

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 (Pirodda 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).

96 *Cross-species comparisons*

97 To facilitate comparisons of energetic consequences across body size, we
 98 present E_{sonar} as 1) the energy cost (kJ), 2) the mass-specific energy cost

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.

99 ($kJ\ kg^{-1}$), and 3) the ratio of energy cost to daily basal metabolic requirements
100 ($E_{sonar} : BMR$). Kleiber's equation for mammals predicts basal metabolic rate
101 as: $BMR = 293.1m^{0.75}$ (kJ/day) (Kleiber, 1975). Given the uncertainty in
102 BMR estimates for large cetaceans and the differences between basal and active
103 metabolic rates, $E_{sonar} : BMR$ should be interpreted as an index of energetic
104 consequence and not an absolute measure of impact.

105 Results

106 Consumption power (P_{in})

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

110 Prey energy per feeding event was empirically derived from acoustic backscatter
111 ter (mysticetes) and stomach samples (odontocetes). Filter feeders consumed the

112 most energy per feeding event. Generally, delphinids targeted more energy-rich
113 prey than Ziphids (Fig. 1).

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

116 *Flight power (P_{out})*

117 Predicted stroke frequencies at cruising speed decreased with length, from
118 1.8 Hz for a 1.22 m *P. phocoena* to 0.09 for a 25 m *B. musculus* (Fig. 3).

119 Across body sizes, P_{out} increased linearly with flight speed (Fig. 4).

120 *Case studies*

121 We modeled the energetic consequence of sonar exposure for four observed
122 behavioral responses. The beaked whale (*M. densirostris* and *Z. cavirostris*)
123 responses were more severe than the rorquals' (*B. bonaerensis* and *B. musculus*)
124 but the mass-specific energetic costs and $E_{sonar} : BMR$ ratio were greater for
125 rorquals (Table 2).

Table 2: Behavioral responses to sonar and estimated energetic consequences of exposure.

Species	Behavioral responses			Energetic consequences					
	t_d (min)	t_f (min)	U_f (m/s)	E_{out} (kJ)	E_{in} (kJ)	E_{sonar} (kJ)	E_{sonar} (kJ kg ⁻¹)	$E_{sonar} : BMR_d$	
M. densirostris	360	30	4.5	3210	20500	23700	27.5	0.509	
Z. cavirostris	360	30	4.5	10400	46700	57000	19.7	0.492	
B. bonaerensis	150	60	3.5	44600	949000	994000	148.0	4.58	
B. musculus	60	5	2.5	79600	14200000	14300000	153.0	9.14	

Note:

t_d is the time displaced from foraging and t_f is the time fleeing the sonar source at the elevated speed, U_f . E_{out} and E_{in} are the energetic costs of increased locomotion and lost feeding, respectively. E_{sonar} is presented as a total cost, as a mass-specific cost, and as a ratio to daily basal metabolic requirements.

126 **Figures**

127 **References**

- 128 Cade, D.E., Friedlaender, A.S., Calambokidis, J., Goldbogen, J.A., 2016.
129 Kinematic diversity in rorqual whale feeding mechanisms. *Current Biology* 26,
130 2617–2624. <https://doi.org/10.1016/j.cub.2016.07.037>
- 131 DeRuiter, S.L., Langrock, R., Skirbutas, T., Goldbogen, J.A., Calambokidis,
132 J., Friedlaender, A.S., Southall, B.L., 2017. A multivariate mixed hidden markov
133 model for blue whale behaviour and responses to sound exposure. *The Annals*
134 *of Applied Statistics* 11, 362–392. <https://doi.org/10.1214/16-AOAS1008>
- 135 DeRuiter, S.L., Southall, B.L., Calambokidis, J., Zimmer, W.M.X., Sadykova,
136 D., Falcone, E.A., Friedlaender, A.S., Joseph, J.E., Moretti, D., Schorr, G.S.,
137 Thomas, L., Tyack, P.L., 2013. First direct measurements of behavioural
138 responses by cuvier’s beaked whales to mid-frequency active sonar. *Biology*
139 *Letters* 9, 20130223–20130223. <https://doi.org/10.1098/rsbl.2013.0223>
- 140 England, G.R., Evans, D., Lautenbacher, C., Morrissey, S., Hogarth, W.,
141 others, 2001. Joint interim report bahamas marine mammal stranding event of
142 15-16 march 2000. US Department of Commerce, US Secretary of the Navy.
- 143 Frantzis, A., 1998. Does acoustic testing strand whales? *Nature* 392, 29–29.
144 <https://doi.org/10.1038/32068>
- 145 Friedlaender, A.S., Hazen, E.L., Goldbogen, J.A., Stimpert, A.K., Calam-
146 bokidis, J., Southall, B.L., 2016. Prey-mediated behavioral responses of feeding
147 blue whales in controlled sound exposure experiments. *Ecological Applications*
148 26, 1075–1085. <https://doi.org/10.1002/15-0783>
- 149 Goldbogen, J.A., Calambokidis, J., Croll, D.A., McKenna, M.F., Oleson,
150 E., Potvin, J., Pyenson, N.D., Schorr, G., Shadwick, R.E., Tershy, B.R., 2012.
151 Scaling of lunge-feeding performance in rorqual whales: Mass-specific energy
152 expenditure increases with body size and progressively limits diving capacity.

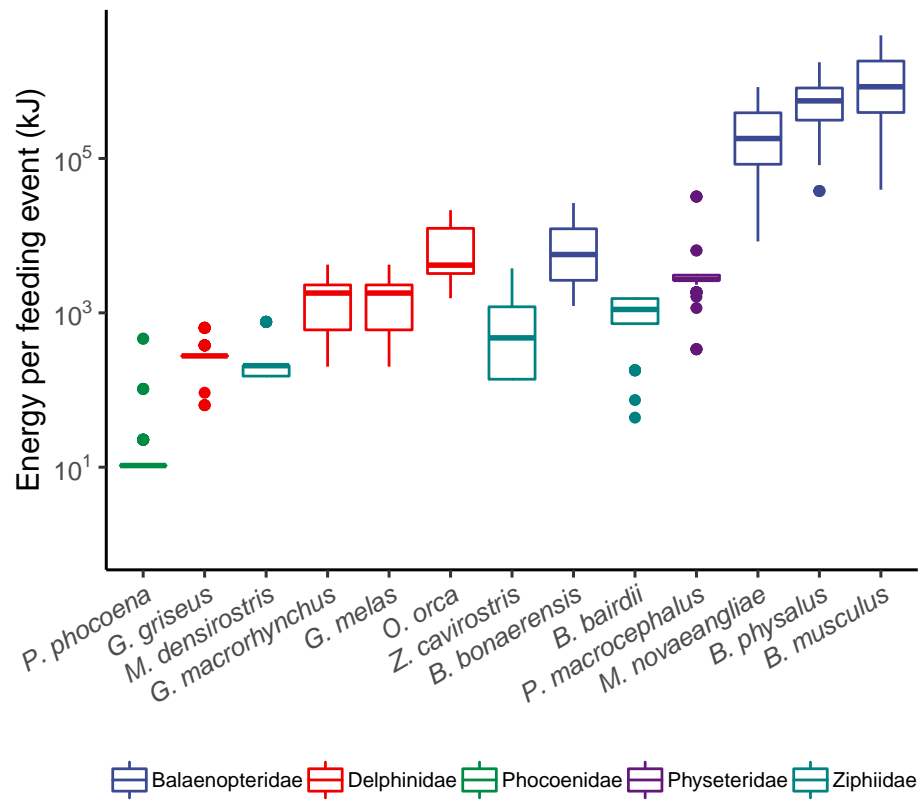


Figure 1: Energy per feeding event. Note log scale on y-axis.

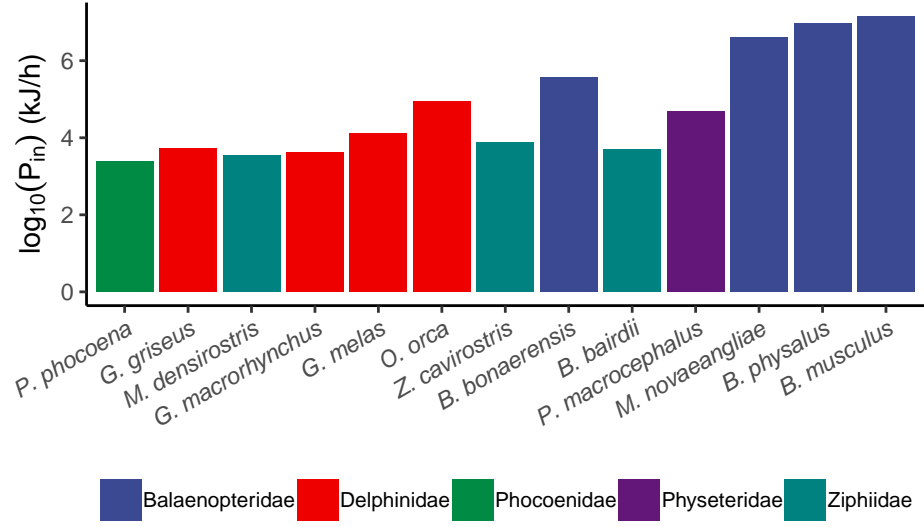


Figure 2: Modeled consumption power (P_{in}).

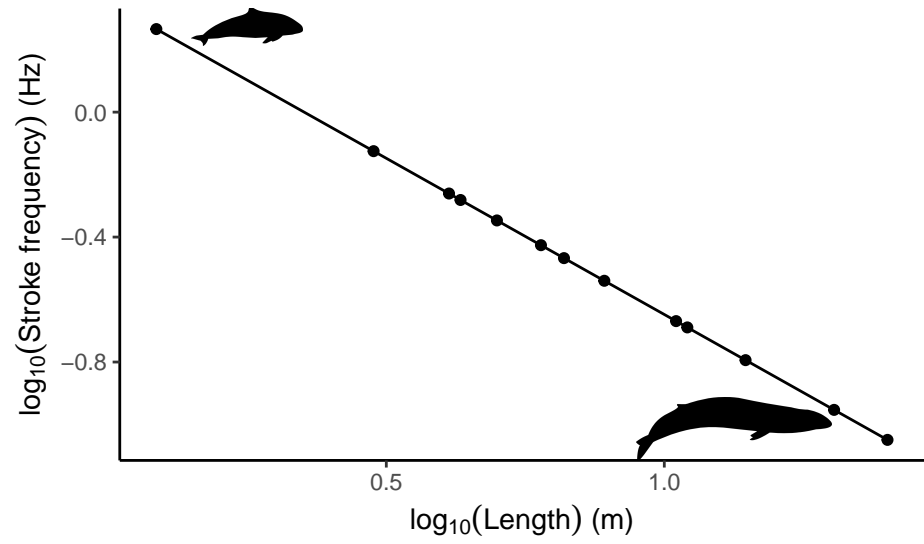


Figure 3: Predicted cruising speed stroke frequencies (f_s).

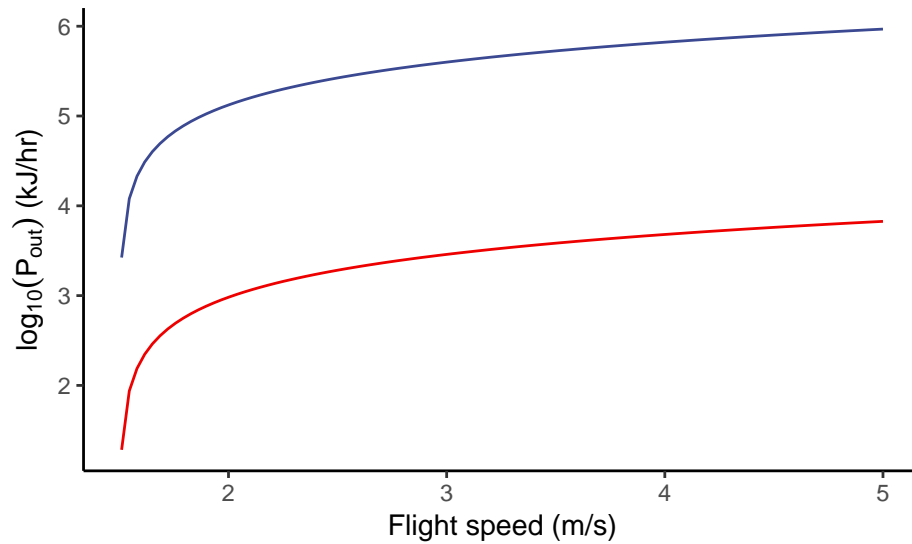


Figure 4: Flight power (P_{out}) by flight speed for *B. musculus* (blue) and *Z. cavistrotris* (red). Note log scale on y-axis.

Functional Ecology 26, 216–226. <https://doi.org/10.1111/j.1365-2435.2011.01905>.

X

Goldbogen, J.A., Southall, B.L., DeRuiter, S.L., Calambokidis, J., Friedlaender, A.S., Hazen, E.L., Falcone, E.A., Schorr, G.S., Douglas, A., Moretti, D.J., Kyburg, C., McKenna, M.F., Tyack, P.L., 2013. Blue whales respond to simulated mid-frequency military sonar. *Proceedings of the Royal Society B: Biological Sciences* 280, 20130657–20130657. <https://doi.org/10.1098/rspb.2013.0657>

Jepson, P.D., Arbelo, M., Deaville, R., Patterson, I.A.P., Castro, P., Baker, J.R., Degollada, E., Ross, H.M., Herráez, P., Pocknell, A.M., Rodríguez, F., Howie, F.E., Espinosa, A., Reid, R.J., Jaber, J.R., Martin, V., Cunningham, A.A., Fernández, A., 2003. Gas-bubble lesions in stranded cetaceans. *Nature* 425, 575–576. <https://doi.org/10.1038/425575a>

Katsufumi, S., Yutaka, W., Akinori, T., J.O, M.P., Hideji, T., Ryo, K., J, P.P., Yves, H., Tomonari, A., Yuuki, W., Yoko, M., P, C.D., Charles-André, B.,

167 Kagari, A., Masao, A., Phil, T., Ari, S., Yasuhiko, N., 2007. Stroke frequency, but
 168 not swimming speed, is related to body size in free-ranging seabirds, pinnipeds
 169 and cetaceans. *Proceedings of the Royal Society B: Biological Sciences* 274,
 170 471–477. <https://doi.org/10.1098/rspb.2006.0005>

171 Kleiber, M., 1975. *The fire of life: An introduction to animal energetics.*
 172 Robert E. Krieger, Huntington.

173 Kvadsheim, P.H., DeRuiter, S., Sivle, L.D., Goldbogen, J., Roland-Hansen,
 174 R., Miller, P.J., Lam, F.-P.A., Calambokidis, J., Friedlaender, A., Visser, F.,
 175 Tyack, P.L., Kleivane, L., Southall, B., 2017. Avoidance responses of minke
 176 whales to 1–4 kHz naval sonar. *Marine Pollution Bulletin* 121, 60–68. <https://doi.org/10.1016/j.marpolbul.2017.05.037>

178 Pirotta, E., Booth, C.G., Costa, D.P., Fleishman, E., Kraus, S.D., Lusseau,
 179 D., Moretti, D., New, L.F., Schick, R.S., Schwarz, L.K., Simmons, S.E., Thomas,
 180 L., Tyack, P.L., Weise, M.J., Wells, R.S., Harwood, J., 2018. Understanding the
 181 population consequences of disturbance. *Ecology and Evolution* 8, 9934–9946.
 182 <https://doi.org/10.1002/ece3.4458>

183 Potvin, J., Goldbogen, J.A., Shadwick, R.E., 2012. Metabolic expenditures
 184 of lunge feeding rorquals across scale: Implications for the evolution of filter
 185 feeding and the limits to maximum body size. *PLOS ONE* 7, e44854. <https://doi.org/10.1371/journal.pone.0044854>

187 Rohr, J.J., Fish, F.E., 2004. Strouhal numbers and optimization of swimming
 188 by odontocete cetaceans. *Journal of Experimental Biology* 207, 1633–1642.
 189 <https://doi.org/10.1242/jeb.00948>

190 Simmonds, M.P., Lopez-Jurado, L.F., 1991. Whales and the military. *Nature*
 191 351, 448. <https://doi.org/10.1038/351448a0>

192 Southall, B.L., DeRuiter, S.L., Friedlaender, A., Stimpert, A.K., Goldbogen,
 193 J.A., Hazen, E., Casey, C., Fregosi, S., Cade, D.E., Allen, A.N., Harris, C.M.,

194 Schorr, G., Moretti, D., Guan, S., Calambokidis, J., 2019. Behavioral responses
 195 of individual blue whales (*balaenoptera musculus*) to mid-frequency military
 196 sonar. The Journal of Experimental Biology 222, jeb190637. [https://doi.org/10.](https://doi.org/10.1242/jeb.190637)
 197 1242/jeb.190637

198 Sumich, J.L., 1983. Swimming velocities, breathing patterns, and estimated
 199 costs of locomotion in migrating gray whales, *eschrictius robustus*. Canadian
 200 Journal of Zoology 61, 647–652. <https://doi.org/10.1139/z83-086>

201 Tyack, P.L., Zimmer, W.M.X., Moretti, D., Southall, B.L., Claridge, D.E.,
 202 Durban, J.W., Clark, C.W., D’Amico, A., DiMarzio, N., Jarvis, S., McCarthy, E.,
 203 Morrissey, R., Ward, J., Boyd, I.L., 2011. Beaked whales respond to simulated
 204 and actual navy sonar. PLoS ONE 6, e17009. [https://doi.org/10.1371/journal.](https://doi.org/10.1371/journal.pone.0017009)
 205 pone.0017009

206 Wensveen, P.J., Saana, I., Hansen, R.R., Benda-Beckmann, A.M. von,
 207 Kleivane, L., IJsselmuide, S. van, Lam, F.-P.A., Kvadsheim, P.H., DeRuiter, S.L.,
 208 Curé, C., Narazaki, T., Tyack, P.L., Miller, P.J., 2019. Northern bottlenose
 209 whales in a pristine environment respond strongly to close and distant navy sonar
 210 signals. Proceedings of the Royal Society B: Biological Sciences 286, 20182592.
 211 <https://doi.org/10.1098/rspb.2018.2592>

212 Werth, A.J., Potvin, J., 2016. Baleen hydrodynamics and morphology of cross-
 213 flow filtration in balaenid whale suspension feeding. PLOS ONE 11, e0150106.
 214 <https://doi.org/10.1371/journal.pone.0150106>

215 Williams, T.M., Friedl, W.A., Haun, J.E., 1993. The physiology of bottlenose
 216 dolphins (*tursiops truncatus*): Heart rate, metabolic rate and plasma lactate
 217 concentration during exercise. Journal of Experimental Biology 179, 31–46.

218 Williams, T.M., Kendall, T.L., Richter, B.P., Ribeiro-French, C.R., John,
 219 J.S., Odell, K.L., Losch, B.A., Feuerbach, D.A., Stamper, M.A., 2017. Swimming
 220 and diving energetics in dolphins: A stroke-by-stroke analysis for predicting

221 the cost of flight responses in wild odontocetes. The Journal of Experimental
222 Biology 220, 1135–1145. <https://doi.org/10.1242/jeb.154245>