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Echolocation is cheap for some mammals: Dolphins conserve oxygen while producing high-intensity clicks

Dawn P. Noren[a,*], Marla M. Holt[a], Robin C. Dunkin[b], Terrie M. Williams[b]

[a] Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, WA 98112, USA

[b] Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Long Marine Laboratory, 115 McAllister Way, Santa Cruz, CA 95060, USA

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ABSTRACT

Toothed whales use echolocation to sense their environment and capture prey. However, their reliance on acoustic information makes them vulnerable to sound exposure. Odontocetes modify echolocation signals in response to ambient noise levels, yet the metabolic cost of producing and modifying echolocation signals are unknown. Studies on bats found that the metabolic cost of producing echolocation signals and modifying sonar parameters is high. Unlike terrestrial mammals, however, the conservation of oxygen is paramount for odontocetes that echolocate underwater on a breath-hold. Flow-through respirometry was used to determine the metabolic costs of producing and modifying echolocations signals in two trained bottlenose dolphins (*Tursiops truncatus*) that produced echolocation clicks with variable sound energy levels. Unlike bats, the metabolic cost of echolocation was negligible in dolphins. On average, the metabolic rate of submerged dolphins producing clicks was 1.1 times greater than the metabolic rate of submerged, silent dolphins. Similar to bats, the metabolic cost of producing echolocation signals increased significantly with acoustic energy in dolphins. Yet, for the sound energy levels produced, metabolic rates of dolphins producing clicks were within the range of metabolic rates measured when the dolphins were silent. These results can be used to better understand some of the energetic costs associated with dolphin foraging behavior as well as assess the relative energetic impacts of different delphinid behavioral responses to anthropogenic disturbance.

1. Introduction

Odontocetes produce acoustic signals for a variety of life functions. Echolocation is the predominant sensory modality for foraging while communicative sounds mediate important social interactions (Janik, 2000). This reliance on acoustic information makes them particularly vulnerable to effects of sound exposure, such as auditory masking, and they readily modify communicative and echolocation signals to compensate (Au et al., 1982, 1985; Au and Penner, 1981; Buckstaff, 2004; Holt et al., 2009; Scheifele et al., 2005). Biological consequences of these responses might include increased energetic costs, degraded communication from modified signals, increased predator or prey detection and/or an elevated stress response (NRC, 2003).

Energetic costs of producing and modifying social sounds have recently been studied in bottlenose dolphins (Holt et al., 2015; Noren et al., 2013), yet the costs of producing and modifying echolocation clicks are unknown. The metabolic cost of click production likely differs from the metabolic cost of social sound production in odontocetes. Whistles are longer and require greater nasal air pressure to produce relative to echolocation clicks (Cranford et al., 2011), which may equate to higher metabolic costs for social sound production. In contrast, clicks are produced at higher sound pressure levels than whistles (Au, 1993; Janik, 2000) and therefore may be more energetically costly to produce. Studies on bats found that the energetic cost of echolocation can be high and that energy expenditure increases with increasing pulse rate (Dechmann et al., 2013; Speakman et al., 1989). Depending on the species and the pulse rate, metabolic rates of echolocating bats range from 1.4–5 times greater than resting metabolic rate (RMR), to as high as 7–12 times greater than basal metabolic rate (BMR, Dechmann et al., 2013; Speakman et al., 1989). During flight, echolocation pulses are coupled with respiratory and wing-beat cycles (Holderied and von Helversen, 2003; Suthers et al., 1972), enabling the larynx to produce high sound pressure level calls with minimal added metabolic cost in bats (Speakman and Racey, 1991; Voigt and Lewanzik, 2012). This mechanism of signal production also enables bats to continually replenish oxygen stores while producing echolocation pulses. In contrast,

* Corresponding author at: Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, WA 98112, USA.
E-mail address: dawn.noren@noaa.gov (D.P. Noren).

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odontocetes have developed physiological and behavioral modifications to minimize oxygen consumption while diving (Kooyman, 1989). Yet, like bats, odontocetes use air to produce echolocation signals while foraging (Kellogg et al., 1953; Norris et al., 1961; Ridgway et al., 1980). The use of air to produce echolocation clicks appears incompatible with the demand to conserve oxygen at depth. Presumably, odontocetes are adapted to minimize oxygen consumption, thereby reducing metabolic costs, while echolocating underwater.

Oxygen consumption was measured in two adult trained bottlenose dolphins during rest and while producing clicks at depth to determine the metabolic cost of producing and modifying echolocation signals. This information is crucial to understanding the metabolic consequences of echolocating underwater as well as evaluating whether modifying echolocation signals, such as when ambient noise levels are high, can affect daily energy budgets.

2. Material and methods

2.1. Subjects

The metabolic cost of click production was measured in two adult male Atlantic bottlenose dolphins (*Tursiops truncatus*) that were 33 (Dolphin A) and 27 (Dolphin B) years old. The dolphins were maintained in outdoor pools (378,541 and 158,987 l, water temperature: 19–21 °C) for 18 years when this study commenced. Animals were fed a diet of herring and capelin supplemented with a daily multivitamin (Seatabs, Mazuri, Richmond, IN, USA).

Both dolphins were trained for over 15 years, using operant conditioning techniques and positive reinforcement, to station under a metabolic hood for the collection of oxygen consumption data. These dolphins had been producing sounds on command while stationed under the hood (Holt et al., 2015; Noren et al., 2013) for two years prior to the initiation of this study. All behaviors were performed voluntarily. The dolphins were free to leave the hood, surface during submerged periods, or stop clicking at any point throughout trials. Such trials, though rare, were discarded from the analysis. All procedures were approved by the University of California, Santa Cruz Institutional Animal Care and Use Committee and conducted under National Marine Fisheries Service permit no. 13602 to T.M.W.

2.2. Experimental design

Experimental trials were conducted with each dolphin separately following an overnight fast, and only one trial was conducted per dolphin each day. Data from each trial were considered to be independent because only one trial was conducted per dolphin each day and metabolic rate naturally varies daily. Acoustic and oxygen consumption data were collected from dolphins during click production (dolphins performed click bouts) and control (dolphins remained silent) trials. Both trial types were a minimum of 22 min 15 s in duration and consisted of three consecutive periods during which one dolphin remained under the metabolic hood for the entire duration of the trial. Click production trials began with one 10-min period when the dolphin remained still and quiet at the water surface to determine baseline resting metabolic rate (RMR); followed by a click production period when the dolphin remained still but submerged just beneath the water surface to perform two one-min clicks bouts, separated by 15 s of silence at the surface, allowing the dolphin to breathe freely; and concluded with a 10-min minimum recovery period when the dolphin remained still and quiet at the surface. When submerged, the dolphins' bodies were completely underwater, but close to the air-water interface. Control (silent) trials were run during the same months that click production trials were run and consisted of three consecutive periods that were identical to click production trials except that the dolphins remained silent throughout the trials, including the submerged periods. Respirations were recorded during all trials. Reinforcement with fish occurred after completing the entire experimental trial.

2.3. Oxygen consumption data collection and analysis

Oxygen consumption ($\dot{V}_{O2}$) was measured via flow-through respirometry. Identical to previous studies on the metabolic cost of social sound production in these dolphins (Noren et al., 2013; Holt et al., 2015), air was drawn into the hood at a flow rate of 300 L min^{-1} and water and CO_2 from subsamples of excurrent air were absorbed using Drierite (W. A. Hammond Drierite Co., Xenia, OH, USA) and Sodasorb (Chemetron, St Louis, MO, USA), respectively, prior to entering the oxygen analyzer. Percentage of oxygen in the sample line was monitored continuously (FMS Field Metabolic Rate System, Sable Systems International, Las Vegas, NV, USA) and recorded by a laptop computer every second during trials. The oxygen analyzer was calibrated daily using dry ambient air (20.95% O_2). The system was checked for leaks and the lag time determined via the N_2 dilution method (Fedak et al., 1981) once per week. The system measured 1–3% deflections in ambient O_2 with an error of ≤ 0.1% during N_2 dilution trials.

Markers for the start and end of the three consecutive periods (baseline, submerged silence/clicks, recovery) were entered into the computer during all trials and adjusted for the system's lag time (36.5 s) prior to analysis. $\dot{V}_{O2}$ for components of each trial were calculated from the $\%O_2$ data by respirometry software (Expedata Data Acquisition & Analysis Program, Sable Systems International, Las Vegas, NV, USA) that incorporated a respiratory quotient of 0.77 in Eq. (4)b from Withers (1977). The first 2 min of the baseline period were excluded from the analysis to eliminate slightly elevated $\dot{V}_{O2}$ values as a result of swimming slowly into the metabolic hood. Baseline RMR was then calculated by averaging $\dot{V}_{O2}$ during the most level 5 min (determined by the "level" function in Expedata) of the last 8 min of the baseline resting period. Metabolic rate (MR) during the 2.25 min submerged clicks bout and MR during the 2.25 min submerged silent bout were both calculated by averaging $\dot{V}_{O2}$ from the beginning to the end of that period. Average MR during the first 2 min of the recovery period (hereafter referred to as "2 min post submerged") was also calculated. "Recovered MR" was calculated by averaging $\dot{V}_{O2}$ during the most level 5 min (determined by the "level" function in Expedata) of the recovery period. Percent change in MR relative to baseline RMR was also calculated for components of each individual click and control trial to account for daily variability in MR and to more precisely evaluate the metabolic cost of echolocation.

2.4. Acoustic data collection and analysis

Click production trials were acoustically monitored in real-time by both the dolphin trainer and an experimenter and also recorded using calibrated equipment. A contact hydrophone (Reson TC 4013 hydrophone molded into a small suction cup) was placed on the midline of the dolphin's melon at 7 cm from the base of the rostrum before each trial and remained in the same position throughout all trials. The hydrophone was then connected through a bandpass filter and amplified (Reson VP 2000). The signal was sent through a DAQ device (IOTech Personal DAQ 3000) which digitized the signal at a sampling rate of 500 kHz. Sound files were stored on a PC laptop. The approximate start time of each click in the sound file was determined using Avisoft SASlab Pro (v5.2.07) pulse train analysis feature. The received peak-to-peak sound pressure level (dB re 1 μPa pp), duration (μsec), inter-click interval (msec), and received energy flux density level (dB re 1 $\mu Pa^2 s$, also known as sound exposure level) of each click, along with the received cumulative energy flux density level (hereafter referred to as cEFD) of all clicks per trial, were determined using customized codes in MATLAB (R2011b or higher versions, MathWorks). The received energy flux density level of each click was based on the 95% accumulated energy content of each click waveform, and the duration was defined as the time window that corresponded to 95% of accumulated energy (Madsen