

The Metabolic Cost of Sound Production in Odontocete Cetaceans

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Award Numbers: N0001411IP20017 / N0001410IP20067 / N000141110341
http://www.nwfsc.noaa.gov/research/divisions/cbd/marine_mammal/marinemammal.cfm

LONG-TERM GOALS

Animals often increase the amplitude (the Lombard effect), duration, and/or repetition rate of their acoustic signals as a strategy to help reduce the probability of masking from environmental sounds (NRC 2003). Although accumulating evidence from recent research (Scheifele et al. 2005, Holt et al. 2009, Parks et al. 2010) illustrates that several marine mammal species readily modify the parameters of their acoustic signals to compensate for masking noise, potential energetic costs of such compensation behavior are unknown. To our knowledge, there is no empirical data on the metabolic cost of sound production for any marine mammal species. Given that changes in vocal behavior in response to masking noise has been documented in several species, assessing the biological significance of these effects is paramount but also very difficult given the life histories of marine mammals. The Population Consequences of Acoustic Disturbance (PCAD) model has been proposed as a framework to address this challenging task (NRC 2005). Data on the energetic cost of dolphin vocalization from this study can be used to assess the biological significance of vocal compensation in response to sound exposure and populate transfer function 2 (transfer function between behavior change to life functions immediately affected) in the PCAD model.

Report Documentation Page				Form Approved OMB No. 0704-0188	
Public reporting burden for the collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington VA 22202-4302. Respondents should be aware that notwithstanding any other provision of law, no person shall be subject to a penalty for failing to comply with a collection of information if it does not display a currently valid OMB control number.					
1. REPORT DATE 30 SEP 2011		2. REPORT TYPE		3. DATES COVERED 00-00-2011 to 00-00-2011	
4. TITLE AND SUBTITLE The Metabolic Cost of Sound Production in Odontocete Cetaceans				5a. CONTRACT NUMBER	
				5b. GRANT NUMBER	
				5c. PROGRAM ELEMENT NUMBER	
6. AUTHOR(S)				5d. PROJECT NUMBER	
				5e. TASK NUMBER	
				5f. WORK UNIT NUMBER	
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) NOAA NMFS Northwest Fisheries Science Center, 2725 Montlake Blvd. East, Seattle, WA, 98112				8. PERFORMING ORGANIZATION REPORT NUMBER	
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)				10. SPONSOR/MONITOR'S ACRONYM(S)	
				11. SPONSOR/MONITOR'S REPORT NUMBER(S)	
12. DISTRIBUTION/AVAILABILITY STATEMENT Approved for public release; distribution unlimited					
13. SUPPLEMENTARY NOTES					
14. ABSTRACT					
15. SUBJECT TERMS					
16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT Same as Report (SAR)	18. NUMBER OF PAGES 11	19a. NAME OF RESPONSIBLE PERSON
a. REPORT unclassified	b. ABSTRACT unclassified	c. THIS PAGE unclassified			

OBJECTIVES

For the first year of this study (Phase 1), oxygen consumption was measured in two captive bottlenose dolphins during sound production of social signals and compared to resting metabolic rates (RMRs) and metabolic costs of other activities, such as performing surface active behaviors (SABs) and/or swimming. The phase of this work was completed in 2010. For the second year of this study (Phase 2, 2011), we aim to measure oxygen consumption in these individuals while they produce the same type of sounds but at different levels and/or durations. This work is ongoing and will continue until the end of the calendar year 2011. These measurements will quantify the potential metabolic cost of vocal compensation as an anti-masking strategy in response to anthropogenic sound exposure.

APPROACH

The metabolic cost of sound production is being measured in two captive male Atlantic bottlenose dolphins (*Tursiops truncatus*) maintained at Dr. Terrie Williams' Mammalian Physiology Laboratory at the University of California, Santa Cruz, Long Marine Laboratory. These individuals were trained by Traci Kendall (Program Manager/Research Training Supervisor) and Beau Richter (Head Trainer) to produce sounds on command while stationed under a metabolic hood to measure oxygen consumption. For Phase 2 of the study, the dolphins have also been trained to produce relatively higher and lower amplitude sounds of the same type on command using two different discriminative stimuli or cues (one for "loud" and one for "quiet"). The sounds of free-ranging Atlantic bottlenose dolphins have been described as clicks, whistles, buzzes, quacks, and pops (Jacobs et al. 1993). The trained sounds of the captive dolphins of the current study are representative of those found in wild, free-ranging populations.

Experimental trials are conducted in the morning. The dolphins are fasted overnight before experimental trials to eliminate the potential for the metabolic cost of digestion to confound oxygen consumption measurements. Thus, food rewards are given after the experimental trial is complete and only one experimental trial is conducted per dolphin per day. Briefly, each experimental trial consists of one dolphin remaining at the water surface under the metabolic hood (details described in next paragraph) for one 10-minute period of rest (to determine baseline metabolic rate), followed by two consecutive one-min bouts of sound production (the two bouts are separated by 15-20 sec of silence), and concluding with a recovery period (at least 10 minutes, or until oxygen consumption values return to resting values). For Phase 2 of the study, either "loud" or "quiet" trials are predetermined before the start of the trial in which the dolphin is asked to produce "loud" or "quiet" sounds during the vocalization period. Both trial types are run within one week's worth of data collection for each dolphin subject so that any seasonal effects of metabolic rates are not confounded with different trial conditions. During all trials, the dolphins are acoustically monitored in real-time and their sounds are recorded for further analysis as described below. The total duration of the rest period, sound production period, and recovery period are recorded for each experimental session. Respirations are also recorded during each of the three periods so that respiration rates can be calculated for the dolphins during rest, sound production, and recovery. The dolphin's behavior during each trial is also video recorded to ensure that body movement is kept to a minimum during all trial periods (baseline rest, vocal period, recovery). See figure 1 for a photograph taken during one experimental session.



Figure 1. Photograph taken during one experimental session showing the equipment set-up which includes the metabolic hood, the dolphin stationed under the metabolic hood, the acoustic recording equipment and operator, the dolphin trainer, and the assistant taking notes and recording respirations. During the trial the dolphin is acoustically monitored and all respirations are recorded during each of the three periods.

The method being used for determining metabolic rates from oxygen consumption values are similar to those used previously on bottlenose dolphins (Williams *et al.* 1993, Noren *et al.* 2011). For this study, the rate of oxygen consumption ($\dot{V}O_2$) is being determined for quiescent dolphins stationed at the water surface and for the same dolphins producing sounds at the water surface. Air is drawn into the hood at a flow rate of 300 L min^{-1} . The flow rate is maintained such that the content of oxygen in the hood will remain above 20%. Water and CO_2 from subsamples of excurrent air from the hood are absorbed using Drierite and Baralyme, respectively, prior to entering the oxygen analyzer. The percentage of oxygen in the sample line is monitored continuously (Phase 1 of the study: TurboFox Complete Field System, Sable Systems International; Phase 2 of the study: FMS field metabolic rate system, Sable Systems International FMS) and recorded by a laptop computer every second during the experimental sessions. $\dot{V}O_2$ for resting and vocalizing dolphins are calculated from the percentage oxygen data by respirometry software (Expedata data acquisition and analysis software, Sable Systems International). Respiration and oxygen consumption data are compared across trial components using one way repeated measures analysis of variance or one way repeated measures analysis of variance on ranks when normality and/or equal variance tests fail. When results are significant, pairwise comparisons are made using the Holm-Sidak method for repeated measures ANOVA and the Tukey Test for repeated measures ANOVA on ranks. Dr. Dawn Noren is responsible for collecting and analyzing the respiration rate and oxygen consumption data.

Sound production during all trials is acoustically monitored in real-time and also recorded using calibrated equipment to quantify the sound pressure level (SPL in dB rms re: 1microPa), duration (in sec) and repetition rate (phonations/min) of the phonations of the dolphins. In Year 2, a contact hydrophone is placed on the dolphin's melon during trials to carefully quantify the received SPL of sounds. This method is being used because the dolphin is stationed at the air-water interface under the hood and small changes in dolphin position can affect how much sound energy is transmitted under water. This will allow comparisons between trials and experimental conditions. The recording equipment includes two calibrated Reson hydrophones. One is positioned in the pool as a monitoring hydrophone (Reson TC 4033) and the other is molded into a small suction cup for contact (TC 4013). The position of both hydrophones is always the same among trials and trial periods (rest, sound production, and recovery). Both hydrophones are connected through a series of filters and amplified (Reson VP 2000) and digitized using the MOTU traveler at a sampling rate of 96 kHz and then recorded (2 channels) and monitored in real-time in the time and frequency domain. Calibration is checked through the entire recording chain on a regular basis with a pistonphone connected to a custom adaptor (42AA with RA78, GRAS Sound & Vibration). Hydrophone placement is the same during all periods (rest, sound production, and recovery) of each experimental session. All sounds produced during trials are analyzed using Avisoft SASlab Pro (v5.1.17). A high pass filter at 1.5 kHz and 2 kHz for trials run with Puka and Primo, respectively, is first applied to the recordings to reduce low frequency extraneous sounds (breaths and water sounds) that occur below the frequency range of dolphin vocalizations. Then, the automated measurement option is used to window each vocalization during a trial period. These windows are manually checked and modified as needed. A number of acoustic parameters are measured in both the time and frequency domains for each vocalization, and these values are averaged across the entire vocalization period for each trial. Means of these means are then calculated and summarized. Dr. Marla Holt is responsible for collecting and analyzing the acoustic data.

WORK COMPLETED

In 2010, four, one week trips to Dr. Terrie Williams' Mammalian Physiology Laboratory at the University of California, Santa Cruz, Long Marine Laboratory for data collection were completed. During the first trip in 2010, technical issues were resolved, and the final protocol for the experimental sessions was determined. During the last three trips, acoustic, metabolic, and respiration data were collected over 28 trials (14 trials per dolphin) for Phase 1 of the study. Preliminary analyses of metabolic, respiration, and acoustic data have been accomplished for Phase 1 and is provided in the Results section below. Data collection for Phase 2 of the study is ongoing in 2011. Thus far, data have been collected over four, one week periods in Dr. Williams' Lab in which 40 trials have been conducted (20 trials per dolphin). Metabolic and respiration data have been visually inspected. Acoustic data have been preliminarily analyzed and are also discussed in the next section. Two additional data collection trips are necessary to complete Phase 2 of the project and are scheduled for the 1st and 3rd weeks of October 2011.

RESULTS

During both phases of the study, each dolphin produced the same sound type during his vocal bouts, but the sounds produced were qualitatively different between the two dolphins. Specifically, Primo produced a whistle while Puka produced what we describe as a pulsed squawk or squeak-like sound as illustrated in the spectrograms of Fig. 2. Puka's pulsed sound is similar to the quack sounds described by Jacobs et al. (1993).

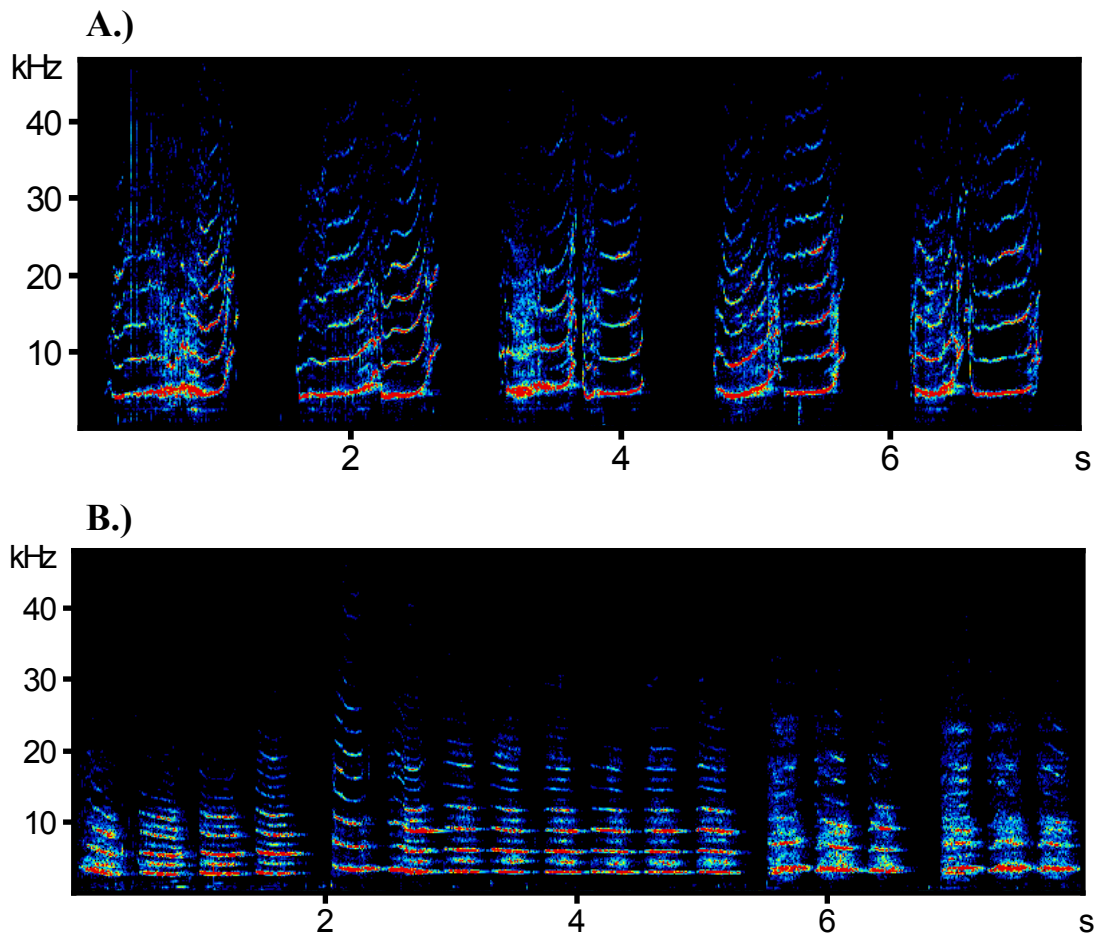


Figure 2. *Spectrograms showing 8 second examples of vocalizations performed by A.) Primo which are five whistles and B.) Puka which are 18 pulsed squeak-like sounds. Both spectrograms show visual representations of vocalizations performed during oxygen consumption data collection with time from 0-8 seconds on the x-axis and frequency from 0-48 kHz on the y-axis. The colors denote relative level or amplitude differences with red indicating higher levels and blue indicating lower levels.*

A total of 13 trials per dolphin are being included in the analysis of Phase 1 data. Primo produced an average of $63.3 (\pm 7.2 \text{ SD})$ whistles during the trial vocal period. Mean whistle duration was 1.08 sec ($\pm 0.26 \text{ SD}$) with a mean interval between the start of each whistle of 1.91 sec ($\pm 0.20 \text{ SD}$). The geometric mean received level of Primo's whistles was 126 dBrms re: $1\mu\text{Pa}$ ($\pm 3.4 \text{ SD}$). During Phase 1, Puka produced an average of 242 squawks ($\pm 42.7 \text{ SD}$) per trial. Mean duration was 0.167 sec ($\pm 0.037 \text{ SD}$) with a mean interval of 0.488 sec ($\pm 0.108 \text{ SD}$). The geometric mean received level of Puka's sounds was 114.6 dBrms re: $1\mu\text{Pa}$ ($\pm 2.0 \text{ SD}$). Little variation in the frequency domain was observed among vocalizations within a dolphin as evident in the spectrograms of Figure 2. It should be emphasized that the received levels reported here were measured from a hydrophone in the test pool (at 0.5 m water depth) to compare vocalization performance between trials and not to estimate source levels since sounds were produced under a reverberant metabolic hood at the air-water interface. Thus, the received levels are likely underestimates of water propagated signals since a significant amount of

sound energy was propagated in air under the hood. In all Phase 2 trials, a contact hydrophone is placed on the dolphin's melon for more precise measurements. The raw percent oxygen data show that both types of vocalizations impact a measurable metabolic cost to dolphins and that recovery to baseline levels occurs gradually after the vocalization period ceases (Fig. 3). Indeed, for both dolphins oxygen consumption ($\text{ml O}_2/\text{min}/\text{kg}$) during the two minute vocal bouts was significantly greater ($P < 0.05$) than baseline resting levels (lowest 2 min measured during the baseline period) and did not return to near baseline levels until well after two minutes post-vocals (Fig. 4). Although metabolic rates during and immediately after sound production were higher than baseline levels, respiration rates recorded for two minutes immediately prior to the vocal bouts, during the two min vocal bouts, and for two minutes immediately following the vocal bouts did not differ significantly for either dolphin (Fig. 5).

The data from Phase 1 of the study demonstrate that this method is successful in assessing the metabolic cost of sound production in odontocete cetaceans. The initial analysis suggests that there is a measurable energetic cost of sound production in bottlenose dolphins, and that it may take up to 5-10 min for dolphins to recover to baseline oxygen consumption values following two consecutive one-min vocal bouts. Furthermore, we found that respiration rates did not change during the three components of the experimental session. These results suggest that increased oxygen consumption during vocal bouts is probably not due to changes in breathing patterns; rather, it is likely due to an increase in metabolic demand related to the production of sound. We are also currently conducting analyses on data collected during Phase 1 to quantify the total metabolic cost of sound production and the duration of time required for dolphins to return to resting metabolism following vocal bouts.

The observed variation in oxygen consumption among Phase 1 trials (within a dolphin, see Fig. 4) might be explained by variations in sound production performance but sample sizes across ranges are limited. Phase 2 (Year 2) of this study aims to determine if variations in oxygen consumption and metabolic rates are explained by variations in vocal performance that are consistent with a metabolic cost of noise-induced vocal compensation (i.e. an increase in sound amplitude or duration is correlated with an increase in oxygen consumption during trials). Data collection is ongoing for Phase 2 of the project and, to date, Puka has produced sounds during "loud" trials that are +11.9 dB relative to his "quiet" trials. Primo, however, has only increased his "loud" trials by approximately +4.1 dB relative to "quiet" trials. Trainers are currently working on conditioning this dolphin to produce a larger difference in vocal amplitude between "quiet" and "loud" trials. Interestingly, both dolphins have a tendency to produce longer vocalizations during "loud" trials as well, although this effect is more pronounced in Primo. Thus, an analysis of sound energy (quantified as sound exposure level or energy flux density) is warranted in addition to exploring increased vocal amplitude or duration as separate effects on metabolic rates.

All analyses described in this report, as well as additional analyses, will be conducted on data collected during Phase 2 to assess the costs of vocal compensation (costs associated with an increase in vocal amplitude and/or duration). The ultimate goals are to assess whether the metabolic cost of sound production and vocal compensation are biologically significant.

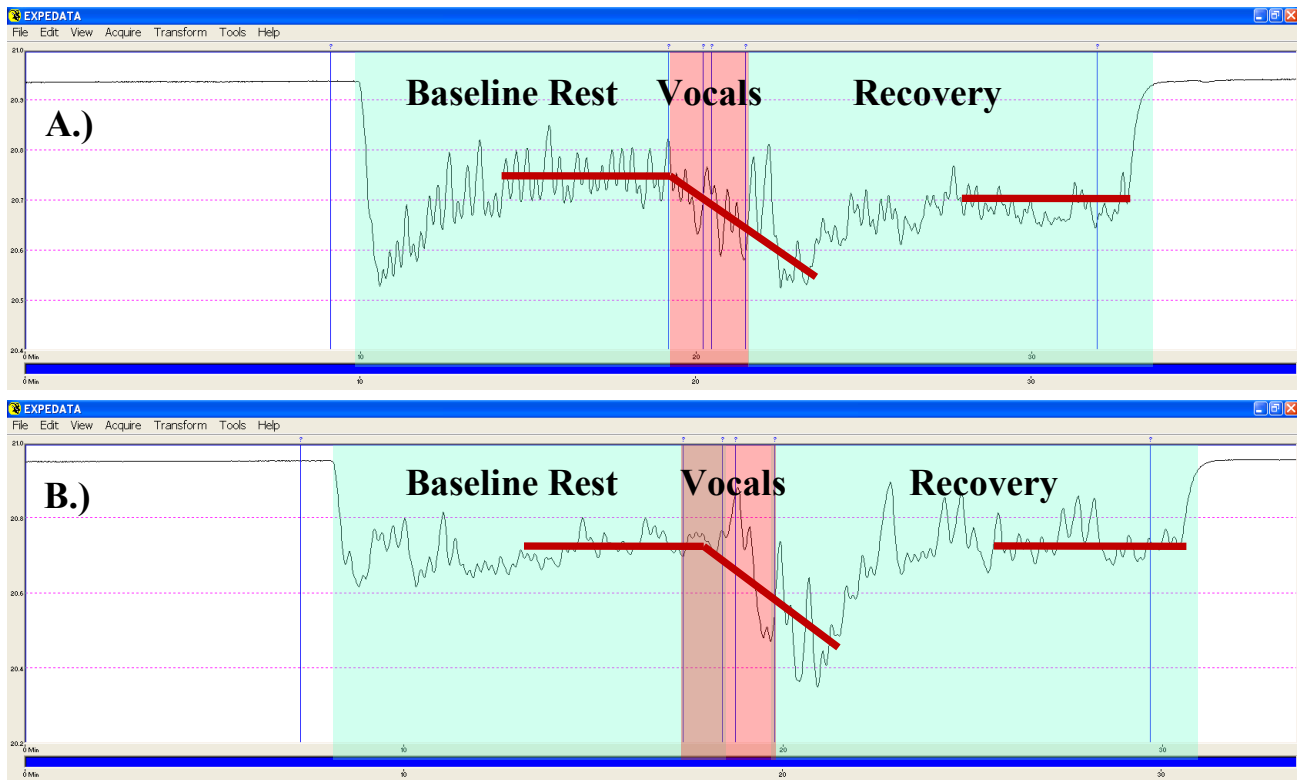


Figure 3. Screen shots from the *Expedata* analysis program (Sable Systems International) showing the concentration of oxygen (%) in the subsample of air from the metabolic hood in relation to time for one experimental session for A.) *Primo* producing whistles and B.) *Puka* producing pulsed squeak-like sounds. The three components of the experimental session (baseline rest, vocal bouts, and recovery) are labeled and shaded. Baseline rest and recovery periods are shaded in cyan while the vocalization period (two consecutive one-min vocal bouts) is shaded in red. For *Primo* (A), average percent oxygen at baseline (horizontal red line within the first cyan shaded region) was approximately 20.75%. Percent oxygen declined (indicating an increase in oxygen consumption) during the vocal bouts (diagonal red line within the red shaded region) to a low of approximately 20.55%. Recovery to pre-vocal percent oxygen levels occurred gradually after the vocal bouts. Average percent oxygen after recovery (horizontal red line within the second cyan shaded region) was approximately 20.7%. For *Puka* (B), average percent oxygen at baseline (horizontal red line within the first cyan shaded region) was approximately 20.75%. Percent oxygen declined (indicating an increase in oxygen consumption) during the vocal bouts (diagonal red line within the red shaded region) to a low of approximately 20.45%. Recovery to pre-vocal percent oxygen levels occurred gradually after the vocal bouts. Average percent oxygen after recovery (horizontal red line within the second cyan shaded region) was approximately 20.75%.

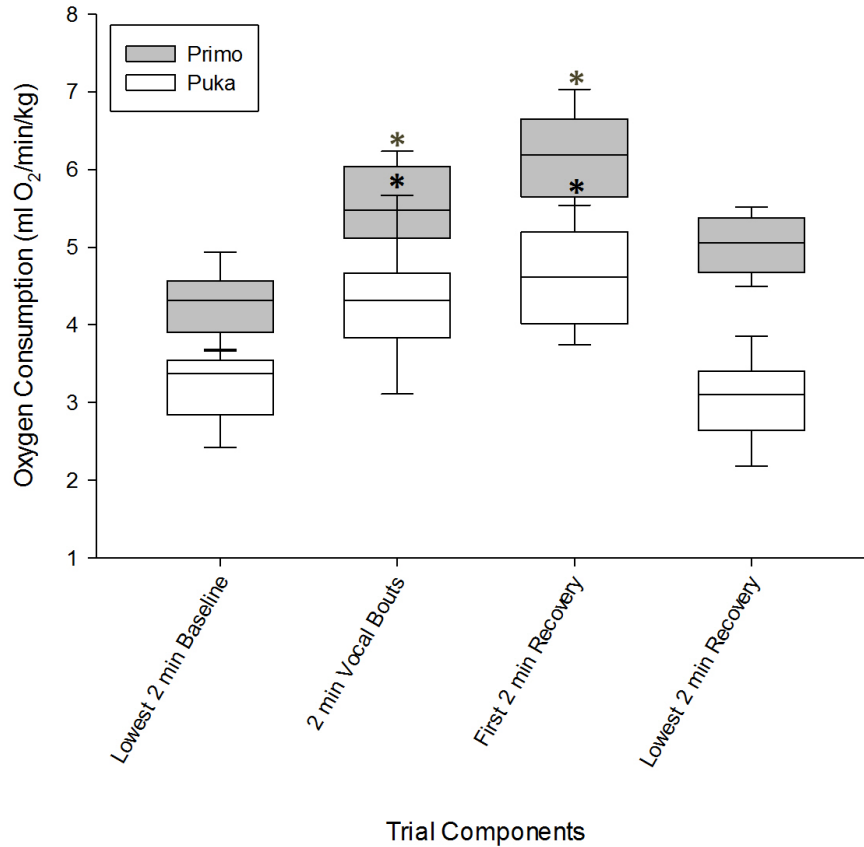


Figure 4. Oxygen consumption (ml O₂/min/kg) measured during components of thirteen experimental trials. The lowest 2 min baseline represents the average lowest resting metabolic rate measured for two minutes during the 10 minute baseline period prior to the vocal bouts (Primo mean: 4.3 ± 0.1 SEM, Puka mean: 3.2 ± 0.1 SEM), the 2 min vocal bouts represents the average metabolic rate measured during the entire two min vocalization period (Primo mean: 5.5 ± 0.2 SEM, Puka mean: 4.3 ± 0.2 SEM), the first 2 min recovery represents the average metabolic rate measured during the two minutes immediately following the vocal bouts (Primo mean: 6.1 ± 0.2 SEM, Puka mean: 4.6 ± 0.2 SEM), and the lowest 2 min recovery represents the average lowest metabolic rate measured for two minutes during the ~10 minute recovery period (Primo mean: 5.0 ± 0.1 SEM, Puka mean: 3.1 ± 0.2 SEM). Data from Primo and Puka are represented by gray and white box plots, respectively, for each of the trial components. For each box plot, the boundary of the box closest to zero indicates the 25th percentile, the solid line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles, respectively. Asterisks (gray for Primo and black for Puka) above the 2 min vocal bouts and the first 2 min recovery box plots designate that these oxygen consumption values are significantly greater ($P < 0.05$) than oxygen consumption values during the lowest 2 min baseline.

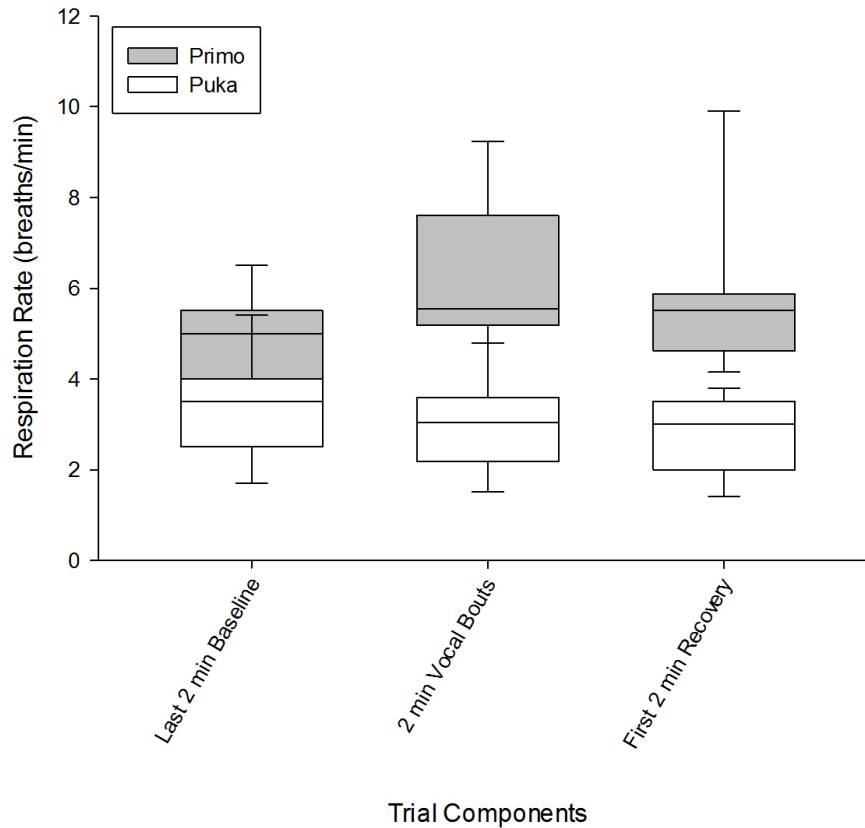


Figure 5. *Respiration rate (breaths/min) recorded during components of thirteen experimental trials. Respiration rates for two minutes immediately prior to the vocal bouts, during the two min vocal bouts, and for two minutes immediately following the vocal bouts are presented. Note for Primo that due to a logistical issue, the sample size for the two minutes immediately following the vocal bouts is twelve, not thirteen. For both dolphins there were no significant differences in respiration rates recorded for two minutes immediately prior to the vocal bouts (Primo mean: 4.9 ± 0.3 SEM, Puka mean: 3.4 ± 0.3 SEM), during the 2 min vocal bouts (Primo mean: 5.9 ± 0.6 SEM, Puka mean: 3.0 ± 0.3 SEM), and for two minutes immediately following the vocal bouts (Primo mean: 5.8 ± 0.5 SEM, Puka mean: 2.8 ± 0.2 SEM). Data from Primo and Puka are represented by gray and white box plots, respectively, for each of the trial components. For each box plot, the boundary of the box closest to zero indicates the 25th percentile, the solid line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles, respectively.*

IMPACT/APPLICATIONS

Currently, there is no empirical data on the metabolic cost of sound production in any marine mammal species. Theoretical assessments of such costs need to factor in variables such as efficiency factors and the relationships between physiological processes and metabolic costs associated with behaviors given that they often do not simply scale according to linear relationships. However, such data needed for theoretical modeling on this topic are also lacking. Empirical data collected from this study will

provide valuable information about sound production costs in odontocetes including costs of modifying acoustic signals in response to anthropogenic sound exposure. For example, if there are significant costs of such behavior as an anti-masking strategy then these effects can impact the energy balance of individuals that in turn affect survival and reproduction. Specifically, this study will provide important input data to populate transfer function 2 in the PCAD model which can then be used to assess the biological significance of such responses to anthropogenic sound exposure.

RELATED PROJECTS

Dr. Terrie Williams' Marine Mammal Physiology Project involves other studies on the two dolphins used in this study. The goal of one related study is to assess the changing energetic demands in cetaceans, and in particular, determine the principle factors in regulating the variable metabolism of cetaceans over the seasons.

http://www.mmpp.ucsc.edu/The_Marine_Mammal_Physiology_Project/Home.html

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Holt, M.M., Noren D.P., and Williams, T.M. 2011. Metabolic rates during sound production in bottlenose dolphins (*Tursiops truncatus*) and evaluating costs of noise-induced vocal compensation. 3rd Symposium on Acoustic Communication by Animals. 1-5 August, Cornell University, Ithaca, NY. p. 60-61.

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Noren, D.P., Dunkin, R.C., Williams, T.M., Holt, M.M. In press. The energetic cost of behaviors performed in response to vessel disturbance: one link in the PCAD Model. In: Anthony Hawkins and Arthur N. Popper, Eds. *The Effects of Noise on Aquatic Life*.