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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 one 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 haulout 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 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.

Key Words: acoustic behavior, reproductive behavior, harbor seal, *Phoca vitulina*, pinnipeds

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 haulouts 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 4 y, 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 nonterritorial) 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 had held territories and produced acoustic cues over multiple years (Hayes et al., 2004). In the Atlantic Ocean, two harbor seal display areas in the Kessock channel in Scotland were each occupied by a single individual over a 3-y 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 similarities in the environmental characteristics of Glacier Bay National Park and Preserve (GBNPP), Alaska, to these other study areas, including its many inlets and narrow corridors between islands, suggest that harbor seal males in this area may establish underwater territories and are likely to be 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, 2015).

Pupping in GBNPP begins in mid to late May (Temte et al., 1991; Mathews & Pendleton, 2006) and is followed by 3 to 5 wks of lactation (Blundell et al., 2011). If this population follows the pattern shown elsewhere, harbor seal males are predicted to 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 haulouts, 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, an increase in acoustic behavior would be expected, 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 were 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 to 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 1). This location was within approximately 8 km of a terrestrial harbor seal haulout. 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-s recordings once per hour for 24 h a day (88-kHz sampling rate). The detection range of the hydrophone was calculated using the passive sonar equation, with a signal to noise ratio (SNR) value of 6 dB re 1 μPa, a source level of 144 dB re 1 μPa for harbor seal roars (Matthews et al., 2017), an ambient 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. This analysis led to an estimated detection range for male roar vocalizations to be 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, which have a primary frequency range of 40 to 500 Hz (Matthews et al., 2017) (Figure 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-s audio clips (.wav format). Each 30-s 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-s 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 taken 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-s sample duration created a snapshot of ambient noise, giving the analyst enough time for assessment with enough spectral data to characterize the sample and provide a sufficient number of averages to smooth the narrow-band spectra (e.g., 30 averages for the 1,000 Hz frequency range).

Seasonality Analysis

To investigate when there were 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 h. Data from 2001 included all months of the year (346 d), and the 2002 data included the months of January through August (213 d). For 2007 and 2008, data were available roughly from May through September (107 and 123 d, respectively). A total of 789 d (18,936 acoustic samples) were available for this analysis.

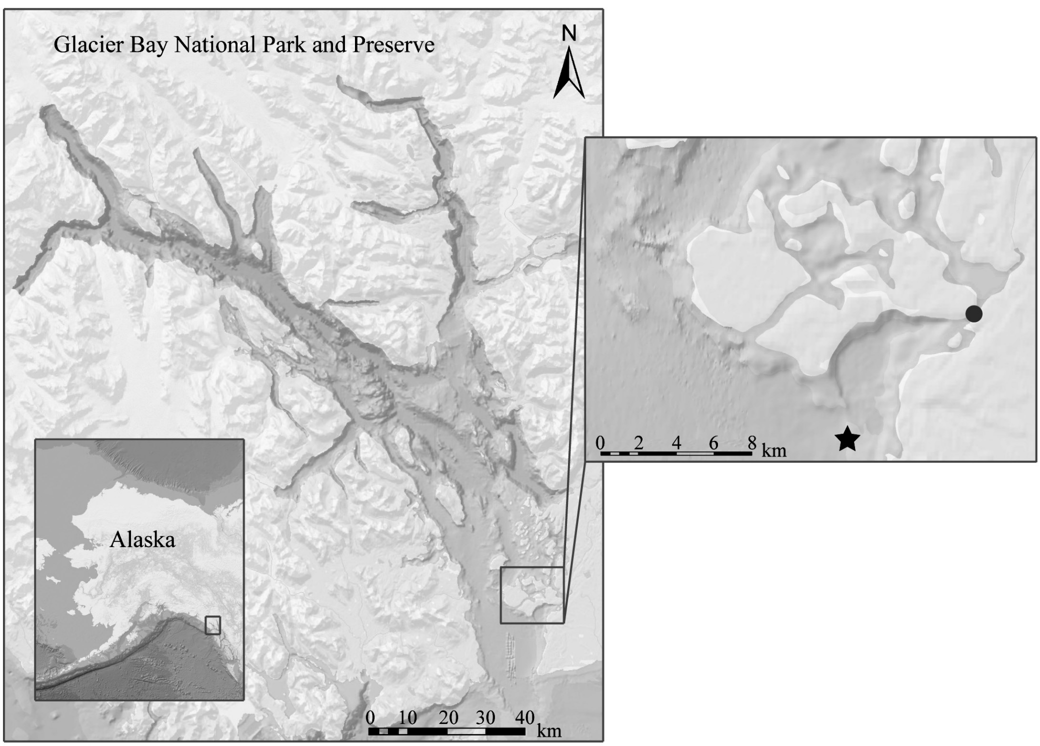

Figure 1. Map of Glacier Bay National Park and Preserve (GBNPP) with the location of the cabled hydrophone system (star) and the closest harbor seal haulout (circle) (Geographic Coordinate System: North American Datum, 1983)

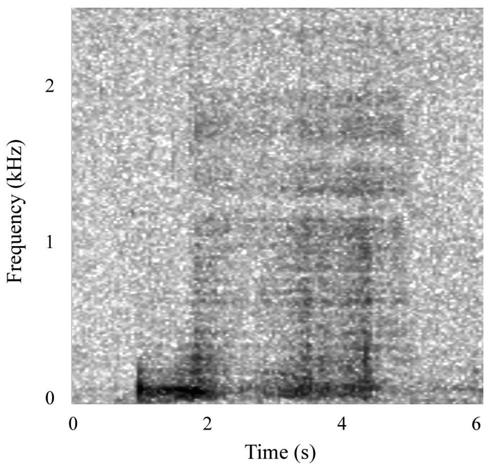

Figure 2. Spectrogram of a harbor seal roar vocalization recorded near Bartlett Cove in GBNPP (spectrogram parameters: Hann window, 50% overlap, discrete Fourier transform [DFT] size = 4,096)

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 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-s audio file was marked with the corresponding tidal height for that date and time as well as the current direction (ebb or flood). Tidal heights were rounded to the nearest quarter meter, and roar presence and absence data were used to calculate the 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 were used for the diel analysis. Because the amount of daylight and night are not equal in the summer in southeastern Alaska, four non-overlapping 2-h time blocks were denoted for sunrise, day, sunset, and night. Sunset and sunrise times were determined using data from the U.S. Naval Observatory (2016), and times were rounded to the nearest hour; the 2-h blocks for sunrise and sunset were centered on these times. The day and night blocks occurred at the midpoint between sunrise and sunset, and between 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
Monthly averages of the number of hours per day with harbor seal detections were calculated to investigate the timing of peaks in acoustic activity. 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 and day as a random effect. Following the model, pairwise post-hoc 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, a tide-by-time interaction, 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*, Version 3.2.3 (R Core Team, 2013).

Results

Analyses of the acoustic activity during the year revealed that the number of hours per day with male harbor seal roaring activity peaked in June and July (Figure 3; Supplemental Table 1—The supplemental tables for this article are available on the Supplementary Material page of the *Aquatic Mammals* website: www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147.) For June, the mean number of hours per day in which harbor seals were acoustically detected was 12.1 h (SD = 8.0). For July, the mean was 18.1 h (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 h (SD = 3.1) and 3.0 h (SD = 4.0), respectively. In February, March, April, and September, vocalizations were detected an average of less than 1 h/d.

No harbor seal roars were detected in the acoustic data in January, October, November, or December for the years in which those months were sampled. 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 (2001-2002 & 2007-2008), but there were statistically significant differences between nonsequential year comparisons (Supplemental Table 2).

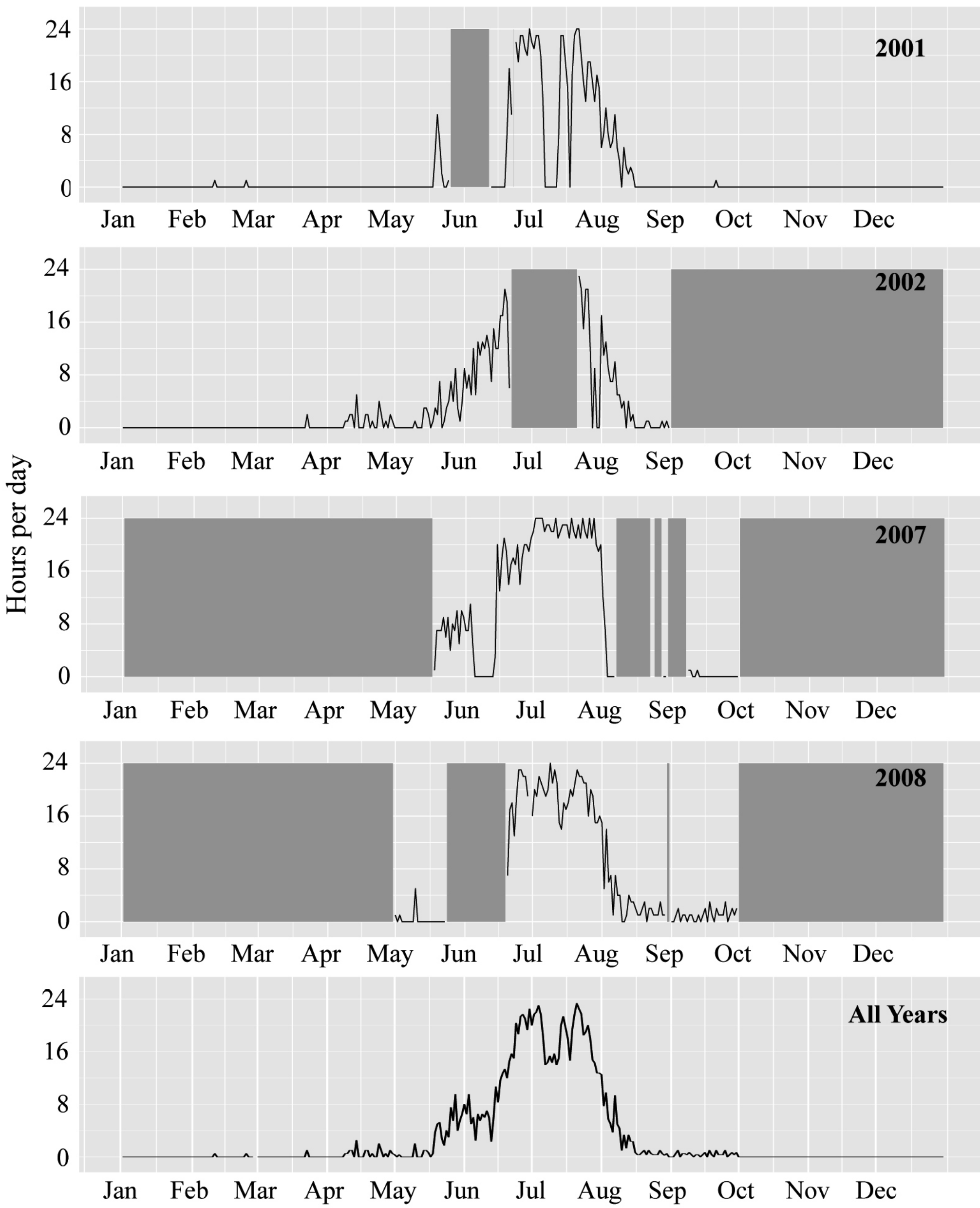

Figure 3. Numbers of hours per day from January through December that harbor seal roar vocalizations were detected from acoustic data. Grey areas indicate missing data. The bottom panel shows the combined data for all 4 y.

Roars were detected across all tidal heights (Figure 4). The minimum probability of detecting harbor seal roars was 55.5% (SD = 50.0%) and was observed at a tidal height of 0 m ($n = 72$). The maximum probability of roar detection was 100% (SD = NA) and occurred at a tidal height of 5.5 m. However, tidal heights this large are rare ($n = 1$) as they occur only during spring tides. The second highest probability of roar detection occurred at 4.75 m and was 85.7% (SD = 35.3%). There was no significant difference in the probability of detecting harbor seal roars during ebb vs flood tides ($p = 0.63$) or spring vs 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 ($p = 0.42$); however, there is a slight increase in call detection at tidal heights of 4 m and greater (Supplemental Table 3).

During peak months of roar activity (June and July), 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 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 (Supplemental Table 4). There was significantly higher detection during the night compared to sunrise ($p < 0.001$) and day ($p < 0.001$). Additionally, there was significantly higher detection during sunset compared to day ($p < 0.001$). There was no difference between the sunrise and sunset periods ($p = 0.15$), sunrise and

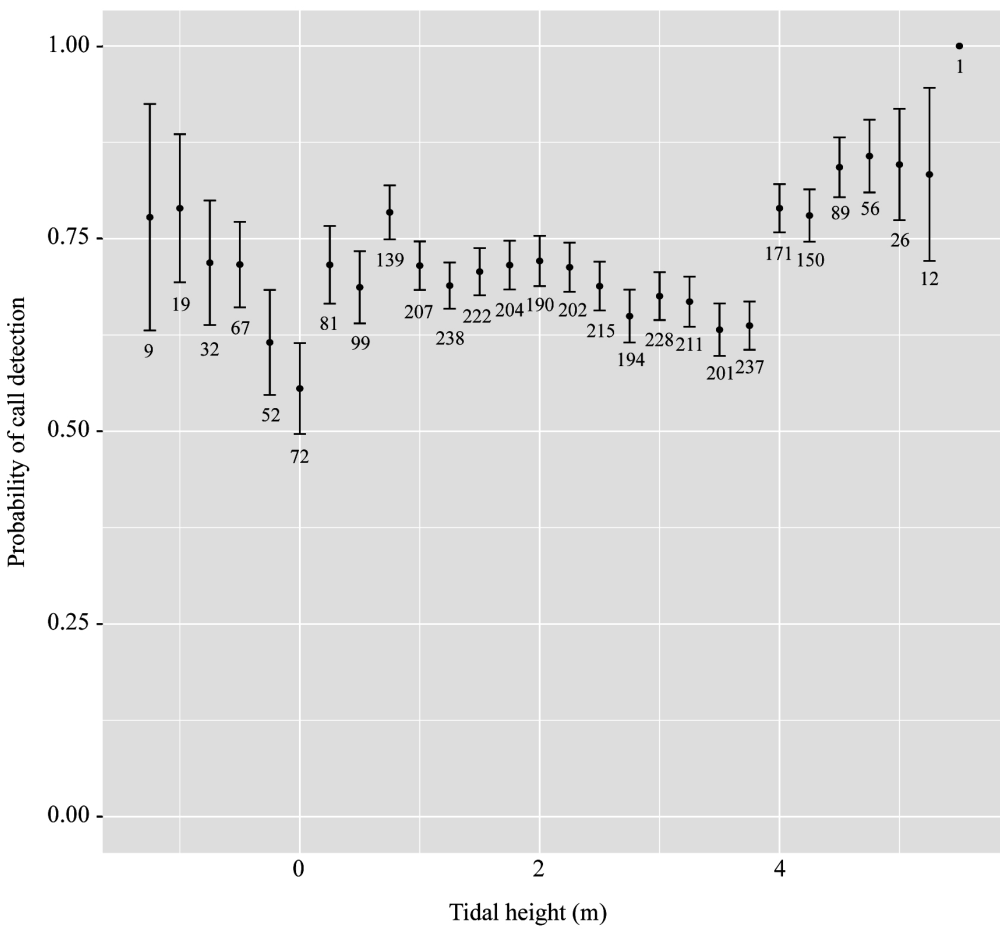

Figure 4. Plot indicating the average probability of harbor seal call detection across all observed tidal heights. The numbers below each bar indicate the sample sizes for each of the tidal height groups.

day periods ($p = 0.17$), and sunset and night periods ($p = 0.34$).

Discussion

Harbor seal roar production in GBNPP was characterized by a strong peak 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 were detected. A few weeks after pupping, as the pups are weaned, female harbor seals begin to make foraging trips. It is during this time that mating is thought to take place (Boness 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 stops before the molting period in August (Calambokidis et al., 1987). Due to the lack of year-round data in all years of the study (Figure 3), it is not possible to rule out that male harbor seals might vocalize during other times of the year. However, the lack of vocalizations during off-peak months in the year-round data from 2001 and the consistency of available months for other years (and GBNPP unpub. data) strongly suggest that roar vocalizations are primarily restricted to the breeding period.

Although there were positive acoustic detections of male harbor seal roars in May and August (Figure 3), these months were significantly different from June and July but not different than the majority of other months. The increase in acoustic detections in May and August 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 prior to the females arriving at 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 herein.

Although there were statistical differences in the seasonality between nonsequential years, this is likely attributed to missing data within each year as the peak in vocal activity begins in June of each year and drops off in August (Figure 3). 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- to 3-mo delayed implantation and a 9- to 11-mo 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. Prey quality and availability can also affect maternal body condition (Jemison & Kelly, 2001). If prey availability affects male body condition, then 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 noncontiguous 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, although there was a slight increase in the detection of calls at higher tidal heights. 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, despite the apparent increase in call detection at higher tidal heights in GBNPP, the difference across all tidal levels was not statistically significant; the presence/

absence data for roars from the 30-s 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 haulout. Male harbor seals defending territories closer to the haulout might be more influenced by tidal state in GBNPP; whereas further offshore, there may be a similar number of animals in the water in all tidal states. 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 (other than sunset). Between May and June, female harbor seals in GBNPP have been shown to make deep dives from 0500 to 2000 h (daylight) and shallower dives from 2100 to 0400 h (sunset and night), thought to be driven by vertically migrating prey moving toward the surface at night (Womble et al., 2014). 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 diurnally 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 UK 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 limitations are a relatively small detection range for roar vocalizations and the inability to localize calling individuals, thus the inability to determine how many calling males are in the sample. In this study, the detection range of the hydrophone did not include the water directly adjacent to the closest haulout but did include areas in which harbor seals have been observed foraging. Additional hydrophones closer to the haulout might detect additional male callers. Without the ability to localize calling animals, it is 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. Evidence from visual spectrogram analysis indicated up to five individuals in a single 30-s audio clip, so although the area of detection was small, there were 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 possible that turnover in specific individuals in this location occurred between 2002 and 2007. A multi-element hydrophone array covering a larger area could help in resolving some of these limitations and facilitate a more complete understanding of the geographic and temporal context of male calling behavior.

This study provides data from the longest acoustic dataset used to monitor harbor seal roar vocalizations published to date. It provides further evidence that PAM is a useful tool for determining the length of the breeding season of harbor seal populations. Additionally, these data complement previous studies on 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 our understanding of social interactions and the role of different pinniped habitats 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.

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