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Behavioral Response of Diving Northern Elephant Seals (*Mirounga angustirostris*) When Exposed to Predator Calls

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BEHAVIORAL RESPONSE OF DIVING NORTHERN ELEPHANT SEALS (*MIROUNGA
ANGUSTIROSTRIS*) WHEN EXPOSED TO PREDATOR CALLS

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Daphne M. Shen

December 2023

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The Designated Thesis Committee Approves the Thesis Titled

BEHAVIORAL RESPONSE OF DIVING NORTHERN ELEPHANT SEALS (*MIROUNGA
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ABSTRACT

BEHAVIORAL RESPONSE OF DIVING NORTHERN ELEPHANT SEALS (*MIROUNGA ANGUSTIROSTRIS*) WHEN EXPOSED TO PREDATOR CALLS

by Daphne M. Shen

Understanding how marine mammals respond to and recover from acoustic stressors is crucial if underwater noise increases. The use of an animal-borne bilogger that combines a speaker with a motion sensor allows for the collection of whole-dive and fine-scale data over repeated exposures under identical experimental parameters. This study determined whether northern elephant seals (*Mirounga angustirostris*), a model for deep-diving marine mammals, exhibited a stereotypical behavioral response when exposed to killer whale whistles, an acoustic stressor. I examined changes in dive characteristics, measured duration of altered response, and observed behavior in response to repeated exposures. When exposed to the playback on ascent, the elephant seals performed an escape response consisting of a dive inversion during which they increased activity and displayed more variation in swimming direction. However, the seals returned to baseline diving behavior immediately after the exposure dives, suggesting they recover quickly from disturbance. After repeated exposures, the seals continued to perform dive inversions but reduced the extent of their responses over time. Even though northern elephant seals appear to recover quickly from this acoustic stressor, the initial strong behavioral response still causes an increase in energy expenditure that could be detrimental over time, especially if they are continuously faced with disturbances. Integrating behavioral responses with physiological measurements will help us fully comprehend how these animals change their diving behavior in response to increased sounds in the ocean.

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Holser, Logan Pallin, Patrick Robinson, Arina Favilla, Theresa Keates, Emma Nicholson, Parker Forman, Luke Keehan, Año Nuevo rangers, and many others for helping with fieldwork and logistics. Finally, thank you to the northern elephant seals that collected data for this project. I'm grateful for the early mornings and late nights spent with so many lovely humans and seals.

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TABLE OF CONTENTS

List of Tables	ix
List of Figures	x
List of Abbreviations	xi
Introduction.....	1
Methods.....	8
Translocation and Instrumentation Procedure	8
AMX Tag Programming	10
Data Processing and Analysis.....	11
Statistical Analysis.....	16
Results.....	21
Exposure Dives vs Non-Exposure Dives	22
Pre-Inversion vs Post-Inversion During Exposure Dives	28
Duration of Behavioral Response Before Returning to Baseline	30
Evidence of Habituation or Sensitization	32
Discussion	38
Behavioral Response to Acoustic Disturbance	38
Duration of Behavioral Responses.....	44
Behavioral Response to Repeated Exposures	46
Conclusion	48
References.....	51

LIST OF TABLES

Table 1.	Summary of 22 Translocated Juvenile Northern Elephant Seals Carrying Acoustic Tags	21
Table 2.	Summary of Northern Elephant Seal Dive Characteristics.....	22
Table 3.	Summary of Northern Elephant Seal Dive Characteristics, Separated Into Three Groups	23
Table 4.	Summary of Results Examining Response to Repeated Exposures of Acoustic Stressors	33

LIST OF FIGURES

Figure 1.	Spectrogram Image of Transient Killer Whale Whistles.....	11
Figure 2.	Illustration Showing When AMX Tag Playbacks can be Triggered	11
Figure 3.	Example Dive Profile of an Elephant Seal's Exposure Dive.....	14
Figure 4.	Example Dive Profiles of Two Types of Acoustic Exposure Dives.....	24
Figure 5.	Dive Duration, Descent Rate, Ascent Rate, and Post Dive Interval for Three Types of Dives	25
Figure 6.	Cluster Analysis for Whole-Dive Variables	27
Figure 7.	Stroke Rate, ODBA, Pitch, and Heading During Pre-Inversion and Post-Inversion Descent	29
Figure 8.	Stroke Rate, ODBA, Pitch, and Heading During Pre-Inversion and Post-Inversion Ascent	30
Figure 9.	Dive Duration, Descent Rate, Ascent Rate, and Post Dive Interval of Exposure Dive Sequence	32
Figure 10.	Dive Duration, Descent Rate, Ascent Rate, and Post Dive Interval During Repeated Exposures of the Acoustic Stressor	35
Figure 11.	Changes in Stroke Rate, ODBA, Pitch, and Heading Between Pre-Inversion and Post-Inversion Descent During Repeated Exposures of the Acoustic Stressor	36
Figure 12.	Changes in Stroke Rate, ODBA, Pitch, and Heading Between Pre-Inversion and Post-Inversion Ascent During Repeated Exposures of the Acoustic Stressor	37

LIST OF ABBREVIATIONS

AMX – audio-motion datalogger
IACUC – Institutional Animal Care and Use Committee
LML – Long Marine Laboratory
MFA – mid-frequency active (sonar)
NMFS – National Marine Fisheries Service
ODBA – overall dynamic body acceleration
PDI – post dive interval
SJSU – San José State University
TDR – time depth recorder
UCSC – University of California, Santa Cruz
VHF – very high frequency

Introduction

Noise in the ocean has increased dramatically in the past 50 years, mostly due to anthropogenic sounds (McDonald et al., 2006). These noises are widespread and may cause disturbance to animals living within a detectable range of the source (Hildebrand, 2005). Marine mammals use sound and hearing for a variety of daily tasks such as foraging, navigation, communication with conspecifics, and detection of nearby predators (Richardson et al., 1995; Tyack, 2008). Excess underwater noise can disrupt many animals' ability to complete these essential tasks. Most marine mammal species have sensitive underwater hearing, making them susceptible to acoustic stimuli. If an unfamiliar or threatening sound is heard, an individual's natural instinct is often to avoid predators or anything else that may cause harm, so the increase in human-made sounds from ships, drilling, naval sonar, or air guns likely impact the behavior of animals in the ocean (Ellison et al., 2012).

Marine mammal responses to noise can be grouped into three categories: behavioral, acoustic, and physiological (Nowacek et al., 2007). Behavioral responses include locomotive changes in dive patterns, surfacing times, or travel direction. Acoustic responses refer to changes in the animal's vocal behavior. Examples of physiological responses include changes to hormone levels, hearing ability, heart rate, and/or oxygen use. Within these categories of responses, behaviors can range from subtle to extreme, and depend on the animal's physiological capabilities and its behavioral state prior to exposure to stimuli (Costa et al., 2016; Ellison et al., 2012). For example, marine mammals are air breathers that spend much of their lives underwater either travelling or foraging, so responses to acoustic stimuli

will be influenced by how long they can stay underwater before needing to surface to replenish their oxygen supply.

There are many short and long-term effects that may result from acoustic stressors. These disruptions include immediately swimming away from projected sound sources, diving deeper, extending dive durations, changing surface intervals, and altering activity metrics (DeRuiter et al., 2013; Goldbogen et al., 2013; Nowacek et al., 2004; Patenaude et al., 2002; Stimpert et al., 2014; Tyack et al., 2011). Many species of toothed and baleen whales decrease or stop feeding behaviors when exposed to various sonar, vessel noise, alert signals (anthropogenic acoustic exposures consisting of a sequence of varying frequencies), or predator noises (Aguilar Soto et al., 2006; DeRuiter et al., 2013; Goldbogen et al., 2013; Isojunno et al., 2016; Nowacek et al., 2004; Sivle et al., 2016; Tyack et al., 2011). Reducing foraging time or spending excess energy avoiding stressors such as noise may lead to long-term negative effects, including decreased fitness or reproduction ability (Braithwaite et al., 2015; Williams, Kendall, et al., 2017). Additionally, one major source of anthropogenic sound, naval sonar, is thought to be a cause of mass stranding events in several species of beaked whales, which is suspected to occur due to decompression sickness that often ends in death (Bernaldo De Quirós et al., 2019; Filadelfo et al., 2009; Simonis et al., 2020). These strandings may be the result of immediate and/or prolonged fine-scale dive behaviors the animals perform following exposure to stressful acoustic stimuli. Although these past studies all examined behavioral changes, it is difficult to generalize responses to acoustic stimuli across and within species because of differences in study design.

The variation between previous studies creates challenges when comparing behavioral responses, mainly due to differences in received sound levels and methods for observing behavior. Playback experiments typically rely on broadcasting acoustic stimuli from nearby boats, or in shallow water, transmitters on the seafloor. The level of exposure is then measured by a hydrophone attached to the animal or by estimating the distance (both horizontally and vertically) between the target animal and the sound source to calculate approximate received sound levels (Goldbogen et al., 2013; Nowacek et al., 2004; Southall et al., 2012; Tyack, 2009; Tyack et al., 2011). Some studies documented the responses of all nearby animals after acoustic stimuli using visual observations, while others tracked one specific individual, usually using a multi-sensor datalogger to examine the underwater response (DeRuiter et al., 2013; Frankel & Clark, 2000; Goldbogen et al., 2013; Sivle et al., 2016; Southall et al., 2019; Stimpert et al., 2014; Tyack et al., 2011). Aspects such as location of sound source, distance, familiarity, or speed of the sound can impact behavioral responses. Since many researchers do not know the behavioral states of their target animals until tags are retrieved, assessing responses to repeated exposures of acoustic stressors under consistent conditions has been challenging. This research field would benefit from studies that can control for more of these factors, including consistent received level of sound and timing of exposures.

The type of acoustic stressor can also impact the behavioral response of marine mammals (Nowacek et al., 2007). Some studies have used natural acoustic stimuli, such as sounds made by conspecifics, other neutral species, or predators. The killer whale (*Orcinus orca*) is one of the top predators of marine mammals, and many species exhibit a fight or flight

response if they see or hear a killer whale (Jefferson et al., 1991; Le Boeuf & Crocker, 1996). Some larger baleen whales may be able to fight off a killer whale, but for deep divers like beaked whales or elephant seals, the safest option is to dive deeper to escape from their predators, which prefer to hunt closer to the surface. Coincidentally, killer whale calls sound similar to a particular type of naval sonar called mid-frequency active (MFA) sonar. These two types of sounds have been observed to cause a comparable reaction in study individuals (Miller et al., 2022; Zimmer & Tyack, 2007). If animals consider sonar to be an equivalent threat as a predator call, triggering them to perform evasive behaviors, then an increase in anthropogenic sounds in the oceans may have increasingly negative effects on marine mammals.

Although many studies have examined marine mammal behavioral responses to acoustic stressors, much less is known about how long it takes an animal to return to normal behavior due to challenges in following individuals for extended periods. Previous studies examined the time it takes animals to return to a geographical area around the sound source (DeRuiter et al., 2013; Tyack et al., 2011), but less is known about return to normal dive patterns and other fine-scale behaviors. Learning how long it takes an animal to return to pre-exposure dive behavior once a threat is gone and how it will react the next time it hears the same stimulus is critical for understanding the impacts of chronic exposures to acoustic stimuli.

To understand potential long-term effects of disturbances, we must test whether animals become habituated or sensitized to acoustic stressors. Survival instincts should discourage an animal to completely habituate to predator and unknown sounds over time, but some animals habituate and start ignoring specific stressors after constant repeated exposure (Cox et al.,

2001). Selective habituation may also occur, in which animals may not waste energy on non-threatening stimuli, but stay alert when threatening or unfamiliar sounds are nearby (Deecke et al., 2002). In contrast, some animals become sensitized to sounds and continue reacting with the same or stronger responses after repeated exposures (Kastak & Schusterman, 1996). To better understand the long-term impacts of acoustic stressors, we must examine how marine mammals respond to controlled repeated exposures.

To better track behavioral responses to repeated acoustic stimuli, a novel biollogger was developed that combines an experimental acoustic playback with a passive acoustic recording system and a three-dimensional movement recorder (Fregosi et al., 2016). This tag allows researchers to control variables such as amplitude of sound, number of playbacks, depth at playback, and distance from sound. Programming this tag to play acoustic stimuli during specific portions of the dive cycle allows for consistent repeated exposures paired with observations of behavioral responses in new and novel ways. By controlling the timing and received level of sound, we can investigate behavioral responses to acoustic stressors and evaluate if responses are consistent through repeated exposures.

Northern elephant seals (*Mirounga angustirostris*) are an ideal study species to test the behavioral response of deep diving marine mammals to acoustic stressors. Their diving behavior is well studied (Le Boeuf et al., 1986; Le Boeuf et al., 1988, 1996; Le Boeuf & Laws, 1994), which allows us to identify how a noise disturbance modifies their behavior. Elephant seals are the premier pinniped diver, capable of performing dives to similar depths as deep diving cetacean species, such as beaked whales, which are thought to be sensitive to anthropogenic noise (Le Boeuf et al., 1988; Robinson et al., 2012; Tyack et al., 2011).

Fortunately, elephant seals are more accessible than whales and handle instrumentation well, making them a model species to represent deep-diving marine mammals (McMahon et al., 2008; Oliver et al., 1998; Worthy et al., 1992). Elephant seals have the best underwater hearing sensitivity of any seal measured so far and are known to respond to various natural and anthropogenic sounds played by a tag (Fregosi et al., 2016; Kastak & Schusterman, 1999). The use of an established translocation protocol allows researchers to retrieve fine-scale data recorded on biologgers that must be recovered from the tagged animal (Oliver et al., 1998).

To predict the behavioral and physiological impacts of acoustic disturbances, we must examine the fine-scale response to controlled repeated exposures and determine how long it takes to return to natural behavior. Data loggers that are synchronized with the experimental acoustic playback can record continuous animal movement before and after the sound exposure, giving us better understanding of each step in the animal's reaction to the acoustic stressor. While the source of the acoustic stimuli in animal-borne biologgers may be artificial, the ability to control timing and received sound level during repeated exposures will allow us to evaluate fine-scale dive behaviors over time. In this study, I investigated the behavioral response to an acoustic stressor. Specifically, I 1) compared dive characteristics of acoustic exposure dives versus non-exposure dives, 2) compared fine-scale behavior before and after dive inversions during acoustic exposure dives only, 3) measured the duration of altered responses following the acoustic stressor before returning to normal behavior, and 4) determined if seals exhibit signs of habituation or sensitization to the acoustic stressor. I hypothesized that the elephant seals would exhibit strong behavioral changes, both at a fine-

scale and whole-dive level, would require time to recover, and would always react to the disturbances. Knowledge gained from studying one model species can be used to provide insight into how other marine mammals are impacted by sounds.

Methods

Translocation and Instrumentation Procedure

Field work was conducted at Año Nuevo State Park (San Mateo County, CA, USA) from March to April in 2018, 2019, and 2021. Twenty-two northern elephant seals were translocated before their annual molt using an established protocol (Oliver et al., 1998). Healthy, unmolted juvenile seals (1-2 years old) were immobilized using an intramuscular (IM) injection of Telazol (~1.2-1.5 mg/kg) (Andrews et al., 1997; Le Boeuf et al., 1988). After the seals were sedated, they were rolled into an aluminum cage and transported 35 km by truck to Long Marine Laboratory (LML) at the University of California, Santa Cruz (UCSC). The seals were weighed in the transport cage upon arrival to LML and moved to an animal holding area until the instrumentation process began.

Following a waiting period of a minimum of 2 hours, the seals were again immobilized with an IM injection of Telazol (<1 mg/kg). After initial sedation, anesthesia was maintained through isoflurane-O₂ gas anesthesia using mask induction followed by intubation (Gales & Mattlin, 1998; Ponganis et al., 2006). Morphometrics (length and girth) were collected before the attachment of devices to determine each seal's body condition and seals were given unique identification tags in the webbing of their hind flippers, if not already present.

Each juvenile elephant seal was instrumented with: 1) an audio-motion datalogger (AMX, Loggerhead Instruments, Sarasota, FL, USA) that played a recorded sound and collected acoustic and motion data; 2) a satellite tag (SPOT6, Wildlife Computers, Redmond, WA, USA) to track the animal's movements during its journey back to the rookery at Año Nuevo; and 3) a very high frequency (VHF) radio transmitter (Advanced Telemetry Systems,

Isanti, MN, USA) that was used to pinpoint the animal's location after its return to the beach. Additionally, a Daily Diary datalogger (Wildlife Computers, Redmond, WA, USA) and an OxyLog physiological datalogger (UFI Instruments, Morro Bay, CA, USA) were attached for use in a separate study. The total weight of the tags represented ~1% of the seal's body mass.

During the instrumentation procedure, data loggers were attached to the dorsal midline and head of each elephant seal. The seal's fur was cleaned to remove debris and dry the area, then instruments were glued to the clean fur with a five-minute marine epoxy (Loctite). The satellite tag was attached to the head to allow for the best transmission of location data via the ARGOS system when the seal surfaced. The acoustic tag was attached just off midline about 0.5 meters behind the ears, the additional tags were placed on or near the midline just behind the center of mass, and the VHF was glued behind the other tags. Once the instrumentation procedure was completed, seals were returned to the metal transport cage for recovery and the intubation tube was removed. The cage was kept in an animal holding room for a minimum of 6 hours while the seal recovered from anesthesia. The seals were then transported 75 km by truck to a beach in Pacific Grove (Monterey County, CA, USA) for release. The instruments recorded sound and movement data as the seals swam across Monterey Bay and returned to Año Nuevo State Park over the next two to ten days, except one seal that was at sea for almost 49 days before returning.

The seal locations were monitored using ARGOS, which allowed for recapture of the animals shortly after their return to land. The seals were immobilized using an IM injection of Telazol (1 mg/kg), and sedation was maintained with intravenous (IV) injections of ketamine (0.5-1 mg/kg) until the recovery procedure was completed. Dataloggers that were

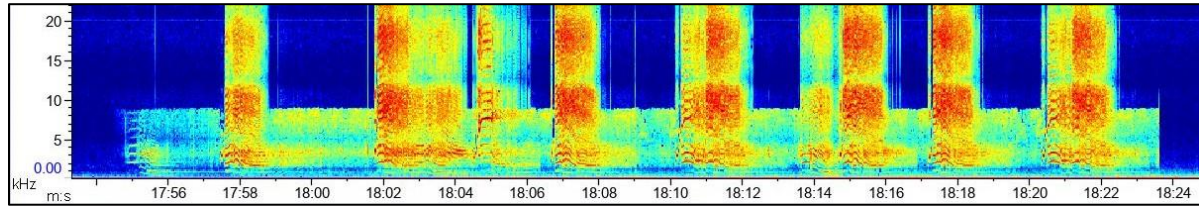
glued to each seal's pelage were removed and any remaining epoxy patches molted off within a few weeks during their annual molt. All research was performed under National Marine Fisheries Service (NMFS) permits #19108 and #23188, UCSC Institutional Animal Care and Use Committee (IACUC) protocol #Costd1912_a1, and San José State University Alternate IACUC approvals #1042 and #AAA-28.

AMX Tag Programming

The AMX tag was designed to record passive acoustics (44.1 kHz), pressure (1 Hz), temperature (1 Hz), light (1 Hz), and three-axis motion (using a tri-axial accelerometer, magnetometer, and gyroscope; all at 100 Hz). Playbacks of a pre-loaded sound file produced the sound exposures experienced by the elephant seals, and since they are solitary animals while in the ocean, the playback was likely only heard by the tagged seal. A 30 second recording of transient killer whale whistles (source levels 130-135 dB_{RMS} re 1 μ Pa @ 1 m, Vancouver Aquarium, Figure 1) was used as the acoustic stressor in this study. The tag used a time-depth sensor to trigger playbacks (exposures) of the pre-loaded sound file at programmed time intervals and dive stages. The tag was set to trigger the exposure upon the elephant seal's dive ascent and was programmed to play the exposure a maximum of 25 times during the translocation. There was a minimum of two hours separating playbacks and the exposure was only triggered when the seals reached 125 meters above maximum dive depth after descending deeper than 250 meters, ensuring that the elephant seal was ascending when the sound was played (Figure 2).

Figure 1

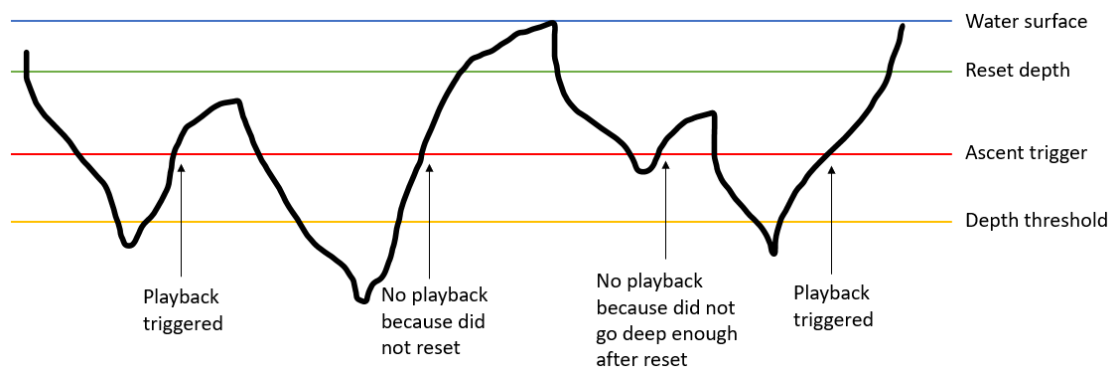
Spectrogram Image of Transient Killer Whale Whistles



Note. This is the 30 second recording that is played from the AMX tag speaker.

Figure 2

Illustration Showing When AMX Tag Playbacks can be Triggered



Note. Our tag is programmed with reset depth (10m), depth threshold (250m), ascent trigger (125m), and playback interval (2h) to ensure the playback gets triggered at the appropriate time in the dive phase. Figure adapted from Loggerhead Instruments' AMX Manual.

Data Processing and Analysis

The data collected by the AMX tag were stored in .amx files that were converted into .wav files using the AMX2WAV converter (Loggerhead Instruments). All motion data were then converted to .csv files to allow for data processing in various software programs. The tag's hydrophone continuously recorded sound throughout the translocation, so Raven Pro 1.6 (K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Ithaca,

NY, USA) was used to audit the sound files to determine when playbacks occurred, as well as note any other potential acoustic stimuli. The elephant seals were exposed to a different number of playbacks depending on each seal's dive patterns, length of time at sea during the translocation, and whether the tag functioned correctly.

All remaining data processing and statistical analyses were conducted using R statistical software version 4.0.3 (R Core Team, R Foundation for Statistical Computing, Vienna, Austria) and MATLAB R2021a (The MathWorks, Inc., Natick, MA, USA). The one-hour segments of data recorded by the tag were concatenated into a single file for each seal. Sequential timestamps were created for the files using the first date and time recorded by the tag for each deployment and the sampling frequency of the sensor (i.e., depth at 1 Hz and accelerometer, magnetometer, and gyroscope at 100 Hz).

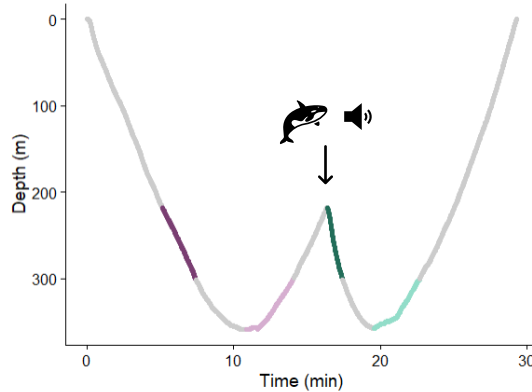
For all two-dimensional movement processing, pressure was converted to depth to create a Time Depth Recorder (TDR) record, which was then analyzed using the IKNOS toolbox (Y. Tremblay, unpublished) in MATLAB. Depth data were zero-offset corrected to account for pressure sensor drift and ensure surface events were accurate. Individual dives were identified from the zero-offset corrected data using programmed thresholds consisting of minimum dive depth of 15 m, minimum dive duration of 30 s, and fixed bottom phase set at 80% of maximum depth. The IKNOS program calculated dive parameters including dive number, date and time for the start of each dive, maximum depth, dive duration, bottom time, descent time, descent rate, ascent time, ascent rate, and post dive surface interval. One complete dive cycle started when the seal descended below the surface and ended at the time it started its next dive. The bottom phase started at the time when the seal descended to 80%

of its maximum depth and ended at the point of its final ascent above that same depth. The descent phase consisted of any time between the surface and the bottom, while the ascent phase consisted of any time between the bottom and the surface. The post dive interval (PDI) comprised of the time the seal returned to the surface until the start of its next dive.

The timings of playbacks, found during the auditing process, were used to separate acoustic exposure dives from non-exposure dives in the dive record. Exposure dives were further separated into two groups based on if the sound playback occurred during the descent or ascent portion of the dive. Although the tag was programmed to only play the recording on dive ascents, the playback was occasionally triggered during the incorrect dive phase. These accidental playbacks on descent likely occurred due to a tag malfunction that caused it to either incorrectly detect a threshold or skip a reset point. For playbacks on ascent, the timestamps matching the start of the dive inversion (a reversal of dive direction, Figure 3) were located to separate the first half of an exposure dive from the second half, which represented pre-inversion and post-inversion. Since the AMX tag was programmed to only play the killer whale whistle recording on dives deeper than 250 m, any non-exposure dives shallower than that depth were removed to better match the parameters of the exposure dives. Dives that did not contain a complete TDR record (from the start of the dive to the start of the next dive) were removed from analyses involving the missing section of data.

Figure 3

Example Dive Profile of an Elephant Seal's Exposure Dive



Note. The recording of the killer whale whistle is played during the seal's initial ascent from a deep dive. The sound causes a dive inversion during which the seal changes direction and descends again before resuming ascent to the surface. The color-coded sections of the exposure dive are compared to each other to examine changes in fine-scale movements. Pre-inversion descent is dark purple, pre-inversion ascent is light purple, post-inversion descent is dark green, and post-inversion ascent is light green.

The three-dimensional movement data (accelerometer and magnetometer), downsampled from 100 Hz to 25 Hz, were used to calculate behavioral dive variables. Flipper strokes were calculated using custom-written code in R. Elephant seals, like all other phocids, stroke side to side with their rear flippers for propulsion, so one set of back-and-forth rear flipper movements was considered one stroke. A Butterworth filter was used to run a 0.1 Hz high-pass filter on the y-axis data to extract the dynamic acceleration, remove the static acceleration, and center the data around zero. Next, the peak detector from the *tagtools* package (DeRuiter, 2017) identified all peaks in the data using set criteria. Blanking time, or the minimum length of time between values for each to be considered separate peaks, was the same for all seals and was chosen because it corresponded to the fastest recorded phocid flipper strokes. The threshold was set to different values for each seal based on the

amplitudes of their strokes. Random trials were then conducted on the data for each seal to check the accuracy of the peak detector against a manual count. The threshold was adjusted and the peak detector was rerun until the detector and manual count were consistent. The timings of the peaks represented each flipper stroke and the time interval between peaks was used to calculate instantaneous stroke rate throughout the translocation.

Overall Dynamic Body Acceleration (ODBA), pitch, and heading were calculated using the respective functions from the *tagtools* package. ODBA is a common acceleration metric that removes the acceleration signal due to gravity from the raw data to quantify an animal's actual movements. It was chosen because it gives a more precise and realistic representation of elephant seal swimming and diving behavior than other acceleration metrics. ODBA is the norm of high-pass-filtered triaxial acceleration and can be computed using several different norms and filters. In this study, it took the dominant stroke frequency into account and was calculated using a FIR filter. Pitch was calculated using triaxial accelerometer data and resulted in angles of rotation around the y-axis, with a descending animal having a negative pitch angle. Heading was calculated by gimbaling the triaxial magnetometer and triaxial accelerometer matrices, resulting in values that are in respect to magnetic north with positive heading in a clockwise rotation around the z-axis.

To examine more fine-scale movements within the exposure dives, the dive profiles were split into four categories. There was a pre-inversion section and a post-inversion section separated by the timestamp at the start of the acoustic stressor playback, visualized as the first “V” and second “V” of a “W”-shaped exposure dive. There was also an ascent and descent section within each of the two “V” sections. The two descent sections started at the

depth of the dive inversion and the two ascent sections started at the maximum depth of their respective halves of the “W”-shaped exposure dives. The four categories created were pre-inversion descent, pre-inversion ascent, post-inversion descent, and post-inversion ascent (Figure 3). Variables calculated from the three-dimensional movement data were split into these four categories, in 60 second segments, for further processing. This period of time was chosen because the killer whale whistle recording is 30 seconds long and comparisons made during a 60 second period would include changes in behavior during the playback and for 30 seconds after the playback ended. Stroke rate was calculated by counting the number of strokes within each category, then dividing by 60 seconds. For ODBA, the mean of the acceleration metric was identified within the 60 s segments. For pitch and heading, the range of the variables were calculated within the 60 s segments by subtracting the minimum value from the maximum value. This calculation provided the greatest amount of change in pitch or heading that was seen during the 60 s intervals of the four categories.

Statistical Analysis

The first objective was to compare acoustic exposure dives and non-exposure dives to determine if seals exhibited changes in diving behavior in response to the acoustic stressor. Separate linear mixed effects models with dive type (exposure dive with playback on ascent, exposure dive with playback on descent, or non-exposure dive) as a fixed effect and individual seal ID as a random effect were used to assess differences between each two-dimensional dive parameter (dive duration, descent rate, ascent rate, and post dive interval). A multivariate cluster analysis was also performed to explore if all the deep dives naturally separated into different groups. The input values for the clustering were the same as above

(dive duration, descent rate, ascent rate, post dive interval) with the added binary variable of whether or not a dive inversion occurred.

The next objective was to compare fine-scale behavior of different sections of the acoustic exposure dives with playback on ascent, before and after the dive inversions that occurred due to the acoustic stressor. Exposure dives with playback on descent were excluded from this analysis because the sound did not play at a consistent depth or time. Separate linear mixed effects models with dive portion (pre-inversion or post-inversion) as a fixed effect and individual exposure as a random effect were used to examine differences between each of the three-dimensional dive variables (stroke rate, ODBA, pitch, and heading). The variables were broken up into the four categories mentioned earlier and calculations were done using stroke rate, mean of ODBA, range of pitch, and range of heading within 60 seconds of the start of that section. For example, the average ODBA during the 60 s after the first deepest point of an exposure dive (pre-inversion ascent) was compared to the 60 s after the second deepest point of an exposure dive (post-inversion ascent).

The third objective was to measure how long it takes for northern elephant seals to return to normal diving behavior following the acoustic disturbances. Separate linear mixed effects models with dive order (baseline, exposure, 1st dive after exposure, or 2nd dive after exposure) as a fixed effect and individual exposure as a random effect were used to investigate when seals returned to baseline following an exposure dive. This was done for each of the four two-dimensional dive parameters (dive duration, descent rate, ascent rate, and post dive interval). Exposure dives with both playback on ascent and descent were

included in the same analysis because my objective was to determine if hearing a killer whale at any point in a dive would influence characteristics of future dives. All dives surrounding the exposure dives were included, no matter the maximum dive depth, and the baseline was determined using the two dives prior to the exposure dives. Since the timing of only two hours between exposures did not allow for many dives to occur, dives after exposure occasionally overlapped with baseline dives of the next exposure dive. In these cases, one of the baseline dives would be removed. If there were even fewer dives between exposures, the latter exposure would be completely removed from analysis because too much information would be lost to accurately compare to other dives.

The final objective was to examine if the seals became habituated or sensitized to a predator call. Separate linear mixed effects models with exposure number (1-25) as a fixed effect and seal ID as a random effect were used to determine if seals changed their dive behavior after repeated exposures of the same acoustic stressor. This analysis was conducted in three sections: comparisons of exposure dives at a whole-dive level, 60 second sections of descent at a fine-scale level, and 60 second sections of ascent at a fine-scale level. The behaviors examined on the full dives were dive duration, descent rate, ascent rate, and post dive interval. Exposure dives with playback on both descent and ascent were used in these analyses to determine if hearing a predator at any point during a dive would influence the seal's degree of response during future disturbances. At a finer scale, I examined how much variation existed between pre-inversion and post-inversion stroke rate, ODBA, pitch, and heading for both the descent and ascent phases within each exposure dive. Only exposure dives with playback on ascent were used for these analyses because they contained the

necessary dive inversions. Since repeated exposures were needed to determine if habituation or sensitization may have occurred, only seals that were exposed to at least five playbacks of the killer whale whistle were included in the analysis of this objective.

Prior to investigating relationships between dive types and sections of dives, correlation analysis was used to test for potential multicollinearity among dive parameters. Dive duration and maximum dive depth were positively correlated (Pearson's correlation test, $r = 0.452$, $p < 0.001$), so all analyses only used dive duration because it was the most relevant variable to this study.

The timing of dives (day vs night) was considered as an explanatory factor, however, this variable was ultimately excluded from the final models as there was not enough variability in daytime and nighttime dives for all the seals for both acoustic exposure and non-exposure dives, likely due to the short time period in which seals were diving deep over the canyon and the parameters the tag was programmed to follow. Since some seals had very few exposure dives, the addition of this covariate would have led to over-parameterized models. Also, since these translocations occurred just before the molting season, the seals were focused on returning to land and therefore performing transiting dives rather than foraging dives, based on the dive types observed (Le Boeuf et al., 1993). Since the seals were not foraging, the timing of dives (day vs night) should not impact dive behavior.

All linear mixed effects models were run using the *lme4* package (Bates et al., 2015) and Tukey post-hoc comparisons were done using the *multcomp* package (Hothorn et al., 2008). Each model's residuals were visually assessed for normality and homoscedasticity. Data were transformed when necessary to meet model assumptions. The selected final models

consisted of the simplest models with the lowest Akaike Information Criterion (AIC) values. Significance was accepted at the level of $p < 0.05$. Due to the multiple pair wise tests performed when comparing pre-inversion and post-inversion data, p-values from those models were adjusted using the Holm's sequential Bonferroni procedure. Reported values are mean \pm standard deviation unless otherwise stated.

Results

Four of the 22 AMX tag deployments failed to record data, but the other 18 deployments collected audio and motion data for 1.48-3.81 days (Table 1). The northern elephant seals were exposed to the recording of the killer whale whistles between 1 and 25 times, with a total of 211 exposures among all the individuals. Of those, 153 of the exposures were played during a dive ascent while the rest played during a dive descent. Every time the acoustic stimulus played on ascent as programmed, the seals performed dive inversions. When the acoustic stressor played on descent, there were no dive inversions, but the seals increased their speed of descent. There was a total of 3613 non-exposure dives but only 705 of those were used for analysis since they had maximum depths greater than 250 m, which was the minimum requirement for the acoustic stressor to play.

Table 1

Summary of 22 Translocated Juvenile Northern Elephant Seals Carrying Acoustic Tags

Seal ID	Capture date	Sex	Age	Standard length (cm)	Mass (kg)	Days at sea	Hours AMX tag recording	Total number of exposures
Ma18_093	4/3/2018	F	2	195	186	8.42	91.43	19
Ma18_095	4/5/2018	F	1	-	151	2.01	Tag failed	0
Ma18_099	4/9/2018	F	1	170	141	1.98	49.83	4
Ma18_104a	4/14/2018	F	1	177	158	2.02	Tag failed	0
Ma18_104b	4/14/2018	M	1	190	172	1.39	35.42	3
Ma19_090	3/31/2019	M	1	183	166	6.98	85.97	9
Ma19_091	4/1/2019	F	1	182	169	7.41	79.08	23
Ma19_092	4/2/2019	F	1	178	164	5.02	86.97	16
Ma19_096	4/6/2019	F	1	170	150	3.46	Tag failed	0
Ma19_098	4/8/2019	F	1	178	157	6.18	80.16	20
Ma19_100b	4/10/2019	F	1	182	155	2.01	47.98	1
Ma19_104	4/14/2019	F	2	198	221	4.20	81.97	3
Ma19_107	4/16/2019	F	1	201	171	5.87	80.17	25
Ma19_111	4/20/2019	M	1	192	177	2.80	71.26	4
Ma21_088	3/29/2021	M	1	179	145	48.45	76.03	25
Ma21_089	3/30/2021	F	1	182	166	9.64	73.91	20
Ma21_091	4/1/2021	F	1	178	159	6.59	83.27	5
Ma21_093	4/3/2021	F	1	175	158	2.60	Tag failed	0
Ma21_101	4/11/2021	F	1	179	168	2.48	63.98	10
Ma21_102	4/12/2021	M	1	196	190	1.51	41.12	3
Ma21_105	4/15/2021	F	1	189	178	3.72	70.97	9
Ma21_106	4/16/2021	F	2	203	237	2.63	66.20	12

Exposure Dives vs Non-Exposure Dives

Dive characteristics (maximum depth, dive duration, bottom time, descent time, descent rate, ascent time, ascent rate, post dive interval) were calculated for each dive and any dives with a maximum depth shallower than 250m were removed from analysis. The remaining data were summarized for exposure dives and non-exposure dives separately (Table 2). Dive duration, descent rate, ascent rate, and post dive interval data from all dives were further separated into two groups depending on whether the acoustic playback occurred during the descent or ascent phase of the dive (Table 3).

Table 2

Summary of Northern Elephant Seal Dive Characteristics

Seal ID	Number of dives		Max depth (m)		Descent time (min)		Bottom time (min)		Ascent time (min)	
	Non-exp	Exp	Non-exp	Exp	Non-exp	Exp	Non-exp	Exp	Non-exp	Exp
Ma18_093	72	19	300.7 ± 57.7	355.1 ± 85.4	5.10 ± 1.22	6.79 ± 2.48	9.03 ± 1.80	11.32 ± 3.95	5.72 ± 1.33	5.82 ± 1.44
Ma18_099	20	4	288.0 ± 38.5	384.0 ± 59.2	5.06 ± 0.97	6.95 ± 1.03	6.59 ± 1.11	12.43 ± 1.95	4.49 ± 0.96	5.17 ± 1.27
Ma18_104b	13	3	401.6 ± 156.2	474.9 ± 66.3	5.73 ± 1.91	7.86 ± 0.01	8.74 ± 1.71	10.18 ± 2.43	6.48 ± 2.04	8.36 ± 0.00
Ma19_090	20	9	319.7 ± 80.4	416.3 ± 101.8	6.29 ± 2.20	8.07 ± 2.49	10.61 ± 3.35	14.51 ± 5.33	6.46 ± 2.37	8.81 ± 3.32
Ma19_091	63	23	376.1 ± 82.4	469.9 ± 132.4	7.13 ± 1.58	9.14 ± 2.69	9.77 ± 2.13	11.72 ± 4.77	8.23 ± 2.27	8.47 ± 2.66
Ma19_092	54	16	361.8 ± 70.3	381.9 ± 52.8	7.11 ± 1.66	8.06 ± 2.07	9.62 ± 2.00	10.85 ± 2.89	7.52 ± 2.27	9.01 ± 3.95
Ma19_098	69	20	354.6 ± 56.5	373.6 ± 76.9	5.58 ± 1.22	6.51 ± 1.60	12.16 ± 2.44	17.47 ± 4.45	6.22 ± 1.24	6.63 ± 2.52
Ma19_100b	2	1	315.4 ± 84.2	404.8 ± 0	6.13 ± 1.70	7.75 ± 0	10.04 ± 0.93	17.27 ± 0	6.29 ± 3.50	6.85 ± 0
Ma19_104	10	3	333.6 ± 57.1	410.2 ± 79.0	5.16 ± 1.10	5.47 ± 1.27	10.32 ± 2.71	22.33 ± 3.87	5.39 ± 1.64	6.27 ± 2.65
Ma19_107	86	25	315.4 ± 49.3	376.4 ± 63.8	5.75 ± 1.14	9.24 ± 4.54	10.57 ± 2.91	12.89 ± 5.57	5.92 ± 1.36	6.43 ± 2.10
Ma19_111	4	4	274.1 ± 22.0	332.2 ± 29.1	5.08 ± 1.02	5.38 ± 1.16	8.66 ± 1.61	13.06 ± 3.19	5.69 ± 1.90	10.81 ± 4.32
Ma21_088	157	25	393.9 ± 62.9	472.3 ± 86.8	5.81 ± 1.09	6.58 ± 1.30	6.63 ± 1.59	8.00 ± 2.47	6.07 ± 0.99	6.27 ± 1.44
Ma21_089	42	20	414.6 ± 97.9	547.5 ± 142.2	8.28 ± 2.62	11.50 ± 4.38	13.20 ± 3.22	15.95 ± 5.62	7.40 ± 2.15	10.22 ± 4.44
Ma21_091	17	5	315.1 ± 33.0	343.3 ± 27.6	7.79 ± 1.45	7.28 ± 1.14	7.53 ± 1.93	15.28 ± 1.21	5.34 ± 1.40	5.18 ± 0.59
Ma21_101	21	10	308.8 ± 62.9	369.6 ± 56.0	7.85 ± 1.87	9.21 ± 2.11	9.70 ± 2.46	13.79 ± 4.37	5.75 ± 1.23	7.80 ± 3.01
Ma21_102	7	3	307.5 ± 51.0	311.8 ± 33.1	7.12 ± 2.38	7.97 ± 2.99	10.14 ± 2.53	10.69 ± 3.50	5.05 ± 1.06	9.31 ± 3.49
Ma21_105	20	9	343.9 ± 144.2	361.8 ± 63.8	7.38 ± 2.12	8.75 ± 3.25	9.65 ± 2.24	13.92 ± 4.63	6.30 ± 2.91	6.50 ± 1.72
Ma21_106	28	12	318.5 ± 48.4	373.2 ± 71.5	5.84 ± 1.35	8.81 ± 3.32	12.05 ± 3.67	17.39 ± 4.74	6.89 ± 2.21	7.26 ± 3.51
Mean ± SD			335.7 ± 40.1	397.7 ± 59.6	6.3 ± 1.1	7.8 ± 1.5	9.7 ± 1.8	13.8 ± 3.4	6.2 ± 0.9	7.5 ± 1.7

Note. The first set of non-exposure dive (white) and exposure dive (gray) columns reports the number of dives for each seal. The remaining columns present the mean ± standard deviation for maximum depth, descent time, bottom time, and ascent time. The bottom row shows the mean ± standard deviation of each column.

Table 3

Summary of Northern Elephant Seal Dive Characteristics, Separated Into Three Groups

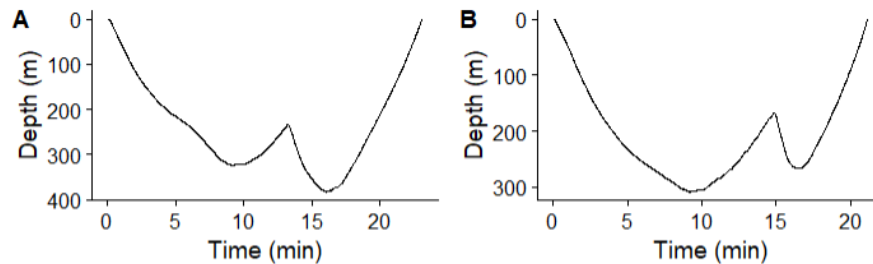
Seal ID	Number of dives			Dive duration (min)			Descent rate (m/s)			Ascent rate (m/s)			Post dive interval (min)		
	Non-exp	Exp (asc)	Exp (desc)	Non-exp	Exp (asc)	Exp (desc)	Non-exp	Exp (asc)	Exp (desc)	Non-exp	Exp (asc)	Exp (desc)	Non-exp	Exp (asc)	Exp (desc)
Ma18_093	72	16	3	19.83 ± 2.73	23.70 ± 2.99	25.12 ± 3.08	0.80 ± 0.12	0.75 ± 0.17	0.70 ± 0.13	0.72 ± 0.14	0.83 ± 0.17	0.88 ± 0.10	2.17 ± 0.99	2.24 ± 1.16	1.91 ± 0.17
Ma18_099	20	4	0	16.14 ± 1.18	24.55 ± 3.18	-	0.77 ± 0.10	0.74 ± 0.10	-	0.88 ± 0.16	1.01 ± 0.09	-	1.69 ± 0.41	1.68 ± 0.44	-
Ma18_104b	13	2	1	20.95 ± 4.03	28.43 ± 0.34	22.32 ± 0	0.94 ± 0.18	0.71 ± 0.25	1.20 ± 0	0.84 ± 0.19	0.78 ± 0.10	0.73 ± 0	2.16 ± 0.43	2.37 ± 0.19	1.88 ± 0
Ma19_090	20	7	2	23.37 ± 3.08	32.87 ± 4.72	26.20 ± 4.12	0.71 ± 0.14	0.69 ± 0.20	0.83 ± 0.02	0.70 ± 0.16	0.70 ± 0.20	0.67 ± 0.41	2.42 ± 0.58	2.39 ± 0.51	2.17 ± 0.64
Ma19_091	63	12	11	25.13 ± 3.95	29.99 ± 3.08	28.61 ± 7.52	0.71 ± 0.12	0.67 ± 0.13	0.74 ± 0.16	0.63 ± 0.15	0.79 ± 0.09	0.72 ± 0.11	3.17 ± 1.68	3.32 ± 1.42	3.35 ± 2.00
Ma19_092	54	13	3	24.25 ± 3.67	26.56 ± 4.71	28.79 ± 4.79	0.70 ± 0.17	0.64 ± 0.13	0.70 ± 0.01	0.67 ± 0.14	0.69 ± 0.27	0.51 ± 0.19	2.14 ± 0.66	1.97 ± 0.71	3.01 ± 1.12
Ma19_098	69	17	3	23.95 ± 3.18	30.91 ± 3.08	28.85 ± 7.06	0.87 ± 0.14	0.79 ± 0.19	0.85 ± 0.14	0.78 ± 0.13	0.83 ± 0.15	0.63 ± 0.17	1.80 ± 0.37	2.69 ± 2.61	2.12 ± 0.31
Ma19_100b	2	1	0	22.47 ± 2.73	31.87 ± 0	-	0.74 ± 0.39	0.70 ± 0	-	0.73 ± 0.23	0.79 ± 0	-	1.99 ± 0.51	3.12 ± 0	-
Ma19_104	10	3	0	20.87 ± 2.89	34.06 ± 5.65	-	0.88 ± 0.11	1.02 ± 0.24	-	0.87 ± 0.18	0.96 ± 0.32	-	2.06 ± 0.54	1.99 ± 0.62	-
Ma19_107	86	22	3	22.23 ± 3.34	29.39 ± 3.77	22.36 ± 1.27	0.75 ± 0.11	0.60 ± 0.21	0.87 ± 0.10	0.73 ± 0.14	0.83 ± 0.16	0.75 ± 0.06	2.28 ± 0.67	2.51 ± 0.93	1.69 ± 0.11
Ma19_111	4	4	0	19.43 ± 1.33	29.25 ± 1.23	-	0.74 ± 0.13	0.86 ± 0.21	-	0.71 ± 0.29	0.46 ± 0.18	-	2.39 ± 0.32	2.86 ± 0.35	-
Ma21_088	157	10	15	18.52 ± 2.08	22.24 ± 2.37	19.91 ± 2.57	0.93 ± 0.18	0.90 ± 0.24	1.05 ± 0.18	0.88 ± 0.12	1.10 ± 0.10	0.97 ± 0.12	3.09 ± 0.96	2.95 ± 0.84	3.28 ± 1.09
Ma21_089	42	9	11	28.87 ± 4.54	37.76 ± 4.40	37.58 ± 9.07	0.70 ± 0.17	0.64 ± 0.18	0.72 ± 0.20	0.78 ± 0.19	0.85 ± 0.27	0.73 ± 0.16	2.48 ± 0.66	2.65 ± 1.04	2.54 ± 0.60
Ma21_091	17	5	0	20.65 ± 3.01	27.74 ± 1.52	-	0.56 ± 0.11	0.64 ± 0.11	-	0.83 ± 0.19	0.90 ± 0.14	-	2.19 ± 0.52	2.36 ± 0.38	-
Ma21_101	21	8	2	23.30 ± 3.20	31.49 ± 3.28	28.01 ± 3.64	0.55 ± 0.14	0.56 ± 0.22	0.60 ± 0.02	0.73 ± 0.13	0.71 ± 0.27	0.72 ± 0.00	2.43 ± 0.55	2.88 ± 1.05	2.55 ± 0.52
Ma21_102	7	3	0	22.30 ± 3.25	27.97 ± 1.84	-	0.60 ± 0.09	0.58 ± 0.22	-	0.84 ± 0.18	0.49 ± 0.20	-	2.60 ± 0.56	2.31 ± 0.63	-
Ma21_105	20	7	2	23.32 ± 5.62	29.45 ± 4.12	28.17 ± 2.73	0.62 ± 0.12	0.59 ± 0.16	0.58 ± 0.06	0.75 ± 0.13	0.81 ± 0.17	0.67 ± 0.14	2.15 ± 1.08	1.92 ± 0.52	2.78 ± 0.75
Ma21_106	28	10	2	24.77 ± 4.26	32.67 ± 5.18	36.11 ± 1.97	0.75 ± 0.10	0.58 ± 0.16	0.79 ± 0.12	0.65 ± 0.13	0.79 ± 0.16	0.59 ± 0.22	1.66 ± 0.33	1.78 ± 0.55	1.77 ± 0.16
Mean ± SD				22.2 ± 2.9	29.5 ± 3.8	27.7 ± 5.2	0.7 ± 0.1	0.7 ± 0.1	0.8 ± 0.2	0.8 ± 0.1	0.8 ± 0.2	0.7 ± 0.1	2.3 ± 0.4	2.4 ± 0.5	2.4 ± 0.6

Note. The three groups are non-exposure dives (white), exposure dives with playback on ascent (light gray), and exposure dives with playback on descent (dark gray). The first set of columns reports the number of dives for each seal. The remaining columns present the mean ± standard deviation for dive duration, descent rate, ascent rate, and post dive interval. The bottom row shows the mean ± standard deviation of each column.

The mean maximum dive depth was 412.6 ± 106.9 meters for exposure dives and 351.8 ± 79.8 meters for non-exposure dives. The deepest dive, at 973.7 m, was performed by Ma19_091 during an exposure dive. Looking specifically at exposure dives, the seals varied in whether they dove deeper during the pre-exposure portion or post-exposure portion of their dives. Of the 153 exposure dives that occurred on ascent and therefore contained a dive inversion, 102 dives had a shallower inversion and 51 had a deeper inversion compared to the initial dive. Some seals consistently performed shallower inversion dives, some consistently performed deeper inversion dives, and most had a combination of shallower and deeper inversion dives (Figure 4). There were no observable trends between characteristics of the original dive and the depth of the inversion dive.

Figure 4

Example Dive Profiles of Two Types of Acoustic Exposure Dives



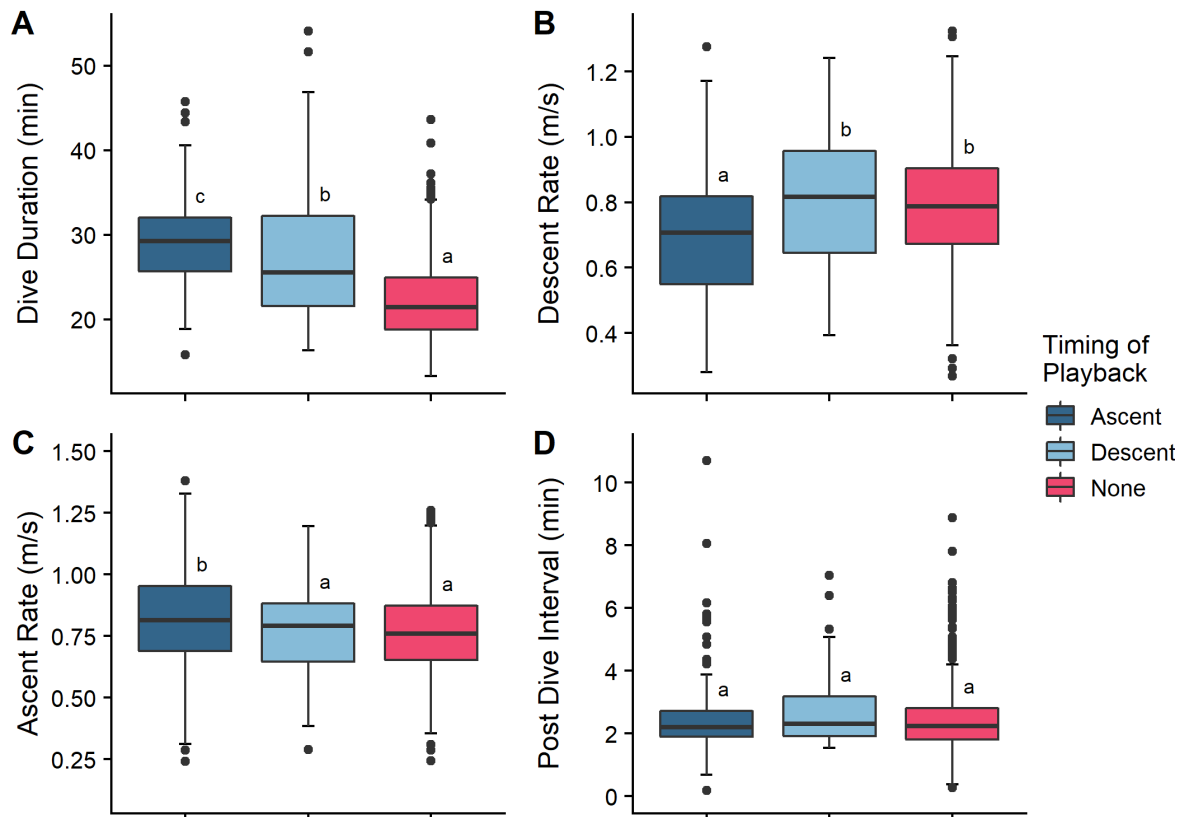
Note. The example dive profiles show (A) an inversion dive that was deeper than the original dive, and (B) an inversion dive that was shallower than the original dive.

There were differences in dive duration between non-exposure dives and both types of exposure dives (Figure 5A; linear mixed effect model, $F_{2,890} = 202.11$, $p < 0.001$). Non-exposure dives had the shortest dive durations at 22.06 ± 4.45 minutes, exposure dives with playback on descent were slightly longer at 27.61 ± 8.35 minutes, and exposure dives when

the playback happened on ascent had the longest dive durations at 29.19 ± 5.15 minutes (Tukey post-hoc, $p < 0.001$). The longest dive, at 54.08 minutes, was performed by Ma21_089 during an exposure dive.

Figure 5

Dive Duration, Descent Rate, Ascent Rate, and Post Dive Interval for Three Types of Dives



Note. (A) Dive duration, (B) descent rate, (C) ascent rate, and (D) post dive interval values during the three types of dives: exposure dives with playback on ascent (dark blue, $n=153$), exposure dives with playback on descent (light blue, $n=58$), and non-exposure dives (pink, $n=705$). The bold line inside the box represents the median, the box shows the interquartile range (IQR) with the lower and upper limits representing the 25th and 75th percentiles, the whiskers extend to the minimum and maximum values within $1.5 \times \text{IQR}$, and the dots represent outliers.

There was a difference in descent rate between the three different types of dives (Figure 5B; linear mixed effect model, $F_{2,891} = 12.842$, $p < 0.001$). Dives when the sound played on ascent had slower descent rates than dives when the sound played on descent (Tukey post-hoc, $p < 0.001$) and non-exposure dives (Tukey post-hoc, $p < 0.001$). When grouped differently, the descent rate of exposure dives with playback on descent was 0.83 ± 0.21 m/s, which was faster than the descent rate of all deep dives with no playback on descent (non-exposure dives and exposure dives with playback on ascent), which was 0.77 ± 0.19 m/s. The quickest descent, at 1.323 m/s, was performed by Ma19_092 during a non-exposure dive while the slowest descent, at 0.268 m/s, was performed by Ma19_091 during a non-exposure dive.

There was a difference in ascent rate between the three different types of dives (Figure 5C; linear mixed effect model, $F_{2,895} = 13.323$, $p < 0.001$). Dives when the sound played on ascent had faster ascent rates than dives when the sound played on descent (Tukey post-hoc, $p = 0.033$) and non-exposure dives (Tukey post-hoc, $p < 0.001$). The quickest ascent, at 1.38 m/s, was performed by Ma19_092 during an exposure dive while the slowest ascent, at 0.241 m/s, was performed by Ma19_111 during an exposure dive.

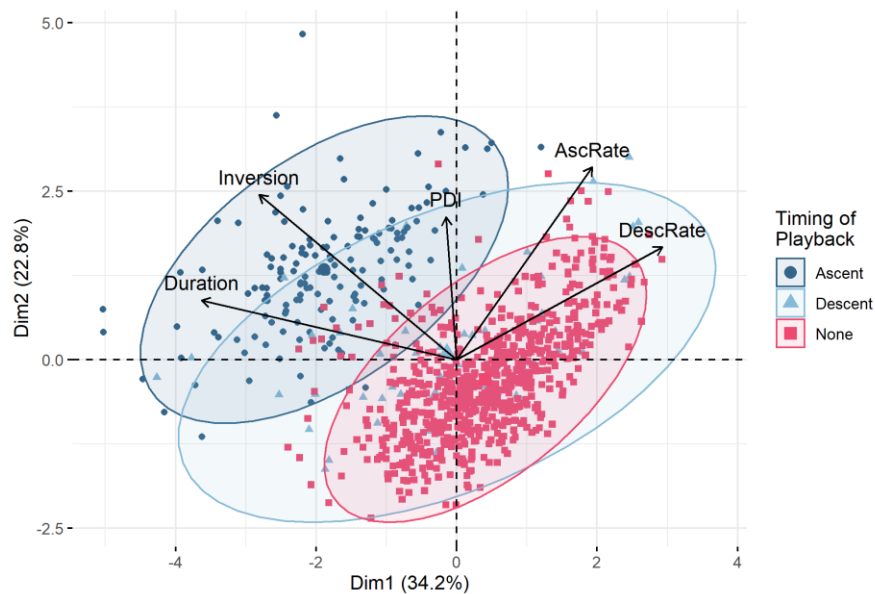
There was no difference in post dive interval between the three dive types (Figure 5D; square root transformed linear mixed effect model, $F_{2,895} = 1.912$, $p = 0.148$). Ma21_088 had the longest PDI at 175.85 minutes following an exposure dive. This particular seal had several extremely long post-dive intervals, both after exposure and non-exposure dives, so it is likely just the behavior of a unique seal and not an effect of the prior dive. These outlier

PDI times were removed from analysis if they were more than three standard deviations away from the mean.

The cluster analysis showed a natural separation between the different types of deep dives (Figure 6). Non-exposure dives and exposure dives with playback on ascent barely overlap, while exposure dives with playback on descent are spread out and have traits of the other two groups. The clustering was mainly driven by dive duration and the inversion criteria, with much less input from the other three variables. If given characteristics of a random deep dive of a juvenile elephant seal, the clustering could be used to predict which category the dive falls into.

Figure 6

Cluster Analysis for Whole-Dive Variables



Note. The points were determined using five dive characteristics. The three colors represent exposure dives with playback on ascent (dark blue), exposure dives with playback on descent (light blue), and non-exposure dives (pink). The ellipses show the clustering for each group. The vectors show the loadings of the dive variables included in the analysis.

Pre-Inversion vs Post-Inversion During Exposure Dives

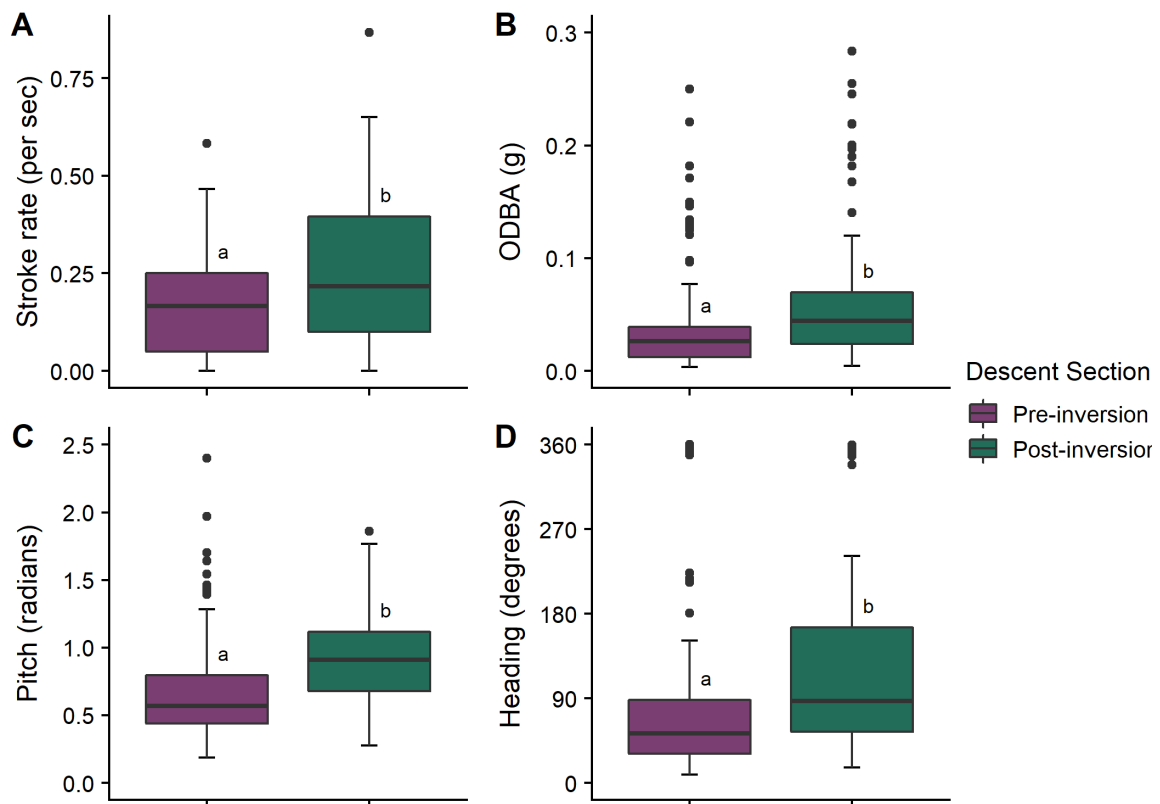
To examine the elephant seal's fine scale behavioral response to the acoustic stressor, I first compared the descent sections of the first "V" and second "V" of the "W"-shaped exposure dives. Stroke rate during the 60 s of descent post-inversion was faster than during the 60 s of descent pre-inversion (Figure 7A; linear mixed effect model, $F_{1,145} = 25.867$, adjusted $p < 0.001$). Mean ODBA of the 60 s of descent post-inversion was greater than during the 60 s of descent pre-inversion (Figure 7B; linear mixed effect model, $F_{1,145} = 54.163$, adjusted $p < 0.001$). Range in pitch varied more during the 60 s of descent post-inversion compared to the 60 s of descent pre-inversion (Figure 7C; linear mixed effect model, $F_{1,145} = 43.795$, adjusted $p < 0.001$). The range in heading during the 60 s of descent post-inversion was greater than during the 60 s of descent pre-inversion (Figure 7D; log-transformed linear mixed effect model, $F_{1,145} = 30.073$, adjusted $p < 0.001$).

Next, I compared the ascent sections of the first "V" and second "V" of the "W"-shaped exposure dives. Stroke rate was faster during the 60 s of ascent post-inversion compared to the 60 s of ascent pre-inversion (Figure 8A; linear mixed effect model, $F_{1,146} = 31.18$, adjusted $p < 0.001$). Mean ODBA of the 60 s of ascent post-inversion was greater than the 60 s of ascent pre-inversion (Figure 8B; linear mixed effect model, $F_{1,146} = 61.205$, adjusted $p < 0.001$). Range in pitch varied more during the 60 s of ascent post-inversion compared to the 60 s of ascent pre-inversion (Figure 8C; linear mixed effect model, $F_{1,146} = 9.249$, adjusted $p = 0.003$). There was more variation in heading during the 60 s of ascent post-inversion compared to the 60 s of ascent pre-inversion (Figure 8D; log-transformed linear mixed effect model, $F_{1,146} = 16.661$, adjusted $p < 0.001$). These fine-scale behavioral responses were also

investigated during 30 s sections, which encompasses only the length of time the killer whale whistle recording plays. The results of all eight of the above analyses were the same, with post-inversion descents and ascents all being significantly greater than their respective pre-inversion counterparts.

Figure 7

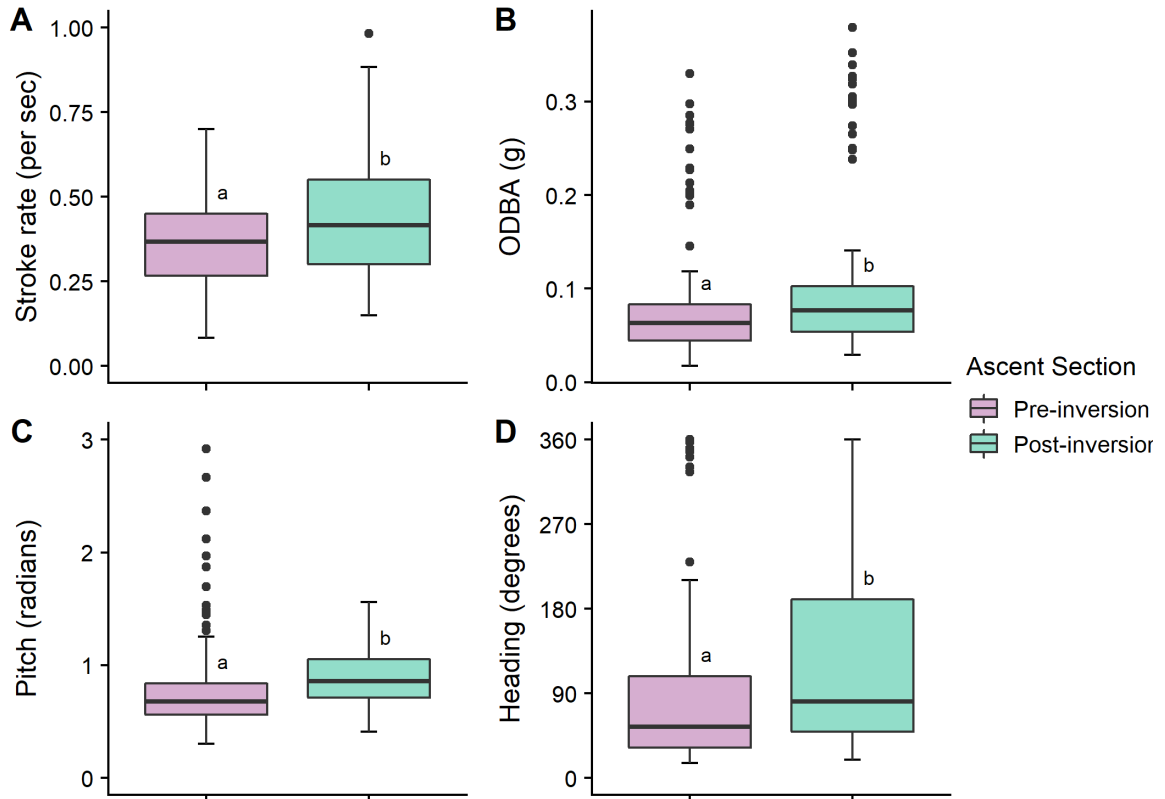
Stroke Rate, ODBA, Pitch, and Heading During Pre-Inversion and Post-Inversion Descent



Note. Comparisons between the 60 second descent sections of exposure dives pre-inversion and post-inversion for (A) mean of stroke rate, (B) mean of ODBA, (C) range of pitch, and (D) range of heading. The bold line inside the box represents the median, the box shows the interquartile range (IQR) with the lower and upper limits representing the 25th and 75th percentiles, the whiskers extend to the minimum and maximum values within 1.5*IQR, and the dots represent outliers.

Figure 8

Stroke Rate, ODBA, Pitch, and Heading During Pre-Inversion and Post-Inversion Ascent



Note. Comparisons between the 60 second ascent sections of exposure dives pre-inversion and post-inversion for (A) mean of stroke rate, (B) mean of ODBA, (C) range of pitch, and (D) range of heading. The bold line inside the box represents the median, the box shows the interquartile range (IQR) with the lower and upper limits representing the 25th and 75th percentiles, the whiskers extend to the minimum and maximum values within 1.5*IQR, and the dots represent outliers.

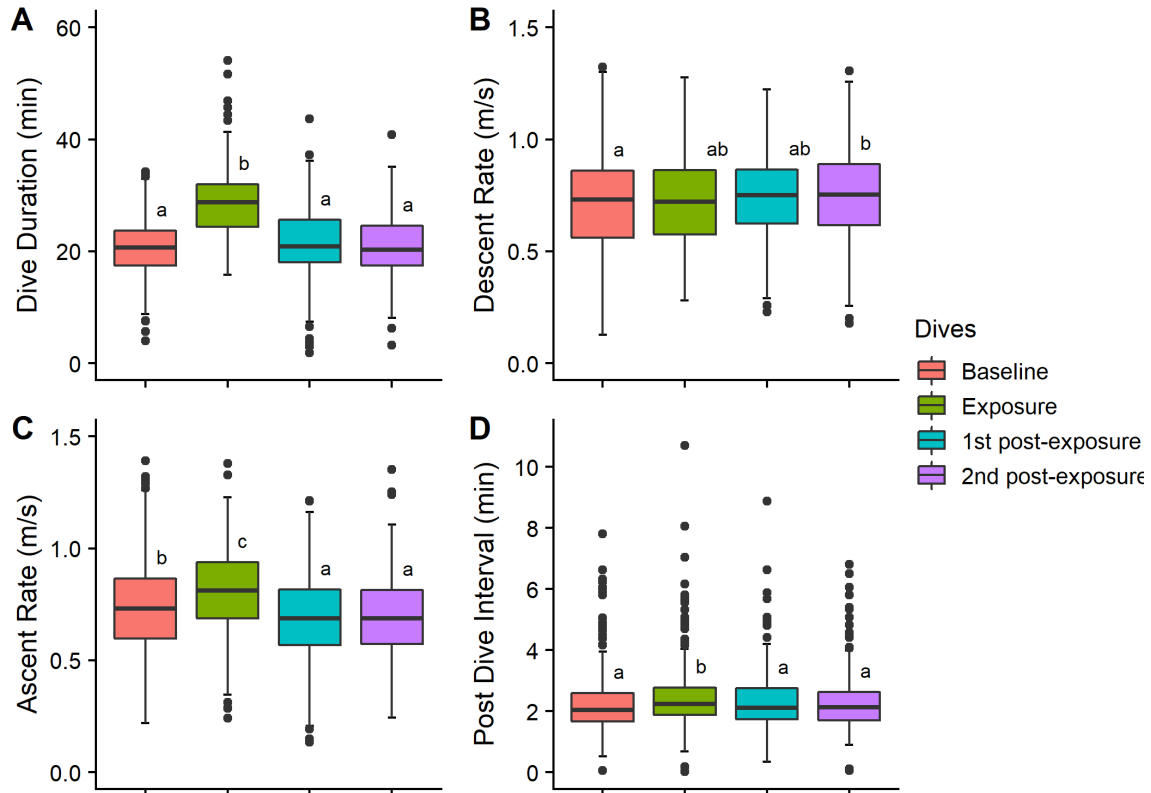
Duration of Behavioral Response Before Returning to Baseline

To examine how long dive behavior was modified in response to the acoustic stressor, I compared dive characteristics between baseline dives, exposure dives, and post-exposure dives. This analysis included all dives, no matter their maximum depth or if the exposure occurred on ascent or descent. Dive duration of exposure dives was longer than non-exposure

dives both before and after the exposure dive (Figure 9A; linear mixed effect model, $F_{3, 781} = 173.89$, $p < 0.001$). Both the first and second dives following the exposure dives were the same as baseline dive durations (Tukey post-hoc, $p < 0.001$). Descent rate differed between baseline dives, exposure dives, and post-exposure dives (Figure 9B; linear mixed effect model, $F_{3, 785} = 3.649$, $p = 0.012$). The set of second post-exposure dives had slightly faster descent rates than baseline dives (Tukey post-hoc, $p = 0.027$) but all other combinations had the same descent rate (Tukey post-hoc, $p > 0.05$). Ascent rate of exposure dives was faster than ascent rate of baseline dives and non-exposure dives following the exposure dive (Figure 9C; linear mixed effect model, $F_{3, 795} = 19.585$, $p < 0.001$). The two post-exposure dives had slower ascent rates than both exposure dives and baseline dives (Tukey post-hoc, $p < 0.001$). Post dive interval of exposure dives was longer than all non-exposure dives (Figure 9D; linear mixed effect model, $F_{3, 789} = 6.428$, $p < 0.001$). PDI of the two dives post-exposure returned to the same length as the post dive interval of baseline dives (Tukey post-hoc, $p < 0.05$).

Figure 9

Dive Duration, Descent Rate, Ascent Rate, and Post Dive Interval of Exposure Dive Sequence



Note. (A) Dive duration, (B) descent rate, (C) ascent rate, and (D) post dive interval values during the sequence of baseline dives (red), an exposure dive (green), and two post-exposure dives (blue and purple). The bold line inside the box represents the median, the box shows the interquartile range (IQR) with the lower and upper limits representing the 25th and 75th percentiles, the whiskers extend to the minimum and maximum values within 1.5*IQR, and the dots represent outliers.

Evidence of Habituation or Sensitization

Finally, I examined behavioral responses over the course of repeated exposures to determine if the seals became habituated or sensitized to the acoustic stressor. The elephant seals showed signs of habituation for some behavioral responses, but most behaviors did not change with repeated exposures (Table 4). No matter the number of repeated exposures, the

elephant seals all continued to perform dive inversions when exposed to the playback on ascent.

Table 4

Summary of Results Examining Response to Repeated Exposures of Acoustic Stressors

Model variables				Fixed effects				Variance explained	
Response variable	Fixed effect	Random effect		(Coefficient Estimate	Standard error	t	p	Marginal R^2	Conditional R^2
Dive duration	Exposure#	SealID	Intercept	1913.932	78.495	24.38	< 0.001	0.103	0.543
		(intercept)	Exposure#	-18.6	3.185	-5.84	< 0.001		
Descent rate	Exposure#	SealID	Intercept	0.674	0.038	17.581	< 0.001	0.009	0.252
		(intercept)	Exposure#	0.003	0.002	1.373	0.171		
Ascent rate	Exposure#	SealID	Intercept	0.738	0.033	22.201	< 0.001	0.041	0.215
		(intercept)	Exposure#	0.006	0.002	2.905	0.004		
Post dive interval	Exposure#	SealID	Intercept	13.095	0.708	18.509	< 0.001	0.061	0.363
		(intercept&slope)	Exposure#	-0.109	0.057	-1.898	0.089		
Stroke rate - descent	Exposure#	SealID	Intercept	7.957	4.262	1.867	0.089	0.073	0.495
		(intercept&slope)	Exposure#	-0.562	0.412	-1.362	0.203		
ODBA - descent	Exposure#	SealID	Intercept	0.021	0.010	2.051	0.064	0.01	0.343
		(intercept&slope)	Exposure#	-0.001	0.001	-0.533	0.605		
Pitch - descent	Exposure#	SealID	Intercept	0.198	0.099	2.003	0.06	0.015	0.344
		(intercept)	Exposure#	0.009	0.006	1.518	0.131		
Heading - descent	Exposure#	SealID	Intercept	1.008	0.14	7.199	< 0.001	0.018	0.162
		(intercept)	Exposure#	0.017	0.011	1.533	0.128		
Stroke rate - ascent	Exposure#	SealID	Intercept	2.747	2.029	1.354	0.205	0.014	0.422
		(intercept&slope)	Exposure#	0.183	0.185	0.992	0.347		
ODBA - ascent	Exposure#	SealID	Intercept	0.012	0.007	1.807	0.086	0.02	0.37
		(intercept)	Exposure#	0.001	0.000	1.83	0.070		
Pitch - ascent	Exposure#	SealID	Intercept	0.803	0.032	25.094	< 0.001	0.019	0.16
		(intercept)	Exposure#	0.004	0.002	1.535	0.127		
Heading - ascent	Exposure#	SealID	Intercept	-0.378	0.124	-3.059	0.003	0.027	0.047
		(intercept)	Exposure#	0.020	0.011	1.858	0.066		

Note. Summary of mixed effects model results examining the influence of repeated exposures to acoustic stressors on dive behavior. Bold values indicate the fixed effect was significant in the model. Marginal R² = variance explained by fixed effects. Conditional R² = variance explained by both the fixed and random effects.

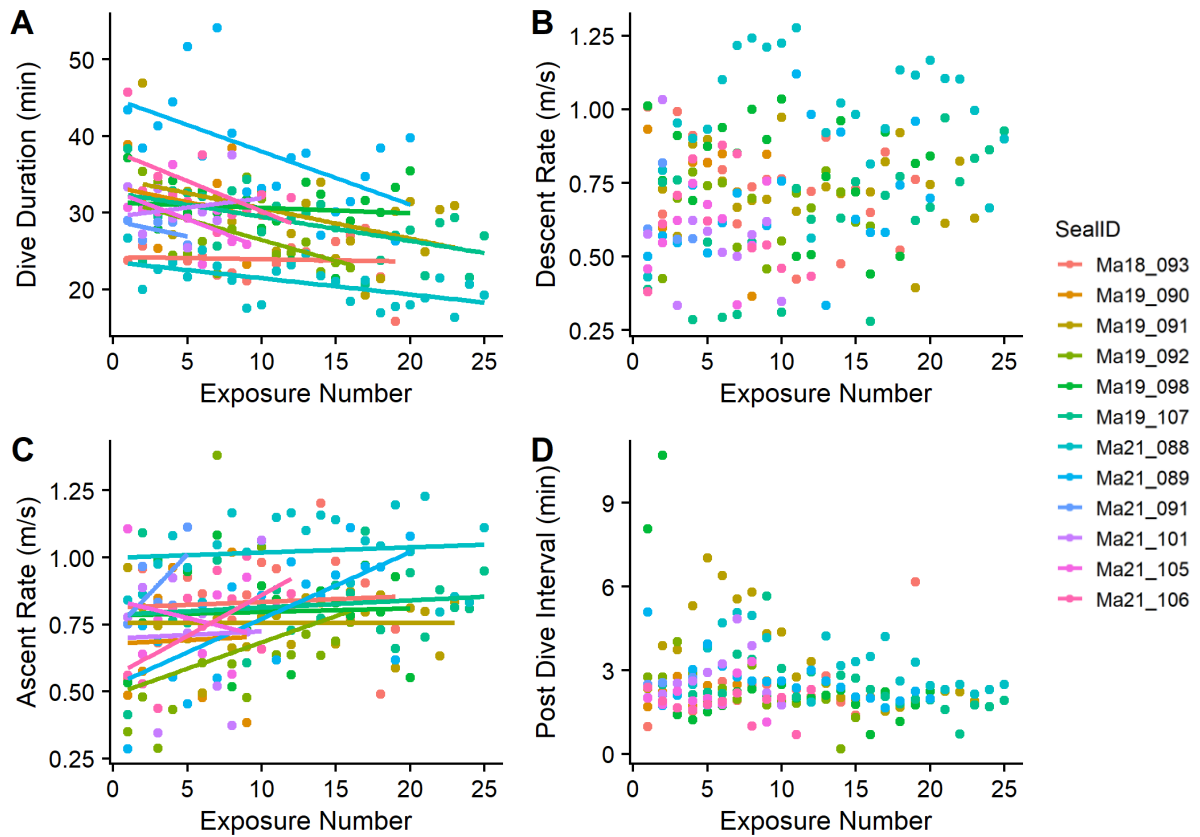
As the elephant seals experienced an increasing number of playbacks, their dive duration during exposure dives decreased (Figure 10A; linear mixed effect model, $F_{1,183} = 34.108$, $p < 0.001$). During exposure 1, the seals averaged a dive duration of 34.7 minutes, but by exposure 10, the average dive duration was 29.5 minutes. At exposure 25, the average dive duration dropped to 23.1 minutes. Almost all seals decreased dive duration with repeated

exposures. Descent rate remained the same as seals were exposed to more playbacks (Figure 10B; linear mixed effect model, $F_{1,188} = 1.885$, $p = 0.171$). The seals increased their ascent rate as they heard repeated exposures (Figure 10C; linear mixed effect model, $F_{1,191} = 8.437$, $p = 0.004$). During the first exposure, seals had an average ascent rate of 0.63 m/s and by exposure 25, the average ascent rate was 1.03 m/s. There was much more variability in the trends seen between seals, with some displaying large increases in ascent rate, some showing small increases, and one decreasing ascent rate with repeated exposures. Post dive interval remained steady as seals were exposed to more playbacks of the acoustic stressor (Figure 10D; square root transformed linear mixed effect model, $F_{1,9} = 3.601$, $p = 0.089$). When examining these four dive variables in relation to increasing numbers of non-exposure dives, no trends were observed for dive duration, descent rate, ascent rate, or post dive interval. Therefore, all results reported for exposure dives were due to repeated exposures to the acoustic stressor and not related to the amount of time the seals spent at-sea.

The juvenile elephant seals did not show signs of habituation or sensitization to the acoustic disturbance at a fine scale during exposure dives. As the number of playbacks increased, the variation of stroke rate, ODBA, pitch, and heading did not differ between the pre-inversion and post-inversion descent (Figure 11, Table 4). The variation of these four fine scale responses also did not change between the pre-inversion and post-inversion ascent with repeated exposures to the acoustic stressor (Figure 12, Table 4).

Figure 10

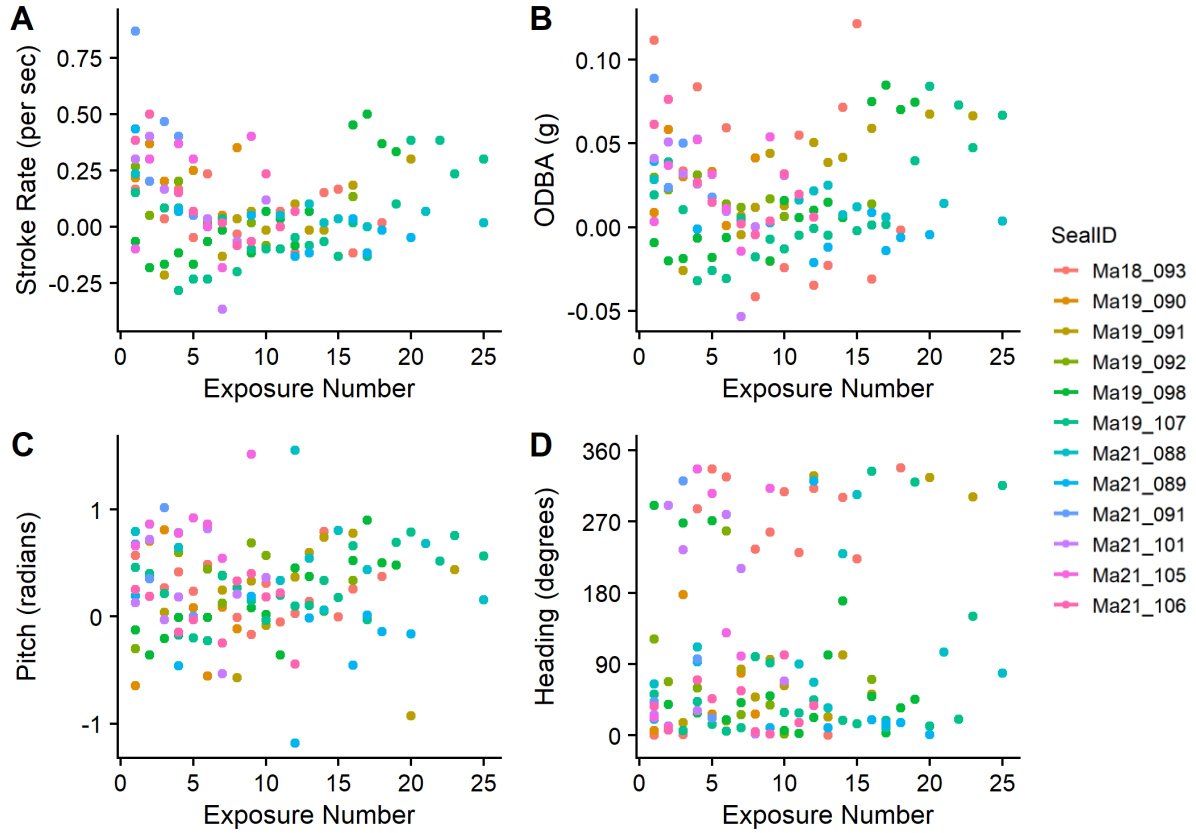
Dive Duration, Descent Rate, Ascent Rate, and Post Dive Interval During Repeated Exposures of the Acoustic Stressor



Note. (A) Dive duration, (B) descent rate, (C) ascent rate, and (D) post dive interval of seals as they were exposed to repeated exposures of the acoustic stressor. Only seals that were exposed to five or more playbacks are included, with 12 seals hearing at least 5 exposures and only 2 seals hearing all 25 exposures.

Figure 11

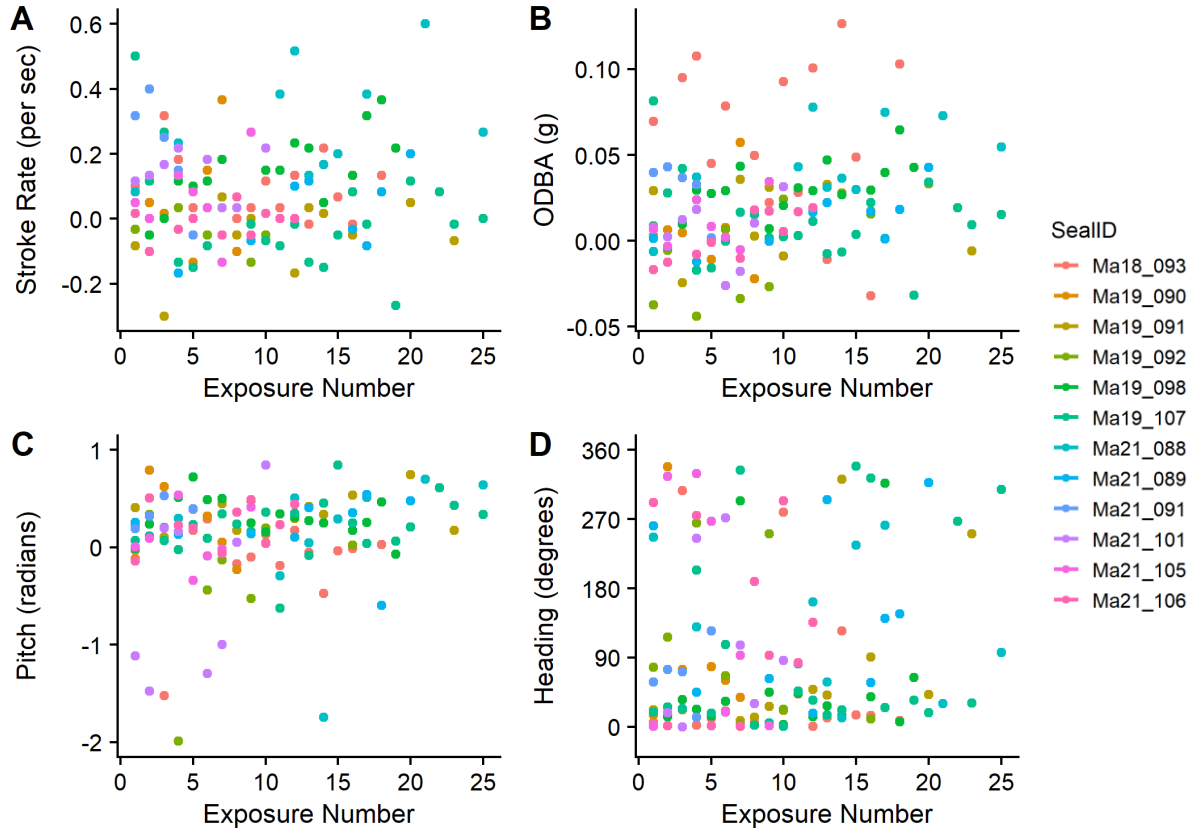
Changes in Stroke Rate, ODBA, Pitch, and Heading Between Pre-Inversion and Post-Inversion Descent During Repeated Exposures of the Acoustic Stressor



Note. Change in (A) stroke rate, (B) ODBA, (C) pitch, and (D) heading of seals during descent phases as they were exposed to repeated exposures of the acoustic stressor. The values for these variables are the difference between pre-inversion and post-inversion 60 second segments. Only seals that were exposed to five or more playbacks are included, with 12 seals hearing at least 5 exposures and only 2 seals hearing all 25 exposures.

Figure 12

Changes in Stroke Rate, ODBA, Pitch, and Heading Between Pre-Inversion and Post-Inversion Ascent During Repeated Exposures of the Acoustic Stressor



Note. Change in (A) stroke rate, (B) ODBA, (C) pitch, and (D) heading of seals during ascent phases as they were exposed to repeated exposures of the acoustic stressor. The values for these variables are the difference between pre-inversion and post-inversion 60 second segments. Only seals that were exposed to five or more playbacks are included, with 12 seals hearing at least 5 exposures and only 2 seals hearing all 25 exposures.

Discussion

In this study, I examined juvenile northern elephant seals during a translocation experiment to understand how a model deep-diving marine mammal responds to and recovers from exposures to acoustic stimuli. The seals exhibited strong behavioral responses to the recording of killer whale whistles, the most distinctive of which was performing dive inversions following each playback on ascent. While elephant seals altered their behavior during acoustic exposure dives, they quickly returned to normal behavior in subsequent dives. Due to the novel technology allowing for the source of the acoustic stimuli to come from an animal-borne biollogger, timing of exposures could be controlled and identical repeated exposures were possible. When subjected to multiple exposures of the killer whale whistles, juvenile elephant seals did not show signs of habituation or sensitization at a fine-scale level, but they appeared to habituate slightly to the sounds over time at a whole-dive level. This study confirmed previous findings that elephant seals respond to acoustic stimuli (Costa et al., 2003; Fregosi et al., 2016), but also added knowledge about fine-scale movements, duration of responses, and behavior in response to repeated exposures.

Behavioral Response to Acoustic Disturbance

The recording of killer whale whistles elicited a strong reaction from juvenile northern elephant seals when they were exposed during the ascent portions of deep dives. Each time the seals were exposed on ascent, they performed a dive inversion, also observed by Fregosi et al. (2016), which led to extended dive durations with acoustic exposure dives averaging 29.19 minutes compared to deep non-exposure dives averaging 22.06 minutes. Several species of whales also dove deeper and extended dive durations when exposed to mid-

frequency active sonar or low-frequency sounds (DeRuiter et al., 2013; Frankel & Clark, 1998; Stimpert et al., 2014). Interestingly, the juvenile seals did not extend their post dive intervals following the longer exposure dives. The only exception was Ma21_088, who had multiple extended PDIs. Since this seal completed a ~49 day migration rather than a quick 2-10 day transit, the behavior more closely matched that of adult female northern elephant seals that occasionally performed extended surface intervals during their long foraging migrations (Le Boeuf et al., 1988). Previous whale studies found that some species shortened PDI and others extended their time at the surface following disturbances (DeRuiter et al., 2013; Nowacek et al., 2004; Patenaude et al., 2002). Breath-hold divers use surface intervals to offload carbon dioxide and replenish oxygen stores, so it was interesting that the seals did not require additional time at the surface to recover after longer dives as some whales do. However, elephant seals are known for performing long, deep dives without extending surface intervals, so the extended dive durations observed probably did not deplete oxygen stores to a level that required longer recovery times (Le Boeuf et al., 1988). Elephant seals likely feel safer at depth since they can dive deeper than their top predators, which are primarily surface hunters, with juvenile northern elephant seals routinely diving to depths greater than 350 m and killer whales and great white sharks averaging dives less than 50 m (Jefferson et al., 1991; Le Boeuf & Crocker, 1996). Therefore, dive inversions, continuous diving, and minimal time spent at the surface likely lead to the best chance at survival.

To be able to extend a deep dive without any issues after unexpected exposure to an acoustic stimulus, elephant seals must have some physiological plasticity that allows them to conserve oxygen. During the exposures, the seals likely faced mixed signals between their

dive response (decreased heart rate), exercise response (increased energy expenditure requiring oxygen), and fear response (freeze reaction similar to dive response), which is similar to reported responses of narwhals exposed to stressful stimuli (Williams et al., 2017). During normal dives, elephant seals exhibit a drastic decline in heart rate at the beginning of dives, then an anticipatory tachycardia as they start their ascent, which becomes more pronounced in the final 15 seconds before surfacing (Andrews et al., 1997). The blood oxygen in elephant seals typically declines throughout a dive but drops more rapidly during the final 15-45 seconds of the ascent (Meir et al., 2009). Additionally, elephant seals do not always fully replenish their oxygen levels during PDIs (Meir et al., 2009). The seals in this study were exposed to the killer whale whistles earlier in the ascent phase, likely before they sharply increase heart rate which depletes their remaining oxygen stores. Therefore, at the time of the acoustic disturbance, the seals are probably still able to ration their remaining oxygen to allow for an extended dive, and longer PDIs are likely unnecessary because their blood oxygen does not need to be fully saturated before starting another dive. Elephant seals are the most impressive pinniped divers, and linking physiological measurements with this behavioral data will inform us of exactly how these seals are able to effortlessly extend their dives.

When exposed to the killer whale whistles on ascent, the juvenile seals also exhibited different descent and ascent rates compared to those during non-exposure dives. Since the exposure does not happen until the seals are starting to return to the surface, no difference was anticipated in descent rates; however, they were actually 0.9 m/s slower than during non-exposure dives. Upon further examination of the data, I noticed some seals performed

extremely long and shallow descents, so the large variability in dive behavior likely led to the unexpected result. On the other hand, the ascent rates of exposure dives with playback on ascent were faster than during non-exposure dives. Similarly, right whales execute rapid high powered ascents following an alert signal (Nowacek et al., 2004); however, this is usually after the whales abandon their dives prematurely. In contrast, some large whales slowly return to the surface after exposure to noise disturbances, suggesting they were cautious of what was at the surface (Allen et al., 2014; DeRuiter et al., 2013; Tyack et al., 2011). The elephant seals' behavior indicates they are trying to return to the surface quicker to offload carbon dioxide and reload oxygen after an extended dive, which also reduces time spent in shallow waters where predators could be hunting. Even though the seals are likely capable of even longer dives, it might be beneficial to quickly ascend to end an extended dive before another disturbance causes the need for an additional dive inversion.

A concern for deep-diving marine mammals is the possibility of decompression sickness, which has been observed in beaked whales (Bernaldo De Quirós et al., 2019). Those whales, like these seals, changed their diving behavior in response to an acoustic stressor.

Decompression sickness may occur because animals return to the surface too quickly, which can lead to nitrogen bubbles forming in their blood and tissues. This phenomenon has not been observed in elephant seals but could be a concern if they increase their ascent rates significantly. Here, the variability of ascent rates between the three categories of dives was relatively equal, so even when ascent rates were faster, they were still within the normal range for diving seals. The elephant seals may understand the threat of the killer whale whistles but are able to adjust their diving in a way that does not negatively impact their

health. Elephant seals have proven to be extremely robust and do not appear to suffer from the same negative effects as some whales when exposed to acoustic stressors.

On a fine-scale, I hypothesized that juvenile elephant seals would increase activity in response to the acoustic stimuli. When examining both descent and ascent sections of the post-inversion portions of exposure dives, activity increased as shown by the faster stroke rate and higher overall dynamic body acceleration, meaning the seals had more power in the additional strokes to help them swim faster. The elephant seals also displayed more variation in their swimming orientation following the dive inversion, with steeper pitch and greater changes in heading. The increased activity metrics and steeper pitch were likely due to the seals trying to escape the predator call then return to the surface more quickly to replenish oxygen stores after extending their dive. The escape response is similar to several whale species where individuals also increased their swim speed, stroke rate, or ODBA in reaction to acoustic stressors (DeRuiter et al., 2013; Stimpert et al., 2014; Williams et al., 2022). Upon closer inspection of the exposure dives, it appeared that many seals spun in circles during the 30 seconds of killer whale whistles, then returned to head in the same direction as they were initially swimming. A possible reason these seals were spinning in circles while on their post-inversion descent could have been to locate the source of the sound to determine which direction to escape. This 360-degree spinning was commonly observed during the acoustic playbacks across many of the seals in this study, showing that they are extremely cognizant of nearby predators and the behavior is not specific to certain individuals, but a trait performed by the species. Other studies have reported several whale species swimming

away from areas with projected sound sources (Allen et al., 2014; DeRuiter et al., 2013; Goldbogen et al., 2013; Tyack et al., 2011), but this spinning behavior has not been reported.

When the predator call played during the descent portions of dives, the elephant seals exhibited different behaviors than when they were exposed on ascent. The seals continued their descent following the sound exposure and there were no dive inversions observed. They still extended their dive durations compared to non-exposure dives, to an average of 27.61 minutes, but not as long as when they were exposed on ascent. All other dive characteristics, including descent rate, ascent rate, and post dive interval, remained the same between non-exposure dives and exposure dives when playback occurred on descent. Since the playback happened early in the dive, it is likely that the seals already recovered from the disturbance before starting their ascent, which led to normal ascent rates and PDIs. The unchanged descent rate was unexpected because previous studies found that some whales increased their swim speed or dove deeper in response to sound stimuli (DeRuiter et al., 2013; Stimpert et al., 2014). If I grouped the dives differently, separating exposure dives with playback on descent from all deep dives with no exposure on descent (which includes non-exposure dives and exposure dives with playback on ascent), seals that were exposed on descent had faster descent rates. These results suggest that hearing the killer whale on descent caused the elephant seals to speed up, matching trends seen in previous studies (Costa et al., 2003; Fregosi et al., 2016). Additionally, upon examination of the dive profiles for each exposure dive, the seals' dive angles become steeper following the exposure when playback occurred on descent.

The northern elephant seals in this study showed consistent behavioral responses to the acoustic stimuli at both the fine-scale and whole-dive levels. At a whole-dive level, there was a wide range in values within each of the three categories of dives, but significant differences were observed for dive duration, descent rate, and ascent rate between the groups. Non-exposure dives and exposure dives with playback on ascent clustered separately while exposure dives with playback on descent overlapped with both other groups. The cluster analysis can be used to predict which type of dive a seal is performing when no hydrophone or video camera is present since finding exposure dives would inform us if a disturbance occurred. The examination of fine-scale movements immediately before and after exposure to an acoustic disturbance has not been studied before due to the difficulty of knowing the exact timing of exposures. These results showed that there was greater three-dimensional movement post-inversion, and when examining these behaviors at 30 and 60 second intervals, the seals appeared to sustain their faster stroking, increased ODBA, and greater variation in heading. If the seals are continuously exposed to acoustic disturbances, their higher energy expenditure could lead to decreased resting or foraging time and therefore overall health. The juvenile seals in this study were mainly transiting, but if individuals in different behavioral states or life stages were exposed, the potential increased energetic costs could be more detrimental.

Duration of Behavioral Responses

Due to the strong behavioral response to the predator calls, I predicted juvenile elephant seals would exhibit altered behavior for a few dives following exposure. While exposure dives were longer with faster ascent rates, the seals returned to normal diving behavior in the

dive immediately following the disturbance (post-exposure dives did not differ from baseline behavior). For this analysis, all dives were included no matter their maximum depth or if the exposure occurred on ascent or descent, because I wanted to know if hearing a killer whale any time during a dive would influence dive characteristics during the following dive. This might explain why PDI was a little longer here but did not change when only comparing deep dives in earlier objectives. The seals immediately decreased dive duration, ascent rate, and PDI during their first post-exposure dives and remained at those lower levels for their second post-exposure dives as well, showing they recover quickly.

The context during which an exposure occurs plays an important role in how marine mammals react to noise (Gomez et al., 2016). Elephant seals reacted strongly to the predator call and took action to avoid the sound but returned to normal behavior immediately. This behavior ensures that extra energy expenditure does not continue when the threat is no longer present during subsequent dives. While these transiting seals appear to recover quickly, greater impacts might be observed during foraging migrations. Actively feeding cetaceans will avoid an area where a sound disturbance occurred for several hours or days, demonstrating that it takes them much longer to recover from disturbances (Goldbogen et al., 2013; Tyack et al., 2011). Antipredator responses could have larger energetic costs during foraging dives because the trade-offs between the risk of predation and benefits gained in continuing foraging are greater than during transiting dives. A study examining behavioral responses of cetaceans to predator and anthropogenic sounds found that the intensity of responses differed depending on how sensitive each species was to predation risk (Miller et al., 2022). Here, I revealed that elephant seals adapt well to stressful scenarios while

transiting, but future studies examining seals in other behavioral states would give us a broader understanding of the effects of sound on dive behavior.

The ability to return to normal behavior quickly could be extremely beneficial for elephant seals as anthropogenic sounds in the ocean continue to increase. With many studies showing that marine mammals react similarly to sonar and killer whales (Fregosi et al., 2016; Miller et al., 2022; Zimmer & Tyack, 2007), it is important to learn more about how acoustic stimuli affects both short-term and long-term behavior. Elephant seals seem to be one of the more robust species, and in addition to handling instrumentation well, they are known to recover quickly from potentially stressful events such as sedation, surgery, and transport (Cooley, 2022; McMahon et al., 2008). We can use elephant seals as a model species to understand the effects of sound and transfer that knowledge to learn about the behavior of more vulnerable cetacean species. The importance of survival should encourage marine mammals to react to threatening sounds whenever they occur, but being able to recover quickly from those events is equally vital to ensure excess energy is not wasted.

Behavioral Response to Repeated Exposures

The final objective of this study was to determine if the seals altered their response when exposed to the stimuli multiple times. The acoustic stimuli came from one of the northern elephant seal's only predators, so I predicted that it would be detrimental for seals to habituate completely to transient killer whale whistles. After being subjected to repeated exposures of the sound playback, the juvenile seals still exhibited a behavioral response, but appeared to show signs of habituation in the dive characteristics measured, with dive duration decreasing with more exposures. Although the seals still performed dive inversions during

later exposures, their dives were shorter, suggesting that they recovered quicker from the later disturbances. Perhaps they were able to more quickly determine that the threat was not following them and could recover from their fear response faster after repeated exposures. This would allow them to not waste excess energy evading a threat that is no longer there.

Factors that may affect how marine mammals respond to ocean noise include individual hearing sensitivity, activity pattern, behavioral state, past exposure to the noise, noise tolerance, and demographic factors (Wartzok et al., 2003). Based on the results, it appears that previous exposures influence the response to later exposures, but there was also a lot of variability in the behavioral responses between the 12 individual seals, especially during the lower exposure numbers. This was especially the case for ascent rate over repeated exposures; some seals performed slow ascents following their first few exposures but faster ascents after later exposures, leading to an increase in ascent rate with more exposures. Perhaps these seals were initially more cautious of predators that could be hunting near the surface (like some large whale species that also perform slow ascents), but then became less concerned after repeated exposures. The large variability in the first few exposures showed that some seals reacted much stronger than others but after repeated exposures, their reactions became more consistent with each other.

When examining the changes in fine-scale behaviors over repeated exposures, the elephant seals did not show signs of habituation or sensitization at the shorter time scale during either the descent or ascent phases of the post-inversion dives. Even though a previous objective showed that stroke rate, ODBA, pitch, and heading all increased during the post-inversion sections of exposure dives, the amount of increase (or the difference between pre-

inversion and post-inversion behavior) remained the same no matter how many times the seals heard the killer whale whistles. The evasive dive maneuvers they performed to escape from the predator call are essential for survival, so at the fine-scale level, it is logical for the seals to continue reacting the same way no matter how many times they hear their predator.

The dive behaviors observed suggest that the elephant seals do not habituate to repeated exposures of the acoustic stimuli at a fine-scale level but do acclimate at a whole-dive level. As in other studies where harbor seals consistently responded to transient killer whale calls (Deecke et al., 2002), elephant seals continued to react to predator calls over repeated exposures. Although the elephant seals never observed a killer whale during the playbacks, the acoustic stimulus elicited a response each time, which is consistent with the idea that biologically important sounds, such as those from a predator, should always lead to a reaction (Ellison et al., 2012). Fully habituating to predator calls could be life-threatening for seals, so the reduced reactions seen in the study animals over time appears to be the best solution. However, if seals consistently respond to naval sonar or other anthropogenic noises the same way they do to killer whale whistles, the increased energy expenditure could be detrimental over time, even if they can recover quickly from the disturbances. More research is needed to discover if elephant seals respond similarly to repeated exposures while in different behavioral states and to different acoustic stimuli.

Conclusion

The ability to collect movement data from marine mammals while controlling timing and received level of acoustic stimuli during repeated exposures is rarely possible. In this study, I used an animal-borne biollogger that was programmed to play a recording of killer whale

whistles at specific times during the translocation of juvenile northern elephant seals. Study animals exhibited stereotypical behavioral responses at both the fine-scale level and the whole-dive level, proving that they can easily adjust diving behavior when confronted with an acoustic stressor. Although the elephant seals all reacted strongly to the stimuli, they were able to quickly return to baseline behavior during subsequent dives, showing that they do not require much time to recover from stressful events. Their behavioral responses were also less intense after repeated exposures to the same acoustic stimuli. The practice of always responding to killer whale whistles is crucial for survival, but the ability to recover quickly and react less to future exposures allows these seals to conserve energy.

As anthropogenic sounds in the oceans increase, there is a need to understand the short-term and long-term impacts of acoustic disturbances on marine mammals. It is also critical to examine how long it takes them to recover from disturbances and how they adjust their behavior during future exposures. Since elephant seals are such a robust species, they are the ideal candidate for this type of research. Studying behavioral responses provides great insight into the visible effects, but integrating these with physiological responses will help us fully comprehend how these animals can change their behavior in the way that they do and how these changes impact their health. Future studies should use similar techniques to examine fine-scale movement data of animals in different age classes or behavioral states (i.e., foraging or resting rather than transiting). A larger sample size, more repeated exposures, additional time between exposures, and the use of different natural and anthropogenic sounds would also be beneficial. As we learn more about how acoustic stimuli impact marine

mammals, we can use this knowledge to guide conservation efforts and manage the increased sounds in the oceans to protect sensitive species.

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