Energetic Consequences of Sonar Exposure

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What are the energetic consequences for cetaceans when exposed to sonar? The following model makes a first order approximation by estimating (1) the energy intake lost to foraging cessation and (2) the additional energy expenditure from increased swim speeds. We considered these two factors in four potential scenarios:

1. No response
2. Cessation of foraging without flight
3. Cessation of foraging with flight
4. Extreme response

The model will be paramterized using data and models from other sources (see table at the end of this document). Functional responses (e.g. displacement distance and duration) will come from the literature. The energy cost of lost feeding opportunities will be estimated with the scaling relationships in Jeremy's scaling paper. The energy cost of increased swim speeds during flight will be estimated using models from Williams et al. 2017. Thus:

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

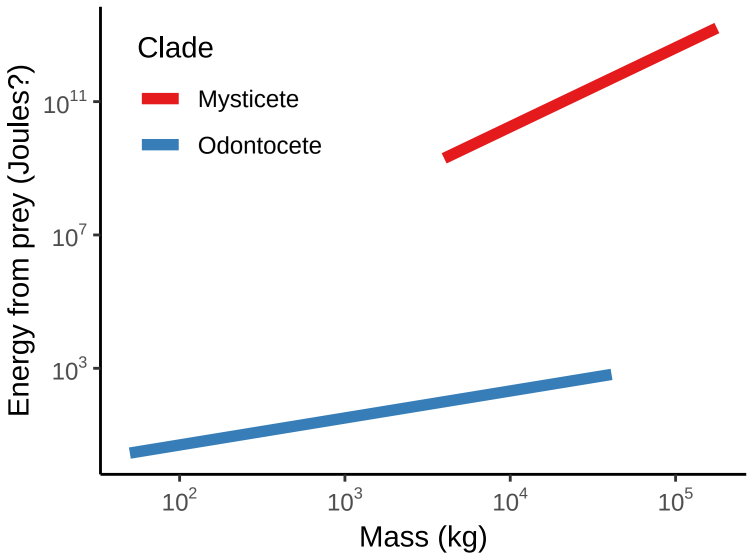
Where $\mathrm{E_{sonar}}$ is the energy cost of sonar exposure, $\mathrm{P_{in}}$ is the rate of energy intake when foraging, $\mathrm{t_d}$ is the displacement time, $\mathrm{P_{out}}$ is the increase in energy expenditure from locomotion due to the flight response, and $\mathrm{t_f}$ is the flight time.

Functional responses

In progress

Energetic parameters

I'm estimating $\mathrm{P_{in}}$ as the product of energy acquired per feeding event ($\mathrm{E_p}$) and feeding rate ($\mathrm{r_f}$). Energy acquired from prey scales sublinearly among odontocetes [$\mathrm{E_p}$=0.12$\mathrm{M_c}^{0.81}$] but superlinearly among mysticetes [$\mathrm{E_p}$=5.83$\mathrm{M_c}^{2.37}$]. *Note: Jeremy's paper has a negative coefficient for mysticete E_p scaling (v8.3:115) but I think that's a mistake.*



If I understand correctly, E_p is energy per feeding event. But how do I get feeding rate? Figure 2 in Jeremy's paper has [feeding events / dive] ~ [dive time - TADL]. Can we get feeding rates from something like that?

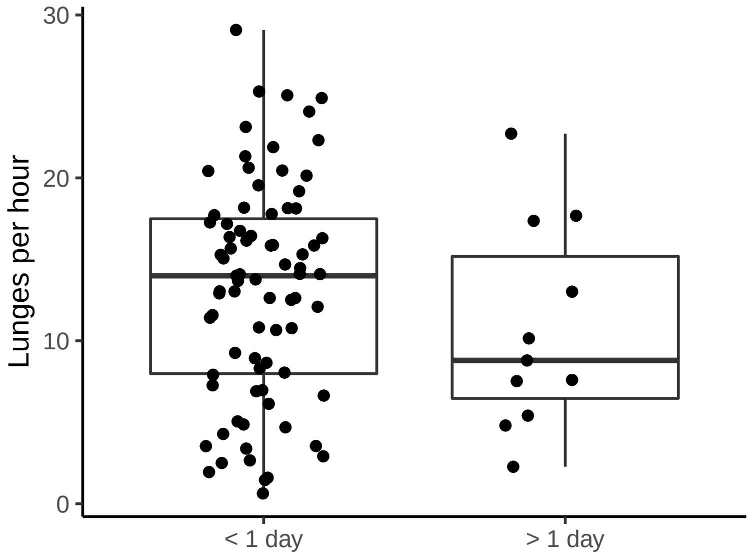
Empirical feeding rates

Prey data from "Cetacea model output BOUT_EXTANT.csv". NOTE: *Ziphius* prey data doesn't sum to 100%.

Species	Sum of prey percentages
Balaenoptera musculus	100.0
Berardius bairdii	100.0
Mesoplodon densirostris	100.1
Ziphius cavirostris	56.2

Blue whales

How should lunge rate be calculated? Lunge rates from tags that lasted more than a day are lower because they capture night time. Should we use the mean lunge rate from <1 day tags because that's the opportunity cost? Or should we use the mean lunge rate from >1 day tags to be conservative? I'm going with the latter for now, which is *10.7 lunges/hour*.



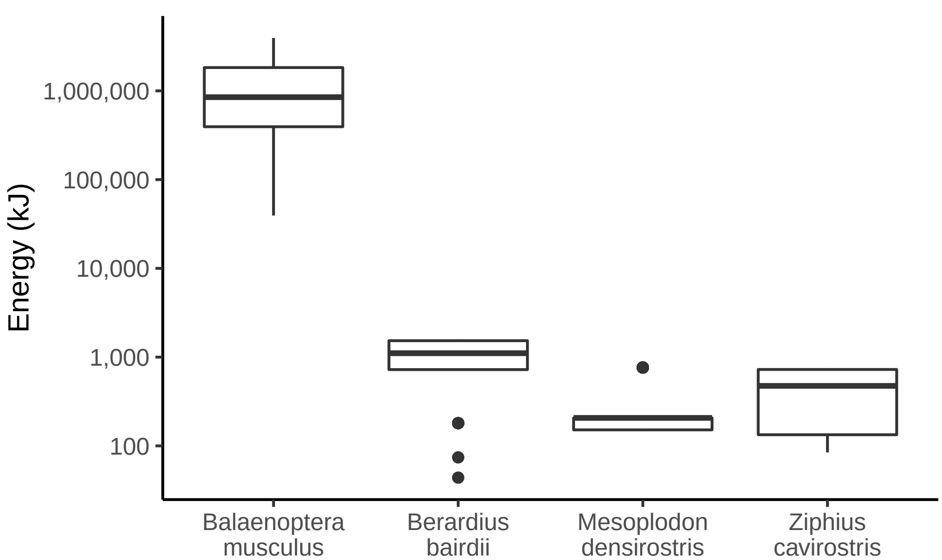
Beaked whales

We have limited beaked whale data. Mean hourly feeding rates are 4.6 for *Berardius* (but N = 1) and ~13 for *Mesoplodon* and *Ziphius*.

Species	N	Buzz rate (per hour)
Berardius bairdii	1	4.6
Mesoplodon densirostris	14	13.0
Ziphius cavirostris	4	12.8

Empirical prey size distributions

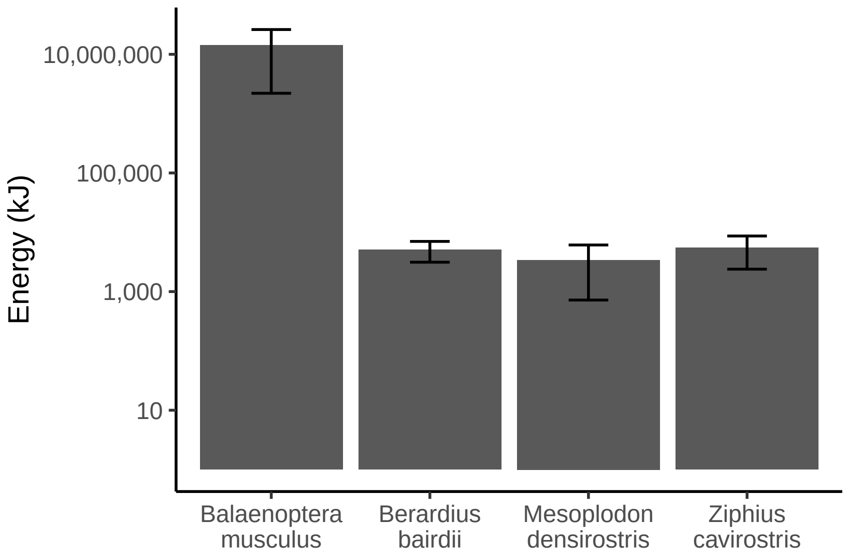
Blue whales engulf several orders of magnitude more energy per feeding event than beaked whales (no surprise there).



Power in

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

Where P_{in} is the rate of energy intake (kJ/hour), E_p is the energy from in one feeding event (kJ), and r_f is the feeding rate (feeding events/hour). The following figure shows estimates of P_{in} for the four study species. Error bars are calculated as $(mean(E_p) \pm sd(E_p)) \times r_f$.



Power out

$$P_{out} = f_f \times m \times (C_{L.max} - C_{L.pref})$$

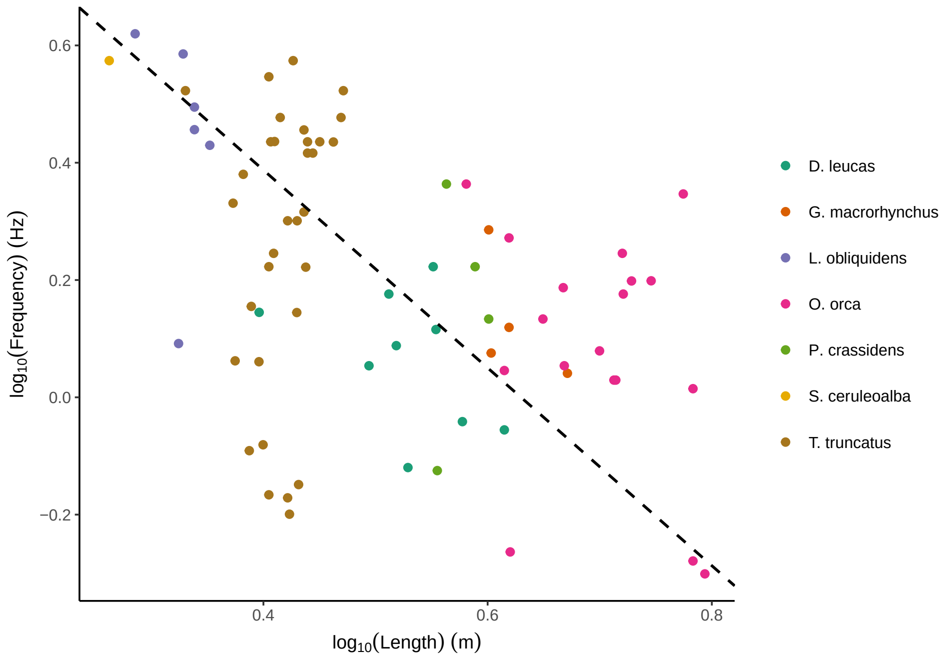
Where f_f is the fluking frequency, m is the mass of the animal, $C_{L.max}$ is the mass-specific cost of locomotion at maximum energetic output and $C_{L.pref}$ is the cost of locomotion at the prefered energetic output. Williams et al. 2017 calculated C_L as:

$$C_{L.pref} = 1.46 + 0.0005m$$
$$C_{L.max} = 5.17 + 0.0002m$$

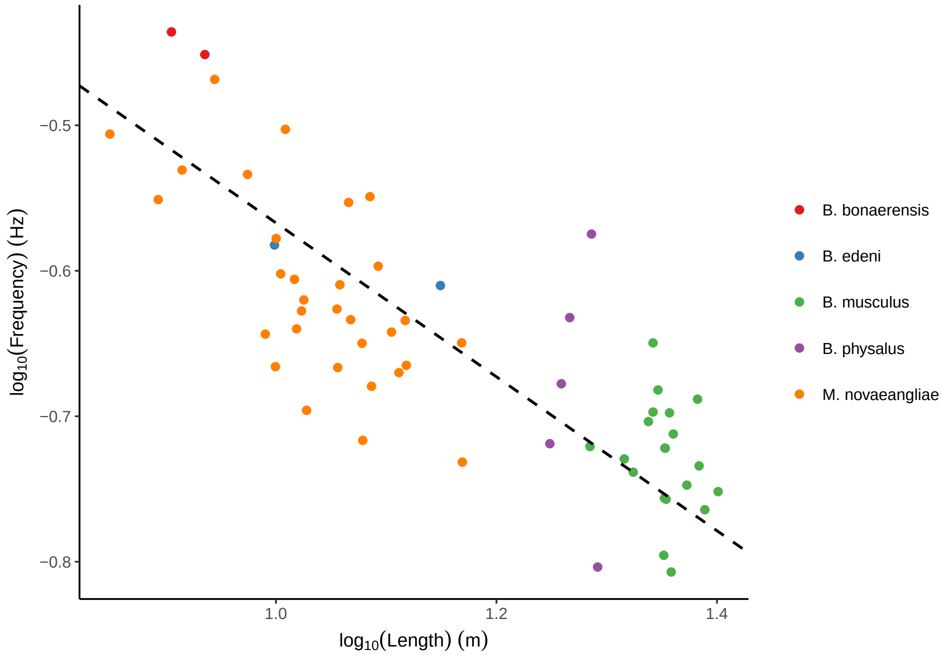
(see equations 6 and 7)

Fluking frequencies

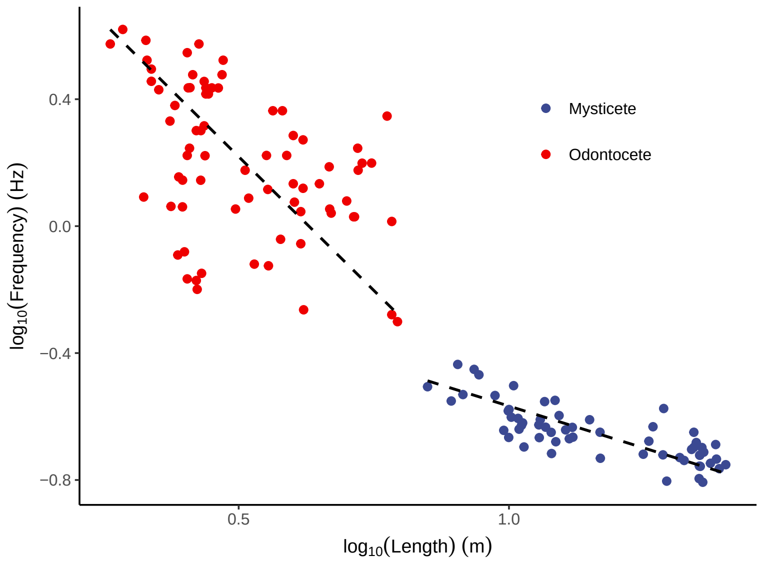
Fluking frequency in odontocetes scales with length as $log_{10}(f) = -1.686 \times log_{10}(m) + 1.062$, but not a lot of variance explained (*r^2=0.20*). Data from Frank Fish via Will G.



Fluking frequency in mysticetes scales with length as $log_{10}(f) = -0.529 \times log_{10}(m) - 0.038$. These are Will's data. Much more variance explained than for odontocetes (*r^2=0.63*)



They don't look terribly similar when plotted together.



These scaling relationships give us the following fluking frequencies:

Species	Length (m)	Fluking frequency (Hz)
Balaenoptera musculus	25.2	0.166
Berardius bairdii	10.5	0.219
Mesoplodon densirostris	4.1	1.068
Ziphius cavirostris	6.6	0.479

Given the equations for P_{out}, $C_{L.pref}$, and $C_{L.max}$, the estimates for power expended from increased fluking are:

Species	Length (m)	$f_f(Hz)$	Mass (kg)	$C_{L.pref}$	$C_{L.max}$	$P_{out}(W)$
B. musculus	25.2	0.166	93000	47.96	23.77	-373854
B. bairdii	10.5	0.219	11900	7.41	7.55	364
M. densirostris	4.1	1.068	860	1.89	5.34	3171
Z. cavirostris	6.6	0.479	2900	2.91	5.75	3942

Note:
C_L is in units of $Jkg^{-1}stroke^{-1}$

This shows the scaling relationship between cost of locomotion and body length derived for odontocetes in Williams et al. 2017 cannot be applied to an animal the size of a blue whale. Furthermore, I don't think the *Berardius* fluke frequency estimate is reliable because 1) *Berardius* is 69% longer than the longest odontocete in the fluking data (*O. orca*, 6.22 m) and 2) the mysticete fluking model wasn't the strongest predictor (r^2=*0.20*).

Literature

Reference	Species	Tags	Notes
Tyack et al. 2011	Mesoplodon densirostris	1	Only 1 tag, but other data from sonar array
DeRuiter et al. 2017	Balaenoptera musculus	37	How did the transition probability from deep feeding to other states change in CEEs?
DeRuiter et al. 2013	Ziphius cavirostris	2	Reduced time foraging in response to proximal sonar, but not distant
Friedlaender et al. 2016	Balaenoptera musculus	9	Includes prey data
Goldbogen et al. 2013	Balaenoptera musculus	17	Basis for Friedlaender et al. 2016 and DeRuiter et al. 2017
Kvadsheim et al. 2017	Balaenoptera acutorostrata	4	SoCal + Norway. 1 CEE + 1 control in each location
Southall et al. 2019	Ziphius cavirostris	0	Prey distribution in SoCal sonar array