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Underwater Vocal Repertoire of the Endangered Hawaiian Monk Seal, Neomonachus Schauinslandi

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UNDERWATER VOCAL REPERTOIRE OF THE ENDANGERED HAWAIIAN MONK SEAL, *NEOMONACHUS SCHAUINSLANDI*

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of the requirements for the degree of

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by

KIRBY PARNELL

June 2018

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Abstract

UNDERWATER VOCAL REPERTOIRE OF THE ENDANGERED HAWAIIAN MONK SEAL, *NEOMONACHUS SCHAUINSLANDI*

by

Kirby E. Parnell

Descriptions of underwater vocalizations produced by aquatically mating phocids are available for many species, but are lacking for the endangered Hawaiian monk seal (*Neomonachus schauinslandi*). We obtained simultaneous year-round audio and video recordings of a captive adult male Hawaiian monk seal to evaluate underwater vocal repertoire and characterize seasonal trends in vocal behavior. A discriminant function analysis based on 17 acoustic parameters revealed that this seal produced at least six discrete underwater vocalizations. Spontaneous aquatic calls were most commonly produced from September through January, during a period coincident with elevated blood testosterone levels and prior to the annual molt. These seasonal patterns in sound production confirm a protracted reproductive season for this tropical species. While limited to a single individual, this first report of underwater sound production expands our understanding of reproductive behavior in *Neomonachus schauinslandi*, and establishes a foundation for future research and population monitoring efforts using passive acoustics.

Acknowledgements

This project would not have been possible without my advisor, Dr. Colleen Reichmuth, and my mentor, Dr. Jillian Sills. They have made my two years of graduate school a positive learning experience, and I am incredibly grateful for the unique opportunity to pursue my master's degree in this lab. I strive to become as organized and thorough as Jillian, and as compassionate and persistent as Colleen. I will forever cherish our project meetings in Colleen's office and the 100 times I interrupted Jillian, as these were the moments I learned the most. I look forward to working with Colleen and Jillian in my future academic career.

My fellow graduate students at the Pinniped Lab, Caroline Casey, Sarah McKay Strobel, and Holly Hermann-Sorensen have continuously supported me in many aspects regarding science and life. Caroline and Sarah McKay helped tremendously with statistics, SoundTrap design, database management, and sound analyses, as well as general graduate school advice. Holly provided supplies for the SoundTrap mount and ever-lasting encouragement through her random sticky-notes and positive attitude. Our post-doc, Juliette Linossier, taught me many skills including programming in R, sound analysis techniques, and how to format documents properly, as well as feedback on my thesis. Ross Nichols set this project up for success by installing cameras, trouble-shooting programs, and advising me on data storage methods and construction of the SoundTrap mount. He and Daniel Mann spent many hours searching the internet for any evidence of underwater sounds produced by Hawaiian monk seals; their efforts are the foundation of this study.

I am grateful to Beau Richter, Traci Kendall, and the volunteers of the Marine Mammal Physiology Project. Beau and Traci were always happy to assist with deploying and retrieving the SoundTrap, and I feel incredibly thankful for the opportunity to collaborate with them. I give all the credit to *Kekoa* for his participation in this unique study. *Kekoa* is an ambassador for his species, and I am thankful for all that we have learned and will learn from him in the years to come.

I am thankful for my committee members, Dr. Terrie M. Williams and Dr. Carl Lamborg, who patiently waited for my thesis and provided thoughtful comments, and to Dr. Matthew Clapham who provided advice on statistical methods for this project and taught me how to code in R.

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I owe my successes to my parents for instilling in me an appreciation of education at a young age, and for supporting my endeavors far from home. My greatest achievement has been making them proud. My mom introduced me to the ocean and its organisms and has always believed in me. My dad has coached me through life and has never doubted my ability to overcome obstacles. My brother encouraged me to explore the world and always visits me wherever I go. I thank them for never complaining about the distance between us and continuously encouraging me to chase my dreams.

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Introduction

The Hawaiian monk seal, *Neomonachus schauinslandi*, is an ancient[1] phocid ("true seal") species endemic to the Main and Northwestern Hawaiian Islands, with subpopulations at Kure Atoll, Midway Atoll, Pearl and Hermes Atoll, Lisianski Island, Laysan Island, French Frigate Shoals, and Necker and Nihao Islands (see Carretta et al. 2017). Monk seals are unique among the 18 extant species of phocids worldwide, as they are non-migratory and inhabit a tropical climate with relatively stable environmental conditions and resources. These unique ecological features influence the atypical reproductive behavior of the Hawaiian monk seal, which involves males competing for breeding access to dispersed estrous females throughout much of the year (Riedman 1990).

Phocids, including seals from the Monachinae (monk seals, elephant seals, Antarctic seals) and Phocinae (most northern-hemisphere seals) lineages, exhibit differences in breeding behavior driven largely by whether copulations take place on shore or in water, how estrous females are distributed in space and time, and the stability of the haul out substrate (Mesnick & Ralls 2002). A similar characteristic shared by adult males of both terrestrial- and aquatic-breeding seals is the production of vocalizations associated with reproductive periods when male-male competition for

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[1] The Hawaiian monk seal belongs to the family Phocidae and subfamily Monachinae, the latter of which comprises monk seals, elephant seals, and Antarctic seals. Monk seals (originally classified as genus *Monachus*) are the earliest diverging lineage of all Monachinae (Berta & Churchill 2012), and include the extinct Caribbean monk seal (*Neomonachus tropicalis*), the critically endangered Mediterranean monk seal (*Monachus monachus*), and the endangered Hawaiian monk seal. Hawaiian and Caribbean monk seals subsequently diverged from *Monachus* ~6.3 million years ago to form a newly recognized genus, *Neomonachus* (Scheel et al. 2014).

territories or females is highest (Van Opzeeland et al. 2010). Adult male seals of shore- or ice-breeding, strongly sexually dimorphic, monachid species—including northern and southern elephant seals, *Mirounga angustirostris* and *Mirounga leonina*—produce structurally complex airborne vocalizations (e.g., Sandegren 1976, Shipley et al. 1986, Galimberti et al. 2000, Sanvito et al. 2007, 2008, Casey et al. 2015), but are not known to produce sounds under water. In contrast, adult males of most aquatically mating species do produce underwater calls during the breeding season (Wartzok & Ketten 1999, Van Parijs 2003, Southall et al. in press). As size does not confer a reproductive advantage to seals that mate aquatically (Stirling & Thomas 2003), behavioral traits including the seasonal production of underwater sounds are of particular importance. As monk seals copulate in water and show slight reverse sexual dimorphism (Kenyon & Rice 1959, Gilmartin & Forcada 2002), it is plausible that mature males of the genera *Monachus* and *Neomonachus* also emit underwater sounds during active reproductive periods, although this has not been confirmed (Charrier et al. 2017, Southall et al. in press).

Few studies have described the airborne acoustic signals of Mediterranean (Muñoz et al. 2011, Charrier et al. 2017) and Hawaiian monk seals (Miller & Job 1992, Job et al. 1995), yet there are no published recordings of underwater vocalizations for either species. An anecdotal account of solitary Hawaiian monk seals producing *foghorn* and *bark* calls was provided by Stirling & Thomas (2003), but the sounds—opportunistically observed by divers and shared as a personal communication—were not recorded and the sex of the calling seals was unknown. A thorough search of a global, publicly accessible video sharing database generated many observations of monk seals in exploratory and social contexts, but relatively few video recordings containing seal vocalizations.[2] Currently, these informal accounts provide the best available evidence of underwater communication in the Hawaiian monk seal. However, fundamental questions about sound production in this species remain unanswered, including those relating to the presence or absence of underwater vocalizations, the typical age and sex of calling individuals, seasonal patterns in sound production, and the types of sounds emitted. Until such data are available, it will not be possible to determine the significance of underwater signaling to reproductive behavior.

Fewer than 1400 Hawaiian monk seals remain in the wild (Carretta et al. 2017, Pacific Islands Fisheries Science Center (PIFSC) 2018), making them one of the most endangered marine mammals and an urgent conservation priority. Historically, the Hawaiian monk seal has confronted numerous pressures, beginning in the 1800s with sealers, guano and feather hunters, and crews of ships that decimated the wild population (Carretta et al. 2017). Now this ancient phocid species is threatened by a combination of anthropogenic and environmental disturbances (National Marine Fisheries Service (NMFS) 2007, Carretta et al. 2017, PIFSC 2018). In the remote Northwestern Hawaiian Islands, threats include shark predation, entanglement in

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[2] The video database YouTube (www.youtube.com) was searched for all available footage of Hawaiian monk seals. This search yielded several examples of underwater vocalizations embedded in the video recordings. High-quality video footage of a male monk seal calling was obtained for the documentary filmmaking for *Jonathan Bird's Blue World,* Season 4, Episode 4: http://www.jonathanbird.net/cgi-bin/vid_search.htm. Additional monk seal vocalizations were detected on video footage posted by the recreational diving tour operator www.oahudiving.com: https://www.youtube.com/watch?v=Eyi-nkRjiek, https://www.youtube.com/watch?v=TLaFgWlq_2I, and by a recreational scuba diver: https://www.youtube.com/watch?v=UDEmY2NkVCs.

marine debris, male conspecific aggression, loss of available habitat due to sea level rise, and food limitation. In the Main Hawaiian Islands, threats include introduced disease (i.e., toxoplasmosis), parasitism, fisheries interactions, vessel collisions, and intentional harm by humans. These mounting pressures could markedly decrease the wild population of Hawaiian monk seals. Thus, investigating every aspect of their biology remains a research priority (NMFS 2007).

The Hawaiian monk seal's remote, tropical environment; threatened status; and aquatic-breeding habits hinder efforts to study reproductive biology in wild individuals despite the importance of such efforts to conservation. However, captive individuals can offer a unique opportunity to study species and behaviors that are otherwise difficult to observe. For example, captive studies on the vocal behavior of harp seals (*Pagophilus groenlandicus*; Serrano & Miller 2000, Serrano 2001), spotted seals (*Phoca largha*; Beier & Wartzok 1979), leopard seals (*Hydrurga leptonyx*; Rogers et al. 1996, Awbrey et al. 2004), northern elephant seals (Reichmuth & Schusterman 2009), bearded seals (*Erignathus barbatus*; Davies et al. 2006), Mediterranean monk seals (Muñoz et al. 2011), and harbor seals (*Phoca vitulina*; Ralls et al. 1985, Khan et al. 2006, Reichmuth & Schusterman 2009, Casey et al. 2016) have revealed information about vocal repertoires, behaviors associated with underwater signals, individual differences in vocalizations, source levels, and seasonal patterns of vocal behavior. These same topics can be studied in non-releasable Hawaiian monk seals by recording their acoustic signals year-round in controlled conditions.

The goals of the present study were to confirm underwater sound production in Hawaiian monk seals and to provide an initial description of their aquatic vocal repertoire. Simultaneous acoustic and video recordings were obtained over a nine-month period for one adult male Hawaiian monk seal living in human care at the University of California Santa Cruz. Underwater calls emitted by this individual were counted, perceptually classified, spectrographically analyzed, and validated as discrete call types. Diurnal and seasonal patterns in vocal behavior were documented relative to annual physiological cycles, including molt and breeding, and were further referenced to the seal's blood testosterone values. These data, although obtained for only one Hawaiian monk seal in an atypical social and environmental context, provide the first quantitative information about the acoustic features of underwater call types and the first description of temporal patterns in aquatic vocal behavior for this species. This foundational knowledge will support future research on monk seal communication and increase understanding of their reproductive behavior, leading to more informed approaches to monitoring and conservation efforts.

Methods

Subject

The subject was a sexually mature (15-16 y) male Hawaiian monk seal identified as *Kekoa* (KE18, NOA0006781). This seal was born at Kure Atoll in the Northwestern Hawaiian Islands and lived in species-typical conditions until the age of 10 y. As a young adult, he was removed from the wild population by the NOAA Pacific Islands Fisheries Science Center's Hawaiian Monk Seal Recovery Program after being deemed a threat to the fragile population; his aberrant behavior included attacking and sometimes killing pup and juvenile conspecifics. To protect the wild population, *Kekoa* was relocated by the National Marine Fisheries Service to Long Marine Laboratory, at the University of California Santa Cruz, to participate in physiological research to promote the conservation of wild monk seals. *Kekoa* was trained to participate in cooperative research over a period of six years. During this time, he was housed without exposure to conspecifics.

During the period of this study (September 2017 to May 2018) *Kekoa* consumed a daily diet of freshly thawed fish (*Clupea harengus*, *Mallotus villosus*) and squid (*Dorytheuthis opalescens*). His diet was established to maintain optimal health and was not constrained for research purposes. During the study, *Kekoa* completed his annual molt (8 February to 13 March 2018). Based on the typical annual cycles of wild monk seals (Atkinson & Gilmartin 1992), this mature seal likely experienced a period of heightened reproductive activity—with coincident high levels of blood testosterone—lasting several months prior to his molt. Blood samples were obtained opportunistically during four veterinary assessments conducted within the study period and serum testosterone levels were measured (Antech Diagnostics, Santa Clara, CA).

Authorizations

Given the endangered and protected status of Hawaiian monk seals, this study was conducted with federal authorization from the National Marine Fisheries Service, under marine mammal research permit 19590. Oversight of research activities was conducted by NMFS Office of Protected Resources and the Institutional Animal Care and Use Committee at the University of California Santa Cruz.

Environment

The seal's primary living enclosure was a 2.1 m deep, 7.6 m diameter round flow-through seawater pool (25,700 gallons) with adjacent haul-out space. This pool was connected to a larger (238,500 gallons) pool that housed three dolphins; a solid gate separated the seal's pool from the dolphin pool. A rectangular, water-filled channel (3 m x 1.5 m x 1.5 m deep) was connected to the seal's primary pool, and the seal was prevented access from this channel by an acoustically transparent (water-filled) PVC gate (Fig. 1, right). On the opposite side of the channel was a 2.4 m deep, 9.1 m diameter round pool that occasionally housed dolphins; a solid gate separated the channel from this pool.

Background noise in the seal's primary living enclosure included typical sounds of water movement and mechanical noise. Median ambient noise spectral density levels generally decreased with increasing frequency from approximately 86 dB re 1 $\mu Pa^2/Hz$ at 80 Hz to approximately 67 dB re 1 $\mu Pa^2/Hz$ at 2 kHz (measurements obtained using a Reson TC4032 low-noise hydrophone and a battery-powered Brüel and Kjær 2270 sound analyzer).

Audio and Video Recording

A SoundTrap 300 STD acoustic recorder (0.02–60 kHz, ±3 dB; Ocean Instruments, Warkworth, Auckland, New Zealand) was placed within a concrete mount at the base of the seal's pool (Fig. 1, upper left). The SoundTrap was programmed to record on a 50% duty cycle (30 min every hour), with a sampling rate of 48 kHz, which was sufficient to capture the full frequency bandwidth of the seal's vocalizations. The SoundTrap was encased in protective, water-filled PVC tubing where only the hydrophone was exposed when submerged (Fig. 1, lower left), and placed in the water-filled channel adjacent to the pool (Fig. 1, right). The SoundTrap unit was retrieved, downloaded, recharged, and re-deployed every two weeks to ensure a continuous record of *Kekoa's* vocal behavior.

Simultaneous, time-linked video data of the seal was obtained via a closed-circuit, infrared surveillance system mounted in the seal's enclosure, with video data banked to an external hard drive (Fig. 2). These data allowed the location of the seal during each call to be determined. During daylight hours, location was scored as either "under water," "surface," or "on deck." Poor video quality at night sometimes hindered our ability to discern underwater from surface vocalizations, so we logged the location of these calls as either "in water" or "on deck."

Acoustic Analyses

The acoustic dataset included 24 30-min files for each day that could be referenced to video data. We analyzed one full day per week—which included 12 h of acoustic data—for nine months, from September 2017 through May 2018. Only sounds confirmed by video to be produced under water, at the water's surface, or in water were considered. Conditioned vocalizations produced during training sessions, environmental noises, and whistles and clicks produced by dolphins in the adjacent pools were excluded from consideration.

We detected and classified different underwater vocal types based on visual inspection of spectrograms for each 30-min recording in the sound analysis software Adobe Audition (Adobe Systems, San Jose, CA). Most of the sounds produced by the seal were individual calls, or sequences of one or more calls, that could be readily isolated and counted. Calls considered to be the same vocal type had common perceptual structure, frequency characteristics, and repeatable features that were recognizable and measurable. Upon detection, the calls were cross-referenced to the video data and then logged, counted, and scored for subjective quality. Initially, each call was categorized into one of ten call types based on perceptual features. These call types were descriptively labeled as *moan*, *ascending moan*, *descending moan*, *croak*, *groan*, *growl*, *gurgle*, *roar*, *rumble*, and *whoop*. To facilitate review and categorization of the calls, representative sound files and spectrographic exemplars were used to train three experienced observers.

Manual counts of calls produced by the monk seal were used to support characterization of diurnal and seasonal temporal patterns in sound production. For diurnal analysis, call production was summarized for each month as the mean number of calls detected per 30-min file within each hourly interval. The photoperiod from the middle of each month was used to bin the data from each day into either a daytime or nighttime interval. For seasonal analysis, mean call production (calls per 30-min file) was summarized for each month, by total number of calls and by call type. Seasonal patterns in calling were further referenced to physiological cycles by considering the timing of the seal's molting period relative to seasonal trends in sound production.

From the manually scored data, a subsample of 20 representative calls per type were selected for spectrographic analysis. These were high-quality calls with signal-to-noise ratio (SNR) greater than 15 dB. SNR was calculated by measuring the root-mean-square (RMS) amplitude of the call (signal) and its surrounding background noise from the waveform using Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY). Both RMS amplitude values were then converted to decibels and the noise value was subtracted from the signal value. Seventeen acoustic features were measured from each call in Raven Pro. These features, described in Table 1, included total duration, duration 90%, center frequency, 1st and 3rd quartile frequencies, inter-quartile range bandwidth, 90% bandwidth upper and lower frequency bounds, 90% bandwidth, peak frequency, 3 dB bandwidth upper and lower frequency bounds, 3 dB bandwidth, 10 dB bandwidth upper and lower frequency bounds, 10 dB bandwidth, and aggregate entropy. Total call duration was determined by manual selection from the waveform. Descriptive parameters observed from the spectrogram or spectrum of each call were noted, including the presence or absence of harmonics and the number of harmonics contained in the call. Frequency parameters were measured from the spectrum over the 90% duration of the call (Window—Type: Hann, size = 4096 samples (= 85.3 ms), 3 dB filter bandwidth: 16.9 Hz; Time grid—Overlap: 90%, Hop size: 410 samples (= 8.54 ms); Frequency grid—DFT size: 4096 samples, Grid spacing: 11.7 Hz). Using the duration 90% enabled consistent (automated) measurement of call duration rather than subjective (manual) determination of duration. If the duration 90% fell below the minimum window dictated by the sampling rate (0.0853 s), then the minimum window allowed by the sampling rate was used for analysis; this was always within 0.03 s of the duration 90%.

In addition to the 17 parameters measured for all calls, additional parameters were measured for a subset of call types. For calls containing harmonics (*ascending moan*, *moan*, *groan*), we also measured fundamental frequency. For *whoops*, we measured inter-pulse interval, call rate, and the number of calls per bout. For *rumbles*, the only pulsed call, we evaluated pulse duration, inter-pulse interval, number of pulses, and pulse rate; these temporal features were measured using Avisoft SAS Lab Pro v.5.2.12 (Avisoft Bioacoustics).

To validate our initial perceptual categorization of the call types emitted by this monk seal while submerged or at the surface, we conducted a preliminary discriminant function analysis (DFA) using the 17 measured call variables obtained for 20 exemplars (when possible) for each of the perceptual call types. Eight call types were considered;

roars and *descending moans* were encountered only 13 and 11 times, respectively, in the data set and were excluded from the DFA due to poor SNRs that prevented spectrographic analysis (< 15 dB). The DFA depicted each of the remaining eight calls in acoustic space, with the pre-assigned subjective call types as group identifiers and acoustic measurements as discriminant variables. The DFA enabled a matrix of percent correct classification scores, which indicated how well the call variables separated into the pre-assigned call types. When the initial DFA was complete, we noted whether certain call types were consistently misclassified as another call type (misclassification rate > 30%). In cases where this occurred, the confounding call types were collapsed into a single category. The DFA and classification matrix were then repeated with a collapsed repertoire of six call types, and an additional cross-validation DFA was computed using the leave-one-out method. To conduct this analysis, we used the 'mass' and 'deducer' package in R Studio v.1.1.423. To create spectrogram figures, we used the 'seewave' package in R Studio v.1.1.423.

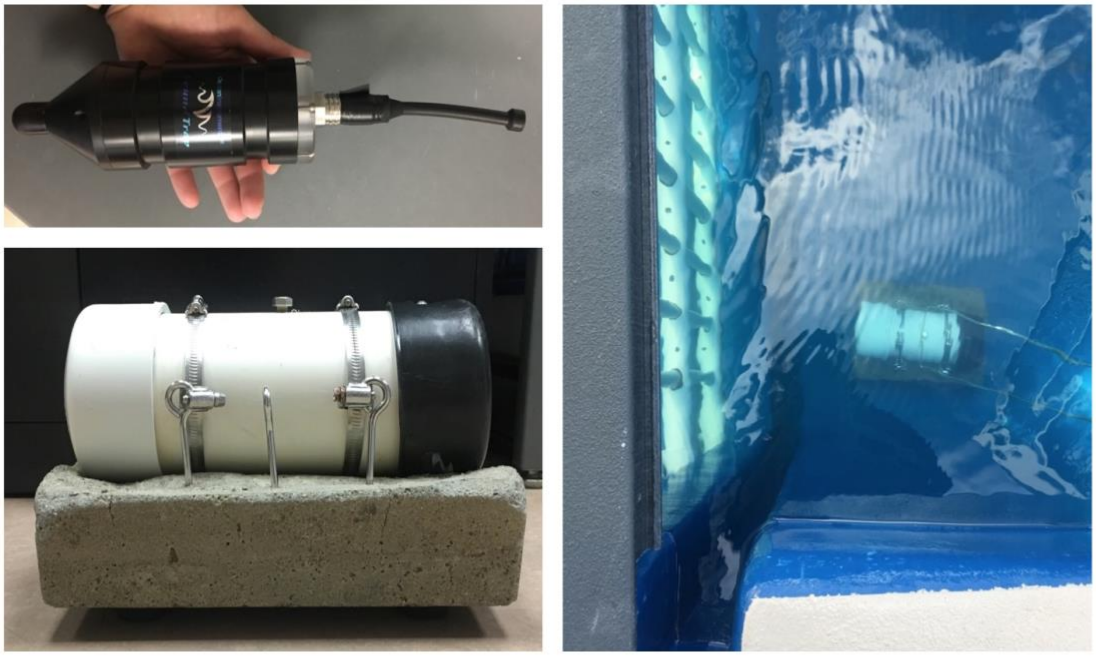
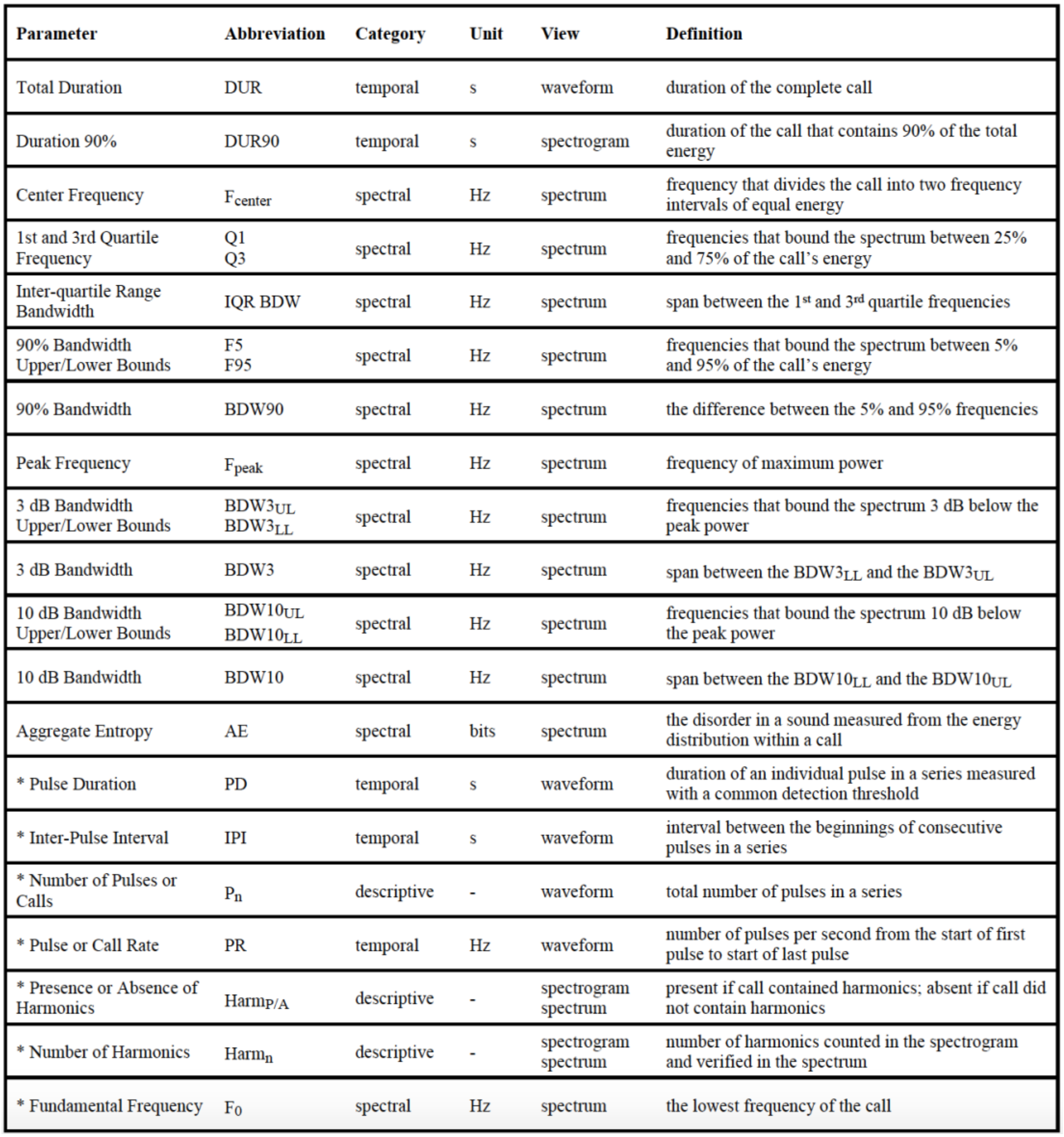


Figure 1. (Upper Left) SoundTrap 300 STD acoustic recorder, with the hydrophone element visible on the left side; note that this end was always oriented toward the monk seal's living enclosure. (Lower Left) SoundTrap recorder encased in PVC tubing and attached to concrete mount for deployment. (Right) SoundTrap recorder deployed in 1.5 m-deep channel with water-filled PVC gate.

Figure 2. Still image extracted from the continuous video feed of the monk seal’s living enclosure. The white PVC, water-filled gate separating the monk seal’s pool from the channel where the SoundTrap was deployed is visible in the upper right portion of the pool.

Table 1. Acoustic parameters measured for the Hawaiian monk seal's vocalizations. Asterisks (*) denote call variables that were discrete or that were measured only for certain call types; these parameters were excluded from the DFA to validate call types.



Parameter	**Abbreviation**	**Category**	**Unit**	**View**	**Definition**
Total Duration	DUR	temporal	s	waveform	duration of the complete call
Duration 90%	DUR90	temporal	s	spectrogram	duration of the call that contains 90% of the total energy
Center Frequency	F_{center}	spectral	Hz	spectrum	frequency that divides the call into two frequency intervals of equal energy
1st and 3rd Quartile Frequency	Q1 Q3	spectral	Hz	spectrum	frequencies that bound the spectrum between 25% and 75% of the call's energy
Inter-quartile Range Bandwidth	IQR BDW	spectral	Hz	spectrum	span between the 1^{st} and 3^{rd} quartile frequencies
90% Bandwidth Upper/Lower Bounds	F5 F95	spectral	Hz	spectrum	frequencies that bound the spectrum between 5% and 95% of the call's energy
90% Bandwidth	BDW90	spectral	Hz	spectrum	the difference between the 5% and 95% frequencies
Peak Frequency	F_{peak}	spectral	Hz	spectrum	frequency of maximum power
3 dB Bandwidth Upper/Lower Bounds	$BDW3_{UL}$ $BDW3_{LL}$	spectral	Hz	spectrum	frequencies that bound the spectrum 3 dB below the peak power
3 dB Bandwidth	BDW3	spectral	Hz	spectrum	span between the $BDW3_{LL}$ and the $BDW3_{UL}$
10 dB Bandwidth Upper/Lower Bounds	$BDW10_{UL}$ $BDW10_{LL}$	spectral	Hz	spectrum	frequencies that bound the spectrum 10 dB below the peak power
10 dB Bandwidth	BDW10	spectral	Hz	spectrum	span between the $BDW10_{LL}$ and the $BDW10_{UL}$
Aggregate Entropy	AE	spectral	bits	spectrum	the disorder in a sound measured from the energy distribution within a call
* Pulse Duration	PD	temporal	s	waveform	duration of an individual pulse in a series measured with a common detection threshold
* Inter-Pulse Interval	IPI	temporal	s	waveform	interval between the beginnings of consecutive pulses in a series
* Number of Pulses or Calls	P_n	descriptive	-	waveform	total number of pulses in a series
* Pulse or Call Rate	PR	temporal	Hz	waveform	number of pulses per second from the start of first pulse to start of last pulse
* Presence or Absence of Harmonics	$Harm_{P/A}$	descriptive	-	spectrogram spectrum	present if call contained harmonics; absent if call did not contain harmonics
* Number of Harmonics	$Harm_n$	descriptive	-	spectrogram spectrum	number of harmonics counted in the spectrogram and verified in the spectrum
* Fundamental Frequency	F_0	spectral	Hz	spectrum	the lowest frequency of the call

Results

Underwater Vocal Repertoire

We initially categorized ten presumptive underwater call types based on aural-visual inspection of spectrograms. However, acoustic variables were measured for only eight of ten call types. *Roars* and *descending moans* were excluded from acoustic analyses and the DFA since they were only observed 13 and 11 times, respectively, and all calls had a SNR less than 15 dB. Two of the perceptually classified call types (*ascending moan*, *gurgle*) had misclassification rates greater than 30% in the initial DFA based on eight vocal types. Half the *ascending moans* were classified as *moans*, and 35% of *gurgles* were classified as *growls*. Therefore, *ascending moans* and *moans* were both re-classified as *moans*, and *gurgles* and *growls* were re-classified as *growls* for the subsequent DFA using only six vocal types.

On the basis of these six primary call types, the DFA correctly identified an average of 77% of vocalizations as their subjective call type. The cross-validated DFA extracted five functions with the first (LD1) and the second (LD2) accounting for 66% and 22% of the total variance, respectively (Fig. 3). LD1 was strongly correlated with aggregate entropy (AE), whereas LD2 was strongly correlated with duration (DUR). The cross-validated DFA correctly classified an average of 63.5% of vocalizations as their subjective call type and revealed significant differences among vocal types (LD1: Wilks' $\lambda = 0.18$, $P < 0.001$; LD2: Wilks' $\lambda = 0.4$, $P < 0.001$). Five of six call types were robustly separated in acoustic space and reliably classified by the cross-validated DFA, as compared to prior (chance) probability of the final call groupings (Fig. 4).

Correct classification rates were high for *moans* (90% correct classification, chance level 26%, n = 40 calls), *growls* (78% correct classification, chance level 26%, n = 40 calls), *rumbles* (70% correct classification, chance level 13%, n = 20 calls), *whoops* (65% correct classification, chance level 13%, n = 20 calls), and *croaks* (60% correct classification, chance level 13%, n = 20 calls). *Croaks* and *whoops* were sometimes confused with one another, with 20% of *croaks* misidentified as *whoops* and 15% of *whoops* misidentified as *croaks*. *Groans*, the call type with the lowest sample size, had the lowest correct classification rate (18% correct classification, chance level 7%, n = 11 calls), with 55% of *groans* classified as *moans* by the cross-validated DFA. Therefore, this monk seal had a vocal repertoire of at least six call types having unique and perceptually recognizable acoustic features, as described individually below (Fig. 5). Underwater calls were often produced in series (Fig. 6), with 89% (1564/1756) of vocalizations produced in a bout comprised of 2 or more discrete or overlapping calls separated by more than 3 s of silence.

Hawaiian monk seal *croaks* (Fig. 7, Table 2) are brief (DUR: 0.28 s ± 0.06), low-frequency calls that sound guttural. They are relatively broadband calls (BDW90: 271 Hz ± 115) with no harmonics, which are similar to *growls* but of much shorter duration. *Croaks* are always discrete, and occur both as isolated signals and within vocal bouts. They are perceptually similar to *whoops*, but have a greater peak frequency (F_{peak}: 258 Hz ± 112), slightly longer duration, and higher aggregate entropy (Fig. 6, upper panel).

Groans (Fig. 8, Table 2) are relatively long (DUR: 1.23 s ± 0.86), tonal, low-frequency vocalizations that sound similar to a foghorn or a bellow. *Groans* are similar in structure to *moans* and *ascending moans*, but reach higher frequencies (F95: 281 Hz ± 179), have a greater fundamental frequency (F_0: 59 Hz ± 18), and contain more harmonics ($Harm_n$: 11 ± 6, range: 3-20). *Groans* are always discrete and occur as isolated signals and within vocal bouts.

Compared to *croaks*, *growls* (Fig. 9, Table 2) are longer (DUR: 3.26 s ± 1.36), but have similar characteristics in being low-frequency, harsh, relatively broadband signals (BDW90: 335 Hz ± 47). *Growls* and *croaks* have the highest aggregate entropy of the six call types (AE: 4.9 bits ± 0.2 and 4.2 bits ± 0.7, respectively). *Growls* lack harmonics and are sometimes preceded by and connected to *ascending moans* (Fig. 6, lower panel). They tend to increase in amplitude and frequency over the duration of the call (Fig. 6). *Gurgles*, one of the ten initial call types, are perceptually similar to *growls*, but have a lower average SNR ratio than growls (SNR: 21.4 dB versus 38.6 dB, respectively); *gurgles* were ultimately categorized as *growls* in the six vocal type DFA.

Moans (Fig. 10, Table 2) are brief (DUR: 0.58 s ± 0.31), low-frequency (F_{peak}: 48 Hz ± 18), tonal calls that have a lower fundamental frequency (F_0: 37 Hz ± 6) and fewer harmonics than *groans* ($Harm_n$: 7 ± 3, range: 2-15). *Moans* have the lowest aggregate entropy (AE: 2.3 bits ± 0.4) of the six vocal types. The *moan*, which is relatively flat in frequency profile, has two variations: *ascending* (Fig. 5) and *descending*. *Ascending moans* have a weak upsweep frequency modulation pattern. They often follow *moans* and precede *growls* (Fig. 6, lower panel). The *descending moan* is a rare variation of the *moan* that resembles a slight downsweep.

Rumbles (Fig. 11, Table 2) are pulsed, low-frequency (F_{peak}: 57 Hz ± 23), relatively long-duration calls (DUR: 2.75 s ± 1.69). *Rumbles* have a greater pulse rate (PR: 14.9 Hz ± 3.5), a longer inter-pulse interval (IPI: 0.07 s ± 0.03), and more pulses per call (P_n: 38 ± 22) than *whoops*. Occasionally, *rumbles* occur as isolated signals, but are typically associated with *moans* and are often followed by and connected to *ascending moans*.

Whoops (Fig. 12, Table 2) are brief calls (DUR: 0.14 s ± 0.04) that occur as a single element or in a series of 2-6 repeating elements with a regular inter-unit interval (IPI: 0.14 s ± 0.07). We counted single or multiple *whoops* as a call when the interval between successive *whoops* was less than 0.5 seconds. *Whoops* are perceptually similar to *croaks* but sound less guttural, have a lower aggregate entropy (AE: 3.8 bits ± 0.7), show a steep upsweep frequency modulation pattern, and have a lower peak frequency than *croaks* (F_{peak}: 193 Hz ± 90). Within a bout of *whoops*, the peak frequency for individual *whoops* varies, sometimes increasing and decreasing over the bout.

Although *roars* were not analyzed for spectrographic parameters, these calls appeared to be very low-frequency (< 100 Hz), long-duration (> 11 s), and low-amplitude calls (SNR range 7-13 dB) that are difficult to discriminate from background noise.

Numerous vocalizations produced by the monk seal while resting out of the water were present in the underwater recordings. These sounds were conducted through the seal’s body into the water through the rigid wooden decks and concrete structure of the pool. Airborne calls were noted when they appeared in underwater recordings; they were counted and descriptively classified but not analyzed further.

Temporal Patterns in Vocal Behavior

A total of 456 h of acoustic data were analyzed for seasonal and diurnal temporal patterns: 1756 vocalizations were produced under water, at the surface, or in water during the intervals sampled over the nine-month study period. A strong seasonal pattern in call production was reflected by overall calling rates (Fig. 13). Call production generally increased from September to January during the suspected breeding season, then decreased markedly from February to May during and following the annual molt. However, no particular call types were emitted only during the suspected breeding season (Fig. 14a-f). Coincident with overall increased call production, the seal's blood testosterone values were high in September and December (210 ng/dL and 304 ng/dL, respectively), and were drastically decreased in February and April (53 ng/dL and <20 ng/dL).

Trends in diurnal patterns in call production for the 9-month study period were less pronounced than trends in overall call production (Fig. 15, with shaded regions denoting intervals between sunset and sunrise). The seal vocalized during more hours of the day from September through January compared to during the molt and post-molt interval from February to May. Additionally, an increase in the number of vocalizations produced in the early morning (from 0500 to 0600 hours) was seen in January and February. Very few vocalizations were produced following sunset in any month.

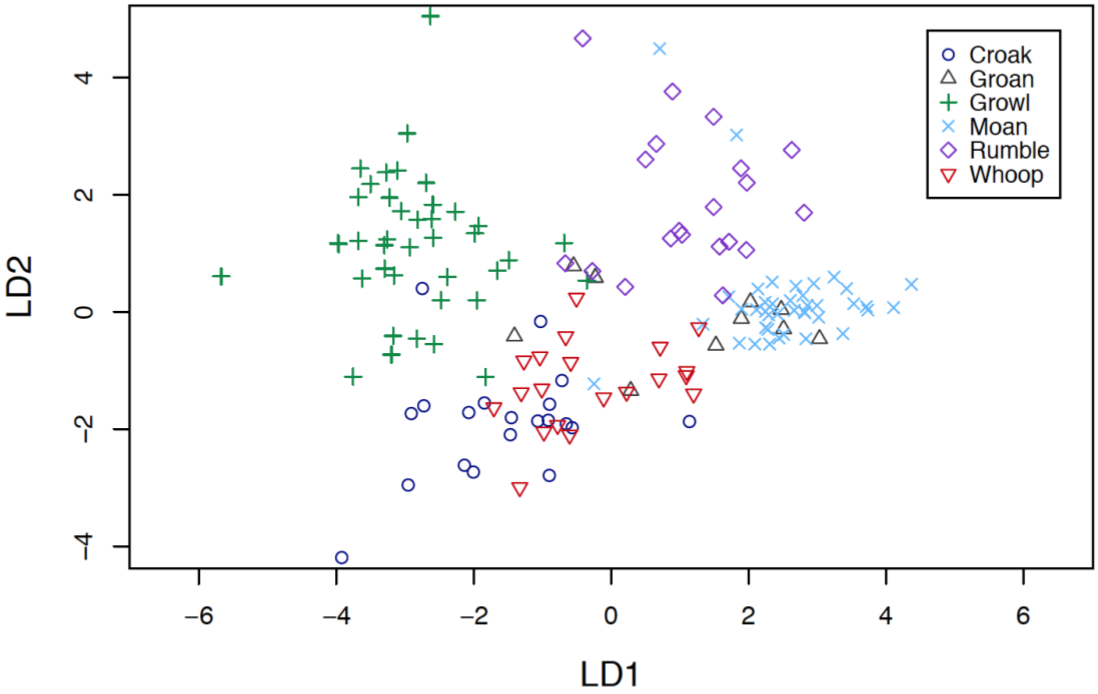
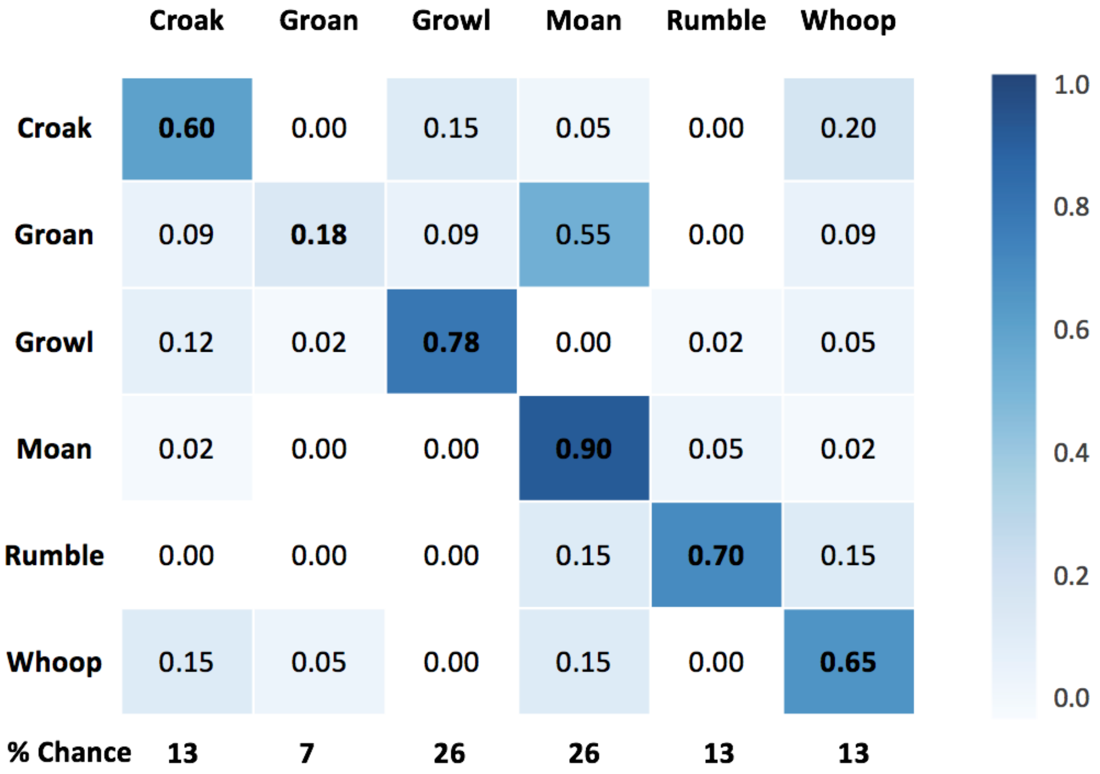


Figure 3. Scatterplot showing the cross-validated DFA results for six different Hawaiian monk seal underwater vocal types. Seventeen acoustic parameters were included in the DFA (see Table 1). n = 40 for *moan* and *growl*; 20 for *croak*, *rumble*, and *whoop*; 11 for *groan*.



	Croak	Groan	Growl	Moan	Rumble	Whoop
Croak	**0.60**	0.00	0.15	0.05	0.00	0.20
Groan	0.09	**0.18**	0.09	0.55	0.00	0.09
Growl	0.12	0.02	**0.78**	0.00	0.02	0.05
Moan	0.02	0.00	0.00	**0.90**	0.05	0.02
Rumble	0.00	0.00	0.00	0.15	**0.70**	0.15
Whoop	0.15	0.05	0.00	0.15	0.00	**0.65**
% Chance	**13**	**7**	**26**	**26**	**13**	**13**

Figure 4. Classification matrix showing the proportion of correctly classified call types from the cross-validated DFA (Fig. 3). Darker colors indicate highest classification rates. Percent correct classification by chance is shown below the matrix. All vocal types were correctly classified at a rate higher than chance. n = 40 for *moan* and *growl*; 20 for *croak*, *rumble*, and *whoop*; 11 for *groan*.

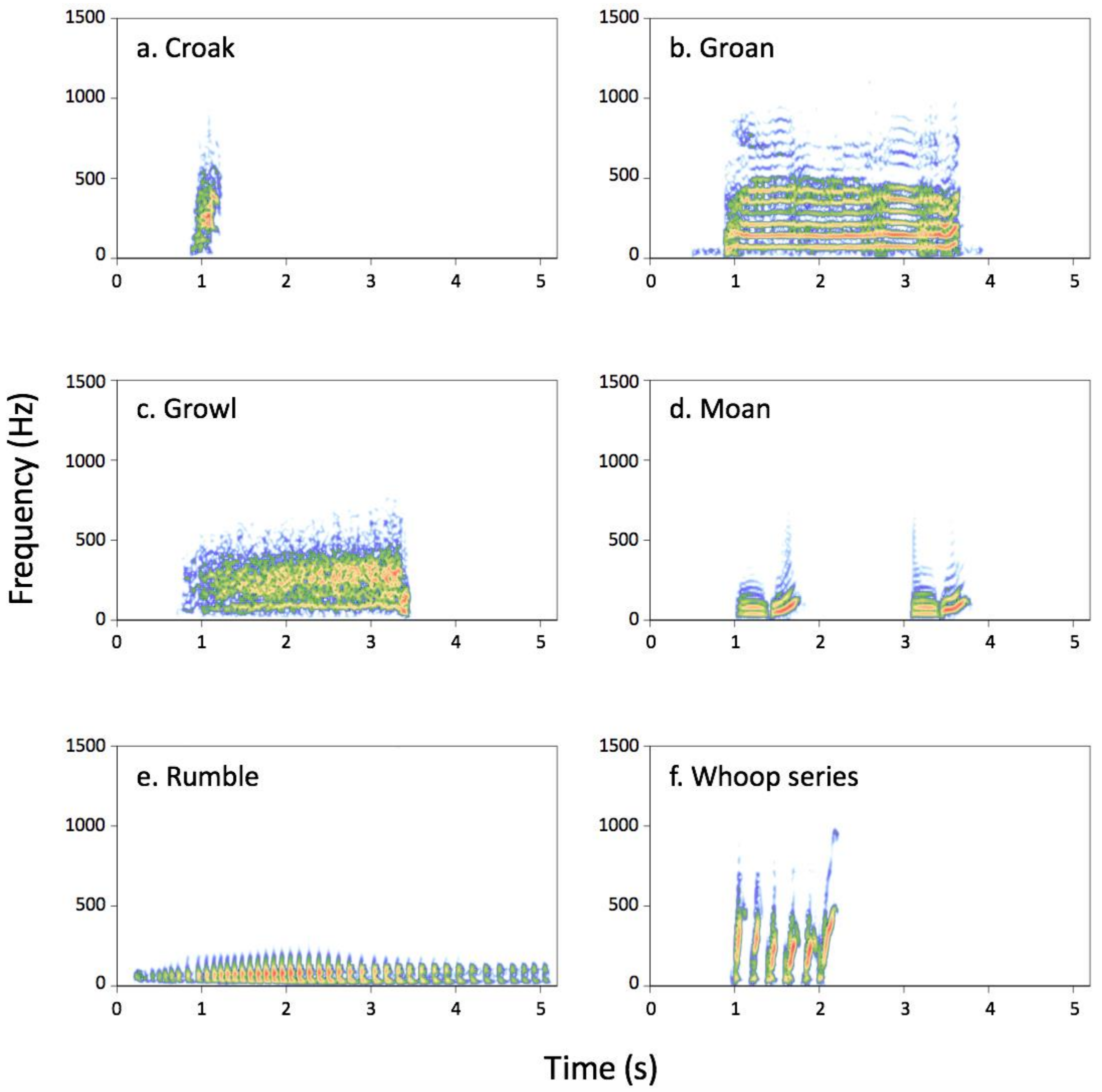


Figure 5. Spectrograms showing the Hawaiian monk seal's underwater vocal repertoire of six vocalizations. In panel d, the first and third vocals are *moans*, and the second and fourth vocals are *ascending moans*. Spectrogram settings: Hanning window, window length: 4096 points, 90% overlap.

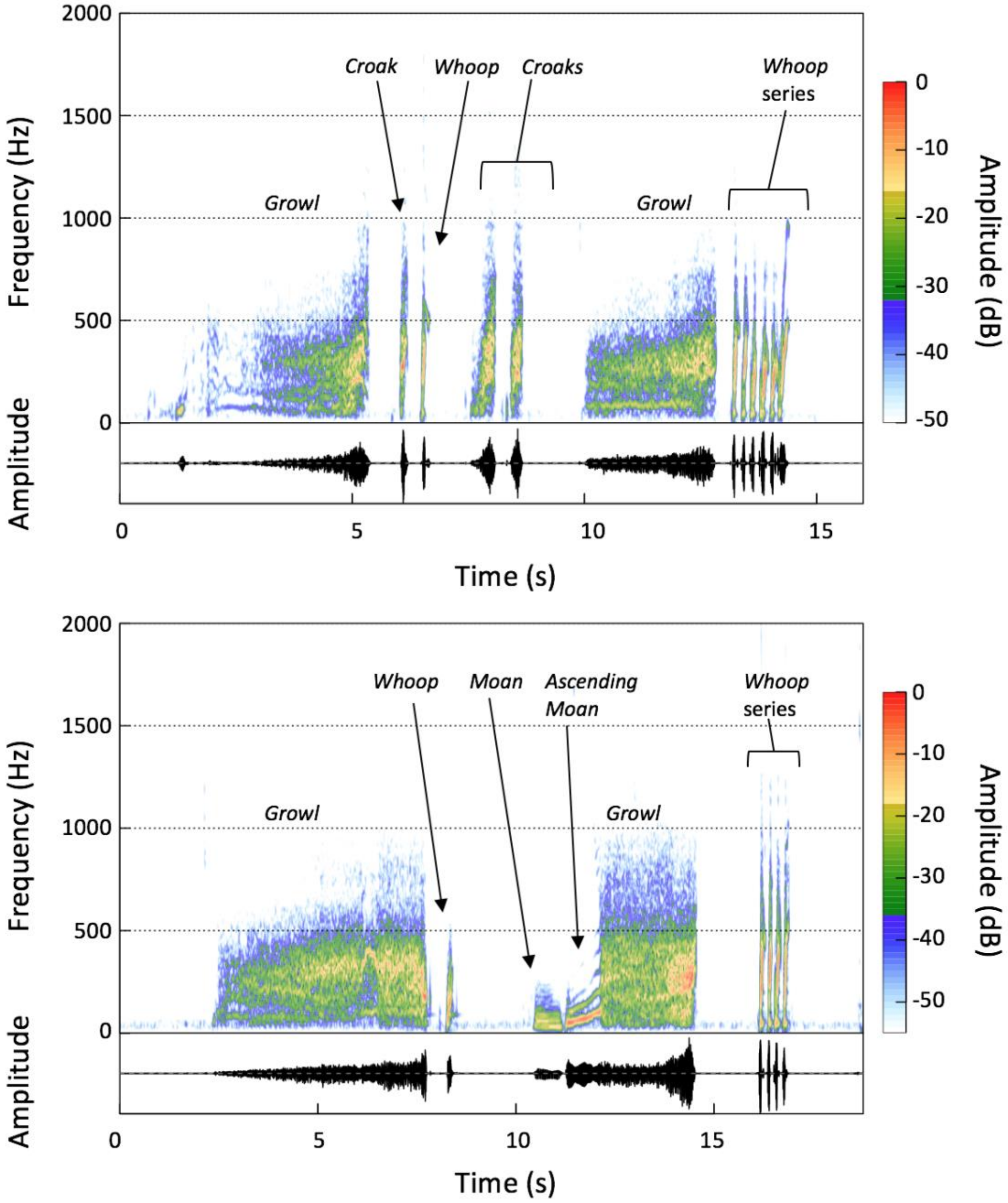


Figure 6. Two exemplars of the monk seal's typical vocal bouts. The spectrogram is shown above the waveform for each exemplar. Spectrogram settings: Hanning window, window length: 4096 points, 90% overlap.

Table 2. Mean (± SD) values of acoustic parameters (see Table 1) measured for each of the six call types. Only good quality calls with SNR > 15 dB were analyzed. Most parameters were measured with Raven Pro 1.5 software (Hann window; DFT size = 4096; 90% overlap, 16.9 Hz 3 dB filter bandwidth). Pulse duration, inter-pulse interval, number of pulses, and pulse rate were measured for *rumbles* with Avisoft SAS Lab Pro v.5.2.12. Asterisks (*) denote call variables that were either descriptive or those that were measured only for certain call types; these parameters were not used in the DFA to validate call types.

Parameter	**Croak** n = 20	**Groan** n = 11	**Growl** n = 40	**Moan** n = 40	**Rumble** n = 20	**Whoop** n = 20
Total Duration (s)	0.28 ± 0.06	1.23 ± 0.86	3.26 ± 1.36	0.58 ± 0.31	2.75 ± 1.69	0.14 ± 0.04
Duration 90% (s)	0.18 ± 0.06	1.02 ± 0.8	2.07 ± 0.85	0.44 ± 0.24	2.26 ± 1.32	0.07 ± 0.02
Center Frequency (Hz)	264 ± 81	142 ± 107	291 ± 47	53 ± 15	63 ± 21	190 ± 75
1st and 3rd Quartile Frequency (Hz)	211 ± 78 321 ± 78	102 ± 51 193 ± 141	229 ± 40 346 ± 41	39 ± 10 66 ± 15	48 ± 13 84 ± 32	154 ± 64 218 ± 87
Inter-quartile Range Bandwidth (Hz)	110 ± 63	91 ± 99	118 ± 27	27 ± 13	36 ± 24	64 ± 52
90% Bandwidth Upper/Lower Bounds (Hz)	406 ± 87 135 ± 75	281 ± 179 58 ±13	436 ± 53 101 ± 22	88 ± 20 29 ± 6	131 ± 52 32 ± 10	298 ± 113 88 ± 60
90% Bandwidth (Hz)	271 ± 115	224 ± 174	335 ± 47	59 ± 19	98 ± 48	209 ± 118
Peak Frequency (Hz)	258 ± 112	150 ± 139	292 ± 67	48 ± 18	57 ± 23	193 ± 90
3 dB Bandwidth Upper/Lower Bounds (Hz)	274 ± 116 242 ± 113	165 ± 148 139 ± 138	328 ± 75 257 ± 61	56 ± 18 41 ± 18	75 ± 26 39 ± 18	220 ± 96 161 ± 68
3 dB Bandwidth (Hz)	31 ± 15	26 ± 24	71 ± 38	15 ± 2	37 ± 22	58 ± 49
10 dB Bandwidth Upper/Lower Bounds (Hz)	325 ± 124 204 ± 95	183 ± 166 113 ± 131	438 ± 44 155 ± 75	78 ± 19 31 ± 16	119 ± 41 24 ± 8	244 ± 106 128 ± 70
10 dB Bandwidth (Hz)	121 ± 73	70 ± 75	284 ± 74	46 ± 18	94 ± 38	116 ± 60
Aggregate Entropy (bits)	4.2 ± 0.7	3.3 ± 1.1	4.9 ± 0.2	2.3 ± 0.4	3.1 ± 0.5	3.8 ± 0.7
* Pulse Duration (s)	-	-	-	-	0.01 ± 0.00	-
* Inter-Pulse Interval (s)	-	-	-	-	0.07 ± 0.03	0.14 ± 0.07
* Number of Pulses or Calls	-	-	-	-	38 ± 22	4 ± 1
* Pulse or Call Rate (Hz)	-	-	-	-	14.9 ± 3.5	4.1 ± 1.0
* Presence or Absence of Harmonics	Absent	Present	Absent	Present	Absent	Absent
* Number of Harmonics	-	11 ± 6	-	7 ± 3	-	-
* Fundamental Frequency (Hz)	-	59 ± 18	-	37 ± 6	-	-

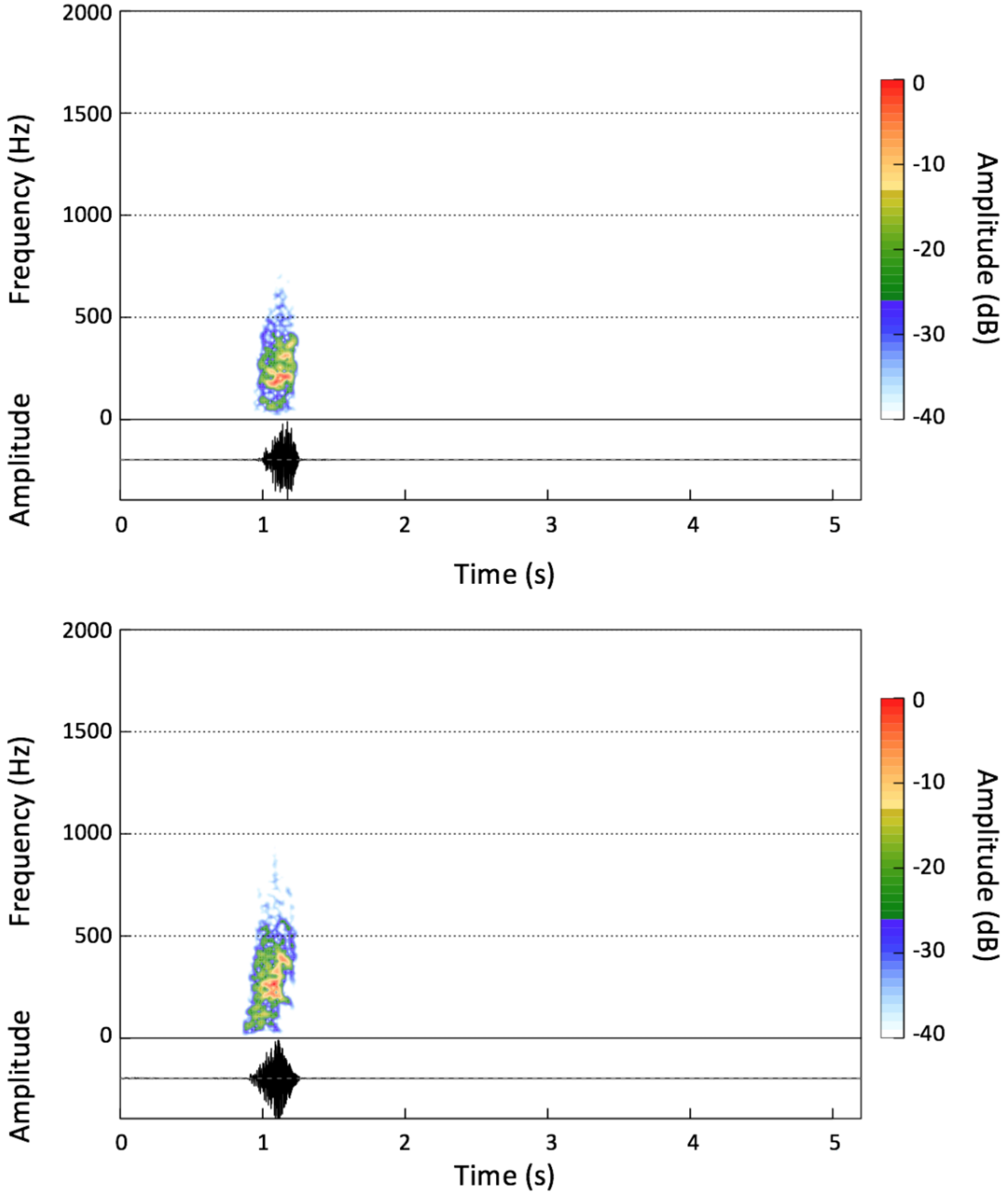


Figure 7. Two exemplars of the monk seal's *croak* vocalization. The spectrogram is shown above the waveform for each exemplar. Spectrogram settings: Hanning window, window length: 4096 points, 90% overlap.

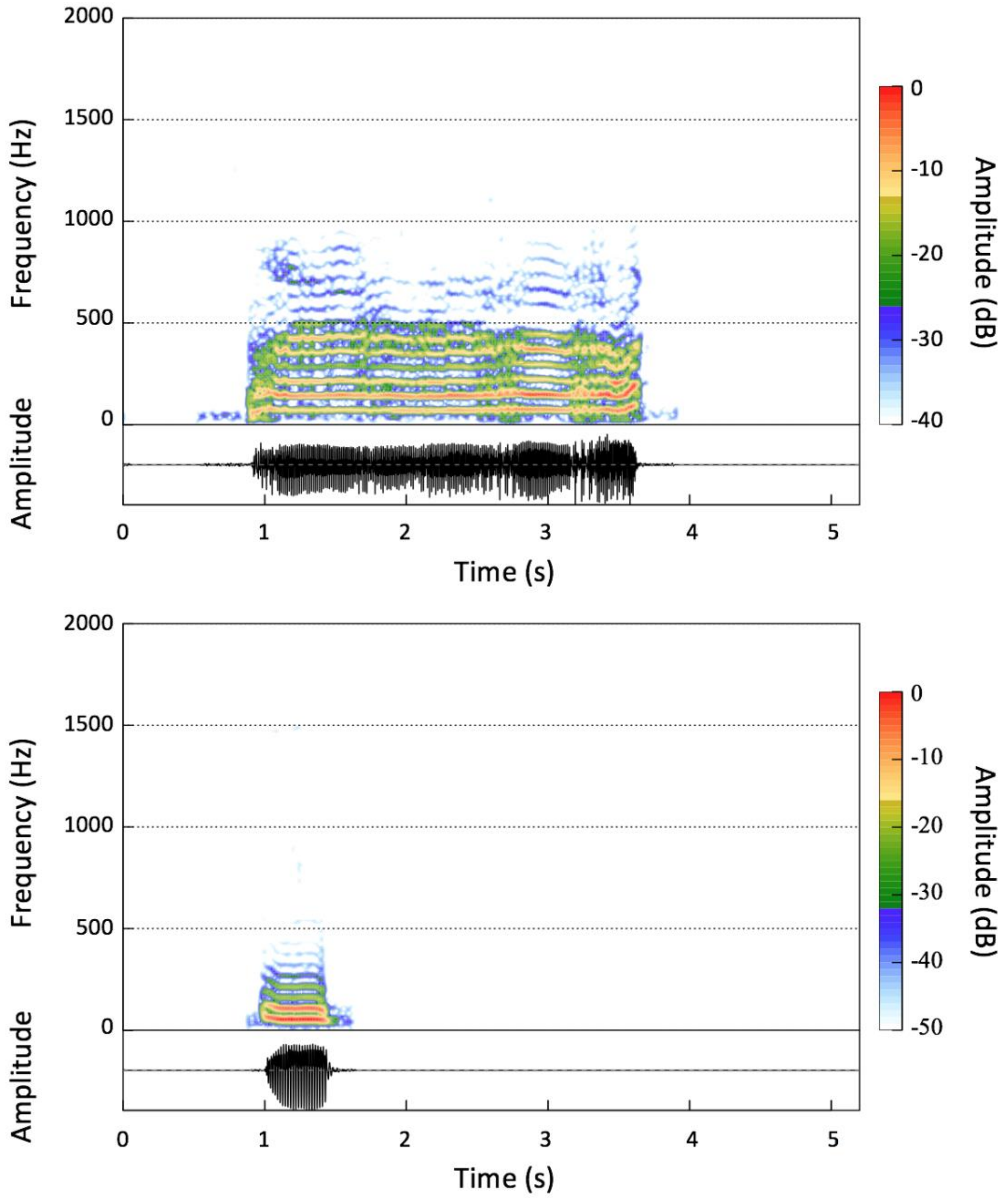


Figure 8. Two exemplars of the monk seal's *groan* vocalization. The spectrogram is shown above the waveform for each exemplar. Spectrogram settings: Hanning window, window length: 4096 points, 90% overlap.

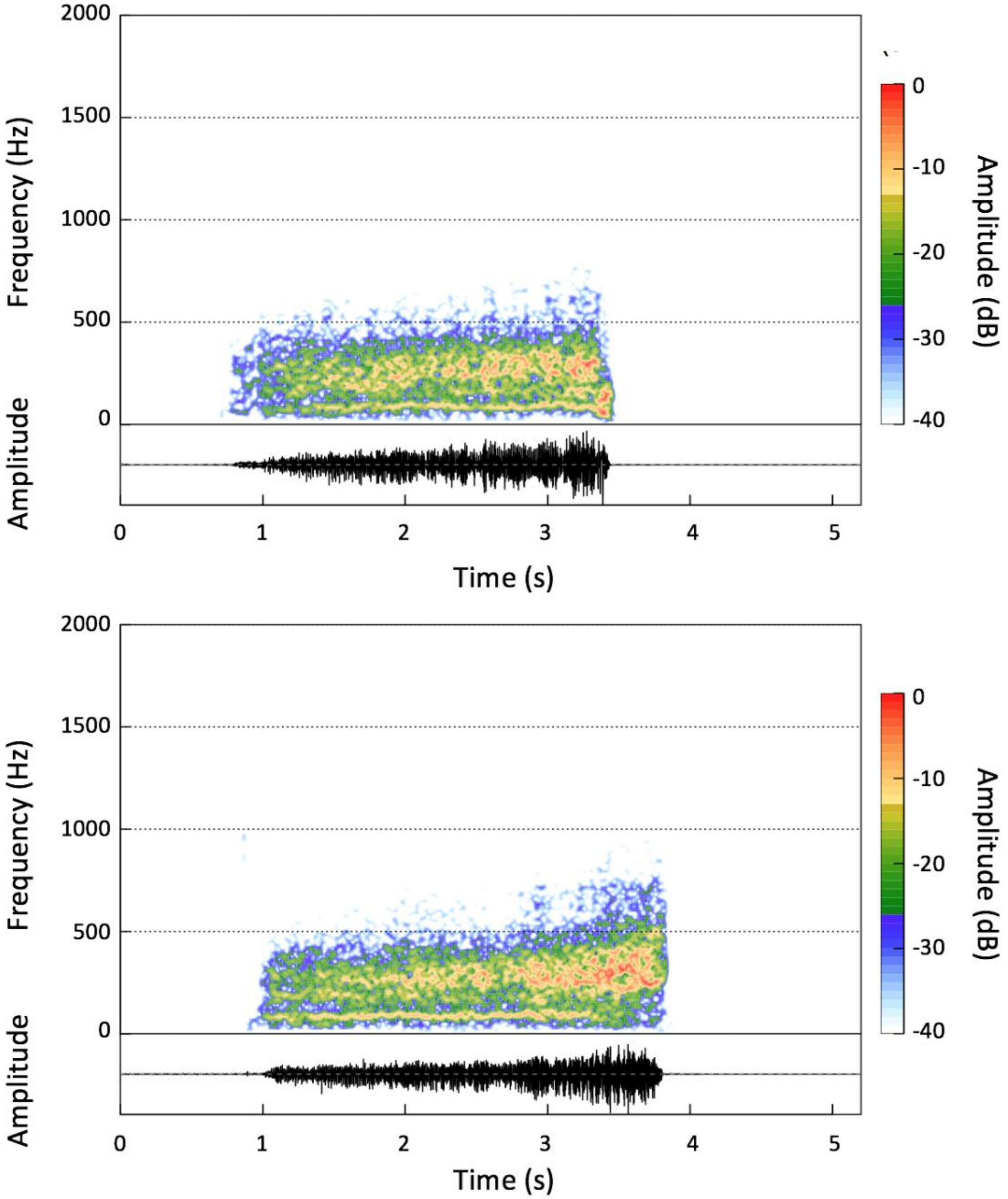


Figure 9. Two exemplars of the monk seal's *growl* vocalization. The spectrogram is shown above the waveform for each exemplar. Spectrogram settings: Hanning window, window length: 4096 points, 90% overlap.

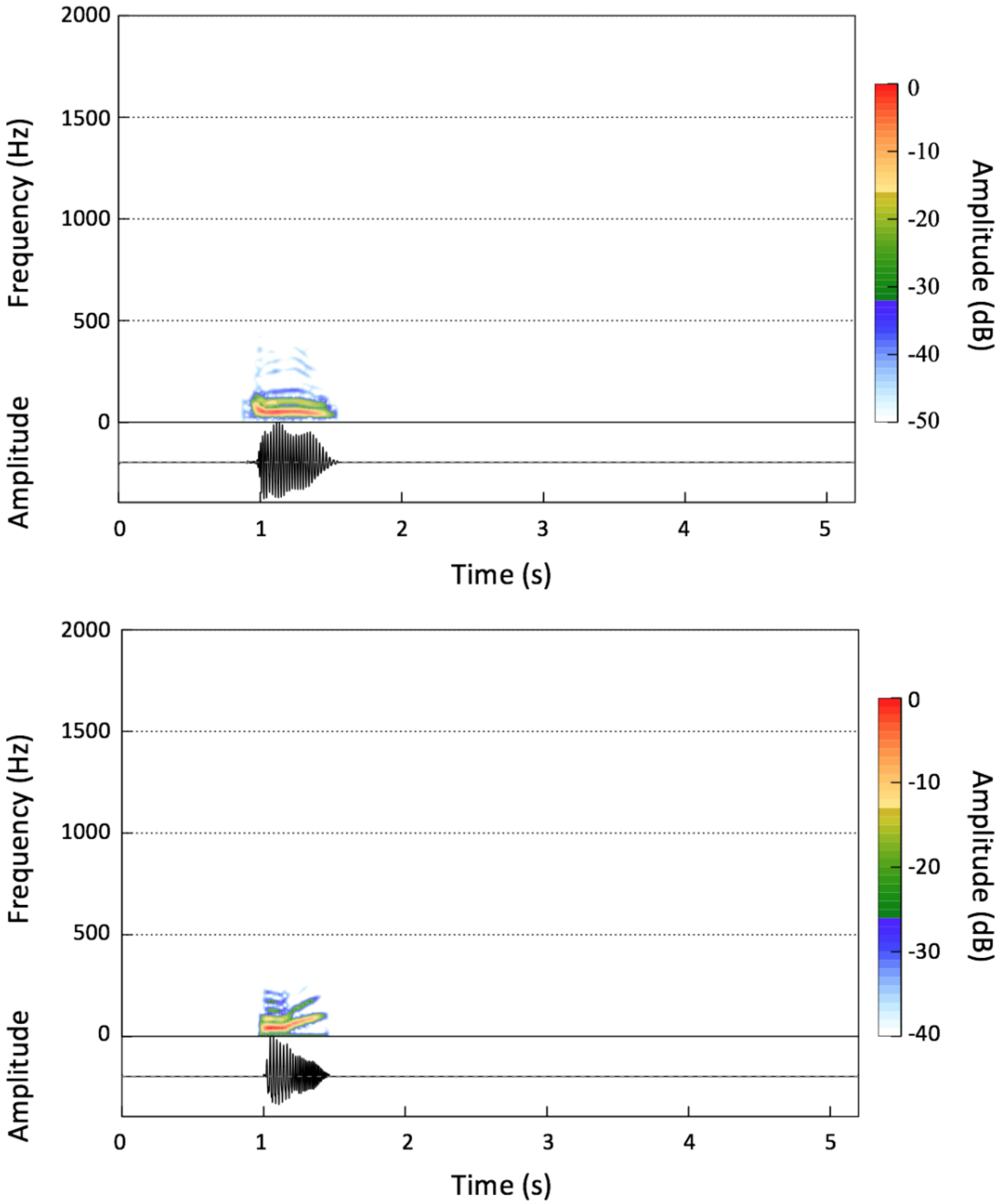


Figure 10. Two exemplars of the monk seal's *moan* vocalization. The spectrogram is shown above the waveform for each exemplar. The upper panel shows a typical *moan*; the lower panel shows an *ascending moan*. Spectrogram settings: Hanning window, window length: 4096 points, 90% overlap.

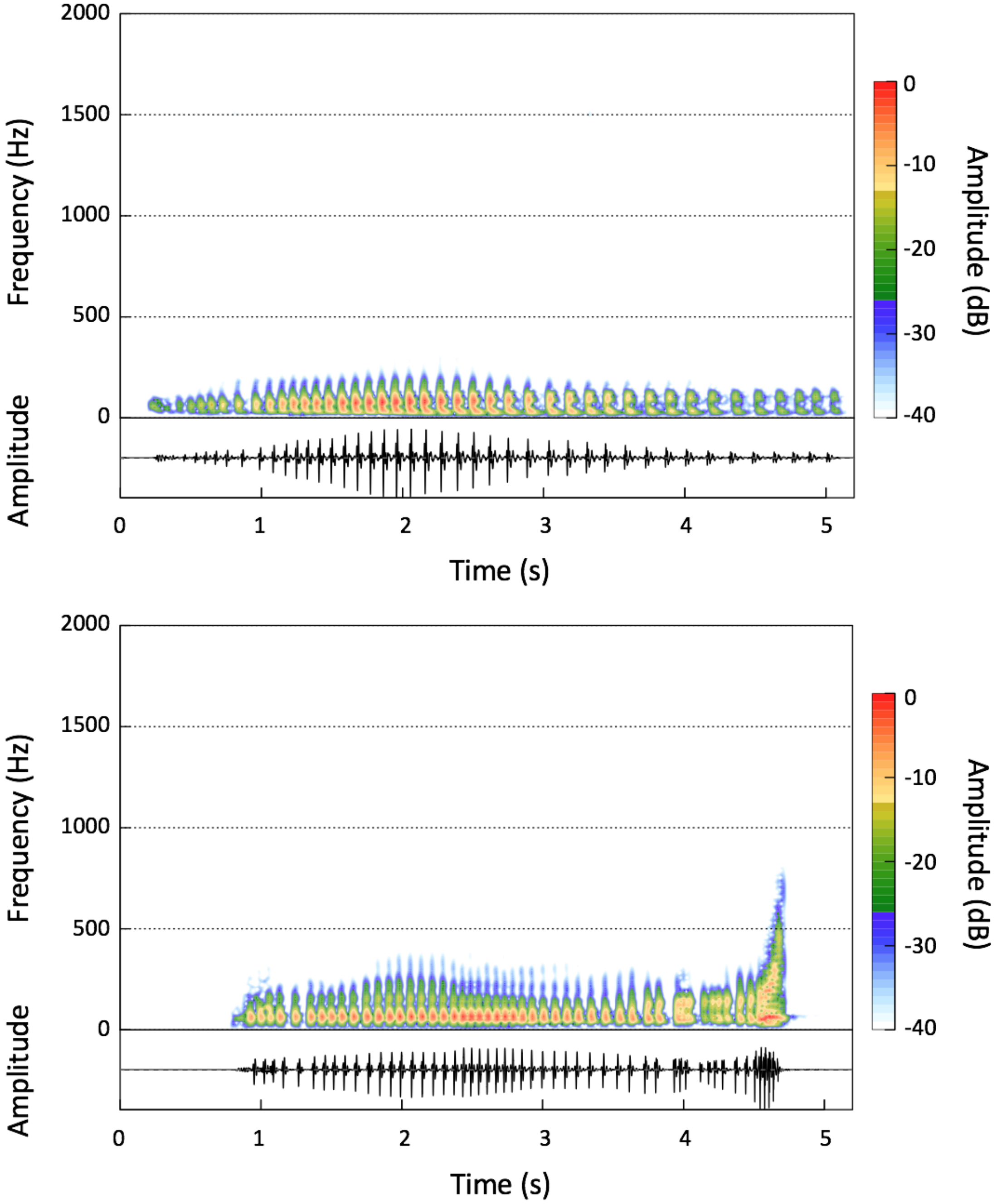


Figure 11. Two exemplars of the monk seal's *rumble* vocalization. The spectrogram is shown above the waveform for each exemplar. Spectrogram settings: Hanning window, window length: 4096 points, 90% overlap.

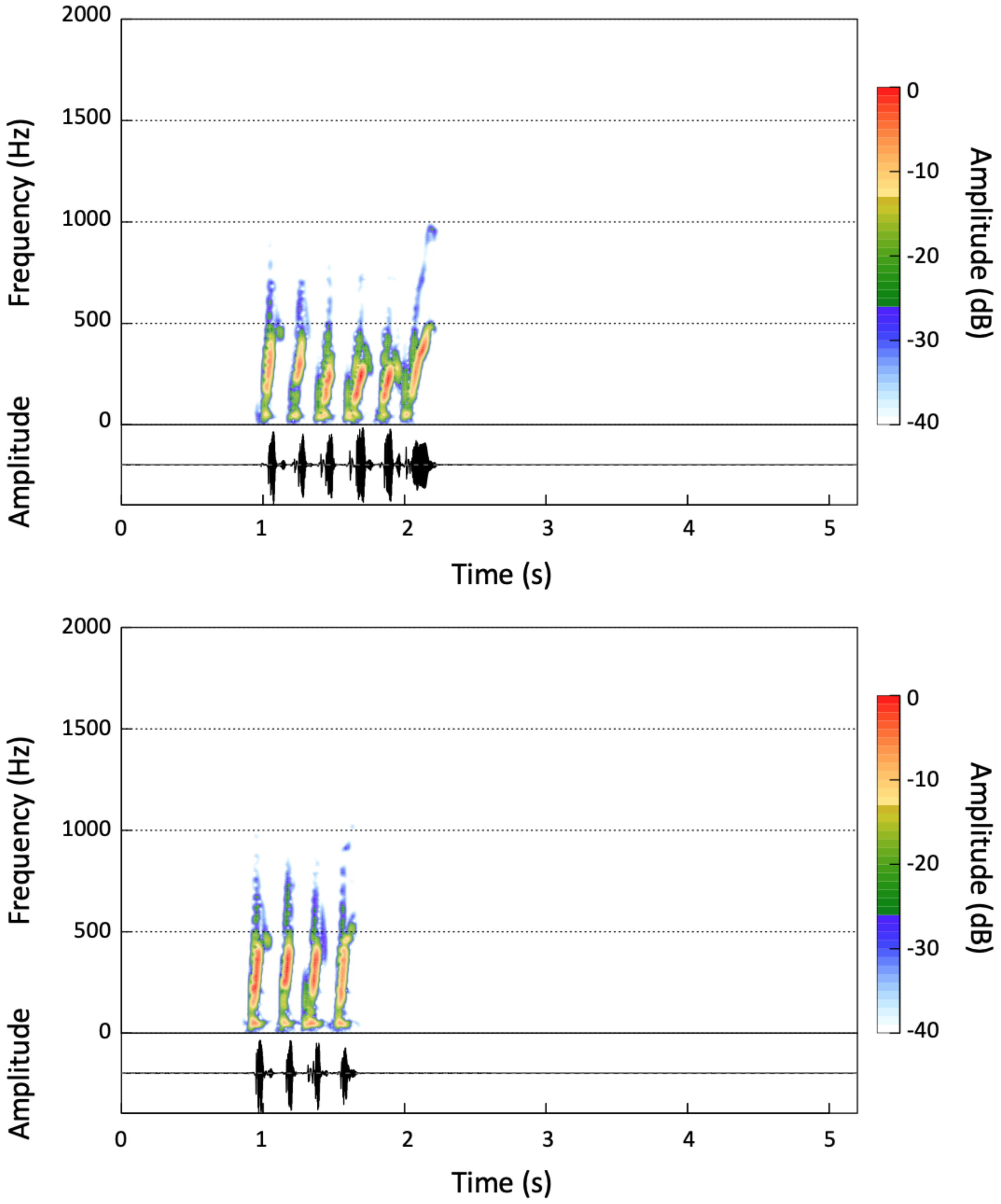


Figure 12. Two exemplars of the monk seal’s *whoop* vocalization, in typical series of six calls (upper panel) and four calls (lower panel). The spectrogram is shown above the waveform for each exemplar. Spectrogram settings: Hanning window, window length: 4096 points, 90% overlap.

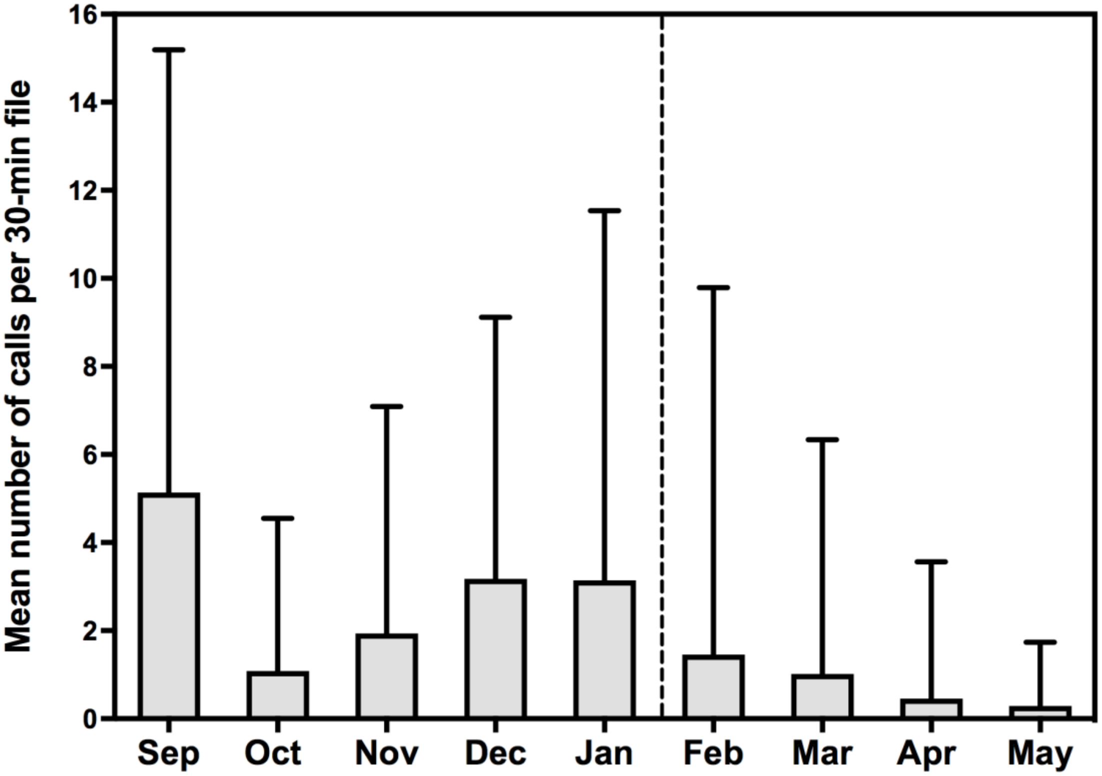


Figure 13. Mean + SD of calls produced by the Hawaiian monk seal per 30-min file per month. All months include 96 30-min files (4 days) except December and March, which include 120 30-min files (5 days). The dotted line separates the suspected breeding season from the molt and post-molt intervals. Blood testosterone levels, opportunistically sampled in September, December, February, and April were 210, 304, 53, and off scale (<20 ng/dL), respectively.

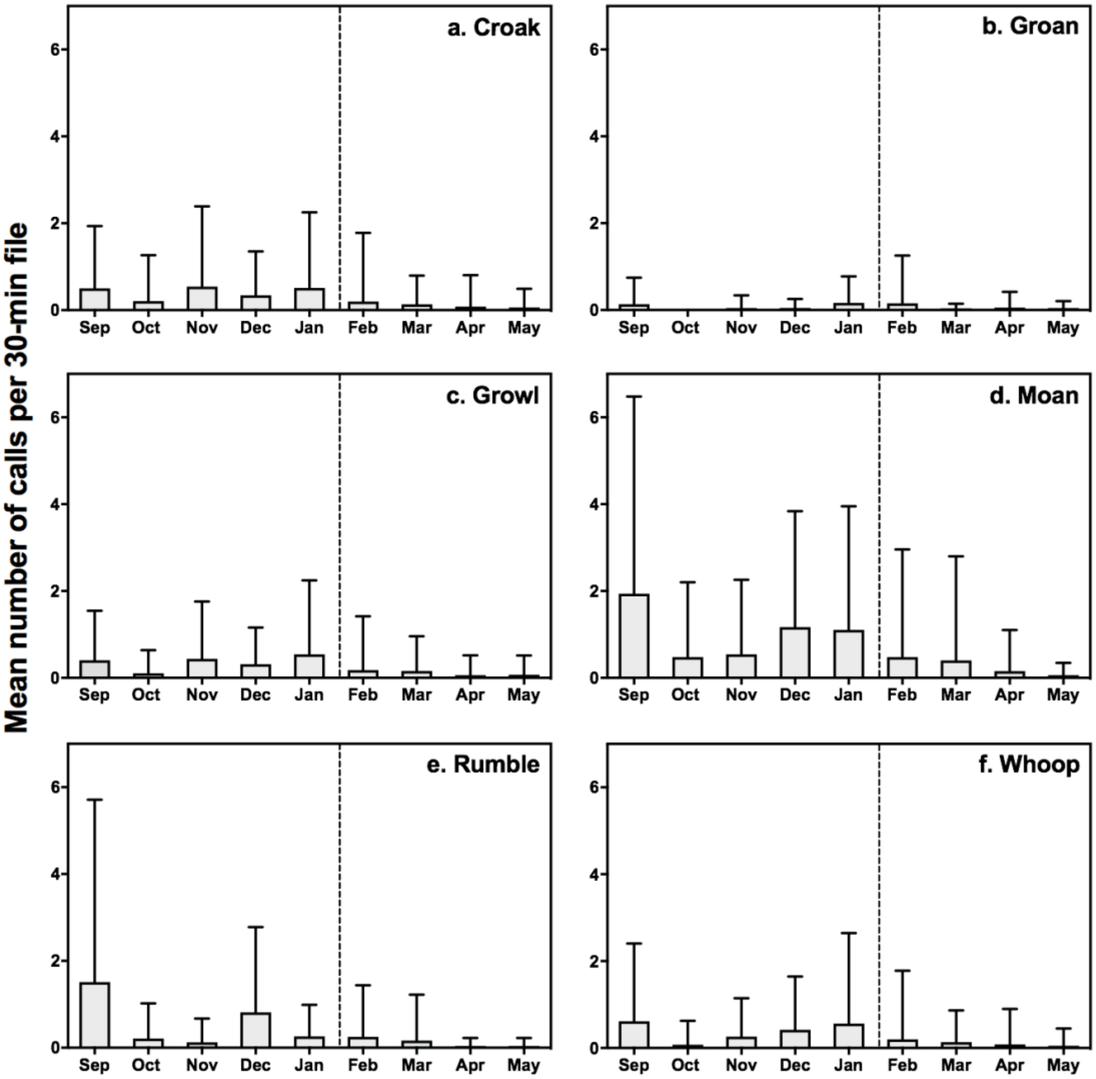


Figure 14. Mean + SD of each call type produced by the Hawaiian monk seal per 30 min file for 9 months. All months include 96 30-min files (4 days) except December and March, which include 120 30-min files (5 days). Plot c includes all *growls* and *gurgles* produced during the 9-month study period. Plot d includes all three *moan* types produced during the 9-month study period. Dotted lines separate the suspected breeding season from molt and post-molt interval.

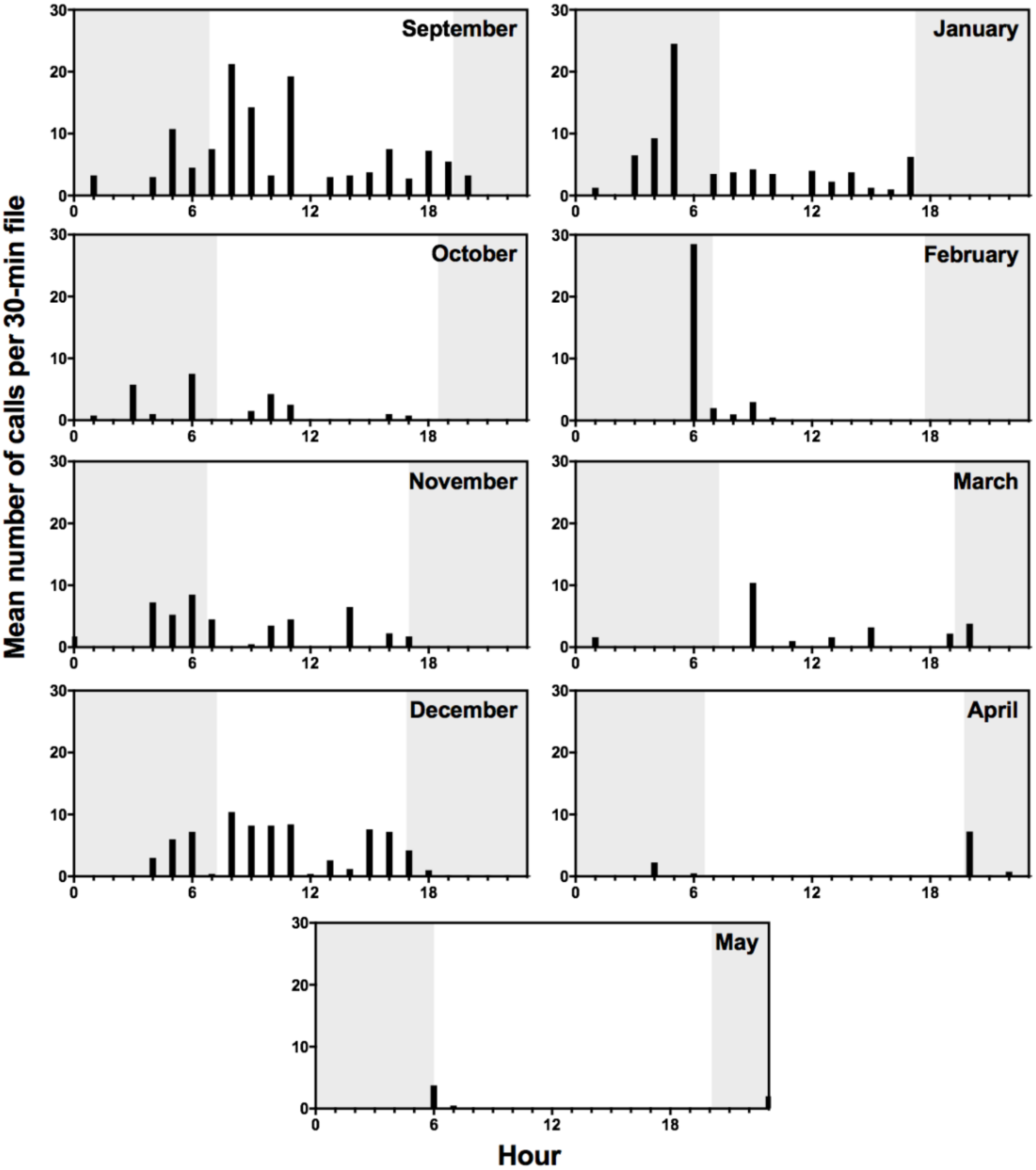


Figure 15. Mean number of calls produced by the Hawaiian monk seal per 30-min file for 9 months binned in hourly intervals. All months include 96 30-min files (4 days) except December and March, which include 120 30-min files (5 days). Shaded regions represent nighttime; white regions represent daylight, based on local photoperiod at the mid-point of each month.

Discussion

Male Hawaiian monk seals possess an underwater vocal repertoire of at least six call types, as shown in the present study of a single individual. The recordings of underwater sound production presented here are the first available for the species, confirming sparse anecdotal observations suggesting a role for acoustic signaling in monk seal underwater social communication (Stirling & Thomas 2003).

The underwater vocal repertoire of the male monk seal identified as *Kekoa* included *croaks*, *groans*, *growls*, *moans*, *rumbles*, and *whoops*, with *ascending* and *descending moans* and *roars* as potential (but rarely encountered) call types. The observed vocalizations were uniformly low in frequency content. Only a few vocalizations contained energy exceeding 1000 Hz. Sounds with tonal qualities or harmonics (*moans, groans*) had fundamental frequencies less than 80 Hz, and all calls had peak frequencies below 400 Hz. The spectral features of the six primary vocalizations produced by this individual suggest that Hawaiian monk seals rely on low-frequency signals to communicate under water. Notably, these findings are incompatible with the measured hearing ability of a single Hawaiian monk seal reported by Thomas and collegues (1990); this study suggested that monk seals would be insensitive to sound frequencies below 8 kHz in water. Additional research to clarify the relationship between call characteristics and sound reception abilities in this species is ongoing at the University of California Santa Cruz (J.M. Sills, personal communication).

Three of *Kekoa's* underwater vocalizations closely resemble airborne vocalizations reported for wild Hawaiian monk seals during the reproductive season (Miller & Job 1992). These underwater calls include the *whoop*, *croak*, and *growl*, which Miller and Job (1992) refer to as the *bubble*, *guttural expiration*, and *roar*, respectively, when these sounds are produced on shore. These calls had similar frequency and duration characteristics whether recorded above or below the water's surface, which suggests that these signal types can be produced amphibiously. Additionally, the qualitative description of *rolling bellows* emitted by adult male monk seals attending females hauled out on beaches (Kenyon & Rice 1959, Johnson & Johnson 1984), is comparable to *Kekoa*'*s groan* vocalization produced in water. We did not record a vocalization in water similar to the airborne *belch-cough* described for adult and sub-adult male seals (Miller & Job 1992).

While the present study emphasized the year-round underwater vocalizations emitted by this Hawaiian monk seal in water, the audio-video recording system also detected vocalizations produced in air while the seal was resting on deck. *Kekoa* produced aerial vocalizations frequently, during every month of the nine-month study period. Each of the six main sound types produced in water were also produced by this monk seal while resting on land. One vocalization emitted solely in air was a pulsed humming sound produced in bouts that typically lasted between 5 and 30 seconds (range: 1 single pulse emitted alone to 1 min 28 s of continuous humming). During emission of this sound, the seal's throat area visibly pulsated with each hum and no exhalation was observed. This nearly continuous, low-frequency, low-amplitude vocalization was similar to the *huh-huhs* produced by wild female monk seals while nursing their pups on shore or prior to giving birth (Miller & Job 1992).

Underwater vocalizations produced by the seal exhibited a seasonal pattern. High vocalization rates were observed from September through January, with a sharp decline in February and continued depression through the end of the study period in May. This pattern suggests a protracted interval of underwater acoustic behavior for this species. Other aquatically mating seals from the monachinae lineage—including the Antarctic Weddell seal (*Leptonychotes weddelli*; Thomas et al. 1987, Green & Burton 1988), leopard seal (Thomas & DeMaster 1982, Rogers et al. 1995, 1996, Van Opzeeland et al. 2010), and Ross seal (*Ommatophoca rossii*; Van Opzeeland et al. 2010)—tend to call under water during their respective 2-3 month breeding seasons (Riedman 1990). Additionally, an increase in underwater vocal behavior during the breeding season has been reported for several seals from the phocinae lineage, including the temperate-breeding harbor seal (Van Parijs et al. 1999, Reichmuth & Schusterman 2009), and the Arctic bearded (Van Parijs et al. 2001) and ringed seals, (*Pusa hispida*; Stirling 1973, Calvert & Stirling 1985). The extended interval of increased calling behavior presumably related to reproduction in this monk seal (> 5 months per year) appears to meet or exceed that reported for both temperate and polar species.

There was an observed relationship between underwater calling rates and reproductive hormones in this Hawaiian monk seal. *Kekoa*'*s* blood testosterone values were at least 4-fold higher in September and December compared to values during and following the annual molt in February and April, respectively. These findings are consistent with hormonal profiles reported by Atkinson and Gilmartin (1992) for four captive Hawaiian monk seals, which showed that testosterone levels peaked six months prior to the annual molt and were lowest in the month following the annual molt. *Kekoa*'*s* calling rates in September and December were at least double those observed in February and April. The simultaneous elevations in both vocal behavior and blood testosterone values preceding the molt, even in the absence of male and female conspecifics, suggest a strong hormonal component in sound production. This is unsurprising given that the calling rates of males vary with reproductive hormones in other pinnipeds including the Weddell seal (Bartsh et al. 1992), the Australian fur seal (*Arctocephalus pusillus*; Tripovich et al. 2009), and the Pacific walrus (*Odobenus rosmarus*; Hughes et al. 2011). As circulating testosterone values increase during breeding seasons for most mammals (Lincoln & Short 1980), heightened vocal behavior and testosterone levels for at least five months prior to *Kekoa*'*s* molt support a prolonged breeding season extending from September (or earlier) through January for this individual.

At a population level, the Hawaiian monk seal breeding season has been reported to extend over at least a nine-month interval (Miller & Job 1992) with breeding occurring throughout the year (Johnson & Johnson 1984) and peaking in summertime (Riedman 1990). The Hawaiian monk seal *Kekoa*, who was housed in temperate California, displayed seasonal physiological cycles that were offset from those of tropical captive seals housed at Sea Life Park in Oahu, Hawaii (Atkinson & Gilmartin 1992); however, the relationship between these cycles and the sustained period of elevated underwater sound production suggests an expected within-individual annual pattern. The offset in his physiological cycles may be attributed to his captive setting in a temperate environment or, alternatively, sexually mature monk seals may exhibit individual variation in seasonal patterns of breeding behavior. Their tropical, aseasonal climate in the Hawaiian archipelago allows female seals to give birth throughout the year, unlike Arctic and Antarctic phocids who are constrained by rapidly changing environmental conditions. Consequently, males may display variability in vocalization rates during extended, individually-timed reproductive seasons.

The moderate size of *Kekoa*'*s* underwater vocal repertoire, compared to that of other pinnipeds, provides insight into reproductive behavior in this species. Stirling and Thomas (2003) categorized the Hawaiian monk seal mating system as having a likely pattern of serial monogamy, based in part on available knowledge of acoustic communication. At the time of their study, only two underwater calls had been anecdotally described for the species. In serially monogamous seals, where females and male competitors are mostly dispersed in space and time, a small vocal repertoire may be sufficient to attract a breeding partner or deter a competitor. Alternatively, in highly polygynous species where receptive females and male competitors aggregate during a short reproductive season, dominant males may require a larger vocal repertoire or complex vocalizations to compete with rival males or for attention from females. Rogers (2003) further suggested that repertoire size in phocids is primarily driven by dispersed or unpredictable access to estrous females. Within these comparative frameworks, *Kekoa*'*s* underwater vocal repertoire of at least six discrete calls suggests a moderate species-typical level of polygyny, relative, for example, to crabeater seals (*Lobodon carcinophaga*) that exhibit low levels of competition for individual females and produce only one aquatic call during a brief breeding season (Stirling & Siniff 1979, Thomas & DeMaster 1982, McCreery & Thomas 2009), and harp seals that are highly promiscuous in dense herds and produce an underwater repertoire of more than 18 discrete call types during a brief breeding season (Terhune & Ronald 1986, Terhune 1994, Perry & Terhune 1999, Serrano 2001). Monk seals have a markedly longer breeding season than other phocid species, during which females are not densely grouped or synchronized in their estrous cycles. Thus, the moderate underwater repertoire of male Hawaiian monk seals supports the view that males serially compete for access to females that come into estrous asynchronously (Kenyon & Rice 1959) and further indicates that underwater social behavior including acoustic communication is a key component of reproductive behavior.

To verify these initial findings with one mature male seal, additional studies should be conducted with other monk seals living in human care to confirm the suspected bias of age and sex in calling behavior; score year-round vocal activity; and assess individual variation in seasonal patterns of vocal behavior, reproductive hormones, and molt. In order to estimate functional communication ranges for different vocal signals, it is also necessary to measure and report call source levels so that probable transmission distances in typical environmental noise can be calculated. Furthermore, documenting the behavioral patterns associated with each vocal type in captive individuals would be beneficial. This practical approach would provide information about context and timing of vocal behavior, and highlight some of the behavioral components associated with different vocal types and the onset and termination of breeding season. Documenting individual behavior, even in atypical environmental or social situations, can clarify our understanding of species-typical reproductive biology, which could in turn guide more targeted field studies of wild populations.

In other marine mammal species, knowledge of typical vocal behavior has been used to document temporal and spatial distribution patterns (e.g., Van Parijs et al. 1999, 2001, MacIntyre et al. 2013), estimate population abundance (e.g., Van Parijs et al. 2002, Marques et al. 2009, 2011, 2013, Küsel et al. 2011), and identify and describe the reproductive strategies and breeding seasons of various species through passive acoustic monitoring (e.g., Stirling & Thomas 2003, Van Parijs et al. 2003, 2004, 2009, Van Parijs & Clark 2006, Van Opzeeland et al. 2010). Passive acoustic monitoring offers an alternative, long-term sampling method for tracking wild populations when visual surveys are difficult to perform due to location, weather, or costs (Mellinger et al. 2007, Marques et al. 2013). The efficient transmission of sound in water can enable the acoustic presence of many species to be detected from towed hydrophone arrays (e.g., Clark & Fristrup 1997, Akamatsu et al. 2001, Oswald et al. 2003, Rankin et al. 2008, Li et al. 2009), fixed moorings (e.g., Marques et al. 2011, MacIntyre et al. 2013, Charrier et al. 2017), underwater autonomous vehicles including gliders (e.g., Baumgartner & Fratantoni 2008), and acoustic tags deployed onto individual animals (e.g., Johnson & Tyack 2003, Van Parijs et al. 2009, Fregosi et al. 2016). The results of our preliminary study suggest that Hawaiian monk seals may be a candidate species for passive acoustic monitoring applications, as males are vocal for a large portion of the year and certain sound types contain repeating and stereotyped spectral and temporal features that could be detected automatically (e.g., *whoops*). However, the low-frequency nature of their vocal repertoire will likely present advantages and challenges for passive acoustics; while low-frequency sounds propagate for long distances under water, allowing for increased probability of detecting vocalizing animals, there is also more ambient noise present at low frequencies in water (Richardson et al. 1995), making some calls types (e.g., *growl*, *croak*) more difficult to detect. The foundational knowledge concerning acoustic behavior gained from this study and subsequent studies can inform passive acoustic monitoring efforts and may support development of long-term passive acoustic recorders and acoustic algorithms capable of detecting wild Hawaiian monk seals in remote habitats. Such advances would enable improved monitoring of wild individuals in sensitive habitats and during reproductive periods, and therefore, have the potential to provide much needed information to mitigate the effects of disturbance on these endangered seals.

In conclusion, this opportunistic study on the vocal behavior of a single male Hawaiian monk seal reveals that *Neomonachus schauinslandi* does in fact produce underwater vocalizations. This male monk seal possessed a vocal repertoire of at least six different underwater call types and was vocally active in all nine months of the study. The extended seasonal pattern of heightened vocal behavior observed suggests a prolonged breeding season spanning at least five months. Such an extended annual breeding season promotes the probability that one male monk seal can mate with multiple females, reinforcing a polygynous mating system. Elevated blood testosterone values concurrent with increased vocal behavior confirms that underwater acoustic communication in this species is related to reproduction in male seals. The fundamental knowledge gained through this study establishes a foundation for future research on the vocal behavior of captive and wild Hawaiian monk seals, and supports planning for conservation and management actions including those based on passive acoustic monitoring.

Bibliography

Akamatsu T, Wang D, Wang K, Wei Z (2001) Comparison between visual and passive acoustic detection of finless porpoises in the Yangtze River, China. J Acoust Soc Am 109:1723–1727

Atkinson S, Gilmartin WG (1992) Seasonal testosterone pattern in Hawaiian monk seals (*Monachus schauinslandi*). J Reprod Fertil 96:35–39

Awbrey FT, Thomas JA, Evans WE (2004) Ultrasonic Underwater Sounds from a Captive Leopard Seal (*Hydrurga leptonyx*). In: Thomas JA, Moss CF, Vater M (eds) Echolocation in Bats and Dolphins. The University of Chicago Press, Chicago, IL, p 535–541

Bartsh SS, Johnston SD, Siniff DB (1992) Territorial behavior and breeding frequency of male Weddell seals (*Leptonychotes weddelli*) in relation to age, size, and concentrations of serum testosterone and cortisol. Can J Zool 70:680–692

Baumgartner MF, Fratantoni DM (2008) Diel periodicity in both sei whale vocalization rates and the vertical migration of their copepod prey observed from ocean gliders. Limnol Oceanogr 53:2197–2209

Beier JC, Wartzok D (1979) Mating behaviour of captive spotted seals (*Phoca largha*). Anim Behav 27:772–781

Berta A, Churchill M (2012) Pinniped taxonomy: Review of currently recognized species and subspecies, and evidence used for their description. Mamm Rev 42:207–234

Calvert W, Stirling I (1985) Winter distribution of ringed seals (*Phoca hispida*) in the Barrow Strait area, Northwest Territories, determined by underwater vocalizations. Can J Fish Aquat Sci 42:1238–1243

Carretta JV, Forney KA, Oleson EM, Weller DW, Lang AR, Baker J, Muto MM, Hanson B, Orr AJ, Huber H, Lowry MS, Barlow J, Moore JE, Lynch D, Carswell L, Brownell Jr RL (2017) U.S. Pacific Marine Mammal Stock Assessments: 2016.

Casey C, Charrier I, Mathevon N, Reichmuth C (2015) Rival assessment among northern elephant seals: evidence of associative learning during male – male contests. R Soc Open Sci 2:1–19

Casey C, Sills J, Reichmuth C (2016) Source level measurements for harbor seals and implications for estimating communication space. Proc Meet Acoust 27:1–9

Charrier I, Marchesseau S, Dendrinos P, Tounta E, Karamanlidis AA (2017) Individual signatures in the vocal repertoire of the endangered Mediterranean monk seal : new perspectives for population monitoring. Endanger Species Res 32:459–470

Clark CW, Fristrup KM (1997) Whales ’95: A combined visual and acoustic survey of blue and fin whales off southern California. Rep Int Whal Comm 47:583–600

Davies CE, Kovacs KM, Lydersen C, Parijs SM Van (2006) Development of display behavior in young captive bearded seals. Mar Mammal Sci 22:952–965

Fregosi S, Klinck H, Horning M, Costa DP, Mann D, Sexton K, Hückstädt LA, Mellinger DK, Southall BL (2016) An animal-borne active acoustic tag for minimally invasive behavioral response studies on marine mammals. Anim Biotelemetry 4:1–15

Galimberti F, Sanvito S, Boitani L (2000) Marking of southern elephant seals with passive integrated transponders. Mar Mammal Sci 16:500–504

Gilmartin WG, Forcada J (2002) Monk Seals. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press, Inc., San Diego, CA, p 756–759

Green K, Burton HR (1988) Annual and diurnal variations in the underwater vocalizations of Weddell seals. Polar Biol 8:161–164

Hughes WR, Reichmuth C, Mulsow JL, Larsen ON (2011) Source characteristics of the underwater knocking displays of a male Pacific walrus (*Odobenus rosmarus divergens*). In: 161st Meeting of the Acoustical Society of America.p 2506

Job DA, Boness DJ, Francis JM (1995) Individual variation in nursing vocalizations of Hawaiian monk seal pups, *Monachus schauinslandi* (Phocidae, Pinnipedia), and lack of maternal recognition. Can J Zool 73:975–983

Johnson BW, Johnson PA (1984) Observations of the Hawaiian monk seal on Laysan Island from 1977 through 1980. NOAA Technical Memorandum NMFS-SWFC-049

Johnson MP, Tyack PL (2003) A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE J Ocean Eng 28:3–12

Kenyon KW, Rice DW (1959) Life History of the Hawaiian monk seal. Pacific Sci 13:215–252

Khan CB, Markowitz H, McCowan B (2006) Vocal development in captive harbor seal pups, *Phoca vitulina richardii* : Age, sex, and individual differences. J Acoust Soc Am 120:1684–1694

Küsel ET, Mellinger DK, Thomas L, Marques TA, Moretti DJ, Ward J (2011) Cetacean population density estimation from single fixed sensors using passive acoustics. J Acoust Soc Am 129:3610–3622

Li S, Akamatsu T, Wang D, Wang K (2009) Localization and tracking of phonating finless porpoises using towed stereo acoustic data-loggers. J Acoust Soc Am 126:468–475

Lincoln GA, Short R V. (1980) Seasonal breeding: nature's contraceptive. In: Proceedings of the 1979 Laurentian Hormone Conference.p 1–52

MacIntyre KQ, Stafford KM, Berchok CL, Boveng PL (2013) Year-round acoustic detection of bearded seals (*Erignathus barbatus*) in the Beaufort Sea relative to changing environmental conditions, 2008-2010. Polar Biol 36:1161–1173

Marques TA, Thomas L, Ward J, DiMarzio N, Tyack PL (2009) Estimating cetacean population density using fixed passive acoustic sensors: an example with Blainville's beaked whales. J Acoust Soc Am 125:1982–1994

Marques TA, Munger L, Thomas L, Wiggins S, Hildebrand JA (2011) Estimating north pacific right whale (*Eubalaena japonica*) density using passive acoustic cue counting. Endanger Species Res 13:163–172

Marques TA, Thomas L, Martin SW, Mellinger DK, Ward JA, Moretti DJ, Harris D, Tyack PL (2013) Estimating animal population density using passive acoustics. Biol Rev 88:287–309

Mellinger D, Stafford K, Moore S, Dziak R, Matsumoto H (2007) An Overview of Fixed Passive Acoustic Observation Methods for Cetaceans. Oceanography 20:36–45

Mesnick SL, Ralls K (2002) Mating Systems. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press, Inc., San Diego, CA, p 726–733

Miller EH, Job DA (1992) Airborne Acoustic Communication in the Hawaiian Monk Seal, *Monachus schauinslandi*. In: Marine Mammal Sensory Systems.p 485–531

Muñoz G, Karamanlidis AA, Dendrinos P, Thomas JA (2011) Aerial vocalizations by wild and rehabilitating Mediterranean monk seals (*Monachus monachus*) in Greece. Aquat Mamm 37:262–279

National Marine Fisheries Service (2007) Recovery Plan for the Hawaiian Monk Seal (*Monachus Schauinslandi*). Second Revision. Silver Spring, MD

Oswald JN, Barlow J, Norris TF (2003) Acoustic identification of nine delphinid species in the eastern tropical Pacific Ocean. Mar Mammal Sci 19:20–37

Pacific Islands Fisheries Science Center (2018) What's the Latest on Hawaiian Monk Seals? NOAA Fisheries

Perry EA, Terhune JM (1999) Variation of harp seal (*Pagophilus groenlandicus*) underwater vocalizations among three breeding locations. J Zool 249:181–186

Ralls K, Fiorelli P, Gish S (1985) Vocalizations and vocal mimicry in captive harbor seals, *Phoca vitulina*. Can J Zool 63:1050–1056

Rankin S, Oswald JN, Barlow J (2008) Passive acoustic methods for population studies. Can Acoust 36:88–92

Reichmuth C, Schusterman RJ (2009) Annual temporal patterning in the vocalizations of captive seals: Two long-term case studies. In: 157th Meeting of the Acoustical Society of America.p 2676–2677

Richardson JW, Charles R. Greene J, Malme CI, Thomson DH (1995) Marine Mammals and Noise. Academic Press, Inc., San Diego, CA

Riedman M (1990) The Pinnipeds: Seals, Sea Lions, and Walruses. University of California Press, Ltd., Berkeley, CA

Rogers TL, Cato DH, Bryden MM (1995) Underwater vocal repertoire of the leopard seal (H*ydrurga leptonyx*) in Prydz Bay, Antarctica. In: Kastelein RA, Thomas JA, Nachtigall PE (eds) Sensory Systems of Aquatic Mammals. De Spil Publishers, Woerden, Netherlands, p 223–236

Rogers TL, Cato DH, Bryden MM (1996) Behavioral Significance of Underwater Vocalizations of Captive Leopard Seals, *Hydurga Leptonyx*. Mar Mammal Sci 12:414–427

Sandegren FE (1976) Agonistic behavior in the male northern elephant seal. Behaviour 57:136–157

Sanvito S, Galimberti F, Miller EH (2007) Vocal signalling of male southern elephant seals is honest but imprecise. Anim Behav 73:287–299

Sanvito S, Galimberti F, Miller EH (2008) Development of Aggressive Vocalizations in Male Southern Elephant Seals (*Mirounga leonina*): Maturation or Learning? Behaviour 145:137–170

Scheel DM, Slater GJ, Kolokotronis SO, Potter CW, Rotstein DS, Tsangaras K, Greenwood AD, Helgen KM (2014) Biogeography and taxonomy of extinct and endangered monk seals illuminated by ancient DNA and skull morphology. Zookeys 409:1–33

Serrano A, Miller EH (2000) How vocal are harp seals (*Pagophilus groenlandicus*)? A captive study of seasonal and diel patterns. Aquat Mamm 26:253–259

Serrano A (2001) New underwater and aerial vocalizations of captive harp seals (*Pagophilus groenlandicus*). Can J Zool 79:75–81

Shipley C, Hines M, Buchwald JS (1986) Vocalizations of Northern Elephant Seal Bulls : Development of Adult Call Characteristics during Puberty. J Mammal 67:526–536

Southall BL, Finneran, JJ, Reichmuth C, Nachtigall PE, Ketten DR, Bowles AE, Ellison WT, Nowacek DP, Tyack PL (in press) Marine mammal noise exposure criteria: auditory weighting functions and TTS/PTS onset. Aquat Mamm

Stirling I (1973) Vocalization in the Ringed Seal (*Phoca hispida*). J Fish Res Board Canada 30:1592–1594

Stirling I, Siniff DB (1979) Underwater vocalizations of leopard seals (*Hydrurga leptonyx*) and crabeater seals (*Lobodon carcinophagus*) near the South Shetland Islands, Antarctica. Can J Zool 57:1244–1248

Stirling I, Thomas JA (2003) Relationships between underwater vocalizations and mating systems in phocid seals. Aquat Mamm 29:227–246

Terhune JM, Ronald K (1986) Distant and near-range functions of harp seal underwater calls. Can J Zool 64:1065–1070

Terhune JM (1994) Geographical variation of harp seal underwater vocalizations. Can J Zool 72:892–897

Thomas JA, DeMaster DP (1982) An acoustic technique for determining diurnal activities in leopard (*Hydrurga leptonyx*) and crabeater (*Lobodon carcinophagus*) seal. Can J Zool 60:2028–2031

Thomas JA, Ferm LM, Kuechle VB (1987) Silence as an anti-predation strategy by Weddell seals. Antarct J 22:232–234

Thomas J, Moore P, Withrow R, Stoermer M (1990) Underwater audiogram of a Hawaiian monk seal (*Monachus schauinslandi*). J Acoust Soc Am 87:417–420

Tripovich JS, Rogers TL, Dutton G (2009) Faecal testosterone concentrations and the acoustic behaviour of two captive male Australian fur seals. Aust Mammal 31:117–122

Van Parijs SM, Hastie GD, Thompson PM (1999) Geographical variation in temporal and spatial vocalization patterns of male harbour seals in the mating season. Anim Behav 58:1231–1239

Van Parijs SM, Kovacs KM, Lydersen C (2001) Spatial and Temporal Distribution of Vocalising Male Bearded Seals: Implications for Male Mating Strategies. Behaviour 138:905–922

Van Parijs SM, Smith J, Corkeron PJ (2002) Using calls to estimate the abundance of inshore dolphins: A case study with Pacific humpback dolphins *Sousa chinensis*. J Appl Ecol 39:853–864

Van Parijs SM (2003) Aquatic mating in pinnipeds: a review. Aquat Mamm 29:214–226

Van Parijs SM, Lydersen C, Kovacs KM (2003) Vocalizations and movements suggest alternative mating tactics in male bearded seals. Anim Behav 65:273–283

Van Parijs SM, Lydersen C, Kovacs KM (2004) Effects of ice cover on the behavioural patterns of aquatic-mating male bearded seals. Anim Behav 68:89–96

Van Parijs SM, Clark CW (2006) Long-term mating tactics in an aquatic-mating pinniped, the bearded seal, *Erignathus barbatus*. Anim Behav 72:1269–1277

Van Parijs SM, Clark CW, Sousa-Lima RS, Parks SE, Rankin S, Risch D, Opzeeland IC Van (2009) Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales. Mar Ecol Prog Ser 395:21–36

Van Opzeeland IC, Parijs SM Van, Bornemann H, Frickenhaus S, Kindermann L, Klinck H, Plötz J, Boebel O (2010) Acoustic ecology of Antarctic pinnipeds. Mar Ecol Prog Ser 414:267–291

Wartzok D, Ketten DR (1999) Marine Mammal Sensory Systems. In: Reynolds III JE, Rommel SA (eds) Biology of Marine Mammals. Smithsonian Institution Press, Washington, DC, p 117–175