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Detecting Feeding and Estimating the Energetic Costs of Diving in California Sea Lions (*Zalophus californianus*) Using 3-Axis Accelerometers

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DETECTING FEEDING AND ESTIMATING THE ENERGETIC COSTS OF DIVING
IN CALIFORNIA SEA LIONS (*ZALOPHUS CALIFORNIANUS*) USING 3-AXIS
ACCELEROMETERS

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

Mason Cole

December 2020

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The Designated Thesis Committee Approves the Thesis Titled

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ABSTRACT

DETECTING FEEDING AND ESTIMATING THE ENERGETIC COSTS OF DIVING IN CALIFORNIA SEA LIONS (*ZALOPHUS CALIFORNIANUS*) USING 3-AXIS ACCELEROMETERS

by Mason Cole

Knowledge of when animals feed and the energetic costs of foraging is key to understanding their foraging ecology and energetic trade-offs. Despite this importance, our ability to collect these data in marine mammals remains limited. In this thesis, I address knowledge gaps in both feeding detection and fine-scale diving energetic costs in a model species, the California sea lion (*Zalophus californianus*). I first developed and tested an analysis method to accurately detect prey capture using 3-axis accelerometers mounted on the head and back of two trained sea lions. An acceleration signal pattern isolated from a ‘training’ subset of synced video and acceleration data was used to build a feeding detector. In blind trials on the remaining data, this detector accurately parsed true feeding from other motions (91-100% true positive rate, 0-4.8% false positive rate), improving upon similar published methods. In a second study, I used depth and acceleration data to estimate the changing body density of 8 wild sea lions throughout dives, and used those data to calculate each sea lion’s energetic expenditure during descent and ascent at fine temporal scales. Energy expenditure patterns closely followed the influence of buoyancy changes with depth. Importantly, sea lions used more energy per second but less energy per meter as dive depth increased, revealing high costs of deep diving. Combined, these studies further our understanding of California sea lion foraging ecology and provide new methods to aid similar future studies.

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Next I have Jim Harvey to thank: Jim responded to my original internship inquiry way back in 2014, effectively granting me a foot in the door toward this career path. Beyond this, as a member of my thesis committee, Jim has provided consistently strong and grounded advice in ecological thought, statistics, and scientific writing style – all while directing MLML through big changes amid unforgiving and challenging world circumstances.

Ever since Jim let me in to the Vertebrate Ecology Lab (VEL) as an intern in 2014, the VEL lab group – interns, students, and faculty – has given me everything from scientific feedback and support to friendship and community. It has been an amazing growing experience with a slowly changing group of people. All of these people deserve their own thank-you, but there isn’t space here: if you’re reading this, know you’re appreciated. This sentiment also expands to the greater MLML community: thank you to all my friends, mentors, teachers, and colleagues; it’s you, the people, who make this famous community what it is.

Leading the VEL charge is my advisor, Gitte McDonald. What a great advisor! Thank you, Gitte, for taking a chance on me as one of your first grad students, for trying

as hard as everyone knows you do, for fostering a positive environment, and for leading the VEL with high but attainable expectations and respect. I've benefitted immensely from the amount of creative freedom you gave me in directing my thesis work, your wealth of knowledge, stats and writing expertise, and the basic respect you always showed me and everyone else in the lab.

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LIST OF ABBREVIATIONS

a – acceleration
 α – compression coefficient: ratio of observed $V_{Resp,depth}$ compression to Boyle’s law
 A_f – frontal surface area
AIC – Akaike information criterion
BMR – basal metabolic rate
 $C_{D,f}$ – drag coefficient referenced to the frontal surface area
COT – cost of transport ($J\ m^{-1}$ or $J\ kg^{-1}\ m^{-1}$)
CSL – California sea lion (plural: CSLs)
DBA – dynamic body acceleration
DLV – diving lung volume
DLW – doubly labeled water
 ρ_{CSL} – sea lion body density
 $\rho_{CSL,depth}$ – sea lion body density as a function of depth
 ρ_{sw} – seawater density
 ϵ – dimensionless factor converting P_i into P_o
ENSO – El Nino Southern Oscillation
 F_B – buoyancy force
 F_D – drag force
FMR – field metabolic rate
FP – false positive
 g – gravity force ($9.81\ m\ s^{-2}$)
GAMM – generalized additive mixed model
Hz – Hertz; a measure of frequency
 M_b – body mass
MSA – minimum specific acceleration
 N_m – muscular efficiency (efficiency of converting chemical energy into muscular work)
 N_p – propeller efficiency
 P_i – metabolic energy needed to produce observed P_o
 P_o – power output required to produce observed swimming thrust
 P_{SMR} – power requirements of CSL standard metabolic rate
RMS – root mean square
RQ – respiratory quotient
S.E. – standard error
SMR – standard metabolic rate
TLC – total lung capacity
TP – true positive
 θ – angle of movement or body (tag) orientation relative to vertical
 U – speed
 $V_{Resp,depth}$ – Respiratory airway volume as a function of depth
 V_{Tissue} – tissue volume
VHF – very high frequency

CHAPTER 1: HEAD-MOUNTED ACCELEROMETRY ACCURATELY DETECTS PREY CAPTURE IN CALIFORNIA SEA LIONS

Introduction

Marine mammal foraging behavior has for decades been assumed from depth profiles (e.g. ‘Wiggles’) and movement patterns (e.g. area-restricted search) during dives and foraging trips (e.g. Feldkamp et al., 1989; Le Boeuf et al., 1992; Costa & Gales, 2003; Kooyman, 2004). While useful to infer behavioral state, these methods cannot resolve individual feeding attempts, and must be ground-truthed to produce reliable quantitative feeding data (Skinner et al., 2009; Viviant et al., 2014; Volpov et al., 2016). Animal borne video cameras can directly record feeding and can be used to estimate prey size and species (Davis et al., 1999; Bowen et al., 2002; Parrish et al., 2005), but are limited by restrictive battery life and may potentially bias results if a light source is used at depth. Furthermore, high costs and extensive video analysis following collection limit the extent of deployments and may render the use of video cameras impractical or unviable for many studies. Prey ingestion can be detected in otariids (sea lions and fur seals; family Otariidae) using stomach temperature transmitters (Kuhn and Costa, 2006), but short and variable retention times make long-duration deployments unreliable. Mandibular gape-angle sensors (IMASEN) can detect jaw opening in pinnipeds (Wilson et al., 2002; Ropert-Coudert et al., 2004; Liebsch et al., 2007), but feeding on small prey is often missed, and cabling may fail or affect the tagged animal over long durations.

For the last ten years, head- or jaw-mounted accelerometers have been investigated as a promising means to identify feeding or attempted prey capture in pinnipeds. These devices are compact, minimally invasive, relatively inexpensive, and have a mid-range

continuous sampling duration, making them an attractive alternative to other methods of feeding detection (Naito et al., 2007; Ydesen et al., 2014; Jeanniard-du-Dot et al., 2017). For appropriate use, however, acceleration signals must be validated, as accelerations of the head and jaw are not limited to feeding motions (Skinner et al., 2009; Iwata et al., 2012; Volpov et al., 2015). Studies vary in their feeding identification criteria. The simplest assume a feeding attempt has occurred when raw or filtered acceleration along one or two axes surpasses a threshold defined from a subset of training data (e.g. Suzuki et al., 2009; Adachi et al., 2018). A variation of this method calculates the variance of those raw acceleration axes within a moving window and applies a similar threshold analysis to those data (Viviant et al., 2010; Volpov et al., 2015; Jeanniard-du-Dot et al., 2017). Due to this simplicity, these analyses invite an increased tendency for false positive feeding detection: any sufficiently strong acceleration along the axis of analysis is identified as feeding (Volpov et al., 2015). Head-mounted (supercranial) triaxial norm Jerk (norm of the differential of each acceleration axis, m s^{-3} ; Simon et al., 2012) reliably indicated prey capture and engulfment by a harbor seal (*Phoca vitulina*) in captive trials (Ydesen et al., 2014), and this method has been applied to harbor porpoises (*Phocoena phocoena*) as well (Wisniewska et al., 2016). However, detection rates and false positive rates were not reported explicitly in these studies. Beyond using only a threshold, Skinner et al. (2009) trained a model based on several acceleration measurements in 2 second windows, but relied only on dynamic (raw minus gravitational component) or differential (head minus body) acceleration data sampling along the surge axis (32-64 Hz). Like other studies, Skinner et al. (2009) reported a substantial number of false positive detections

(86 false positive detections with 75 true positive detections).

Back-mounted accelerometry presents a more desirable but less promising means to detect prey capture in pinnipeds. When positioned in the mid-back to approximate the animal's center of mass, back-mounted accelerometers are more practically situated than head-mounted accelerometers to detect propulsive strokes (Ladds et al., 2017; Tift et al., 2017) and measure overall body acceleration or activity metrics (e.g. Wilson et al., 2006; Qasem et al., 2012; Simon et al., 2012; Ware et al., 2016). This mid-back position allows accelerometers to be incorporated into a larger or more well-equipped biologging instrument than would be appropriate to attach to the head of many pinniped species. Acceleration data from back-mounted tags on pinnipeds often feature strong and abnormal acceleration patterns at depth that clearly differ from the typical signature of propulsive strokes (Ladds et al., 2017; Tift et al., 2017), but these patterns, even if they indicate foraging behavior, cannot yet yield fine-scale quantitative feeding data. Body pitch angle, calculated from an accelerometer, has been used to identify foraging behavior of benthically foraging Hawaiian monk seals (*Neomonachus schauinslandi*) below 3 m depth with variable accuracy, as validated by video (Wilson et al., 2017), but this method is unlikely to be of much use for generalist or non-benthic foraging pinniped species. Skinner et al. (2009) reported that head-mounted accelerometers on Steller sea lions (*Eumetopias jubatus*) performed similarly to the difference between head- and back-mounted accelerometers, indicating that back-mounted accelerometers alone largely missed the acceleration signals of feeding. Use of the back-mounted accelerometer alone, however, was not reported in their study. Back-mounted accelerometers have

successfully detected prey captures by little penguins (*Eudyptula minor*) by detecting a stereotyped body motion while handling prey (Carroll et al., 2014), but it is unclear if a similar method would work well in pinnipeds given the differences in body size and anatomy.

This study investigated the use of head- and back-mounted accelerometry to detect feeding by California sea lions (CSLs), *Zalophus californianus*. I used controlled feeding trials with two trained adult CSLs in a seawater pool to sync video and acceleration data precisely and to analyze acceleration signals due to feeding at high temporal resolution. Both CSLs used the same stereotyped movements of the head and neck to capture and handle prey for consumption. In both CSLs, these movements produced reliable acceleration signals in head-mounted accelerometers but not in back-mounted accelerometers. From head-mounted accelerometry, feeding events were best detected using both acceleration and Jerk, combined in particular temporal patterns to yield specific detection criteria. I used a training dataset to isolate a stereotyped acceleration and Jerk pattern ‘phrase’ that consistently matched head movements during feeding, developed a detector to identify this phrase in each sea lion, and blindly tested these detectors against a non-training dataset for each sea lion. I found true positive detection rates (91-100% at 50-333 Hz) consistent with the best reported rates in the literature, while achieving consistently minimal false positive rates (0-4.8%) at all sampling rates, improving upon published false positive rates. I also found that the adult female’s detector could be used to accurately identify feeding by the adult male within a range of mid-speed sampling rates (32-100 Hz). This would seem counterintuitive, but I found that

at the highest sampling rates, differences in Jerk thresholds become more pronounced between individuals, which made true positive detection more difficult. At mid-frequencies, however, these differences are minimal, indicating the potential use of a universal detector for adult *Z. californianus*. Prey length was related to acceleration metrics of detected feeding events, particularly to the integrated magnitudes of heave-axis Jerk and surge-axis dynamic acceleration, but these relationships varied between the two CSLs.

Materials and Methods

Experimental Procedure

Experiments were carried out at the SLEWTHS facility (Moss Landing Marine Laboratories, Moss Landing, CA), with two trained adult CSLs (72 kg female ‘Cali’, 135 kg neutered male ‘Nemo’). The subjects represented a wide range of movement variability within the species: Cali is small and could swim and maneuver rapidly in the pool, whereas Nemo moved more slowly due to his larger size and vision impairment (cataracts). Both were trained to wear a custom-built 1 mm neoprene head strap which held a small accelerometer (OpenTag, Loggerhead Instruments, Sarasota, FL) snugly against the dorsal surface of the skull. In each experimental trial, the sea lion was sent by a trainer to swim across a large seawater pool, capture and consume a dead fish of known total length (herring *Clupea pallasii* or capelin *Mallotus villosus*, 15.1 – 23.5 cm), and return to the trainer. Fish were presented within 1 m of two underwater GoPro video cameras (60 frames s⁻¹) positioned at different angles to capture the full feeding event. A third GoPro video camera recorded the entire experimental area from above water.

Three types of trials were performed: prey capture trials with the accelerometer (1) head-mounted as described above (Cali: n = 90; Nemo: n = 67) or (2) held against the mid-back near the center of gravity by harnesses (Cali: n = 32; Nemo: n=44), or (3) non-feeding ‘control’ trials with a head-mounted accelerometer to account for the acceleration signals of swimming and turning without prey capture (Cali: n = 75; Nemo: n = 56). During prey capture trials (trial types 1 and 2), sea lions displayed a tendency to anticipate the location of the dead fish. The control trials (trial type 3) were introduced after trial types 1 and 2 had finished to account for the resulting consistent full-body movements; in these trials, the sea lions were trained to swim the same route at the same pace, but no prey was presented and they were called back to the trainer as they were approaching the target.

Data Syncing and Video Analysis

In all trials the OpenTag was set to record acceleration at 333 Hz with 16 bit resolution along 3 axes (heave, surge, sway). Static acceleration along each axis was calibrated before and after each experimental session (12 sessions, 6 to 23 trials per sea lion per session) by allowing the tag to sit steady in each of six stable resting orientations along each axis, recording maxima and minima for each axis, and scaling data to [1, -1], the range expected due to gravity (Ware et al., 2016). Care was taken to sync the OpenTag precisely with each GoPro: all GoPros continuously recorded the entire experimental session, capturing deliberate acceleration markers (stationary accelerometer flicked four times consecutively) before, between, and after trials in each session. Precise GoPro and OpenTag timestamps were recorded for each acceleration marker, and from

these the relative drift between the OpenTag and GoPros was calculated and corrected between each marked point. All signal analyses were performed in MATLAB 2015b or 2016b (MathWorks, Natick, MA, USA).

Prior to analyzing acceleration patterns, framewise GoPro video analysis in Adobe Premier Pro was used to record timestamps in all trials at 1) 5 frames after initial OpenTag submergence once the sea lion left the trainer, 2) initial mouth opening for prey capture (if applicable), 3) lower jaw closure following either suction feeding or the moment of raptorial prey capture (if applicable), 4) any repetitions of steps 2 and 3 (in the case of prey handling following initial capture), 5) the approximate end of stereotyped prey capture head movements, marked by final closing of the jaw (if different than 3), and 6) five frames before the OpenTag visually surfacing from the water. The five-frame buffer in timestamps 1 and 6 was used to avoid acceleration artifacts caused by the tag nearing and breaking the water surface. In control trials, only timestamps 1 (submergence) and 6 (surfacing) were recorded.

Additionally, biomechanics of prey capture were noted from video analysis and used to inform the detector selection process (described below). Stereotyped feeding motions of the head, mouth, and neck were observed with particular attention to the movement imposed on the OpenTag. These biomechanical observations guided the order and timing of the acceleration patterns sought by the detector. For both sea lions, framewise video analysis revealed a consistent, stereotyped feeding motion consisting of 1) mouth opening, 2) a nearly-concurrent rapid head retraction or stalling, peaking approximately during maximum gape; 3) a sharp forward head jolt as the jaw closed, and sometimes a

rapid repetition of steps 1 through 3, if further prey handling was necessary to engulf prey.

Head-Mounted Accelerometry: Training and Testing the Prey Capture Detector

Head-mounted acceleration data from prey capture and control trials were divided into training and non-training datasets. The training datasets, which were composed of a subset of each sea lion's prey capture trials (prey capture training subsets, Cali: $n = 24$, Nemo: $n = 22$) and control trials (control training subsets, Cali: $n = 16$; Nemo: $n = 14$), were used to identify the combination of acceleration patterns that most accurately identified feeding, following guidance from biomechanical observations. Acceleration data marked with video analysis timestamps (see above) were first visually inspected to identify a suite of patterns that appeared repeatedly, aligned with expectations from biomechanical video observations, and could potentially indicate prey capture. These patterns were then used in an iterative testing process, using only training subsets, to determine which pattern combinations most accurately identified true prey capture denoted by timestamps. This process was applied to raw data (333 Hz), and to data subsampled by decimation to 200 Hz, 100 Hz, 50 Hz, 32 Hz, 20 Hz, and 16 Hz, to evaluate the consequences of lower sampling rate to prolong deployment in the field.

For visual pattern inspection, acceleration data were considered in a variety of forms. These forms were raw acceleration data in each axis, estimates of dynamic acceleration along each axis (raw acceleration minus gravitational acceleration as estimated with a moving mean), the triaxial Jerk, and individual-axis Jerk (rate of change of acceleration data). All forms were plotted for each trial in the training subset and were overlain with

timestamps recorded from video analysis for visual pattern inspection. This process identified a suite of possible indicative patterns (magnitude, duration, and directionality of signals) from each data form, yielding numerous combinations or ‘phrases’ of these patterns.

An iterative testing process was used to select the combination of these patterns that best identified true prey capture events (True Positive) in prey capture training data, and ignored other motions associated with swimming or turning in experimental and control training data (False Positive). This process occurred separately for Nemo and Cali. In each test iteration, a different combination of patterns, thresholds, and timing requirements were applied to the training subset as search criteria in custom-written MATLAB script, and the accuracy of prey capture detection was recorded. All pattern combinations identified from visual inspection were tested.

Iterative testing of the training datasets produced an optimized set of detection criteria that described the biomechanics of the prey capture motion well in both Cali and Nemo (Fig. 1.1). The resulting detector required that data contain three components (A-C), each corresponding to a rapid motion during prey capture. A) An initial spike in heave-axis (dorso-ventral relative to the head) smoothed Jerk signal surpassing a threshold calculated from sampling rate (see below). Here, heave-axis Jerk was smoothed with a moving mean over a window size of (sampling rate / 20). This component traced a sharp increase in vertical acceleration due to mouth opening (step 1). B) Within 0.2 seconds of the end of (A), surge-axis (parallel to forward swimming direction) filtered deceleration must surpass -0.7 g ($1\text{ g} = 9.81\text{ m s}^{-2}$). Here, filtered acceleration is calculated as the

difference between raw acceleration and the moving mean of raw acceleration calculated over a window of (sampling rate / 2) data points). This component results from head retraction to facilitate suction feeding (step 2). C) Following within 0.5 seconds of (B), surge-axis acceleration must surpass 1.0 g. This component reflects the sharp forward jolt of the head during raptorial biting (step 3).

Furthermore, the sequence of components A-B must exceed 0.05 seconds, to prevent detection of some rapid motions such as shaking. In the case of prey handling, in which the sea lion does not successfully swallow prey during initial suction (steps 1-3 or A-C), the pattern of steps A-C is repeated one or more times until prey is consumed. To be considered prey handling, any repetitions of A-C must occur within 1 second of the end of the previous A-C sequence; otherwise it is categorized as a new feeding event.

Because Jerk values are dependent on sampling rate, it was necessary to describe the heave-axis Jerk threshold (step 1,A) as a function of sampling rate. Threshold values were first determined separately for each sea lion, at each sampling rate, as part of the iterative testing process described above. These ideal values were plotted against their respective sampling rates.

Fig. 1.1 Prey capture detection model: acceleration and Jerk pattern combination that most accurately identified prey capture. For prey capture detection, the model required (A) a peak in smoothed heave-axis Jerk data surpassing a threshold (*'Jerk threshold'*) empirically determined with the training dataset (Figure 2), resulting from sharp acceleration as the head tilted dorsally when the jaw opened; (B) a surge-axis dynamic deceleration surpassing -0.7 g (*'Deceleration threshold'*; $1 \text{ g} = 9.81 \text{ m s}^{-2}$) within 0.2 s of A, corresponding to head retraction upon reaching prey to allow time for suction or pierce feeding; and (C) a surge axis dynamic acceleration surpassing 1.0 g (*'Acceleration threshold'*) within 0.5 s of B, as the mouth closes and head jolts forward or rocks ventrally.

For both sea lions, a power curve best described the heave-axis jerk threshold as a function of accelerometer analysis rate (Fig. 1.2). These curves diverged substantially at greater sampling rates, as inter-individual differences in the speed and acceleration of the initial mouth opening motion were amplified at increasing sampling rates by the calculation of Jerk.

Fig. 1.2. Relationships between empirically determined heave-axis Jerk threshold and sampling rate.

Detectors were tested on the non-training trial and control subsets to determine their accuracy in identifying true positive prey capture events, ignoring false positive detections during feeding trials, and minimizing false positive detections of the qualitatively similar rapid head and body movements in control trials. Tests were conducted at 333, 200, 100, 50, 32, 20, and 16 Hz. True positive detections (TP) were

defined as ($\# \text{ true detections} / \# \text{ actual prey captures}$), false positive detections during feeding trials (Trial FP) were defined as ($\# \text{ false detections} / \# \text{ actual prey captures}$), and false positive control trial detections (Control FP) were defined as ($\# \text{ control movement detections} / \# \text{ control trials}$).

To assess another promising method for comparison, I also calculated TP and FP rates for the same non-training datasets using root mean squared (RMS) triaxial Jerk over an averaging window of 250 ms, a simpler method that works well in harbor seals and harbor porpoises (Ydesen et al., 2014; Wisniewska et al., 2016). The optimal cutoff threshold was calculated from training datasets for each sampling rate.

Confident application of the method presented here to wild subjects requires a single general detector, but optimum detectors differed between sea lions. Because Cali approached and captured prey more quickly and deliberately, she was judged to be the more representative model of a wild subject. The detector calibrated for Cali was thus tested against Nemo's data, across the full range of sampling rates, to assess the robustness of Cali's detector to variation between subjects.

Head-Mounted Accelerometry: Predicting Prey Size

I investigated if variations in prey size were correlated with characteristics of the prey capture detection signal. As variations in prey size may produce differences in gape angle, feeding mechanism (e.g. suction, pierce, or raptorial), speed of movement, and prey handling time before consumption (Marshall et al., 2015; Hocking et al., 2015, 2016; Kienle et al., 2018), these differences may affect prey capture detection signals (Ydesen et al., 2014). Using the selected prey capture detectors for Nemo and Cali, a

suite of possible indicators were extracted from acceleration and Jerk signals of true positive detections at each sampling rate; these indicators were i) total duration of the prey capture, ii) maximum heave-axis Jerk (smoothed signal, as described above), iii) maximum surge-axis filtered acceleration, iv) the integral of heave-axis smoothed Jerk, and v) the integral of the absolute value of surge-axis acceleration. Linear regressions were used to examine relationships between these indicators and prey length at each sampling rate, as all assumptions for this test were met in each comparison.

Back-Mounted Accelerometry

A random subset of back-mounted accelerometry trials was used as a training dataset (Cali: $n = 16$; Nemo: $n = 20$). Timestamps from GoPro video analysis were overlain on relevant patterns derived from accelerometer tags (single-axis acceleration, triaxial Jerk, single- and double-axis Jerk) for each trial in the training dataset, as described above for head-mounted accelerometry, and visual inspection was used to find any possible patterns, or combinations of patterns, indicative of feeding. No such patterns were found, so no further analyses were conducted.

Results

Head-Mounted Accelerometry: Prey Capture Detection Accuracy

Individually optimized prey capture detectors performed accurately at high sampling rates (Fig. 1.3A). True positive (TP) detection rate ($\# \text{ true prey capture detections} / \# \text{ feeding trials}$) was high at sampling rates of 32 Hz and above, peaking at 100-200 Hz for Cali and Nemo. A slight decrease in TP detection rates at 333 Hz resulted from the need for a stricter heave axis Jerk threshold to help filter out noise from non-feeding signals,

which tended to increase with sampling rate. TP detection rates were slightly greater for Cali than for Nemo at all sampling rates except 333 Hz. Overall, TP detection rates were notably similar between Cali and Nemo across sampling rates. There were no Trial FP detections for either sea lion, at any sampling rate, indicating that propulsive strokes and head movements while searching for prey before capture were not mistaken for feeding.

Cali's detector identified Nemo's feeding events relatively accurately between 32 and 100 Hz (Fig. 1.3A). True positive detection peaked at 50 Hz (91.11%), equivalent to Nemo's optimized detector at the same sampling rate. At 50 Hz and below, detection rates mimicked those of the optimized model. For 100-333 Hz, detection rates decreased with greater sampling rate. This is expected given the criteria in the detector: at higher sampling rates, it becomes increasingly difficult for Nemo's heave axis Jerk data to reach the threshold set by Cali's detector (due to differences shown in Fig. 1.2).

In all control trials, including when Cali's detector was applied to Nemo's data, FP rates were low or zero across all sampling rates for both subjects (Fig. 1.3A; Cali: 0-1.51%, Nemo: 0-4.76%), with maximums of 1 and 2 FP detections for Cali and Nemo's control trials, respectively. The control trials that were falsely detected were qualitatively similar to prey capture in head movement: in these trials, and in several others that were not falsely detected, the sea lion stationed at a target (rapid deceleration) and then actively pushed the target (acceleration) before being called back to the trainer.

In contrast to the detector, the triaxial RMS Jerk method produced high TP detection rates at all sampling frequencies, but greatly elevated FP detection rates (Fig. 1.3B).

Fig. 1.3. True positive (TP) and false positive (FP) prey capture detection rates across sampling rate. Shown are detection rates for A) the detector outlined in Figure 1 using individually optimized parameters, and B) RMS Jerk summed over a 250 ms window with individually optimized thresholds (adjusted from Ydesen et al. (2014) for this study). TP rates are # TP detections / # feeding trials. Control FP rates are the percentage of control trials that were falsely detected as prey capture # control trial FP detections / # control trials. Feeding Trial FP rates are false detections that occurred during feeding trials (# feeding trial FP detection / # feeding trials). TP and FP detection rates of Nemo's data using Cali's detector are labeled 'Cali's detector'.

Head-Mounted Accelerometry: Predicting Prey Size

Prey size was related to some calculated indicators, but results varied between Cali and Nemo and across sampling rates (Table 1.1).

Table 1.1. Relationships between prey length and characteristics of true positive detections in head-mounted feeding trials

Sampling Rate	DF	Prey capture duration		Max. Heave Jerk		Max. Surge Deceleration		Heave Jerk Integral		Surge accel. Integral	
		<i>p-value</i>	<i>R</i> ²	<i>p-value</i>	<i>R</i> ²	<i>p-value</i>	<i>R</i> ²	<i>p-value</i>	<i>R</i> ²	<i>p-value</i>	<i>R</i> ²
CALI											
333 Hz	54	< 0.0001	0.254	0.214	0.029	0.098	0.051	0.0003	0.221	< 0.0001	0.346
200 Hz	54	< 0.0003	0.226	0.351	0.016	0.079	0.057	< 0.0001	0.271	< 0.0001	0.399
100 Hz	55	< 0.0001	0.284	0.487	0.009	0.056	0.066	< 0.0001	0.269	< 0.0001	0.435
50 Hz	54	< 0.0001	0.357	0.224	0.028	0.221	0.028	< 0.0001	0.28	< 0.0001	0.482
32 Hz	50	< 0.0001	0.314	0.292	0.025	0.275	0.024	0.002	0.18	0.0004	0.225
20 Hz	34	0.243	0.041	0.372	0.024	0.89	< 0.001	0.026	0.142	0.027	0.14
16 Hz	25	0.157	0.082	0.416	0.028	0.667	0.008	0.005	0.285	0.006	0.277
NEMO											
333 Hz	41	0.098	0.067	0.841	0.001	0.151	0.051	0.084	0.073	0.111	0.062
200 Hz	43	0.108	0.06	0.774	0.002	0.113	0.059	0.044	0.093	0.078	0.072
100 Hz	43	0.087	0.068	0.838	0.001	0.114	0.059	0.049	0.089	0.049	0.089
50 Hz	38	0.234	0.038	0.387	0.02	0.2	0.044	0.165	0.051	0.244	0.037
32 Hz	18	0.105	0.147	0.36	0.05	0.64	0.013	0.169	0.108	0.238	0.081
20 Hz	17	0.619	0.016	0.528	0.025	0.06	0.205	0.697	0.009	0.791	0.005
16 Hz	7	0.386	0.127	0.127	0.343	0.782	0.014	0.364	0.139	0.936	0.001

Coefficients of determination (R^2) and p-values are italicized for significant relationships (linear regressions). For each relationship, sample size (n) = DF + 1; this varies across sampling rate because indicators were only calculated from true positive detections.

In Cali's data, integrated heave-axis Jerk and integrated absolute value of surge-axis acceleration signals were the best predictors of prey length; however, prey length only explained a moderate amount of the variation in the data (max. $R^2=0.482$). In Nemo's data, all relationships were weak or not significant. Maximum heave-axis Jerk and

maximum surge-axis deceleration signals showed no significant relationship with prey length in either animal at any sampling rate.

Back-Mounted Accelerometry

Back-mounted accelerometers did not record any combination of acceleration or Jerk patterns, that aligned consistently with the timing of feeding (Fig. 1.4).

Fig. 1.4. Typical 3-axis acceleration (top) and triaxial Jerk (bottom) data from a feeding trial with a back-mounted accelerometer. Timing of events, from video, are marked on the plot or labeled with corresponding photos. The timing of feeding (B-D) is highlighted in an orange band, concurrent with a lack of any distinct data signal.

In all but one trial included in training subsets (20 of 20 for Nemo, 15 of 16 for Cali), acceleration and Jerk patterns during feeding movements were nearly absent and indistinguishable from acceleration and Jerk patterns of passive gliding or non-propulsive floating. In Cali's one trial that did have pronounced rhythmic acceleration and Jerk patterns during feeding, GoPro video suggested these patterns were caused by fluttering of the harness strap holding the accelerometer (e.g. Ware et al., 2016). Since no patterns due to feeding could be identified from back-mounted accelerometers, we could neither develop nor test a detection model applicable to back-mounted accelerometry.

Discussion

Head-Mounted Accelerometry: Implications

Using supercranial acceleration data at 50 Hz or above, the stereotyped head movements of prey capture can be identified with high accuracy in CSLs. Whereas similar acceleration-based procedures for detecting prey capture (or attempted prey capture) in pinnipeds exist, the optimized prey capture detector outlined here builds and improves upon such methods by employing selective search criteria to minimize false positive detections, while maintaining high true positive detection rates.

For CSLs, a selective detector appears necessary to discern feeding from other movements. Though triaxial Jerk appeared sufficient for high TP detection, control trial FP detections were similar to FP data reported in other published accelerometry based feeding detection methods (Skinner et al., 2009; Volpov et al., 2015; Adachi et al., 2018). In contrast, this study found that searching for a specific pattern in certain metrics was key to minimizing FP detection. By precisely syncing high resolution acceleration data

with high-speed video, I was able to observe those acceleration and Jerk data patterns, occurring at times scales of tens to hundreds of milliseconds, that reliably and repeatedly aligned with specific prey capture head movements.

Our findings that specific, biologically-informed pattern recognition improves detection accuracy are consistent with observations from previous studies in otariids. Skinner et al. (2009) found that dynamic surge-axis acceleration (at 32 or 64 Hz) correctly detected >80% of TP fish capture attempts (75 of 92), but erroneously detected 86 FP fish capture attempts. Nearly all FP detections occurred while chasing fish, highlighting the need for specific pattern recognition to better discern between high-acceleration behaviors. Similarly, Volpov et al. (2015) found that the calculated variance of individual-axis acceleration successfully detected true feeding events, but also reported high FP detection rates (range 26.1 – 58.6%, calculated in their study as $(TP / (TP + FP))$), with much of this error attributed to head movements unrelated to feeding.

Sampling rate proved crucial to the detector's accuracy. Whereas FP detections remained low across all sampling rates, TP detection rate decreased sharply below 32 Hz, due to loss of details in the acceleration signal. Because the best descriptors of prey capture (Fig. 1.1) often occurred over approximately 0.05 to 0.1 seconds per spike, sampling at a low rate resulted in acceleration and Jerk signals that mischaracterized the true head movements (Fig. 1.5). At our greatest sampling rates, however, the detection model was less robust to inter-individual differences (Fig. 1.3A). Combining these results, our data indicate a 'sweet spot' at around 50Hz for this detector.

Fig. 1.5. The effect of sampling rate on surge filtered acceleration and smoothed heave Jerk signals. Timing of key prey capture movements (from video) are shown with dotted lines. Surge dynamic acceleration signals are relatively conserved above 20 Hz, whereas smoothed heave Jerk signals are strongly affected by sampling rate, with timing and magnitude particularly obscured at 32 Hz and below.

Results varied between individuals, rendering this model's ability to reliably predict prey length inconclusive. Handling time (time needed to engulf prey following capture) appeared to drive significant relationships in Cali's, but not Nemo's, prey length predictions (Table 1.1). Individual qualities of Cali and Nemo likely drove these

differences: Cali found and consumed prey rapidly, whereas Nemo often displayed prolonged searching and prey handling, likely due to vision trouble. In these cases, prey length was unlikely to drive Nemo's handling time. Adachi et al. (2018) found that the number of acceleration signals (peaks above a threshold) per inferred feeding event differed among prey size grouping and correlated with prey length, supporting the idea that the extent of prey handling can help infer prey size.

Head-Mounted Accelerometry: Limitations and Use on Wild Otariids

This model should be directly applicable to studies of feeding patterns in wild CSLs, and likely other otariids. However, limitations exist when applying methods validated in controlled settings to wild animals. These limitations generally reflect behavioral differences between subjects, differences in prey, and settings within the detector.

Individual subjects may differ in their ideal model parameters (Volpov et al., 2015). In our case, prey capture detections were optimized with different personalized heave-axis thresholds, reflecting strong inter-individual differences. Despite this, we found that Cali's personalized detector accurately identified Nemo's feeding when used at moderate sampling rates (32-100 Hz). This result supports the use of a single, generalized detector at moderate sampling rates (~50 Hz) to accurately detect prey capture events in wild CSLs. The detector optimized for Cali is recommended, as her movements were judged to be more representative of wild foraging sea lions, and particularly those of adult female size. MATLAB code for Cali's detection model is available upon request.

Validation using dead prey presented in a controlled environment allows for detailed isolation of prey capture signals, but yields a limited range of observations. Vigorous

prey pursuit or extended prey handling could produce acceleration signals not observed during captive validations with dead prey (Skinner et al., 2009; Iwata et al., 2009; Volpov et al., 2015). Although this study could not test these scenarios, the detectors were effective in minimizing FPs in both feeding and control trials. When Cali's detector is applied to wild individuals, FPs should be decreased relative to past studies with simpler criteria.

Larger and live prey in wild settings should not negatively affect this detector's performance. Within pinniped species, the head and jaw kinematics of initial prey capture (suction, pierce, or raptorial feeding) comprise a narrow range of stereotyped movements (Hocking et al., 2014, 2015; Marshall et al., 2015; Keinle et al., 2018). The prey size prediction trends reported here indicate that larger prey elicit extended, but not fundamentally different, prey capture acceleration and Jerk signals. The use of small dead prey in this study ensures that minimal prey capture signals are detected, whereas larger and actively swimming prey should produce similar but stronger acceleration patterns (Skinner et al., 2009; Ydesen et al., 2014). So long as a prey capture motion (raptorial, suction, or mixture) is present, subsequent accelerations due to tearing and handling of large prey will not negate the initial detection.

Captive validated detectors have practical limits to wild application. Because prey sizes were restricted, this study could not fully validate relationships between detection signals and prey size. Larger prey will likely require more handling time, including tearing at the surface (Hocking et al., 2015, 2016); this detector was not calibrated for tearing or thrashing, and should not be used to infer these behaviors. Additionally, like

other methods, this detector is likely to detect a subset of attempted but unsuccessful prey captures (Skinner et al., 2009; Volpov et al., 2015). Relative to past studies, however, the strict detection requirements imposed here likely will detect an increased ratio of successful to unsuccessful attempts. Finally, this model should be applied in appropriate diving context: breaking the air-water barrier and shallow-water conspecific interactions are likely to produce acceleration signals that mimic prey capture by chance.

Back-Mounted Accelerometry

Feeding by California sea lions did not produce discernable signals in back-mounted accelerometer data. However, a similar method performs reliably in Little Penguins (*Eudyptula minor*; Carroll et al., 2014), indicating that differences in size, anatomy, or feeding kinematics may prevent feeding motions (e.g. Fig. 1.1) from creating acceleration signals at the mid-back in California sea lions.

Because the sea lions were fed only relatively small (15.1 - 23.5 cm) dead fish, they did not need to chase or extensively handle their prey during these trials. These dynamic movements would likely produce strong, abnormal acceleration and Jerk signals in a back-mounted accelerometer. With these behaviors absent, the results of this study indicate that the head and neck movements of feeding alone (head striking, mouth opening, head retraction, mouth closing, and prey handling) do not themselves produce acceleration signals that are discernable by a back-mounted accelerometer. Studies attempting to use back-mounted accelerometers to indicate feeding, therefore, would need to infer feeding from dynamic full-body movements such as prey chasing and handling of large or difficult prey. A variety of behavioral classification techniques using

various combinations of acceleration and depth profile data can be used to identify behavioral modes in diving pinnipeds and seabirds, but none of these can collect data at the resolution of individual feeding attempts (Heerah et al., 2014; Viviant et al., 2014; Carter et al., 2016; Volpov et al., 2016; Chessa et al., 2017).

Importance and Conclusion

Knowledge of feeding patterns is key to understanding an animal's ecological role and energetic trade-offs, yet methods to identify prey capture by marine mammals, and otariids in particular, remain relatively inaccurate or expensive. Fine-scale feeding data informs our understanding of ecosystem impact, ecological niche, and rates of energetic gain from prey, the latter of which further affects reproductive success and ultimately population trends (Melin et al., 2008; Estes et al., 2013; Jeglinski et al., 2013; Villegas-Amtmann et al., 2008, 2013; Kelaher et al., 2015; McClatchie et al., 2016; McHuron et al., 2016, 2018; Jeanniard-du-Dot et al., 2017).

The detector presented here builds upon the trend of accelerometry-based feeding detection, improving accuracy by employing stricter detection requirements to help filter out false positive detections. The accuracy of this detector is robust to inter-individual variability at moderate sampling rates, with best performance at 50 Hz. Whereas inferences about prey size and feeding success remain limited, I am optimistic that this selective detector will decrease the gap between captive validation and wild application.

CHAPTER 2: ENERGETIC CONSEQUENCES OF DIVE DEPTH REVEALED WITH FINE-SCALE ANALYSES IN CALIFORNIA SEA LIONS

Introduction

Foraging is one of the most energetically expensive behaviors for predators (Gorman et al., 1998; Goldbogen et al., 2008; Wilson et al., 2013; Williams et al., 2014). For marine predators that perform breath-hold dives to find prey, these costs can stem primarily from vertical travel to and from a targeted foraging zone (Hind & Gurney, 1997; Skinner et al., 2014; McHuron et al., 2018). Because diving behavior influences reproductive success and survival in breath-hold divers (Costa, 1993; Melin et al., 2008; Jeanniard du Dot et al., 2018), determining the energetic costs of diving to depth, and what drives variation in those costs, has been an important topic in diving mammal and seabird ecological research for decades (Lovvorn and Jones, 1991; Wilson et al., 1992; Speakman, 1997; Costa and Gales, 2000, 2003; Hansen and Ricklefs, 2004; Trassinelli, 2016; McHuron et al., 2018).

The cost of breath-hold foraging most often has been investigated with indirect calorimetry methods that estimate metabolic rates but lack the capacity to pinpoint drivers of diving cost variability in wild animals. One such method, open-flow respirometry, measures changes in oxygen consumption and/or carbon dioxide production and compares these rates across behavioral states (Feldkamp, 1987b; Culik et al., 1994; Thometz et al., 2014). While useful to sum or compare among the relative costs of behaviors such as diving, transiting, and resting (e.g. Thometz et al., 2014), respirometry cannot be applied to freely foraging wild animals diving at sea (with the possible exception of Weddell seals *via* the ice hole technique, e.g. Kooyman et al.,

1973), nor can it establish mechanistic drivers of within-activity cost variation. For example, Fahlman et al. (2008) found that manipulated buoyancy did not affect the metabolic cost of shallow dives in captive Steller sea lions *Eumetopias jubatus* but could not investigate the likely behavioral influence of volitional adjustments to lung volume. Another method, the doubly-labeled water (DLW) technique (Speakman, 1997), has for almost three decades been the premier method to measure the field metabolic rate (FMR) of freely foraging breath-hold divers (Boyd et al., 1995; Costa and Gales, 2000, 2003; McHuron et al., 2018, 2019). DLW measures dilution of hydrogen and oxygen isotopes in the blood over time to determine an accurate estimate of CO₂ production. The coarse temporal resolution of measurements, however, often makes identifying drivers of FMR variation difficult or impossible. While correlations of FMR with behavior or time-activity budgets can indicate drivers of overall FMR variability (Costa and Gales, 2000; McHuron et al., 2018), potential trends are often masked by individual differences such as variable basal metabolic rate (e.g. McHuron et al., 2018, 2019).

Estimating energetic cost at fine time scales is therefore necessary to more clearly parse out drivers of variation in the energy expenditure of breath-hold divers. A variety of methods have been used to this end, enabled by fine-scale movement data from animal-borne dataloggers. The two most common methods, stroke rate and dynamic body acceleration (DBA; Wilson et al., 2006; Qasem et al., 2012), produce relative proxies of energy expenditure from acceleration data. The use of either stroke rate or DBA for this purpose relies on the assumption that the chosen method predicts relative changes in energy expenditure. Both methods significantly predict oxygen consumption

in controlled environments (Williams et al., 2004, 2017; Wilson et al., 2006, 2020), and both have been used extensively to estimate energy expenditure in wild breath-hold divers at a variety of time scales (Wilson et al., 2006, 2010; Shepard et al., 2010; Sato et al., 2011, 2013; Elliott et al., 2013; Adachi et al., 2014; Jeanniard-du-Dot et al., 2016; Hicks et al., 2017; Tift et al., 2017; Grémillet et al., 2018). Validation of these methods against oxygen consumption, however, is limited by logistics of respirometry to ≥ 3 minutes (Barstow et al., 1993; Halsey et al., 2011; Wilson et al., 2020). Hence, the precision and accuracy with which these methods estimate energy expenditure at fine time scales in wild breath-hold divers remains unvalidated.

Bioenergetic modeling offers a more direct means to calculate the propulsive energy expenditure of wild diving animals at fine time scales. Propulsive thrust and swimming power can be calculated from the drag opposing movement through seawater and the buoyant force acting upon the diver at a given depth (Lovvorn and Jones, 1991; Wilson et al., 1992; Hansen and Ricklefs, 2004; Sato et al., 2010; Miller et al., 2012, Trassinelli, 2016). These calculations require knowledge or estimation of morphological parameters and variables (e.g. drag coefficient, frontal surface area, body density), which have traditionally been determined using videography (Feldkamp, 1987b; Lovvorn and Jones, 1991). With fine-scale depth and movement sensors common in animal-borne dataloggers, these morphological parameters can now be estimated at fine temporal scales in wild animals from hydrodynamic gliding performance (Biuw et al., 2003; Miller et al., 2004, 2012, 2016; Aoki et al., 2011, 2017; Narazaki et al., 2018). This hydrodynamic

gliding analysis, however, has not yet been applied to estimate the fine-scale energy expenditure of wild breath-hold divers.

This fine-scale bioenergetic modeling approach can address the open question of how dive depth affects energy expenditure in wild breath-hold divers. Dive depth is expected to drive non-linear variations in cost due to intersecting effects of buoyancy, drag, and behavior (Miller et al., 2012; Trassinelli, 2016). Most air spaces in marine mammals and birds are compressible and thus decrease in volume under increasing pressure with depth (Kooyman, 1973; Ponganis et al., 2015), increasing a diver's density and decreasing buoyancy. As body density deviates from neutral in the surrounding seawater, the buoyant force acts to aid or hinder a diver's vertical movement. When buoyancy aids movement sufficiently to outweigh the drag resisting movement, burst-and-glide swimming or prolonged gliding can be used to minimize overall travel costs (Clark and Bemis, 1979; Lighthill, 1971; Skrovan et al., 1999; Williams, 2000). However, the costs saved in the direction aided by buoyancy must be repaid in the direction hindered by buoyancy (Hays et al., 2007; Miller et al., 2012; Adachi et al., 2014). Recent bioenergetic models of diving pinnipeds, dolphins, and penguins predict that the round-trip cost of a dive to a given depth increases as mean body density deviates from that of the surrounding seawater (Miller et al., 2012; Trassinelli, 2016). By extension, mean round-trip swimming power (J s^{-1}) and Cost of Transport (COT; energy to move one meter; J m^{-1} ; Schmidt-Nielsen, 1972) are predicted to be minimized in dives to twice the depth of neutral buoyancy (because round-trip buoyancy is neutral), and are predicted to increase in shallower or deeper dives (Trassinelli, 2016).

In the wild, dive depth (thus foraging strategy) is likely driven by targeted prey. It is expected, therefore, that mean swimming power and COT vary as a byproduct of dive depth rather than driving dive depth. Deep diving or high-cost strategies are observed in a variety of diving species (or individuals within species), indicating that potential prey reward can motivate or outweigh elevated energetic cost (Aoki et al., 2017; Friedlaender et al., 2019; McHuron et al., 2016, 2018). Furthermore, deep and long-duration dives can approach the limits of an animal's oxygen stores (Ponganis et al., 2007; McDonald & Ponganis, 2013). Sufficient foraging time to find and catch prey at depth (and offset dive costs) is thus a top priority in such extreme dives, demanding optimal travel efficiency by way of a minimized COT. Deep divers, therefore, are expected to swim at the medium to fast speeds that minimize COT, likely incurring elevated rates of swimming power (energetic cost) as a result (Feldkamp, 1987b; Rosen and Trites, 2002).

The California sea lion *Zalophus californianus* (CSL) is a model species to investigate the effects of dive depth on foraging costs using fine-scale bioenergetic calculations. Bioenergetic modeling of density and dive costs is relatively simple in CSLs, as they often descend and ascend nearly vertically (*this study*) and have key morphometric and hydrodynamic coefficients reported from controlled studies (Feldkamp, 1987b). Adult female CSLs dive to a wide range of depths, with foraging strategy varying both within and among individuals (Melin et al., 2008; Kuhn and Costa, 2014; McHuron et al., 2016, 2018). CSLs appear to dive on inhalation (McDonald and Ponganis, 2012), resulting in positive buoyancy near the surface. However, they also have a relatively low lipid mass typical of otariids (Liwanag et al., 2012), which underlies

negative tissue buoyancy in seawater. This combination of diving on inhalation and presumably high tissue density should produce a shift between strong positive buoyancy in shallow depths and strong negative buoyancy at deeper depths. Such a shift may reveal an effect of buoyancy on foraging costs. Furthermore, CSLs swim with a fore flipper propulsion mechanism comprising a brief power stroke and subsequent glide of varying duration (Feldkamp, 1987a) that is typical of otariids and many seabirds (Clark and Bemis, 1979; Fish, 1994, 1996). Thus, results found for CSLs could be applied with caution to a variety of other diving species. These combined traits and the rich literature on CSLs provide an ideal system to investigate changes in fine-scale energy expenditure with depth and the effect of dive depth on energetic cost.

In this study I used bioenergetic models to calculate the energy expenditure of free-ranging adult female CSLs at fine temporal scales during ascents and descents, and expanded those fine-scale data to investigate the effect of dive depth on energetic cost per second (Power) and per meter (COT) during round-trip vertical transit. The bottom phase of dives could not be included because speed could not be reliably estimated; thus, power and COT results give measures of the energetic cost incurred by achieving the observed depth, without including variability from the duration or activity during the bottom phase. I hypothesized that (1) patterns of swimming thrust and power would vary with depth due to changes in buoyancy, reflecting tissue density and compression of air in the lungs; and that (2) round-trip swimming power and COT would vary with dive depth. Specifically, I predicted that (2a) round-trip swimming power would increase with dive depth due to increasingly negative mean buoyancy and faster swimming; and that (2b) round-trip COT

would decrease with depth, reflecting an increasing need to save oxygen by swimming at speeds that cover distance more efficiently.

Materials and Methods

Sea Lion Capture, Instrumentation, and Recapture

Lactating adult female CSLs were captured with custom hoop nets at San Nicolas Island, CA in November 2012 (n=4) and 2014 (n=4). CSLs were weighed (± 0.1 kg), physically restrained, and the standard length and circumference of maximum girth were recorded (cm).

CSLs were instrumented under isoflurane gas anesthesia (Gales and Mattlin, 1998; McDonald and Ponganis, 2013) with VHF radio transmitters and dataloggers.

Instruments were mounted on a neoprene base attached to mesh netting with cable ties; this package was glued with quick-set epoxy to the pelage on the dorsal midline to approximate the location of the center of mass (e.g. McDonald and Ponganis, 2014; McHuron et al., 2016, 2018). In 2012 dataloggers were Daily Diary tags (Wildlife Computers, Redmond, WA) recording pressure and temperature at 1 Hz and 3-axis acceleration at 16 Hz. In 2014 dataloggers were OpenTags (Loggerhead Instruments, Sarasota, FL) recording pressure and temperature at 10 Hz and acceleration, orientation (magnetometer), and rotational velocity (gyroscope) along 3 axes each at 50 Hz.

After instrumentation, CSLs were placed in a large kennel to allow safe recovery from anesthesia (up to 60 min.) and released. Following one or more trips to sea, CSLs were recaptured and instruments were removed under manual restraint (approximately 10 minutes total).

Data Calibration and Initial Processing

Raw OpenTag data were processed in MATLAB 2015b and 2016b. Depth data were calculated from pressure and temperature data at the sampling rate of the tag (10 Hz), then corrected for zero-offset with custom-written scripts. Daily Diary data (corrected depth, temperature, 3-axis acceleration) were converted with Wildlife Computers DAP Processor and loaded into MATLAB 2016b. Acceleration data from both tags were calibrated to [-1 1], the range expected due to gravity, along each axis (Ware et al, 2016).

Overview: Calculating Density, Thrust, and Swimming Power

Thrust and P_i were calculated in 5 s intervals following published and modified methods (Feldkamp, 1987b; Miller et al., 2004, 2012; Sato et al., 2010; Aoki et al., 2011; Trassinelli, 2016). Briefly, the thrust needed for a swimming animal to achieve an observed speed can be estimated from the drag (F_D) and buoyancy (F_B) forces acting on the animal. The forces F_D and F_B must be estimated at fine scales, as F_D varies as a function of morphometrics and swim speed and F_B is estimated from animal density relative to the surrounding media. In marine mammals, body density (ρ_{CSL}) increases with depth as the volume of air spaces is compressed under hydrostatic pressure. When ρ_{CSL} sufficiently surpasses seawater density (ρ_{sw}) below a given depth, negative F_B aiding descent outweighs F_D opposing descent, allowing the animal to glide passively to depth. I used these periods of gliding descent, in which glide speed is not influenced by active swimming, to estimate ρ_{CSL} in 5 s time intervals using published equations. For each CSL, I described mean ρ_{CSL} as a function of depth with a simple best fit model

based on air space compression, DLV, and tissue density (ρ_{Tissue}). This allowed an estimate of each CSL's mean F_B across the full range of observed depths during both descent and ascent. During vertical transit at a given depth, the F_B and F_D vectors acting on the CSL together give the thrust (N; force) produced by the CSL to achieve the observed speed. The power output (J s^{-1} ; rate of energy) needed to produce that thrust is the product of the thrust and swim speed. Elements of this process are described in detail below.

Estimating Body Density from Hydrodynamic Gliding Performance

The acceleration or deceleration that a CSL experiences during gliding descent is the result of the buoyancy and drag forces (F_B and F_D , both in Newtons (N)) acting upon it. Drag resists the CSL's forward motion through seawater, and is described as a function of seawater density (ρ_{sw} , kg m^{-3}), the CSL's frontal surface area (A_f , m^2) calculated from the maximum girth measurement assuming a circular cross section (Aoki et al., 2011, 2017), the drag coefficient referenced to the frontal surface area ($C_{Df} = 0.07$; Feldkamp, 1987b; Aoki et al., 2011, 2017), and the square of observed speed (U , m s^{-1}):

$$F_D = -\frac{1}{2}C_{Df}\rho_{\text{sw}}A_fU^2 \quad (1)$$

Buoyancy results from the difference in density between the CSL's body (ρ_{CSL} ; kg m^{-3} , including air spaces) and that of the surrounding seawater (ρ_{sw}):

$$F_B = \frac{(\rho_{\text{sw}} - \rho_{\text{CSL}})m_{\text{CSL}}g}{\rho_{\text{CSL}}} \quad (2)$$

Where m_{CSL} is the mass of the CSL (kg), and g is gravity. Acceleration in the direction of motion during gliding descent results from the difference between F_B and F_D , weighted by the descent angle (θ) relative to the gravitational force (Miller et al., 2004; Aoki et al., 2011):

$$m_{CSL}a = F_B \sin\theta - F_D \quad (3)$$

Eqns 1-3 can then be combined (Aoki et al., 2011) and rearranged to solve for CSL density as a function of known and measured variables during gliding descent:

$$\rho_{CSL} = \frac{g \sin\theta \rho_{sw}}{0.5 \frac{C_{D,f} A_f}{m_{CSL}} \rho_{sw} U^2 + g \sin\theta + a} \quad (4)$$

I wrote custom MATLAB code to identify and analyze periods of gliding descent that maintained near-vertical body orientation (within 10 degrees of vertical). Body orientation (θ) was measured from the heave axis (parallel to swimming path) of the accelerometer. I excluded shallow-angle glides to avoid the increased influence of lift generated by the relatively large fore flippers at less vertical swim angles (Aoki et al., 2011; Narazaki et al., 2018). Additionally, all active stroking was excluded from analysis, along with a 5 s buffer after the last stroke. These strokes, and other sharp accelerations that could influence glide speed, were identified from peaks in the acceleration metric Minimum Specific Acceleration (MSA; calculated from 3-axis acceleration following Simon et al., 2012) during descent, similar to published methods (Miller et al., 2016; Aoki et al., 2017). MSA peaks were considered strokes if they exceeded a conservative threshold of 0.13 g (threshold estimated from visual inspection).

Raw data (depth, time, Θ) from each gliding descent were extracted in 5 s intervals (Miller et al., 2004, 2016; Aoki et al., 2011, 2017).

From those raw data, I calculated additional variables (speed (U), acceleration (a), and ρ_{sw}) needed to estimate ρ_{CSL} in each 5 s interval using Eqn 4. U was calculated as the change in depth over the time interval, weighted by descent angle (e.g. Miller et al., 2004). A curve was fit to each CSL's observed glide speed data (U) across depth (Fig. 2.1, left), and that curve was then used to calculate ΔU , and hence acceleration ($\Delta U/\text{time}$), as a function of measured depth at the beginning (t_1) and end (t_2) of each 5 s interval (Fig. 2.1, right).

Fig. 2.1. Estimating acceleration during gliding descent. Glide speed as a function of depth from CSL C3 (left graph). For each CSL, a best fit curve was used to describe glide speed as a function of depth (right graph). Using this curve, acceleration was estimated as the change in glide speed (ΔU) over the time interval.

ρ_{sw} was calculated at the sampling rate of the pressure and temperature sensor of each biollogger using the International Equation of State of Seawater (UNESCO, 1981), assuming a salinity of 34.84‰ (Vogel, 1994; Aoki et al., 2011, 2017), and was averaged in 5s intervals. ρ_{CSL} was calculated in each identified glide interval using equation 4.

Mean ρ_{CSL} was then modeled as a function of depth for each CSL, a step that was necessary to estimate F_B during active swimming (when ρ_{CSL} could not be directly calculated). For each CSL, a mathematical model for ρ_{CSL} based on gas compression due to hydrostatic pressure was fitted to calculated ρ_{CSL} data, as a function of depth:

$$\rho_{CSL,depth} = \frac{mass}{V_{Tissue} + V_{Resp,depth}} \quad (5)$$

where:

$$V_{Tissue} = \frac{mass}{\rho_{Tissue}}$$

$$V_{Resp,depth} = \frac{DLV}{1 + (\alpha \cdot \frac{depth}{10})}$$

Here, V_{Tissue} (L) is the tissue volume excluding air spaces, $V_{Resp,depth}$ (L) is the respiratory volume at a given depth, DLV (L) is the diving lung volume or respiratory volume at the surface preceding a dive, ρ_{Tissue} (kg m⁻³) is the density of tissue excluding air spaces, and α is a constant between 0 and 1, introduced here, that describes the ratio of observed air space compression relative to that expected from Boyle's law.

In this model, three unknown parameters were estimated: ρ_{Tissue} , DLV , and α . For each CSL, the best fit model parameters were selected following iterative testing of

combinations of the three parameters over realistic ranges of values. The range of ρ_{Tissue} was set between 1030 and 1090 kg m⁻³ at increments of 0.5 kg m⁻³. DLV was set over a range of 2 to 10 L at 0.1 L increments. The resulting DLV estimate gives a mean value for each individual. The range of α was set between 0 and 1, and was tested in increments of 0.01. The best fit model for each CSL was used to estimate density as a function of depth, and to extrapolate body density at depths shallower and deeper than those observed during glides.

Calculating Thrust and Power During Ascent and Descent

The relationships established between depth and ρ_{CSL} permit the calculation of F_B (Eqn 2), allowing calculation of the thrust and power used in active swimming. U , depth, ρ_{CSL} , and ρ_{SW} were calculated or measured for each 5 s interval (using methods described in the previous section) in both ascents and descents, and these were used to calculate F_B , F_D , thrust, and power (P_o and P_i , described below). As with the ρ_{CSL} analysis, intervals were only included in analysis if CSL body orientation remained within 10 degrees of vertical, to minimize confounding effects of foreflipper lift generation (Narazaki et al., 2018).

The swimming thrust force (N) necessary to achieve an observed ascent or descent speed is given by the sum of the buoyancy (F_B) and drag (F_D) vectors acting on the CSL:

$$Thrust = F_B \sin\theta + F_D \quad (6)$$

and the power output (P_o , in Watts (W)) needed to produce that thrust is given as the product of the observed thrust and speed:

$$P_o = Thrust \cdot U \quad (7)$$

This power output (P_o) is related to metabolic power input (P_i) by a dimensionless conversion factor (ε), which represents the efficiency in converting P_i into P_o (Watanabe et al., 2011). This conversion factor is given as the product of propeller efficiency (N_p) and the efficiency of converting chemical energy into muscular work (N_m ; muscular efficiency), where N_m is approximately 0.25 at optimal contraction speed (Cavagna et al., 1964; Webb, 1975; Miller et al., 2012):

$$P_i = P_o / \varepsilon \quad (8)$$

where:

$$\varepsilon = N_p \times N_m$$

Feldkamp (1987b) found that N_p in CSLs increased with U and reached a plateau above 2.5 m s^{-1} . I multiplied those published N_p data (Fig. 8 in Feldkamp, 1987b) by an N_m value of 0.25 to find ε , then fit a 3rd order polynomial to the resulting relationship (as in Feldkamp, 1987b), to obtain ε as a function of U . In each 5 s interval, ε was determined using this relationship and observed U .

Calculating Mean Dive Thrust, P_i , and Cost of Transport During Vertical Transit

Fine-scale estimates of energy expenditure were expanded to evaluate energetic costs and benefits of different dive strategies. This analysis focused on the combined travel costs of descent and ascent, giving estimates of the energy per second and per meter that CSLs used to achieve observed dive depths. Bottom time dive costs were not included in this analysis because fine-scale swimming costs were not estimated at shallow swim angles (previous section). Because bottom time was excluded, the data presented here estimate round-trip vertical travel costs rather than the overall energy expenditure of a

full dive. For each full ascent and descent, mean costs were estimated by averaging data from all 5 s intervals of that dive phase. Only ascents and descents with complete data were included (594 ± 227 (Mean $\pm$ S.E.) ascents and 560 ± 278 descents, representing 61.6 ± 21.1 of total ascents and 54.4 ± 22.9 of total descents); those missing data from any 5 s interval (e.g. due to horizontal excursions; criteria presented earlier in methods) were excluded.

Two complimentary estimates of energetic costs, P_i and COT, were calculated for each full ascent and descent from fine-scale data. P_i holds clear importance to CSLs and other divers, as variation due to dive depth would indicate that dive strategy influences energy expenditure. COT is similarly important: for CSLs operating near their physiological limits in deep dives (McDonald and Ponganis, 2013), efficient vertical travel (low COT) should help maximize foraging time at depth. Thrust, which is the force output by the CSL, was calculated alongside these energetic estimates for comparison.

COT, the energy needed to move a CSL a given distance (J m^{-1}), was calculated here as the total energy input divided by the distance traveled:

$$COT = \frac{(P_i + P_{SMR})time}{distance} \quad (9)$$

where:

$$P_{SMR} = \frac{19.84}{60} \times SMR \times mass$$

Here, the total energy cost (J) is the sum of the metabolic power input from swimming (P_i) and a constant basal or standard metabolic rate (P_{SMR}), both measures of energy per second, multiplied by ascent or descent time (s). In this equation, P_i is the mean of all 5 s

intervals in that full descent or ascent. The total energy cost is divided by the distance traveled to find mean COT (J m^{-1}) for that descent or ascent. For some analyses, mass-specific COT ($\text{J kg}^{-1} \text{m}^{-1}$) was calculated by dividing COT by body mass. To calculate P_{SMR} , I used an SMR of $10.23 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ found for female CSLs in conditions defined for BMR (Hurley and Costa, 2001). I assumed a calorific equivalent of $19.84 \text{ J mlO}_2^{-1}$ at a respiratory quotient (RQ) value calculated as 0.75 in swimming CSLs that was unaffected by swim speed (Feldkamp, 1987b). This constant RQ ignores the possibility of CSLs entering anaerobic metabolism during their longest and deepest dives (which would alter the RQ and SMR rates), as this study could not measure the onset of anaerobic metabolism. The calorific cost of thermoregulation was not included as it is considered negligible during foraging behaviors due to thermal substitution (Hind and Gurney, 1997; Lovvorn, 2007).

For both descents and ascents, means of thrust, P_i , and COT were binned by maximum dive depth, with bin sizes of 10 m. For each 10 m bin, mean thrust, P_i , and COT were calculated for both descent and ascent. For each bin value (10 m depth range), descent and ascent means of each data type (thrust, P_i , and COT) were averaged to give overall mean thrust, P_i , and COT values for vertical transit (descent plus ascent).

Statistical analyses

This study comprised two goals; the first was to calculate CSL body density and energy expenditure at fine temporal scales during dives and to describe these patterns as a function of depth. Results of this first goal were not tested statistically because all

explanatory variables were used in the calculation procedure. These descriptive results were instead evaluated qualitatively in the context of published data.

The second goal was to investigate the effect of dive depth on the estimated energetic cost of vertical travel (thrust, P_i , and COT); these data were tested statistically. To investigate the effect of dive depth on estimated energetic cost, I ran Generalized Additive Mixed Models (GAMMs) using the *mgcv* package in R (Zuur et al., 2009; Wood, 2011; R Core Team, 2017) to investigate these relationships while accounting for the violation of data independence due to repeated sampling from few individuals. Thrust, P_i , and COT were each the response variable for two GAMMs: one with and one without dive depth as a fixed effect, with both including CSL ID as a random effect. AIC values were used to evaluate the effect of dive depth (fixed effect) on each response variable. Coefficients of variation (R^2 adj.) estimated by GAMM models were used to assess the overall fit of each model. Each GAMM model was validated by examining normalized residuals against fixed effects (if applicable) and fitted values (Zuur et al., 2009).

Results

Body Density Estimates Across a Range of Depths

As predicted, ρ_{CSL} increased with depth in agreement with air space compression for all CSLs (Fig. 2.2). In most CSLs, passive gliding was observed at or below depths where ρ_{CSL} slightly exceeded ρ_{sw} ($\sim 1027 \text{ kg m}^{-3}$), consistent with expected behavioral minimization of swimming cost. One CSL (C20) only began prolonged glides at deeper depths and at slightly increased ρ_{CSL} , limiting the depth range of her ρ_{CSL} observations.

Fig. 2.2. Body density calculated using Eqn 4 for each sea lion during 5 s gliding descent intervals (dots), shown with best-fit body density models (Eqn 5, Table 2.1) extrapolated to a depth range of 0-300 m.

Inter-individual differences were apparent between best fit models (Fig. 2.2, Table 2.1). Average CSL ρ_{Tissue} was estimated to be $1059.3 \pm 1.6 \text{ kg m}^{-3}$, with individual CSL estimates ranging from 1053 and 1071 kg m^{-3} (Table 2.1). Average DLV at the onset of dives was estimated as $5.3 \pm 0.6 \text{ L}$ (Table 2.1; range 3.5 – 7.95 L among individuals). One variable estimated by iteration in best fit models did not differ among CSLs: α , the parameter introduced to describe the ratio of observed to unopposed gas compression in air spaces, was 0.3 in all CSLs (Table 2.1).

Table 2.1. Body mass (M_b), CSL ID, number of 5 s gliding descent intervals analyzed (N), and best-fit parameters (tissue density ρ_{Tissue} , diving lung volume (DLV), and air space compressibility (α)) modeled for each sea lion in this study.

CSL ID	M_b (kg)	ρ_{Tissue} (kg m ⁻³)	DLV (L)	α	N
C22	95.4	1071	7.95	0.3	767
C20	82.8	1054	6.5	0.3	647
C14	86.2	1053	4.5	0.3	191
C16	94.2	1063	7.5	0.3	612
S2	95	1056.5	4.9	0.3	992
S4	73.8	1062	4	0.3	148
S7	72.8	1060	3.5	0.3	180
S8	70.4	1055	3.5	0.3	416
83.8 ± 3.5		1059.3 ± 1.9	5.3 ± 0.6		

Thrust and Swimming Power (P_i) during Descent and Ascent

As expected, all CSLs adjusted thrust and P_i during descent and ascent to account for changes in buoyancy across their range of depth (Fig. 2.3). CSLs began descent by producing powerful thrust with elevated P_i to counter positive buoyancy near the surface; with continued descent, CSLs decreased thrust and P_i to zero as the hinderance of positive buoyancy gradually shifted to aid from negative buoyancy (Fig. 2.3). Individual descent trends of thrust and P_i magnitude varied, but showed two dominant patterns with depth: six CSLs ceased active swimming between 50-80 m depth and produced lower thrust and P_i at a given depth, whereas the other two CSLs continued active swimming until over 200 m depth and produced elevated thrust and P_i relative to the other CSLs at a given depth (Fig. 2.3).

Fig. 2.3. Patterns of thrust, swimming power (P_i), and Minimum Specific Acceleration (MSA) during descents and ascents. A) depth (black) and raw MSA (orange) during a descent (left) and ascent (right) of a representative dive to 300 m. **B)** Observed thrust and P_i trends with depth during descent (left) and ascent (right). Mean $\pm$ SE trends of 5 s interval data from each CSL are shown with a LOESS smoother.

Notably, ρ_{CSL} alone did not appear to drive these inter-individual differences, indicating that behaviors and choices such as preferred descent speed and the use of stroke-and-glide swimming during deeper descent do not always follow from body density.

During ascent, all CSLs exhibited the highest thrust and P_i values at the onset of ascent at depth, which slowly decreased toward the surface, and more sharply decreased within the top 25-50 m, eventually approaching 0 at or near the surface (Fig. 2.3, top two rows, right column). As with descent, these patterns reflect buoyancy, showing that deep-diving CSLs incur elevated ascent costs to swim against negative buoyancy. Despite this similarity, the magnitude of thrust and P_i at depth varied among individuals. Unlike with descent, increased P_i and especially thrust at a given depth appeared to be driven by increased ρ_{Tissue} (Fig. 2.3 right column, top row. ρ_{Tissue} denoted by color as in Fig. 2.2). Whereas seven of the eight CSLs continued stroking until near the surface, one individual (C20, yellow in Figs. 2.2 & 2.3) appeared to reach positive buoyancy at a deeper depth during ascent (e.g. Fig. 2.2, yellow), allowing it to glide upward with minimal or no effort in the shallowest ~30-40 m of ascent (Fig. 2.3, right column, top 2 rows).

The Effect of Dive Depth on the Average Cost of Vertical Travel

As hypothesized, the average thrust and P_i of vertical travel increased with dive depth (Table 2.2, Fig. 2.4). Generally, this means deeper dives require more thrust and metabolic energy input per unit time of vertical travel. Most CSLs increased average thrust and P_i with increasing dive depth, although at least two CSLs had more complex trends (Fig. 2.4A). Mean thrust and P_i increased sharply as dive depth increased from approximately

Table 2.2. Generalized Additive Mixed Effects Models (GAMMs) examining the effect of dive depth on mean thrust, swimming power (P_i), and cost of transport (COT) during vertical travel.

Model Variables			Results						
Response	Effects		Fixed Effects					Random effect	
	Fixed	Random	AIC	est. df	F	P-value	adj. R^2	F	P-value
Mean Thrust	Dive Depth	CSL ID	-602.81	3.19	15.47	< 0.0001	0.667	29.43	< 0.0001
Mean Thrust		CSL ID	-568.64					25.63	< 0.0001
Mean P_i	Dive Depth	CSL ID	68.3554	3.75	16.38	< 0.0001	0.716	32.71	< 0.0001
Mean P_i		CSL ID	111.139					29.48	< 0.0001
Mean COT	Dive Depth	CSL ID	30.4478	4.60	9.949	< 0.0001	0.486	14.25	< 0.0001
Mean COT		CSL ID	57.705					7.599	< 0.0001

CSL ID was included as a random effect in each GAMM to account for repeated sampling of data from few individuals. For each response variable, dive depth improved GAMM models when added as a fixed effect as indicated by lower AIC values.

Adj. R^2 is an estimate of overall variation explained by a GAMM model.

20 to 100 m, and more gradually between 100 m and 300+ m (Fig. 2.4B, left and middle).

Data from most individuals agreed with this trend (Fig. 2.4A).

In contrast, the average COT of the vertical phases of dives decreased with dive depth (Table 2.2, Fig. 2.4). This trend was largely driven by shallower dives: mean COT for vertical travel is generally greatest in the shallowest dives, decreasing with dive depth in 6 of the 8 CSLs until dive depths of approximately 50-75 m depth (Fig. 2.4A, circles). As dive depth increased beyond this, COT trends in individual CSLs became somewhat ambiguous (S7, S8, C14, C20), increased slightly (C22, C16), or decreased slightly (S4, S2). The average trend among all CSLs determined by the GAMM smoother (Fig. 2.4B, right) indicated that mean COT decreased relatively sharply as dive depth increased from 20 m to about 75 m, then decreased gradually with increasing dive depth.

Fig. 2.4. The effect of dive depth on mean mass-specific thrust, swimming power (P_i), and cost of transport (COT) during vertical travel (ascent plus descent). A) Mean $\pm$ SE thrust (squares), P_i (triangles), and COT (circles) for each CSL, binned (10 m bins) by dive depth. B) Cubic regression spline smoothers determined by GAMM models showing overall trends of thrust, P_i , and COT as a function of dive depth. Y-axes show deviation from a zero mean.

Discussion

This study quantified free-ranging swimming effort of adult female CSLs during descents and ascents at a fine temporal scale, and calculated from these data that vertical travel uses more energy per unit time, but less per unit distance, as dive depth increases. These results indicate CSLs adjust swim speed to suit energetic priorities that shift from energy preservation (low P_i , high COT) in shallow dives to oxygen management and transit efficiency (high P_i , low COT) in deep dives. Given their similar swimming mechanisms and diving patterns, results and methods from this study likely apply to other diving bird and mammal species that use a fore flipper or wing propulsion mechanism while diving (e.g. otariids, alcids, and penguins).

Modeling Body Density Across Depth

The CSL body density estimates and models reported here (Fig. 2.2, Table 2.1), which form the basis for thrust, P_i , and COT calculations, are corroborated by isotope dilution and allometric equations. Because four of the CSLs (C22, C20, C14, C16) in this analysis were also injected with doubly labelled water (DLW) for a separate study (McHuron et al., 2018), tissue density (ρ_{Tissue}) could be calculated from isotope dilution data for comparison (Nagy, 1980; Speakman, 1997). These tissue densities were calculated with total body lipid and total body protein derived from available total body water data (Arnould et al., 1996; Aoki et al., 2011; McHuron et al., 2018), and a total body ash content of 2.8% (Reilly and Fedak, 1990). ρ_{Tissue} estimated by our model was only $0.50 \pm 0.38\%$ (range -0.44 to 1.6%) different than these densities calculated from this isotope dilution method, the same order of accuracy as expected from isotope

dilution alone (Lukaski, 1987; Aoki et al., 2011). Furthermore, the estimated mean DLV for each CSL averaged $74.2 \pm 6.1\%$ (range: 57.1-100%) of the total lung capacity (TLC) estimated from one allometric equation based on marine mammals ($TLC = 0.1 \times M_b^{0.96}$; Kooyman, 1989), and $65.7 \pm 5.5\%$ of TLC estimated from another ($TLC = 0.135 \times M_b^{0.96}$; Kooyman, 1973, Fahlman, 2011). This estimated range agrees with reports that CSLs dive following inhalation (Kooyman and Sinnett, 1982). These averages are derived from static mean DLV estimates for each sea lion, which likely contributed much of the variability around each individual's density-depth model (Fig. 2.2) as CSLs moderate their DLV (McDonald and Ponganis, 2012). Despite this, comparisons with TLC and isotope dilution provide confidence that the density models in this study accurately approximate mean body density for each sea lion as a function of depth.

Despite model accuracy, factors driving density at various depths are more complex than assumed here and in other models (e.g. Aoki et al., 2011; Miller et al., 2016; Trassinelli, 2016). Body densities calculated with Eqn 4 (shown in Fig. 2.2) indicate that increased hydrostatic pressure during descent causes compression of a CSL's air space at a rate substantially slower than that predicted by Boyle's law. The term α (Eqn 5) was introduced here to quantify the observed rate of gas compression relative to the rate of gas compression that would occur unopposed; for instance, in a balloon filled with air. My observed value of $\alpha = 0.3$ for all CSLs (Table 2.1) indicates that, in all 8 of the CSLs in this study, total gas in the body compressed at an average of 0.3 times the rate expected from Boyle's law alone. The respiratory tract tissues of CSLs and other marine mammals vary in compliance and compressibility (Scholander, 1940; Kooyman, 1973;

Fahlman et al., 2011, 2014, 2015); hence, the compressibility of marine mammal body air spaces changes with depth (Fitz-Clarke, 2007; Fahlman et al., 2014). Laboratory tests on live, dead, and excised CSL respiratory tracts found that lung compliance (change in lung volume as a function of transpulmonary pressure) varies strongly between individuals and as a function of air volume in the lung (Fahlman et al., 2014), providing support for this concept. Additionally, active exhaling during a dive or ‘braking’ by increasing drag with the fore flippers can cause calculated body density or swim speed to deviate from model predictions (Sato et al., 2002, 2011; Hooker et al., 2005). In lieu of attempting to model this complexity, the term α may act as a ‘catch-all’ correction that, along with parameters DLV and ρ_{Tissue} , describes the difference between the theoretical and observed average gas compression.

Tissue Density and DLV Across Depth

Tissue density of all CSLs in this study was substantially greater than seawater (Table 2.1), producing strong negative buoyancy at depth (Fig. 2.2). Buoyancy while diving is in large part a function of body condition, and particularly lipid stores (Beck et al., 2000; Biuw et al., 2003; Trassinelli, 2016). I estimated tissue densities that exceed those reported for adult cetaceans (Miller et al., 2004, 2016; Aoki et al, 2017; Narazaki et al., 2018) and phocids (Aoki et al., 2011; Sato et al., 2013) indicating lower proportional lipid content in this species or poor body condition in the tagged individuals. Each CSL’s tissue density affected its mean depth of neutral buoyancy (Fig. 2.2), thereby influencing the proportion of ascents and descents that are positively or negatively buoyant in CSLs, with cascading consequences for F_B , thrust, P_i , and COT.

DLV affects body density at shallow depths, influencing the depth of neutral buoyancy and the patterns of energetic costs during descent and ascent, despite its relatively minor impact on overall work during transit compared with the effect of tissue density (Trassinelli, 2016). CSLs dive on inhalation like other otariids (Kooyman, 1973; Hooker et al., 2005) and appear to adjust their DLV to planned dive depth (McDonald and Ponganis, 2012) to maximize respiratory oxygen stores, like Adelie (*Pygoscelis adeliae*), King (*Aptenodytes patagonicus*), and Emperor (*Aptenodytes forsteri*) penguins (Sato et al., 2002, 2011) but unlike Antarctic fur seals (*Arctocephalus gazella*) and Northern bottlenose whales (*Hyperoodon ampullatus*; Hooker et al., 2005; Miller et al., 2016). Relative to marine mammals that dive after exhalation or to much greater depths, the DLV of CSLs (and likely other otariids) should have increased effect on density and, by extension, energetic costs (Miller et al., 2012; Trassinelli, 2016). In this study, CSL body density continued to increase to depths of more than 300 m and contributed to inter- and intra-individual variation in body density throughout dives, likely contributing to variability around best-fit density models (Fig. 2.2). In contrast, the effect of residual gas volume on the body density and overall buoyancy of exhalation divers (e.g. elephant seals) is considered negligible below 100 m (Biuw et al., 2003; Miller et al., 2004; Aoki et al., 2011).

Fine-Scale Swimming Costs During Descent and Ascent

As expected, the curvature of thrust and P_i trends relative to depth strongly reflects buoyancy changes resulting from air space compression or re-expansion (Fig. 2.3B). This result confirms that CSLs adjust their swimming effort according to the aid or hinderance

they experience from buoyancy, as reported for mysticetes (Nowacek et al., 2001; Narazaki et al., 2018), odontocetes (Skrovan et al., 1999; Williams et al., 2000; Miller et al., 2004, 2016; Martín López et al., 2015; Aoki et al., 2017), phocids (Webb et al., 1998; Watanabe et al., 2006; Gallon et al., 2007; Aoki et al., 2011; Miller et al., 2012; Adachi et al., 2014), otariids (Crocker et al., 2001; Hooker et al., 2005), penguins (Sato et al., 2002, 2011;), and alcids (Lovvorn et al., 1999; Watanuki et al., 2003, 2006). The clarity of this trend in each CSL indicates the prevalence of cost-saving transit strategies (gliding and stroke-and-glide swimming; e.g. Williams et al., 2000), and highlights the strong effect of buoyancy on patterns of CSL swimming effort.

Although buoyancy drove changes in swimming effort with depth, the magnitude of mass-specific thrust and P_i at a given depth varied between individuals (Fig. 2.3B). Buoyancy, as determined by body density (as a function of DLV and tissue density) contributes heavily to this variation: at a given depth during ascent, mean thrust and P_i vary between individuals roughly according to tissue density (Fig. 2.3B; tissue density denoted by line colors). Alongside buoyancy, drag affects thrust as a square function of swim speed (Eqn 1). Swim speed further influences P_i by determining the conversion efficiency (ϵ) between muscular energy expenditure (P_i) and observed power output (Eqn 7). Thus, swim speed and buoyancy are important determinants of swimming costs in CSLs, as observed extensively in marine mammals (Watanabe et al., 2011; Miller et al., 2012; Suzuki et al., 2014; Trassinelli, 2016; Aoki et al., 2017).

Trade-Off Between Cost Saving and Travel Efficiency Across Dive Depth

As dive depth increases, adult female CSLs transit to and from depth using energy at a faster average rate (increased mean P_i) but cover that distance more efficiently (decreased mean COT). CSLs may thus modify behavior to suit energetic priorities that vary with dive depth. During deep dives, lowered COT serves to maximize oxygen available for foraging. In shallower dives, where oxygen stores are less limited, decreased P_i minimizes overall energetic cost. CSLs may behaviorally achieve this shift by modifying swim speed, although buoyancy likely also influenced P_i and COT trends across depth. The role of each is explored in the following discussion. The results presented here support the assertion that deeper diving may be a high-risk, high-reward strategy in this species (McHuron et al., 2018).

Based on results presented here, I hypothesize that the increased need to preserve oxygen in deep dives drives the observed trends of decreased COT and increased energy expenditure in deeper dives. The trends of COT and P_i with depth mirror each other inversely (Fig. 2.4B), suggesting a shifting swimming strategy that favors overall energy saving in shallow dives and travel efficiency (minimized COT) in deeper dives. Oxygen preservation should grow in importance with dive depth, secondary to prolonged duration underwater and to greater travel distance (and thus increased overall work). Free ranging adult female CSLs exhibit a graded physiological dive response that intensifies with dive depth and duration (McDonald and Ponganis, 2013, 2014; Tift et al., 2017), supporting this interpretation. The results presented here suggest that, alongside this graded dive response, CSLs alter their swimming behavior with dive depth in a manner that meets

energetic priorities. In deeper dives, reduced mean COT (Fig. 2.4B) allows CSLs to cover distance more efficiently and thus maximize oxygen available for foraging at depth, despite incurring greater overall rates of energy expenditure (P_i , Fig. 2.4B). In shallower dives, by comparison, CSLs use a travel strategy that reduces their rate of energy expenditure (lower mean thrust and P_i) relative to deeper dives but results in elevated COT. Vertical travel efficiency therefore appears to be outweighed on average by the benefit of overall energy savings in shallower dives, but to demand elevated energy expenditure in deeper dives.

The effect of bottom time is absent from the reported trends (Fig. 2.4), and it is unclear how it would influence the effects of depth reported here. Many CSL prey encounters are assumed to occur at the bottom of dives (Feldkamp et al., 1989; Melin et al., 2008; McHuron et al., 2016, 2018); hence, mean P_i or COT of each full dive will likely depend strongly on the presence, duration, and intensity of prey pursuit and capture. It is currently unknown how these factors will influence mean bottom time P_i or COT as a function of depth. In contrast, P_i and COT will likely be minimized at neutral buoyancy (~15-70 m in CSLs, Fig. 2.2), where effort is not needed to maintain vertical position within the water column (Sato et al., 2013). COT and P_i are therefore expected to be quite variable during the bottom phase as a function of prey capture effort. This study removed this bottom phase variability and thus clarified the influence of vertical travel, which can be understood as the cost of accessing a targeted foraging zone.

Using Swim Speed to Prioritize P_i or COT According to Dive Depth

Swim speed is a major behavioral mechanism by which CSLs can respond to shifting oxygen management demands as a function of dive depth (Gallon et al., 2007; Watanabe et al., 2011; Trassinelli, 2016; Aoki et al., 2017), and it appears to contribute to the different trends of COT and P_i with dive depth (Fig. 2.5). Faster swimming requires elevated thrust (Eqn 1) and power output (P_o ; Eqn 7), but also increases the efficiency by which muscular metabolic energy input (P_i) is converted to P_o (Eqn 8). As swim speed was directly used to calculate P_i and COT in this study, the effect of swim speed on P_i and COT was not described statistically. Examining these relationships graphically, however, can help clarify the role of swim speed. With increasing dive depth, mean swim speed of most CSLs increased during both descent and ascent (Fig. 2.5A). This trend indicated that swim speed contributed to the increase in P_i and decrease in COT observed with increased dive depth (e.g. Fig. 2.4). Direct plots of P_i and COT against swim speed support this interpretation: in most CSLs, increasing mean swim speed was indeed associated with increasing mean P_i and decreasing mean COT when each was averaged over full descents and ascents (Fig. 2.5B). In fact, when all CSL data are pooled for ascents and descents, the mean swim speed at 25 m predicts low or minimized P_i and moderately elevated COT, whereas mean swim speed at 300 m predicts elevated P_i but low or minimized COT (Fig. 2.5A and B). Thus, the data qualitatively indicate that adult female CSLs generally transit vertically at speeds that prioritize cost savings in shallow dives and prioritize efficient travel in deeper dives.

The relationships between speed and P_i and COT (Fig. 2.5B) are consistent in value and trend to those reported in controlled respirometry studies with juvenile CSLs (Feldkamp, 1987b) and juvenile Steller sea lions *Eumetopias jubatus* (Rosen and Trites, 2002), even though subjects in those studies were swimming horizontally at neutral buoyancy. Using data published by Feldkamp (1987b), Miller et al. (2012) produced models of COT against swim speed that were similar to those presented here (Fig. 2.5B), but that showed a more pronounced U-shape and minimum COT. This difference likely stems from the use of a P_i to P_o efficiency conversion parameter (ϵ) that was assumed constant in Miller et al., (2012) rather than varying more than four-fold with observed speed as in this study and Feldkamp (1987b), and may also reflect an effect of buoyancy.

The Effect of Buoyancy on Swim Speed, P_i , and COT

At fine temporal scales (all 5 s intervals of ascents and descents combined), swim speed of most CSLs increases when buoyancy opposes swimming (Fig. 2.5C), suggesting that the effects of mean dive swim speeds on P_i and COT (explored above and in Fig. 2.5A and B) may be driven in part by behavioral responses to buoyancy across depth (by increasing the rate or force of strokes, e.g. Martín López et al., 2015; Tift et al., 2017). This trend is clear in 5 of the 8 CSLs; the others exhibited slower (C20 & C14) or faster (C16) swim speeds that did not clearly shift with buoyancy. The apparent importance of buoyancy to swim speed, COT, and P_i reported here aligns in some regards with theoretical and modeling work. The increase in swim speed as buoyancy hinders movement may support the Actuator Disc bioenergetic model (Weis-Fogh, 1972; Ellington, 1984; Miller et al., 2012), and bioenergetic modeling of diving dolphins and

Fig. 2.5. Relationships of swim speed with dive depth, swimming power (P_i), cost of transport (COT), and the effect of buoyancy. Straight red (descent) and black (ascent) lines in (A) and (B) indicate the overall observed mean swim speed for 25 m dives (solid lines) and 300 m dives (dashed lines). A) Mean ascent and descent swim speed plotted against dive depth. Dots represent full ascents or descents. Black curves show swim speed trends with depth when all CSL data is pooled. B) Mean P_i and COT as a function of mean swim speed for ascents and descents. Dots represent full ascents or descents. C) Swim speed (mean $\pm$ SE) binned by the magnitude (2 N bins) of aid or hinderance acting on CSLs. Dots represent 5 s intervals.

penguins by Trassinelli (2016), which both predict that the speed of minimum COT increases with deviation of body density from neutral. Since mean ρ_{CSL} during vertical transit increasingly deviates from neutral in dives below 50-80 m (Fig. 2.2), the swim speed that minimizes COT in CSLs should increase with dive depths below that point. Hence, CSLs should swim faster in deeper dives to minimize mean COT during vertical travel. Swim speeds in this study likely reflect this influence of buoyancy during deeper dives (when COT is prioritized), and a behavioral shift to slower speeds favoring lower P_i in shallow dives where oxygen management is less crucial.

Theoretical and modeling work also suggests that mean buoyancy affects round trip COT and P_i of breath-hold divers independently of swim speed. When swim speed is held constant, mean COT and P_i (or work) of vertical transit are both predicted to increase as mean dive body density (and thus buoyancy) deviates from neutral (Sato et al., 2010; Miller et al., 2012; Trassinelli, 2016). This is because the effort expended in the direction hindered by buoyancy is expected to outweigh the associated effort saved by gliding with the help of buoyancy (Miller et al., 2012; Trassinelli, 2016). Mean vertical transit ρ_{CSL} in this study becomes increasingly deviant from neutral in deep dives (most CSLs were neutrally buoyant at 15-50 m; e.g. Fig. 2.2), meaning the strong mean negative buoyancy of deep dives likely influenced COT and P_i independently of swim speed. P_i indeed increases with dive depth, but COT notably does not (Fig. 2.4), indicating that the behavioral effect of swim speed (Fig. 2.5B and C) likely overwhelmed the presumed effect of buoyancy.

The Influence of Body Condition and DLV

CSL buoyancy is influenced by tissue density and DLV; thus, body condition and inspired pre-dive air volume likely contribute to P_i and COT trends. Poor body condition (low blubber %) raises tissue density, likely causing neutral buoyancy to occur at shallower depths. This would increase the hinderance due to buoyancy during initial ascent in mid to deep dives, likely encouraging faster swimming behavior (Fig. 2.5C; predicted by Trassinelli, 2016) that results in raised P_i and lowered COT. This suspected behavioral effect would augment the direct increase in energy costs associated with a body density highly deviant from neutral (Sato et al., 2010, 2013; Miller et al., 2012; Adachi et al., 2014; Trassinelli, 2016).

DLV likely affects swim speed during initial descent, where a greater inspired air volume before diving (increased DLV) increases the hinderance due to buoyancy (Trassinelli, 2016). Because adult female CSLs often increase DLV with dive depth (McDonald and Ponganis, 2012), this effect is probably stronger in deeper dives. Increased hinderance from buoyancy, due to body condition, DLV, and dive depth, may therefore help explain the observed increase in mean ascent and descent speeds of deeper dives, thereby influencing trends of mean transit P_i and COT with dive depth (Fig. 2.4).

Behavioral Flexibility in Shallow Dives, and Inter-Individual Variability

Swim speed data also indicate widened behavioral flexibility in shallower dives (Fig. 2.5A), consistent with the interpretation that oxygen management increases in importance in dive depth and duration, and therefore drove changes in mean P_i and COT across depth (Figs. 2.4 & 2.5B). In this study, the range of observed ascent and descent speed

decreased with dive depth, narrowing around 2 m s^{-1} , a speed that corresponds to near-minimum COT (Fig. 2.5A). This may indicate increasingly strict adherence to transit strategies that minimize oxygen consumption in deeper dives. By comparison, observed descent speed in shallow dives varied widely (between $>0.5\text{-}3 \text{ m s}^{-1}$ in $\sim 25 \text{ m}$ dives), producing the full breadth of observed COT and P_i values (Fig. 2.5A and B). These shallow dives, generally of short duration (McDonald and Ponganis, 2014), are less likely to approach the limit of a CSL's oxygen stores (McDonald and Ponganis, 2013) and should thereby permit a widened range of swim speeds. This concept is supported by elevated variability in both oxygen depletion and heart rate in shallow dives compared with deep dives in CSLs (McDonald and Ponganis, 2013, 2014)

The effect of dive depth on P_i , COT, and swim speed, and the effect of buoyancy on swim speed, varied among individuals (Figs. 2.4, 2.5), highlighting the importance of behavioral differences among individuals. For each of these relationships, a minority of CSLs exhibited patterns that differed qualitatively from the overall trend. Most notably, individual C16 used elevated swim speeds averaging above 2 m s^{-1} across her full range of observed buoyancy (Fig. 2.5B), unlike all other CSLs in this study. This behavior likely explains her elevated mean thrust and P_i in shallow and mid depth dives relative to deep dives, which was also unique among the CSLs in this study (Fig. 2.4A).

Unsurprisingly, shallow dives to less than 100 m had the clearest variation in P_i and COT patterns among individuals (Fig. 2.4A). This variability, alongside sharp increases in mean COT in some CSLs (Fig. 2.4A), points to behavioral flexibility. High-activity foraging behavior such as prey pursuit could lead to increased vertical transit swim

speeds and associated changes in P_i and COT. Similarly, actively swimming when passive gliding is possible may allow CSLs to more rapidly access a prey patch, but would also lead to increased mean energetic cost of vertical travel (e.g. Williams et al., 2000).

Dive Depth and Foraging Strategy

Deep diving appears to be a high-risk energetic strategy, and the increased costs may affect CSL body condition, survivorship, and reproductive success. As shown here, deep dives produce elevated P_i (Fig. 2.4), which was maintained over an extended vertical transit duration and distance. This result provides mechanistic support for the recent finding by McHuron et al. (2018) that an increased prevalence of deep diving is associated with greater total energy costs (FMR) in CSLs that dive with a mixed depth strategy. In addition to increased swimming costs, these longer and deeper dives are more likely to require anaerobic metabolism, prolonging the subsequent surface interval needed for recovery, thereby reducing time spent foraging relative to energy spent (Kooyman et al., 1980; Ponganis et al., 1997; McHuron et al., 2016). These increased costs of deep diving add to the list of difficulties facing adult female CSLs in years of poor prey availability near rookeries. Anomalous oceanographic patterns during ENSO events have been associated with increasingly offshore travel in both male and female CSLs, and with deeper, longer duration dives, alongside early termination of lactation and increased adult mortality, in adult female CSLs (DeLong et al., 1991; Feldkamp et al., 1991; Trillmich et al., 1991; Weise et al., 2006; Melin et al., 2008). Change in prey availability and nutritional quality in these years has been linked to greater theoretical

energy requirements in adult female CSLs (McHuron et al., 2017) and decreased pup mass resulting in elevated CSL pup stranding and starvation (McClatchie et al., 2016). If shifted prey distribution indeed leads to deeper average diving in adult female CSLs, the resulting elevated P_i of these deep dives could potentially drive high FMR in deep-diving generalist individuals (McHuron et al., 2018), further compounding the energetic stress caused by low prey availability.

Given the elevated energetic cost, is deep diving a less preferable strategy for CSLs? CSLs are traditionally described as epipelagic divers, with a generalist epipelagic diet targeting nutritious schooling prey such as sardine (Antonelis et al., 1984; Feldkamp et al., 1989; Lowry et al., 1991; Lowry & Carretta, 1999; Orr et al., 2011; Melin et al., 2012; Kuhn and Costa, 2014; McHuron et al., 2016). However, dive depth and duration increase substantially during anomalously low prey availability (Feldkamp et al., 1991; Melin et al., 2008; Weise et al., 2010), and during seasonal drops in productivity (Villegas-Amtmann et al., 2011), suggesting CSLs prefer shallow diving when prey are abundant. Decreased abundance of shallow prey (i.e. McClatchie et al., 2016), therefore, may drive CSLs to rely more heavily on deep dives, potentially requiring CSLs to seek larger calorific rewards to make up for increased energetic costs of deep diving.

Alternatively, some CSLs may specialize in this high cost, high-reward strategy. CSLs use three main strategies: an epipelagic strategy, a mixed epipelagic/benthic strategy, and a deep diving strategy (Weise et al., 2010; Villegas-Amtmann et al., 2011; McHuron et al., 2016). Some adult female CSLs specialize in one strategy, whereas others switch freely between strategies (McHuron et al., 2016). Notably, deep-diving

specialists exhibited intermediate field metabolic rates (FMR), whereas the FMR of mixed-strategy foragers increased with dive depth (McHuron et al., 2016, 2018). Prey quality may contribute to these trends: deep mesopelagic divers likely target a consistent stock of mesopelagic fishes of greater nutritional quality at predictable locations, whereas the mixed epipelagic/benthic foragers appear to target less nutritious adult Pacific hake (*Merluccius productus*; Bailey et al., 1982; Lowry et al. 1991; Huynh and Kitts, 2009; Litz, 2010; Orr et al., 2011; Melin et al., 2012; McHuron et al., 2016, 2018). If mesopelagic prey are indeed both predictably available and of high quality, deep diving specialists may achieve lower FMRs by minimizing the dives needed to meet their energetic demands, despite increased costs while diving. For example, fin whales (*Balaenoptera physalus*) overcome increased energetic costs by increasing their energy intake four-fold in deeper dives (Friedlaender et al., 2019). Perhaps similarly to deep-diving CSLs, deep-diving and negatively buoyant long-finned pilot whales (*Globicephala melas*) appear to use a high-cost strategy, presumably seeking large energetic rewards (Aoki et al., 2017). Future studies combining fine-scale energetic cost estimates (as in this study) with prey capture data (i.e. from accelerometry and/or video) will help clarify the effects of dive depth, dive type (benthic, pelagic), and habitat on patterns of at-sea energy balance in CSLs and likely in other species.

Conclusions

Foraging costs in California sea lions are strongly tied to buoyancy at fine temporal scales, due to high tissue densities and compression of a moderate to high DLV (~57-100% TLC) during deep dives to >300 m. Depth of neutral tissue density varies widely

among individuals (~20-40 m; but one individual ~80 m) as a function of both tissue density and DLV, and this inter-individual variation is reflected in thrust and P_i trends with depth. Despite inter-individual variation, all CSLs exhibited thrust and P_i patterns that indicate a primary role of buoyancy in determining swimming cost in a given moment, with initial descent and the majority of ascent depths (below ~80 m) accounting for much of the dive cost.

CSLs appear to use swimming behavior that prioritizes cost saving (low P_i) in shallow dives and shifts gradually to favor travel efficiency (minimized COT) in deep dives. Buoyancy effects and the behavioral response of swim speed appear to drive the observed results. The high travel efficiency in deep dives allows CSLs to exploit prey in dives that approach limits of oxygen stores, but comes at the cost of greater energy spent per unit time. Deep diving may therefore be an energetically expensive strategy, although these costs could be buffered by a decreased dive rate or offset by increased energy gain as part of a high-cost, high-reward strategy.

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