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tazzy</td>
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<td>0.00</td>
<td>0.00</td>
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<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
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</tr>
</tbody>
</table>
Figure 6.1: Line graphs illustrating the number of approaches made to the playback speaker during the first year of playbacks (A) and second year of playbacks (B).
Conclusions and Future Directions

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The results presented here provide the evidence that the underwater acoustic behavior of male harbor seals in Glacier Bay National Park and Preserve, Alaska during the breeding season is, in some ways, similar to that of other harbor seal populations. Seasonal and diel trends in vocal behavior appear to be consistent across populations, while still more investigation is needed to understand the role of tidal state. Future studies should compare the influence of tidal state on vocal production with the distance from the breeding haul out. It is possible that males advertising farther away from the haul out are not influenced by tidal height, while males displaying close to the haul out adjust their behavior based on this environmental parameter.

Future studies should also use multi-year acoustic data to compare acoustic display areas in Glacier Bay across years. As with previous studies, the territories seen in this study are non-adjacent. However, unlike previous studies that show year-to-year site fidelity, it is unknown if harbor seals in Glacier Bay occupy to same areas in consecutive years. It would also be of interest to investigate other possible territories that were unable to be detected on the hydrophone array. It would also be important to do a paternity study, as has been done with other populations, to understand the level of polygyny in the Glacier Bay population. Other studies consistently show low levels of polygyny within harbor seal populations. The Glacier Bay population differs from other populations in that territorial males are displaying in sub-optimal locations with strong currents. If females are selecting territorial males because of their ability to maintain these territories, then it is possible that there are higher levels of polygyny than have been documented thus far.

One of the most notable results of this study is the relationship between the female preference experiments and the impacts of vessel noise on acoustic behavior of male harbor seals. During periods of vessel noise, male harbor seals shift their vocalizations away from the
acoustic characteristics that are preferred by females. If females are using underwater vocalizations to choose mates, these acoustic changes could directly impact reproductive success. Future work should continue playback experiments and test if female behavior changes in the presence of noise.

As noted in previous chapters, while the harbor seals studied here occupy terrestrial haul outs, the majority of harbor seals in Glacier Bay inhabit glacial ice floes. These glacial ice harbor seals are highly understudied compared to harbor seals in other habitats. It is of great interest to understand the similarities and differences of underwater breeding behavior between terrestrial and glacial haul outs, as separate management and conservation efforts might be necessary to protect the species in both habitats.

These chapters add to the general understanding of harbor seal behavior during the breeding season and provide insight into the effects of vessel noise on aquatically breeding pinnipeds, an understudied area of marine mammal biology and conservation. The future directions outlined here will even further clarify how harbor seal reproductive behavior varies with the environment and anthropogenic influences.
VITA

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