Energetic Consequences of SONAR Exposure (preliminary)

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Abstract

This is a tool intended for resource managers to understand the energetic sub-lethal effects of SONAR exposure on cetaceans. The model makes a first order approximation by estimating (1) the energy intake lost to foraging cessation and (2) the additional locomotor costs from increased swim speeds. Energetic parameters for the model come from empirical data and theoretical scaling relationships.

Here I present the model derivation and apply it to four case studies of hypothetical behavioral responses. The results indicate even minor behavioral responses from filter feeders can have immense energetic costs, several times greater than daily basal metabolic requirements. Conversely, strong responses from raptorial feeders cost only a fraction of basal metabolic requirements. So although raptorial feeders (especially beaked whales) are the majority of mass strandings associated with SONAR (ref?), sub-lethal effects of energy loss probably have a greater impact on rorquals.

Energetic model

The energetic consequences of SONAR exposure, as modeled here, take the form:

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

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.

The first term ($P_{in} \times t_d$) is the energy the animal would have consumed during foraging. The second term ($P_{out}(U_f) \times t_f$) is the additional energy spent in elevated locomotion.

Consumption power (P_{in})

The rate of consumption is the product of feeding rates and prey quality. We estimated feeding rates from tag data (lunges for rorquals, buzzes for odontocetes) and prey quality from active acoustics (rorquals) or stomach contents (odontocetes).

$$P_{in} = r_f \times E_p$$

Where r_f is the feeding rate and E_p is the energy from prey consumed per feeding event.

Empirical feeding rates (r_f)

Feeding rates were empirically derived from tag data. Lunges for rorquals and buzzes for odontocetes.

Mysticetes

The mysticete feeding rate is defined as the mean number of lunges per hour of deployment for deployments exceeding 24 hours. Shorter deployments tend to have higher lunge rates due to diel foraging patterns. Overall, lunge rates decrease with body size.

| Species	N	Lunge rate
B. bonaerensis	3	44.1
M. novaeangliae	6	17.2
B. physalus	3	13.3
B. musculus	11	10.7
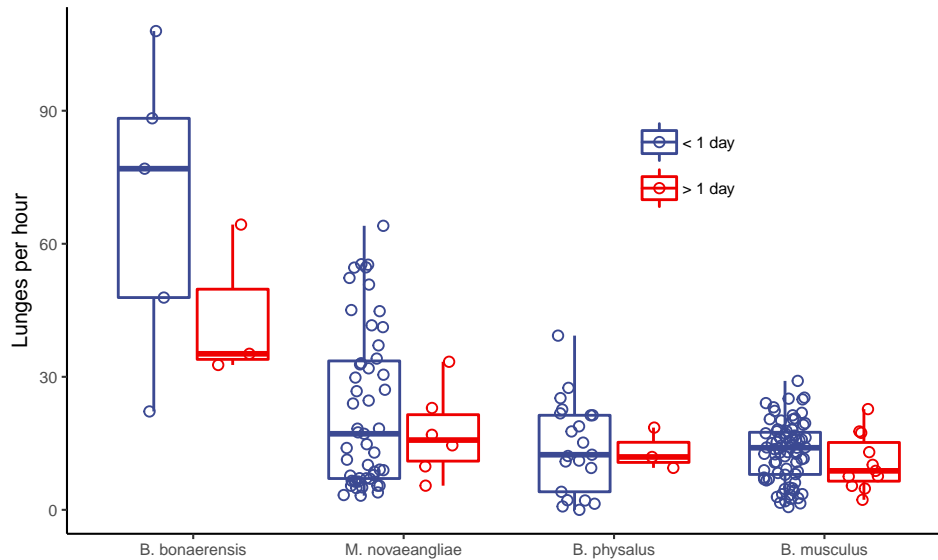
Odontocetes

Odontocete feeding events are identifiable by the acoustic signature of echolocation (buzzes). Feeding rates are estimated as buzzes per hour. Tagging durations on odontocetes rarely exceed 24 hours, so I used all available data. The relationship between feeding rates and body size is more variable than for mysticetes. This makes sense given the wider range of prey and dive depths for odontocetes.

Note: there's a Pm with NA for buzz count.

Species	N	Buzz rate (per hour)
P. phocoena	8	96.8
G. griseus	17	17.7
M. densirostris	14	13.0
G. macrorhynchus	2	2.5
G. melas	9	7.9
O. orca	10	9.7
Z. cavirostris	4	12.8
B. bairdii	1	4.6
P. macrocephalus	36	12.5

P. phocoena not shown, mean buzz rate = 96.8/hr
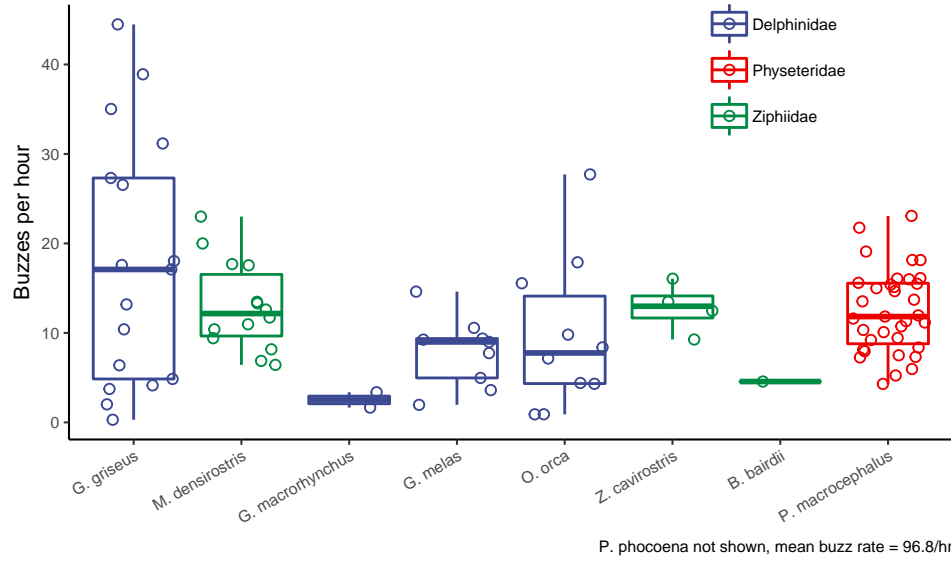
Empirical prey energy (E_p)

Prey energy was empirically derived from acoustic backscatter (mysticetes) and stomach samples (odontocetes). Filter feeders consume the most energy per feeding event. Delphinids target more energy-rich prey than Ziphids.
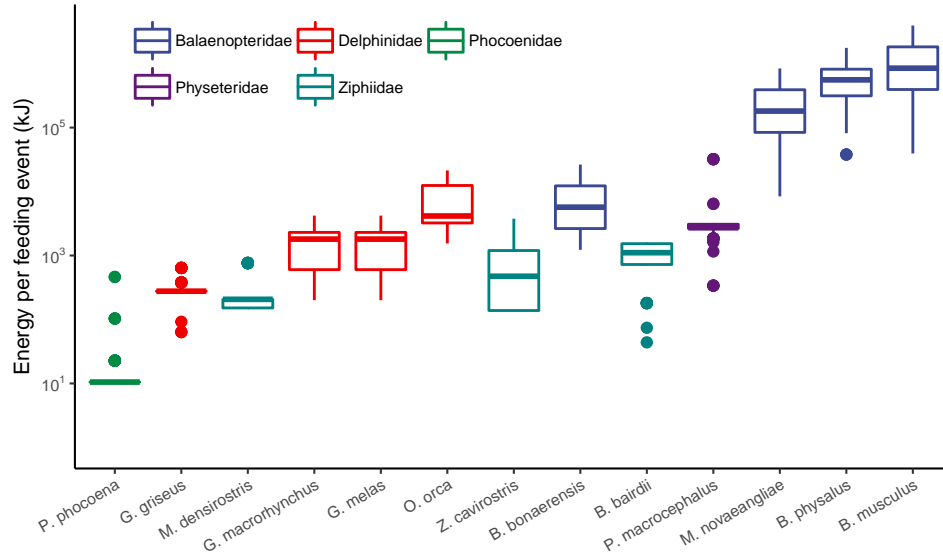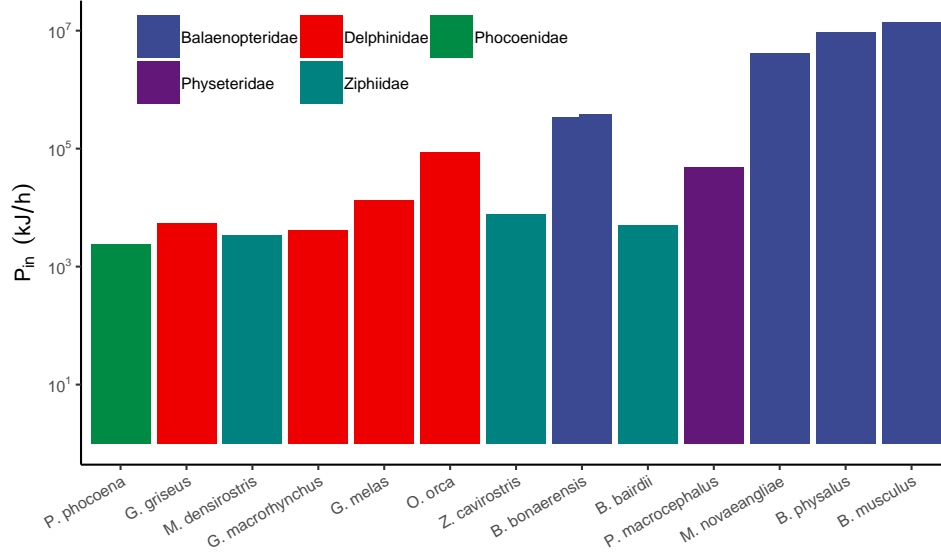

Modeled P_{in}

From before:

$$P_{in} = r_f \times E_p$$

Based on empirical feeding rates and prey energy density, the rate of energy consumption covers four orders of magnitude: from 2.4e3 kJ/hr (P. phocoena) to 1.4e7 kJ/hr (B. musculus).

The ratio of P_{in} to basal metabolic rate (BMR, estimated in kJ/day with Kleiber's equation $BMR = 293.1 \times m^{0.75}$ (Kleiber 1975)) puts the consumption rates of mysticetes into perspective. Odontocetes consume energy up to approximately 10 times BMR. The larger mysticetes, however, exceed 100 times BMR. This probably reflects both the high costs of lunge feeding as well as the demands of a capital breeding strategy.
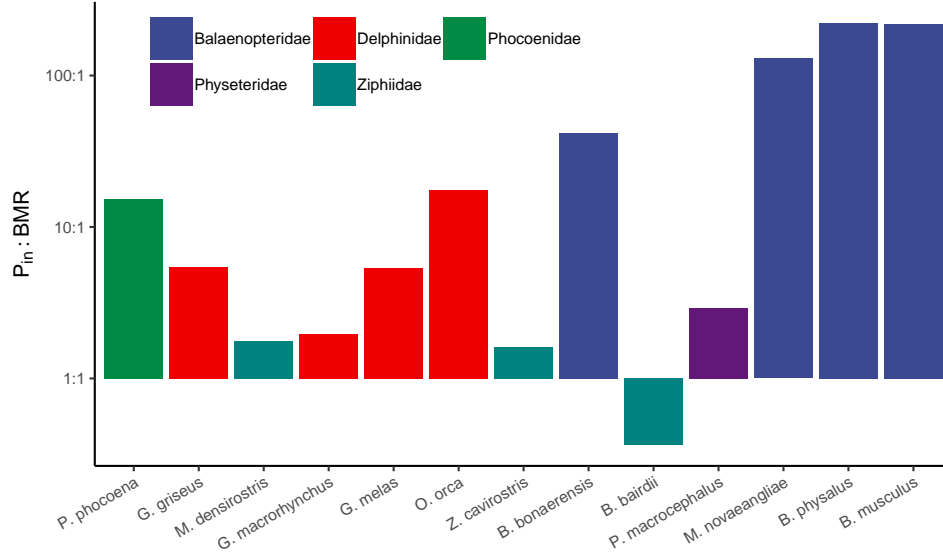
Flight power (P_{out})

The rate of energy expenditure during the flight response (flight power) is a function of the animals' elevated speed. In turn, stroke frequency has a relationship with body length dependent on speed. I modeled flight power as:

$$P_{out}(U_f) = (f_s(U_f) - f_s(U_b)) \times C_L \times m$$

Where f_s is a function relating stroke frequency to swimming speed, U_f and U_b are the animal's speed during the flight response and the basal, undisturbed state, C_L is the mass-specific locomotor cost of a stroke (Williams et al. 2017), and m is the animal's mass.

Fluking frequencies (f_f)

Animals can swim efficiently by maintaining a Strouhal number of approximately 0.3 (Rohr and Fish 2004). The Strouhal number is a dimensionless ratio of the form:

$$S_t = \frac{f}{U}A$$

Where A is the stroke amplitude. Cetacean stroke amplitudes are typically one fifth body length (ref?), so by fixing S_t at 0.3 I estimate stroking frequencies for a given speed as:

$$f = \frac{1.5U}{L}$$

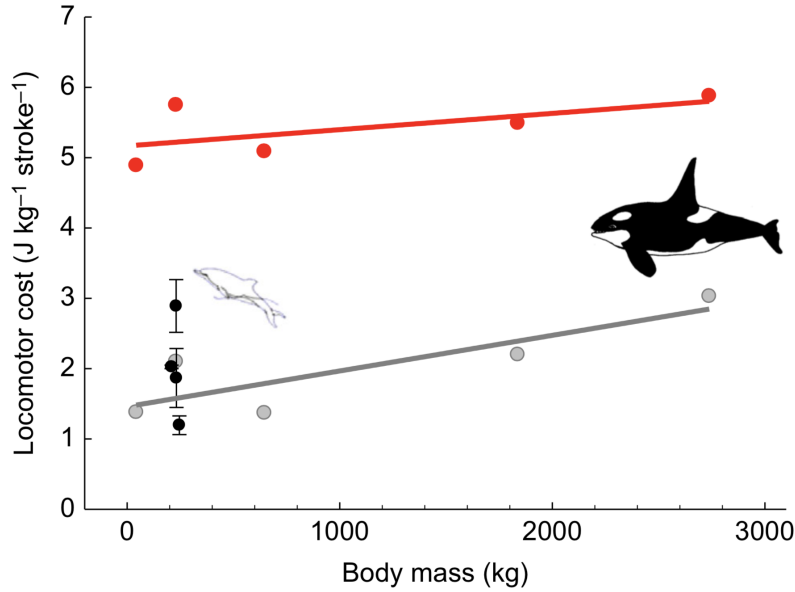Where L is the length of the animal.

The cruising speed of swimming animals is invariant with size (Sato Katsufumi et al. 2007), about 1.5 m/s. The predicted stroking frequencies for cetaceans in this study at cruising speed are:
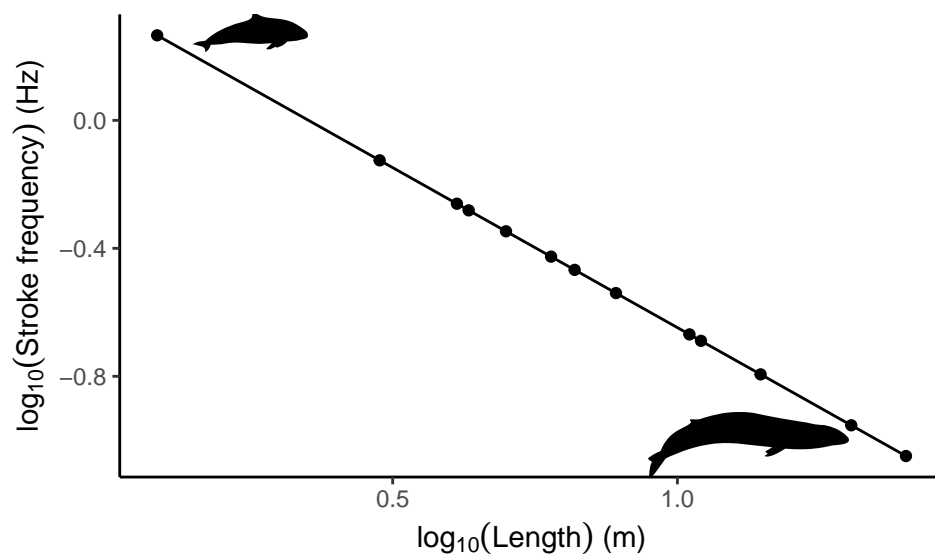
Locomotor cost (C_L)

(Williams et al. 2017) calculated C_L for cruising speeds as:

$$C_L = 1.46 + 0.0005m$$

The grey line in this figure (reproduced from (Williams et al. 2017)) is C_L at cruising speeds and the red line is at maximum aerobic output. I extrapolated the grey line to estimate C_L for all cetaceans, which I recognize is dodgy but it's the best available data.

Modeled P_{out}

Across body sizes, P_{out} increases steeply with flight speed until an inflection point at approximately 1.8 m/s, then increases with a shallow slope.
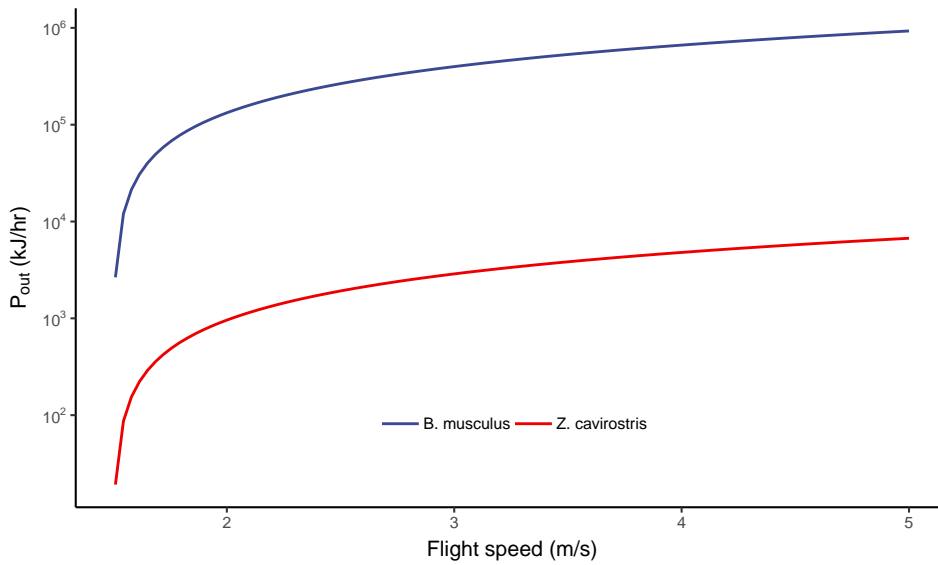
Total energetic cost (E_{sonar})

In summary, the energetic cost model combines lost consumption and additional stroking costs:

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

I derived P_{in} using empirical feeding rates and prey quality:

$$P_{in} = r_f \times E_p$$

The equation for P_{out} is based on (1) a general theoretical relationship between stroke rates and swim speeds and (2) an empirically derived scaling relationship between body size and per-stroke costs.

$$P_{out}(U_f) = (f_s(U_f) - f_s(U_b)) \times C_L \times m$$

Where U_b is fixed at 1.5 m/s. The relationship between stroke frequency and speed is:

$$f = \frac{1.5U}{L}$$

Combining these equations, the full model takes the form:

$$E_{sonar} = r_f \times E_p \times t_d + \left(\frac{1.5(U_f - 1.5)}{L} \right) \times C_L \times m \times t_f$$

TODO: Present 4 (?) case studies. Get good estimates for t_d, U_f and t_f. *Which species do we have good data for?* For now, given these hypothetical functional responses:

Species	t_d (min)	t_f (min)	U_f (m/s)	Reference
M. densirostris	360	30	4.5	DeRuiter et al. 2013 Fig 1.
Z. cavirostris	360	30	4.5	DeRuiter et al. 2013 Fig 1.
B. bonaerensis	150	60	3.5	Kvadsheim et al. 2017 Fig 2.
B. musculus	60	5	2.5	Southall et al. 2019 bw11_219b

I predict these energetic costs:

Species	E_{out}(kJ)	E_{in}(kJ)	E_{sonar}(kJ)	$E_{sonar} : BMR_d$
M. densirostris	3210	20500	23700	0.509
Z. cavirostris	10400	46700	57000	0.492
B. bonaerensis	44600	949000	994000	4.58
B. musculus	79600	14200000	14300000	9.14

In these examples, blue whales react weakly to sonar ($t_f = 5\ min, t_d = 1\ hr, U_f = 2.5\ m/s$) but the cost is still over 9x daily BMR. Conversely, a much stronger reaction from Ziphids ($t_f = 30\ min, t_d = 6\ hr, U_f = 4.5\ m/s$) only costs about half daily BMR. When considering the sub-lethal effects of SONAR, this model suggests filter feeders are a greater conservation concern than raptorial feeders, even though the latter are the majority in mass stranding events.

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