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EXAMINING THE PLASTICITY OF THE DIVE RESPONSE IN RELATION TO DIVE
BEHAVIOR OF NORTHERN ELEPHANT SEALS (*MIROUNGA ANGUSTIROSTRIS*)

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

Shawn M. Hannah

August 2023

The Designated Thesis Committee Approves the Thesis Titled

EXAMINING THE PLASTICITY OF THE DIVE RESPONSE IN RELATION TO DIVE
BEHAVIOR OF NORTHERN ELEPHANT SEALS (*MIROUNGA ANGUSTIORSTRIS*)

by

Shawn M. Hannah

APPROVED FOR THE DEPARTMENT OF MARINE SCIENCE

SAN JOSÉ STATE UNIVERSITY

August 2023

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ABSTRACT

EXAMINING THE PLASTICITY OF THE DIVE RESPONSE IN RELATION TO DIVE
BEHAVIOR OF NORTHERN ELEPHANT SEALS (*MIROUNGA ANGUSTIROSTRIS*)

By Shawn M. Hannah

Marine mammals face an extraordinary challenge as they must actively hunt during breath-hold dives. This challenge is conquered by the dive response (the decreased heart rate and increased peripheral vasoconstriction associated with a breath hold) and is influenced by dive duration, depth, exercise, and cognitive control. I studied the dive response of one of the deepest diving marine mammals, the northern elephant seal, across two years to determine interactions between behavioral and physiological factors on a fine scale. I examined the influence of dive depth, duration, and activity (ODBA) on dive heart rate (f_H), pre- and post-dive f_H, post-dive surface interval and f_H at fine scale (20s). Dive depth and duration influenced dive f_H more than activity. When analyzed on a fine scale, however, northern elephant seals did adjust their f_H in response to activity, primarily in the bottom and ascent phases of their dive. These results suggest that these seals actively regulate their oxygen stores during dives. Overall, these seals are prioritizing oxygen conservation to replenishing oxygen-depleted muscle tissue, as the relationship between dive depth and duration to dive f_H was stronger than dive activity to dive f_H. They do provide relief to muscle tissue in small increments at fine scale, however, by briefly increasing f_H. Their incredibly adapted dive response, exercise modulation, and dive behavior allows northern elephant seals to regularly dive within their aerobic dive limit (ADL) and minimize their recovery time at the surface.

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First, I'll start with my advisor Gitte. Gitte, thank you for choosing me to be part of your incredible lab. I am so grateful for all the experiences I've gained through your leadership and mentorship. I am a better scientist because of you, and I hope we get to work together again someday (hopefully with less tag, pandemic, and data issues… and maybe less falling but probably not). Thank you for continuing to push me when things got hard, and for your compassionate, effective guidance.

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This thesis was part of a larger project studying diving physiology in northern elephant seals, and there were many who contributed to the success of the project. First, the seven Principal Investigators on the project included: Drs. Birgitte McDonald, Cassondra Williams, Allyson Hindle, Paul Ponganis, Markus Horning, Holger Klinck, and Dan Costa. These seven scientists all bring not only their amazing intelligence, but each their own unique craftsmanship to the field. There were so many people who aided the project and were integral in its success: thank you to Dr. Rachel Holser, Dr. Logan Pallin, Dr. Jason John, Dr. Chhavi Goenka, Luke Keehan, Dr. Patrick Robinson, Parker Forman, Emma Nicholson, Mason Cole, Jenni Johnson, Dr. Luis Hückstädt, Arina Favilla, Theresa Keates, and others

The best thing MLML did for me was introduce me to Matthew Elliott. Thank you, Matthew, for your unconditional love and support. Through times when I really didn't think I would make it to this point, you were always there for me. You are my best friend and rock.

Thank you to my family and friends for your continued support over these several years – we did it… finally! To my parents and my brother, thank you for never giving up on me and giving me the confidence to go after my dreams. To my dear friend, Patty, thank you for answering my FaceTimes, calls, texts and being a huge support system for me – I couldn't have done this without you. I also want to shout out the following people whose support helped me so much through these years: Georgia, Katie E., Lolo, Kelley, Nina, Dom. I love you all.

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LIST OF ABBREVIATIONS

ADL – Aerobic dive limit
AIC - Akaike information criterion
cADL – Calculated aerobic dive limit
ECG – Electrocardiogram
f_H – Heart rate
IACUC - Institutional animal care and use committee
if_H – Instantaneous heart rate
LMM – Linear mixed-effects model
MSA – Minimum specific acceleration
NMFS – National Marine Fisheries Service
NSF – National Science Foundation
ODBA – Overall dynamic body acceleration
TDR – Daily diary time-depth-recorder
VHF – Very high frequency radio transmitter

INTRODUCTION

The recurrent task of searching and capturing prey is an extraordinary challenge for marine mammals, as these animals must actively hunt during a breath-hold dive. This challenge is conquered through a suite of physiological adaptations known as the dive response. The dive response is comprised of breath-hold (apnea), lowered heart rate (bradycardia; Kooyman, 1985), and peripheral vasoconstriction (Grinnell et al., 1942; Zapol et al., 1979). This response increases the dive capacity of marine mammals by lowering the rate that oxygen stores are used (Kooyman, 1985) while maintaining physiological homeostasis and prolonging the duration of aerobic metabolism (Ponganis et al., 2017; Davis, 2019). The dive response is dynamic, where the central nervous system adjusts the degree of the response based on the animal's dive behavior (Ponganis et al., 2017). This allows an animal to conserve oxygen at different stages of the dive. Many of the physiological mechanisms and fine-scale drivers underlying the dynamic capabilities of the dive response, however, are still unknown. Marine mammals depend on this response to succeed in their habitat; therefore, it is imperative to understand these unknown aspects of the dive response to determine how these apex predators will be affected by climate change and anthropogenic disturbance altering their environment.

Dive depth, duration, and exercise influence the dive response (Ridgway et al., 1975; Williams et al., 1991; Andrews et al., 1997; Davis and Williams, 2012; McDonald and Ponganis, 2014; Elmegaard et al., 2016; McDonald et al., 2018). To study these impacts on the dive response in freely-diving marine mammals, heart rate (f_H) is often used as a proxy. This is because measuring vasoconstriction is difficult, and the onset of bradycardia and

vasoconstriction after apnea are highly associated (Grinnell et al., 1942). Using f_H as a proxy, the intensity of the dive response increases as dive depth and duration increase in voluntary and free-range dives (Elsner, 1965; Williams et al., 1991; Hindell et al., 1992; Andrews et al., 1997; Davis and Williams, 2012; McDonald and Ponganis, 2014). More recently, it has been suggested that exercise influences the dive response (Williams et al., 2004; Davis and Williams, 2012; Williams et al., 2015; Ponganis et al., 2017; McDonald et al., 2018). For instance, free-ranging Weddell seals (*Leptonychotes weddellii*) experienced an increased f_H during brief bursts of exercise activity to compensate for muscle oxygen demand (Davis and Williams, 2012). Therefore, dive f_H is thought to be exercise-modulated, temporarily increasing f_H to provide oxygenated blood to the skeletal muscle when exercising.

Exercise-modulation of the dive response may be the answer to a long-standing paradox. During exercise, terrestrial mammals experience tachycardia (increased f_H), hyperventilation, peripheral vasodilation, and increased cardiac output to minimize lactate buildup from anaerobic muscle metabolism (Davis and Williams, 2012; Poole and Erickson, 2015). In contrast, given the physiological characteristics of the dive response, marine mammals should have high lactate buildup when exercising. Yet, these animals exercise during dives while appearing to stay within their aerobic dive limit (ADL; Hindell et al., 1998; Williams et al., 2015; Ponganis et al., 2017), the maximum duration they can perform a breath-hold dive before using anaerobic metabolism resulting in the accumulation of lactate (Kooyman et al., 1983). This is possible because the decreased cardiac output and associated peripheral vasoconstriction reduce the amount of blood perfusing exercising muscle, leading the muscle to rely on oxygen stored in the myoglobin (Kooyman, 1985). During incidences of increased

activity during a dive, myoglobin is depleted of oxygen, which could result in the onset of anaerobic metabolism, lactate build-up, and ultimately muscle acidosis (Kanatous et al., 2002; Williams et al., 2011). An exercise-modulated dive response would allow for temporary increases in f_H associated with increased activity to deliver blood-oxygen stored in hemoglobin to oxygen-depleted myoglobin (Davis and Williams, 2012). These temporary increases in blood flow to the muscle reduce the need for anaerobic metabolism.

The dive response also is under a degree of cognitive control where marine mammals regulate their dive response based on anticipation (Harrison et al., 1972; Lin et al., 1972; Ridgway et al., 1975; Jobsis et al., 2001; McDonald and Ponganis, 2014; Elmegaard et al., 2016). For example, pre-dive f_H was higher before longer dives than shorter dives in California sea lions (*Zalophus californianus*), presumably to facilitate more loading of blood oxygen in preparation for the dive (McDonald and Ponganis, 2014). More recently, it was found that harbor seals (*Phoca vitulina*) have some degree of cognitive control over their vasoconstriction and redistribution of oxygen in anticipation of and during their dive response (McKnight et al., 2019). Cognitive regulation of the dive response allows these animals to manage their blood oxygen stores based on anticipated dive activity and changes in behavior during the dive.

As demonstrated above, there is support that dive depth, duration, exercise, and anticipation influence the dive response, but less is known about the relationship among these variables and the degree to which they influence the dive at a fine scale for most species. Northern elephant seals (*Mirounga angustirostris*) are a model species to determine the relationship between dive behavior and the dive response, as well as the plasticity of the dive

response in a deep diving species. Elephant seals have been extensively studied as they handle instrumentation well and return to the same beach allowing for instrument retrieval (Andrews et al., 1997; Oliver et al., 1998; Meir et al., 2009; Maresh et al., 2014). Northern elephant seals are one of the deepest diving pinnipeds (Stewart and Delong, 1993), on average diving to 350-650m for 30 minutes when foraging (Le Boeuf et al., 1988; Delong and Stewart, 1991); however, they are capable of dives deeper than 1500m and longer than an hour (Le Boeuf et al., 1996). These seals dive continuously (spending 88 ± 2.7 % of time at sea submerged; Le Boeuf et al., 1996) while spending minimal time (less than 3 minutes) recovering during surface intervals (Andrews et al., 1997; Le Boeuf et al., 2000b; Davis et al., 2001). The ADL has not been measured in northern elephant seals, but it has been calculated (cADL) to be approximately 30 minutes for adult females (Hassrick et al., 2010). Northern elephant seals, however, routinely exceed the cADL while maintaining short surface intervals (Hassrick et al., 2010). It is suggested that northern elephant seals prolong aerobic metabolism by passively gliding during some portions of their dive descent when they are negatively buoyant, minimizing the level of activity during a dive (Williams et al., 1996, 2000; Davis et al., 2001). Similar to other species, elephant seals' dive f_H is negatively correlated with increased dive depth and duration (Andrews et al., 1997), but it is unknown how their dive response relates to dive activity. Additionally, although it has been suggested that northern elephant seals may have cognitive control over their dive response based on the observed anticipatory tachycardia before surfacing to maximize the efficiency of CO_2 offloading and O_2 onloading (Andrews et al., 1997), it is unclear if they prepare for dives or make other cognitive adjustments during the dive.

While there have been important studies on the dive response of northern elephant seals, some questions remain. In this study I investigated the relationship between dive depth, duration, and activity (stroke rate; overall dynamic body acceleration, ODBA) and their influence on pre, post, and dive f_H of juvenile (~1-2-year-old) northern elephant seals, to determine the plasticity of the dive response. Heart rate (f_H), a proxy for dive response, was continuously measured using an electrocardiogram (ECG) biologger. Dive depth and acceleration were collected with a time-depth-recorder (TDR). This study focused on juvenile elephant seals as they are easier to transport and recover compared with adults. Additionally, although they perform shorter dives, their dive behavior and dive response are similar to adults (Le Boeuf et al., 1996). I hypothesized that 1) dive f_H will be lower on longer, deep dives, but higher on more active dives (higher stroke rate/ODBA), also 2) at a fine scale (20 s intervals) there will be a negative relationship between depth/duration and f_H and a positive relationship between activity and f_H; these relationships will be more pronounced at fine scale. The relationship between activity and f_H, however, will be influenced by dive depth/duration, 3) post-dive f_H will be higher after longer, deeper, and more active dives, but there will be no difference in the length of surface recovery duration based on dive behavior (e.g., high activity vs low activity dive), and 4) pre-dive f_H will be high before longer, deep dives to maximize O_2 stores before longer dives. This study will provide essential information about the capabilities, oxygen management, and dive response in a deep-diving marine species.

METHODS

Animal Translocation and Instrumentation

Six juvenile northern elephant seals were translocated from Año Nuevo State Park (Año) during the 2018 and 2019 molting seasons (April-May) using the well-established translocation protocol (Fig. 1; Andrews et al., 1997; Oliver et al., 1998; Meir et al., 2009; Maresh et al., 2014). Healthy, pre-molt seals were immobilized by administering Telazol (1.2 – 1.5 mg/kg) intramuscularly (Le Boeuf et al., 2000a). Once immobilized, seals were placed in a metal cage lined with mesh shading. Seals were transported 35km by truck to Long Marine Laboratory (LML) in Santa Cruz for instrumentation.

Upon arriving at LML, seals were weighed and placed in the lab. After 2-3 hours, the instrumentation procedure began. First, seals were anesthetized with an injection of Telazol (< 1mg/kg) intramuscularly. Once sedated, a custom-built oxygen mask was placed over their head and 5% isoflurane-O_2 was delivered. This continued until the seal was relaxed enough to safely intubate, then 1-2% isoflurane-O_2 was administered for the remainder of the procedure (Ponganis et al., 2006; Stockard et al., 2007; Meir et al., 2009). Morphometric data (lengths, girths, and blubber depths) were measured.

Each seal was instrumented with: **1)** OxyLog datalogger (UFI, Inc., 3x10 cm cylinder) that measured ECG, venous partial pressure of O_2 (PO_2), temperature, and pressure (see details below); **2)** Daily Diary diving behavior datalogger (TDR tag, MK-10DD, Wildlife Computers, ~5x3x1.5 cm) that measured depth and acceleration; **3)** a satellite tag (SPOT tag, Wildlife Computers) used to track the animal at sea; and **4)** a very high frequency (VHF) radio transmitter used to locate seals when they return to the beach (Fig. 2). Tags were
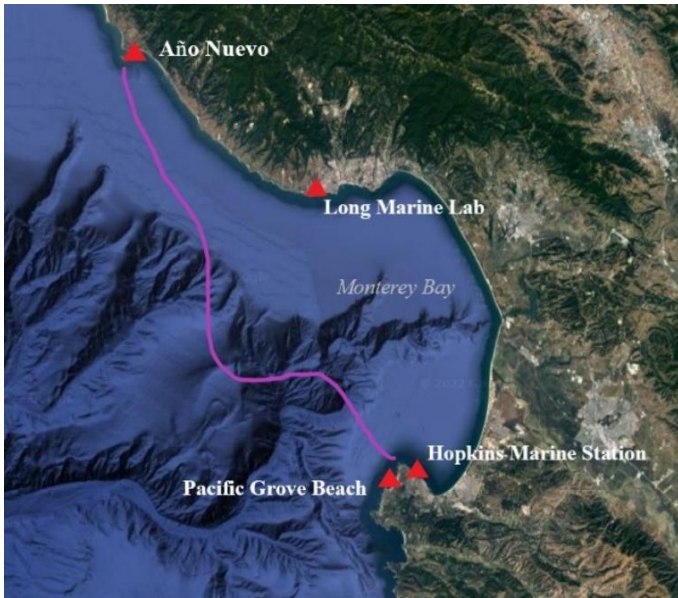
Fig. 1. Monterey Bay, California with key study sites. Red triangles mark key locations during this study: Año Nuevo was the capture site, Long Marine Lab was the tagging site, and Hopkins Marine Lab and Pacific Grove Beach were the release sites. The purple line demonstrates a possible track of a northern elephant seal when translocated from Año Nuevo State Park and released at Hopkins Marine Station, Monterey.

attached using 5-minute quick set epoxy (Loctite) and cable ties (Meir et al., 2009). After instrumentation, seals remained at LML in a holding area to recover either for the rest of the day or overnight. Later that evening or the next morning, seals were transported via truck to Pacific Grove, CA (75km from LML), where they were released.

Seals were tracked at sea using the satellite tag. Once on land seals were relocated using the VHF tag for tag removal. It took 2-9 days for seals to return to Año. One seal swam to the Piedras Blancas rookery in San Simeon, CA. Before tag removal, seals were immobilized on the beach with an intramuscular injection of Telazol (1.2-1.5 mg/kg), and immobilization was maintained with intravenous injections of ketamine (0.5–1 mg/kg) (Meir et al., 2009). After tag removal, seals were monitored on the beach while recovering from sedation.
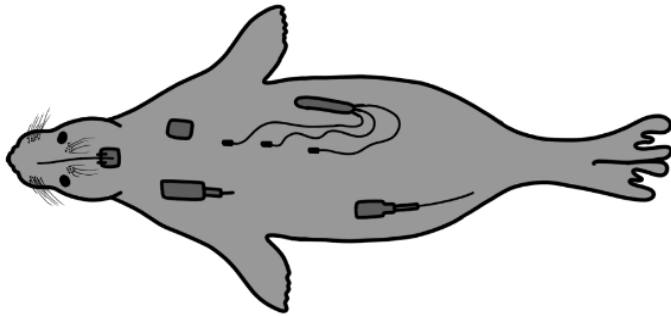
Fig. 2. Schematic of tag placement on an elephant seal. A) The tag placement on the northern elephant seals. Tag placement: satellite tag on the seals head, TDR on the right shoulder, VHF on the left hip, and OxyLog datalogger on the right side of midline. The fifth tag, on the left shoulder of the seal, was not used in this study.

The study was performed under both National Marine Fisheries Service (NMFS) permits (#19108 and #23188) and permission from the San José State University and University of California, Santa Cruz Institutional Animal Care and Use Committees (SJSU protocol # 1042 & AAA-28, UCSC protocol # Costd1701).

OxyLog Datalogger

The OxyLog data logger records the electrocardiogram (ECG, 50-100 Hz), venous PO_2 (1 Hz), temperature (1 Hz), and pressure (1 Hz). The OxyLog was placed on the seals dorsal midline ~ 45-50 cm behind the foreflippers (Fig. 2). A sterile bipolar pacing ECG electrode (model 006225; C.R. Bard, Lowell, MA, USA) was inserted percutaneously into the extradural vein through a peel-away catheter (5Fr; Cook Medical, Bloomington, IN or Braun XXX, USA). The electrode was inserted ~30 cm into the vein and then connected to the datalogger. The same aseptic procedure was performed for the PO_2 electrode (Licox C1.1 Revoxode; Integra Life Sciences) and thermistor (model 554; Yellow Springs Instruments) with extradural venous placements about 10 cm behind the ECG sensor. The incision sites

and cables were protected using neoprene patches. The described procedure is per established protocols (Ponganis et al., 2006; Stockard et al., 2007; Meir et al., 2009; McDonald and Ponganis, 2013, 2014), and instrumentation has proven not to interfere with seal locomotion.

Data Processing and Analysis

Custom-written scripts were used in MatLab (The MathWorks, Inc., Natick, MA, USA) to detect R-wave peaks in the ECG data. The identified peaks were confirmed by visual inspection and corrected if necessary. Instantaneous f_H (if_H, beats min^{-1}) for each heartbeat was calculated using R-R peak intervals ($if_H = 60$/R-R interval).

Depth data from the TDR tag was processed using custom-written scripts and the *diveMove* package in R (Luque, 2007; v.1.1.419, R Foundation for Statistical Computing). I used the zero-offset correction given by the TDR in the output dataset from the tag. I identified a dive, using the following criteria: minimum duration of 20s and minimum depth of 5m (McDonald and Ponganis, 2014). Each dive was segmented into descent, bottom, and ascent phases using the following criteria: descent (submersion to 80% of maximum depth), bottom (time spent at greater than 80% of maximum depth), ascent (80% maximum depth back to surface; Andrews et al., 1997; McDonald and Ponganis, 2014).

I determined seal activity during dives with stroke rate, MSA, and ODBA using the raw TDR 3-axis accelerometry data. I calculated stroke rate by using the y-axis accelerometry values from the TDR. The values were smoothed over a 5-second interval and low-frequency static acceleration was eliminated using a 0.4 Hz high-pass Butterworth filter (0.4 Hz was chosen as it was the best signal-to-noise ratio for the y-axis acceleration data; Tift et al., 2017). Once the data were smoothed and run through the Butterworth filter, I used

'*detect_peaks*' to identify a flipper stroke from the *tagtools* package in R (Sweeney et al., 2019; v.1.1.419, R Foundation for Statistical Computing). Using the time interval between two strokes I calculated instantaneous stroke rate (stroke rate = 60/stroke interval). Additionally, I calculated MSA, an underestimation of an animal's specific acceleration obtained by removing the gravitational acceleration (1g; g=9.81 ms^{-2}) from the absolute value of the norm of acceleration (Simon et al., 2012). To calculate MSA, I ran all three axes of raw acceleration data through the '*msa*' function in the *tagtools* package in R (Sweeney et al., 2019). Lastly, I calculated ODBA, which is an animal's dynamic acceleration and is measured by subtracting smoothed three-axis acceleration from the corresponding unsmoothed acceleration to remove the gravitational acceleration, then adding up the resulting three-axes values (Wilson et al., 2006). To calculate ODBA, I ran all three axes of raw acceleration data through the *'odba'* function in the *tagtools* package in R (Sweeney et al., 2019). I found that MSA did not accurately describe acceleration for northern elephant seals, as the values would drift from zero while the seals were not actively accelerating. This is likely due to northern elephant seals passively descending into the water column; they stroke-and-glide while descending, but will also undergo a falling-leaf pattern when they rest during descent (Davis et al., 2001; Mitani et al., 2010; Kendall-Bar et al., 2023). This resulted in higher mean MSA values, therefore, I did not include MSA in further analysis. I investigated the relationship between ODBA and stroke rate and found that they were positively correlated (Fig. 3; Pearson's correlation test, correlation coefficient = 0.74, $P <$ 0.001). I used ODBA as my activity index in the models, as the calculation for ODBA incorporates amplitude and was deemed a more accurate representation of seal activity.
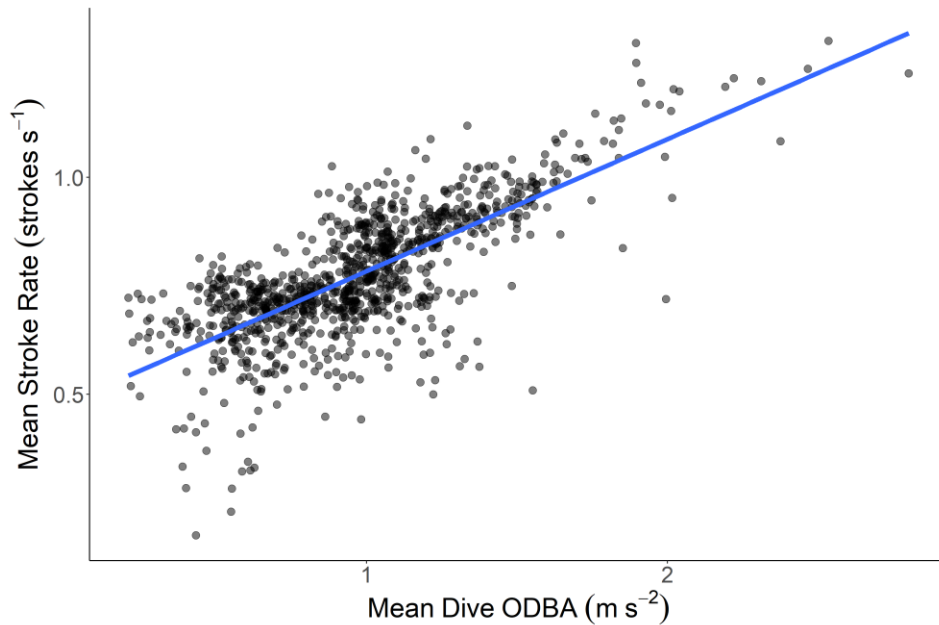
Fig. 3. Relationship between Dive ODBA and stroke rate. A positive correlation between mean dive ODBA and mean dive stroke rate was determined using Pearson's correlation test (correlation coefficient = 0.74 , p-value < 2.2e-16). ODBA was used as the activity index for analyses as the error in calculating this index is lower than stroke rate.

1. *Dive Analysis*

To investigate the relationship between dive behavior and dive f_H, I used linear mixed effects models (LMM). I ran these models in R using the *'lme'* function from package *nlme* (Pinheiro et al., 2022). Dives less than 3 minutes duration were removed for the LMM analyses, as the physiological constraint of oxygen conservation is not as severe in these short dives. For all models, seal ID was a random effect to account for the lack of independence of multiple dives stemming from an individual seal. All models contained a correlation structure, corAR1, to account for autocorrelation in time series data. The following are the dependent variables of each model: 1) dive f_H, 2) bottom-dive f_H, 3) pre-dive f_H (30s before dive), 4) post-dive f_H (30s after dive), and 5) post-dive surface interval.

The mean value of each dive was used for the previously mentioned variables, with post-dive surface interval as the exception as this value was the full time-lapse between each dive. Maximum dive depth or dive duration, mean dive ODBA, and the interaction between depth or duration and ODBA were fixed effects. Dive duration and dive depth were positively correlated (Pearson's correlation test, correlation coefficient = 0.863, p-value < 0.001), so I used the variable that led to a better model. This varied among models and was tested using both Akaike information criterion (AIC) scores and effect size for each model. I selected the most parsimonious models by removing a single variable and comparing the models' AIC score, until removing a variable did not improve the score. Only the best-fit models are presented in the results. Residuals were examined for all models to check normality and homoscedasticity.

2. *Dive Interval Analysis*

Similarly, to analyze the fine-scale relationship between dive behavior and if_H within a dive I used LMM for the 20s interval data of dives greater than 3 minutes long. Intervals with mean dive depths less than 10m were removed to prevent surface if_H from influencing the analyses at the start and end of each dive. I tested each phase (descent, bottom, ascent) individually. Seal ID was a random effect. All models contained a correlation structure, corAR1. Interval if_H was the dependent variable. Maximum interval depth, mean interval ODBA, and the interaction between depth and ODBA were fixed effects. I selected the most parsimonious models by removing a single variable and comparing the models' AIC scores. Only the best-fit models are presented in the results. Residuals were examined for all models to check normality and homoscedasticity.

RESULTS

General Dive Summary

I analyzed 924 dives from six seals (Table 1). Mean dive duration was 17.1 ± 6.0 (mean ± SD) minutes and mean dive depth was 159.5 ± 124.5 meters. Fryxell had the longest dive duration at 37 minutes and 6 seconds, and Baikal had the deepest dive at 692.5 meters. Surface intervals were consistent across seals (Table 1). Mean post-dive surface interval was 2 minutes ± 53 seconds.

ODBA differed among the three dive phases (ANOVA, F(2,2769) = 429.8, $P < 0.001$, Fig. 4); ODBA was lowest during descent (0.6 ± 0.8 m/s^2) and highest during ascent (1.2 ± 1.0 m/s^2; Tukey HSD post-hoc comparison, $P < 0.001$). Similarly, stroke rate varied between dive phase (ANOVA, F(2,2726) = 195.2, $P < 0.001$). Stroke rate was highest during ascent phase (50 ± 22 strokes/min; Tukey HSD post-hoc comparison, $P < 0.001$), but there was no significant difference between descent and bottom stroke rate. Mean dive stroke rate was 47 ± 20 strokes per minute, and mean dive ODBA was 0.9 ± 0.9 m/s^2 (Table 1).

Mean dive f_H was 41.7 ± 7.4 bpm (Table 2). Mean f_H was variable among individuals, but consistent between the three dive phases (Table 2, Fig. 4). The mean pre- and post-dive f_H's were 108 ± 12.2 and 102.7 ± 8.1 bpm, respectively. Heart rate (f_H) fell drastically at the onset of a dive and increased dramatically at the end of a dive (Fig. 4). The lowest instantaneous f_H recorded was 4.1 bpm.

Dive Analysis

1. Dive behavior and dive f_H

Max dive depth and mean dive ODBA influenced mean dive f_H (Table 3). Deeper

	Congaree	Everglades	Glacier	Baikal	Fryxell	Huron	Mean
Table 1. Summarized Dive Behavior Data							
Seal ID	Congaree	Everglades	Glacier	Baikal	Fryxell	Huron	Mean
Sex	Female	Male	Female	Female	Female	Female	
Age (years)	1	Juvenile (1-2)	1	1	1	1	
Mass (kg)	232	256	222	253	241	239	
Mean ODBA (m/s^2)							
Dive ODBA	1.1 ± 0.9	0.7 ± 0.9	1.1 ± 1.0	1.1 ± 0.8	0.9 ± 0.9	0.9 ± 0.9	0.9 ± 0.9
Descent ODBA	0.9 ± 0.8	0.5 ± 0.7	0.5 ± 0.6	1.0 ± 0.7	0.7 ± 0.8	0.8 ± 1.0	0.6 ± 0.8[a]
Bottom ODBA	1.0 ± 0.8	0.7 ± 0.9	1.0 ± 1.0	1.1 ± 0.8	0.8 ± 0.8	0.9 ± 0.9	0.8 ± 0.9[b]
Ascent ODBA	1.6 ± 1.0	1.0 ± 0.9	1.9 ± 1.1	1.3 ± 0.9	1.2 ± 1.0	1.3 ± 1.0	1.2 ± 1.0[c]
Mean Stroke Rate (strokes/min)							
Dive Stroke Rate	50 ± 18	44 ± 21	55 ± 21	53 ± 21	45 ± 20	45 ± 21	47 ± 20
Descent Stroke Rate	49 ± 20	45 ± 22	52 ± 30	49 ± 24	44 ± 21	43 ± 23	45 ± 22[a]
Bottom Stroke Rate	48 ± 19	40 ± 22	51 ± 23	52 ± 21	43 ± 21	46 ± 21	45 ± 22[a]
Ascent Stroke Rate	54 ± 13	48 ± 17	60 ± 16	57 ± 19	48 ± 18	48 ± 18	50 ± 18[b]
Dive Depth (m)							
Mean Dive Depth	91.5 ± 111	177 ± 129.5	125.5 ± 82	54.5 ± 24	215 ± 120.5	69 ± 65.5	159.5 ± 124.5
Max Dive Depth	527.5	569	390.5	692.5	542.5	390	
Dive Durations (min)							
Mean Dive Duration	10.9 ± 5.0	18.2 ± 4.6	12.8 ± 3.3	9.39 ± 3.0	20.7 ± 5.6	13.1 ± 5.1	17.1 ± 6.0
Max Dive Duration	20.4	29.3	18.3	14.9	37.1	24.3	
Surface Intervals (min)							
Mean Post-Dive Surface Interval	1.6 ± 1.7	2.5 ± 0.9	1.8 ± 0.4	1.6 ± 1.3	1.9 ± 0.3	1.4 ± 0.5	2.0 ± 0.9
Dive Totals							**Sum**
Total Dives	107	290	116	32	212	167	924

Means are reported ± s.d. Overall dynamic body acceleration, ODBA. Superscripts "a", "b", and "c" represent statistical significance (ANOVA, $\alpha = 0.05$) between means in respective categories.
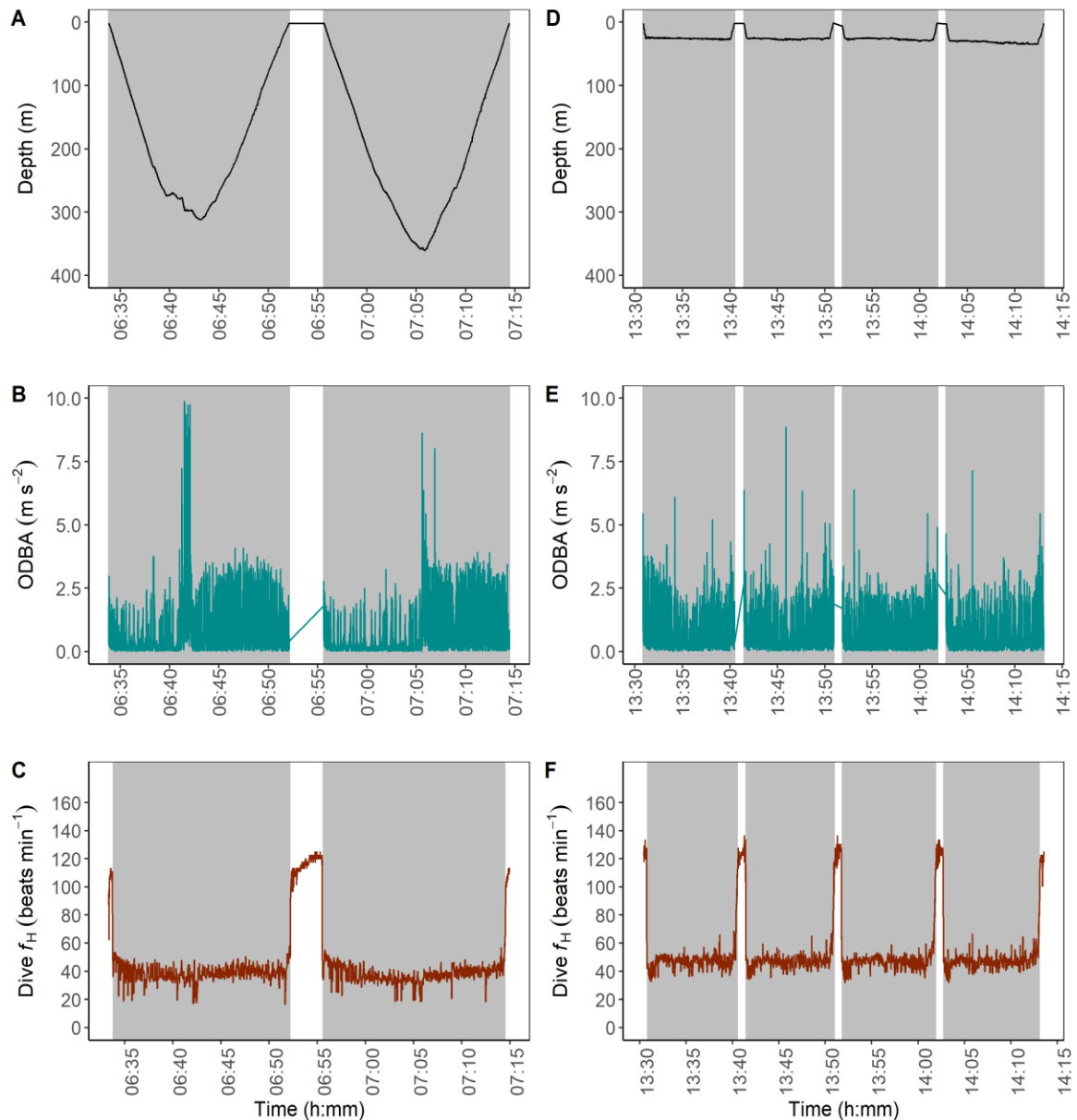
Fig. 4. Dive depth, activity (ODBA), and heart rate (f_H) profiles of a northern elephant seal. Example of two ~20 min dives (A,B,C) and four ~10 min dives (D,E,F) of a juvenile northern elephant (Everglades). Dives are highlighted in gray. The depth profile of the two long, deep dives almost reaching 400m (A) and four short dives shallower than 100m (D). Activity profiles (ODBA) of two long, deep dives show that activity increases greatly at the end of the dive when seals are fighting against buoyancy (B). Activity profiles (ODBA) of four short, shallow dives show activity stays consistent during shallow dives (E). Instantaneous f_H (if_H) profile of long, deep dives (C) and short, shallow dives (F). In both profiles (C,F) if_H decreases dramatically at the start of a dive and increases dramatically at the end of a dive.

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Table 2. Summarized Dive Heart Rate Data							
Seal ID	**Congaree**	**Everglades**	**Glacier**	**Baikal**	**Fryxell**	**Huron**	**Mean**
Mean Heart Rate (total beats/duration)							
Dive f_H	39.4 ± 2.1	41.3 ± 5.5	46.7 ± 7.0	47.0 ± 3.2	34.7 ± 6.9	48.2 ± 5.0	41.7 ± 7.4
Descent f_H	39.3 ± 5.1	42.0 ± 5.4	46.1 ± 7.1	47.3 ± 7.1	37.4 ± 8.1	44.4 ± 8.6	41.8 ± 7.6
Bottom f_H	38.4 ± 2.7	40.9 ± 5.4	46.3 ± 7.5	46.0 ± 3.4	34.9 ± 7.1	46.8 ± 6.3	41.1 ± 7.4
Ascent f_H	40.0 ± 2.9	41.4 ± 5.3	47.3 ± 7.7	47.1 ± 3.5	34.9 ± 6.9	47.9 ± 5.4	41.8 ± 7.4
Pre-Dive f_H	98.6 ± 14.1	109.1 ± 13.3	99.0 ± 9.2	112.0 ± 13.8	111.8 ± 8.6	109.4 ± 9.9	108.0 ± 12.2
Post-Dive f_H	101.6 ± 5.8	101.2 ± 8.9	104.6 ± 4.9	109.4 ± 7.5	100.0 ± 7.2	108.2 ± 6.3	102.7 ± 8.1
Instantaneous Heart Rate (beats/min)							
Mean Dive if_H	40.1 ± 8.5	42.0 ± 8.4	47.0 ± 8.7	48.3 ± 8.8	37.3 ± 10.9	48.9 ± 7.9	42.5 ± 10.0
Minimum if_H	4.9	4.7	4.7	14.6	4.1	4.5	

Means are reported ± s.d. Heart rate, f_H; Instantaneous heart rate, if_H. 924 dives from six seals were summarized.

dives (longer duration) resulted in lower mean dive f_H (Table 3, Fig. 5A; coefficient and error = -0.03 ± 0.0, $t = -21.36$, $P < 0.001$). When max dive depth decreased from 100m or less to 400m or more, mean dive f_H decreased from 46.4 bpm to 31.5 bpm, a decrease of 32% (Fig. 5A). More active dives resulted in a higher mean dive f_H (Table 3, Fig. 5B; coefficient and error = 3.01 ± 0.88, $t = 3.44$, $P = 0.001$). Although there is no significant interaction between ODBA and depth, dive f_H increased with increasing ODBA when dive depth was below 100m and greater than 400m (Fig. 5B); these values heavily influenced the relationship between ODBA and dive f_H. However, increased ODBA does not noticeably change dive f_H at dive depths of 100-400m (Fig. 5B). It is likely that the relationship between mean dive ODBA and dive f_H is not biologically important, as a 1 m/s^2 increase in ODBA only resulted in an increase in mean dive f_H of 3.4 bpm and ODBA alone accounted for less than 5% of the variation in mean dive f_H (Table 3).

Table 3. Linear Mixed-Effects Models Examining the Relationship of Dive Behavior to Dive Heart Rate (f_H) and Post-Dive Surface Interval

	Coefficient	Intercept	Max Dive Depth (m)	Mean Dive ODBA (m/s²)	Dive Duration (s)	Mean ODBA (m/s²) * Dive Duration (s)
Post-Dive Surface Interval (s)	Estimate	44.67		8.83	0.04	0.02
	St. Error	10.53		8.39	0.01	0.01
	t	4.24		1.05	2.72	2.35
	P-Value	**<0.001**		0.293	**0.007**	**0.019**
Mean Post-Dive f_H (beats/duration)	Estimate	99.45		4.71		
	St. Error	1.72		1.51		
	t	57.71		3.13		
	P-Value	**<0.001**		**0.002**		
Mean Pre-Dive f_H (beats/duration)	Estimate	111.48		-10.67	-0.01	0.02
	St. Error	6.78		5.21	0.00	0.00
	t	16.44		-2.05	-1.97	3.64
	P-Value	**<0.001**		**0.041**	**0.049**	**<0.001**
Bottom-Phase Mean Dive f_H (beats/duration)	Estimate	39.81	-0.04			
	St. Error	1.70	0.00			
	t	23.45	-18.10			
	P-Value	**<0.001**	**<0.001**			
Mean Dive f_H (beats/duration)	Estimate	44.24	-0.03	3.01		
	St. Error	1.70	0.00	0.88		
	t	25.99	-21.36	3.44		
	P-Value	**<0.001**	**<0.001**	**0.001**		

Random Effects

	ICC	Observations	Marginal R² / Conditional R²
Post-Dive Surface Interval (s)	0.00	917	0.253 / 0.253
Mean Post-Dive f_H	0.18	917	0.036 / 0.212
Mean Pre-Dive f_H	0.29	911	0.045 / 0.319
Bottom-Phase Mean Dive f_H	0.38	924	0.393 / 0.625
Mean Dive f_H	0.51	924	0.472 / 0.742

Seal ID was included as a random effect in each linear mixed-effects model (LMM). A correlation structure (corAR1) was included in each LMM model to account for autocorrelation in time-series data. Significant p-values are bolded. Intraclass correlation coefficient (ICC), is provided to show how similar dives performed by one seal are compared to dives performed by other seals; this explains how much variation is due to an individual. Observations represent the number of dives used in each model. Marginal R^2 and Conditional R^2 represent the goodness of fit for each model; where Marginal R^2 is variance explained by fixed effects and Conditional R^2 is variance explained by fixed and random effects.

Heart rate, f_H; Overall dynamic body acceleration, ODBA.
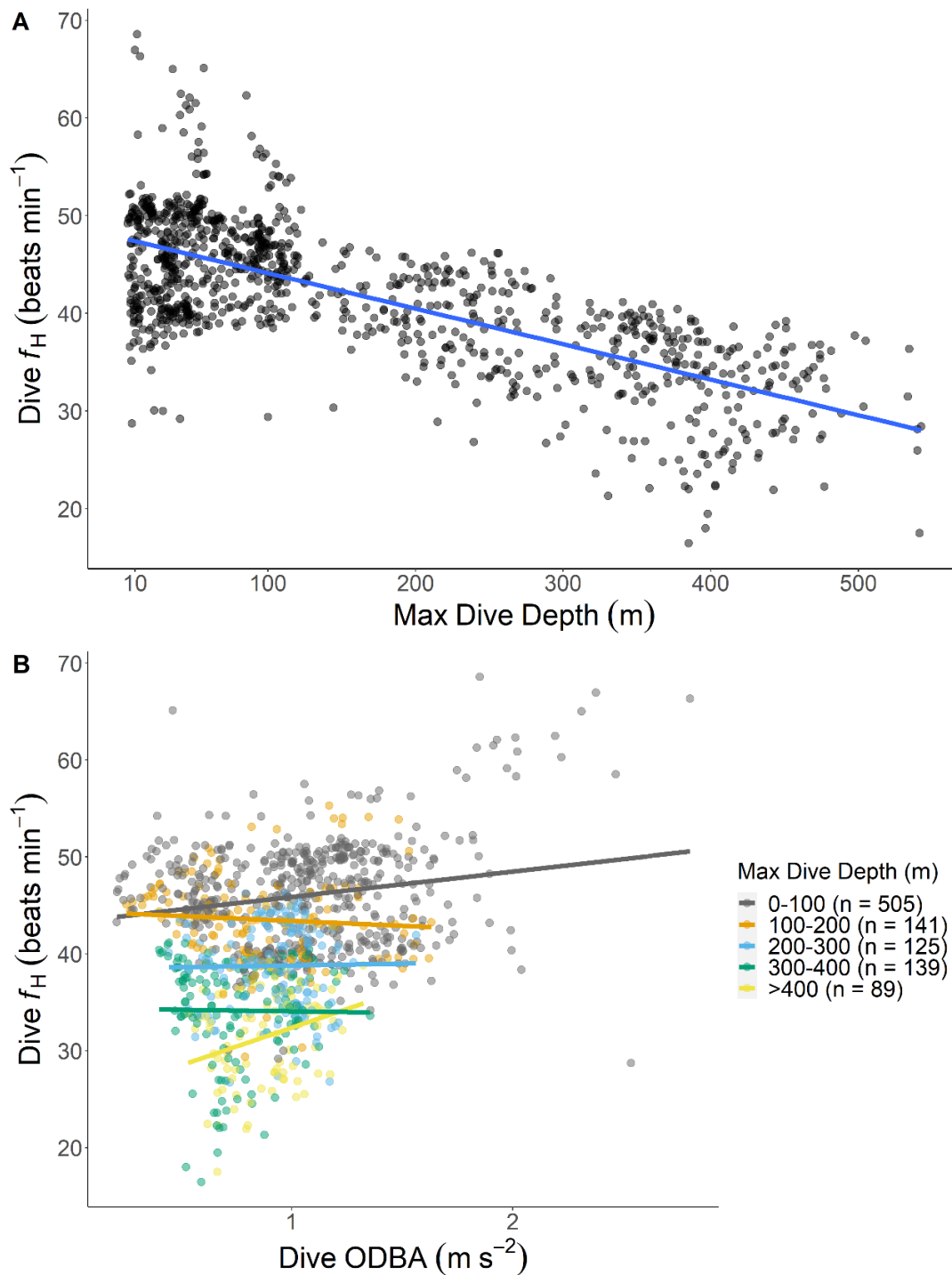
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Fig. 5. Relationship between dive depth and activity (ODBA) to dive heart rate (f_H). A) Dive heart rate is lower in deeper dives (Table 3: f_H=44.24+3.01(ODBA)-0.03(Depth)+(Seal ID and ODBA correction), R^2=0.74). **B)** The relationship between ODBA and dive f_H was significant but minor.

Whereas max dive depth accounted for 43% of the variation in mean dive f_H and is a stronger influencer of mean dive f_H (Table 3).

2. Bottom phase dive behavior to dive f_H

Only max dive depth influenced bottom phase dive f_H. Heart rate was lower in deeper dives (Table 3, Fig. 6; coefficient and error = -0.04 ± 0.0, t = -18.10, P < 0.001). Max dive depth accounted for 39% of the variation in bottom phase mean dive f_H.

3. Dive behavior to pre- and post- dive f_H

Dive duration and mean dive ODBA weakly influenced pre-dive f_H. Pre-dive f_H was lower before longer dives (Table 3, Fig. 7A; coefficient and error = -0.01 ± 0.0, t = -1.97, P = 0.049). The relationship between mean dive ODBA and pre-dive f_H was influenced by dive duration (Table 3, Fig. 7A; coefficient and error = -10.67 ± 5.21, t = -2.05, P = 0.041, interaction P < 0.001). As ODBA increased, pre-dive f_H decreased for dive durations of 5-15 min and greater than 25 min. At intermediate durations of 15-25 min, increased ODBA resulted in increased pre-dive f_H. Though the results of this LMM were significant, the relationships between dive duration, ODBA, and pre-dive f_H are likely not biologically important, as dive duration and ODBA only accounted for 4.5% of the variation in pre-dive f_H and had small effect sizes.

There was a weak positive relationship between dive activity and post-dive f_H (Table 3, Fig. 7B; coefficient and error = 4.7 ± 1.51, t = 3.13, P = 0.002). When ODBA doubled from 1 to 2 m/s^2, post-dive f_H only increased 13 bpm (12% increase). Furthermore, ODBA only accounted for 3.6% of the variation in post-dive f_H, therefore, this relationship is likely not biologically important.
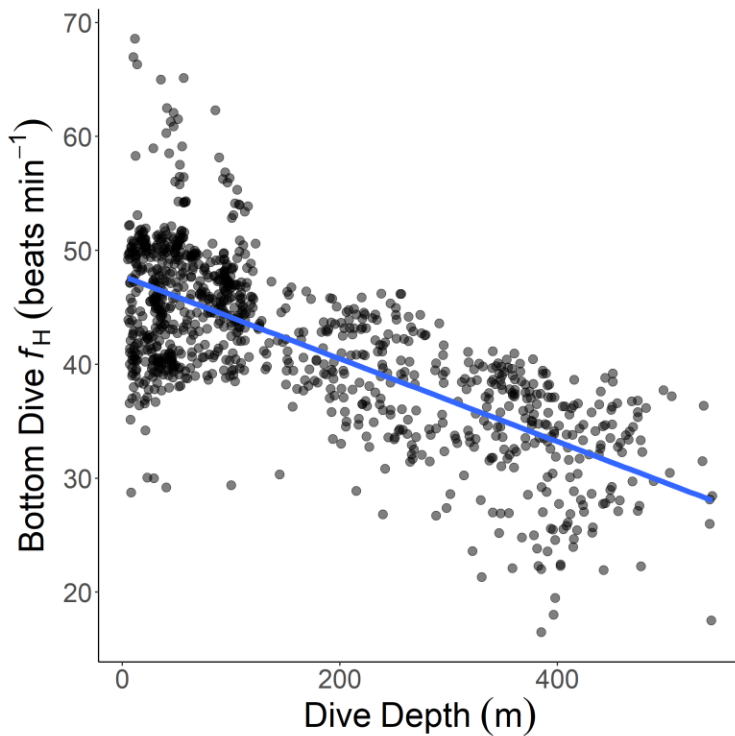
Fig. 6. Relationship of bottom dive heart rate (f_H) to dive depth. Bottom dive f_H decreases with increased dive depth (Table 3: f_H=39.81-0.04(Max Depth)+(Seal ID and ODBA correction), R^2=0.63). There was no relationship between mean bottom-phase f_H and mean bottom-phase ODBA.

4. *Dive behavior to post-dive surface interval duration*

Dive duration influenced the duration of the post-dive surface interval. Longer dives resulted in greater post-dive surface intervals (Table 3, Fig. 8; coefficient and error = 0.04 ± 0.01, t = 2.72, P = 0.007). The relationship between mean dive ODBA and post-dive surface interval was not significant, but the interaction between dive duration and mean dive ODBA was significant (Table 3, Fig 8; coefficient and error = 8.83 ± 8.39, t = 1.05, P = 0.292, interaction P = 0.019). A higher mean dive ODBA resulted in a longer post-dive surface interval when dive duration was less than 15 minutes, but active dives with a dive duration

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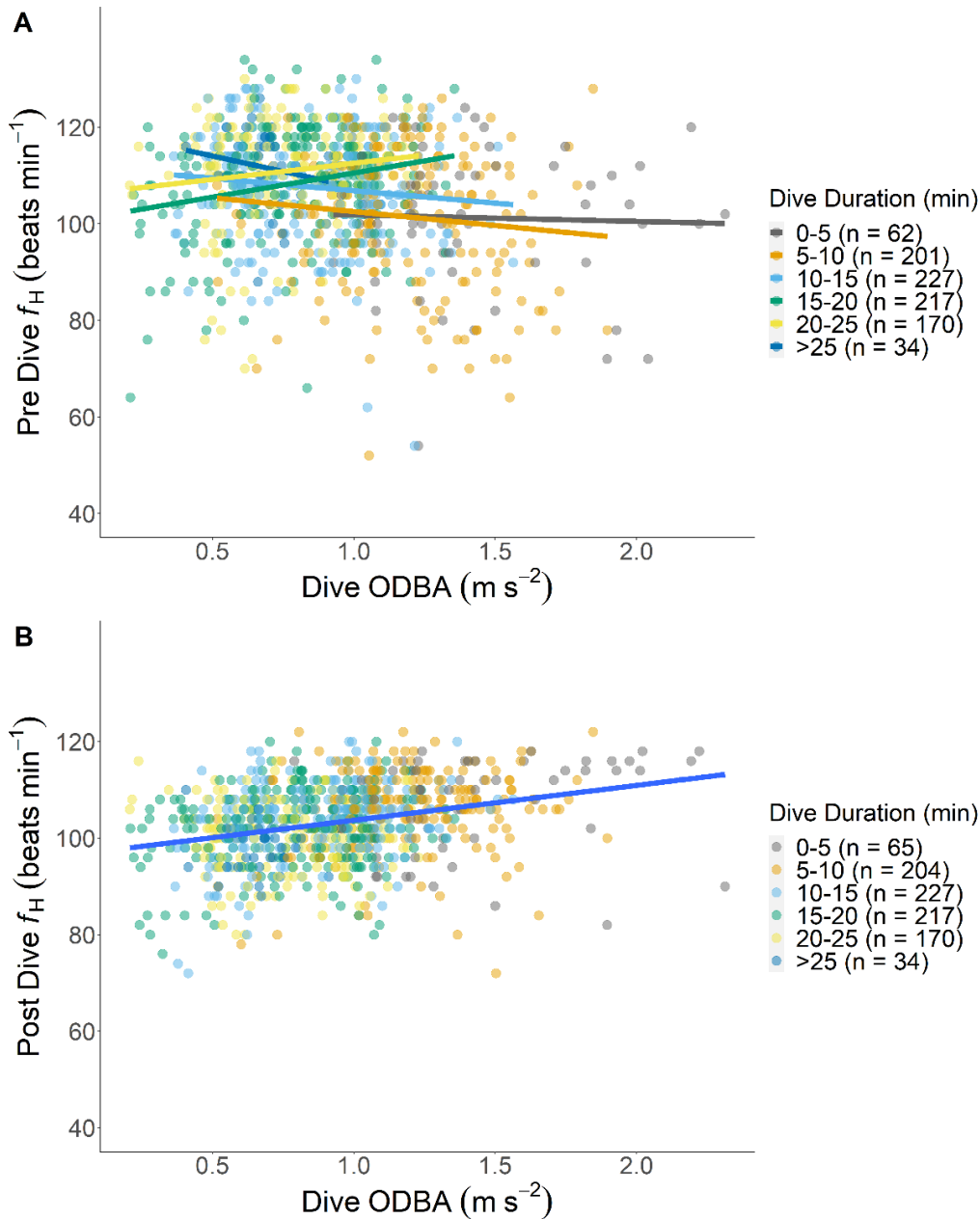
Fig. 7. Pre- and post-dive heart rate (f_H) in relation to dive behavior. A) The relationship between pre-dive f_H and ODBA depends on dive duration (Table 3: f_H=111.48-10.67(ODBA)-0.01(Dive Duration)+0.02(ODBA*Dive Duration)+(Seal ID and ODBA correction), R^2=0.32). Pre-dive f_H decreases before longer dives. More active dives have a lower pre-dive f_H when dives are less than 15 minutes or greater than 25 minutes. More active dives between 15-25 minutes in duration have a higher pre-dive f_H. **B)** There is a weak positive relationship between post-dive f_H and mean dive ODBA (Table 3: f_H=99.45+4.71(ODBA)+(Seal ID and ODBA correction), R^2=0.21). There was no relationship between post-dive f_H and dive duration nor depth.

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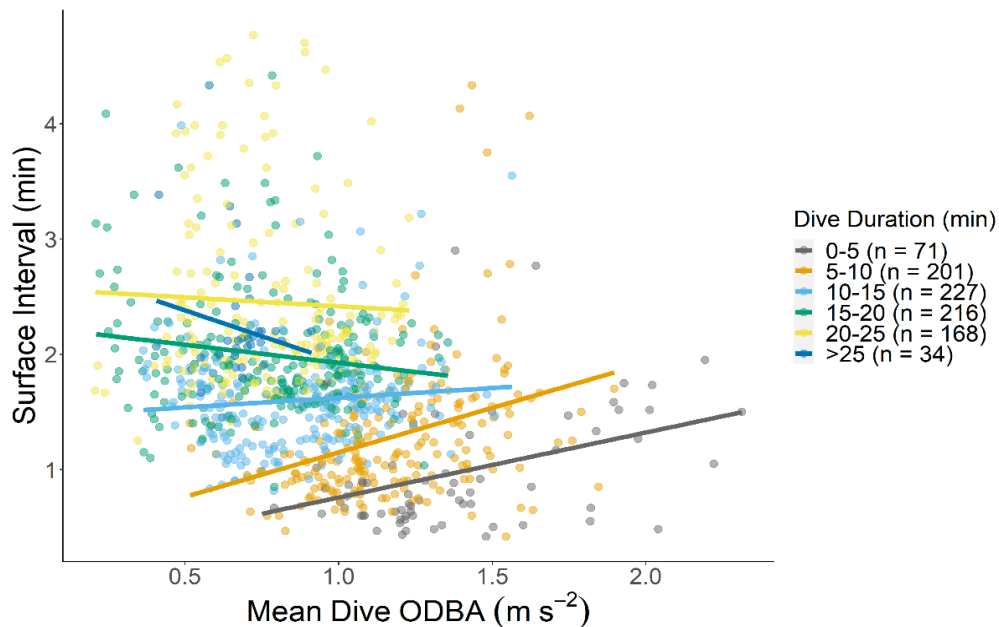
Fig. 8. Post-dive surface interval is influenced by dive duration and weakly influenced by mean dive ODBA. Post-dive surface interval is positively related to dive duration. There is a weak positive relationship between mean dive ODBA and post-dive surface interval when dives are shorter than 15 minutes in duration. Dives greater than 15 minutes in duration have a weak negative relationship between mean dive ODBA and post-dive surface interval (Table 3: surface interval = 44.67+8.83(ODBA)+0.04(Dive Duration)+0.02(ODBA*Dive Duration)+(Seal ID and Dive Duration correction), $R^2=0.25$).

longer than 15 minutes resulted in a decrease in post-dive surface interval. When dives were less than 15 minutes, post-dive surface interval had a mean duration of 1 minute 28 seconds, whereas when dives were 15 minutes or greater the post-dive surface interval duration increased by 51% to a duration of 2 minutes 13 seconds. When mean dive ODBA increased by 1.0 m/s^2 (from 0.5 to 1.5 m/s^2) there was only a 12% decrease in post-dive surface interval duration from 2 minutes 12 seconds to 1 minute 58 seconds. Together dive duration and ODBA accounted for 25% of the variation in the post-dive surface interval (Table 3). Alone dive duration accounted for 15% of the variation in the post-dive surface interval, and mean dive ODBA accounted for only 1.7% in the variation.

Dive Interval Analysis

1. Dive if_H and dive behavior within a dive

Dive-interval data were analyzed separately by dive phase. During the descent phase, if_H was influenced by both depth and ODBA. In general, as the seal descended, if_H decreased (Table 4, Fig. 9A; coefficient and error = -0.02 ± 0, t = -12.31, P < 0.001). More active descents resulted in higher descent if_H at depths less than 100m and greater than 300m, but at intermediate depths of 100-300m an increase in interval activity resulted in a lower descent if_H (Table 4, Fig. 9A; coefficient and error = 7.54 ± 1.66, t = 4.54, P < 0.001, interaction P-value < 0.001). Depth and ODBA accounted for 26% of the variation of descent if_H.

When at the bottom phase of their dives, if_H was influenced by depth and ODBA. During the bottom phase, there was a negative relationship between depth and if_H (Table 4, Fig. 9B; coefficient and error = -0.05 ± 0, t = -58.36, P < 0.001). Yet, as ODBA increased, if_H increased in the bottom phase (Table 4, Fig. 9B; coefficient and error = 1.99 ± 0.36, t = 5.48, P < 0.001). Bottom if_H increased the most with activity for dives deeper than 500m (Figure 9B). Together depth and ODBA accounted for 59% of the variation in if_H in the bottom phase of the dive.

During the ascent phase, depth and ODBA influenced if_H. As seals ascended to the surface, their if_H increased (Table 4, Fig. 9C; coefficient and error = -0.06 ± 0, t = -67.54, P < 0.001). When ascending, ODBA had a positive relationship with if_H (Table 4, Fig. 9C; coefficient and error = 1.42 ± 0.66, t = 2.15, P = 0.032). Depth and ODBA accounted for 39% of the variation in if_H in the ascent phase of the dive.

Table 4. Linear Mixed-Effects Models Examining the Relationship of Dive Interval Behavior to Dive Interval Instantaneous Heart Rate (if_H)

Coefficient	Ascent Dive Interval if_H (beats/min)				Bottom Dive Interval if_H (beats/min)				Descent Dive Interval if_H (beats/min)			
	P-Value	t	St. Error	Estimate	P-Value	t	St. Error	Estimate	P-Value	t	St. Error	Estimate
Intercept	**<0.001**	23.95	2.03	48.59 (44.62 – 52.57)	**<0.001**	242.10	0.20	47.46 (47.07 – 47.84)	**<0.001**	17.52	2.29	40.05
Mean Interval ODBA (m/s²)	**0.032**	2.15	0.66	1.42 (0.12 – 2.71)	**<0.001**	5.48	0.36	1.99 (1.28 – 2.70)	**<0.001**	4.54	1.66	7.54
Max Interval Depth (m)	**<0.001**	-67.54	0.00	-0.06 (-0.06 – -0.06)	**<0.001**	-58.36	0.00	-0.05 (-0.05 – -0.05)	**<0.001**	-12.31	0.00	-0.02
Mean Interval ODBA (m/s²) * Max Interval Depth (m)									**<0.001**	-19.60	0.00	-0.03
Random Effects												
ICC	0.32				0.02				0.33			
Observations / N	7376 / 827				21453 / 902				7556 / 807			
Marginal R² / Conditional R²	0.391 / 0.585				0.592 / 0.600				0.262 / 0.507			

Seal ID was included as a random effect in each linear mixed-effects model (LMM). A correlation structure (corAR1) was included in each LMM model to account for autocorrelation in time-series data. Significant p-values are bolded. Intraclass correlation coefficient (ICC), is provided to show how similar dives performed by one seal are compared to dives performed by other seals; this explains how much variation is due to an individual. Observations represent the number of 20 second intervals in N (number of dives) used in each model. Marginal R^2 and Conditional R^2 represent the goodness of fit for each model; where Marginal R^2 is variance explained by fixed effects and Conditional R^2 is variance explained by fixed and random effects. Instantaneous heart rate, if_H; Overall dynamic body acceleration, ODBA.
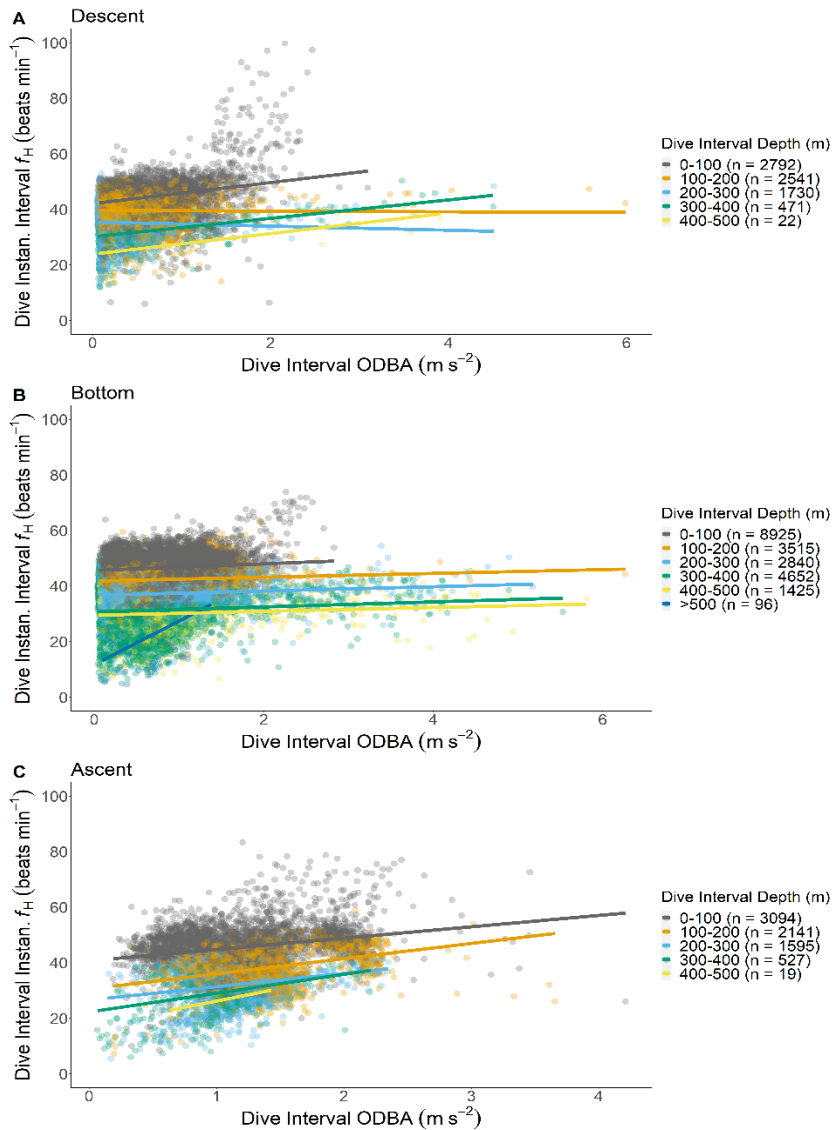
Fig. 9. Dive-interval instantaneous heart rate (if_H) is influenced by dive-interval ODBA and depth. A) There is a positive relationship between mean descent dive-interval if_H and mean descent dive-interval ODBA at interval depths <100m or >300m, but a negative relationship occurs at depths between 100-300m. There is a negative relationship between descent dive-interval if_H and max descent dive-interval depth (Table 4: if_H=40.05+7.54(ODBA)-0.02(Max Depth)-0.03(ODBA*Max Depth)+(Seal ID and ODBA correction), R^2=0.51). **B)** There is a positive relationship between mean bottom dive-interval if_H and mean bottom dive-interval ODBA and a negative relationship between bottom dive-interval if_H and max bottom dive-interval depth (Table 4: if_H=47.46+1.99(ODBA)-0.05(Max Depth) +(Seal ID and OBDA correction), R^2=0.60). **C)** There is a positive relationship between mean ascent dive-interval if_H and mean ascent dive-interval ODBA and a negative relationship between ascent dive-interval if_H and max ascent dive-interval depth (Table 4: if_H=48.59+1.42(ODBA)-0.06(Max Depth) +(Seal ID and OBDA correction), R^2=0.59).

DISCUSSION

Research during the last several decades has debunked any notion that the dive response is a strict reflex. The dive response is dynamic and physiologically complex, influenced by dive duration, depth, anticipation, and exercise (Kooyman, 1967; Williams et al., 1991; Andrews et al., 1997; Noren et al., 2004; Froget et al., 2004; Davis and Williams, 2012; Noren et al., 2012; McDonald and Ponganis, 2014; Elmegaard et al., 2016; McDonald et al., 2018). My results suggest that dive duration and depth are the primary predictors of dive f_H when analyzing dives at the whole-dive scale. When I analyzed the dives on a fine scale, however, I learned that northern elephant seals also are adjusting their f_H in response to their activity. Whereas the relationships between dive behavior and dive f_H have been investigated in a few species, it is clear the influence of dive duration, depth, and activity varies among species, indicating that these relationships are species-specific or determined by dive behavior (e.g., shallow, moderate, deep divers). Additionally, when dives are evaluated at fine scale, the relationship between behavior and physiology proves to be more dynamic than previously thought (McDonald et al., 2020).

Dive Behavior Influences f_H

I tested the hypothesis that dive f_H will be lower in longer, deeper dives, but increase with increased dive activity. I compared the relationship of dive behavior to dive f_H of juvenile northern elephant seals. Dive f_H in short, shallow dives (< 100m) was 46.5 beats/duration, while in deeper, longer dives (>400m) dive f_H was 31.5 beats/duration. This supports the hypothesis that dive f_H is lower on longer, deeper dives (Fig. 5-A). These results indicate that the dive response is stronger in deeper dives. This is consistent with findings in other marine

mammals, such as California sea lions (*Zalophus californianus*), blue whales (*Balaenoptera musculus*), and grey seals (*Halichoerus grypus*; Thompson and Fedak, 1993; McDonald and Ponganis, 2014; Goldbogen et al., 2019; McDonald et al., 2020). The f_H of blue whales was typically between 4-8 bpm during the bottom-phase of the dive, which was about ⅓ to ½ the predicted resting f_H (Goldbogen et al., 2019). Reducing f_H with increased dive duration and depth conserves oxygen and reduces the use of anaerobic metabolism, which is important for species that spend less time recovering at surface (i.e., northern elephant seals, blue whales).

To further support the hypothesis that dive f_H is lower on longer, deeper dives I investigated the relationship between bottom-phase f_H, depth, and activity. In doing so, I aimed to eliminate the influences of the rapid decrease during descent and increase during ascent of f_H. I found that activity did not have a relationship with bottom-phase f_H. However, dive f_H decreased 4 bpm for every 100m increase in dive depth, meaning a dive to 500m would have a dive f_H 16 bpm lower than a dive f_H at 100m. These results further suggest that dive depth and duration have a greater influence on dive response than activity at depth.

The hypothesis that more active dives would result in a higher dive f_H was weakly supported, the relationship was minor as activity explained less than 5% of the variation in dive f_H. Furthermore, an increase of 1 m/s^2 in ODBA (range of ODBA observed was 0.02–2.3 m/s^2) only resulted in a change of 3 bpm of dive f_H (Table 3, Fig. 5). In similar studies, however, an increase in activity increased the mean dive f_H in captive harbor porpoises (*Phocoena phocoena*), and wild bottlenose dolphins (*Tursiops truncatus*), blue whales, and Weddell seals (Noren et al., 2012; McDonald et al., 2018; Goldbogen et al., 2019; Williams et al., 2015). Weddell seals, in particular, when at a dive depth of 200m showed an increase

of about 10 bpm with an increase of physical exertion (measured by stroke frequency) from 0 strokes/minute to 40-45 strokes/minute (Williams et al., 2015). Although blue whales showed a relationship between dive f_H and dive duration, unlike the northern elephant seal, blue whales did show a strong relationship between f_H and activity during lunge feeds. When blue whales drastically increase their stroke rate to ascend for lunge feeding events, their dive f_H increases 2.5 folds above their diving f_H minima (on average 4-8 bpm; Goldbogen et al., 2019). Northern elephant seals do not participate in foraging activities as taxing as lunge feeding is to blue whales, which could explain why we do not see as strong a relationship between activity and f_H in elephant seals. In addition, Weddell seals do not have as long of dive bouts as northern elephant seals; therefore, it is possible Weddell seals' ability to reach the surface to recover sooner and remain at the surface longer gives them the flexibility to have a more plastic relationship between their dive response and their dive activity. The differences observed among species suggest that there are species-specific approaches to regulating dive response, likely based on a combination of lifestyle and dive behavior.

The degree to which the dive response changes throughout a dive or between dives seems to vary among species. Weddell seals (*Leptonychotes weddellii*) have a consistent dive response in regard to depth and duration of their dive, unless diving beyond their ADL; yet they do modulate their dive response based on their activity (stroke rate) during the dive (Hill et al., 1987; Williams et al., 2015). Similarly, wild harbor porpoises did not show a strong correlation between dive duration and dive f_H, and instead had a more consistent, moderate bradycardia. However, these wild porpoises did not show an exercise modulated dive (McDonald et al., 2021). The two lifestyles of these species vary drastically. Weddell seals

are deep-diving pinnipeds; they spend about 5 minutes at the surface between dives and return to the ice surface to rest after about 12-hour bouts of dives (Castellini et al., 1992). In shallow Danish waters, harbor porpoises perform short, continuous dives. Although they experience a dive response, it is not as pronounced as a deep-diving species. These cetaceans will spend minimal time at the surface between dives (McDonald et al., 2021). Northern elephant seals, on the other hand, dive continuously for days, with minimal time spent at the surface. On average these juvenile elephant seals dive for 17 minutes to 160 meters, spending less than 3 minutes to recover at the surface. Northern elephant seals are most vulnerable to predators at the surface; therefore, limiting their time recovering is beneficial. Their incredible diving physiology allows them to dive well within their cADL, reducing their lactic acid build-up, oxygen depletion, and in turn their surface recovery duration. Clearly there are behavioral differences among species that could lead to physiological differences in dive response.

Fine-scale Dive Behavior Influences Interval *if*$_H$

Northern elephant seals are not as active as lunge feeding whales. They spend most of their descent passively descending in stroke-and-glide or falling-leaf patterns (Davis et al., 2001; Mitani et al., 2010; Kendall-Bar et al., 2023). Their dive response is so well adapted that they typically are diving well within their cADL and limiting the use of anaerobic metabolism. I believed it important, however, to analyze their dive response on a fine scale to determine if there are small physiological changes they make in response to dive behavior. To test the hypothesis that at fine-scale (20s intervals) there will be a negative relationship between depth/duration and f_H but a positive relationship between activity and f_H, I broke

each dive down into 20s intervals to look at fine-scale relationships between dive behavior and if_H. These intervals were grouped by dive phase. For all three dive phases, interval if_H was influenced by both interval depth and activity. In all three dive phases, interval if_H was lower in deeper intervals, but increased interval activity only increased if_H in bottom- and ascent-phases. Unlike bottom- and ascent-phases where there were clear positive relationships between if_H and activity, the relationship between descent-phase if_H and activity depended on depth. Due to the small sample size and lesser variation in the level of activity in deeper depths (>300m) it was difficult to investigate the relationship between activity and heart rate in deeper intervals. At shallow depths (< 100m), seals stroke more frequently during descent to fight their positive buoyancy, which led to a positive relationship between activity and f_H. After their initial dive descent (>100m), seals become negatively buoyant and passively descend using both stroke-and-glide and falling-leaf behaviors (Davis et al., 2001; Mitani et al., 2010; Kendall-Bar et al., 2023). These two common behaviors require little stroking, in turn reducing the seals activity during this phase of the dive. During these moderate descent-interval depths (100-300m), f_H was not influenced by the minimal activity.

Unlike the variable relationships between depth and activity during descent, if_H was positively related to activity during the bottom-phase of the dive. There also was a strong, negative relationship between if_H and bottom-interval depth. These results suggest that depth/duration have a stronger influence on dive f_H, but small increases in f_H associated with increased activity may be important to increase blood flow to perfuse muscle of oxygenated blood. Overall, this perfusion of blood to muscle tissues during times of increased activity likely reduces lactic acid buildup and maximizes aerobic metabolism (Davis and Williams,

2012; Williams et al., 2015). These findings are consistent with studies that examined exercise modulation in other species (Davis and Williams, 2012; Goldbogen et al., 2019; McDonald et al., 2020). For example, California sea lions showed a relationship between dive f_H and activity (MSA) at fine scale (10s intervals), and similar to my findings with northern elephant seals, this relationship was based on dive duration (McDonald et al., 2020). Small changes in their dive response may be what allows northern elephant seals to reduce their lactic acid build-up; they maintain a strong dive response but make minor adjustments in fine-scale moments of high activity. Since these seals are diving well within their cADL and making fine-scale adjustments to do so, they are a species that will likely have the capacity to adjust in response to climate change and anthropogenic stress. For example, if their prey moves farther or deeper to cooler waters, it appears that northern elephant seals will have enough conserved oxygen to compensate for these changes. If their diving behaviors do begin to change with changing ocean conditions, however, it would be important to study if their abilities to dive within their cADL and quickly recover at the surface are altered.

The dive response of the northern elephant seal is clearly influenced by depth/duration, but when analyzed on a finer scale it is evident that there is a degree of exercise modulation. The diving activities of juvenile northern elephant seals during this translocation study were minimal. There are five dive types commonly seen in northern elephant seals (Le Boeuf et al., 1988, 1992, & 1993), but transit dives (category A) are the primary dive type seen during these translocation studies. Category A dives are "V" shaped and described as a direct descent to a max depth followed by a sharp ascent to the surface (Le Boeuf et al., 1988).

Foraging dives (category D and E), however, are categorized as decent to depth, swimming at depth, then ascent to the surface, and are typically longer in duration (Le Boeuf et al., 1988). In more active foraging dives, or with greater variation of dive times, a relationship between dive activity and dive heart rate may be more apparent. However, at a fine scale, when you can observe a greater range of activity, there was evidence that seals modulate their dive response when exercising. Their dive response is plastic, but further research on more active, foraging dives should be studied to truly understand to what extent this species regulates its dive response.

Dive Behavior Does Not Influence Pre-dive f_H

I compared the pre-dive f_H with dive behavior to test the hypothesis that pre-dive f_H would be high before longer, deep dives. Past studies have suggested that marine mammals have a degree of cognitive control over their dives and may make physiological adjustments to prepare for longer dives, (Froget et al., 2004; McDonald and Ponganis, 2014; Elmegaard et al., 2016). For example, pre-dive f_H was higher before longer dives compared with shorter dives in California sea lions, likely to increase O_2 on-loading before the dive (McDonald and Ponganis, 2014). In contrast to my prediction, northern elephant seals do not show the same anticipatory behavior. While there was a negative relationship between pre-dive f_H with both dive duration and activity, which means longer, deeper, more active dives would have a lower pre-dive f_H, the relationship was minor. The effect size was small, with a decrease of 1 bpm for every 10 min increase of dive duration and an 11 bpm decrease for 1 m/s^2 increase in activity. Additionally, dive duration and activity only explained 5% of the variation of pre-dive f_H. Northern elephant seals are not anticipating their dive durations. It is possible that the

dive durations of these transit dives are within a range where they do not have to alter their dive response drastically to manage oxygen stores. Furthermore, the fine-scale adjustments they do make during moments of high activity may reduce their need to prepare beforehand. It would be interesting to measure fine-scale dive behavior on foraging dives, when they spend more time swimming at the bottom of their dive, to determine if their anticipatory behavior changes with dive type.

Although northern elephant seals did not anticipate longer dives with a higher pre-dive f_H, they had anticipatory tachycardia before surfacing at the end of their dives. This anticipatory tachycardia in the last seconds of a dive is commonly seen in marine animals such as bottlenose dolphins, northern elephant seals, harbor porpoises, blue whales, and king penguins (*Aptenodytes patagonicus*; Andrews et al., 1997; Froget et al., 2004; Noren et al., 2004; Noren et al., 2012; Goldbogen et al., 2019; Elmegaard et al., 2019). Increased f_H just before reaching the surface allows for efficient CO_2 off-loading and O_2 on-loading as soon as an animal reaches the surface. I found that the mean if_H in the last 20 seconds was 64.0 bpm, whereas the mean ascent-phase if_H was 47.5 bpm (26% increase). My data supports Andrews et al. (1997) findings from 25 years ago, that northern elephant seals have anticipatory tachycardia to increase the efficiency of gas exchange at the surface.

Dive Behavior Does Not Influence Post-dive f_H

One of the most remarkable diving traits of northern elephant seals is their ability to make deep dives after spending minimal time resting at the surface (Andrews et al., 1997; Le Boeuf et al., 2000b; Davis et al., 2001). I investigated how post-dive f_H and post-dive surface interval related to dive behavior to test the hypothesis that post-dive f_H was higher after

longer, deep, active dives, but that there was no difference in surface recovery duration based on dive behavior. Dive duration did not influence post-dive f_H, and there was little support for activity influencing post-dive f_H. While there was a positive relationship between dive activity and post-dive f_H, a doubling of activity from 1 to 2 m/s^2 (some of the highest values I observed) only resulted in an increase in f_H of 13 bpm (12% increase). Moreover, activity and dive duration only explained 4% of the variation in the data. Therefore, my hypothesis that post-dive f_H would be higher after longer, deep dives and active dives was not supported. These juvenile seals may not have exceeded a threshold of dive duration, depth, nor activity that would require greater post-dive f_H. Furthermore, the post-dive f_H may not have been as elevated due to these seals actively regulating their dive response during their dive; their fine-scale exercise modulation may lower the necessity of a high post-dive f_H on recovery.

Dive Behavior Influences Post-dive Surface Interval Duration

Post-dive surface interval increased with increased dive duration which negates my hypothesis. Activity had no influence on the post-dive surface interval; an increase in 1 m/s^2 in activity resulted in a decrease of post-dive surface duration of only 12%. Additionally, this relationship was influenced by dive duration. The mean post-dive surface interval was 2 minutes which is consistent with previous studies (Le Boeuf, 1994; Andrews et al., 1997). Northern elephant seals rarely recovered at the surface for more than 3 minutes; only 7.5% of dives resulted in a recovery greater than 3 minutes. When seals dove for greater than 15 minutes, however, their post-dive surface interval duration increased 51%. This was an increase of 45 seconds to a post-dive surface duration of 2 minutes 13 seconds. Dive duration influences the recovery of these seals, but it does not push them to increase their recovery

duration past 3 minutes regularly. Northern elephant seals are most vulnerable to predation at the surface; therefore, it is within their best interest to recover quickly. Their strong dive response and diving behavior allow them to spend less time at the surface recovering. For instance, by passively descending into their dive they conserve oxygen for more active moments of their dive. Similarly, their anticipatory tachycardia before surfacing maximizes their gas-exchange on recovery. These seals are so well adapted to diving deep and continuously with minimal recovery, because they actively regulate their dive response and dive within their cADL.

CONCLUSION

The dive response is a dynamic reflex that is influenced by dive depth, duration, activity, and anticipation. Investigating these variables at a fine scale is important to reveal more about how marine mammals regulate their dive response to maximize their oxygen stores. In this study I examined the relationship between dive behavior and dive f_H to determine how a model species, the northern elephant seal, regulates their dive response. I found that northern elephant seals' dive response is strongly influenced by dive depth and/or duration. Longer, deeper dives resulted in a lower dive f_H. On a finer scale, activity does influence f_H, suggesting that there is a degree of exercise modulation. However, this relationship was only seen in the bottom and ascent phases of the dive. During the descent phase of the dive, seals rely on negative buoyancy to passively drift or stroke-and-glide to depth. Additionally, this relationship between f_H and activity was not as strong as the relationship between depth and/or duration and f_H. Northern elephant seals likely make minor adjustments to provide O_2 to working muscle. It is fair to assume this activity-based regulation of the dive response maximizes aerobic metabolism and limits anaerobic metabolism (Davis and Williams, 2012; Williams et al., 2015).

Northern elephant seals did not show any sign of adjusting their f_H pre- nor post-dive after longer, deeper dives. Their post-dive surface interval duration was typically less than 2 minutes and rarely exceeded 3 minutes. Seals did rest 51% longer (45 seconds longer), however, in dives greater than 15 minutes. Northern elephant seals use their incredibly adapted dive response and dive behavior to minimize their time recovering at the surface. It is likely that these seals are diving below their ADL and regulate their dive response to

minimize lactic acid build-up and maximize aerobic metabolism, thereby minimizing surface intervals. These adaptations and dive behaviors are important, as northern elephant seals are most vulnerable to predators when at the surface. By making fine-scale physiological adjustments, such as increased f_H with increased activity or anticipatory tachycardia, they limit their use of anaerobic metabolism and conserve their oxygen stores. These adjustments allow them to regularly dive below their cADL and recover quickly at the surface.

This study determined that a deep-diving model species, the northern elephant seal, has a plastic dive response. Instead of making anticipatory changes before dives, elephant seals actively adjust their dive response during their dives. These remarkable divers limit their use of anaerobic metabolism and lactic acid buildup, likely due to the active regulation of their dive response in moments of increased activity or anticipatory surfacing. This plastic dive response could make northern elephant seals more tolerable of anthropogenic stressors (e.g., sonar, boat strikes, food availability). These findings suggest that deep-diving marine mammals may be regulating their dive response in real time, have an exercise-modulated dive response to manage O_2 in their muscle tissue, and maximize efficiency such as an anticipatory tachycardia.

Future studies should focus on adult northern elephant seals and more active dives (e.g., foraging dives) to analyze the relationship between activity and dive response on a fine scale. Though juvenile northern elephant seals do not have the dive capacity of adults, their dive response and behavior are similar to adults (Le Boeuf et al., 1996). I would expect similar relationships, therefore, like the ones found in this study, and for these relationships to possibly be stronger. To fully understand the dynamic regulation of the adult dive response,

however, it would be important to measure these variables in adults. As biologging

technology continues to advance, the possibility of repeating this study on adults becomes

more possible.

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