Received Date: 01-Sep-2016

Revised Date : 20-Dec-2016

Accepted Date: 20-Dec-2016

Article type : Article

LRH: MARINE MAMMAL SCIENCE, VOL. **, NO. *, ****

RRH: SHORTER ET AL.: BIO-LOGGING TAGS FOR IMPROVED ANIMAL WELL-

BEING

A day in the life of a dolphin: Using bio-logging tags for improved animal health and well-being

K. ALEX SHORTER, 1 YUNLI SHAO, LAURO OJEDA, KIRA BARTON, Department of Mechanical Engineering, University of Michigan, Ann Arbor, Michigan 48109, U.S.A.; Julie Rocho-Levine, Dolphin Quest Oahu, Honolulu, Hawaii 96816, U.S.A.; Julie van der Hoop and Michael Moore, Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, U.S.A.

ABSTRACT

Little quantitative information on the behavior, health, and activity level of managed marine mammals is currently collected, though it has the potential to significantly contribute to management and welfare of these animals. To

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the <u>Version of Record</u>. Please cite this article as <u>doi: 10.1111/mms.12408</u>

This article is protected by copyright. All rights reserved

address this, high-resolution motion-sensing Digital Acoustic Recording Tags (DTAGs) collected data from animals under human care (n = 5) during their daily routine, and classification algorithms were used for gait analysis and event detection. We collected and examined ~57 h of data from five bottlenose dolphins (Tursiops truncatus). Day-scale changes in behavior and activity level were observed and diurnal changes were detected with lower activity at night (n = 1). During the day, animals spent about 70% of their time swimming. The deepest part of the lagoon is ~3 m and individual dives were typically shallow (~1 m) with the dolphins tending to utilize a fluke and glide gait pattern. Activity level was quantified using overall dynamic body acceleration. A significant relationship between normalized activity level and glide duration during different portions of the dive was measured; animals fluked more during descent and glided more during ascent. This could indicate that even during very shallow dives the dolphins use their positive buoyancy to improve energy economy.

Key words: persistent monitoring, gait, time budget, enrichment,
wellness, activity level.

Bio-logging devices or tags are frequently used to monitor the behavior of wild cetaceans. Data from these tags have resulted in discoveries about basic animal behavior and provide a means to quantify impact from human activity on marine mammals (Nowacek et al. 2007, Southall et al. 2008, Tyack 2009). These devices enable the quantification of normative behavior as well as offer insight into an animal's response to changing environmental conditions on a precise timeline (Johnson and Tyack 2003, Tyack et al. 2003, Nowacek et al. 2004). Importantly, these bio-logging devices are the only way to

record sophisticated behavioral information from animals that spend the majority of their time in an environment where direct behavioral observation is not always possible (Cooke et al. 2004, Ropert-Coudert et al. 2007, Johnson et al. 2009). Further, tag data combined with new analysis methods are enabling the quantification of foraging and locomotor efforts of animals, resulting in an improved ability to detect subtle responses and to interpret their biological significance (Johnson et al. 2004, Miller et al. 2004, Aguilar et al. 2008). While bio-logging devices are used widely with animals in the wild, their use with animals in human care has been limited.

Marine mammals garner tremendous public support, which is reflected by the growing whale-watching industry and the large number of visitors who travel to zoos and aquariums to view these animals. Some estimates put the worldwide number of visitors to zoos and aquariums as high as 700 million annually (Gusset and Dick 2011). Marine park and zoo animals in human care educate visitors about marine mammals, as well as provide facilities for rehabilitation and scientific research (Clayton et al. 2009). These organizations prioritize animal health and well-being. As such, observational monitoring and proactive animal management practices are an important element of daily animal care, in addition to routine preventative medical health assessment. What, when, and how much the animals eat, where and how the animals spend their time, and even social conspecific interactions are all monitored and managed by the staff caring for the animals. Current monitoring approaches tend to rely on qualitative behavioral observations recorded in daily logs. As such, direct measurement of animal behavior in a quantifiable

manner would provide an important additional tool to inform animal care.

Tags have been used with managed animals to collect biomechanics data during controlled experiments, but relatively little work has been conducted using bio-logging tags for long term monitoring of health and well-being (van der Hoop et al. 2014, Akiyama et al. 2015). Tag size and cost, as well as lack of algorithms to quantify motion, have all contributed to the limited use of these technologies with managed animals. Here we use a high-resolution motion-sensing digital acoustic recording tag (DTAG), to collect data from animals during their daily routines at Dolphin Quest Oahu, and develop classification algorithms to quantify the data (Johnson et al. 2000, Johnson and Tyack 2003). This work presents a set of analysis tools to describe the behavior of managed dolphins, offers new insights into behavior and has the potential to help enhance the overall health and well-being of managed animals. Although we use parameters and classification tools from existing literature (e.g., overall dynamic body acceleration (ODBA) or frequency analysis) (Shepard et al. 2008, McClune et al. 2014), the comprehensive automated algorithms that are developed for gait and event detection in this work along with the resulting analysis methodology represent an important contribution to the literature, and can be extended to data sets from other swimming animals.

METHODS

Experimental Facilities and Equipment

We studied the daily behavior of five Atlantic bottlenose dolphins (*Tursiops truncatus*) in human care at Dolphin Quest Oahu (Honolulu, Hawaii) (Table 1). The animals inhabit a system

of four lagoons separated by floating docks and underwater barriers that cover about 1,400 m². The largest area, the main lagoon, is about 750 m² (40 m in diameter) and 3.4 m deep (see Fig. 1a and b). The remaining lagoons are 360 m^2 , 190 m^2 , and 120 m^2 m², with each of the smaller pools having a deepest point of ~2.4 m. Six deployments were conducted with five of the six dolphins at Dolphin Quest Oahu (Table 1). The trials were conducted between 23 and 27 September 2013, and during an additional deployment conducted on 10 March 2015. These deployments are referred to as TT1-TT6 in the text, with the TT02 and TT06 data recorded from the same animal. For all of the deployments (TT01-TT06), the tag was attached to the back of the animal ahead of the dorsal fin (see Fig. 1c). For five of the trials (TT02-TT06), the tags were attached between 0800 and 1000 and removed from the animals between 1500 and 1700. For the sixth trial (TT01), the tag was placed on the animal in the afternoon and removed the following day, providing a record of activity level during the day and night. The tag location was selected to replicate the location of tags placed on wild animals in Sarasota Bay (Wells et al. 2013). The animals' daily routines were not modified during these trials, enabling the opportunistic collection of a range of behaviors such as: selfselected swimming, human trainer interactions, enrichment activities, and conspecific interactions.

The DTAG (version 3) is approximately 150 mm in length, with four silicon rubber suction cups used to create a secure attachment to the animal. The 64 GB of memory and 500 mAh lithium-polymer battery enable continuous day scale recordings. The DTAG contains a 3-axis accelerometer (Kionix KXSC7, range \pm 6 g), 3-axis magnetometer (Honeywell HMC1043, \pm 6 Gauss), a

pressure sensor (Keller Series PA L3, range 200 bar), custom stereo hydrophones, and a temperature sensor. During a deployment, the accelerometers were sampled at 250 Hz to capture dynamic animal behavior, while the magnetometer was sampled at 125 Hz, and the pressure and temperature were sampled at 25 Hz. All sensor data were then resampled to a uniform 25 Hz for processing. The animal's swimming depth was estimated by the pressure sensor. Additionally, pitch, roll, heading, and ODBA were estimated using a combination of accelerometer and magnetometer sensor data and used to parameterize behavior (Johnson and Tyack 2003, Wilson et al. 2006). ODBA is a method that has been widely adopted by researchers to estimate specific acceleration components of tagged animals. Because of the availability of accelerometer tags, accelerometer data have been used to characterize a diverse range of behaviors including: diving (Laich et al. 2008, Mitani et al. 2010, Ropert-Coudert et al. 2009), swimming (Miller et al. 2004), feeding (Wisniewska et al. 2014), and breathing (Okuyama et al. 2009). Classification Methods

To identify animal behavior, we developed a supervised classification method that automatically clustered data into segments based on behavioral classes defined using observations (Watanabe *et al.* 2005, Halsey and White 2010, Okuyama *et al.* 2009).

Surface event detection—In our analysis, the signals were first segmented into periods when the animal was either underwater or at the surface using depth estimations from the pressure sensor. An extended period (>5 s) when the animal was within 0.45 m of the surface was classified as a surface event. The 0.45 m threshold was selected based on direct observation of

the animal and inspection of the depth estimates. Extended periods of time at the surface often occurred when the animal was interacting closely with the training staff. A detailed behavioral analysis at the surface was outside the scope of this work.

Dives and swimming behavior-A dive was defined as a period of underwater (>0.45 m) swimming between two surfacing events. To facilitate within-animal and between-animal comparisons, temporal and spatial parameters were identified for each dive. Dive depth was defined as the maximum depth reached during the dive, and dive time as the time between surfacing events. Each dive was divided into three intervals following a surfacing event: descent, bottom time and ascent (Sato et al. 2003, Miller et al. 2004). Respiration often occurs during surfacing, while fluking and gliding occur during the underwater intervals. Descriptive parameters to quantify animal behavior were calculated using data from each interval, facilitating statistical analysis and class detection with supervised classification. Pressure measurements were used to identify periods of descent and ascent for each dive. Descent was initiated after a surfacing event and was defined as the interval beginning after the animal reached a depth of at least 0.45 m and ending at the first local minimum in the pressure measurement. The ascent was defined as the period between the last local pressure minimum and the next surfacing event. Time at the bottom occurred between the end of the descent and the beginning of the ascent. Time durations for the descent, bottom, and ascent were calculated for each dive. A representative dive with identified behavioral classes is presented in Figure 2a.

Fluke detection—Surge acceleration data measurements along the length of the animal in the direction of swimming were used to identify fluking (see Fig. 2b). As the dolphins swam, periodic oscillations were observed in the surge accelerations. The behavioral signature in the data was used to identify the frequency and magnitude of the stroke. A representative sinusoidal function was used to model fluke stroke ($A_{\rm fluke}$).

$$A_{\text{fluke}} = \alpha_{\text{dom}} \sin(s\pi f_{\text{dom}} t + \varphi) \tag{1}$$

In Equation (1), α_{dom} represents the dominant amplitude, f_{dom} is the dominant frequency of oscillation, φ is the phase shift, and t is time. A bout of fluking was defined by two or more consecutive cycles. Synchronized video and tag recordings of animals performing straight-line swimming tasks were used as training data to create and evaluate the fluking identification template. Specifically, our training data consisted of periods of time when the dolphin swam continuously between two trainers located about 50 m apart. Data from one leg of a straight-line swimming trial is presented in Figure 2.

Expertly identified periods of fluking in the surge acceleration data were used to calculate the parameters for the fluking template. Ten fluking intervals, each with several consecutive fluke strokes, were selected using visual inspection of the surge acceleration data (Fig, 3a, b). The dominant frequency (f_{dom}) and amplitude (α_{dom}) were calculated from each interval (see Fig. 3c, d) to form the template parameters. A discrete Fourier transform was used to identify the dominant frequency in a given bout of fluking, and binned peak values were used to determine the dominant amplitude of the fluking signal. The example parameters from the data presented in Figure 3 are shown in Table 2. During classification, data that fell

within an error band of twice the standard deviation was used to identify fluking. Identified bouts of fluking were then further parameterized using: average pitch angle, average surge acceleration, variability of the surge acceleration, dominate fluking frequency, and dominant amplitude of the surge acceleration. Additionally, Overall Dynamic Body Acceleration (ODBA) was used to estimate the specific acceleration of the animal during swimming. ODBA values were also normalized for between animal comparisons during the ascent, bottom, and descent portions of the dive with duty factor.

$$\overline{ODBA_{ij}} = \frac{ODBA_{ij}}{\frac{1}{3} \sum_{j=1}^{3} ODBA_{ij}}$$

In Equation (2), i corresponds to the individual animal and j represents the swimming event (e.g., ascent, bottom, descent).

Glide detection—Gliding in the data was identified from surge acceleration, with extended periods of smooth acceleration indicative of a glide. A gliding event occurred when the time interval between two peaks in the surge acceleration exceeded 1.5 times the dominant fluking period ($t_{\rm gap} > 1.5 \times 1/f_{\rm dom}$). The threshold was selected iteratively using expert—identified periods of gliding and video recordings of behavior. An example is shown in Figure 2b, where the glide begins during the bottom phase of the dive and continues through the animal's ascent. The duty factor (DF), gliding time divided by total length of the phase, was used to characterize the percentage of time that the animals spent gliding.

Statistical analysis—We performed statistical tests to examine differences in ODBA and duty factor as a function of the dive phase (descent, time at the bottom, ascent), using repeated measures ANOVA (α = 0.05). A post hoc Tukey's test was used to examine differences in discrete conditions. Linear regression was used to test significance of linear dependence between normalized ODBA and duty factor.

RESULTS

Animal Time Budgets

For the approximately 57 h of recorded data, the animals spent more time under water than at the surface with training staff or between dives (Fig. 4). For this work, dolphin behavior was divided into two major classes: swimming and surfacing events. Detailed time budgets are presented in Figure 5, with the 24 h tag data set for animal TT01 further detailed in Figure 6. During a typical day, the animals spent roughly 72% of their time swimming. Swimming was further segmented into individual dives, with the dive times segmented into periods of fluking (23%), gliding (17%), surfacing (6%), and other/unidentified (26%). In addition to swimming, the dolphins spent approximately 28% of their time in a surfacing event, typically while working closely with a trainer.

Overnight tag data from TT01 were used to provide a qualitative comparison between day and night activity levels (Fig. 6). During this trial, the tag became detached from the animal for about three hours beginning at ~1900. The tag was retrieved from the lagoon and placed back on the animal at ~2215 for the remainder of the trial. The data during the period of detachment were excluded from the analysis. Estimates of ODBA indicate that the animal was more active during the day than at

night, and that activity levels began to increase again at sunrise (~ 0600). In addition to the lower ODBA measurements, the animal appears to spend slightly more time swimming at night (87% vs. 81%) with longer and more frequent periods of gliding (41% vs. 29%) compared to during the day.

Swimming Analysis

Swimming data were segmented into a series of individual dives, and then further divided into periods of descent, time at the bottom, and ascent. Table 3 presents the summary measures (mean ± SD) for 600 dives collected during the six tag deployments. On average, the dives lasted about 22 s and were relatively shallow (around 1 m). Dives tended to be characterized by a period of slow descent $(5.3 \pm 1 \text{ s})$, time at the bottom of the dive $(8.4 \pm 3 \text{ s})$, and a slow ascent $(4.7 \pm 1 \text{ s})$ s). During the dives, bouts of fluking with interspersed periods of gliding were observed as the animals swam in the lagoons. Duty factor was used to quantify the percentage of time spent gliding during each portion of the dive; higher duty factors indicate more gliding during a period of swimming. The length of the dive had a significant effect on both ODBA and duty factor (ODBA: P = 0.0002; duty factor: P = 0.0001; repeated measures ANOVA). Duty factor was significantly higher during the ascent (0.52 ± 0.1) than during either time at the bottom (0.34 ± 0.08) P = 0.0049) or the descent (0.2 ± 0.08, P = 0.0021). ODBA was significantly higher during the descent $(0.56 \pm 0.06 g)$ than during the bottom of the dive $(0.53 \pm 0.07 g)$ or the ascent $(0.50 \pm 0.05 \, g, P = 0.0002; \text{ Table 3}). \text{ Normalized ODBA and duty}$ factor were significantly correlated (P = 0.0011; $R^2 = 0.50$; Fig. 7); a decreasing trend in normalized ODBA during the different portions of the dives was observed. As duty factor increases,

normalized ODBA decreases, indicating that the dolphins tend to fluke more on the descent and glide more on the ascent. Tag data also has the potential to identify changes in animal gait and behavior during structured enrichment activities. Figure 8 shows an example where the magnitude of an individual animal's recorded acceleration is three times larger during a structured boat following task than during self-selected swimming.

DISCUSSION

The work presented here provides a methodology for systematic monitoring of animals in human care. Working with managed animals offers the unique opportunity to develop motion profiles specific to an individual in a consistent environment. The ability to provide quantitative information, currently not readily available for managed marine mammals, about behavior, health, and relative activity level has the potential to significantly enhance the management and overall welfare of these animals. Here we presented tools and techniques to enable persistent monitoring, as well as data sets for the formulation of behavioral parameters for the resident animals at Dolphin Ouest Oahu.

During a typical day (24 h) the Dolphin Quest animals spend ~3 h engaging in session activities, including in-water encounters with guests, and the remaining ~21 h free-swimming in their habitat with different social mates and occasionally (no more than 30 min at a time) solo. Session activities are varied on a daily basis and consist of combinations of five different session types: learning, exercise, play, gating, and husbandry. Learning sessions focus on mental stimulation and physical exercise. Exercise sessions are structured around physical exercise and enrichment. Play sessions emphasize physical

exercise, enrichment, and mental stimulation. Gating sessions encourage environmental exploration and fission fusion of social groups. Husbandry sessions develop mental stimulation and facilitate medical assessments by training the animals to participate in health assessment protocols. Information about how the animals perform during sessions and use their environment are particularly important for the staff who are continually working to optimize animal wellness.

Currently, wellness is assessed behaviorally, socially and medically for the animals. A daily assessment of the quality of the animals' engagement with their trainers during all sessions is used to assess behavioral wellness. The trainers and staff also observe and record daily observations on animal interactions with their social mates. Strong social alliances, interactions and breeding are all signs of social wellness. Regularly scheduled blood, fecal, chuff, gastric, and urine samples are collected and analyzed to create baseline values that are used during medical assessments of health and wellness. To complement these measures of wellness, tag data can now be used to investigate and quantify swimming behavior in the lagoon environment.

In this work, we collected ~57 h of data from five of the six animals in the habitat during both session actives and free swimming. Swimming typically consisted of 20 s dives to depths of around a meter. During these dives the animals tended to employ a fluke and glide gait pattern, but the percent of gliding within the gait (duty factor) differed during dive phase (e.g., descent, time at the bottom, and ascent). Tagged animals had the highest ODBA values and lowest duty factor during the descent, and the lowest ODBA values and largest duty factor

during the ascent (Fig. 7 and Table 3). This could be an indication that the animals were using their positive buoyancy to improve energy economy as they came to the surface between dives.

Modified swimming behavior in response to buoyancy has been observed in other marine mammals (Nowacek et al 2001, Miller et al. 2004, López et al. 2015). Positive buoyancy forces are created by soft tissue (e.g., blubber) and air carried in the lungs. These forces directly oppose downward swimming motion during a dive. However, at depth, ambient pressure created by the water column compresses air in the animal's lungs resulting in negative buoyancy. During the descent portion of the dive, animals will fluke to overcome their positive buoyancy until they become negatively buoyant. At this point the animals will reduce fluking rates and spend more time gliding to their desired depth, resulting in improved energy economy. During the ascent the opposite occurs; animals fluke until they become positively buoyant and then tend to glide to the surface. In our work, we observed the Dolphin Quest animals, in their shallow water environment, gliding more often as they came to the surface between dives. Descents to >1 m will cause less than a 1.5 psi change in ambient pressure, likely having little effect on buoyancy. As such, it is unlikely that changes in lung volume are driving the change in gait observed with the Dolphin Quest animals; instead, the dolphins are likely overcoming their positive buoyancy on descent and then taking advantage of it on ascent (Williams et al. 2000, Aoki et al. 2011). This may indicate that shallow water animals take advantage of buoyancy to improve swimming efficiency.

The results presented here indicate that animals at Dolphin Quest Oahu spend ~72% of their time swimming, during which 40% of the time is spent actively fluking and gliding, 6% surfacing, and 26% classified as unidentified behavior, with dives averaging 22 s. While time budgets for wild dolphins calculated using the types tags and analysis algorithms described here have yet to be published, these results can be compared to others in the literature. Wild dolphins have been observed spending ~50%-60% of time traveling, ~15%-20% feeding, and ~15%-20% milling about (Hanson and Defran 1993, Powell and Wells 2011, Wells et al. 2013). Resting behaviors may be population variability (e.g., Hanson and Defran 1993) but other studies have observed animals resting for 7%-18% of time (Wells et al. 2013). Average dive times for coastal Tursiops spp. range from 20 s to 40 s (reviewed in Shane 1990, Mate et al. 1995). Our future work will be directed at applying the types of analysis presented here to data collected from similar tags on wild animals.

In addition to swimming classification, changes in behavior related to activity in and around the animal's environment were evident in the data. While the conclusions that can be made from these data are limited by factors such as small sample size (n = 5) and skewed sampling (only one night recording), they are the first of their kind for dolphins in a managed environment. For example, there was a large drop in average ODBA shortly after noon Hawaii Standard Time (HST) corresponding to a period when the trainers left the lagoon area and no structured activities where conducted with the animals (Fig. 5a). Activity levels then increase in the afternoon as the trainers returned to continue the animal's planned behavioral program. Tag data may also be used to detect diurnal changes in animal behavior, and examples

were observed in the single day scale data record presented in Figure 6. The animal's average ODBA level was lower throughout the night, and then steadily increased at sunrise. ODBA continued to increase as the training staff arrived on site (~0730) and the animals began their behavioral program (~0900). The increased swimming time observed at night could be the result of the lack of structured time with the trainers during this period. While these are just examples from two animals that may be subject to individual variation, they illustrate the potential for tag-based persistent monitoring to identify day-scale trends in the activity levels.

The findings and techniques presented here offer unique insights into these animals' behavior, with and without trainers present, but are subject to limitations. The tags used to collect data from the animals increase hydrodynamic loading as the animals swim. Simulation and experimental work has been used to show that the tags generate about ~5 N of drag on simplified geometry at swimming speeds (3 m/s) that are in the range of those observed with the animals at Dolphin Quest (Shorter et al. 2014). Even though this is a relatively small amount of additional drag, we cannot say for sure that it did not affect the behavior of the animals (van der Hoop et al. 2014). Most data were collected at the same time of year with only one overnight data recording. In order to draw stronger conclusions about animal behavior, more tag data from different seasons and times of day will need to be collected. Further, the tags collect both acoustic and movement data, and our classification algorithms were mostly limited to the identification of swimming events. Thus, future work will be directed at including acoustic data in the analysis and identifying more behaviors in the data

to form a more complete picture of how animals in the cohort may contribute to changes in focal animal behavior.

Additionally, the ability to infer behavior from tag data in this work was limited by the single point measurements on the animal's body. For example, tag data were used to identify when the animals were fluking and even the frequency of the motion. But, we were not able to quantify the amplitude of the stroke at the fluke or the relative phasing between the motion of the fluke and the body. Additionally, information about how the animal was maneuvering in the environment was limited to the orientation of the body. The ability to quantify how much time the animals are swimming in a straight line compared to time spent turning would provide additional perspective about how the animals are using their habitat and could inform habitat and pool design. While it is not possible to localize the animal in the pool with tag data alone, our future work will involve integrating positional updates from pool-mounted overhead cameras with the tag data to improve spatial localization.

Future work may also involve the use of tag data for the assessment of long- and short-term effects of enrichment and training activities. Environmental enrichment is used to increase animal activity and improve animal welfare (Mason et al. 2007). During some of the tag deployments presented in this work, the animals were trained to follow a remote-controlled boat in circular loops around the lagoon. When tag data collected during the trained behavior were compared directly with a period of unstructured swimming, the accelerometers measured three times more motion during enrichment (Fig. 8 top). The increased activity level could be due to the faster swimming speed and the use of a continuous fluking gait to keep up with

the boat, as opposed to the self-selected fluke and glide gait observed during unstructured swimming (Fig. 8 bottom). This brief example demonstrates the ability to use tag data to provide quantitative information about how the biomechanics of the animal may be modified in response to trained behavior.

The combination of traditional qualitative behavioral observations made by the training staff, combined with quantitative behavioral measures made possible by bio-logging tags and analysis algorithms have the potential to significantly enhance the care, overall health and well-being of these animals. It is possible that these tags would also derive useful information about the recovery of animals if being treated medically. In this work, we demonstrated tools and a structured methodology that can be used to provide objective and quantifiable measures of the behavior of bottlenose dolphins in human care. The data collected and analyzed here provide a baseline behavioral record that can be used to facilitate future work. Importantly, five of the six animals present at the Dolphin Quest Oahu facility were successfully trained to wear the tag for extended periods of time. This will enable future studies that examine behavioral changes in the presence of environmental or seasonal changes. Further, the ability to tag multiple animals in the lagoon environment will offer unique insights into social conspecific interactions between the resident animals.

ACKNOWLEDGMENTS

The authors give special thanks to Dolphin Quest Oahu whose dolphin interactive facility at The Kahala Hotel and Resort served as a critically important controlled environment for this study. The collection of these data for the benefit of wild

populations would not have been possible without the support of Dolphin Quest, their expert animal behaviorists and the amazing animals in their care. Additionally, we would also like to thank Ding Zhang for his assistance with this work. The study protocol was approved by WHOI Institutional Animal Care and Use Committee.

This project was funded by the National Oceanographic Partnership Program (National Science Foundation *via* the Office of Naval Research N00014-11-1-0113). Dolphin Quest provided kind support of animals, crew, and access to resources.

LITERATURE CITED

- Aguilar de Soto, N., M. P. Johnson, P. T. Madsen, F. Díaz, I. Domínguez, A. Brito and P. Tyack. 2008. Cheetahs of the deep sea: Deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). Journal of Animal Ecology 77:936-947.
- Akiyama, Y., Y. Matsuda, N. Sakurai and K. Sato. 2015.

 Evaluation of wave drag on bottlenose dolphin *Tursiops*truncatus from swimming effort. Coastal Marine Science
 38:42-46.
- Aoki, K., Y. Y. Watanabe, D. E. Crocker, et al. 2011. Northern elephant seals adjust gliding and stroking patterns with changes in buoyancy: Validation of at-sea metrics of body density. Journal of Experimental Biology 214:2973-2987.
- Clayton, S., J. Fraser and C. D. Saunders. 2009. Zoo experiences: Conversations, connections, and concern for animals. Zoo Biology 28:377-397.

- Cooke, S. J., S. G. Hinch, et al. 2004. Biotelemetry: A mechanistic approach to ecology. Trends in Ecology and Evolution 19:334-343.
- Gusset, M., and G. Dick. 2011. The global reach of zoos and aquariums in visitor numbers and conservation expenditures.

 Zoo Biology 30:566-569.
- Halsey, Lewis G., and Craig R. White. 2010. Measuring energetics and behaviour using accelerometry in cane toads *Bufo marinus*. PLoS ONE 5(4):e10170.
- Hanson, M. T., and R. H. Defran. 1993. The behavior and feeding ecology of the Pacific coast bottlenose dolphin, *Tursiops truncatus*. Aquatic Mammals 19:127-127.
- Johnson, M. P., and P. L. Tyack. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE Journal of Oceanic Engineering 28:3-12.
- Johnson, M., P. Tyack, D. Nowacek and A. Shorter. 2000. A digital acoustic recording tag for measuring the response of marine mammals to sound. The Journal of the Acoustical Society of America 108:2582-2583.
- Johnson, M., P. T. Madsen, W. Zimmer, N. Aguilar De Soto and P. L. Tyack. 2004. Beaked whales echolocate on prey.

 Proceedings of the Royal Society B, 271:S383-S386.
- Johnson, M., N. Aguilar de Soto and P. T. Madsen. 2009. Studying the behaviour and sensory ecology of marine mammals using acoustic recording tags: A review. Marine Ecology Progress Series 395:55-73.
- Laich, A. G., R. P. Wilson, F. Quintana and E. L. C. Shepard. 2008. Identification of imperial cormorant Phalacrocorax

- atriceps behaviour using accelerometers. Endangered Species Research 10:29-37.
- López, L. M. M., P. J. O. Miller, N. Aguilar de Soto and M. Johnson. 2015. Gait switches in deep-diving beaked whales: Biomechanical strategies for long-duration dives. Journal of Experimental Biology 218:1325-1338.
- Mason, G., R. Clubb, N. Latham and S. Vickery. 2007. Why and how should we use environmental enrichment to tackle stereotypic behaviour? Applied Animal Behaviour Science 102:163-188.
- Mate, B. R., K. A. Rossbach, S. L. Nieukirk, R. S. Wells, A. B. Irvine, M. D. Scott and A. J. Read. 1995. Satellitemonitored movements and dive behavior of a bottlenose dolphin (*Tursiops Truncatus*) in Tampa Bay, Florida. Marine Mammal Science 11:452-463.
- McClune, D. W., N. J. Marks, R. P. Wilson, et al. 2014. Triaxial accelerometers quantify behaviour in the Eurasian badger (Meles meles): Towards an automated interpretation of field data. Animal Biotelemetry 2:5.
- Miller, P. J. O., M. P. Johnson, P. L. Tyack and E. A. Terray. 2004. Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. Journal of Experimental Biology 207:1953-1967.
- Mitani, Y., R. D. Andrews, K. Sato, A. Kato, Y. Naito and D. P. Costa. 2010. Three-dimensional resting behaviour of northern elephant seals: Drifting like a falling leaf.

 Biology Letters 6:163-166.
- Nowacek, D. P., M. P. Johnson, P. L. Tyack, K. A. Shorter, W. A. McLellan and A. Pabst. 2001. Buoyant balaenids: The ups and

- downs of buoyancy in right whales. Proceedings of the Royal Society of London B: Biological Sciences 268:1811-1816.
- Nowacek, D. P., M. P. Johnson and P. L. Tyack. 2004. North

 Atlantic right whales (*Eubalaena glacialis*) ignore ships
 but respond to alerting stimuli. Proceedings of the Royal

 Society of London B: Biological Sciences 271:227-231.
- Nowacek, D. P., L. H. Thorne, D. W. Johnston and P. L. Tyack.

 2007. Responses of cetaceans to anthropogenic noise. Mammal
 Review 37:81-115.
- Powell, J. R., and R. S. Wells. 2011. Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. Marine Mammal Science 27:111-129.
- Okuyama, J., Y. Kawabata, Y. Naito, N. Arai and M. Kobayashi.

 2009. Monitoring beak movements with an acceleration
 datalogger: A useful technique for assessing the feeding
 and breathing behaviors of sea turtles. Endangered Species
 Research 10:39-45.
- Ropert-Coudert, Y., M. Beaulieu, N. Hanuise and A. Kato. 2009.

 Diving into the world of biologging. Endangered Species

 Research 10:21-27.
- Sato, K., Y. Mitani, M. F. Cameron, D. B. Siniff and Y. Naito. 2003. Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. Journal of experimental Biology 206:1461-1470.
- Shane, S. H. 1990. Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. Pages 541-558 in S. Leatherwood and R. R.

- Reeves, eds. The bottlenose dolphin. Academic Press, San Diego, CA.
- Shepard, E. L. C., R. P. Wilson, L. G. Halsey, et al. 2008.

 Derivation of body motion via appropriate smoothing of acceleration data. Aquatic Biology 4:235-241.
- Shorter, K. A., M. M. Murray, M. Johnson, M. Moore and L. E. Howle. 2014. Drag of suction cup tags on swimming animals:

 Modeling and measurement. Marine Mammal Science 30:726-746.
- Southall, B. L., A. E. Bowles, W. T. Ellison, et al. 2008.

 Marine mammal noise-exposure criteria: Initial scientific recommendations. Bioacoustics 17:273-275.
- Tyack, P. L. 2009. Effects of human-generated sound on marine mammals. Physics Today 62:39-44.
- Tyack, P., J. Gordon and D. Thompson. 2003. Controlled exposure experiments to determine the effects of noise on marine mammals. Marine Technology Society Journal 37:41-53.
- van der Hoop, J. M., A. Fahlman, T. Hurst, J. Rocho-Levine, K. A. Shorter, V. Petrov and M. J. Moore. 2014. Bottlenose dolphins modify behavior to reduce metabolic effect of tag attachment. Journal of Experimental Biology 217:4229-4236.
- Watanabe, S., M. Izawa, A. Kato, Y. Ropert-Coudert and Y. Naito. 2005. A new technique for monitoring the detailed behaviour of terrestrial animals: A case study with the domestic cat. Applied Animal Behaviour Science 94:117-131.
- Wells, R., K. A. McHugh, D. C. Douglas, S. Shippee, E. J. B. McCabe, N. B. Barros and G. T. Phillips. 2013. Evaluation of potential protective factors against metabolic syndrome in bottlenose dolphins: Feeding and activity patterns of

dolphins in Sarasota Bay, Florida. Frontiers in Endocrinology 4:139.

- Wilson, R. P., C. R. White, F. Quintana, L. G. Halsey, N. Liebsch, G. R. Martin and P. J. Butler. 2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. Journal of Animal Ecology 75:1081-1090.
- Wisniewska, D. M., M. Johnson, P. E. Nachtigall and P. T.

 Madsen. 2014. Buzzing during biosonar-based interception of prey in the delphinids *Tursiops truncatus* and *Pseudorca crassidens*. Journal of Experimental Biology 217:4279-4282.
- Williams, T. M., R. W. Davis, L. A. Fuiman, et al. 2000. Sink or swim: Strategies for cost-efficient diving by marine mammals. Science 288:133-136.

Received: 1 September 2016

Accepted: 20 December 2016

Figure 1. (A) A dimensioned illustration of the main lagoon with the depth shown in meters, and a sketch of a lagoon cross-section (red line) is shown below the main lagoon with depth in meters. (B) A photo of the main Dolphin Quest lagoon. (C) The tag shown on a bottlenose dolphin with dimensions in millimeters. Tags were placed on the dorsal side of the animal between the dorsal fin and the blow hole.

Figure 2. An example of a straight-line swimming behavior used to develop the template for identifying fluking motions in the tag data. (A) Depth data from the pressure sensor for one dive; (B) Surge acceleration during the dive with periods of fluking and gliding; (C) Pitch calculated from the tag sensors with a representative fluke cycle highlighted in red; (D) Pitch

during the representative fluke cycle with an illustration of the corresponding animal posture.

Figure 3. Representative example of the data used to create the template used for fluke detection TT06). (A) Acceleration data from a full day trial; (B) a representative bout of fluking (*); (C) FFT of the bout of fluking; and (D) a histogram used to identify the amplitude used in the fluking template.

Figure 4. A histogram of 57 h of pressure data for all six tag deployments from the five animals. Data has been separated into time at the surface (black), as defined by the $0.45~\mathrm{m}$ threshold, and time underwater.

Figure 5. (A) Overall activity trends for a representative animal (TT06). Both the time series ODBA signal and the half-hour average ODBA values are plotted against local time of day.

(B) Normalized time budget for the animals during swimming, with the percentage of time spent fluking, gliding, and surfacing separately identified. Local time (HST) is shown on the plot.

(C) The percentage of time surface events were detected in the data. A surface event was defined as an extended period of time (>5 s) when the animal was at the surface (<0.45 m). Data from the six tagged animals is presented along with the average time budget for all the animals.

Figure 6. (A) Overall activity trends for TT01 during a nearly 24 h period. Both the time series ODBA signal and the half-hour average ODBA values are plotted against local time of day. Normalized time budgets that capture the percentage of time the animal spent performing certain classified behaviors are also presented for both the day and night. Local time (HST) is shown on the plot. (B) Time budgets for the animal during swimming, percentage of time spent fluking, gliding, and

surfacing. (C) The percentage of time surface events were detected in the data. A surface event was defined as an extended period of time (>5 s) when the animal was at the surface (<0.45 m).

Figure 7. Normalized ODBA plotted against average duty factor for each of the six tag deployments during the segmented descent, bottom, and ascent phases of the dive. Larger duty factors indicate more gliding during a period of swimming. As the duty factor increases average ODBA decreases and the dolphins tend to fluke more on the descent and glide more on the ascent.

Figure 8. Example data comparing animal behavior during a novel enrichment activity, following a remote controlled boat, and a period of free swimming. The top plots compare the magnitude of the acceleration measured by the tag. The bottom plots present a subset of the pitch estimates for the animals. The pitch data can be used to identify different gaits used by the animals. In this case, the animal had to employ a continuous fluking gait to follow the boat, but self-selected a fluke and glide gait during the period of free swimming presented.

Table 1. Information about the animals and the tag duration for each data set.

Tag ID	Animal ID	Age	Sex	Mass (kg)	Length (m)	Tag on (HST)	Tag off	Duration
TT01	90N6	15	Male	179	2.5	1557	1409	23 h 12 min ^a
TT02	99L7	13	Male	165	2.5	838	1643	8 h 5 min

¹ Corresponding author (e-mail: kshorter@umich.edu).

TT03	01L5	18	Male	155	2.4	947	1615	5 h 28 min
TT04	63Н4	22	Male	182	2.5	822	1654	8 h 32 min
TT05	9FL3	28	Male	247	2.7	839	1540	7 h 1 min
TT06	99L7	15	Male	171	2.6	906	1635	7 h 29 min

^a The tag became detached for 3 h during data collection.

Table 2. Dominant frequency $(f_{\rm dom})$ and amplitude $(\alpha_{\rm dom})$ of 10 selected fluking intervals from an example trial (TT06). An error band of twice the standard deviation was used to define the limits for the template 0.95 Hz (± 0.36) and 0.26 g (± 0.08).

Interval	f _{dom} (Hz)	$\alpha_{ ext{dom}}$ (g)
1	0.83	0.23
2	1.03	0.28
3	0.79	0.23
4	0.63	0.19
5	1.05	0.27
6	1.19	0.31
7	1.12	0.27
8	0.81	0.22
9	1.02	0.28
10	1.09	0.30
Average	0.95	0.26
SD (σ)	0.18	0.04

Table 3. Summary parameters of entire dives and portions of dives (descent, bottom, ascent) used to quantify swimming behavior from the data collected during the study. The mean and standard deviation (SD) for the different sections of the dives are presented for both the individual trails (TT1-TT6) and for the group. See text for abbreviations.

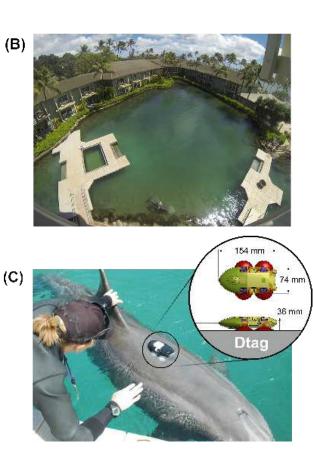
ISO	TT01	TT02	TT03	TT04	TT05	ТТ06	Group average
Dives							
Depth (m)	1.3 (0.5)	0.9 (0.4)	1.2 (0.4)	1.1 (0.5)	1.1 (0.4)	1.1 (0.5)	1.1 (0.1)
Durations (s)	21.8 (17.4)	13.7 (8.5)	27.2 (11.7)	25.3 (12.8)	24.8 (15.6)	18.0 (9.4)	21.8 (5.1)
Descent							
Duty Factor	0.33 (0.33)	0.20 (0.24)	0.24 (0.28)	0.18 (0.25)	0.17 (0.27)	0.10 (0.21)	0.20 (0.08)
$ODBA\left(g ight)$	0.63 (0.40)	0.56 (0.36)	0.57 (0.31)	0.51 (0.30)	0.48 (0.29)	0.61 (0.33)	0.56 (0.06)
$f_{\sf dom}$ (Hz)	0.89 (0.40)	0.95 (0.45)	0.89 (0.71)	0.87 (0.49)	0.89 (0.39)	0.97 (0.28)	0.91 (0.04)
$lpha_{dom}\left(g ight)$	0.23 (0.08)	0.26 (0.08)	0.20 (0.06)	0.24 (0.06)	0.24 (0.07)	0.27 (0.07)	0.24 (0.02)
Duration (s)	5.1 (4.0)	4.5 (4.0)	6.3 (3.2)	6.2 (3.7)	5.5 (3.5)	4.2 (3.0)	5.3 (0.9)
Bottom							

This article is protected by copyright. All rights reserved

Γ	4	3	3	4	1	_	2	C
L	т.	J	J	ı			4	_

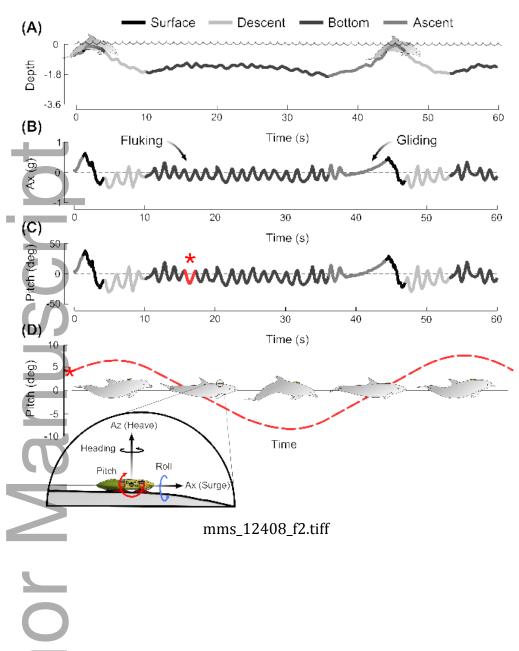
Duty Factor	0.40 (0.30)	0.37 (0.38)	0.37 (0.33)	0.40 (0.36)	0.32 (0.29)	0.20 (0.27)	0.34 (0.08)
ODBA (g)	0.59 (0.39)	0.57 (0.36)	0.57 (0.34)	0.46 (0.29)	0.42 (0.25)	0.59 (0.34)	0.53 (0.07)
$f_{ m dom}$ (Hz)	0.79 (0.25)	0.88 (0.27)	0.85 (0.65)	0.79 (0.17)	0.80 (0.32)	0.99 (0.24)	0.85 (0.08)
$lpha_{ ext{dom}}\left(g ight)$	0.21 (0.06)	0.26 (0.07)	0.19 (0.05)	0.22 (0.05)	0.21 (0.05)	0.28 (0.06)	0.23 (0.03)
Duration (s)	9.0 (13.4)	3.7 (6.0)	9.1 (10.5)	8.2 (10.4)	13.3 (15.2)	7.1 (8.1)	8.4 (3.1)
Ascent							
Duty Factor	0.54 (0.31)	0.41 (0.36)	0.45 (0.32)	0.59 (0.33)	0.67 (0.31)	0.49 (0.33)	0.52 (0.10)
$ODBA\left(g\right)$	0.55 (0.36)	0.52 (0.32)	0.54 (0.31)	0.42 (0.29)	0.45 (0.30)	0.51 (0.30)	0.50 (0.05)
$f_{ m dom}$ (Hz)	0.94 (0.47)	0.92 (0.51)	0.79 (0.18)	0.83 (0.21)	0.88 (0.33)	0.98 (0.29)	0.89 (0.07)
$\alpha_{ ext{dom}}\left(g ight)$	0.22 (0.07)	0.23 (0.08)	0.17 (0.04)	0.20 (0.06)	0.22 (0.11)	0.26 (0.08)	0.22 (0.03)

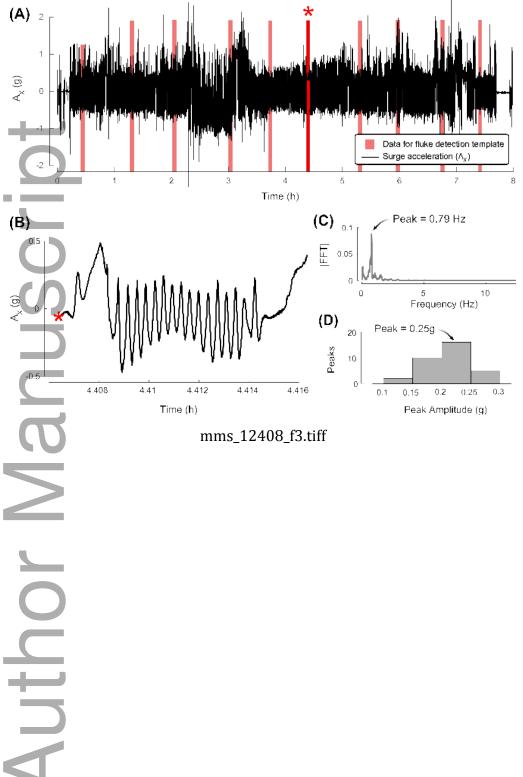
This article is protected by copyright. All rights reserved

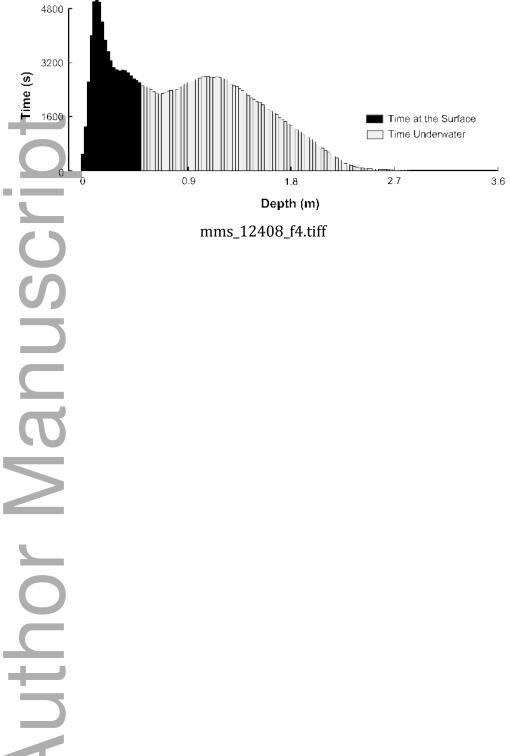


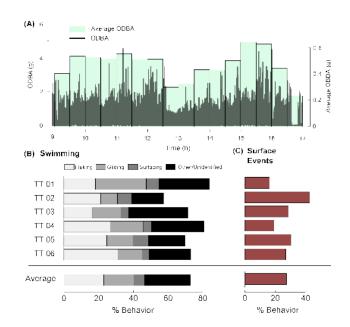
 $mms_12408_f1.tiff$

Dock

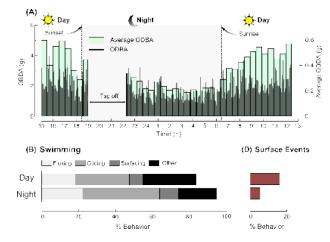




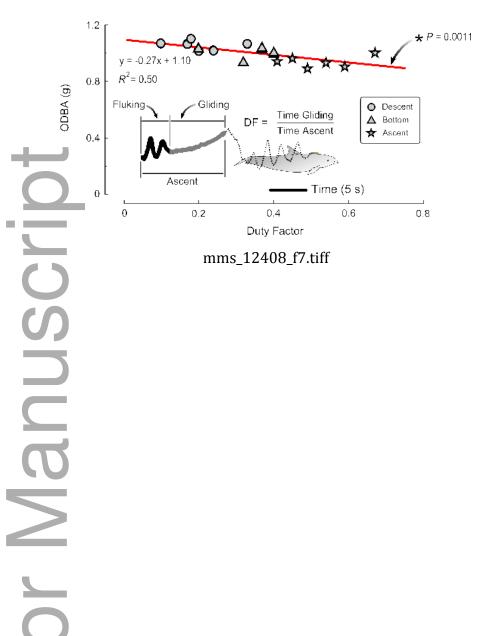


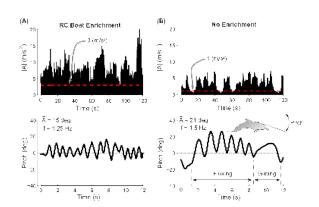


 $mms_12408_f5.tiff$



 $mms_12408_f6.tiff$





 $mms_12408_f8.tiff$