

# 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 sub-lethal 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., 2017,

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2013; Friedlaender et al., 2016; Goldbogen et al., 2013; Kvadsheim et al., 2017;  
Southall et al., 2019; Tyack et al., 2011; Wensveen et al., 2019). Quantitatively  
linking these behaviors to demographics requires an understanding of the impacts  
on individuals' health (Pirrotta 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

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

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

## 49 **Methods**

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

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

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

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 ( $E_p$ ):

$$P_{in} = r_f \times E_p \quad (2)$$

62  $r_f$  was calculated as the lunge rate for rorquals and buzz rate for odontocetes  
63 using tag sensors.  $E_p$  was derived using active acoustics (rorquals) and stomach  
64 contents (odontocetes) [ref?].

65 *Flight power ( $P_{out}$ )*

66 The locomotor costs associated with fleeing the sonar source is the energetic  
67 cost of swimming at  $U_f$  relative to the cruising swim speed. Using the relationship  
68 between stroke frequency and swimming speed and a scaling relationship for  
69 mass-specific stroke costs, we calculate  $P_{out}$  as:

$$P_{out}(U_f) = (f_s(U_f) - f_s(U_c)) \times C_L \times m \quad (3)$$

70 Where  $f_s$  is a function relating stroke frequency to swimming speed,  $U_f$  and  
71  $U_c$  are the swimming speeds during the flight response and cruising,  $C_L$  is the  
72 mass-specific locomotor cost of a stroke, and  $m$  is the animal's mass. Equation  
73 (2) assumes, during the flight response, cetaceans increase swimming speed and  
74 stroke frequency, but the mass-specific locomotor cost of a stroke remains the  
75 same regardless of speed. Although  $C_L$  increases with swimming speed, the  
76 scaling relationships do not hold for larger cetaceans (Williams et al., 2017). To

77 be conservative, we use the  $C_L$  scaling relationship for cruising speeds, estimated  
 78 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  
 79 on size-invariant scaling of cruising speeds (Katsufumi et al., 2007). Assuming  
 80 cetaceans maintain a Strouhal number of 0.3 and stroke amplitude is one fifth  
 81 body length, stroking frequency as a function of body length is:

$$S_t = \frac{Af}{U}$$

$$f = \frac{1.5U}{L} \quad (4)$$

## 82 *Case studies*

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

Table 1: Cetacean feeding rates

Group	Species	$r_f$	N
Odontocete	<i>Phocoena phocoena</i>	96.8	8
Odontocete	<i>Grampus griseus</i>	17.7	17
Odontocete	<i>Mesoplodon densirostris</i>	13.0	14
Odontocete	<i>Globicephala macrorhynchus</i>	2.5	2
Odontocete	<i>Globicephala melas</i>	7.9	9
Odontocete	<i>Orcinus orca</i>	9.7	10
Odontocete	<i>Ziphius cavirostris</i>	12.8	4
Odontocete	<i>Berardius bairdii</i>	4.6	1
Odontocete	<i>Physeter macrocephalus</i>	12.5	36
Rorqual	<i>Balaenoptera bonaerensis</i>	44.1	3
Rorqual	<i>Megaptera novaeangliae</i>	17.2	6
Rorqual	<i>Balaenoptera physalus</i>	13.3	3
Rorqual	<i>Balaenoptera musculus</i>	10.7	11

*Note:*

$r_f$  is lunges/hour (rorquals) or buzzes/hour (odontocetes)

Species ordered by size within groups.

## 96 Results

### 97 Consumption power ( $P_{in}$ )

98 Feeding rates were derived from tag data and tended to decrease with body  
99 size. Rorqual feeding rates ranged from 10.7 to 44.1 lunges/hour and odontocete  
100 feeding rates ranged from 2.5 to 96.8 buzzes/hour (Table 1).

101 Prey energy per feeding event was empirically derived from acoustic backscat-  
102 ter (mysticetes) and stomach samples (odontocetes). Filter feeders consumed the  
103 most energy per feeding event. Generally, delphinids targeted more energy-rich  
104 prey than Ziphids (Fig. 1).

105 Modeled consumption power covered four orders of magnitude: from 2.4e3  
106 kJ/hr (*P. phocoena*) to 1.4e7 kJ/hr (*B. musculus*) (Fig. 2).

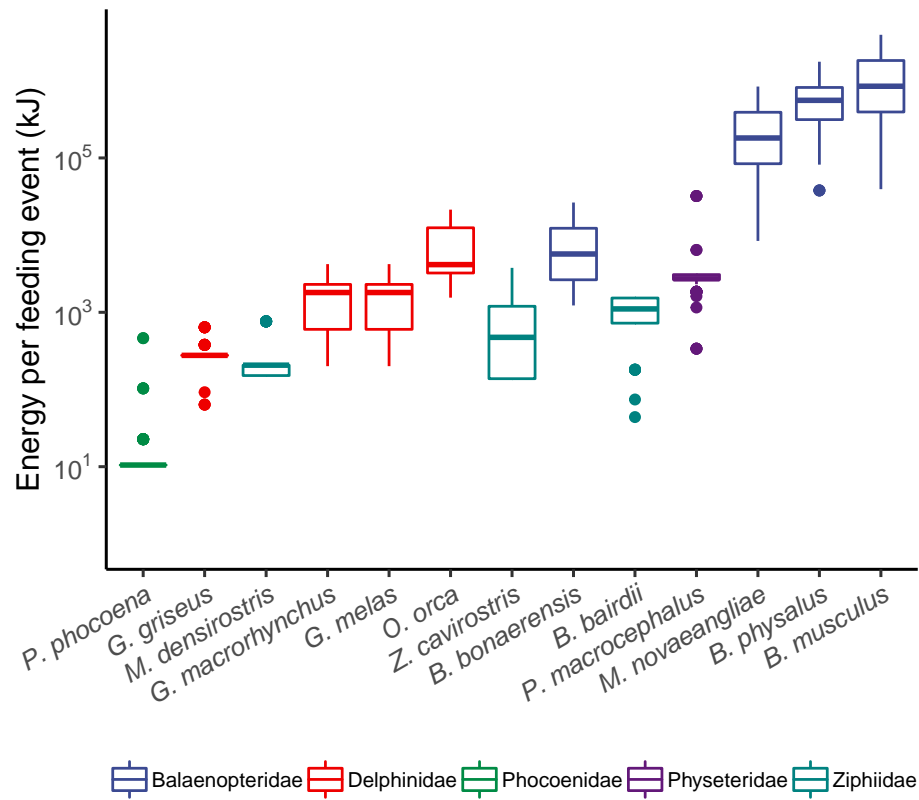


Figure 1: Energy per feeding event. Note log scale on y-axis.

107 *Flight power ( $P_{out}$ )*

108 *Case studies*

109 **Figures**

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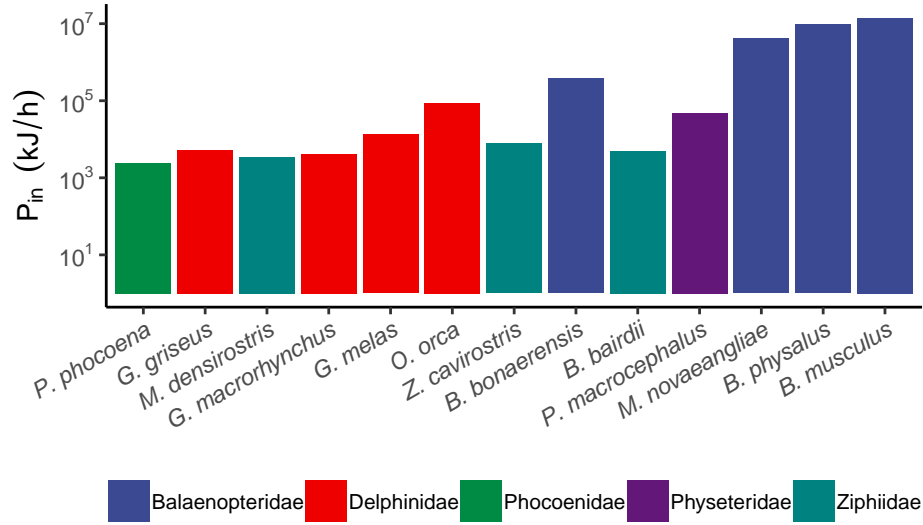


Figure 2: Modeled consumption power ( $P_{in}$ ).

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