Energetic Consequences of Sonar Exposure for Cetaceans

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Abstract

The sub-lethal effects of sonar exposure for cetaceans is not well enough understood to predict population consequences. To better inform conservation planning, we developed a model to predict the energetic costs of sonar avoidance behavior. When avoiding sonar sources, cetaceans may cease foraging and/or flee the area. We estimate the potential energy intake lost to foraging cessation and the additional locomotor costs from increased swim speeds.

Although medium-sized cetaceans, especially beaked whales, make up the majority of mass strandings associated with naval sonar, our results indicate sublethal effects cause the most harm to large baleen whales. A severe response by a Cuvier's beaked whale (6.5 hour foraging cessation and 30 minutes of elevated swim speeds at 4.5 m/s) cost 49% of its daily basal metabolic requirements. Conversely, a moderate response by a blue whale (1 hour foraging cessation and 5 minutes of elevated swim speeds at 2.5 m/s) cost more than nine times its daily basal metabolic requirements. These results may be used to reduce harm to endangered cetacean species.

1. Introduction

Naval exercises involving sonar have been linked to mass strandings of cetaceans worldwide since at least the 1980's (England et al., 2001; Frantzis, 1998; Jepson et al., 2003; Simmonds and Lopez-Jurado, 1991). However, the population consequences of sub-lethal effects are not as well understood. Controlled exposure experiments (CEEs) show that behavioral responses may include cessation of feeding and/or fleeing the sonar source at elevated speed (DeRuiter et al.,

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2017, 2013; Friedlaender et al., 2016; Goldbogen et al., 2013; Kvadsheim et al., 2017; Southall et al., 2019; Tyack et al., 2011; Wensveen Paul J. et al., 2019). Quantitatively linking these behaviors to demographics requires an understanding of the impacts on individuals' health (Pirotta et al., 2018). The mechanism addressed here is reduced energy stores due to lost foraging opportunities and increased locomotor costs.

The two extant clades of cetaceans differ in their feeding styles. Toothed whales (odontocetes) are raptorial feeders and locate prey using echolocation [ref?]. Baleen whales (mysticetes) are filter feeders and capture prey by lunging (Goldbogen et al., 2012) or continuous ram filter feeding (Werth and Potvin, 2016). These feeding styles have profound effects on feeding rate, energy per feeding event, dive depth, and body size. Odontocetes feed at higher rates on smaller prey and most larger odontocetes must dive to extreme depths to find sufficient prey [ref?]. Lunge-feeding mysticetes (rorquals) engulf enormous quantities of prey-laden water, increasing the energy intake per feeding event but limiting dive depth and duration (Goldbogen et al., 2012).

Feeding rates and the energy obtained per feeding event can be empirically measured with multi-sensor tags, active acoustics, and stomach contents [jeremy's paper?]. The rapid echolocation clicking (buzzes) preceeding odontocete prey capture events have a kinematic and acoustic signature that register on tag sensors [ref?]. Similarly, rorqual lunges can be identified from an increase in speed followed by a rapid deceleration, usually associated with high pitch and roll angles (Cade et al., 2016). Simultaneous prey mapping with tagging efforts using active acoustics have measured the biomass density of fish and krill schools targeted by rorquals. The sizes of squid beaks and fish otoliths *(?)* in odontocete stomach samples are a record of prey sizes and energy per feeding event.

Empirical estimates of cetacean metabolic rates are logistically challenging for

smaller species and infeasible for larger species. Oxygen consumption has been measured for captive odontocetes trained to swim under a metabolic hood using open-flow respirometry, showing that mass-specific stroke costs are largely size invariant (Williams et al., 1993, 2017). Whether these metabolic estimates scale to larger odontocetes or mysticetes is unknown, so other methods of estimating energy expediture include breathing rates and hydrodynamic models (Potvin et al., 2012; Sumich, 1983).

Animals swim efficiently by cruising at 1-2 m/s and maintaining a Strouhal number of 0.25 - 0.3 (Rohr and Fish, 2004; Sato Katsufumi et al., 2007). The Strouhal number is a dimensionless quantity $St = \frac{Af}{U}$ where A is stroke amplitude, f is stroke frequency, and U is swimming speed. Cetacean stroke amplitudes are approximately one fifth body length [ref?] so there is a linear relationship between swimming speed and stroke frequency for animals of a given body size [gough?].

Methods

We considered the potential energy intake of lost feeding opportunities and additional energy expenditure from elevated swimming speeds in modeling the energetic consequences of sonar exposure. The model takes the form:

$$E_{sonar} = P_{in} \times t_d + P_{out}(U_f) \times t_f \qquad (1)$$

Where E_{sonar} is the energy cost of sonar exposure, P_{in} is consumption power (i.e. rate of energy intake) during undisturbed foraging, t_d is the time displaced from foraging, P_{out} is flight power (i.e. increased rate of locomotor costs), U_f is the animal's speed during flight, and t_f is the flight time. P_{in} and P_{out} are species-specific values and t_d, U_f, and t_f are dependent on the individual's

3

58 behavioral response to sonar exposure.

59 *Consumption power (P_{in})*

60   The rate of energy intake is the product of feeding rate (r_f) and prey energy

61 per feeding event (E_p). r_f was calculated as the lunge rate for rorquals and buzz

62 rate for odontocetes using tag sensors. E_p was derived using active acoustics

63 (rorquals) and stomach contents (odontocetes) [ref?].

64 *Flight power (P_{out})*

65   The locomotor costs associated with fleeing the sonar source is the energetic

66 cost of swimming at U_f relative to the cruising swim speed. Using the relationship

67 between stroke frequency and swimming speed and a scaling relationship for

68 mass-specific stroke costs, we calculate P_{out} as:

$$P_{out}(U_f) = (f_s(U_f) - f_s(U_c)) \times C_L \times m \qquad (2)$$

69   Where f_s is a function relating stroke frequency to swimming speed, U_f and

70 U_c are the swimming speeds during the flight response and cruising, C_L is the

71 mass-specific locomotor cost of a stroke, and m is the animal's mass. Equation

72 (2) assumes, during the flight response, cetaceans increase swimming speed and

73 stroke frequency, but the mass-specific locomotor cost of a stroke remains the

74 same regardless of speed. Although C_L increases with swimming speed, the

75 scaling relationships do not hold for larger cetaceans (Williams et al., 2017). To

76 be conservative, we use the C_L scaling relationship for cruising speeds, estimated

77 as $C_L = 1.46 + 0.0005m$ in $J \cdot stroke^{-1} \cdot kg^{-1}$. We chose 1.5 m/s for U_c based on

78 size-invariant scaling of cruising speeds (Sato Katsufumi et al., 2007). Assuming

79 cetaceans maintain a Strouhal number of 0.3 and stroke amplitude is one fifth

80 body length, stroking frequency as a function of body length is:

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$$S_t = \frac{Af}{U}$$
$$f = \frac{1.5U}{L} \qquad (3)$$

Case studies

We analyzed tag data from four controlled exposure experiments (CEEs) and applied the E_{sonar} model to estimate energetic costs of observed behavioral responses to sonar exposure [BRS ref?]. As part of an on-going behavioral response study to naval sonar, in 2011-2015 *(???)* Blainville's beaked whales (*Mesoplodon densirostris*), Cuvier's beaked whales (*Ziphius cavirostris*), northern minke whales (*Balaenoptera acutorostrata*), and blue whales (*B. musculus*) were tracked with multi-sensor tags and exposed to mid-frequency active sonar in Southern California. Time displaced from foraging (t_d), time in flight (t_f), and speed of flight (U_f) were selected based on tag data. These values should be considered realistic scenarios, but not the typical or most common response. Behavioral responses to sonar exposure are highly variable and seem to depend on received sound level, distance to source, foraging behavior, and habituation (Southall et al., 2019; Wensveen Paul J. et al., 2019).

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5

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