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

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SANTA CRUZ

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

A thesis submitted in partial satisfaction
of the requirements for the degree of

MASTER OF SCIENCE

in

OCEAN SCIENCES

by

KIRBY PARNELL

June 2018

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is approved:

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Tyrus Miller
Vice Provost and Dean of Graduate Studies
# Table of Contents

List of Tables and Figures ........................................................................................................ iv

Abstract ....................................................................................................................................... vi

Acknowledgements ....................................................................................................................... vii

Introduction ................................................................................................................................. 1

Methods ....................................................................................................................................... 6

Subject ....................................................................................................................................... 6

Authorizations ............................................................................................................................. 7

Environment ............................................................................................................................... 7

Audio and Video Recording ......................................................................................................... 8

Acoustic Analyses ....................................................................................................................... 9

Results ......................................................................................................................................... 16

Underwater Vocal Repertoire ..................................................................................................... 16

Temporal Patterns in Vocal Behavior ......................................................................................... 21

Discussion .................................................................................................................................... 36

Bibliography ............................................................................................................................... 45
List of Tables and Figures

Methods

Figure 1: SoundTrap 300 STD acoustic recorder.................................................13
Figure 2: Still image extracted from the continuous video feed of the monk seal’s living enclosure.................................................................14
Table 1: Acoustic parameters measured for the Hawaiian monk seal’s vocalizations.................................................................15

Results

Figure 3: Scatterplot showing the cross-validated discriminant function analysis results for six different Hawaiian monk seal underwater vocal types...........22
Figure 4: Classification matrix showing the proportion of correctly classified call types from the cross-validated discriminant function analysis..............23
Figure 5: Spectrograms showing the Hawaiian monk seal’s underwater vocal repertoire of six vocalizations........................................24
Figure 6: Two exemplars of the monk seal’s typical vocal bouts......................25
Table 2: Mean (± SD) values of acoustic parameters measured for each of the six call types.............................................................26
Figure 7: Two spectrograms of the monk seal’s croak vocalization...............27
Figure 8: Two spectrograms of the monk seal’s groan vocalization...............28
Figure 9: Two spectrograms of the monk seal’s growl vocalization..............29
Figure 10: Two spectrograms of the monk seal’s moan vocalization.............30
Figure 11: Two spectrograms of the monk seal’s rumble vocalization..........31
Figure 12: Two spectrograms of the monk seal’s *whoop* vocalization..................32

Figure 13: Seasonal patterns in overall calling behavior.................................33

Figure 14: Seasonal patterns in calling behavior for each vocal type......................34

Figure 15: Diurnal patterns in overall calling behavior.....................................35
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.

My team (human and animals) at the Pinniped Lab has cheered me on through the finish line. They started as friends, but have turned into family. I have enjoyed working side-by-side with each and every one of them, especially while cleaning F7, dancing in fish house to Lil’ Jon, running the discrimination experiment every day, fleeing from wild elephant seals, playing dungeons and dragons, sitting with Sprouts, and celebrating the smallest victories. I am especially thankful for Jenna Sullivan, who took me under her wing and taught me how to clearly communicate with humans and animals. She has always been honest and open, and I thank her for becoming my biggest cheerleader. My roommate, Michelle, has never objected treats during stressful times. She made our house a home, listened to my endless daily struggles, encouraged me, watched numerous Netflix series with me, and ultimately made my time in Santa Cruz an unforgettable experience. I am grateful for the hard work and dedication my monk
seal team (Chloe, Taylor, and Vanessa) exhibited. I will cherish every teaching and learning moment we shared together in the purple office and in the compound while staring at Kekoa.

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.

My boyfriend, Tyler, has loved and supported me halfway across the country for the last five years. In our busy lives full of sports and school, he has somehow managed to tolerate my absence and dedication to academia. Tyler has accepted and embraced my interests in marine mammals and conservation, and has encouraged me to pursue them, no matter the distance between us.

I am grateful to the Gates Millennium Scholarship Program, the Dr. Earl and Ethel Myers Oceanographic and Marine Biology Trust, the Friends of Seymour Marine Discovery Center, and the Navy’s Living Marine Resources Program for their financial support.
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. 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 (*Doryteuthis 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 µPa²/Hz at 80 Hz to approximately 67 dB re 1 µPa²/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.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Abbreviation</th>
<th>Category</th>
<th>Unit</th>
<th>View</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Duration</td>
<td>DUR</td>
<td>temporal</td>
<td>s</td>
<td>waveform</td>
<td>duration of the complete call</td>
</tr>
<tr>
<td>Duration 90%</td>
<td>DUR90</td>
<td>temporal</td>
<td>s</td>
<td>spectrogram</td>
<td>duration of the call that contains 90% of the total energy</td>
</tr>
<tr>
<td>Center Frequency</td>
<td>$F_{\text{center}}$</td>
<td>spectral</td>
<td>Hz</td>
<td>spectrum</td>
<td>frequency that divides the call into two frequency intervals of equal energy</td>
</tr>
<tr>
<td>1st and 3rd Quartile Frequency</td>
<td>Q1, Q3</td>
<td>spectral</td>
<td>Hz</td>
<td>spectrum</td>
<td>frequencies that bound the spectrum between 25% and 75% of the call’s energy</td>
</tr>
<tr>
<td>Inter-quartile Range Bandwidth</td>
<td>IQR BDW</td>
<td>spectral</td>
<td>Hz</td>
<td>spectrum</td>
<td>span between the 1st and 3rd quartile frequencies</td>
</tr>
<tr>
<td>90% Bandwidth Upper/Lower Bounds</td>
<td>F5, F95</td>
<td>spectral</td>
<td>Hz</td>
<td>spectrum</td>
<td>frequencies that bound the spectrum between 5% and 95% of the call’s energy</td>
</tr>
<tr>
<td>90% Bandwidth BDW90</td>
<td>spectral</td>
<td>Hz</td>
<td>spectrum</td>
<td>the difference between the 5% and 95% frequencies</td>
<td></td>
</tr>
<tr>
<td>Peak Frequency</td>
<td>$F_{\text{peak}}$</td>
<td>spectral</td>
<td>Hz</td>
<td>spectrum</td>
<td>frequency of maximum power</td>
</tr>
<tr>
<td>3 dB Bandwidth Upper/Lower Bounds</td>
<td>BDW3UL, BDW3LL</td>
<td>spectral</td>
<td>Hz</td>
<td>spectrum</td>
<td>frequencies that bound the spectrum 3 dB below the peak power</td>
</tr>
<tr>
<td>5 dB Bandwidth BDW3</td>
<td>spectral</td>
<td>Hz</td>
<td>spectrum</td>
<td>span between the BDW3UL and the BDW3LL</td>
<td></td>
</tr>
<tr>
<td>10 dB Bandwidth Upper/Lower Bounds</td>
<td>BDW10UL, BDW10LL</td>
<td>spectral</td>
<td>Hz</td>
<td>spectrum</td>
<td>frequencies that bound the spectrum 10 dB below the peak power</td>
</tr>
<tr>
<td>10 dB Bandwidth BDW10</td>
<td>spectral</td>
<td>Hz</td>
<td>spectrum</td>
<td>span between the BDW10UL and the BDW10LL</td>
<td></td>
</tr>
<tr>
<td>Aggregate Entropy</td>
<td>AE</td>
<td>spectral</td>
<td>bits</td>
<td>spectrum</td>
<td>the disorder in a sound measured from the energy distribution within a call</td>
</tr>
<tr>
<td>* Pulse Duration</td>
<td>PD</td>
<td>temporal</td>
<td>s</td>
<td>waveform</td>
<td>duration of an individual pulse in a series measured with a common detection threshold</td>
</tr>
<tr>
<td>* Inter-Pulse Interval</td>
<td>IPI</td>
<td>temporal</td>
<td>s</td>
<td>waveform</td>
<td>interval between the beginnings of consecutive pulses in a series</td>
</tr>
<tr>
<td>* Number of Pulses or Calls</td>
<td>$P_n$</td>
<td>descriptive</td>
<td>-</td>
<td>waveform</td>
<td>total number of pulses in a series</td>
</tr>
<tr>
<td>* Pulse or Call Rate</td>
<td>PR</td>
<td>temporal</td>
<td>Hz</td>
<td>waveform</td>
<td>number of pulses per second from the start of first pulse to start of last pulse</td>
</tr>
<tr>
<td>* Presence or Absence of Harmonics</td>
<td>HarmonicsA</td>
<td>descriptive</td>
<td>-</td>
<td>spectrogram spectrum</td>
<td>present if call contained harmonics; absent if call did not contain harmonics</td>
</tr>
<tr>
<td>* Number of Harmonics</td>
<td>Harmonics</td>
<td>descriptive</td>
<td>-</td>
<td>spectrogram spectrum</td>
<td>number of harmonics counted in the spectrogram and verified in the spectrum</td>
</tr>
<tr>
<td>* Fundamental Frequency</td>
<td>$F_0$</td>
<td>spectral</td>
<td>Hz</td>
<td>spectrum</td>
<td>the lowest frequency of the call</td>
</tr>
</tbody>
</table>
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\(_{\text{peak}}\): 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 (F0: 59 Hz ± 18), and contain more harmonics (Harmn: 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 (Fpeak: 48 Hz ± 18), tonal calls that have a lower fundamental frequency (F0: 37 Hz ± 6) and fewer harmonics than *groans* (Harmn: 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 (Fpeak: 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 (Pn: 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 (Fpeak: 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.
**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.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Croak n = 20</th>
<th>Groan n = 11</th>
<th>Growl n = 40</th>
<th>Moan n = 40</th>
<th>Rumble n = 20</th>
<th>Whoop n = 20</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Duration (s)</td>
<td>0.28 ± 0.06</td>
<td>1.23 ± 0.86</td>
<td>3.26 ± 1.36</td>
<td>0.58 ± 0.31</td>
<td>2.75 ± 1.69</td>
<td>0.14 ± 0.04</td>
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<td>Duration 90% (s)</td>
<td>0.18 ± 0.06</td>
<td>1.02 ± 0.8</td>
<td>2.07 ± 0.85</td>
<td>0.44 ± 0.24</td>
<td>2.26 ± 1.32</td>
<td>0.07 ± 0.02</td>
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<td>Center Frequency (Hz)</td>
<td>264 ± 81</td>
<td>142 ± 107</td>
<td>291 ± 47</td>
<td>53 ± 15</td>
<td>63 ± 21</td>
<td>190 ± 75</td>
</tr>
<tr>
<td>1st and 3rd Quartile Frequency (Hz)</td>
<td>211 ± 78</td>
<td>102 ± 51</td>
<td>229 ± 40</td>
<td>39 ± 10</td>
<td>48 ± 13</td>
<td>154 ± 64</td>
</tr>
<tr>
<td>Inter-quartile Range Bandwidth (Hz)</td>
<td>110 ± 63</td>
<td>91 ± 99</td>
<td>118 ± 27</td>
<td>27 ± 13</td>
<td>36 ± 24</td>
<td>64 ± 52</td>
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<td>90% Bandwidth Upper/Lower Bounds (Hz)</td>
<td>406 ± 87</td>
<td>281 ± 179</td>
<td>436 ± 53</td>
<td>88 ± 20</td>
<td>131 ± 52</td>
<td>298 ± 113</td>
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<td>90% Bandwidth (Hz)</td>
<td>271 ± 115</td>
<td>224 ± 174</td>
<td>335 ± 47</td>
<td>59 ± 19</td>
<td>98 ± 48</td>
<td>209 ± 118</td>
</tr>
<tr>
<td>Peak Frequency (Hz)</td>
<td>258 ± 112</td>
<td>150 ± 139</td>
<td>292 ± 67</td>
<td>48 ± 18</td>
<td>57 ± 23</td>
<td>193 ± 90</td>
</tr>
<tr>
<td>3 dB Bandwidth Upper/Lower Bounds (Hz)</td>
<td>274 ± 116</td>
<td>165 ± 148</td>
<td>328 ± 75</td>
<td>56 ± 18</td>
<td>75 ± 26</td>
<td>220 ± 96</td>
</tr>
<tr>
<td>3 dB Bandwidth (Hz)</td>
<td>31 ± 15</td>
<td>26 ± 24</td>
<td>71 ± 38</td>
<td>15 ± 2</td>
<td>37 ± 22</td>
<td>58 ± 49</td>
</tr>
<tr>
<td>10 dB Bandwidth Upper/Lower Bounds (Hz)</td>
<td>325 ± 124</td>
<td>183 ± 166</td>
<td>438 ± 44</td>
<td>78 ± 19</td>
<td>119 ± 41</td>
<td>244 ± 106</td>
</tr>
<tr>
<td>10 dB Bandwidth (Hz)</td>
<td>121 ± 73</td>
<td>70 ± 75</td>
<td>284 ± 74</td>
<td>46 ± 18</td>
<td>94 ± 38</td>
<td>116 ± 60</td>
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<tr>
<td>Aggregate Entropy (bits)</td>
<td>4.2 ± 0.7</td>
<td>3.3 ± 1.1</td>
<td>4.9 ± 0.2</td>
<td>2.3 ± 0.4</td>
<td>3.1 ± 0.5</td>
<td>3.8 ± 0.7</td>
</tr>
<tr>
<td>* Pulse Duration (s)</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>0.01 ± 0.00</td>
<td>-</td>
</tr>
<tr>
<td>* Inter-Pulse Interval (s)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.07 ± 0.03</td>
<td>0.14 ± 0.07</td>
</tr>
<tr>
<td>* Number of Pulses or Calls</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>38 ± 22</td>
<td>4 ± 1</td>
</tr>
<tr>
<td>* Pulse or Call Rate (Hz)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>14.9 ± 3.5</td>
<td>4.1 ± 1.0</td>
</tr>
<tr>
<td>* Presence or Absence of Harmonics</td>
<td>Absent</td>
<td>Present</td>
<td>Absent</td>
<td>Present</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>* Number of Harmonics</td>
<td>-</td>
<td>11 ± 6</td>
<td>-</td>
<td>7 ± 3</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>* Fundamental Frequency (Hz)</td>
<td>-</td>
<td>59 ± 18</td>
<td>-</td>
<td>37 ± 6</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
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 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 underwater. Notably, these findings are incompatible with the measured hearing ability of a single Hawaiian monk seal reported by Thomas and colleagues (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 rossi*; 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


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


