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Publication Date

2025

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

ACOUSTIC BIOLOGY OF HAWAIIAN MONK SEALS

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

DOCTOR OF PHILOSOPHY

in

OCEAN SCIENCES

by

Brandi Ruscher

March 2025

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ACOUSTIC BIOLOGY OF HAWAIIAN MONK SEALS

Brandi Ruscher

Abstract

Like other marine mammals, True seals (Family Phocidae) rely on acoustic cues for orientation, communication, and prey and predator detection. Because of their amphibious life histories, the auditory systems of seals must operate efficiently both in air and water—environments with very different physical characteristics. While all seals exhibit common evolutionary traits related to hearing, the extent of auditory adaptations varies between phylogenetic lineages and, in some cases, may differ among species. The functional significance of these differences remains to be resolved. The most complete dataset describing amphibious hearing in seals is for the Phocinae subfamily (most temperate and polar phocid species of the Northern Hemisphere). There are few hearing data available for seals from the Monachinae subfamily (the Southern Ocean seals, monk seals, and elephant seals). However, the limited evidence suggests potential subfamily-level differences in hearing. Additional audiometric measurements are needed within the Monachinae lineage of seals to inform our understanding of auditory adaptations from an evolutionary perspective.

The first two chapters of this dissertation aim to expand knowledge of amphibious hearing in seals—particularly from the lesser known Monachinae lineage—by utilizing classic behavioral methods with two individual Hawaiian monk seals (*Neomonachus schauinslandi*) conditioned to voluntarily participate in hearing trials. These efforts generated and validated the first terrestrial audiogram, provided the first auditory masking measurements, and resolved discrepancies between two prior underwater hearing profiles for monk seals. The findings suggest reduced terrestrial hearing sensitivity may be related to physiological differences in soft tissue within the peripheral auditory system among seal species, which could inhibit the reception of airborne sound. Together, the results confirm that the hearing abilities of monk seals differ from those of related species and are informative for evolutionary considerations of hearing in seals.

From an applied perspective, these hearing data suggest that terrestrial communication is limited for the species. However, a lack of data describing the amplitude of Hawaiian monk seal airborne vocalizations has precluded any communication range estimates. For Chapter 3, I describe the spectral characteristics of and provide the first source level measurements for low-frequency calls emitted by this species in air. These amplitude and spectral data are combined with hearing thresholds and representative ambient noise levels to estimate the distances over which these seals can effectively communicate with conspecifics. Findings suggest that terrestrial communication is limited by the poor hearing sensitivity and moderate vocal amplitudes of the species and is further constrained by ambient noise in the environment.

This series of audiometric measurements advances knowledge of acoustic sensitivity in an endangered species, contributes comparative information about hearing for a data-poor marine mammal lineage, and increases our understanding of the evolution of hearing in the amphibious true seals. Finally, by combining hearing data with information about sound production, we can better understand the acoustic communication system of Hawaiian monk seals, ultimately supporting conservation and management efforts for this endangered species.

Dedication

I dedicate this dissertation to the many flippered scientists I have had the honor to work alongside for the last decade of my life—Kekoa, Hoʻailona, Rio, Sprouts, Ronan, Amak, Tunu, Natchek, Nayak, Selka, Siku, Noatak, Saktuliq, Kunik, and Raindrop. Thank you for teaching me.

All for one, and one for all.

Acknowledgements

As anyone who has gone on this academic journey knows, it takes a village to raise and support a graduate student. And my village was truly extensive. First and foremost, I want to acknowledge the entirety of the Pinniped Lab—past, present, and future. There is nothing like this place, these animals, and these humans. What an honor it has been to have spent over a decade of my life learning, growing, struggling, persevering, and laughing with you all. No matter what comes next, I know this extended ‘pinniped family’ will always be there.

Most importantly, I’d like to thank my advisor Dr. Colleen Reichmuth. I am beyond grateful to belong to the small group of graduate students who have come through your program. The love you have for your team (human and flippered) and the science is inspiring. I also would not have reached this milestone without Dr. Jillian Sills, my unofficial but very official advisor. Jillian has been my mentor, partner, and friend throughout this entire journey, and I owe many of my strengths to her. Together, these two amazing women have taught me so many invaluable lessons about being a thoughtful and thorough scientist. Especially to always ‘leave breadcrumbs,’ ‘close the loop,’ and ‘work the problem.’ I am the scientist (and person) I am today because of their mentorship.

Thank you to the many amazing women scientists who have inspired and guided me along the way—Jenna Sullivan, Dr. Caroline Casey, Dr. Sarah McKay Strobel, Sonny Knaub, Asila Ghoul, and Dr. Nicole Thometz. Thank you to the graduate students, research technicians, and lab friends who have been my steadfast mentors and support system through various portions of this very long journey—Maddie Meranda, Emma Levy, Madilyn Pardini, Ryan Jones, Noah Packard, Sarah Pryce, Holly Hermann-Sorensen, Michelle Conroy, Kirby Parnell, Micaela Wood, Andrew Rouse, Ross Nichols, and so many more. I would be remiss if I didn't especially acknowledge, Maddie. We have been on quite a journey together over the last few years. Thank you for being my daily partner and sharing custody of our 'one brain cell.' I am grateful for your friendship. Additionally, I am so appreciative of the support provided by Drs. Brandon Southall and Ari Friedlaender. Thank you for finding ways to include me in fieldwork and get me out on the water. Finally, I am grateful for the time, advice, and support provided by my dissertation committee—Drs. Ari Friedlaender, Jerome Fiechter, John Terhune, and Terrie Williams.

There are a handful of people outside of the science world who have managed to be patient with me these last seven years of graduate school. To my freshman-year college roommates and longtime support system Amalia Fuentes and Lauren Korth, thank you for helping to remind me (when I would let you) that there is life beyond graduate school, seals, and deadlines. I am especially grateful for my nearest and dearest friends, the Nothwang Family. Riki, I am so lucky to have had your friendship for two decades.

Reed, thank you for always bringing laughter into my life. And to the three beautiful, vibrant, and silly Nothwang children (Ellie, Noble, and Haven), you remind me why what I do is important. To my family, thank you for introducing me to nature and exploration as a child and then attempting to understand my complete disappearance into academic pursuits as an adult. I formally apologize for all the missed holidays and unanswered phone calls. Finally, I owe so much gratitude to my husband, Jesse. Thank you for always being genuinely interested in my work, humoring me by pointing out every wild animal you see, providing me with endless encouragement, and being incredibly devoted to my well-being during this very intense journey. I am so lucky for your partnership.

This dissertation is the result of several multi-institutional collaborations necessary to pursue research with endangered species, including funding sources, government agencies, zoological organizations, and animal care specialists. First, I'd like to acknowledge the US Navy's Living Marine Resources Program for supporting the initial project and for recognizing the importance of our additional proposals. Additionally, this research would not have been possible without the animal care agreements between Long Marine Lab, SeaLife Park, and the Waikīkī Aquarium, and the support of the National Marine Fisheries Services OPR and PIFSC Hawaiian Monk Seal Research Program. In particular, I am grateful for the partnership of Dr. Terrie Williams and her dedicated animal care team. Specifically, I am so thankful for the patience of animal care specialists Traci Kendall, Beau Richter, Alyssa Sandage, and

Bryan Tom during my countless technical difficulties. Thank you to the incredible veterinary team at UC Santa Cruz—Drs. Dave Casper and Megan Moriarty. Your ingenuity and dedication to animal care is inspiring. Finally, I'd like to acknowledge the additional funding resources that supplemented me throughout graduate school. Thank you to the Friends of Long Marine Lab, the Myers Family Oceanographic and Marine Biology Trust, the Rebecca and Steve Sooy Graduate Fellowship, and the Ocean Sciences Department. In particular, the travel funding provided by the Ocean Sciences Department supported my very last-minute travel to Hawaiʻi for fieldwork.

The third chapter of this dissertation would not have been possible without Kirby Parnell, Dr. Michelle Barbieri, Tracy Mercer, Glauco Puig-Santana, Maddie Duda, and the community of Kalaupapa. And of course, I owe Colleen a huge thank you as well. She had a 'shot in the dark' idea, which we followed with a very well-timed email to Kirby, and then, within just a few months, I was in Hawaiʻi. My time with wild monk seals and the Kalaupapa Community was a privilege for which I will forever be grateful. I am in awe of the natural and historical beauty of Kalaupapa.

Finally, it's very important to recognize the inspiration for this dissertation, and the animals who made this all possible. I, of course, must acknowledge the efforts of monk seals Kekoa and Hoʻa. These projects were not easy, and these two were constantly challenging my abilities as a researcher and animal behaviorist. Beyond this dissertation, these two seals have made remarkable contributions to conservation, education, and science. I am grateful to the marine mammal scientists who came before me and laid the groundwork for monk seal bioacoustic research, especially Drs. Jeanette Thomas and Ted Miller who provided the first glimpse into the acoustic world of these endangered seals. In particular, the research presented in this dissertation became possible because Colleen and Jillian poured their hearts into a collaboration that provided the opportunity to work with Kekoa. Prior to pursuing graduate school, I worked closely with Jillian to investigate Kekoa's underwater hearing abilities. These efforts resulted in my coauthorship on a comprehensive publication describing monk seal underwater sound reception and production (see Sills et al. 2021), which inspired the continued investigation of monk seal bioacoustics discussed in this dissertation. I am honored to follow in the footsteps of these incredible scientists and to have contributed valuable data for an endangered species—every little kid's dream.

Statement of Contribution

The text of this dissertation includes reprints of the following previously published material:

Chapter 1: Ruscher B, Sills JM, Richter BP, Reichmuth C (2021) In-air hearing in Hawaiian monk seals: implications for understanding the auditory biology of Monachinae seals. J Comp Physiol A 207:561–573. https://doi.org/10.1007/s00359-021-01498-y

Chapter 2: Ruscher B, Sills JM, Packard N, Kendall TL, Williams TM, Reichmuth C (2025) Psychoacoustic data confirm reduced hearing sensitivity in Hawaiian monk seals relative to Phocinae seals. Endang Species Res 56:19–26. https://doi.org/10.3354/esr01377

Note that small adjustments to the reprinted articles were made to accommodate formatting guidelines for this dissertation. Supplemental video media for each manuscript are available through the associated journal. These manuscripts were published open access under a CC-BY license; as such, no permission is necessary per journal guidelines. This work was original research by Brandi Ruscher. Specifically, B. Ruscher was responsible for experimental design, data collection and analysis, and manuscript preparation. Co-authors Drs. Reichmuth and Sills directed and supervised the research that forms the basis for this dissertation. Co-authors Richter, Packard, Kendall, and Dr. Williams assisted with aspects of project conceptualization, data collection, and manuscript preparation.

General Introduction

Pinnipeds comprise a broad taxonomic grouping of semi-aquatic marine carnivores that includes true seals (Family Phocidae), sea lions and fur seals (Family Otariidae), and walruses (Family Odobenidae). Species in this group exhibit varying degrees of aquatic adaptations and amphibious life history characteristics, but all receive and process acoustic information on land and at sea. Sound behaves differently in these disparate physical environments, with waterborne sounds traveling faster with less absorption and longer wavelengths than airborne sounds of the same frequency content. These medium-dependent characteristics of sound can be considered for a given pinniped species relative to their phylogenetic relationships, anatomical adaptations, and acoustic biology.

Pinnipeds, like other mammals, use acoustic cues to gather meaningful information during movement and orientation, predator and prey detection, and social communication—including mother-pup affiliative interactions and breeding displays used by males to defend territories and attract females (see Hanke and Reichmuth 2022). Thus, efficient sound reception is essential to their routine behavior and survival. As secondarily aquatic mammals, pinnipeds have retained or modified auditory structures shared with terrestrial relatives to support their acoustic sensitivity in air and water (Nummela 2008).

The basic form of the terrestrial mammalian ear remains intact in pinnipeds. The outer ear encompasses the pinna (ear flap) and the external auditory meatus (outer ear canal), which ends at the tympanic membrane (eardrum). The air-filled middle ear contains three ossicles (malleus, incus, stapes) that interconnect to bridge the eardrum to the fluid-filled inner ear. The inner ear includes the semicircular canals and vestibule—which primarily function as part of the vestibular system—and the cochlea, which houses the main auditory organ where sensorineural transduction occurs (the organ of Corti). In most mammals, sound waves are collected by the pinna, directed through the external auditory meatus, and amplified and transformed as they are conducted through the ossicular chain to the oval window of the cochlea. Here, sound energy is translated by sensory cells into neural impulses that eventually reach the brain (Yost 2000). The placement of two ears on the bilaterally symmetrical mammalian form aids in the localization of sounds reaching the central auditory system through two separate peripheral paths.

While the prototypical mammalian ear has primarily evolved to receive airborne sounds, the ears of pinnipeds have been modified to varying degrees to allow these animals to operate under water (Nummela 2008). The most significant challenge of moving an air-filled ear into the water is the extreme pressure experienced at depth, which can subject diving animals to barotrauma. Additionally, the densities of soft tissue and bone are similar to or greater than the surrounding underwater environment, allowing sound to pass more readily through the body and influencing potential sound reception or sound-ducting pathways. This similarity in acoustic impedance—the intrinsic resistance of a medium or mechanism to transmitting sound—decreases the sound energy normally lost at air-water boundaries and increases the permeability of the body to incident sound (Nummela and Thewissen 2008). As a result, sound localization becomes less accurate in water than in air. On an evolutionary scale, transitioning an air-adapted auditory system to water is difficult, especially when the same system must retain some operational efficiency in air, as for amphibious mammals.

Among the pinnipeds and other marine carnivores—including sea otters (*Enhydra lutris*) and polar bears (*Ursus maritimus*)—true seals of the family Phocidae have the most derived auditory traits to support the production and reception of both waterborne and airborne sounds and/or to protect air spaces in the ear during deep diving. Seals have retained acute terrestrial hearing sensitivity while gaining aquatic acoustic specializations (Wartzok and Ketten 1999). Many, if not all, species are known to emit vocalizations when submerged (Charrier and Casey 2022). Seals are probably the best-studied marine carnivores with respect to hearing, auditory anatomy, and sound production (Hanke and Reichmuth 2022); there are available descriptions and measurements of specific bony and soft tissue adaptations, portions of hearing pathways, demonstrated hearing abilities, and vocal behavior. However, many questions remain about the acoustic biology of particular species and differences between phylogenetic lineages.

Biology of True Seals

True seals, known as phocids or ‘earless’ seals, are superficially distinguished from other pinnipeds by their lack of external ear pinnae and a pelvis that does not rotate underneath the body for terrestrial locomotion. They are presently found worldwide in polar, sub-polar, temperate, and tropical environments. Seals are tied to land or ice for critical biological functions such as whelping, nursing, and resting but also display a high degree of aquatic specialization, exclusively utilizing the marine environment for prey resources (Riedman 1990). Seals are typically generalist predators, feeding on a variety of fish, mollusks, and crustaceans. Foraging ecology varies among species, with some utilizing relatively shallow (< 100 m) waters and benthos along the continental shelf and others routinely diving upwards of 1000 m to forage on mesopelagic prey (Bowen and Jonsen 2022). The vast horizontal and vertical spatial scales utilized by phocids in diverse marine habitats greatly influence the degree of their species-typical aquatic adaptations.

The ancestors of modern seals transitioned to semi-aquatic living more than 25 million years ago to take advantage of abundant coastal prey resources supported by productive upwelling conditions (Berta 2012). Due to scattered and incomplete fossil records, key details of their phylogenetic history are unknown. Early seals are thought to share bear-like or otter-like qualities with terrestrial Arctoid carnivores of that time (Berta et al.

2018). Modern phocids include 18 species within two major lineages, the Monachinae and Phocinae subfamilies. This divergence occurred more than 15 million years ago (Higdon et al. 2007; Berta et al. 2018; Rule et al. 2021), and for the most part, these lineages have retained geographic separation. The eight extant species of Monachinae seals are sometimes referred to as the clade of ‘southern’ seals and include the elephant, monk, and Antarctic seals. Most of these species presently inhabit the waters of the Southern Hemisphere, with three of the most basal species occurring in the Northern Hemisphere. The ten species of Phocinae seals, or ‘northern’ seals, include polar and most temperate seals of the Northern Hemisphere. Phocinae seals, especially the ubiquitous harbor seal (*Phoca vitulina*), are historically better studied due to their widespread presence in both the Atlantic and Pacific waters of the Northern Hemisphere. We know less about Monachinae seals; however, some species—such as the Weddell seal (*Leptonychotes weddellii*) and northern elephant seal (*Mirounga angustirostris*)—have been studied in more detail because of their accessibility and unique physiology (Beltran et al. 2022; Le Boeuf and Naito 2022; Shero and Burns 2022).

The auditory biology of true seals reflects their strongly amphibious life histories. Sound is vital in terrestrial and marine environments but is especially critical under water, where other sensory cues attenuate more rapidly (Kröger 2008; Nummela and Thewissen 2008). Seals utilize underwater sound to orient themselves within three-dimensional marine habitats (Schusterman et al. 2000), for intra-specific communication (Charrier and Casey 2022), and to identify the presence of sound sources including predators and other threats (Deecke et al. 2002). The reliance of seals on acoustic information in air and water is supported by their impressive hearing capabilities in both environments. Some species are known to have aerial hearing almost as acute as the best terrestrial carnivores and underwater hearing nearly as sensitive as fully aquatic marine mammals (Fay 1988; Reichmuth et al. 2013; Southall et al. 2019). The study of hearing in seals is especially interesting because of the conflicting selective pressures on the auditory system posed by dual physical environments. How seals balance these conflicting demands while retaining acute amphibious hearing abilities with a terrestrially derived auditory system is perplexing.

Sound Reception

Aspects of auditory function (hearing) in true seals have been measured using classic psychophysical methods with trained individuals since early studies of hearing sensitivity and pitch discrimination in the 1960s (Møhl 1964, 1967, 1968a, 1968b). For the first comprehensive study of hearing in seals, Bertel Møhl worked with a trained harbor seal living in an outdoor pen in Strib, Denmark. Møhl conditioned the seal to perform a cooperative hearing test at the water's surface and when voluntarily submerged using a combination of desired fish rewards and aversive puffs of air (Møhl 1968a). In this way, Møhl described the seal's amphibious hearing ability as a measure of sensitivity (detection threshold) determined for frequencies across the range of hearing. Since that time, similar hearing profiles, or ‘audiograms,’ have been reported for additional harbor seals (e.g., Kastelein et al. 2009; Reichmuth et al. 2013) as well as bearded (*Erignathus barbatus*; Sills et al. 2020), Caspian (*Pusa capsica*; Babushina 1997), harp (*Pagophilus groenlandicus*; Terhune and Ronald 1971, 1972), spotted (*Phoca largha*; Sills et al. 2014), ringed (*Pusa hispida*; Terhune and Ronald 1975a, Sills et al. 2015), Hawaiian monk (*Neomonachus schauinslandi*; e.g., Sills et al. 2021), and northern elephant seals (e.g., Kastak and Schusterman 1999; for review see Erbe et al. 2016, Southall et al. 2019). These studies have employed similar operant conditioning methods to examine the frequency and intensity limits of sound reception, as well as more complex aspects of hearing—including studies of directional hearing, temporal processing, and auditory masking (e.g., Cunningham et al. 2014; Sills et al. 2017). More than half a century following Møhl’s original study, behavioral conditioning methods remain the most accurate way to measure auditory performance in these amphibious marine mammals.

In addition to behavioral methods, neurophysiological methods have also been applied with phocids to measure evoked responses to auditory stimuli (e.g., Wolski et al. 2003; Bornemann et al. 2007; Houser et al. 2007, 2008; Mulsow and Reichmuth 2007; Reichmuth et al. 2007; Tripovich et al. 2011). These passive methods seem to work well for odontocete cetaceans (toothed whales) at mid- to high-frequencies and for pinnipeds at relatively high frequencies in air. However, these methods have not proven useful for studying hearing at lower frequencies or for measuring the hearing of seals in water (Supin et al. 2001; Mulsow et al. 2012). Therefore, current knowledge of hearing abilities in seals relies upon standard behavioral threshold measurements obtained from individuals trained to cooperate in various sound detection and discrimination tasks (Hanke and Reichmuth 2022).

Among the true seals, most auditory data are available for Phocinae species. Hearing profiles indicate that these ‘northern’ seals have the most acute amphibious abilities of the marine carnivores (Owen and Bowles 2011; Reichmuth et al. 2013; Ghoul and Reichmuth 2014). Initial behavioral data for harbor, harp, Caspian, and ringed seals suggested these seals had better hearing in water than in air and, thus, were considered to be aquatic specialists (Møhl 1968a; Terhune and Ronald 1971, 1972, 1975a; Terhune 1988, 1989, 1991; Babushina 1997). However, these hearing measurements rarely extended to frequencies below 1 kHz, restricting the ability to capture the complete hearing profile of these seals. Further, most studies were conducted outdoors, which may have constrained absolute hearing measurements.

More recent behavioral studies have provided new perspectives into the hearing abilities of seals. Research with harbor, ringed, spotted, and bearded seals have confirmed previous assertions that the underwater hearing sensitivity of seals is quite acute (Southall et al. 2019; Sills et al. 2020). In contrast, hearing measurements obtained for most of the same species in the highly controlled, quiet environment of an acoustic chamber have revealed greater absolute sensitivity to airborne sound than previously reported (Reichmuth et al. 2013; Sills et al. 2014, 2015). Collectively, hearing data from multiple species confirm that Phocinae seals have a broad range of underwater hearing (< 0.1 to > 70 kHz) with best sensitivity near 50 dB re 1 µPa, nearly as good as fully aquatic marine mammals, albeit at lower frequencies (Southall et al. 2019). Notably, Phocinae seals have the best demonstrated low-frequency hearing of marine mammal species that have been behaviorally tested. Additionally, these seals have been reported to have surprising ultra-high-frequency hearing abilities in water, with detection thresholds less than 140 dB re 1 µPa measured at frequencies up to 180 kHz (Cunningham and Reichmuth 2016)—although frequency discrimination ability above 60 kHz is poor (Møhl 1968b).

In air, the frequency range of hearing for these Phocinae seals is narrower (< 0.1 to ~ 50 kHz) with best sensitivity as low as -13 dB re 20 µPa at frequencies of a few kHz (Reichmuth et al. 2013; Sills et al. 2014, 2015; Southall et al. 2019), superior to humans and rivaling the best terrestrial carnivores (Fay 1988). The acute hearing abilities of these Phocinae seals in air and under water are remarkable, given that both sensory modes involve the same auditory structures. Amphibious hearing profiles measured in water and in air are generally in agreement for harbor, spotted, and ringed seals (the species that have been tested in both media). Thus, the hearing abilities of Phocinae seal species are well known and considered to be similar across the clade (Sills et al. 2020).

Fewer behavioral audiometric data are available for species from the Monachinae lineage and include data only for the northern elephant seal and the Hawaiian monk seal. Both species show relatively poorer hearing abilities when compared to their Phocinae counterparts. While the elephant seal's underwater hearing profile is generally similar to that of the Phocinae seals, the thresholds for the single seal tested are somewhat elevated across most of the hearing range (Kastak and Schusterman 1999). Terrestrial measurements obtained with the same individual suggest this species has markedly reduced sensitivity to airborne sounds (Reichmuth et al. 2013). Hearing in Hawaiian monk seals has been studied in two individuals, but the available auditory profiles are inconsistent with one another. An initial report by Thomas et al. (1990) suggested that monk seals perceive underwater sounds across a more restricted frequency range (~ 10 to 40 kHz) than other seals. In contrast, Sills et al. (2021) describe a much broader range of hearing in water (< 0.1 to > 40 kHz), although with sensitivity poorer than 73 dB re 1 µPa. Given these limited data, the hearing abilities of Monachinae seals remain poorly understood.

A notable auditory feature shared by Phocinae and Monanchinae seals is an extreme high-frequency hearing ability. For Phocinae seals, the hearing range in water extends above 70 kHz, almost an octave above that of most terrestrial carnivores (Fay 1988). While their high-frequency hearing limit in water is reduced compared to fully aquatic odontocetes—who rely on the reception of high-frequency sounds for echolocation—it is still impressive and comparable to that of fully aquatic sirenians (Gerstein et al.

1999; Gaspard et al. 2012; Southall et al. 2019). This indicates a derived trait of special neural encoding for the resolution of high-frequency sounds within the cochlea of seals (Hemilä et al. 2006; Cunningham and Reichmuth 2016). Although similar high-frequency hearing ability is possible for airborne sounds based on these sensorineural adaptations, inertial constraints of the auditory system operating in air may limit high-frequency hearing to ~ 50 kHz in seals (Hemilä et al. 2006).

Descriptions of hearing frequency range and sensitivity are strengthened by studies of auditory masking, which reveal how the perception of relevant sounds is altered in the presence of interfering noise (Yost 2000). Studies of masking are a critical addition to more basic measurements of hearing abilities, as they describe how different species are adapted to receive sound in representative noise conditions. Auditory masking is commonly studied by testing a subject's ability to detect a target sound presented within simultaneous (overlapping) noise. One frequency-dependent metric that results from masking studies is the critical ratio, defined as the difference between the sound pressure level of a just-audible tonal signal and the spectrum level of the masking noise in the same spectral frequency range (Fletcher 1940; Scharf 1970). Thus, lower critical ratio values correspond to a greater ability to detect signals in noise. Critical ratios typically increase with increasing frequency, but this relationship appears to change at the lower frequencies (Erbe et al. 2016; Branstetter and Sills 2022).

Auditory masking and critical ratios have been measured for several Phocinae seals at frequencies between 0.1 and 32 kHz. These include bearded (Sills et al. 2020), harbor (e.g., Terhune 1991), harp (Terhune and Ronald 1971), spotted (Sills et al. 2014), and ringed seals (Terhune and Ronald 1975b; Sills et al. 2015). For Monachinae species, only the northern elephant seal has been similarly evaluated (Southall et al. 2000, 2003a; for review see Erbe et al. 2016, Branstetter and Sills 2022). The critical ratios measured for seals relative to other pinnipeds and terrestrial mammals suggest they have an enhanced ability to hear well in noisy environments (Fay 1988; Branstetter and Sills 2022). This specialization may be linked to their evolutionary history in marine environments where sound is a critical sensory modality (Schusterman et al. 2000; Southall et al. 2003a; Reichmuth 2012). Additional information about auditory masking for Monachinae species is needed and would be informative to understanding masking adaptations as derived traits in marine mammals.

Auditory Anatomy

Among the pinniped clades, true seals have the most derived auditory anatomy to support semi-aquatic life (Wartzok and Ketten 1999). They lack external pinnae and have muscular attachments for voluntary control of the meatal openings. Their auditory canals are narrow, tortuous, and lined with cavernous tissue (Møhl 1968b; Ramprashad et al. 1973; Repenning 1972; King 1983). The ossicles of the middle ear are hypertrophied with altered shape and proportions, and the middle ear cavity is relatively large and extensively lined with cavernous tissue. The cavernous tissue associated with the outer and middle ear can swell and engorge with blood to reduce the air volume within these spaces, which is likely an adaptation for pressure regulation while diving (Møhl 1968b; Repenning 1972). Compared to similarly sized terrestrial carnivores, seals have a large tympanic membrane separating the outer and middle ear and an enlarged oval window membrane leading from the middle ear to the fluid-filled cochlea. The area ratio between these two membranes impacts the amplification of sound as it passes through the middle ear (i.e., pressure is increased and, thus, sound is amplified more when the tympanic membrane is much larger than the oval window). The area ratio between the tympanic membrane and the oval window, the extent of ossicle hypertrophy and derivation of shape, and the development of cavernous tissue have been documented to vary between true seal species (Repenning 1972; Ramprashad et al. 1973; King 1983).

All phocids have a greatly enlarged round window—a membrane-covered opening in the cochlea that typically connects the inner ear to the middle ear and relieves the pressure of sound energy traveling through the cochlea by moving in the opposite direction as the oval window. The round window is well shielded from the cavernous tissue by the surrounding fossula and appears to open externally to the skull rather than into the middle ear cavity as in other mammals (Repenning 1972; Ramprashad et al. 1975; Koper et al. 2021). Within the inner ear, the cochlear anatomy of seals resembles that of terrestrial mammals. Some descriptions indicate that the basal whorl of the spiral cochlea structure is enlarged and oriented more laterally than that of terrestrial carnivores to aid in sound reception under water through resonant reaction at the side of the head (Repenning 1972; Ramprashad et al. 1975).

Regarding neural anatomy associated with auditory structures, seals have large cochlear nerves with high densities of axons relative to terrestrial carnivores (Smodlaka et al. 2019). Their demonstrated high-frequency hearing ability (> 70 kHz) demands cochlear anatomy with neural receptors tuned to these frequencies, and this phocid trait is perhaps the most derived feature of hearing among the pinnipeds.

These anatomical modifications from the terrestrial form of the auditory system are likely shared among many or all true seals. However, much of this information is gathered from a few representative species, particularly within the Phocinae subfamily. Less is known about how auditory structures vary by species and what the resulting consequences on sensory performance may be. Some notable anatomical variations between the species examined thus far suggest possible differences at the phylogenetic level. While most of the differences described reflect bony anatomy and gross tissues (e.g., Møhl 1968b, Repenning 1972; Ramprashad et al. 1975; Marsh 2001; Smodlaka et al. 2019; Koper et al. 2021), emerging techniques are allowing for fine-scale imaging of neural tissues and individual cells. For example, scanning electron microscopy and immunofluorescence have recently been used to examine the ultrastructure of the sensory epithelium within the cochlea of harbor seals (Rojas et al. 2023). This high-resolution description of auditory structures in a ubiquitous species enables correlations between morphological features and hearing abilities, including the specific neural adaptations that support transduction and differentiation of high-frequency sounds.

Monachinae seals have some gross anatomical features that suggest differences in acoustic perception compared to Phocinae seals. All Monachinae species have an extremely small meatal opening that is often closed and/or occluded with hair (King 1983). It is unknown whether their auditory meatal canal is air filled or collapsed while resting on land. King (1969) noted that the portion of the canal immediately behind the meatal opening has a longer unsupported section in Ross seals (*Ommatophoca rossii*) than in Phocinae species. Thus, it seems reasonable to conclude that the ability of Monachinae seals to receive airborne sounds through the conventional terrestrial pathway may be reduced due to tissue obstruction (e.g., Kastak and Schusterman 1999). In contrast, the orifice of the external ear of Phocinae seals—who possess acute in-air hearing abilities—is large and surrounded by muscles that enable voluntary opening and closing of the channel leading to the auditory canal. When these seals listen in air, the ear is open wide with an apparently air-filled canal, allowing efficient hearing through the conventional terrestrial pathway (Møhl 1968b). The opening or occlusion of the external ear has significant consequences on hearing ability. For perspective, occluding the human meatal opening with a finger, palm, or tragus causes a 25 to 45 dB reduction in hearing thresholds (Holland 1967). Interestingly, the complete closure of the external meatus is a feature that Monachinae seals share with fully aquatic marine mammals, including sirenians and cetaceans (Wartzok and Ketten 1999; Nummela 2008). It is intriguing that the semi-aquatic Monachinae seals have converged on a similar solution to protect the ear from water intrusion and other challenges of aquatic life.

Other features of Monachinae auditory anatomy also suggest a divergence between the two phocid subfamilies. Within the middle ear, Monachinae seals have a smaller area ratio between the tympanic membrane and oval window (King 1983), which could indicate relatively poor sensitivity to terrestrial sounds. More anatomical data are needed, but this ratio has been measured as 18-38:1 versus 9-10:1 in Phocinae and Monachinae species, respectively (Repenning 1972; King 1983). The higher tympanic membrane to oval window ratio in Phocinae seals is more similar to that of terrestrial carnivores that possess sensitive in-air hearing (>35:1; King 1983). While this ratio is not a proxy for hearing sensitivity, a lower value for the Monachinae species suggests[1] poorer middle ear function and, thus, reduced terrestrial hearing ability (Rosowski 1994; Mason 2016). In addition, it has been noted that the ossicles are extremely large and heavy in northern elephant seals compared to Phocinae seals (Marsh 2001). As the ossicles have not been described in other Monachinae species, it is unknown whether this trait is present within the clade or is a specific adaptation to coping with intense pressure in a very deep-diving species. This trait likely influences hearing ability in air

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[1] The tympanic membrane to oval window ratio of Monachinae species also suggests an increased pressure tolerance during submersion which may be helpful to deep-diving species, such as the closely related northern elephant seal (Repenning 1972).

as large, heavy bones do not conduct airborne sound energy efficiently through the ancestral mammalian auditory pathway (e.g., Hemilä et al. 2006). The size of membranes and auditory ossicles of some Monachinae seals suggest that their hearing abilities may differ from those of related species. Still, a greater understanding of comparative aspects of both structure (anatomy) and function (hearing) is needed to further assess subfamily and species-level differences in auditory biology.

Sound Production and Communication

True seals produce a variety of sounds to communicate with conspecifics. When hauled out on land or ice, seals may emit a variety of mother-pup contact calls, threats, displays, and other social vocalizations, such as grunts and growls, with frequencies that fall primarily between 0.02 and 10 kHz (see Southall et al. 2019). In water, sounds produced by seals are generally associated with breeding behavior, with males of aquatically mating species producing seasonal acoustic displays that are thought to serve in either male-male competition or female attraction (Charrier and Casey 2022). The frequency content of underwater vocalizations extends over a broader frequency range, typically from 0.01 to 30 kHz, though energy content above 100 kHz has been documented in the calls of Weddell (Cziko et al. 2020) and leopard seals (*Hydrurga leptonyx*; see Southall et al. 2019). The extent to which these species utilize acoustic energy above 60 kHz in complex vocalizations is unclear (Cziko et al. 2020).

A fundamental component to enhance our understanding of acoustic signals is to consider the ‘active space’ of a signal in the environment. Active space, or communication range, refers to the distance from a source over which a sound remains detectable by a listener in the same environment (see Marten and Marler 1977; Brenowitz 1982; Janik 2000). Calculating the communication range of a signal requires knowledge of the sound being produced, signal degradation as a function of distance, the ambient noise of the environment, and the auditory capabilities of the listener. Aspects of active space have been investigated for some highly vocal species, including birds (e.g., Brenowitz 1982), amphibians (e.g., Gerhardt 1975), primates (e.g., Brown 1989), cetaceans (e.g., Erbe and Farmer 2000; Janik 2000), and pinnipeds (e.g., Southall 2002; Southall et al. 2003b; Casey et al. 2016; Sills et al. 2021). These studies rely on comprehensive field data describing environmental conditions and vocal behavior and laboratory data on sound production and reception to support these estimates; however, calculations are still made with many simplifying assumptions, especially when considering the complex nature of signal propagation, auditory masking, and requirements for effective communication (see Southall et al. 2003b). Regardless, assessing sound production and sound reception together provides a fuller understanding of species-typical acoustic communication and the extent to which it could be impacted by anthropogenic noise.

The Hawaiian Monk Seal

The Hawaiian monk seal is a Monachinae species with limited bioacoustic data available until recently. They are endemic to the Northwestern and Main Hawaiian Islands of the Pacific Ocean and are of significant conservation concern, with approximately 1,600 individuals remaining in the wild (NOAA Fisheries 2024; Fig. 1). Monk seals differ from phocids living at higher latitudes as they experience relatively stable environmental conditions and resources year round. For this reason, monk seals do not breed synchronously during a brief, predictable period each year like temperate and polar seals that show stronger seasonality in behavior. Instead, Hawaiian monk seals have an unusually prolonged reproductive period spanning at least nine months at the population level (Miller and Job 1992). Monk seals forage extensively within the reefs surrounding the islands and undertake short foraging trips to nearby seamounts and submerged reefs and banks (Stewart et al. 2006; Bowen and Jonsen 2022). They consume a wide variety of fish, cephalopods, and crustaceans, many of which are predominately benthic species (Robinson et al. 2022). Typical dive depths appear to depend on biological resources and geological features of foraging areas. Most dives are relatively shallow (< 150 m) and short (< 5 min), with some deeper, longer dives recorded upwards of 500 m (Stewart et al. 2006). Among other conservation concerns, the relatively nearshore foraging behavior of Hawaiian monk seals within the Main Hawaiian Islands has increased their overlap with areas of human use and, thus, the potential for negative interactions with humans and fishing gear (Robinson et al. 2022). Additionally, they inhabit areas very close to US military activities and are regularly exposed to high levels of anthropogenic noise, but the extent of how this might impact them is still unclear.

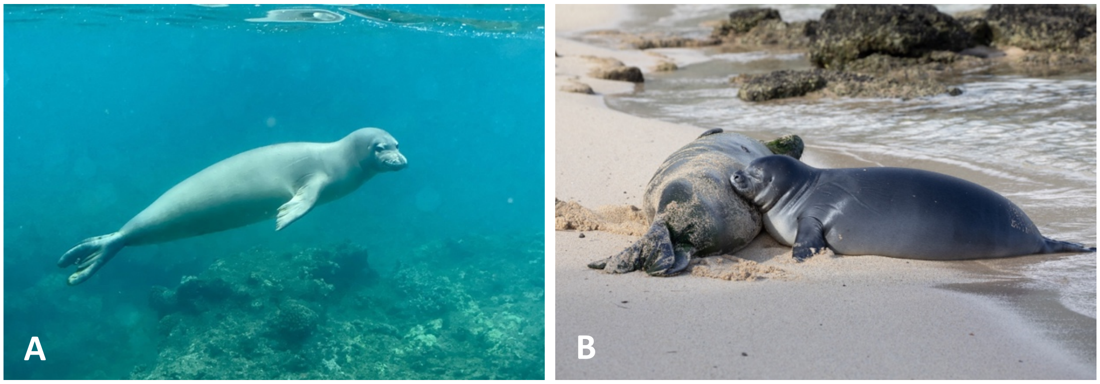

Fig. 1 Hawaiian monk seal swimming along a reef (**Panel A**; O‘ahu, HI, USA) and an adult female with a dependent pup resting on the beach (**Panel B**; Kalaupapa National Historical Park, Moloka‘i, HI, USA). Photo credit: N. Kincaid (Panel A) and G. Puig-Santana (Panel B; NMFS permit 22677).

Monk seals are particularly interesting from an evolutionary perspective as they are the oldest species within the Monachinae lineage, having separated from their nearest living relatives more than 12 million years ago (Higdon et al. 2007; Berta et al. 2018; Rule et al. 2021). Like elephant seals from the genus *Mirounga*, Hawaiian monk seals have an annual catastrophic molt in which they shed their fur and top layer of skin. Other aspects of their life history and ecology are also quite different from the remaining Monachinae seals that inhabit the cold, productive waters of the Southern Ocean. Given their long evolutionary and biogeographical isolation, it is perhaps not surprising that they have an auditory biology that differs from that of other seals.

While we know quite a bit about the general biology of this endangered species, we do not yet have a complete picture of their auditory biology. Descriptions of terrestrial vocal behavior provide some initial insight into their acoustic biology. Hawaiian monk seals emit low-frequency (< 1 – 2 kHz) vocalizations while on shore, which include mother and pup contact calls, threats, and a few other rumbling sounds (Kenyon and Rice 1959; Miller and Job 1992; Job et al. 1995). There are some detailed observations of terrestrial vocal behavior, and certain spectral parameters (e.g., frequency, duration, pulse rates) have been measured for these calls, but there have been no measurements of call amplitude (Miller and Job 1992). While the species was previously thought to be silent in water, recent work has identified a moderate repertoire of at least six low-frequency (< 1 kHz) vocalizations with apparent reproductive function that are produced by mature males (Terhune 2019; Sills et al. 2021).

In terms of sound reception, the two available audiometric studies of individual Hawaiian monk seals have yielded conflicting underwater hearing profiles (Thomas et al. 1990; Sills et al. 2021), and there are no terrestrial audiometric measurements available for the species (see Southall et al. 2019). Although the underwater hearing profiles described in the two studies do not match, both monk seals displayed similarly limited high-frequency hearing compared to all other species behaviorally tested. Specifically, hearing sensitivity in these monk seals decreased above ~ 36 kHz, rather than ~ 50 kHz in other species (e.g., Sills et al. 2014, 2015, 2020, 2021). This reduction compared to Phocinae seals and the more closely related elephant seals is significant.

It may indicate that high-frequency hearing in seals is an adaptation that emerged after the divergence of the monk seals and separately within the two Phocidae lineages. The generation of uniformly low-frequency calls in air and water might suggest acute or enhanced low-frequency hearing abilities in this species. This is apparently not true for Hawaiian monk seals in water, as the data from Sills et al. (2021) suggest underwater hearing thresholds < 1 kHz are at least 15 dB worse than those of Phocinae seals. Because we do not know the terrestrial hearing capabilities of monk seals or the amplitudes of their airborne calls, it remains unknown to what extent monk seals can detect the biologically relevant low-frequency sounds they produce in air.

There are some clues that monk seals exhibit certain ‘basal’ auditory traits consistent with their early divergence from other seals. Specifically, these included the extent of cavernous tissue within the middle ear, morphological differences in the bony structures surrounding the inner ear, and the spiral structure of the cochlea, which is reduced at the basal section (Repenning 1972; Repenning and Ray 1977; Wyss 1988). These features suggest that the hearing abilities of monk seals may differ from those of related species, but more information is needed to further assess how these differences relate to hearing performance. Given the unique life-history characteristics, phylogenetic status, and auditory anatomy of Hawaiian monk seals, further audiometric measurements with at least one additional individual trained to cooperate in behavioral hearing tests should greatly improve our understanding of sound reception in this species, provide updated guidance for management of noise-related disturbance, and, more generally, increase knowledge of auditory biology in Monachinae seals. Similarly, quantitative information about the amplitude and characteristics of the calls emitted by Hawaiian monk seals, along with representative data concerning typical ambient noise conditions, would allow for the examination of the active space associated with biologically relevant vocalizations. Such data would advance our understanding of social communication and the auditory effects of environmental disturbance.

Dissertation Scope

This dissertation focuses on the auditory capabilities of true seals, with particular emphasis on contributing new information for the lesser known Monachinae subfamily. The research is inspired by complementary studies of underwater hearing and communication in Hawaiian monk seals conducted at the University of California Santa Cruz (Sills et al. 2021). The scope of work includes both laboratory and field studies of this endangered seal species to address significant data gaps.

The first two chapters of the dissertation aim to clarify the typical hearing abilities of the Hawaiian monk seal. Audiometric measurements were obtained from captive, highly trained seals at the University of California Santa Cruz. Chapter 1 provides the first available terrestrial hearing profile and masking measurements for the species, including descriptions of hearing range, sensitivity, and masking parameters (critical ratios). These auditory measurements, obtained in highly controlled conditions, allow for direct comparison to available data for related seal species. Information about hearing ability is presented alongside a detailed comparative consideration of the external auditory anatomy of Monachinae seals in order to link aspects of auditory structure and function. Chapter 2 resolves the conflicting underwater hearing profiles previously collected for this species and validates the in-air hearing profile collected in Chapter 1, thus confirming hearing abilities at the species level for Hawaiian monk seals. Together, these studies advance knowledge of Hawaiian monk seal auditory biology by providing necessary measurements while exploring and emphasizing potential differences in hearing and anatomy between the two Phocidae subfamilies.

The terrestrial hearing data presented in Chapters 1 and 2 suggest that monk seal communication is likely limited in air relative to other well-studied seals. To investigate this, Chapter 3 incorporates field observations and recordings of spontaneous calls produced by free-ranging Hawaiian monk seals at Kalaupapa National Historical Park (Moloka‘i, HI, USA) to provide the first source level estimates for their airborne groan vocalizations. These data are combined with descriptions of typical environmental conditions—including ambient noise profiles and aspects of sound transmission loss—and frequency-specific masked and absolute hearing sensitivity measurements to estimate distances over which monk seals can hear the calls of conspecifics.

Collectively, the work presented in this dissertation contributes fundamental knowledge about hearing capabilities in seals and informs our understanding of sensory biology and communication in an endangered species. In particular, the combination of hearing and sound production data illustrates how hearing and communication may be constrained by ambient or human-generated noise in the environment, which will support decision-making about anthropogenic noise exposures that may be relevant to conservation efforts.

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Chapter 1

In-air hearing in Hawaiian monk seals: implications for understanding the auditory biology of Monachinae seals

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Ruscher B, Sills JM, Richter BP, Reichmuth C (2021) In-air hearing in Hawaiian monk seals: implications for understanding the auditory biology of Monachinae seals. J Comp Physiol A 207:561–573. https://doi.org/10.1007/s00359-021-01498-y

Abstract

The auditory biology of Monachinae seals is poorly understood. Limited audiometric data and certain anatomical features suggest that these seals may have reduced sensitivity to airborne sounds compared to related species. Here we describe the in-air hearing abilities of a Hawaiian monk seal (*Neomonachus schauinslandi*) trained to participate in a psychophysical paradigm. We report absolute (unmasked) thresholds for narrowband signals measured in quiet conditions across the range of hearing and masked thresholds measured in the presence of octave-band noise at two frequencies. The behavioral audiogram indicates a functional hearing range from 0.1 to 33 kHz and poor sensitivity, with detection thresholds above 40 dB re 20 μPa. Critical ratio measurements are elevated compared to those of other seals. The apparently reduced terrestrial hearing ability of this individual—considered with available auditory data for a northern elephant seal (*Mirounga angustirostris*)—suggests that hearing in Monachinae seals differs from that of the highly sensitive Phocinae seals. Exploration of phylogenetic relationships and anatomical traits support this claim. This work advances understanding of the evolution of hearing in amphibious marine mammals and provides updated information that can be used for management and conservation of endangered Hawaiian monk seals.

Introduction

The Hawaiian monk seal, *Neomonachus schauinslandi*, is a phocid (true seal) species endemic to the Northwestern and main Hawaiian Islands. There is significant conservation concern for this endangered marine mammal, with approximately 1,400 individuals remaining in the wild (Carretta et al. 2017; Pacific Islands Fisheries Science Center 2020). Monk seals are unique in comparison to seals living at higher latitudes as they experience relatively stable environmental conditions and resources year round. For this reason, monk seals do not breed synchronously during a brief, predictable period each year like temperate and polar seals that show much stronger seasonality in behavior. Instead, Hawaiian monk seals have an unusually prolonged reproductive period spanning at least nine months at the population level (Miller and Job 1992). While parturition tends to occur during spring and summer, females can give birth throughout much of the year (Kenyon and Rice 1959; Johnson and Johnson 1984; Johanos et al. 1994). This enables males to continuously compete for access to dispersed females that apparently come into estrous within a few weeks of weaning their pups (Johnson and Johnson 1984; Atkinson and Gilmartin 1992; Johanos et al 1994).

From a phylogenetic perspective, it is noteworthy that monk seals—including the extant Hawaiian monk seal and Mediterranean monk seal (*Monachus monachus*)—have been separated from their nearest living relatives for about 12 million years (Berta et al. 2018; Higdon et al. 2007; Rule et al. 2020). A more complete understanding of their biogeography is just emerging from recently discovered fossil data (Rule et al. 2020), which indicate that monk seals primarily evolved in the southern hemisphere. Monk seals belong to the Monachinae lineage of phocid Carnivores (Family Phocidae), which split from its sister lineage of Phocinae seals more than 15 million years ago (Berta et al. 2018; Higdon et al. 2007; Rule et al. 2020). Monachinae seals are sometimes referred to as the clade of 'southern' seals and also include the elephant seals and Antarctic seals. These species have some anatomical differences from Phocinae seals, including with respect to their auditory anatomy. While all true seals have hypertrophied ossicles, cavernous tissue in the middle ear, and a muscular external ear opening that lacks a pinna (see Nummela 2008), Monachinae species have a much smaller external ear opening (King 1983) and a long and unsupported ear canal relative to Phocinae species (King 1969). Monachinae seals also have a relatively small fenestra vestibuli (oval window) compared to the size of the tympanum (King 1983). These features could indicate poor sensitivity to terrestrial sounds. Furthermore, monk seals exhibit certain 'basal' auditory traits, specifically with respect to tissues in the middle ear and the morphology of bony structures surrounding the inner ear (Repenning 1972; Repenning and Ray 1977; Wyss 1988). The retention of these traits suggests that the hearing abilities of monk seals may differ from those of related species.

Few audiometric studies have attempted to describe hearing in Monachinae seals. Rather, most auditory data are available for Phocinae species. These hearing profiles indicate a broad range of underwater hearing (< 0.1 to > 70 kHz) with best sensitivity near 50 dB re 1 μPa. The frequency range of hearing is narrower in air (< 0.1 to > 30 kHz) with best sensitivity as low as -13 dB re 20 μPa (Reichmuth et al. 2013; Southall et al. 2019a), rivaling the best terrestrial carnivores (Fay 1988). There is a good understanding of amphibious auditory abilities in Phocinae species including harbor seals (*Phoca vitulina*), spotted seals (*Phoca largha*), and ringed seals (*Pusa hispida*). Conversely, audiometric data are available for only two Monachinae species and both show relatively poorer hearing abilities. One northern elephant seal (*Mirounga angustirostris*) had an underwater hearing profile that was generally similar to that of the Phocinae seals but with somewhat elevated thresholds (Kastak and Schusterman 1999). Aerial measurements obtained with the same individual suggested reduced sensitivity to airborne sounds (Reichmuth et al. 2013). Hearing in Hawaiian monk seals has also been studied. An initial report by Thomas et al. (1990) suggested that monk seals perceive underwater sounds across a more restricted frequency range (~10-30 kHz) than other seals. In contrast, Sills et al. (2021) describe a much broader range of hearing in water (< 0.1 to > 60 kHz), although with sensitivity poorer than 73 dB re 1 μPa. No in-air audiometric data are available for Hawaiian monk seals.

Descriptions of vocal behavior provide some additional clues about the auditory biology of this species. Hawaiian monk seals emit low-frequency (< 1 kHz) vocalizations while on shore, which include mother-pup contact calls, threats, and other social vocalizations (*e.g.* Kenyon and Rice 1959; Miller and Job 1992; Job et al. 1995).

While this species was previously thought to be silent under water, recent work has identified a moderate repertoire of low-frequency (< 1 kHz) vocalizations with apparent reproductive function that are produced by mature males (Sills et al. 2021). The generation of uniformly low-frequency sounds might suggest acute low-frequency hearing abilities in this species. This is apparently not true for Hawaiian monk seals in water, however, and it is unknown to what extent they can hear biologically relevant sounds in air.

In this study, we evaluated the in-air hearing sensitivity of a highly trained Hawaiian monk seal whose underwater hearing had previously been described (Sills et al. 2021). Using similar methods, we conducted in-air audiometric testing in a specialized acoustic chamber to allow for direct comparison to related species. We measured (1) absolute (unmasked) auditory thresholds across the range of hearing from 0.1 to 33.2 kHz, and (2) masked thresholds in the presence of spectrally flat, octave-band noise to reveal critical ratios at 0.8 and 3.2 kHz. Given the unique life-history characteristics, phylogenetic status, and auditory anatomy of Hawaiian monk seals, these measurements improve our understanding of sound reception in this species, provide updated guidance for management of noise-related disturbance, and, more generally, increase knowledge of auditory biology in Monachinae seals.

Materials and Methods

Subject

The subject was an adult male Hawaiian monk seal identified as KE18 (NOA0006781; also known as *Kaimalino* or *Kekoa*) (Figure 1), who lived in the waters surrounding the Northwestern Hawaiian Islands for his first ten years of life. After exhibiting aberrant aggressive behavior towards conspecifics, he was removed from the wild by the U.S. National Marine Fisheries Service and relocated to Long Marine Laboratory at the University of California Santa Cruz to participate in behavioral research to support conservation and management of the species. KE18 was in good health with no known history of ear injury or exposure to ototoxic medication. At the start of the study, he was 17 years of age and weighed approximately 200 kg. With respect to his external ears, curvilinear interaural distance was 26 cm (measured as the dorsal curvilinear length between meatal openings), while direct interaural distance (straight length) was 21 cm. Prior to this study, KE18 completed a similar behavioral assessment of underwater hearing (Sills et al. 2021).

KE18 was trained using operant conditioning methods and fish reinforcement for voluntary participation in husbandry and research sessions. He received one-third to one-half of his daily diet of freshly thawed fish and squid during audiometric sessions; his diet was not constrained for experimental purposes. The monk seal typically participated in one audiometric session per day, five days per week. Data collection occurred over a 12-month period beginning in April 2019.

Testing Environment

Audiometric testing was conducted in a sound-attenuating, hemi-anechoic acoustic chamber (Eckel Industries, Cambridge, MA, USA) that was located 30 m from the seal's living enclosure. This custom chamber had a 3.3 x 2.3 x 2.2 m testing room with double paneled stainless-steel walls and ceiling lined with fiberglass-filled aluminum wedges. The floor of the chamber was covered with thick (>2 cm) foam mats. Sessions were controlled by a technician from an adjacent, sound-isolated room and monitored in real time with a video surveillance system.

Ambient noise in the acoustic chamber was measured prior to each session in the absence of the animal. One-minute, unweighted measurements were obtained with a battery-powered 2250 or 2270 sound analyzer (Brüel and Kjær A/S, Nærum, Denmark) with a calibrated Brüel and Kjær 4189 free-field microphone (flat frequency response 0.006–20 kHz), which was placed at the location corresponding to the center of the monk seal's head during testing. We calculated percentile statistics of 1/3-octave band noise levels from equivalent continuous sound pressure levels (L_{eq}) for frequencies from 0.04 to 20 kHz. Power spectral density levels for the entire study period were then calculated from the median of daily 1/3-octave band 50th percentile measurements (L50) that included each test frequency. Equipment limitations prevented absolute noise measurements above 20 kHz.

Audiometric Procedure

We used cooperative behavioral methods to measure hearing sensitivity with a ‘go/no-go’ psychoacoustic procedure (Stebbins 1970) (Online Resource 1). After voluntarily leaving his home pool to enter the acoustic chamber with a trainer, KE18 placed his head on a polyvinyl chloride (PVC) listening station that ensured consistent positioning of his ears 0.3 m above the foam mat within a calibrated sound field. The trainer remained to the right of the seal, at least 1 m behind the station. A PVC response target was located 23 cm to the left of the station, and a light in front of the station indicated the 5-s window during which a signal could be presented. Each trial began when the monk seal was settled in the station and ended either when he touched the response target to indicate the presence of a signal or withheld this response for the full 5-s trial interval when he did not perceive a signal. Correct responses—remaining still at the station when no signal was present or touching the response target on signal-present trials—were marked with a conditioned acoustic reinforcer (buzzer) followed by primary reinforcement (fish) delivered by the trainer. Incorrect responses—remaining still on the station during a signal-present trial (miss) or touching the response target on a signal-absent trial (false alarm, FA)—were not reinforced and KE18 continued on to the next trial after a brief pause. The trainer received instructions via headphones and was unaware of individual trial conditions; even so, to prevent inadvertent cuing, the trainer was positioned out of the seal’s view on each trial.

An adaptive staircase method was used to estimate hearing threshold (Cornsweet 1962). For each session, frequency was held constant and signal amplitude was manipulated. Sessions began with signals presented at an easily detectable level (~20 dB above expected threshold), after which signal amplitude was decreased by 4 dB after each correct detection (hit) until the first miss. Signal amplitude was then increased by 4 dB following each miss and decreased by 2 dB following each correct detection. After five hit-to-miss transitions within a span of 6 dB, the signal was returned to an easily detectable level for multiple trials to maintain stimulus control at the end of the session. Sessions included 40 – 60 trials in a predetermined, pseudorandom order with signals presented on 50 – 70% of trials. This ratio was manipulated between sessions to maintain a consistent response bias over the study interval. False alarm rate was calculated as the number of FAs out of the total number of signal-absent trials during the 'test-phase' of the session—that is, between the first and fifth consistent hit-to-miss transitions.

Testing was completed at each frequency when performance was stable, and the average miss level fell within 3 dB across three sessions. A psychometric function was fit to the proportion of correct detections at each signal level presented, and an inverse prediction was applied to determine threshold as the sound pressure level (SPL, dB re 20 μPa) corresponding to 50% correct detection (see Finney 1971). Threshold criteria required 95% confidence intervals to be less than 4 dB and corresponding FA rate to be above 0.0 and below 0.3. We tested frequencies to completion in random order, and repeated testing at two frequencies to ensure no learning effect over the course of the experiment.

Absolute Hearing Thresholds

We measured auditory sensitivity at 11 frequencies across the range of hearing: in octave steps from 0.1 to 25.6 kHz and at 33.2 kHz, the highest frequency to which KE18 exhibited reliable responses. Additionally, we measured hearing at 18.1 kHz to complement his underwater audiogram (Sills et al. 2021). This frequency was of particular interest due to increased sensitivity noted under water in this region by Thomas et al. (1990).

Acoustic stimuli were 500 ms frequency modulated upsweeps with 10% bandwidth (+/- 5% from center frequency) and 5% rise/fall times, generated using Hearing Test Program (HTP) software (Finneran 2003). The stimuli were sent through a USB-6259 BNC M-series data acquisition module (update rate 500 kHz; NI, Austin, TX, USA), a 3364 anti-aliasing bandpass filter (Krohn-Hite, Brockton, MA, USA), and a PA5 digital attenuator (Tucker-Davis Technologies, Alachua, FL, USA) to the designated speaker in the acoustic chamber. Signals were projected through a 2245H speaker (JBL Incorporated, Northridge, CA, USA) for 0.1 kHz signals, a JBL 2123H speaker for 0.2 to 6.4 kHz signals, or a FT96H speaker (Fostex Company, Tokyo, Japan) for 12.8 to 33.2 kHz signals. These transducers were positioned 0.8 to 1.4 m in front of and on axis with the station. We determined speaker locations through spatial mapping of the sound field, which we conducted at each frequency to ensure that variability in received signals did not exceed +/- 3 dB across 14 positions. The mapping grid included each ear and six points surrounding each ear with 2 cm spacing (forward/backward, left/right, and up/down from the ear position). This grid encompassed all possible locations of the external ears during testing.

Signals were calibrated daily at the location of the external ear that had the higher received level during spatial mapping. Signals were measured at a range of amplitudes and evaluated in the time and frequency domains to ensure integrity. During spatial mapping and calibration, signals were received by a MK301 microphone capsule (0.005–100 kHz, ±2 dB; Microtech Gefell GmbH, Gefell, Germany) with a C617 body (Josephson Engineering, Santa Cruz, CA, USA) and BPS-1 power supply (Stewart Electronics, Rancho Cordova, CA, USA) and passed through the same filter and data acquisition hardware used for signal generation before being measured in HTP. Sound field mapping and daily calibration were conducted in the absence of the animal.

Masked Hearing Thresholds

We measured masked hearing thresholds at the two frequencies with lowest absolute thresholds (800 Hz and 3200 Hz) in the presence of octave-band white noise centered at each test frequency. Critical ratios (CRs) were calculated as the difference between the SPL of the masked threshold and the power spectral density level of the masking noise (Fletcher 1940). Due to KE18's elevated absolute thresholds, testing was limited to the two frequencies of best sensitivity where maximum signal level did not need to exceed 90 dB re 20 µPa during audiometry[2].

The auditory masking paradigm was similar to that used for the audiogram, with the addition of masking noise paired with the onset of the trial light. Masking noise was generated and spectrally flattened with custom LabVIEW software (NI, Austin, TX, USA), projected through the computer sound card, and mixed with the test signal at a P1000 power amplifier (Hafler Professional, Tempe, AZ, USA) before reaching the JBL 2123H speaker. Masker duration was 8 s (500 ms rise/fall time) with the received spectral density level 10 dB above the corresponding absolute hearing threshold. Masked thresholds were measured using the same adaptive staircase procedure described earlier.

We spatially mapped the masking noise to ensure a stable sound field using the 14-position grid described previously. The 1/3-octave band levels comprising the octave-band masker were measured to confirm acceptable variability (≤ 6 dB) of all three bands across the mapping grid. Additionally, mapping confirmed that the center 1/3-octave band level measured at all 14 positions fell within 3 dB of that received at the

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[2] Levels required for testing at other frequencies were above those authorized by the National Marine Fisheries Service (marine mammal research permit 19590 to T. Williams).

daily calibration position. The masker was calibrated prior to each session to confirm that the center 1/3-octave band was within 1 dB of expected and that the surrounding 1/3-octave bands were within 3 dB of expected. During spatial mapping and calibration, masking noise was received through the Microtech microphone and analyzed with Spectra-PLUS software v.5.2.0.14 (Pioneer Hill Software LLC, Poulsbo, WA, USA) on a laptop computer.

External Ear Morphology

To evaluate external ear anatomy in relation to what is known about hearing capabilities in the two Phocidae subfamilies, we conducted a simple comparison of the sizes of the external ear openings for the 18 extant true seal species. We used Adobe Illustrator v.23.1.1 (Adobe Inc., San Jose, CA, USA) to digitally trace a silhouette of each species from reference photos, including the meatal opening and other anatomical landmarks. Seals were hauled out or at the surface of the water in all photos.

Results

Audiogram

Absolute (unmasked) in-air hearing thresholds, false alarm rates, ambient noise levels, and threshold-to-noise offsets are provided for one Hawaiian monk seal in Table 1. The resulting audiogram and associated ambient noise floor, along with representative auditory data for Monachinae and Phocinae seals, are shown in Figure 2. Psychometric functions for the thresholds are provided in Online Resource 2.

The audiogram lacked the characteristic U-shape of mammalian hearing curves and instead was relatively flat with a distinct elevation at 6.4 kHz. The functional range of hearing—the range of frequencies audible at 60 dB re 20 µPa (as in Heffner and Heffner 2007)—fell between 0.1 and 33 kHz, spanning almost eight octaves across the audiogram. The lowest threshold of 40 dB re 20 µPa was measured at 0.8 and 3.2 kHz, indicating relatively poor overall sensitivity to airborne sounds. The difference between the low- and high-frequency hearing limits and best hearing was only 20 dB. Additionally, the low- and high-frequency regions of the audiogram did not show pronounced declines in sensitivity; the low-frequency slope was approximately 7 dB per octave, while the high-frequency slope was approximately 18 dB per octave. Audiometric signals transitioned from inaudible (0% detection) to reliably detectable (100% detection) over a range of 6 to 10 dB.

The measured audiogram fell well above the ambient noise floor with threshold-to-noise offsets ranging from 47 to 82 dB. Repeated testing revealed differences of 3 dB or less for thresholds at both 6.4 and 12.8 kHz. KE18's average false alarm rate throughout testing was 0.16 (range: 0.05-0.25).

Critical Ratios

Masked thresholds, masking noise levels, critical ratios, and false alarm rates evaluated at two frequencies are provided in Table 1. Critical ratios were 23 and 28 dB at 0.8 and 3.2 kHz, respectively. These data are shown in Figure 3 with representative data from several Phocinae and Monachinae seal species. KE18's average false alarm rate during these measurements was 0.17 (range: 0.16-0.18).

Comparative Auditory Anatomy

Digitally illustrated silhouettes of all 18 extant true seals are provided in Figure 4a for a comparison of the external auditory meatal opening size relative to other anatomical landmarks. This depiction shows that all Monachinae seals have an extremely small and essentially closed meatal orifice compared to the relatively larger meatal openings of Phocinae species. A phylogenetic representation of the Phocidae family, which references species for which recent audiometric data are available (Figure 2, Figure 3), is provided in Figure 4b.

Discussion

This Hawaiian monk seal exhibited notably poor terrestrial hearing, with best sensitivity of 40 dB re 20 µPa and a range of functional hearing extending from 0.1 to 33 kHz. Hearing range was constrained in both the low- and high-frequency regions of the audiogram relative to that of Phocinae seals evaluated under the same conditions; best sensitivity was approximately 50 dB higher. The distinct upward notch at 6.4 kHz, which is also evident in the underwater audiogram of this individual (Sills et al. 2021), does not occur in other true seals. Overall, as observed for KE18's underwater audiogram, this hearing curve does not correspond well with those of related species but best matches that of the northern elephant seal (Reichmuth et al. 2013)—the only other Monachinae seal for which auditory data are available.

The elevated thresholds of this individual compared to Phocinae seals cannot be explained by experimental conditions or animal behavior. High threshold-to-noise offsets indicate that ambient noise in the acoustic chamber did not influence measured hearing thresholds. Rather, auditory thresholds were well above noise levels at all frequencies. Typically, species-specific critical ratios are compared to threshold-to-noise offsets to determine whether thresholds could have been limited by background noise. As the only critical ratios available for Hawaiian monk seals are the two from this study, we used available data for other true seals for the remaining frequencies (Erbe et al. 2016; Sills et al. 2020). Threshold-to-noise offsets generously exceeded predicted critical ratios at each frequency (by 30-61 dB). In addition, KE18 did not exhibit an overly conservative response bias, which could have prevented the measurement of lower thresholds. Finally, the seal's reliable behavior during testing and subsequent repeated testing at two frequencies confirms that his performance did not improve after additional experience with the task. Thus, the measurement of elevated absolute (unmasked) hearing thresholds cannot be attributed to insufficient practice on the behavioral task.

Critical ratios at 0.8 and 3.2 kHz were 3 to 10 dB higher than representative data from both true seal subfamilies. However, these values did increase with increasing frequency at a similar rate as for other true seals. Additional data are needed for a more complete comparison of masked hearing abilities, but further testing was not possible in this case. Our limited masking data suggest that Hawaiian monk seals may not have the same derived ability as other true seals to hear well in noisy environments.

These auditory data are available for only one subject, as is the case for the northern elephant seal (Reichmuth et al. 2013). Therefore, the high auditory thresholds measured for this seal across the frequency range of hearing could potentially be due to individual differences and not representative of all conspecifics. However, the poor terrestrial hearing of the two Monachinae seals tested thus far is consistent with the evolutionary biology of true seals, especially with respect to auditory anatomy.

Relevance to Auditory Anatomy

Certain aspects of Hawaiian monk seal auditory anatomy may help explain the apparently reduced hearing sensitivity of this species. In particular, features of the external auditory meatus of Monachinae seals likely limit terrestrial auditory abilities;

this opening can be qualitatively described as a pinhole that is often occluded with hair, making it essentially closed in air. Further, it is unknown whether the auditory canal is air filled or collapsed when these seals are resting on land. Thus, it seems reasonable to conclude that the ability of Monachinae seals to receive airborne sounds through the conventional terrestrial pathway is reduced (e.g., Kastak and Schusterman 1999). In contrast, the orifice of the external ear opening of Phocinae seals—who possess acute in-air hearing abilities—is large and surrounded by muscles that enable voluntary opening and closing of the channel leading to the auditory canal. When these seals are listening in air, this canal is thought to remain open and air filled, enabling hearing to occur efficiently through the conventional pathway (Møhl 1968). To put these anatomical differences into perspective, occluding the human meatal opening with finger, palm, or tragus causes a 25 to 45 dB reduction in hearing threshold (Holland 1967), enough to largely account for the elevated hearing thresholds observed in the two Monachinae seals evaluated thus far. A further reduction in terrestrial hearing ability may occur within the auditory canal, as King (1969) notes that the portion of the canal immediately behind the meatal opening has a longer unsupported section than in Phocinae species. Based on these anatomical considerations, it appears that the reception of airborne sounds may be constrained in all Monachinae seals by their peripheral auditory anatomy (as illustrated in Figure 4a). These anatomical characteristics explain both elevated aerial hearing thresholds measured behaviorally in Hawaiian monk seals and northern elephant seals, as well as small-amplitude auditory evoked potentials (AEPs) measured electrophysiologically in several

Monachinae species, including northern and southern elephant seals, *Mirounga leonina* (Bornemann et al. 2007; Houser et al. 2007; Reichmuth et al. 2007; Houser et al. 2008) and leopard seals, *Hydrurga leptonyx* (Tripovich et al. 2010).

While many features of the middle ear are shared among true seals, there are anatomical indications that suggest a divergence between the two subfamilies. The ossicles of the middle ear are heavy and enlarged in northern elephant seals (Marsh 2001), a trait that could also influence sound conduction (if present) in other Monachinae seals. Another notable difference is the area ratio between the tympanic membrane and the oval window. Terrestrial hearing is improved when this ratio is large (*i.e.*, the oval window is relatively small), because ossicular movement is amplified upon reaching the cochlea. More anatomical data are needed, but this ratio has been measured as 18-38:1 versus 9-10:1 in Phocinae and Monachinae species, respectively (Repenning 1972; King 1983). The higher tympanic membrane to oval window ratio in Phocinae seals is more similar to that of terrestrial Carnivores with sensitive in-air hearing (>35:1; King 1983). While this area ratio cannot be used to estimate hearing sensitivity, a lower value for the Monachinae species suggests relatively poorer middle ear function with reduced hearing ability (Rosowski 1994, Mason 2016), as well as increased pressure tolerance during submersion (Repenning 1972). A final intriguing characteristic of the middle ear of Hawaiian monk seals concerns the distribution of cavernous tissue lining the middle ear cavity. Their particular distribution is notably similar to that of the distantly related otariid Carnivores (Repenning 1972; Repenning and Ray 1977) and can be considered a basal or more ‘primitive’ auditory trait (Wyss 1988).

In terms of skull morphology, the petrous bone—a pyramid-shaped portion of the temporal bone housing the inner ear—differs in monk seals relative to other true seals. Monk seals have a dorsoventrally flattened petrosal apex with a v-shaped outline in contrast to the hypertrophied bone at the petrosal apex of most other seals (Repenning and Ray 1977; Wyss 1988). In Hawaiian monk seals, the dorsal part of the petrosum is unexpanded; conversely, this surface is enlarged in Phocinae seals and may be linked to sensitive underwater hearing (Repenning and Ray 1977; Wyss 1988). This feature of the petrosum in Hawaiian monk seals is not only unique among extant seals, but among fossil species as well. Unlike other true seals, monk seals also have vestigial remnants of the petrosal lip roof of the internal auditory meatus (Wyss 1988), which suggests similarities to otarrid and odobenid Carnivores and may imply less derived auditory anatomy than other true seals. With respect to the cochlea, it has been noted that the basal whorl of the Hawaiian monk seal cochlea is relatively small compared to those of other seals (Repenning and Ray 1977); in addition, the distinct upward notch of this audiogram at 6.4 kHz suggests a cochlear anatomy that may be unique to the species. Together, these features of the inner ear and surrounding skull suggest that Hawaiian monk seals may have the least derived auditory anatomy of all true seals, which could help to explain the reduced sensitivity of this species to both airborne and waterborne sounds.

Relevance to Phylogenetic Relationships

Observed anatomical differences between Phocidae subfamilies may not be unexpected given the evolutionary history of this group. Recently, fossils dating to the Pliocene (~3-5 mya) were discovered in New Zealand and identified as a new species of monk seal—the first monk seal ever found in the southern hemisphere (Rule et al. 2020). This finding contradicts the prevailing theory that monk seals evolved exclusively in the northern hemisphere. Instead, these new data suggest that all three Monachinae tribes coexisted in the southern hemisphere and that Monachinae evolution primarily occurred in isolation from the northern Phocinae seals. This discovery has profound impacts on our biogeographical understanding of true seal evolution. Analysis of the monk seal lineage based on both fossil and genetic evidence suggests that Hawaiian monk seals are the oldest species in this group (Rule et al. 2020), contrary to recent categorization of the Mediterranean monk seal as the earlier diverging species (Scheel et al. 2014). This new interpretation of monk seal evolution may explain the 'primitive' auditory anatomy observed in this species and, thus, their apparently reduced hearing abilities.

Because monk seals are the oldest branch within the Monachinae lineage, similarities in hearing ability with the more recently derived, deep-diving elephant seals suggest common selective pressures on ancestral species more than 12 million years ago.

However, audiometric measurements obtained with additional Monachinae species are needed to confirm this idea. As most hearing data in marine mammals come from a few representative species, our unexpected findings for Hawaiian monk seals underscore the importance of sampling within and across phylogenetic clades to better understand auditory adaptations from an evolutionary perspective.

Relevance to Social Communication

The auditory data reported in this study confirm that, while Hawaiian monk seals have poor sensitivity to airborne sounds in general, they are capable of detecting their own low-frequency vocalizations. However, their elevated thresholds indicate that terrestrial signaling probably occurs over relatively short ranges (as noted in Miller and Job 1992) or could rely on the production of high-amplitude calls. For example, male northern elephant seals overcome poor hearing sensitivity by emitting airborne calls that are among the loudest measured to date (Southall et al. 2019b). The source levels of Hawaiian monk seal airborne vocalizations have not yet been measured but do not seem to be of particularly high amplitude (Stacie Robinson, personal communication). It is possible that multimodal cues including acoustic, seismic, visual, or olfactory components (Miller and Job 1992) facilitate social communication during the extended breeding season in this species.

Implications for Conservation and Management

The auditory measurements reported for this individual address significant gaps in our understanding of sensory systems—including the use of sound—in Hawaiian monk seals. From a management perspective, we note that the reported audiogram is captured by the Phocid Carnivores in Air (PCA) hearing group proposed in recent marine mammal noise exposure criteria (Southall et al. 2019a). Thus, the application of the PCA weighting function to predict potential noise effects is likely conservative for this species. However, elevated critical ratio measurements suggest that Hawaiian monk seals do not have efficient hearing in noise and therefore may be more susceptible to auditory masking. As critical ratios can be applied to predict masking in terrestrial and aquatic environments (see Richardson et al. 1995; Reichmuth 2012; Erbe et al. 2016), these data enable estimation of auditory masking induced by natural and anthropogenic noise in both media.

This study advances knowledge of the acoustic ecology of Hawaiian monk seals, including auditory adaptations, evolutionary considerations, and social communication. While additional behavioral measurements describing auditory capabilities for this species and other Monachinae seals will be difficult and expensive to obtain, such data are needed to validate these findings and conclusions.

Acknowledgements

This work would not have been possible without the significant support of T. Williams and T. L. Kendall at the Marine Mammal Physiology Project and the ongoing encouragement and guidance of A. Kumar and M. Shoemaker at the US Navy's Living Marine Resources Program. We thank the committed husbandry and research teams of Long Marine Laboratory, especially R. Jones for technical support and R. Rozin for assistance with data curation. Reference photographs for digital illustrations were provided by: R. S. Beltran, C. Casey, A. S. Friedlaender, and M. Meranda at UC Santa Cruz; M. Cameron at NOAA; E. Levy at Humboldt State University; and N. Lubcker at University of Pretoria. J. Finneran of the U.S. Navy Marine Mammal Program provided access to custom LabVIEW software for the measurement of auditory thresholds and the generation of masking noise. At UC Santa Cruz, we thank D. Casper for veterinary care, J. Fiechter and T. Williams for reviewing this manuscript, and J. Kendall-Bar for inspirational scientific illustration workshops. We thank J. Terhune at University of New Brunswick and two anonymous reviewers for helpful comments on this manuscript. Lastly, we acknowledge the continued support of this research by J. Pawloski at SeaLife Park and A. Sloan at the National Marine Fisheries Service. A portion of this work was presented at the 178th meeting of the Acoustical Society of America.

Declarations

Funding

Funding for this study was provided by the U.S. Navy's Living Marine Resources Program. Supplemental funding to B. Ruscher was provided through the Dr. Earl H. Myers and Ethel M. Myers Oceanographic and Marine Biology Trust and the Friends of Seymour Marine Discovery Center. B. P. Richter was supported in part by the Office of Naval Research.

Compliance with Ethical Standards

Research was conducted with approval and oversight from the Institutional Animal Care and Use Committee at the University of California Santa Cruz, with authorization from the National Marine Fisheries Service of the United States (research permit 19590 to T. Williams).

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Chapter 1: Figures and Tables

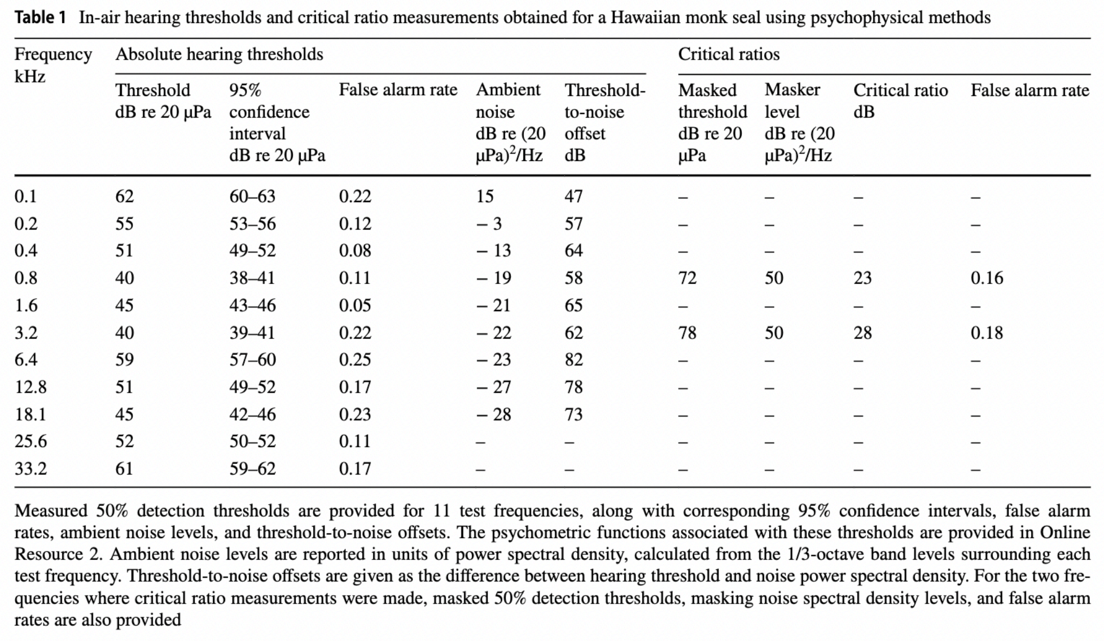


Table 1 In-air hearing thresholds and critical ratio measurements obtained for a Hawaiian monk seal using psychophysical methods

Frequency kHz	Absolute hearing thresholds					Critical ratios			
	Threshold dB re 20 μPa	95% confidence interval dB re 20 μPa	False alarm rate	Ambient noise dB re (20 μPa)^2/Hz	Threshold-to-noise offset dB	Masked threshold dB re 20 μPa	Masker level dB re (20 μPa)^2/Hz	Critical ratio dB	False alarm rate
0.1	62	60–63	0.22	15	47	–	–	–	–
0.2	55	53–56	0.12	− 3	57	–	–	–	–
0.4	51	49–52	0.08	− 13	64	–	–	–	–
0.8	40	38–41	0.11	− 19	58	72	50	23	0.16
1.6	45	43–46	0.05	− 21	65	–	–	–	–
3.2	40	39–41	0.22	− 22	62	78	50	28	0.18
6.4	59	57–60	0.25	− 23	82	–	–	–	–
12.8	51	49–52	0.17	− 27	78	–	–	–	–
18.1	45	42–46	0.23	− 28	73	–	–	–	–
25.6	52	50–52	0.11	–	–	–	–	–	–
33.2	61	59–62	0.17	–	–	–	–	–	–

Measured 50% detection thresholds are provided for 11 test frequencies, along with corresponding 95% confidence intervals, false alarm rates, ambient noise levels, and threshold-to-noise offsets. The psychometric functions associated with these thresholds are provided in Online Resource 2. Ambient noise levels are reported in units of power spectral density, calculated from the 1/3-octave band levels surrounding each test frequency. Threshold-to-noise offsets are given as the difference between hearing threshold and noise power spectral density. For the two frequencies where critical ratio measurements were made, masked 50% detection thresholds, masking noise spectral density levels, and false alarm rates are also provided

Fig. 1. Hawaiian monk seal KE18. Photo collection authorized under NMFS permit 19590. Photo credit: C. Reichmuth

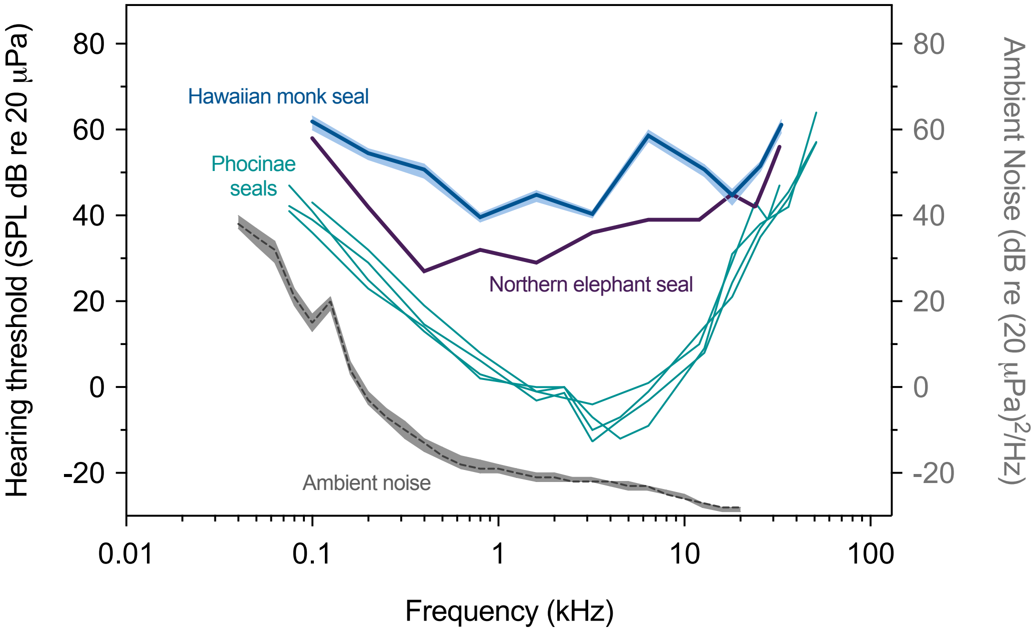


Fig. 2. In-air audiogram for one Hawaiian monk seal, obtained using psychophysical methods; the shaded area around the audiogram depicts 95% confidence intervals. Associated hearing data are provided in Table 1. Ambient noise in the testing environment (dashed line corresponding to the right y-axis) is reported in terms of power spectral density levels; this noise curve is bounded by the 10th (above) and 90th (below) percentile statistics of the noise distribution. For comparison, audiograms are shown for representative species from each subfamily of true seals. Hearing data for the Phocinae subfamily include audiograms for harbor [n=1, (Reichmuth et al. 2013)], spotted [n=2, (Sills et al. 2014)], and ringed seals [n=1, (Sills et al. 2015)]. For the Monachinae subfamily, data are only available for the northern elephant seal [n=1, (Reichmuth et al. 2013)] (Color online)

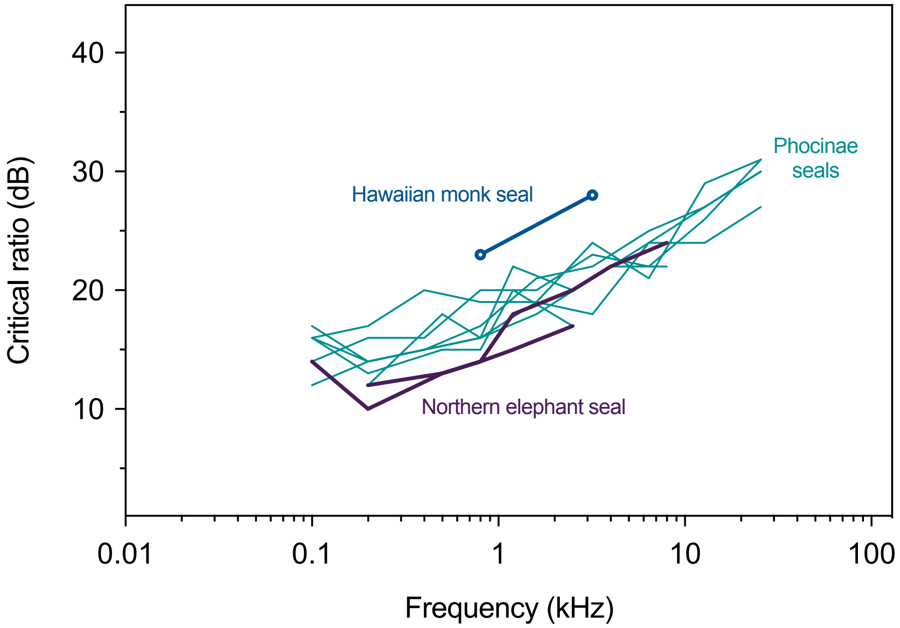
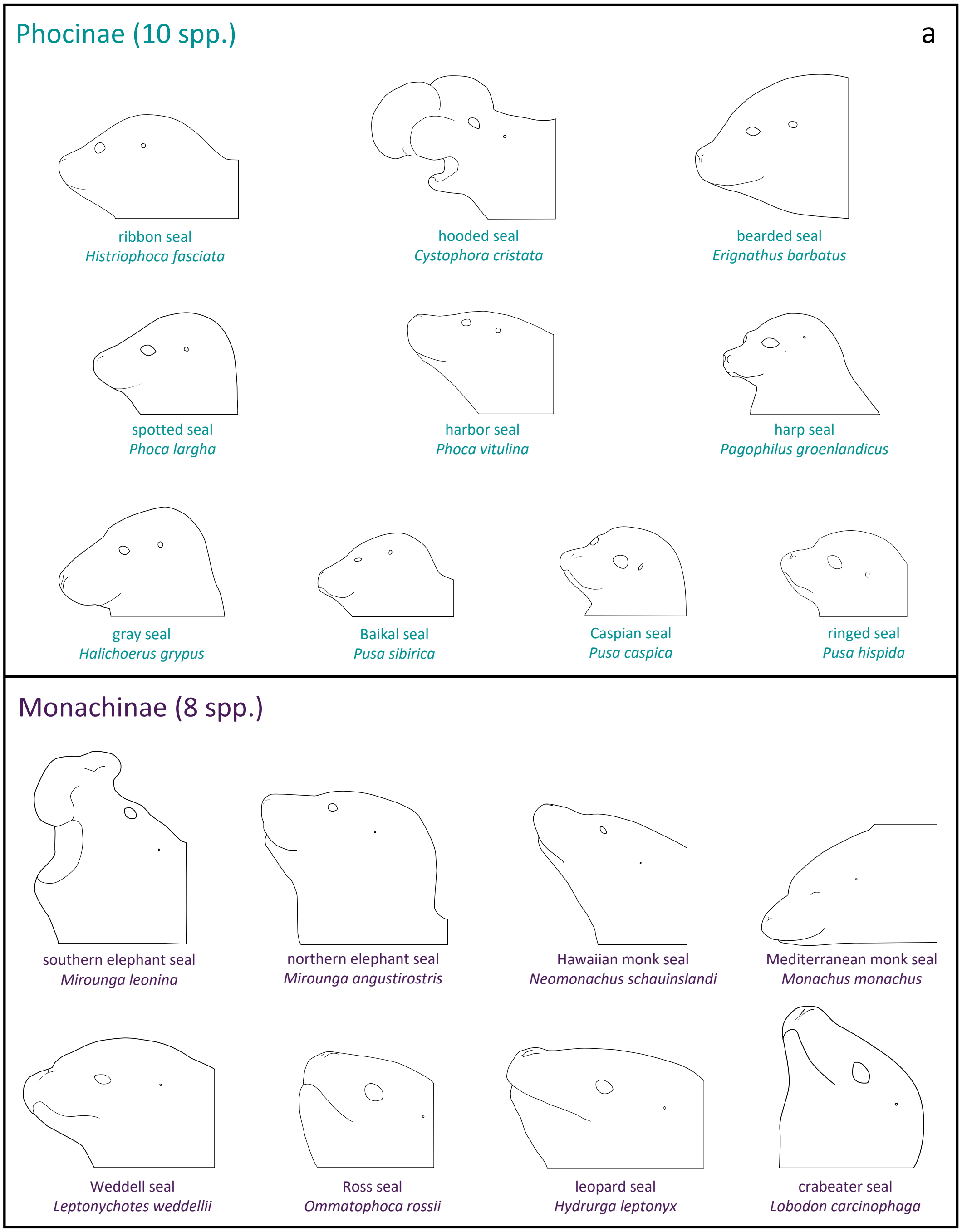


Fig. 3. Critical ratio measurements for one Hawaiian monk seal at 0.8 and 3.2 kHz (open circles). For comparison, critical ratios are shown for representative species from each subfamily of true seals. Data are provided for bearded, *Erignathus barbatus* [n=1, (Sills et al. 2020)], harbor [n=1, (Southall et al. 2000, 2003)], ringed [n=2, (Sills et al. 2015)], and spotted seals [n=2, (Sills et al. 2014)] of the Phocinae subfamily. For the Monachinae subfamily, critical ratio measurements are only available for the northern elephant seal [n=1, (Southall et al. 2000, 2003)] (Color online)


Phocinae (10 spp.)
a
ribbon seal
Histriophoca fasciata
hooded seal
Cystophora cristata
bearded seal
Erignathus barbatus
spotted seal
Phoca largha
harbor seal
Phoca vitulina
harp seal
Pagophilus groenlandicus
gray seal
Halichoerus grypus
Baikal seal
Pusa sibirica
Caspian seal
Pusa caspica
ringed seal
Pusa hispida
Monachinae (8 spp.)
southern elephant seal
Mirounga leonina
northern elephant seal
Mirounga angustirostris
Hawaiian monk seal
Neomonachus schauinslandi
Mediterranean monk seal
Monachus monachus
Weddell seal
Leptonychotes weddellii
Ross seal
Ommatophoca rossii
leopard seal
Hydrurga leptonyx
crabeater seal
Lobodon carcinophaga

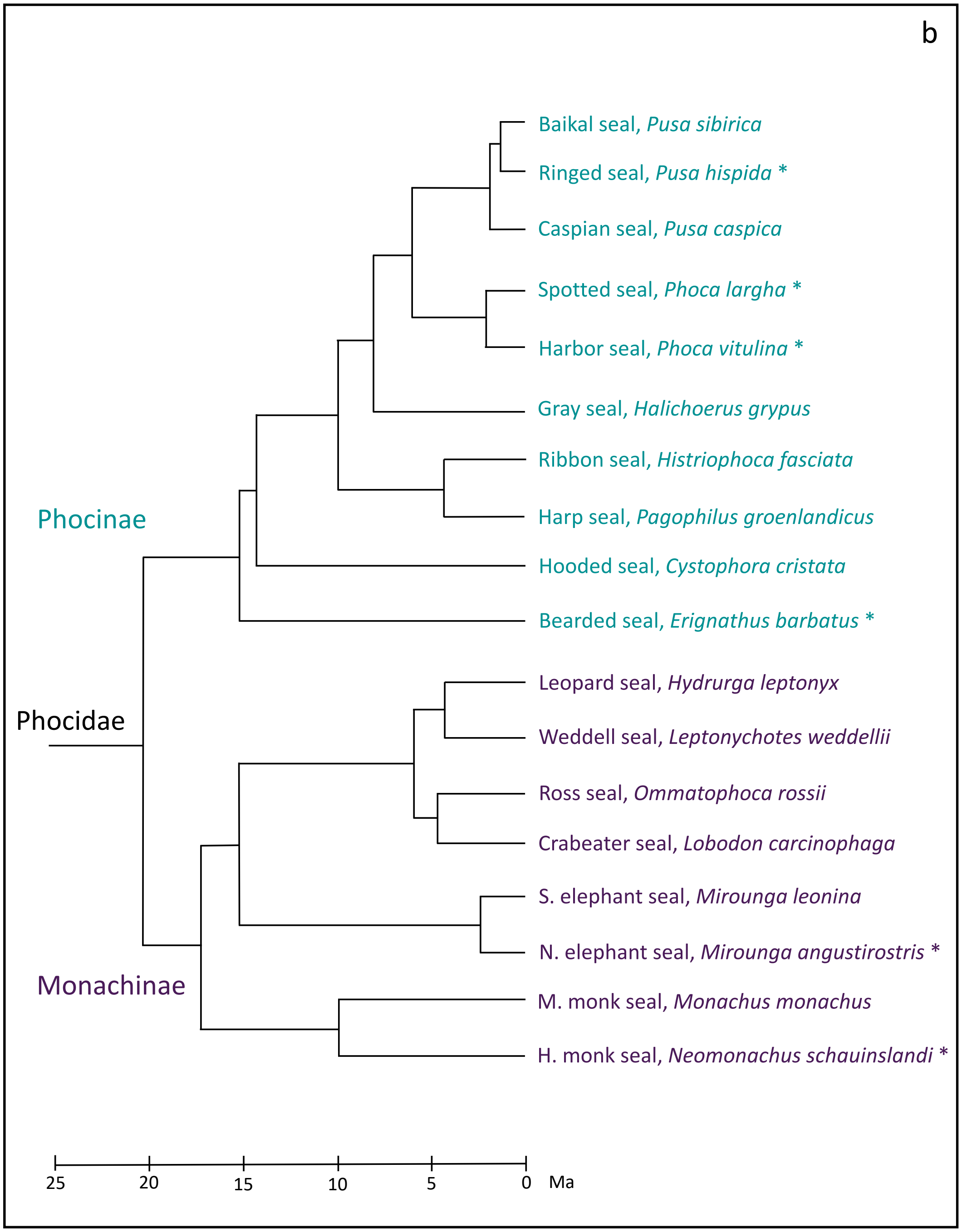
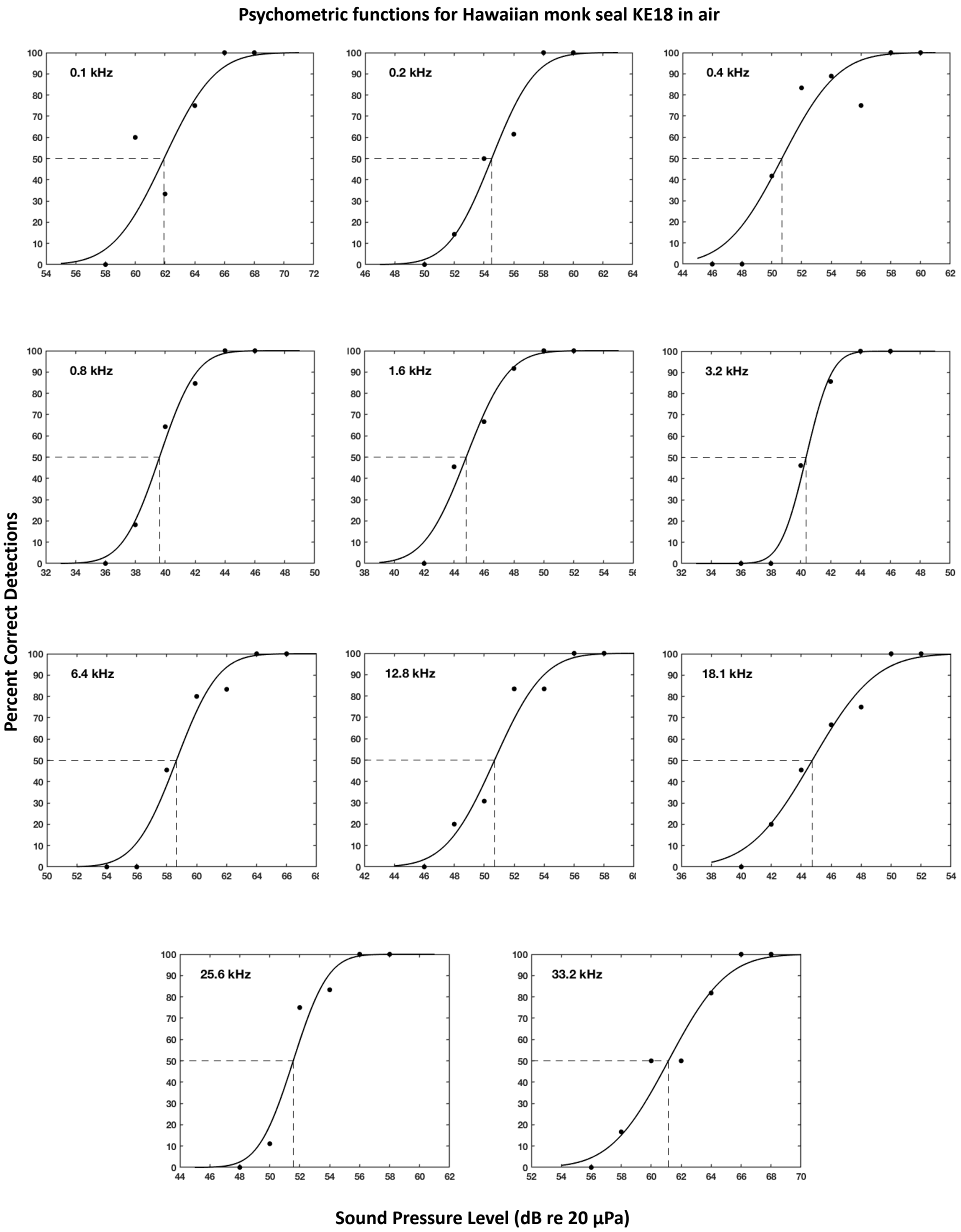

b
Baikal seal, *Pusa sibirica*
Ringed seal, *Pusa hispida* *
Caspian seal, *Pusa caspica*
Spotted seal, *Phoca largha* *
Harbor seal, *Phoca vitulina* *
Gray seal, *Halichoerus grypus*
Ribbon seal, *Histriophoca fasciata*
Harp seal, *Pagophilus groenlandicus*
Hooded seal, *Cystophora cristata*
Bearded seal, *Erignathus barbatus* *
Leopard seal, *Hydrurga leptonyx*
Weddell seal, *Leptonychotes weddellii*
Ross seal, *Ommatophoca rossii*
Crabeater seal, *Lobodon carcinophaga*
S. elephant seal, *Mirounga leonina*
N. elephant seal, *Mirounga angustirostris* *
M. monk seal, *Monachus monachus*
H. monk seal, *Neomonachus schauinslandi* *
Phocinae
Phocidae
Monachinae
25
20
15
10
5
0
Ma

Fig. 4. Silhouettes of the 18 extant seal species of family Phocidae and their phylogenetic relationships. a) Evaluation of external auditory meatus opening size between the Monachinae and Phocinae subfamilies reveals that all Monachinae species have extremely small, likely occluded meatal orifices while those of the Phocinae species are comparatively large and open. Images were traced from reference photographs of seals while hauled out or at the water's surface and are approximately scaled to reflect differences in head size across species. Illustrations are internally consistent, with accurate representation of the relative position and size of key facial features. b) The scaled Phocidae phylogeny is adapted from Rule et al. (2020), with both subfamilies rotated at the first node so the earlier diverging species are at the base. Extinct lineages are not shown. Some details of the Phocidae phylogeny remain to be resolved (see Árnason et al. 2006; Higdon et al. 2007; Fulton and Strobeck 2010; Berta et al. 2018; Rule et al. 2020). The six seal species with recent behavioral hearing data (see Figure 2, Figure 3) are marked with an asterisk (*)

Chapter 1: Supplementary Material

Online Resource 1. Examples of auditory go/no-go trials conducted with a Hawaiian monk seal in the acoustic chamber at Long Marine Laboratory, Santa Cruz, CA

*This supplementary video file can be accessed through the following link:
https://doi.org/10.1007/s00359-021-01498-y



Online Resource 2. Psychometric functions obtained for one Hawaiian monk seal at 11 frequencies in air, with percent correct detection on signal-present trials (y-axis) shown as a function of sound pressure level in dB re 20 µPa (x-axis). Probit analysis was used to fit these functions to the percent correct detection at each stimulus level presented (6-8 SPLs and 38-51 trials pooled from three final staircase sessions for each frequency). The dashed line represents the stimulus level corresponding to 50% correct detection, as measured using an inverse prediction

Chapter 2

Psychoacoustic data confirm reduced hearing sensitivity in Hawaiian monk seals relative to Phocinae seals

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Ruscher B, Sills JM, Packard N, Kendall TL, Williams TM, Reichmuth C (2025) Psychoacoustic data confirm reduced hearing sensitivity in Hawaiian monk seals relative to Phocinae seals. Endang Species Res 56:19-26.
https://doi.org/10.3354/esr01377

Abstract

We presently have an incomplete understanding of hearing in Hawaiian monk seals (*Neomonachus schauinslandi)*. Their auditory biology is important from a conservation perspective and is especially intriguing given their long evolutionary isolation from related seal species. Available audiometric data for two individuals are conflicting but suggest that monk seals have limited aquatic and terrestrial hearing abilities compared to the more well-studied species in the Phocinae subfamily of seals. To resolve representative amphibious hearing profiles for Hawaiian monk seals, we describe auditory sensitivity for one additional seal trained to participate in a psychophysical task while submerged and on land. Detection thresholds were measured for narrowband signals across the frequency range of hearing under water and at select frequencies in air. This individual demonstrated poor sensitivity in both media, with notable insensitivity to high-frequency waterborne sounds and an overall decreased ability to detect airborne sounds. The range of functional hearing was wider in water (< 0.1 – 40 kHz) than in air (0.1 – 33 kHz), with peak sensitivities of 73 dB re 1 µPa (at 18 kHz) and 42 dB re 20 µPa (at 3.2 kHz), respectively. These data confirm recently published behavioral audiograms as typical for the species. When considered with the limited available data for related species, these findings suggest that hearing within the Monachinae subfamily of seals differs from that of the highly sensitive Phocinae seals. This study advances knowledge of the evolution of hearing in amphibious marine

mammals and supports conservation and management decisions for the endangered Hawaiian monk seal.

Introduction

True seals—the semi-aquatic carnivores of the family Phocidae—have evolved to utilize sound in two very different physical environments, with waterborne sounds traveling faster and attenuating less than airborne sounds of the same frequency content. The consequences of these medium-dependent characteristics of sound for different seal species can be considered relative to their phylogenetic relationships, anatomical adaptations, and specific hearing abilities. Our knowledge of hearing in seals has increased substantially in recent decades, but several questions and data gaps remain (see Southall et al. 2019). The most complete dataset describing amphibious hearing is for the Phocinae subfamily (polar and most temperate seals of the Northern Hemisphere). These data indicate that Phocinae seals have acute amphibious hearing abilities, with best sensitivities rivaling those of aquatic and terrestrial mammalian specialists in their respective media (Kastelein et al. 2009, Reichmuth et al. 2013, Sills et al. 2014, 2015, 2020). Conversely, there are few hearing data for seals from the Monachinae subfamily (the Southern Ocean seals as well as elephant and monk seals). Hearing profiles from one elephant seal and two monk seals suggest that Monachinae species have significantly reduced abilities in air and water relative to other true seals, with especially poor sensitivity to airborne sound (Thomas et al. 1990, Kastak & Schusterman 1999, Reichmuth et al. 2013, Ruscher et al. 2021, Sills et al. 2021). While the available audiometric data indicate potential subfamily-level differences in hearing, additional information is needed to improve our understanding of similarities and differences in auditory biology among true seals.

Of the Monachinae species, the monk seals are of particular interest due to their Vulnerable or Endangered conservation status (Littnan et al. 2015, Karamanlidis et al. 2023) and their long evolutionary and biogeographical isolation from other true seals (Rule et al. 2021). The auditory biology of extant monk seals (*Monachus monachus* and *Neomonachus schauinslandi)* remains incompletely understood, though some hearing data are available for two Hawaiian monk seals *N. schauinslandi* studied in zoological settings. An initial underwater audiogram by Thomas et al. (1990) suggested that a young male Hawaiian monk seal was insensitive to sounds below 10 kHz, indicating that hearing in this species could differ from that of other true seals. More recently, comprehensive audiometric measurements were obtained to describe amphibious hearing capabilities in another Hawaiian monk seal. Sills et al. (2021) reported a much broader range of hearing in water, more similar to that of Phocinae seals despite a somewhat lower high-frequency hearing limit and elevated thresholds overall. Ruscher et al. (2021) reported poor sensitivity to airborne sounds in the same individual, with an unusually flattened audiogram and peak sensitivity approximately 50 dB higher than that measured for Phocinae seals. While these data collectively suggest that monk seals have reduced hearing abilities both above and below the water's surface, the unexpectedly high thresholds in both media and the discrepancies between the two underwater studies at frequencies below 10 kHz make the available audiograms difficult to interpret. More data are needed from at least one additional individual to characterize typical auditory sensitivity in Hawaiian monk seals and to help inform higher-level questions about hearing in related species.

By obtaining comprehensive behavioral hearing measurements in air and in water with a third Hawaiian monk seal and comparing these results to those of Ruscher et al. (2021), Sills et al. (2021), and Thomas et al. (1990), we resolve inconsistencies in available auditory data and confirm typical amphibious hearing abilities for *N. schauinslandi*. These findings improve our understanding of the evolution of hearing within the phocid clade of carnivores and support conservation and management decisions involving anthropogenic noise for monk seals and possibly other Monachinae species.

Materials and Methods

Subject

The subject was an adult male Hawaiian monk seal identified as KP2 (NOA0006753, also known as *Hoʻailona*). This seal was born in the wild but brought into permanent human care after his habituation to humans rendered him non-releasable (Williams 2012). KP2 participated in this auditory study at Long Marine Laboratory at the University of California (Santa Cruz, CA, USA) while on loan from the Waikīkī Aquarium (Honolulu, HI, USA). KP2 was 13 years old at the start of testing and weighed approximately 170 kg. His curvilinear interaural distance was 24 cm measured dorsally, while the straight length between his meatal openings was 19 cm. He had no known ear pathologies or exposure to ototoxic medications other than a short course (7 days) of topical tobramycin eyedrops at age five years, which was considered unlikely to be harmful to auditory structures (C. Field, personal communication). However, this seal had bilateral hypermature cataracts and lens-induced uveitis, resulting in significant permanent visual impairment.

KP2 participated in one audiometric session per day, up to five days per week. He received one-third to one-half of his scheduled daily diet of thawed fish and squid during this session. His prescribed diet was established for optimal health and was not constrained for experimental purposes. This seal had experience with operant conditioning using positive (fish) reinforcement for behavioral management and cooperative physiological research (Williams et al. 2011, Williams 2012, Kienle et al. 2019, 2020, John et al. 2021); however, he had no prior experience with auditory testing and was gradually trained over a 6-month period to respond to airborne and waterborne acoustic signals. Subsequent audiometric testing occurred in water from April 2022 to July 2023 and in air from January to August 2023.

Research was conducted with approval and oversight from the Institutional Animal Care and Use Committee at the University of California Santa Cruz, with authorization from the National Marine Fisheries Service of the United States under marine mammal research permits 24054 to T. Williams and 23554 to C. Reichmuth. Behavioral audiometry was conducted without harm, stress, or food deprivation using positively conditioned voluntary responses to tonal sounds.

Underwater Hearing Measurements

To provide direct comparative data, we replicated the underwater hearing study conducted previously with Hawaiian monk seal KE18 (NOA0006781; Sills et al. 2021) with minor adjustments. In the present study, auditory measurements for monk seal KP2 were obtained either in the same circular, partially in-ground, seawater-filled pool (1.8 m deep and 7.6 m diameter; test frequencies 0.8 kHz and above) or in an adjacent pool of the same size (0.4 kHz and below). The training methods, acoustic calibration protocols, testing apparatus, and environmental controls matched those used previously for monk seal KE18. The audiometric procedure was generally similar, with minor differences in threshold determination (see Text S1 and Table S1 in the Supplement for a detailed comparison of threshold methodology). Several items in the equipment chain, including the underwater sound projector, were different (see Fig. S1 for a detailed equipment schematic).

Underwater hearing was evaluated using a behavioral ‘go/no-go’ psychoacoustic procedure (Stebbins 1970) at 14 frequencies spanning 0.1 – 60.9 kHz (Video S1 at www.int-res.com/articles/suppl/n056p019_supp/). Hearing thresholds were measured using an adaptive staircase procedure (Cornsweet 1962), where frequency was held constant and signal level was varied based on subject performance. In practice, this involved presenting the seal with 40 – 60 successive trials within a session, 50 – 70% of which contained a narrowband signal. Each session contained at least three transitions between trials in which the signal was successfully detected and those in which the subject failed to respond after the signal level was lowered by 2 dB (i.e., hit-to-miss transitions). Sessions were repeated until performance on signal-present and signal-absent trials was stable. Within a session, only the plateau of consecutive signal trials with hit-to-miss transitions within 6 dB of one another was used to calculate threshold. Final threshold was determined as the average of 15 hit-to-miss transitions across 3 – 4 sessions with a standard deviation < 3 dB and with a pooled false alarm rate > 0 and < 0.30. False alarm rate for an individual session was defined as the proportion of signal-absent trials between the first and last hit-to-miss transitions on which KP2 incorrectly reported a signal detection[1]. Frequencies were tested in a pseudorandom order, with the first hearing threshold remeasured near the end of the experiment to evaluate the possibility of a practice effect. At each test frequency, threshold-to-noise offset was calculated as the difference between hearing threshold and ambient noise spectral density level.

Acoustic stimuli were 500 ms frequency modulated upsweeps with a 10% bandwidth (± 5% from center frequency) and 5% rise and fall times. Signals were generated in

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[1] Responses prior to signal presentation on signal-present trials were also considered false alarms.

LabVIEW (NI) using custom Hearing Test Program (HTP) software (Finneran 2003). They passed through an NI USB-6259 BNC M-series data acquisition module (500 kHz update rate), a Krohn-Hite 3364 bandpass digital filter, a Tucker-Davis Technologies PA5 digital attenuator, and in some cases a Behringer NX1000 power amplifier prior to reaching the designated speaker. Signals were projected from one of three speakers, depending on frequency: a Naval Undersea Warfare Center (NUWC) J-11 transducer for 0.1 – 0.4 kHz, a NUWC J-9 transducer for 0.8 – 6.4 kHz, or an International Transducer Corporation 1042 projecting hydrophone for 12.8 – 60.9 kHz. The transducers were suspended into the pool approximately 6 m behind the seal and decoupled from the subject's listening station. Exact speaker positions were determined by spatial mapping of the sound field to ensure acceptable variability of the test stimuli (± 3 dB) within a 14 x 14 x 14 cm grid surrounding the location of the seal's head during testing. For sound field mapping and daily calibration, signals were received in the absence of the seal through a calibrated Reson TC4032 low-noise hydrophone (0.01 – 80 kHz, ± 2.5 dB) with a Reson EC6076 active input module, passed through the same data acquisition board, and measured in HTP. The entire system was checked regularly with a GRAS 42AA pistonphone with an RA0046 adapter.

Sound field mapping and daily calibration ensured that the acoustic conditions replicated Sills et al. (2021). As in Sills et al. (2021), ambient noise conditions in the pool were measured in 1/3-octave bands prior to every session using the TC4032 hydrophone and a self-powered Brüel and Kjær 2270 sound level meter (sampling rate

48 kHz). The median of daily, 1-min unweighted 50th percentile measurements (L50) were converted to units of power spectral density. On a subset of days, ambient noise was recorded above 24 kHz with the hydrophone and a battery-powered Fostex FR-2 Field Memory Recorder (sampling rate 192 kHz). At the end of testing, thresholds and ambient noise levels were adjusted based on the frequency-specific sensitivity of the TC4032 hydrophone used.

In-air Hearing Measurements

Prior auditory testing with monk seal KE18 demonstrated poor sensitivity to airborne sounds, even when evaluated in the very quiet conditions of a hemi-anechoic acoustic chamber (Ruscher et al. 2021). Therefore, we elected to conduct testing more efficiently with KP2 in a semi-controlled outdoor environment. Test frequencies were chosen to ensure that expected thresholds were sufficiently elevated above background noise. The theoretical lowest thresholds measurable outdoors were predicted by adding actual or extrapolated monk seal critical ratios (Ruscher et al. 2021) to ambient noise spectral density levels at corresponding frequencies. KE18's thresholds were all higher than the lowest values that could be measured outdoors, indicating that KP2's auditory thresholds—if his hearing were similar—could be accurately measured in this environment. Specifically, we tested six frequencies with sufficient separation (5 – 48 dB) between theoretical lowest thresholds and KE18's measured thresholds to allow for typical individual variation in detection abilities. At these frequencies, thresholds measured outdoors for KP2 were ultimately compared to theoretical lowest thresholds to evaluate whether hearing was influenced by background noise. Measurements falling well above theoretical lowest thresholds reflected absolute hearing sensitivity. Conversely, any thresholds similar to or below theoretical lowest thresholds were likely constrained by noise. The latter would reveal that KP2's auditory sensitivity is more acute than KE18's, thus requiring further testing in quieter conditions.

Auditory measurements were obtained at 0.2, 3.2, 6.4, 12.8, 18.1, and 33.2 kHz in a semi-enclosed 4 x 3 m triangular holding area adjacent to the underwater testing pools (Video S1). This area was covered with a shade cloth, and had vertical walls of HDPE, plexiglass, or vinyl-coated chain link. The floor was composite decking material. A listening station was positioned so the monk seal rested comfortably in an open doorway at the front of the holding area with his ear openings 19 cm above the deck. A response target was located 13 cm to his left and the space behind it remained open to the adjacent pool. The speakers used to generate test signals were positioned in front of KP2 on axis with his midline. Padding was added between the listening station and speaker as needed to reduce variability in the sound field (characterized during spatial mapping of received signals) due to nearby reflective surfaces. Frequencies were tested in a pseudorandom order, with one hearing threshold remeasured near the end of the experiment to evaluate the possibility of a practice effect.

Acoustic stimuli had the same parameters as for in-water testing and were generated in the same manner using HTP software. Signals were passed through an NI USB-6251 data acquisition module (500 kHz update rate), a 0.1 – 250 kHz Krohn-Hite bandpass active filter module, and a Radial two-channel Mix 2:1 passive mixer, before being projected through a Neumann KH 80 DSP powered studio monitor (0.057 – 21 kHz, ± 3 dB). For testing at 33.2 kHz, filtered signals were passed from the data acquisition module straight to an Avisoft ultrasonic power amplifier, and were projected with an Avisoft Vifa ultrasonic dynamic speaker (1 – 120 kHz, ± 12 dB). Speakers were positioned 0.8 – 1.3 m in front of the seal. Their exact locations were determined by spatial mapping of the received sound field in the absence of the seal to confirm acceptable variability (± 3 dB) of the test stimuli across 14 positions in a 4 x 4 x 4 cm grid surrounding the location of each of the seal's ears during testing. For spatial mapping and daily calibration at 0.2 – 18.1 kHz, signals were received by a Brüel and Kjær battery-powered 2250 sound level meter (sampling rate 48 kHz) with a free-field 4966 1/2-in microphone (0.005 – 20 kHz, ± 2 dB), passed through the data acquisition board, and measured in HTP. For 33.2 kHz, signals were received by a Microtech Gefell MK301 microphone capsule (0.005 – 100 kHz, ± 2 dB) with a Josephson C617 body and a Stewart Electronics BPS-1 power supply, passed through the same data acquisition board, and measured in HTP. The entire system was checked regularly with a RION NC-73 sound level calibrator.

Training procedures and test stimuli matched those used for monk seal KP2's underwater audiogram and for monk seal KE18 in air (Ruscher et al. 2021). Threshold determination followed the methodology used for KP2 in water and by Jones et al. (2023) for odobenid and otariid carnivores. Acoustic calibration protocols and most equipment (see Fig. S1 for a detailed equipment schematic) were consistent with those used by Jones et al. (2023). As in water, ambient noise was measured prior to each session in 1/3-octave bands and converted to power spectral density levels. Below 20 kHz, measurements were obtained with the 2250 sound level meter and the 4966 microphone. Ambient noise measurements were limited above 20 kHz by the self-noise of the Fostex FR-2 recording system that was used for high-frequency noise measurements in water.

Results

Underwater and in-air thresholds, false alarm rates, ambient noise levels, and threshold-to-noise offsets at each frequency are provided for monk seal KP2 in Table 1. The associated underwater audiogram and in-air thresholds are plotted along with comparative auditory data (Fig. 1). Thresholds collected for KP2 fell within 4 dB of KE18's auditory data on average (maximum of 11 dB difference at 33.2 kHz in air).

KP2's underwater audiogram was relatively flat (7 dB range) from 0.8 – 25.6 kHz, with a peak sensitivity of 73 dB re 1 µPa at 18 kHz. The functional range of hearing (frequencies audible at 120 dB re 1 µPa, see Houser & Finneran 2006) extended from < 0.1 kHz to approximately 40 kHz. The 20 dB range of best sensitivity—defined as the frequency range of thresholds within 20 dB of peak sensitivity (see Reichmuth et al. 2013)—spanned from approximately 0.16 – 36 kHz. Above this range, thresholds increased by about 30 dB within a half octave. Sensitivity decreased more slowly at the low-frequency end of the audiogram, with a slope of 7 dB per octave on the roll-off.

The six in-air hearing thresholds measured for KP2 suggest that he has a flattened audiogram similar to that of KE18, with a relatively shallow curve compared to the typical mammalian U-shape. Best sensitivity was 42 dB re 20 µPa at 3.2 kHz and, like KE18, KP2's data exhibited a distinct upward notch at 6.4 kHz. Overall, KP2's thresholds indicate that both the functional range of hearing—defined as frequencies audible at 60 dB re 20 µPa (see Heffner & Heffner 2007)—and the 20 dB band of best sensitivity would fall between approximately 0.1 and 33 kHz for this individual. KP2's high-frequency hearing appears to decrease in sensitivity earlier and at a steeper rate than KE18's, with a slope of approximately 22 dB per octave. All six thresholds measured in air were at least 8 dB above the theoretical lowest thresholds predicted for this outdoor testing environment.

Repeated testing at 12.8 kHz in water and 18.1 kHz in air revealed differences of < 3 dB, confirming the absence of a practice effect and demonstrating that KP2's performance on the task was reliable. Average response bias was similar in both testing environments, with a combined mean false alarm rate of 0.16 (range: 0.03 – 0.27); KP2 did not have an overly conservative response bias that could explain elevated thresholds. Additionally, threshold-to-noise offsets exceeded 28 dB in all cases, indicating that the auditory data were likely not masked by ambient noise and accurately reflect KP2's auditory capabilities in both media.

Discussion

The underwater audiogram and in-air thresholds collected for Hawaiian monk seal KP2 closely follow the hearing curves collected previously with monk seal KE18 (Ruscher et al. 2021, Sills et al. 2021). These individuals were tested more than two years apart, with some methodological differences across studies. These included minor changes in signal production and calibration equipment and methods of psychophysical threshold determination in both media. Most notably, the testing environment and associated noise conditions were different between the acoustic chamber used for monk seal KE18 and the outdoor testing conditions used for monk seal KP2 in air. Nevertheless, the detection thresholds measured for KP2 and KE18 fell within 6 dB of one another in nearly every case (19 out of 20 comparisons). This between-subject variation is similar to that of other seal species when tested in identical experimental configurations (e.g., Kastelein et al. 2009, Sills et al. 2014). Thus, we can now fully validate amphibious hearing profiles for Hawaiian monk seals, resolving the discrepancies in underwater hearing between Thomas et al. (1990) and Sills et al. (2021) and confirming the surprisingly poor terrestrial sensitivity described by Ruscher et al. (2021). The complete aquatic and terrestrial audiograms reported previously for monk seal KE18 are, in fact, representative of *N. schauinslandi*. We conclude that Hawaiian monk seals have auditory abilities and adaptations that are consistent with their evolutionary isolation within the Monachinae lineage of true seals.

The excellent agreement on the high-frequency portion of the three available underwater audiograms verifies that Hawaiian monk seals have a reduced high-frequency hearing ability, with a functional upper-frequency hearing limit near 40 kHz. Their hearing range is constrained even when compared to the more closely related northern elephant seal, which has an upper-frequency hearing limit extending to about 55 kHz (Kastak & Schusterman 1999)—similar to that of seals from the Phocinae lineage (Southall et al. 2019, Sills et al. 2020). This reduced sensitivity of monk seals at high frequencies may not be ecologically significant. However, it does suggest that the derived trait of expanded underwater high-frequency hearing occurred less than 15 million years ago (Rule et al. 2021) and separately within each seal subfamily.

These validation data for Hawaiian monk seals show that auditory sensitivity in both media is most similar to that of the northern elephant seal from the Monachinae lineage. Auditory thresholds are higher than measured for one northern elephant seal and significantly elevated in comparison to four species of Phocinae seals (as illustrated in Fig. 1). Despite this, sound reception in water—particularly at the low frequencies—

may be more important for monk seals than was previously concluded from the original Thomas et al. (1990) hearing curve. With respect to social communication, this validated audiogram combined with the recently described underwater vocal repertoire (Sills et al. 2021) collectively confirm that monk seals likely rely on acoustic communication underwater. Conversely, elevated in-air thresholds suggest that monk seal terrestrial communication is probably acoustically limited, likely occurring effectively over relatively short ranges and possibly including multimodal cues (i.e., acoustic, seismic, visual, or olfactory stimuli, as suggested by Miller & Job 1992). From an applied perspective, poor terrestrial hearing suggests that the use of acoustic deterrents—a common tool to mitigate marine mammal and human interactions—may not be very effective for this species.

This study, combined with Sills et al. (2021) and Ruscher et al. (2021), provides a core understanding of auditory biology in Hawaiian monk seals. The findings have implications for the conservation of Mediterranean monk seals (*M. monachus)*—a vulnerable species with no existing hearing data and a currently developing knowledge of vocal behavior (Muñoz et al. 2011, Charrier et al. 2017, 2023, Muñoz-Duque et al. 2024). While the results of the present study strongly indicate subfamily-level differences in hearing among true seals, additional Monachinae species need to be tested to confirm whether related species share similar auditory traits.

On the basis of the hearing data now available, we consider the functional grouping of all seals to be appropriate and conservative (for monk seals, northern elephant seals, and possibly the other five Monachinae seals) in terms of regulatory guidance on the effects of noise (see Southall et al. 2019). More applied bioacoustic research is needed to support the conservation of both extant monk seal species (e.g., passive acoustic monitoring, development of call detectors) and to resolve questions about the evolutionary biology of hearing among true seals, including Antarctic species.

Acknowledgements

This work was made possible by the generous animal loan agreement from the Waikīkī Aquarium, and through collaboration with the National Marine Fisheries Service OPR and PIFSC Hawaiian Monk Seal Research Program. Funding for this study was provided by the US Navy's Living Marine Resources Program under awards N62473-17-20018 and N39430-24-C-2003, and we are grateful to M. Shoemaker and A. Kumar and for their guidance and support. We thank J. Rivers of US Pacific Fleet, A. Sloan of the National Marine Fisheries Service, P. Nachtigall of University of Hawai‘i, A. Rossiter of the Waikīkī Aquarium, and J. Palowski of SeaLife Park for their encouragement and advice. We thank R. Specht of Avisoft Bioacoustics and K. Eyster of Naval Undersea Warfare Center for their support in identifying and resolving technical issues; J. Finneran of the US Navy Marine Mammal Program for access to custom LabVIEW software; D. Casper for expert veterinary care; and J. Terhune for helpful comments on this manuscript. A portion of this work was presented at the 7th International Meeting of the Effects of Sound in the Ocean on Marine Mammals. B. Ruscher received supplementary funding from the Rebecca and Steve Sooy Graduate Fellowship, N. Packard by the California Ocean Alliance, and T. L. Kendall by the Office of Naval Research.

We are grateful to the dedicated research, husbandry, and facilities teams of Long Marine Laboratory, including: J. Sullivan, C. Casey, M. Garcia, S. Pryce, M. Meranda,

B. Farmer, N. Doeden, G. Dulay, I. Anderson, B. Wong, E. Zawacki, S. Stoll, S. Caamaño, A. Klein, B. Peterson, A. Reyes, E. Santos, K. Kolda, F. Mulhern, I. Mabon, M. Klos, M. Puentes, N. Renshaw, A. Roberts, P. Zhang, C. Hood, P. Gremore, B. Theders, S. Aldana, J. Whisler, H. Jackson, N. Whitman, N. Sprenger, K. Jagit, M. Weiner, and T. Beckon. We especially thank R. Jones for technical support, B. Tom and A. Sandage for husbandry support, and J. Raimondi for facilities support.

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Chapter 2: Figures and Tables

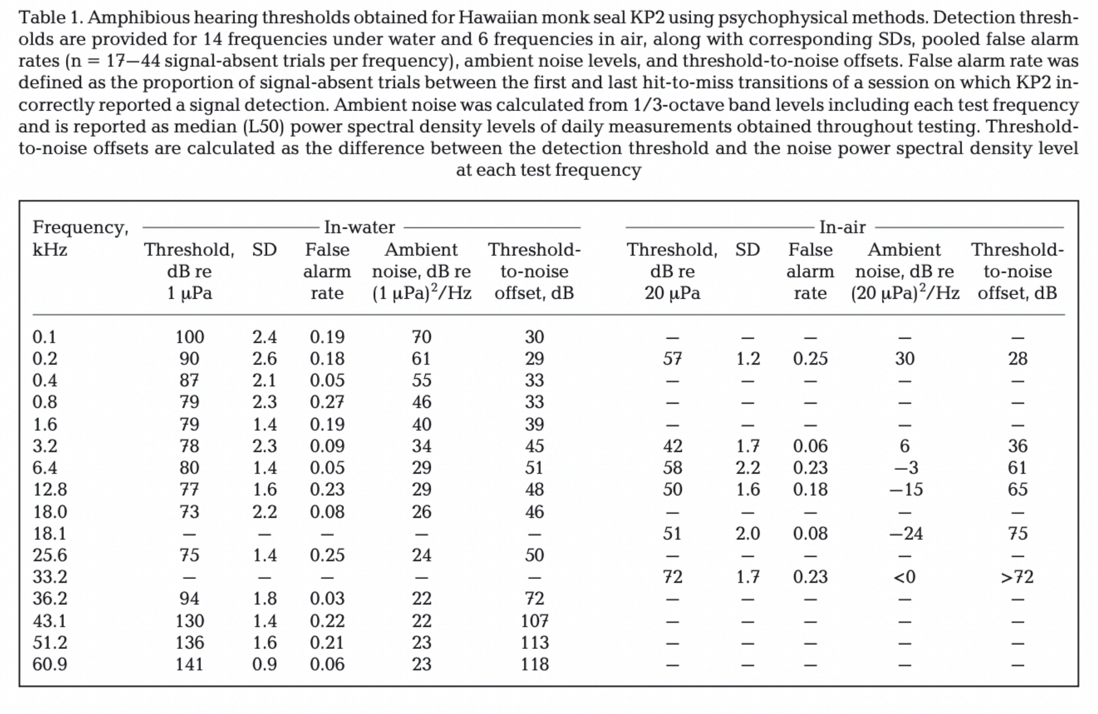
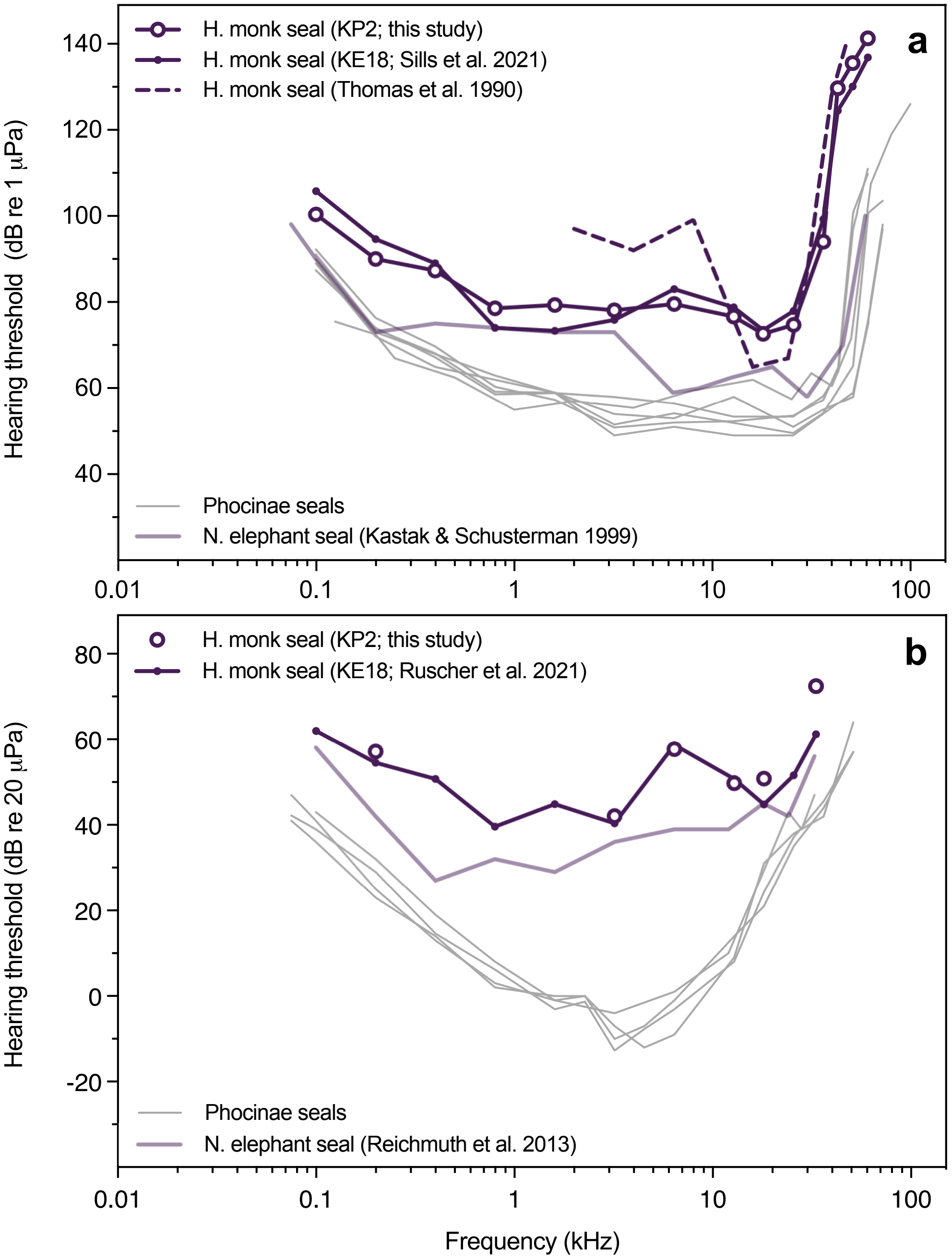


Table 1. Amphibious hearing thresholds obtained for Hawaiian monk seal KP2 using psychophysical methods. Detection thresholds are provided for 14 frequencies under water and 6 frequencies in air, along with corresponding SDs, pooled false alarm rates (n = 17–44 signal-absent trials per frequency), ambient noise levels, and threshold-to-noise offsets. False alarm rate was defined as the proportion of signal-absent trials between the first and last hit-to-miss transitions of a session on which KP2 incorrectly reported a signal detection. Ambient noise was calculated from 1/3-octave band levels including each test frequency and is reported as median (L50) power spectral density levels of daily measurements obtained throughout testing. Threshold-to-noise offsets are calculated as the difference between the detection threshold and the noise power spectral density level at each test frequency

Frequency, kHz	In-water					In-air				
	Threshold, dB re 1 μPa	SD	False alarm rate	Ambient noise, dB re (1 μPa)^2/Hz	Threshold-to-noise offset, dB	Threshold, dB re 20 μPa	SD	False alarm rate	Ambient noise, dB re (20 μPa)^2/Hz	Threshold-to-noise offset, dB
0.1	100	2.4	0.19	70	30	–	–	–	–	–
0.2	90	2.6	0.18	61	29	57	1.2	0.25	30	28
0.4	87	2.1	0.05	55	33	–	–	–	–	–
0.8	79	2.3	0.27	46	33	–	–	–	–	–
1.6	79	1.4	0.19	40	39	–	–	–	–	–
3.2	78	2.3	0.09	34	45	42	1.7	0.06	6	36
6.4	80	1.4	0.05	29	51	58	2.2	0.23	−3	61
12.8	77	1.6	0.23	29	48	50	1.6	0.18	−15	65
18.0	73	2.2	0.08	26	46	–	–	–	–	–
18.1	–	–	–	–	–	51	2.0	0.08	−24	75
25.6	75	1.4	0.25	24	50	–	–	–	–	–
33.2	–	–	–	–	–	72	1.7	0.23	<0	>72
36.2	94	1.8	0.03	22	72	–	–	–	–	–
43.1	130	1.4	0.22	22	107	–	–	–	–	–
51.2	136	1.6	0.21	23	113	–	–	–	–	–
60.9	141	0.9	0.06	23	118	–	–	–	–	–



a
H. monk seal (KP2; this study)
H. monk seal (KE18; Sills et al. 2021)
H. monk seal (Thomas et al. 1990)
Phocinae seals
N. elephant seal (Kastak & Schusterman 1999)
Hearing threshold (dB re 1 μPa)
140
120
100
80
60
40
0.01
0.1
1
10
100
b
H. monk seal (KP2; this study)
H. monk seal (KE18; Ruscher et al. 2021)
Phocinae seals
N. elephant seal (Reichmuth et al. 2013)
Hearing threshold (dB re 20 μPa)
80
60
40
20
0
-20
0.01
0.1
1
10
100
Frequency (kHz)

Fig. 1. Amphibious detection thresholds for one Hawaiian monk seal (KP2) obtained using psychophysical methods. For comparison, representative hearing data from each subfamily of true seals are provided. (**a**) Underwater audiogram for monk seal KP2. For the Monachinae subfamily, audiograms are included for other Hawaiian monk seals (n=2, Thomas et al. 1990, Sills et al. 2021) and northern elephant seals *Mirounga angustirostris* (n=1, Kastak & Schusterman 1999). Data for the Phocinae subfamily include bearded *Erignathus barbatus* (n=2, Sills et al. 2020), harbor *Phoca vitulina* (n=2, Kastelein et al. 2009), ringed *Pusa hispida* (n=1, Sills et al. 2015), and spotted seals *Phoca largha* (n=2, Sills et al. 2014). (**b**) In-air hearing thresholds for KP2 at six frequencies tested in outdoor ambient conditions. Additional Monachinae hearing data are represented by the Hawaiian monk seal (n=1, Ruscher et al. 2021) and northern elephant seal (n=1, Reichmuth et al. 2013). For Phocinae seals, audiograms are shown for harbor (n=1, Reichmuth et al. 2013), ringed ([n=1, Sills et al. 2015), and spotted seals (n=2, Sills et al. 2014). Associated hearing data and ambient noise values for this study are provided in Table 1.

Chapter 2: Supplementary Material

Supplementary Video S1*. Video examples of underwater and in-air auditory go/no-go trials conducted with Hawaiian monk seal KP2 at Long Marine Laboratory, Santa Cruz, CA**.**

*This supplementary video file can be accessed through the following link: https://doi.org/10.3354/esr01377

Text S1. In behavioral psychophysics, various methods are used to determine detection thresholds. Two standard approaches are 1) averaging hit-to-miss transitions (Cornsweet 1962) and 2) probit analysis (Finney 1971). Thresholds derived from either method are often compared, but the validity of this direct comparison has not been evaluated. In Table S1, we provide detection thresholds calculated with both threshold determination methods using the same underlying auditory data. Hearing data were obtained from two Hawaiian monk seals in water and in air (this study, Ruscher et al. 2021, Sills et al. 2021). The two methods of threshold determination are described below. Resulting thresholds are provided for each method (Table S1).

Hit-to-miss transitions are defined as transitions between trials in which the signal was successfully detected (hit) and those in which the subject failed to respond (miss) after the signal level was lowered. Each session required a minimum of at least three hit-to-miss transitions within 6 dB of one other. Detection thresholds were calculated by averaging the signal level of 15 stable hit-to-miss transitions across 3 – 4 sessions. Testing was complete when performance stabilized across both signal-present (standard deviation < 3 dB) and signal-absent trials (false alarm rate greater than 0 and less than 0.3). The underwater and in-air hearing data reported for monk seal KP2 in the main text of this paper were calculated using this method. This change in threshold determination method from Sills et al. (2021) and Ruscher et al. (2021) was made to improve efficiency of auditory data collection with KP2.

For probit analysis, average thresholds for a session were calculated from the last five stable hit-to-miss transitions (within 6 dB of one another). Testing was considered complete when the average threshold fell within 3 dB across three sessions, and performance on signal-absent trials was considered stable (false alarm rate between 0.0 and 0.3). Final thresholds were then determined by fitting a psychometric (sigmoid) function to the proportion of correct detections at each signal level presented between the five hit-to-miss transitions in each of the three pooled sessions. An inverse prediction was applied to determine threshold as the sound pressure level corresponding to 50% correct detection (Finney 1971). Threshold criteria required 95% confidence intervals to be less than 4 dB (see e.g., Sills et al. 2014, 2015). The underwater and in-air hearing thresholds for monk seal KE18 were calculated using this method (Sills et al. 2021, Ruscher et al. 2021).

Threshold differences are reported as the absolute difference between the two methods (Table S1). To facilitate comparison, these values are provided to the nearest tenth of a dB. Detection thresholds were not consistently higher with one method versus the other. For all comparisons, absolute threshold differences were < 1 dB. As seen in Table S1, in terms of reported thresholds there is no practical difference between these two threshold determination methods. Thus, behavioral auditory data collected with either method can be compared directly. This applies specifically to these data collected for monk seals KE18 and KP2, but also more generally across behavioral hearing experiments utilizing these two threshold methods.

Text S1 References

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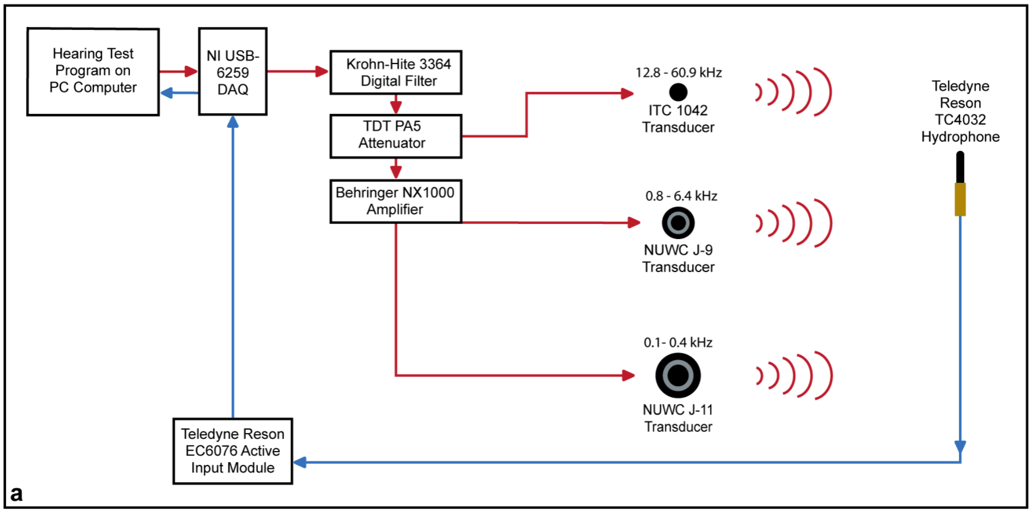
Table S1. See Text S1

	seal KP2 in water (dB re 1 µPa)			**seal KE18 in water (dB re 1 µPa)**			**seal KE18 in air (dB re 20 µPa)**		
Frequency kHz	Probit threshold	Hit-to-miss transition threshold	Threshold difference	Probit threshold	Hit-to-miss transition threshold	Threshold difference	Probit threshold	Hit-to-miss transition threshold	Threshold difference
0.1	-	-	-	106	106	0.2	62	62	0.4
0.2	-	-	-	95	95	0.1	55	55	0.1
0.4	-	-	-	89	89	0.3	51	50	0.4
0.8	79	79	0.4	74	74	0.2	40	39	0.4
1.6	80	79	0.6	73	73	0.1	45	45	0.2
3.2	78	78	0.1	76	76	0.2	40	40	0.4
6.4	80	80	0.1	83	83	0.1	59	58	0.6
12.8	77	77	0.4	79	79	0.0	51	51	0.2
18.0	72	73	0.2	74	73	0.5	-	-	-
18.1	-	-	-	-	-	-	45	45	0.3
25.6	75	75	0.2	78	78	0.1	52	52	0.2
33.2	-	-	-	-	-	-	61	61	0.3
36.2	94	94	0.2	99	99	0.1	-	-	-
43.1	130	130	0.1	125	125	0.0	-	-	-
51.2	135	136	1.0	130	130	0.1	-	-	-
60.9	142	141	0.3	137	137	0.4	-	-	-

In-Water Audiometry Equipment



In-Air Audiometry Equipment

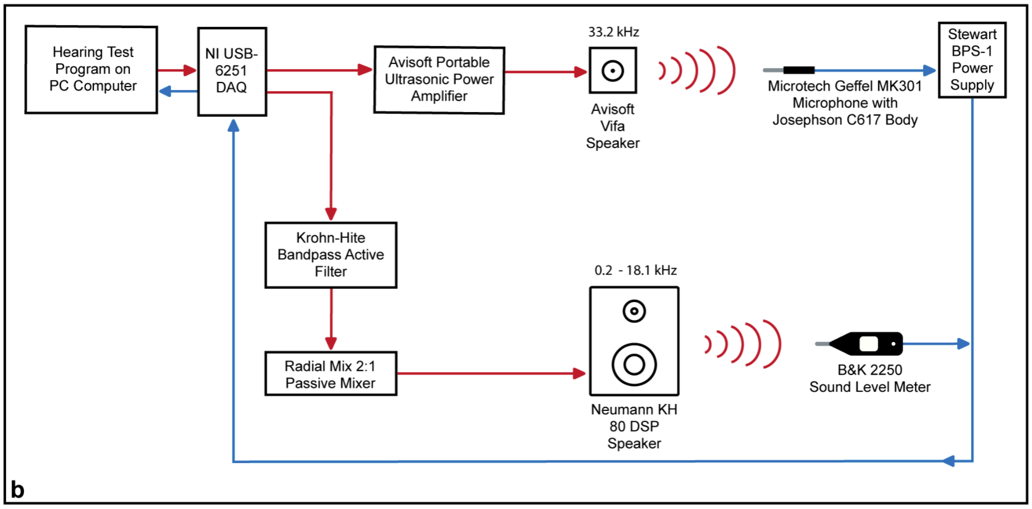


Fig. S1. Equipment schematics are provided for the in-water (a) and in-air (b) audiometry experiments. Acoustic stimuli were generated, spatially mapped, and calibrated following the detailed methods of Sills et al. (2021) in water and Ruscher et al. (2021) or Jones et al. (2023) in air. While some of the equipment was the same as in the prior studies, specific details are provided within the main text.

Fig. S1 References

Ruscher B, Sills JM, Richter BP, Reichmuth C (2021) In-air hearing in Hawaiian monk seals: implications for understanding the auditory biology of Monachinae seals. J Comp Physiol A 207:561–573

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Chapter 3

Terrestrial vocal behavior and communication range estimates in Hawaiian monk seals

Abstract

The acoustic biology of Hawaiian monk seals (*Neomonachus schauinslandi*) is a compelling topic due to their evolutionary and biogeographical separation from related species, prolonged reproductive season, and endangered status. Studies of hearing ability suggest that terrestrial communication will be constrained by poor hearing, but limited available information about species' vocal behavior and typical environmental conditions preclude communication range estimates. We recorded spontaneous vocalizations from free-ranging monk seals at Kalaupapa National Historical Park (Moloka‘i, HI, USA) to provide source level estimates of airborne, low-frequency calls emitted by this species. Sound pressure levels measured over the 90% call duration recorded within 7 m from resting seals were used to approximate vocalization source levels at 1 m. Amplitude and spectral characteristics of recorded calls were combined with monk seal hearing data and representative metrics of ambient conditions (ambient noise levels and propagation loss) to estimate the distances over which seals can communicate with conspecifics in air. Communication ranges for female *groans* (< 40 m) and pup *groans* (< 95 m) were limited by moderate vocal amplitudes and primarily their relatively poor hearing sensitivity at low frequencies. These detection ranges are

constricted further when considering the conditions needed for discrimination, recognition, and effective communication. Findings indicate that acoustic communication in Hawaiian monk seals is restricted in terrestrial environments and is likely further reduced by low-frequency anthropogenic noise exposures.

Introduction

The acoustic biology of Hawaiian monk seals (*Neomonachus schauinslandi*) is intriguing due to their endangered status (Littnan et al. 2015) and evolutionary and geographical isolation from other seal species (Rule et al. 2021). As a result of relatively stable environmental conditions and resources available year-round, monk seals do not breed during a brief, predictable period each year like other seals. Instead, they have an unusually prolonged reproductive period spanning at least nine months at the population level (Miller & Job 1992). Along with their history of isolation, this seasonal asynchrony likely has consequences for their social and acoustic behavior.

Though Hawaiian monk seals are polygamous and capital breeders, their asynchronous reproductive season does not promote aggregated breeding colonies like other pinniped species. Mating occurs at sea and males do not maintain specific terrestrial breeding territories or monopolize females on the beaches, though they often approach and rest near available females on land (Robinson et al. 2022). Females stay with their pups and fast during the entire nursing period (~ 40 days), and weaning occurs abruptly when the female's resources are depleted (Robinson et al. 2022). The female and pup remain near the birth site throughout the duration of dependency, swimming together in the shallows or hauling out to rest and nurse. Mother-pup pairs occur in low densities, and nursing females are noted to be particularly asocial (Robinson et al. 2022). Despite being well-spaced, aggressive interactions have been reported to result in pupswitching and fostering; thus, the ability of females to recognize their biological pup is unclear (see Robinson et al. 2022).

While the general biology of Hawaiian monk seals is well known, more detailed information about their hearing abilities and sound production behavior is just beginning to emerge. These data are especially relevant given the intensity of US military activity around the Hawaiian Archipelago, resulting in the introduction of underwater and in-air noise to monk seal habitats. Additionally, as monk seal conservation efforts enable increasing population numbers near the Main Hawaiian Islands, the exposure of these seals to coastal human activities is increasing.

In terms of sound production, Hawaiian monk seals are known to emit low-frequency vocalizations (< 1 – 2 kHz) both above and below the water's surface. Underwater vocal behavior has only recently been described for mature males living in human care. Sills et al. (2021) provide detailed descriptions—including spectral and temporal parameters and estimates of call amplitude—for a moderate repertoire of low-frequency vocalizations with apparent reproductive function. In air, low-frequency sounds have been reported for wild individuals of all age classes, including mother-pup affiliative calls, threats, and a few other social sounds (Kenyon and Rice 1959; Miller and Job 1992; Job et al. 1995; Chaudun et al. 2018). Miller and Job (1992) describe the spectral and temporal characteristics of these terrestrial calls paired with detailed behavioral observations. This study reports that airborne communication seems to occur over short distances and suggests that vocal cues are likely unimportant for the species at long ranges. However, measures of vocal amplitude were not reported, prohibiting a more complete understanding of acoustic communication—including terrestrial communication ranges for the species.

Regarding sound reception, recently available data confirm that monk seals have reduced hearing sensitivity in water and especially poor terrestrial hearing relative to other seal species (Chapters 1 and 2; Ruscher et al. 2021; Sills et al. 2021; Ruscher et al. 2025). At some frequencies in air, auditory detection thresholds for monk seals are 50 dB worse than for other phocid species tested in the same conditions. These audiometric data indicate that acoustic communication may be limited by the sound reception abilities of monk seals in both media, which supports the behavioral observations of Miller and Job (1992).

Active space—also termed communication space or communication range—refers to the distance from a source over which a sound remains detectable by a listener in the same environment (see Marten and Marler 1977; Brenowitz 1982; Janik 2000). Calculating the communication range of a signal requires knowledge of the sound being produced, signal degradation as a function of distance, ambient noise in the environment, and auditory capabilities of potential listeners. Aspects of active space have been investigated for some vocal species, including birds (e.g., Brenowitz 1982; Lohr et al. 2003), amphibians (e.g., Gerhardt 1975), primates (e.g., Brown 1989), elephants (e.g., Larom et al. 1997), cetaceans (e.g., Erbe and Farmer 2000; Janik 2000), and pinnipeds (e.g., Reiman and Terhune 1993; Southall 2002; Southall et al. 2003a; Casey et al. 2016; Sills et al. 2021). These studies rely on combining comprehensive field and laboratory data describing environmental conditions, vocal behavior, and sound reception abilities. Simplifying assumptions are often used for these calculations, especially when considering the complex nature of signal propagation, auditory masking, and requirements for effective communication (see Southall et al. 2003a; Branstetter and Sills 2022). Even so, estimates of communication space provide an important method for assessing acoustic behavior in dynamic conditions, which is particularly interesting when considering the dual physical environments experienced by seals.

For the semi-aquatic marine mammals of the Phocidae family (true seals), intra-specific communication is enabled by the effective production and reception of sound both above and below the water's surface. While aspects of hearing and vocal behavior are known for some true seal species, there are still many questions about how seals acoustically experience their terrestrial and aquatic environments—including the spatial use of important communication signals. Under water, communication ranges have been estimated for harbor (*Phoca vitulina;* Casey et al. 2016), spotted (*Phoca largha*; Sills et al. 2017), and Hawaiian monk seals (Sills et al. 2021). In air, communication ranges have been estimated for harbor seals at the water's surface (Reiman and Terhune 1993) and northern elephant seals (*Mirounga angustirostris*) on beaches (Southall 2002; Southall et al. 2003a). While estimates vary depending on environmental conditions, amplitude and spectral features of the vocal type, and specific hearing abilities of the listener, communication space in water is generally predicted to be much larger than that in air. The estimates of communication ranges for monk seals under water suggest that the detection of conspecific vocals is limited by poor hearing abilities in a representative underwater soundscape (Sills et al. 2021). Similar measurements have not yet been made for monk seals in air.

This study aims to further describe the terrestrial acoustic behavior of Hawaiian monk seals and report the first source level estimates of female and pup groan vocalizations. Additionally, we characterize ambient noise conditions of a representative environment, report relevant spectral parameters of vocalizations, and investigate how calls propagate in typical conditions. These direct measurements are combined with available auditory data to calculate potential in-air communication ranges for this endangered species, which will support conservation and management efforts.

Materials and Methods

Field Site

Research was conducted at Kalaupapa National Historical Park (KNHP; Molokaʻi, HI, USA; 21.199° N, 156.981° W) in July and August 2024, coinciding with the end of Hawaiian monk seal peak pupping season. Access to the site was permitted by the

National Park Service and the State of Hawai‘i Department of Health. Research was conducted with authorization from the United States National Marine Fisheries Service under marine mammal research permit 22677, with approval and oversight from the University of California Santa Cruz Institutional Animal Care and Use Committee.

KNHP encompasses ~ 44 km^2 of protected land and water resources on the north side of Moloka‘i (Fig. 1). This area includes a peninsula (~ 12 km^2) that is the site of the small community of Kalaupapa. Due to the small human population (< 50 residents) and Kalaupapa community codes, anthropogenic activity is well-regulated and reduced relative to other easily accessible sites utilized by monk seals in the Main Hawaiian Islands. However, seals are still exposed to some anthropogenic noise from nearby roads and maintenance activities. Additionally, this isolated peninsula is primarily accessed by plane and is used for landing training, resulting in frequent small aircraft traffic. The exposed peninsula typically experiences constant trade winds blowing from the east/northeast, and temperatures ranging from 15 – 33° C.

KNHP is frequented by approximately 40 – 50 monk seals annually, and most pups born on Moloka‘i each year (~ 5 – 12) are birthed at this site. For this study, we monitored the easily accessible haul-out beaches and rocks along the leeward side of the peninsula. We collected acoustic data at two beaches (Papaloa and ‘Iliopi‘i) where female monk seals typically pup each year (Fig. 1).

Behavioral and Environmental Observations

Behavioral observations of monk seals were conducted daily between 0700 and 1900 from 25 July – 1 August and 14 – 19 August 2024. We first surveyed the shoreline to identify seals sparsely distributed along beaches, rocks, or in the shallows. Our subsequent observations comprised focal and ad libitum recordings of social and acoustic interactions of seals with conspecifics or the environment. To avoid disturbing the seals, researchers remained concealed behind vegetation along the beach (~ 10 – 30 m from the animals).

A subset of seals in this area—including most females and young animals—had alphanumeric tags placed in their rear flippers as part of long-term population monitoring efforts for this endangered species (see Robinson et al. 2022). Other individuals could, in some cases, be reliably identified by alphanumeric dye marks on their fur, unique scars, or other marks. As possible, unknown animals were sexed and assigned age classes based on size and behavior (e.g., large seals patrolling beaches were typically assigned as adult males based on the known behavior of the species, see Robinson et al. 2022).

Due to their accessible locations at KNHP and predictable rest behavior, we identified three females with dependent pups as the focal study animals. When feasible to do so without disturbance, we obtained paired audio-video recordings of the interactions of these individuals. Two pairs were observed just prior to weaning (pups 29 – 38 days old). The last pair was observed near the start and end of the lactation period (pup 6 – 13 days and 25 – 31 days old). Other seals were opportunistically observed and recorded, especially adult males who patrolled the shoreline throughout the day and would often haul out to investigate the mother-pup pairs.

Associated environmental data (relative humidity, temperature, and wind speed) were taken with a handheld Kestrel 3000 Weather Meter ad libitum during or after acoustic recordings. We obtained measurements at the height and placement of the acoustic recorder on the beach as well as at ~ 2 m height windward of the windbreak provided by vegetation along the beaches.

Ambient Noise Measurements

Ambient noise measurements were obtained throughout field efforts at KNHP. A Brüel and Kjær (B&K) 2250 self-powered sound level meter (sampling rate 48 kHz) with a free-field ½-in type 4966 microphone and a UA1650 windscreen was used to record noise samples. The microphone was placed at the approximate ear height of a monk seal in a relaxed position with their head slightly raised (0.2 m). We obtained 47 unweighted, 1-min noise samples during daytime hours (between 0800 and 1800). Measurements were taken in representative weather conditions and in typical resting locations along the beaches (within ~ 15 m of the shore break). Noise levels were determined as power spectral density levels calculated from the median of the 1/3-octave band 10th, 50th, and 90th percentile measurements (L10, L50, L90).

Transmission Loss Measurements

We conducted a simple transmission loss study on the focal beaches at KNHP in representative environmental conditions to determine how airborne monk seal vocalizations propagate through this environment. Brief tonal signals (2 s, 5% rise/fall time) were generated at 0.1, 0.2, 0.5, 1, and 2 kHz in Audacity software (version 3.0.5). Signals were projected from a small bluetooth speaker (JBL Charge 3; +/- 5 dB from 0.1 – 15 kHz) mounted 0.2 m above the sand, at approximate monk seal ear height. Signals were recorded with the B&K 2250 on axis to the speaker at distances of 1, 2, 4, 8, 16, and 32 m. Transmission loss measurements were conducted in the absence of seals. To further minimize potential disturbance, signal levels were set as low as possible while still exceeding ambient noise at the same frequencies (source levels ~ 80 – 90 dB re 20 μPa). We collected transmission loss measurements for all frequencies in a crosswind condition. On an additional day, a subset of frequencies (0.2, 0.5, and 1 kHz) were also recorded at shorter distances in crosswind, upwind, and downwind conditions to investigate the influence of wind direction. Signal received levels were determined for five replicate signal presentations per frequency and distance combination. Median received levels were compared to those expected from a spherical spreading model ($20 \log R$). Finally, we used simple linear regressions of median levels as a function of log(distance) to determine the propagation term for each frequency and wind condition.

Audio and Video Recording

Spontaneous vocalizations produced by free-ranging monk seals were obtained using a continuously recording Wildlife Acoustics Song Meter SM4 with two omnidirectional microphones (+/- 5 dB from < 0.15 – 10 kHz; 48 kHz sampling rate). This small, self-powered listening device was inconspicuously placed 4 – 15 m from Hawaiian monk seals hauled out on the beach or on exposed rock (Fig. 2). The recorder was gently deployed and retrieved by hand without disturbing the animals. Recording sessions were typically 0.5 – 2.5 hours and generally ended when the seals returned to water. To simultaneously document behavior associated with vocalizations, we paired a GoPro Hero10 (with an external battery pack) with the acoustic recorder (Fig. 2). Metadata corresponding to vocal events (e.g., time, seal IDs, sex, age, weather conditions, distance and orientation of seals from microphone, behavioral state) were also logged by hand throughout each recording period. Distances were visually estimated referenced to an adult female monk seal's average body length. When possible, distances were also directly measured after animals left the area. The orientation of the animal relative to the recording microphone was not controlled in this study, and calls were recorded between 0° and 180°.

Vocal Analysis

Audio data were reviewed using Adobe Audition software (Build 22.0.0.96). Discrete vocalizations were aurally and visually identified. Each call was referenced to the associated video data and observational notes to identify the caller, the caller's distance and orientation relative to the SM4 recorder, and additional details relevant to behavioral context of vocalizations or environmental conditions were noted. Sounds with common perceptual structure and frequency characteristics were labeled as the same call type. Each call was logged and scored for subjective quality (very poor, poor, fair, good, or excellent) based on the presence of other simultaneous sounds and general sound quality.

We quantitatively described the most common contact calls produced by mother (female *groan*) and pup (pup *groan*) by measuring a range of variables in amplitude, temporal, and spectral domains. Seventeen spectral and temporal features were measured using Raven Pro software (v.1.6.1; settings: Hann window DFT size 4096 samples 90% overlap, 3 dB filter bandwidth 16.9 Hz) for five female groans and five pup groans with a good or excellent subjective quality score and a signal-to-noise ratio > 7 dB. These parameters included call total duration, 90% duration, center frequency, inter-quartile range bandwidth (and 1st and 3rd quartile frequencies), 90% bandwidth (and upper and lower frequency bounds), peak frequency, 3-dB bandwidth (and upper and lower frequency bounds), 10-dB bandwidth (and upper and lower frequency bounds), and aggregate entropy (see Table 2 for descriptions). Total call duration was measured from manual selection on the waveform and frequency parameters were measured from the spectrum over the 90% duration of the call (see Sills et al. 2021). Fundamental frequency and number of harmonics were also measured for both call types.

Call amplitude was measured in dB RMS over the 90% call duration in terms of both broadband level and 1/3-octave band levels. The broadband received sound pressure levels were measured in Raven Pro and were referenced to a 1 kHz calibration tone. This tone was produced in Audacity software, projected from the JBL Charge 3 speaker, and recorded on axis at 1 m on the SM4. Received levels at 1 m were verified by the B&K 2250 sound level meter. Similarly, 1/3-octave band received levels were calibrated and measured across the 10-dB bandwidth of each call using Spectra-PLUS sound analysis software (v.5.3.1.1). Vocalization source levels at 1 m were then determined in each 1/3-octave band, with frequency-specific transmission loss terms informed by the results of the propagation study. Specifically, the exact transmission term applied for each 1/3-octave band was the one determined at the closest frequency (within the same or nearest octave band) evaluated in the transmission loss study. Broadband source levels were approximated from the broadband received levels with a spherical spreading model of transmission loss. As most of these calls were not recorded on axis with the caller, the broadband and 1/3-octave band sound pressure levels are considered apparent source levels that approximate true on-axis source levels (see Sills and Reichmuth 2022).

Communication Range Estimates

Calculations of communication range were made for the *groan* calls produced by female and pup Hawaiian monk seals. These were informed by characteristics of the vocal signal (frequency and amplitude, measured in this study), ambient noise levels and transmission loss terms (measured in this study), and previously published hearing data (hearing thresholds and masking critical ratios, Ruscher et al. 2021).

First, we evaluated whether the detection of conspecific calls was likely to be limited by biological constraints (absolute hearing abilities) or environmental constraints (masking noise). This was determined by comparing absolute hearing thresholds at relevant frequencies to the minimum values theoretically possible in the environment (i.e., theoretical lowest thresholds). The latter were calculated at each frequency as the ambient noise spectral density level plus a metric of auditory masking—the critical ratio. Critical ratios describe the amount by which a signal must exceed simultaneous, overlapping noise in order to be detectable (see Fletcher 1940; Scharf 1970). Detection is limited by hearing when absolute thresholds fall above the theoretical lowest thresholds that can be measured in the environment. Conversely, when hearing thresholds are below theoretical lowest thresholds, detection is likely to be masked or limited by the ambient noise environment.

Across the frequency span of vocalizations, we compared median L50 spectral density levels of ambient noise at KHNP in each 1/3-octave band to species hearing data (Chapter 1; Ruscher et al. 2021) in the same bands. We used 1/3-octave bands as a reasonable approximation of mammalian auditory processing capability (see Richardson et al. 1995). At frequencies where direct auditory measurements were unavailable, we predicted hearing thresholds and critical ratio values. The hearing thresholds for each 1/3-octave band were extrapolated or interpolated from absolute detection thresholds reported by Ruscher et al. (2021). The critical ratio predictions for each 1/3-octave band were informed by the few values reported by Ruscher et al. (2021). As these data are limited to two frequencies, supporting data were used from one northern elephant seal (Southall et al. 2000, 2003b)—the most closely related species with auditory masking measurements available.

Communication range estimates were then calculated using appropriate variants of the following equation:

$$DT = SL - Xlog(R)$$

Here, DT (detection threshold) is either the Hawaiian monk seal terrestrial hearing threshold or the ambient noise spectral density level plus the critical ratio within the relevant 1/3-octave band (based on whether *DT* is expected to be limited by biological or environmental constraints, respectively), *SL* (source level) is the sound pressure level of each vocal within the 1/3-octave band containing the most signal excess (see below), *Xlog(R)* is the transmission loss term (*X* is frequency dependent and determined by the propagation study), and *R* (in m) is the detection distance from the source. The use of absolute (50% detection) hearing thresholds provides maximum distances over which monk seals can acoustically detect conspecifics. As higher received levels are likely needed to facilitate successful communication (see Lohr et al. 2003), calculations were also made with *DT* increased by 10 dB (as in Terhune 2017).

Communication range estimates for species that emit broadband vocalizations are often calculated from the sound pressure level in the loudest portion of the call (i.e., the relevant auditory filter band containing peak frequency; see Casey et al. 2016; Sills et al. 2021). However, this method does not always coincide with the band containing the most energy above detection threshold (i.e., highest sensation level), which may be what drives perception of acoustic signals. Here, we calculated communication range using the 1/3-octave band with the most excess signal energy. Specifically, signal excess was determined by subtracting detection threshold from the source level in each 1/3-octave band within the 10-dB bandwidth of the call (see Fig. 3). In other words, the band containing the highest sensation level (see Erbe and Farmer 2000; Southall 2002; Southall et al. 2003a) was used to predict communication range.

Excess environmental attenuation (e.g., from atmospheric absorption, thermal gradients, ground effects) is sometimes included explicitly in calculations of communication space. In this case, excess attenuation was inherently accounted for within the transmission terms empirically measured from our propagation study.

Results

Environmental Conditions at the Field Site

During the 15-day field effort, environmental conditions along the leeward beaches of KNHP were relatively consistent and typical of windward areas of Hawaiʻi—warm, windy, and humid with occasional, brief tropical squalls. At ~ 2 m height just windward of the vegetation windbreak, the median temperature was 28 °C (range 19 – 32 °C), median relative humidity was 67% (range 57 – 89%), median average wind speed was 3.1 m/s (range 1.5 – 5.4 m/s), and median maximum wind speed was 5.0 m/s (range 2.5 – 7.0 m/s). At the acoustic recording site on the beaches and at the height of the microphone (0.2 m), the temperature and relative humidity measurements were generally similar (temperature: 23 – 33 °C, median 28 °C; relative humidity: 50 – 87%, median 65%), but wind speeds were decreased. Average wind speed was reduced to 1.4 m/s (range 0.3 – 4.5 m/s) and maximum wind speed to 2.4 m/s (range 1.1 to 7 m/s).

Perceptually, ambient noise at KNHP was driven primarily by wind—particularly noise created by ironwood and date palm trees along the beaches—and wave action along the rocky and sandy shores. As expected, the L50 spectral density levels decreased with increasing frequency (see Supplement 1). At low frequencies—where the predominant energy of female and pup groans falls—the L50 levels decreased from 33 dB re (20 μPa)^2/Hz at 0.05 kHz to 15 dB re (20 μPa)^2/Hz at 2 kHz.

Estimates of Transmission Loss

Tonal signals at five frequencies from 0.1 to 2 kHz attenuated with distance at rates similar to or greater than predicted by spherical spreading ($20logR$) over short ranges (< 32 m) in crosswind, upwind, and downwind conditions (see Table 1). Measured transmission loss was well approximated by spherical spreading at 0.1 kHz in crosswind conditions and at 0.2 kHz in all three wind conditions. Measurements at the three higher frequencies indicated that attenuation was greater than modeled by spherical spreading and possibly dynamic depending on the direction of the wind. At 0.5 kHz, transmission loss varied between crosswind ($32logR$) and upwind/downwind ($22logR$) conditions. At 1 and 2 kHz, signal attenuation with distance was described by approximately $30logR$. Transmission loss at 1 kHz was consistent across wind conditions. Across all measured frequencies and wind conditions, the median transmission loss term was $26logR$.

Behavioral Observations

Approximately 25 monk seals of all age classes were observed at KNHP during about 40 hours of behavioral observations. Known animals included three adult female and dependent pup pairs, about five weanlings, one subadult female, and one adult male. Approximately 10 to 12 additional unmarked adult males were sighted throughout field efforts, but these individuals were not identifiable in real time.

Monk seals around the leeward coast of KNHP were most reliably spotted when resting onshore and were typically distributed by age class. Weanlings were found hauled out on the beaches and rocky outcrops along the southern portion of the peninsula, females with pups were distributed along the two large beaches in the middle, and adult males were mostly found at the rocky northern point of the peninsula. Individuals were generally well spaced and appeared to avoid resting in the areas used by the mother-pup pairs. However, weanling seals were sometimes found relatively close to each other. Along the shoreline, the weanling seals were observed socializing in small ephemeral groups but were not notably vocal. Adult males were generally observed alone in the water. They were most often observed quietly cruising back and forth along the beaches and haul-out areas, presumably searching for access to receptive females (see Robinson et al. 2022).

The majority of observed airborne acoustic signaling occurred between the three focal pairs of female seals and their pups. Vocalizations were typically produced as a call and response between mom and pup on land or at the water’s surface (Fig. 4). Vocal exchanges usually occurred when mom and pup were beginning to move apart or attempting to reunite after separation. This calling behavior was observed to occur when mother and pup were in close contact or separated at distances up to about 30 m. For the youngest pup (PM10) observed (age 6 – 13 days and 25 – 31 days during field efforts), the rate of in-air contact calls between the pair increased when they were swimming in the shallows. Pups would also call to elicit nursing and were generally noted to vocalize more frequently than their moms. For the mom-pup pair observed over the longest period during lactation (female RT22 and pup PM10), the female appeared relatively more responsive when the pup was younger. She was observed to be more acoustically, visually, and olfactorily reactive to her surroundings compared to later in her lactation period and to the other two females with pups older than 28 days. This was qualitatively apparent in her sensitivity to common surrounding items in the environment, such as small flags used to mark turtle nests and leaves blowing in the wind, and to the presence of researchers moving in the vegetation.

Seals of all age classes produced in-air vocalizations directed toward one another during agonistic interactions. In air this included groans, bouts of *whoops* (described underwater by Sills et al. 2021 and as *bubbling* in air by Miller and Job 1992), and harsh guttural vocalizations (variations described in Miller and Job 1992). Most agonistic interactions were instigated by subadult and adult male seals patrolling beaches. The intensity and duration of interactions between males and females with pups appeared to vary based on the proximity and speed of the male's approach. Males who approached slowly and rested further than 5 m from the pair were apparently more readily accepted. They elicited less vocal behavior and were tolerated for longer durations (> 5 min) than males who approached closer or were more insistent. Generally, when a male approached, moms would initially ignore his presence and then vocalize if he continued to move toward the mom-pup pair. If the male did not respond to acoustic threats, he would typically retreat after she reoriented her body or moved only a few meters toward him. During or after these interactions, a resting female typically did not leave to water with the male unless their pup followed that male's retreat. Interactions between patrolling males and females without pups were infrequently observed but were notably longer (several minutes to over an hour).

Multimodal cues reported for other seal species (e.g., ritualized chest slamming on the sand by northern elephant seals; Sandegren 1976) were not observed to occur simultaneously with monk seal vocalizations. However, the seals apparently relied on olfactory cues in addition to acoustic behavior. The use of olfaction was particularly notable from males patrolling the beaches. Observers noted that we could reliably hear males sniffing from over 20 m away as they swam along the shoreline. The olfactory behavior of mom-pup pairs was less audible to researchers; however, face-to-face or face-to-body contact was often observed before and after vocal behavior following short separations of the pair.

Audio Summary

From 17 recording sessions, we collected 1160 minutes of acoustic data with corresponding video and identified 972 individual vocalizations. Of these calls, 188 were confirmed to be produced by the three focal females (RL04, RG30, and RT22) and 474 by the three focal pups (PM8, PM9, and PM10). The remaining 310 vocals were identified to be produced by subadult female (RQ32), adult male (RKB2), and approximately 10 to 12 unknown adult males. Besides occasional snorts and sneezes, most sounds emitted by the pups were identified as *groans*. Female contact calls with their pups were exclusively *groans*, which were also produced in non-affiliative interactions. *Whoops*, *sneezes*, *snorts*, and other non-affiliative calls were also recorded but were not explicitly labeled by call type or analyzed further. Representative high-quality (signal-to-noise ratio > 7 dB) female *groans* and pup *groans* were analyzed for amplitude, temporal, and spectral metrics.

Female and Pup Groans

Female and pup *groans* were similar in their broadband, harmonic structure, though energy in the pup call extended to slightly higher frequencies. *Groans* were typically produced in the absence of other vocal types but occasionally were preceded or succeeded by *whoops*. The groans sometimes concluded in a harsh expiration (*snort* or *sneeze*) that overlapped the end of the call.

Seventeen spectral and temporal parameters are reported for both calls in Table 2. Female *groans* (Fig. 4) were on average 1.3 s (total call duration). The mean 10-dB bandwidth ranged from 55 (+/- 7) to 509 (+/- 49) Hz. The mean fundamental frequency was 70 Hz, and female *groans* contained an average of 13 harmonics. The total call duration for pup *groans* (Fig. 4) was shorter (0.7 s), and these calls contained more energy at higher frequencies. The mean 10-dB bandwidth was 73 (+/- 8) to 595 (+/- 364) Hz. Additionally, they had a higher mean fundamental frequency (87 Hz) but a similar average number of identifiable harmonics (14). Spectrograms for both call types indicated that there were likely more harmonics at frequencies above where we could confidently count. In terms of amplitude, broadband source levels (at 1 m) were on average 85 dB RMS re 20 μPa for the mom and 83 dB RMS re 20 μPa for the pup.

Communication Ranges

Signal excess analysis across the 10-dB bandwidth of representative female and pup *groans* (see Fig. 3) suggested which salient frequency bands (i.e., 1/3-octave bands with the highest sensation levels) were likely driving detection ranges. Thus, communication ranges were calculated in the 0.4 and 0.5 kHz 1/3-octave bands for the female *groan* and the 0.25, 0.4, 0.8, and 1 kHz 1/3-octave bands for the pup *groan*. Based on the relative, frequency-specific levels of mom and pup vocalizations, hearing parameters (i.e., absolute thresholds and critical ratios), and ambient noise in the environment, detection of the female *groan* was likely limited by auditory capabilities at all frequencies. Detection of the pup *groan* was likely constrained by hearing capabilities at lower frequencies (0.25 – 0.4 kHz) and by background noise at higher frequencies (0.8 – 1 kHz).

We estimate that the maximum distance over which female *groans* can be detected by conspecifics is 40 m with spherical spreading loss (Fig. 5). This predicted range is reduced to 11 m if we assume excess energy is lost to the environment, as is likely based on the propagation study. If detection thresholds are increased to account for the necessity of higher received levels for effective discrimination, recognition, and communication, this detection range decreases to 6 – 13 m (Fig. 5). For the pup *groan*, the maximum detection range assuming spherical spreading is estimated to be 94 m but is reduced to 6 m if we account for increased environmental attenuation (Fig. 5). For effective communication, this range decreases to 2 – 30 m (Fig. 5). Minimum distances were calculated with the largest measured frequency-specific transmission loss term and are illustrated in Fig. 5.

Discussion

This study provides the first source levels for airborne vocalizations produced by Hawaiian monk seals, with broadband source levels (at 1 m) of approximately 84 dB RMS re 20 μPa for the female *groan* and pup *groan*. Along with vocal parameters, we describe the relevant characteristics of a representative terrestrial habitat used by monk seals, including measures of signal transmission loss and ambient noise.

The calls measured here have generally similar spectral and temporal parameters to those previously reported for Hawaiian monk seals (Miller and Job 1992; Job et al. 1995; Chaudun 2018). For both female and pup *groans*, duration is < 2 s, fundamental frequency below 100 Hz, and predominant call energy is below about 2 kHz. In general, the female *groan* is somewhat longer, has a lower fundamental frequency, and has a lower frequency distribution relative to the pup *groan*. Minor variations between studies are likely due to different recording methodologies, sample sizes, and environmental conditions, but all descriptions support that monk seal calls are low-frequency, broadband sounds with strong harmonic structure.

Communication Range Estimates for Hawaiian Monk Seals

The communication ranges we estimated (< 100 m) suggest that the detection of common Hawaiian monk seal calls is dynamic but limited to short ranges on shore. The predicted ranges are even shorter (< 30 m for the pup *groan* and < 15 m for the female *groan*) when we consider the received levels that are likely needed for effective communication between conspecific individuals. Detection thresholds over the low-frequency call spectra were limited by the seals' hearing abilities between 0.05 – 0.8 kHz and by ambient noise between 0.8 and 1 kHz. However, at the frequencies where hearing limits detection, absolute detection thresholds exceed the theoretical lowest thresholds in this environment by < 10 dB. This suggests that, even if detection is currently limited by auditory sensitivity at most relevant frequencies, communication range could easily be reduced further with the addition of more low-frequency noise to the environment.

While the *groan* vocalizations described here are particularly relevant for communication between mothers and their dependent pups, the female *groan* is perceptually similar to calls used by other subadult and adult monk seals. Thus, the communication ranges provided for the female *groan* are likely applicable to other *groan* variations or similar call types.

These communication space estimates for Hawaiian monk seals fall on the low end of the ranges that have been estimated in air for harbor seals and the more closely related northern elephant seal. This certainly reflects differences in auditory sensitivity and vocal amplitude between species, environmental conditions, and potentially methodological differences between studies. Reiman and Terhune (1993) investigated the distance over which a female harbor seal can detect a pup's airborne call with both of their heads above the water's surface. They utilized actual measurements of environmental noise and sound propagation loss in representative habitats paired with harbor seal auditory data available at the time. Data suggested that the 0.5 kHz energy component of a pup's call could be detected almost 1 km away. However, successful recognition (considered to be $DT + 10$ dB) was predicted to be less than 150 m. If the amplitude of the call was decreased, recognition was further reduced to < 20 m. As in the present study, this work accounted for relevant environmental parameters and the sensitivity of the listeners' auditory system.

Similarly, a comprehensive study of northern elephant seal bioacoustics provided estimated communication ranges on beaches for multiple vocal types, including mother-pup affiliative calls and female and male threat calls (Southall 2002; Southall et al. 2003a). Communication ranges were calculated from extensive sound recordings—including measurements of source levels and the sensitivity of sound pressure levels to recording orientation from the caller, frequency-specific transmission loss, and ambient noise levels in several environmental conditions experienced within the breeding colony. The reported communication ranges suggest that elephant seal calls are detectable by conspecific listeners between 5 and > 500 m, with shorter ranges for female and pup affiliative calls and longer ranges for the higher-amplitude adult male and female threat calls. Similar to the monk seal data, calls produced by pups have energy at higher frequencies and are detectable at longer ranges than female affiliative calls.

Collectively, these studies and our data for monk seals demonstrate the dynamic nature of communication space in the terrestrial environment and suggest that the detection of important communication signals in some cases may be limited to short ranges relative to calls produced by some seal species under water (Casey et al. 2016; Sills et al. 2017; Sills et al. 2021). As airborne vocal communication on shore and at the water's surface has implications for the reproductive success of many seal species, understanding their communication ranges and sensitivity to increased ambient noise is relevant for conservation and management efforts.

Behavioral Context of Acoustic Signals

In this study, most acoustic communication between a Hawaiian monk seal female and her dependent pup was observed to occur well within the maximum detection ranges estimated for both call types. This makes sense, given that mother and pup are rarely separated at such distances for the general safety of the pup. Additionally, this aligns with the asynchronous, low-density, capital breeding system of Hawaiian monk seals, which likely puts less pressure on effective long-range acoustic communication between mother-pup pairs than other higher-density pinniped breeding colonies. Finally, the increased calling behavior observed for one mom-pup pair swimming in the shallows also suggests that successful communication is particularly important in the more dynamic aquatic environment where the pair could easily become separated.

Despite active vocal communication not typically occurring at the maximum ranges possible, behavioral observations indicated that animals were collecting information from vocalizations received at a distance. Specifically, one roaming male patrolling the beaches was observed to respond to a female groan produced 150 to 200 m away. The male was swimming in the opposite direction when a mom and her pup began vocalizing in the shallows. The male immediately turned around and started swimming toward the mom-pup pair. Despite detecting this acoustic signal, it became apparent that the male struggled to localize the pair’s location at that distance. In this particular case, the vocal exchange between mom and pup had reduced in calling rate and become less salient to human observers by the time the male approached, and he apparently did not locate the pair. Regardless, this scenario provides anecdotal evidence that acoustic signals may be biologically relevant for Hawaiian monk seals at longer distances than these communication range data suggest. Further, this demonstrates the importance of behavioral observations describing natural history to complement acoustic data.

Simplifying Assumptions Associated with Active Space Estimates

It is important to note that any calculations of communication space rely on a range of assumptions about the sound signaler, environment, and receiver, and thus are a simple approximation of true communication ranges.

For the signaler, error is most often introduced with the value used for the source level. For this study and the elephant seal data (Southall 2002; Southall et al. 2003a), source levels are estimated from received levels measured at distance from calling seals. Thus, these values rely on accurate real-time estimates of distance between the calling animal and recording microphone. Furthermore, Southall (2002) reported that relative to on-axis values, received levels for a male elephant seal threat call were reduced by approximately 2 dB at 90° to 7 dB at 180° from the calling animal. Therefore, because we did not control for call directionality in this study, source levels for these calls are likely an underestimate of the true on-axis source levels.

In terms of the environment, the calculations applied here do not fully account for all the factors that influence sound propagation, including vertical wind and temperature gradients, vegetation and other surrounding obstacles, and the effects of ground reflections. However, our use of empirically measured transmission loss terms—which, in this case, suggested that signals attenuate similar to or greater than the rate expected by a spherical spreading model—attempts to encompass variability in excess attenuation across relevant frequencies. Additionally, the ambient noise measurements used to determine detection thresholds are based on median 50th percentile values in conditions experienced during a short window of time within the summer season. These values likely change seasonally with increased noise from storms or in areas with more intense wave action and would likely also increase with a greater anthropogenic presence.

The characteristics of listeners are also difficult to fully describe. What an animal can detect in simplified listening scenarios in controlled laboratory conditions does not fully encapsulate the complex nature of auditory perception (see Branstetter and Sills 2022). The simplified calculations used here do not account for the ability of animals to detect complex signals in temporally, spectrally, and spatially varying background noise (Branstetter and Sills 2022). The use of absolute hearing thresholds provides maximum distances for conspecific detection, but it is likely that higher received levels are needed to facilitate successful communication. Psychophysical data collected with birds listening for biologically relevant sounds suggest that discrimination requires an increase of 2 – 5 dB over detection thresholds (Lohr et al. 2003). For humans, comfortable understanding occurs 15 dB above absolute hearing thresholds (Franklin et al. 2006; Freyaldenhoven et al. 2006). While there are no available data describing how loud a signal must be above detection thresholds for successful discrimination, recognition, and communication in seals, psychophysical data can inform levels needed for 100% detection. Across all frequencies behaviorally tested with Hawaiian monk seals, detection increased from 50% to 100% within 7 dB in air and 4 dB in water on average and within a maximum of 10 dB in both media (see psychometric functions in Ruscher et al. 2021 and Sills et al. 2021). Sills et al. (2021) opted to use the average value (4 dB) to model effective communication ranges. Similarly, Terhune et al. (2017) used 90% detection thresholds for harbor seals (+ 10 dB from 50% detection) to investigate detection of Weddell seal (*Leptonychotes weddellii*) underwater calls by conspecifics hauled out on ice. Here, we set detection thresholds for effective communication as $DT + 10$ dB.

Finally, estimates of active space are further complicated when we consider how energy in a call is perceived by a listener. Here, we assume detection is driven by the 1/3-octave band with the greatest signal excess, but whether peak frequency or other elements are driving detection is unclear. While measurements of active space would improve if we could better model the perception of complex signals, the widely used method of peak frequency or the highest sensation level within a relevant auditory filter bandwidth provides a conservative initial estimate (see Southall 2002). Given the complexity of auditory perception in realistic listening scenarios and the limited available data for marine mammals, all the approximations used are appropriate for providing conservative estimates of the relative magnitude of communication ranges for Hawaiian monk seals.

Conclusions

Despite the acknowledged limitations in models of active space, assessing sound production and sound reception holistically is a valuable step in characterizing the acoustic behavior of Hawaiian monk seals. The communication ranges proposed herein are dynamic values that vary with environmental conditions, the sound being produced, and the ability of the listener to perceive and understand the signal. These conservatively estimated data improve understanding of Hawaiian monk seal vocal behavior and their acoustic habitats and are relevant to predicting how terrestrial communication may be constrained by ambient or human-generated noise in the environment.

Acknowledgements

This research was facilitated by partnerships with the NMFS Hawaiian Monk Seal Research Program and the National Park Service. Specifically, we are grateful for the support of K. Parnell, M. Barbieri, T. Mercer, L. McCue, G. Puig-Santana, M. Duda, K. Moore, and the entire community of Kalaupapa. We thank E. Levy, K. Jagit, S. Aldana, N. Packard, and J. Raimondi for help with field preparation, data analysis, and figure curation. B. Ruscher was supported in part by the US Navy's Living Marine Resources Program and the UC Santa Cruz Ocean Science Department. A portion of this work was presented at the 187th Meeting of the Acoustical Society of America (virtual).

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Chapter 3: Figures and Tables

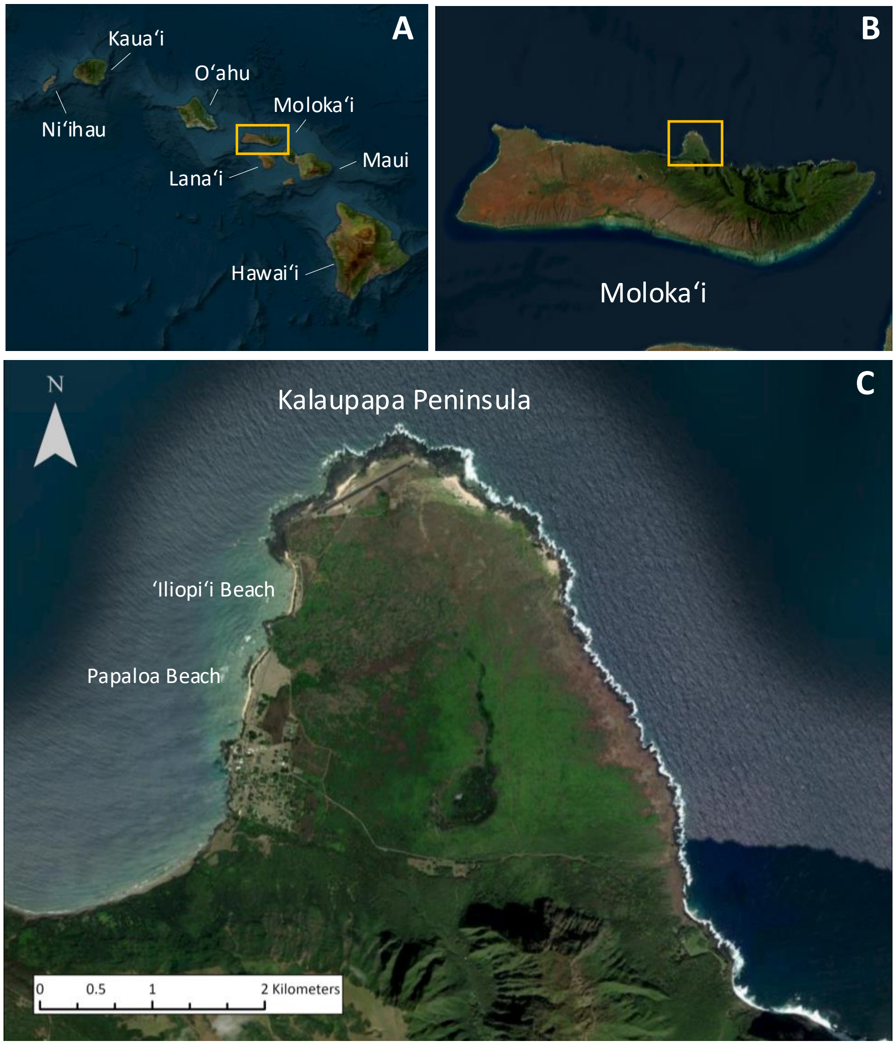


Fig. 1. The study site in Kalaupapa National Historical Park (Moloka'i, HI, USA). **Panel A** indicates the position of Moloka'i (yellow box) among the Main Hawaiian Islands, and **panel B** highlights the Kalaupapa Peninsula (yellow box) on the north side of Moloka'i. **Panel C** zooms into the Kalaupapa Peninsula and identifies the two beaches on the leeward side of the peninsula where all acoustic data were collected. The scale bar in panel C is only relative to that image. Satellite images obtained with ArcGIS Pro (courtesy of E. Levy).

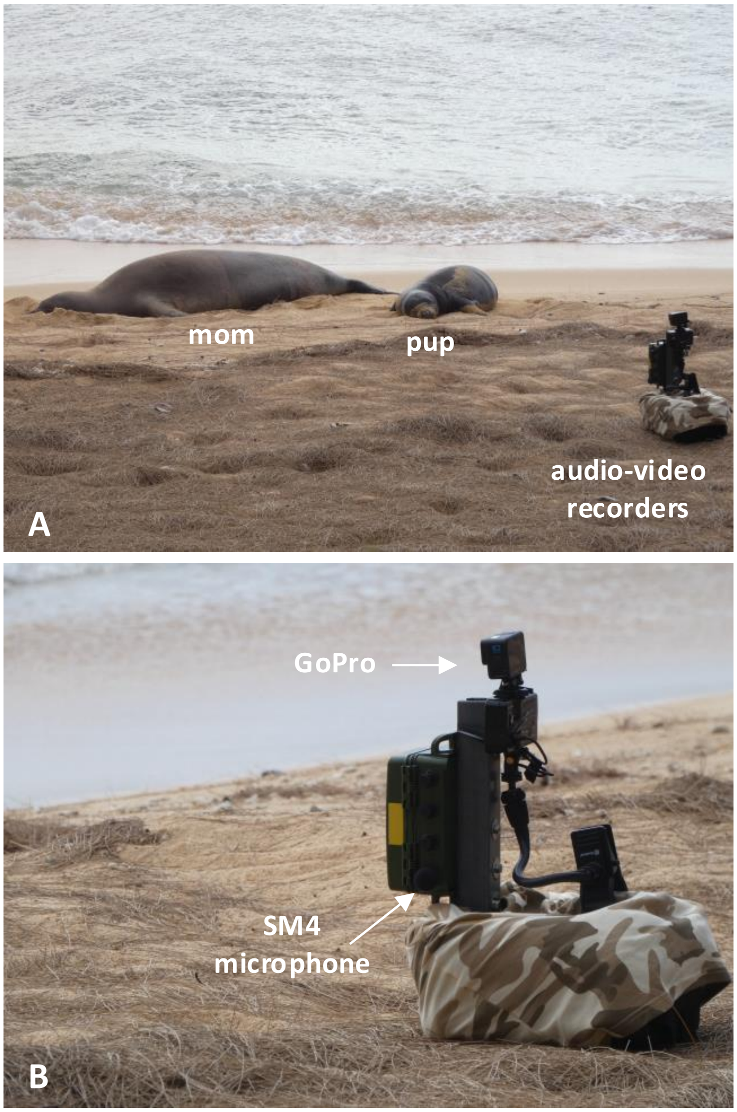


Fig. 2. Panel A shows a female Hawaiian monk seal and her dependent pup resting on the beach with the autonomous audio-video recorders placed within 10 m. **Panel B** shows the location of the video recorder and one microphone in the equipment setup. The Wildlife Acoustics SongMeter SM4 is mounted so that the dual microphones (located on either side of the SM4 box) are stably fixed at 0.2 m height. The base of the mount is wrapped in thin neoprene to acoustically dampen the case and is covered in camouflage-patterned cloth to make the whole setup less conspicuous to the animals. The GoPro Hero 10 wide-angle camera and external battery pack are mounted above and behind the acoustic recorder. Photos: B. Ruscher, NMFS permit 22677.

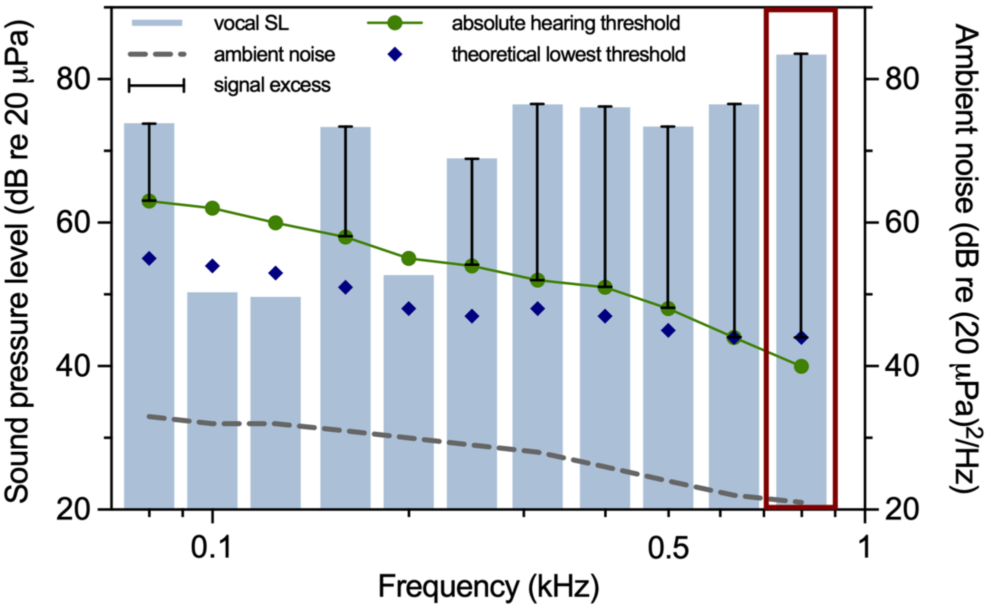


Fig. 3. Overview of the signal excess analysis conducted to determine the 1/3-octave band within a call to be used for communication range calculations. For one representative Hawaiian monk seal pup *groan* vocalization, source levels (SL) are plotted in SPL (blue bars) for the 1/3-octave bands within the 10-dB bandwidth of the call. These SL values are estimated from received levels at the microphone using spherical spreading, or 20*logR*. Associated ambient noise in the environment is reported as unweighted, 50th percentile power spectral density levels (grey dashed line corresponding to the right y-axis). Detection threshold (DT) for each 1/3-octave band is defined either as the absolute hearing threshold (green circles) or the theoretical lowest threshold in the environment (ambient noise plus critical ratio; blue diamonds), depending on which value is greater at a particular frequency. Auditory data are from Ruscher et al. 2021—where values were not directly reported, hearing thresholds or critical ratios are extrapolated or interpolated (see text for details). Signal excess (black vertical lines) is calculated as the difference between SL and DT within the same 1/3-octave band. The 1/3-octave band with the greatest signal excess is ultimately used to calculate communication range. In this example, the 0.8 kHz 1/3-octave band has the largest signal excess (red box).

Table 1. Frequency-specific transmission loss terms estimated at relevant frequencies (0.1 – 2 kHz) in typical ambient conditions over two days. Pure tones were recorded at distances from 1 to 32 m in three possible wind conditions. Sound pressure level was measured for five replicates at each distance. Simple linear regressions of median received levels were calculated as a function of log(distance) for each frequency and wind condition. For 0.1 and 2 kHz, transmission terms were only estimated once in the crosswind condition. For 0.2 and 1 kHz, transmission terms were similar between both days and all three wind conditions and, thus, are presented as a median value of all data. At 0.5 kHz, transmission terms were variable between the crosswind and up/downwind conditions, so they are presented as median values of both crosswind datasets, up and downwind data, and all three wind conditions. Sample size refers to the number of propagation estimates conducted. In all cases, transmission loss is ≥ spherical spreading (20*logR*).

Frequency (kHz)	Wind direction	Sample size	Transmission term
0.1	crosswind	n = 1	20logR
0.2	cross/up/downwind	n = 4	22logR
0.5	crosswind	n = 2	32logR
	up/downwind	n = 2	22logR
	cross/up/downwind	n = 4	27logR
1	cross/up/downwind	n = 4	31logR
2	crosswind	n = 1	29logR
all	cross/up/downwind	n = 18	26logR

Table 2. Mean ± SD values and ranges for acoustic parameters measured for two call types (female *groan* and pup *groan*) produced in air by free-ranging Hawaiian monk seals. Five calls with signal-to-noise ratios > 7 dB were analyzed for each call type. Vocal parameters were measured in Raven Pro v.1.6.1 (Hann window; DFT size 4096 samples; 90% overlap; 3 dB filter bandwidth 16.9 Hz). Asterisks (*) denote spectral parameters that were influenced by ambient noise for a subset of analyzed calls; for these parameters, values were reported for only three female *groans* and two pup *groans* with signal-to-noise ratios > 10 dB. Broadband source levels were approximated with a spherical spreading model from broadband received levels recorded at < 7 m from seals.

Parameter	Definition	Female groan		Pup groan	
		Mean ± SD	Range	Mean ± SD	Range
Total duration (s)	Complete call duration	1.27 ± 0.47	0.78 - 1.99	0.68 ± 0.21	0.40 - 0.98
90% duration (s)	Duration containing 90% of the call's total energy	1.05 ± 0.40	0.63 - 1.68	0.53 ± 0.18	0.32 - 0.80
Center frequency (Hz)*	Frequency dividing the call into 2 frequency intervals of equal energy	359 ± 36	328 - 398	439 ± 373	176 - 703
First quartile frequency (Hz)*	Frequency bounding the spectrum betweenat 25% of the call's energy	266 ± 34	246 - 305	217 ± 191	82 - 352
Third quartile frequency (Hz)*	Frequency bounding the spectrum betweenat 75% of the call's energy	426 ± 36	387 - 457	938 ± 249	762 - 1113
Inter-quartile range bandwidth (Hz)*	Span between first and third quartile frequencies	160 ± 24	141 - 188	721 ± 439	410 - 1031
90% bandwidth upper bound (Hz)*	Frequency bounding the spectrum at 95% of the call's energy	531 ± 119	457 - 668	1107 ± 373	844 - 1371
90% bandwidth lower bound (Hz)*	Frequency bounding the spectrum at 5% of the call's energy	59 ± 12	47 - 70	76 ± 8	70 - 82
90% bandwidth (Hz)*	Difference between 5 and 95% frequencies	473 ± 129	398 - 621	1031 ± 381	762 - 1301
Peak frequency (Hz)	Frequency of maximum power	359 ± 57	305 - 445	223 ± 302	82 - 762
3 dB bandwidth upper bound (Hz)	Upper frequency bounding the spectrum 3 dB below peak power	437 ± 46	378 - 486	270 ± 293	87 - 785
3 dB bandwidth lower bound (Hz)	Lower frequency bounding the spectrum 3 dB below peak power	166 ± 146	58 - 380	215 ± 298	76 - 748
3 dB bandwidth (Hz)	Span between upper and lower 3 dB bandwidth bounds	271 ± 150	84 - 421	55 ± 48	11 - 112
10 dB bandwidth upper bound (Hz)	Upper frequency bounding the spectrum 10 dB below peak power	509 ± 49	458 - 565	595 ± 364	266 - 1118
10 dB bandwidth lower bound (Hz)	Lower frequency bounding the spectrum 10 dB below peak power	55 ± 7	48 - 64	73 ± 8	67 - 86
10 dB bandwidth (Hz)	Span between upper and lower 10 dB bandwidth bounds	455 ± 53	406 - 514	522 ± 366	199 - 1051
Aggregate entropy (bits)	Disorder in a sound measured from energy distribution within a call	4.77 ± 0.48	4.22 - 5.24	5.13 ± 0.69	4.26 - 5.82
Number of harmonics	Number of harmonics	13 ± 1	12 - 15	14 ± 6	4 - 18
Fundamental frequency (Hz)	Lowest frequency of the call harmonics	70 ± 8	59 - 82	87 ± 11	82 - 106
Broadband received level (dB RMS re 20 μPa)	Calibrated level of the call measured < 7 m from the animal	72 ± 2	71 - 77	71 ± 1	70 - 72
Broadband source level (dB RMS re 20 μPa)	Estimated level of the call @ 1 m. Approximated from received level	85 ± 2	83 - 89	83 ± 2	81 - 86

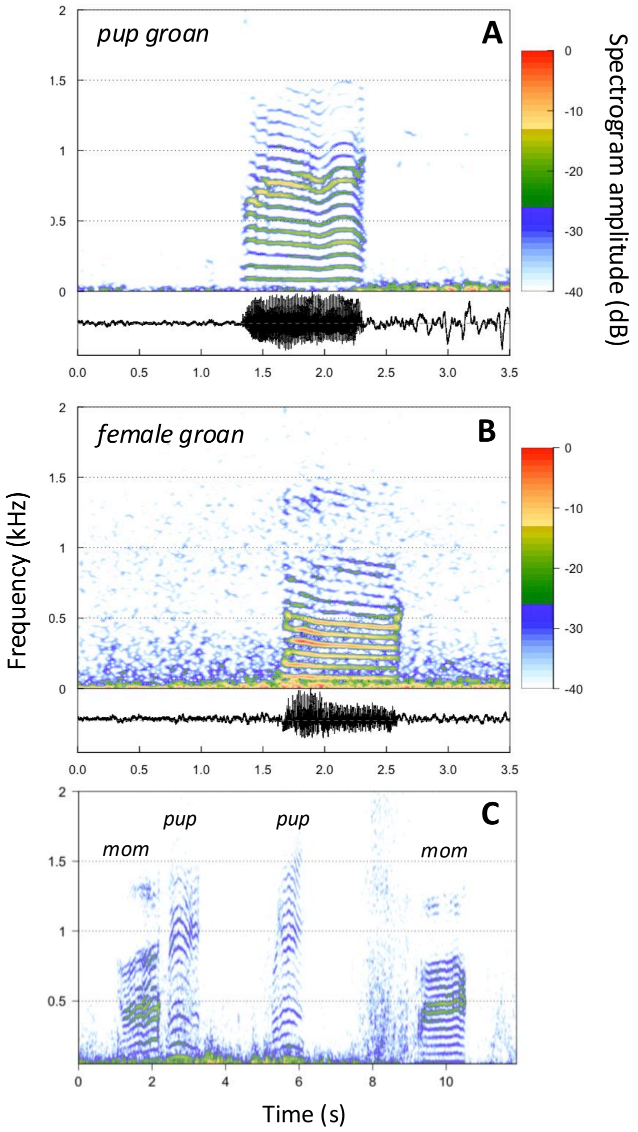


Fig. 4. Spectrograms for two calls produced in air by Hawaiian monk seals. **Panel A** displays a pup *groan*. **Panel B** displays an adult female *groan*. Relative amplitude is shown by corresponding waveforms (below each plot) and the vertical scalebar (right). **Panel C** shows a typical vocal exchange between mother and pup. Note the different time scales of the x-axis for the solitary calls versus the vocal bout. Spectrogram settings: Hanning window, window length 4096 points, 90% overlap.

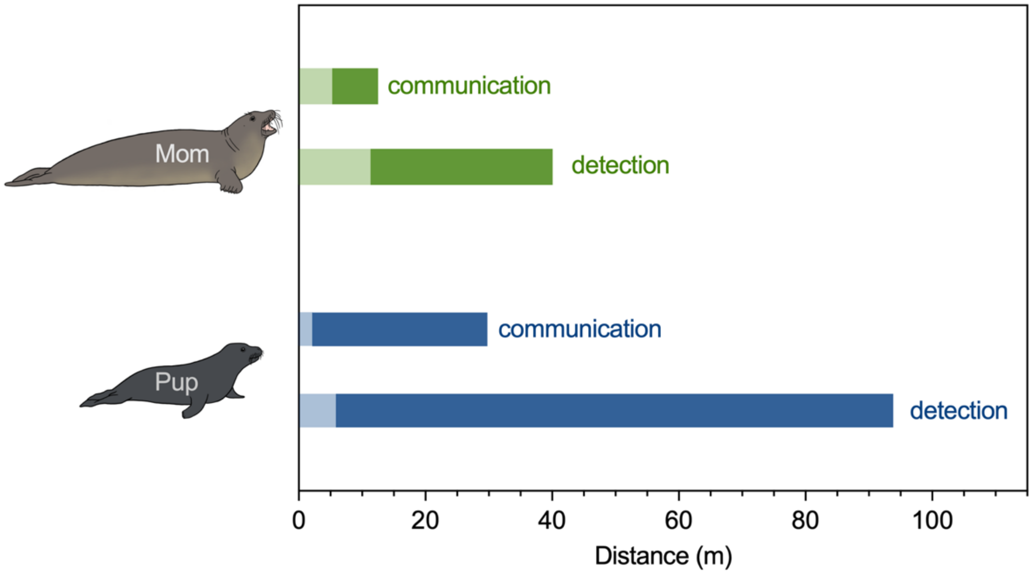
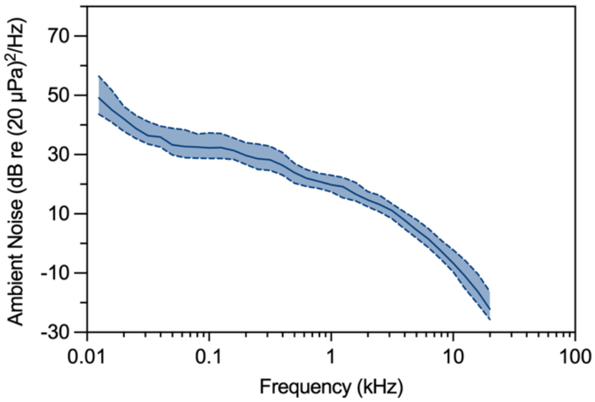


Fig. 5. Estimated communication ranges for calls emitted by Hawaiian monk seal mother (green) and pup (blue). Range was calculated in each case for the 1/3-octave band containing the greatest signal excess (see Fig. 3) and is provided as the predicted distance (in m) over which detection (determined by detection thresholds; see Fig. 3) or 'effective' communication (approximated by detection thresholds plus 10 dB) can occur. The darker portion on the right side of each bar denotes the minimum and maximum predicted communication range for each call type (n = 5, signal-to-noise ratio > 7 dB), with variation driven by transmission loss estimates (see Table 1). For all conditions, maximum distances were calculated based on spherical spreading ($20logR$), while minimum distances were determined from the frequency- and wind-dependent transmission terms (between 26 and $32logR$) estimated in this study. Female *groans* (green) are predicted to be detectable over distances of up to 11 to 40 m, while pup *groans* (blue) are likely detectable at distances of up to 6 to 94 m from the vocalizing individual. At thresholds more ecologically relevant for effective communication, distances decrease to 6 to 13 m (female *groan*) and 2 to 30 m (pup *groan*). The broad ranges of communication estimates calculated for Hawaiian monk seals are influenced by amplitude and spectral variation of calls, as well as by dynamic environmental conditions.

Chapter 3: Terrestrial vocal behavior and communication range estimates in Hawaiian monk seals

Supplement 1: Terrestrial ambient noise at Kalaupapa National Historical Park

Ambient noise was recorded on the beaches of Kalaupapa National Historical Park (KNHP) over 15 days in July and August 2024. A Brüel and Kjær 2250 self-powered sound level meter (sampling rate 48 kHz) with a free-field ½-in type 4966 microphone and a UA1650 windscreen were used to record 47 1-min, unweighted ambient noise samples. Measurements were taken in representative weather conditions between 0800 and 1800 in locations utilized by Hawaiian monk seals at KNHP. Power spectral density levels were calculated from the median of 1/3-octave band 10th (L10), 50th (L50), and 90th (L90) percentile measurements. These values describe the noise levels which were exceeded 10, 50, and 90% of the time. L50 ambient noise is plotted as a solid line and is bounded by the 10th (above) and 90th (below) percentile statistics of the noise distribution. Associated values are provided in the table.



Frequency (Hz)	Ambient noise (dB re (20 µPa)^2/Hz)		
	L10	L50	L90
12.5	56	49	44
16	52	45	41
20	46	42	38
25	43	39	36
31.5	41	36	34
40	40	36	33
50	39	33	30
63	38	33	29
80	37	33	29
100	37	32	29
125	37	32	29
160	36	31	28
200	34	30	27
250	34	29	25
315	33	28	25
400	31	26	23
500	27	24	20
630	25	22	19
800	24	21	19
1000	23	20	17
1250	22	19	15
1600	21	17	14
2000	18	15	12
2500	16	13	11
3150	13	11	8
4000	11	8	5
5000	8	5	2
6300	5	1	-1
8000	1	-3	-6
10000	-2	-7	-10
12500	-6	-11	-15
16000	-10	-16	-20
20000	-16	-22	-26

General Discussion

This dissertation addresses some intriguing gaps in our knowledge of acoustic behavior in Hawaiian monk seals (*Neomonachus schauinslandi*) —a true seal species endemic to the Hawaiian Archipelago. Research on the population biology and ecology of this species intensified with the onset of widespread conservation concerns following their designation in 1976 as 'depleted' under the US Marine Mammal Protection Act and 'endangered' under the US Endangered Species Act. Though the population numbers have begun to rebound, this species is still granted 'endangered' status under the IUCN Red List (Littnan et al. 2015). Rigorous population monitoring and mitigation of threats, both natural (e.g., shark predation, food limitation, male aggression) and anthropogenic (e.g., introduced diseases, debris entanglement, fisheries interactions, human disturbance), are ongoing by the National Marine Fisheries Service Hawaiian Monk Seal Research Program (for review, see Robinson et al. 2022).

During the initial phases of recovery efforts, there were a few studies focused on bioacoustics. These included reports of Hawaiian monk seal sound production in air (Miller and Job 1992; Job et al. 1995) and sound reception in water (Thomas et al. 1990), which provided a first glimpse into the acoustic lives of these unique tropical seals. In particular, the audiometric data collected in an abbreviated study by Thomas et al. (1990) was quite unexpected. Specifically, the data indicated that monk seals were insensitive to underwater sounds below 10 kHz, suggesting a very constricted hearing range relative to other, more well-studied seal species that can detect underwater sounds below 0.1 kHz (see Southall et al. 2019). This preliminary monk seal underwater audiogram (Thomas et al. 1990) called into question the potential use of acoustic communication signals under water—which had not yet been documented—and suggested that monk seals may be similarly insensitive to low-frequency sounds contained within their airborne calls (Miller and Job 1992; Job et al. 1995). However, no terrestrial auditory measurements were made at the time.

These early studies and unresolved data gaps in our understanding of the acoustic biology of monk seals inspired a comprehensive study conducted by Sills et al. (2021). The research team, including myself (B. Ruscher), carried out a thorough examination of underwater sound reception and vocal production in this species. Our work resulted in an updated hearing profile for one additional monk seal and the first published description of underwater calling behavior by two mature males living in human care (Sills et al. 2021). These data confirmed the frequent and year-round production of low-frequency vocalizations in water, comparable to some of the sounds produced on shore. Furthermore, audiometric data indicated that these seals do, in fact, have a broad enough underwater hearing range (< 0.1 – 40 kHz) to enable detection of their calls. However, the apparent misalignment of auditory thresholds at the low frequencies between Sills et al. (2021) and Thomas et al. (1990) inhibited our ability to confirm species-typical hearing for Hawaiian monk seals.

The remaining questions about monk seal bioacoustics following the Sills et al. (2021) study inspired the body of work presented in this dissertation. Chapter 1 (Ruscher et al. 2021) contributed the first in-air hearing profile and auditory masking metrics (critical ratios) for the species. The audiogram is surprisingly elevated compared to those of other seal species (see Southall et al. 2019), indicating that monk seals are relatively insensitive to airborne sounds. When considered alongside a comparative review of the external auditory anatomy of true seals, these data suggest subfamily to species-level differences in anatomical adaptations and acoustic sensitivity. Chapter 2 (Ruscher et al. 2025) addressed the important issue of whether the available hearing data could be considered representative for the species. This work added detailed amphibious hearing data for a second seal. It revealed an additional underwater audiogram for Hawaiian monk seals that is consistent with Sills et al. (2021) and six terrestrial hearing thresholds that confirm the shallow hearing profile described in Chapter 1. Combined with the hearing data from Sills et al. (2021), the psychophysical measurements reported in this dissertation provide comprehensive hearing profiles for the species. We can now confidently describe species-typical hearing abilities in air and under water for Hawaiian monk seals.

In terms of sound production, Hawaiian monk seals are now known to emit low-frequency vocalizations both above and below the water's surface. In-air, these include mother-pup affiliative calls, threats, and a few other social sounds (Kenyon and Rice 1959; Miller and Job 1992; Job et al. 1995; Chaudun et al. 2018). However, the high auditory thresholds presented for Hawaiian monk seals in Chapters 1 and 2 indicate that the effective use of airborne acoustic signals is likely limited for the species—supporting reports of limited long-range communication by monk seals in air (Miller and Job 1992). Chapter 3 reports spectral, temporal, and amplitude metrics of spontaneous calls produced by free-ranging Hawaiian monk seals at Kalaupapa National Historical Park (Molokaʻi, HI, USA), providing the first source level estimates for airborne vocalizations produced by this species. Data for female and pup calls were combined with descriptions of typical environmental conditions—including ambient noise profiles and aspects of sound transmission loss—and frequency-specific masked and absolute hearing sensitivity to calculate potential communication distances for monk seals. These confirm that the detection of these airborne sounds is limited to < 100 m for the species and is likely shorter (< 30 m) if we consider requirements for effective communication.

Collectively, these amphibious auditory data measured in controlled laboratory conditions, observations and measurements of spontaneous vocal behavior in wild individuals, and characterizations of representative environments inhabited by these seals enrich our understanding of the acoustic world of Hawaiian monk seals. Although the estimated communication ranges are small and monk seals are not particularly acoustically sensitive in air, behavioral observations confirm that they still use acoustic cues to move within their environment and communicate with conspecifics. Though they are primarily limited by hearing abilities at frequencies relevant to their vocalizations, hearing thresholds are within 10 dB of ambient noise in a representative terrestrial environment. Thus, any increase in background noise, whether natural or anthropogenic, could further reduce their ability to detect biologically relevant sounds. In particular, the effective detection and recognition of sounds related to reproductive success (e.g., mother-pup affiliative calls) is vital given their endangered species status. The threat of anthropogenic noise impacting communication is especially relevant for this species due to their presence around human activity in the Main Hawaiian Islands and US military activity throughout their entire population range. While their hearing data and behavioral observations suggest that they are fairly resilient to acoustic disturbance, communication in this species is still susceptible to auditory masking by anthropogenic noise sources.

Relevance to Other Species

These acoustic data for Hawaiian monk seals are relevant to our understanding of lesser-studied true seal species. Hearing data for seals are mostly available for species from the Phocinae subfamily—most temperate and all polar seals of the Northern Hemisphere (i.e., 'northern' seals). Hawaiian monk seals belong to the Monachinae subfamily or 'southern' seals, which includes the monk, elephant, and Antarctic seals. The northern elephant seal (*Mirounga angustirostris*) is presently the only other species behaviorally tested from this lineage, with data available for just one individual tested in air and water (e.g., Kastak and Schusterman 1999; Reichmuth et al. 2013). These limited but valuable data suggest that elephant seals also have limited hearing abilities relative to the Phocinae species. While psychophysical data from more Monachinae species will be needed to determine if there are differences in auditory biology at the subfamily level, the confirmation of species-typical hearing for Hawaiian monk seal provides insights into auditory abilities of unstudied species.

The growing body of auditory data for Hawaiian monk seals is particularly relevant to the Mediterranean monk seal (*Monachus monachus*), the only other extant monk seal species. Mediterranean monk seals were recently relisted from ‘endangered’ to ‘vulnerable’ under the IUCN Red List (Karamanlidis et al. 2023), but conservation efforts are ongoing for this elusive species. While insight into their sound production behavior is emerging (Muñoz et al. 2011; Charrier et al. 2017, 2023; Muñoz-Duque et al. 2024), there are currently no available audiometric data available for this species (Southall et al. 2019). The hearing data highlighted here for Hawaiian monk seals will certainly inform conservation and management efforts regarding anthropogenic noise within Mediterranean monk seal habitats. Additionally, there are no available behavioral audiometric data for the Antarctic seals (see Southall et al. 2019). This leaves a significant gap in our understanding of the hearing within this clade of Monachinae seals, which is increasingly relevant given the increased presence of human activity in Antarctica (e.g., tourism, krill fisheries).

The subfamily-level differences in hearing sensitivities for true seals highlighted in Chapters 1 and 2 (Ruscher et al. 2021, 2025) reflect the importance of sampling within and across phylogenetic clades for a deeper understanding of the evolution of hearing in highly specialized marine mammals. In terms of current regulatory guidance on the effects of noise (see Southall et al. 2019), we have filled a key data gap for one vulnerable species. The psychophysical data reported in this dissertation confirm that we can consider the in-air and underwater functional hearing groups of phocid carnivores—based primarily on hearing data from Phocinae seals—to be conservative for Hawaiian monk seals, and likely the understudied Mediterranean monk seal and Antarctic seal species of the Monachinae lineage.

Conclusions

The work presented in this dissertation contributes fundamental knowledge about hearing capabilities and acoustic communication in endangered Hawaiian monk seals. In particular, the combination of detailed measurements concerning sound reception and sound production illustrate how hearing and communication may be constrained by ambient or human-generated noise in the dual environments used by the species. This dissertation provides comprehensive marine and terrestrial data to support decision-making about anthropogenic noise exposures that may be relevant to conservation efforts for Hawaiian monk seals.

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