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RESEARCH ARTICLE

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Modelling short-term energetic costs of sonar disturbance to cetaceans using high-resolution foraging data

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Abstract

1. Anthropogenic noise is a pervasive and increasing source of disturbance to wildlife. Marine mammals exhibit behavioural and physiological responses to naval sonar and other sound sources. The lost foraging opportunities and elevated locomotor effort associated with sonar disturbance likely carry energetic costs, which may lead to population-level consequences.
2. We modelled the energetic costs associated with behavioural responses using (a) empirical datasets of cetacean feeding rates and prey characteristics and (b) allometry of swimming performance and metabolic rates.
3. We applied our model to compare the short-term (i.e. the scale of the disturbance response; hours to days) energetic costs of a variety of observed behavioural responses. Efficient foragers (e.g. baleen whales) incur a greater relative energetic cost for mild behavioural responses as compared to the most extreme observed response for larger odontocetes (e.g. beaked whales). Energetic costs are more sensitive to lost feeding opportunities than increased energy expenditure from elevated locomotor effort.
4. To scale up from short-term costs to long-term effects (months to years), future research should address individuals' capacity to compensate for energetic losses as well as energetic thresholds for demographic rates (survival, fecundity). We discuss how relative energetic costs correlate with species' pace of life and the implications for conservation planning.
5. *Synthesis and applications*. Current approaches towards understanding the Population Consequences of Disturbance (PCoD) often must rely on expert opinion due to data deficiency. Our model provides an empirical method for linking behaviour to energetics, which is critical for managers to make informed decisions on actions that may affect marine mammal species. Furthermore, our model is applicable to other forms of disturbance, such as vessel traffic or seismic exploration, and our scaling approach enables risk projections for understudied species.

Abbreviations: A, Stroke amplitude (m); C_L, Mass-specific locomotor cost of a stroke (kJ stroke^{-1} kg^{-1}); E, Energy cost of disturbance (kJ); E^*, Relative energetic cost of disturbance (unitless); E_p, Energy acquired per prey capture event (kJ/event); f, Stroke frequency (Hz); Δf, Change in stroke frequency (Hz); P_a, Rate of energy acquisition (kJ/hr); ΔP_e, Change in rate of energy expenditure (kJ/hr); PCoD, Population Consequences of Disturbance; r_f, Feeding rate (event/hr); St, Strouhal number (unitless); t_d, Time displaced from feeding (hr); t_f, Time spent in flight response (hr); U_f, Swim speed during flight response (m/s).

KEYWORDS
anthropogenic noise, cetaceans, disturbance, energetics, foraging behaviour, predator–prey, sonar, sublethal effects

1 | INTRODUCTION

Human activity is profoundly altering terrestrial and marine soundscapes, with impacts expected to increase in the future (Barber et al., 2010; Frisk, 2012; Kaplan & Solomon, 2016; McDonald et al., 2006). Like other forms of disturbance, anthropogenic noise can induce behavioural and physiological responses with population-level consequences (Frid & Dill, 2002; Shannon et al., 2016; Sutherland, 2007). Effects can be acute, including mortality (Simpson et al., 2016), or chronic, such as reduced reproductive success (Injaian et al., 2018; Kleist et al., 2018). Sound moves more efficiently in water than in air, so the impacts of increasing anthropogenic noise are particularly cause for concern in marine ecosystems (Duarte et al., 2021; Hildebrand, 2009; Popper & Hawkins, 2012).

Sound is a critical aspect of cetacean life history, especially for toothed whales (Odontoceti). Odontocetes (porpoises, dolphins, beaked and sperm whales), use echolocation to locate and capture prey in light-limited environments, from turbid rivers to ocean depths up to 3 km (Lindberg & Pyenson, 2007; Shearer et al., 2019). Both toothed and baleen whales (Mysticeti) use sound in communication and social behaviour (Jensen et al., 2012; Sørensen et al., 2018; Stafford et al., 1998; Tyack, 1986). Critically, in certain states and contexts, cetaceans may respond to anthropogenic sound sources, sometimes with fatal results. Severe responses to military mid-frequency active sonar have been directly linked to mortality in odontocetes (Cox et al., 2006; D'Amico et al., 2009; Jepson et al., 2003; Parsons, 2017). Sonar-associated mass stranding events in the 1990s and 2000s led to a series of behavioural response studies (Table 1), showing that cetaceans exposed to sonar cease foraging, swim faster and flee the sound source (Harris et al., 2017; Southall et al., 2016). The biological significance of these sublethal responses remains largely unknown.

Behavioural responses, such as foraging cessation and elevated locomotion, carry energetic costs that may negatively impact individuals and populations. However, behavioural changes alone do not necessarily lead to population declines (Gill et al., 2001; Griffin et al., 2007). The Population Consequences of Disturbance (PCoD) conceptual framework addresses this issue using transfer functions to link changes in individuals' behaviour and physiology to population dynamics (Harwood et al., 2016; Pirotta et al., 2018). However, data are lacking for many of these transfer functions, necessitating expert solicitation for model parameterization (King et al., 2016). These 'interim' models have provided valuable insight by demonstrating, for example, how life-history stage (Farmer et al., 2018; Villegas-Amtmann et al., 2015) and resource availability (Hin et al., 2019; New et al., 2013) can mitigate or exacerbate the effects

TABLE 1 Controlled exposure experiments quantifying behavioural responses of cetaceans to low- and mid-frequency active sonar. Mysticetes in bold. *N* is the number of individuals exposed to sonar

Species	*N*	Region	Example feeding cessation	Example flight response	Reference
Berardius bairdii	1	E Pacific	50 min	30 min, 3 m/s	Stimpert et al. (2014)
Globicephala melas	6	Arctic			Antunes et al. (2014)
Hyperoodon ampullatus	1	Arctic	>8 hr		Miller et al. (2015)
Hyperoodon ampullatus	1	Arctic	>6 hr	10 min, 4 m/s	Sivle et al. (2015)
Hyperoodon ampullatus	3	Arctic	>8 hr	12 min, 3 m/s	Wensveen et al. (2019)
Mesoplodon densirostris	1	W Atlantic			Tyack et al. (2011)
Orcinus orca	8	Arctic			Miller et al. (2014)
Ziphius cavirostris	2	E Pacific	6.6 hr	1.6 hr, 2.6 m/s	DeRuiter et al. (2013)
Balaenoptera acutorostrata	1	Arctic			Sivle et al. (2015)
Balaenoptera acutorostrata	2	E Pacific, Arctic	70 min		Kvadsheim et al. (2017)
Balaenoptera musculus	17	E Pacific	62 min	5 min, 3 m/s	Goldbogen et al. (2013)
Balaenoptera musculus	9	E Pacific			Friedlaender et al. (2016)
Balaenoptera musculus	42	E Pacific	>1 hr	5 min, 3 m/s	Southall et al. (2019)
Megaptera novaeangliae	11	Arctic			Sivle et al. (2015)
Megaptera novaeangliae	13	Arctic			Sivle et al. (2016)

of disturbance, but they also highlight the need for empirically quantifying undisturbed behaviour, physiology and demography to establish a baseline.

Quantifying the foraging and movement energetics of wild cetaceans presents numerous challenges. Direct measurements of energy expenditure are limited to small- to medium-sized toothed whale species using respirometry or doubly labelled water techniques (Fahlman et al., 2016; Rojano-Doñate et al., 2018; Williams et al., 1993). Baleen whale metabolic rates have never been measured directly but have been inferred from models parameterized primarily with breathing rate data (Blix & Folkow, 1995; Sumich, 1983). For behavioural response studies, the theoretical relationship between exercise kinematics, such as fluke stroking rates, and swimming speed across body sizes (grounded in biomechanical constraints) provides a first approximation of increases in metabolism due to changes in locomotion (Dial et al., 2008; Fahlman et al., 2016). Stroking rates recorded for captive animals show a consistent relationship with speed and size (Rohr & Fish, 2004), which is supported by studies of wild animals (Gough et al., 2019; Sato et al., 2007; Watanabe et al., 2011, 2015).

Empirical estimates of energy intake are possible for a wider range of species, though still present logistical challenges. The biomass and energy obtained per feeding event for rorqual whales (the 'pleated' baleen whales such as blues, *Balaenoptera musculus*, and humpbacks, *Megaptera novaeangliae*) have been measured by combining active acoustics with animal-borne sensors and morphology of the engulfment apparatus (Goldbogen et al., 2019). Active acoustic techniques, also called prey mapping, use the backscatter of high-frequency sound from prey to measure the composition, extent and density of schools of crustaceans, squid and fish (Benoit-Bird & Lawson, 2016). Rorqual lunge feeding behaviour is characterized by distinct kinematic signatures that are readily captured by high-resolution animal-borne accelerometer tags. The whale accelerates as it approaches a prey school, engulfs a large quantity of prey-laden water and rapidly decelerates while filtering the engulfed water mass through baleen plates (Cade et al., 2016; Goldbogen et al., 2017). In contrast, toothed whales use echolocation to forage, and sound-recording tags can detect the acoustic signatures (i.e. high-rate click trains, or buzzes, and prey echoes) associated with prey capture (Johnson et al., 2004; Miller et al., 2004; Wisniewska et al., 2016). Odontocete diet composition and prey size have been estimated from non-digestible parts in stomach samples, such as squid beaks and fish otoliths (Clarke, 1996), and with active acoustic techniques (Wisniewska et al., 2016).

Here, we use empirical estimates of cetacean energy intake to predict the energetic costs of sonar disturbance and address the following questions. First, are energetic costs more sensitive to lost feeding opportunities (reduced acquisition) or elevated locomotor effort (increased expenditure)? We hypothesize that lost feeding opportunities are more important because of the low cost of cetacean locomotion (Williams, 1999) and high foraging efficiency conferred by adaptations such as echolocation and bulk filter feeding (Goldbogen et al., 2017; van der Hoop et al., 2019; Watwood et al., 2006). Second, which species face the greatest immediate energetic costs relative to body size? The biological consequences of energy costs depend on energetic requirements; a 1,000 kJ cost will have greater consequences for a small porpoise than a large baleen whale. Mass-specific energy costs are inappropriate for comparison because energetic requirements (basal or field metabolic rate) are not isometrically proportional to body size (Kleiber, 1975; Nagy, 2005). Therefore, we define the relative energetic cost of a behavioural response as the ratio of its absolute energetic cost to the allometrically predicted daily basal metabolic rate. Although basal metabolic rates do not account for important energetic demands, such as lactation, they are correlated with many phylogenetic, physiological and ecological parameters and, as such, are a useful proxy for energy requirements (White & Seymour, 2004). This ratio facilitates interspecific comparisons by accounting for differential energy budgets across large body size ranges, but it is not appropriate for intraspecific comparisons where energy budget variability is influenced by other factors (such as life-history stage) more than body size. As feeding efficiency increases with body size among mysticetes, but decreases with body size among odontocetes (Goldbogen et al., 2019), we hypothesize that relative energetic costs are greatest for very large and small species compared to intermediate sizes. This scaling approach facilitates assessments for understudied species and is broadly applicable to other forms of disturbance, such as vessel traffic and seismic exploration.

2 | MATERIALS AND METHODS

We modelled the energetic cost of sonar exposure as the sum of energetic costs due to lost feeding opportunities and elevated locomotion during the flight response (Equation 1) for 11 species, selected on the basis of available feeding rate and prey energy content data (Table 2). See Figure 1 for a flowchart showing how the model combines species-specific energetics and behavioural scenarios to predict absolute and relative energetic costs.

$$E = P_a t_d + \Delta P_e \left(U_f\right) t_f, \quad (1)$$

where:

E is the energetic cost of sonar exposure in kJ.

P_a is the undisturbed rate of energy acquisition in kJ/hr.

t_d is the time displaced from feeding in hours.

ΔP_e is the increase in rate of energy expenditure when fleeing in kJ/hr (a function of swim speed).

U_f is the swim speed during the flight response in m/s.

t_f is the duration of the flight response in hours.

Together, t_d, U_f and t_f parameterize the behavioural response. Because the behavioural response can be highly variable, depending on the animal's behavioural state and the amplitude, frequency, and distance of the sound source, we leave these parameters to model users' discretion to allow greater flexibility (Ellison et al., 2012; Friedlaender et al., 2016). Energy acquisition and expenditure rates

TABLE 2 Cetacean species used in developing the model, covering three orders of magnitude in body size. Length and mass taken from (Goldbogen et al., 2019). Only *P. macrocephalus* exhibits strong sexual dimorphism; size here is for females. Mysticetes (all rorquals) in bold

Species	Length (m)	Mass (kg)	Family
Harbour porpoise (*Phocoena phocoena*, *Pp*)	1.2	31	Phocoenidae
Risso's dolphin (*Grampus griseus*, *Gg*)	3	350	Delphinidae
Blainville's beaked whale (*Mesoplodon densirostris*, *Md*)	4.1	860	Ziphiidae
Short-finned pilot whale (*Globicephala macrorhynchus*, *Gma*)	4.3	980	Delphinidae
Long-finned pilot whale (*Globicephala melas*, *Gme*)	5	1,200	Delphinidae
Cuvier's beaked whale (*Ziphius cavirostris*, *Zc*)	6.6	2,900	Ziphiidae
Minke whale (*Balaenoptera bonaerensis*, *Bb*)	7.8	6,700	Balaenopteridae
Sperm whale *Physeter macrocephalus*, *Pm*)	11	15,000	Physeteridae
Humpback whale (*Megaptera novaeangliae*, *Mn*)	14	36,000	Balaenopteridae
Fin whale (*Balaenoptera physalus*, *Bp*)	20.2	53,000	Balaenopteridae
Blue whale (*Balaenoptera musculus*, *Bm*)	25.2	93,000	Balaenopteridae

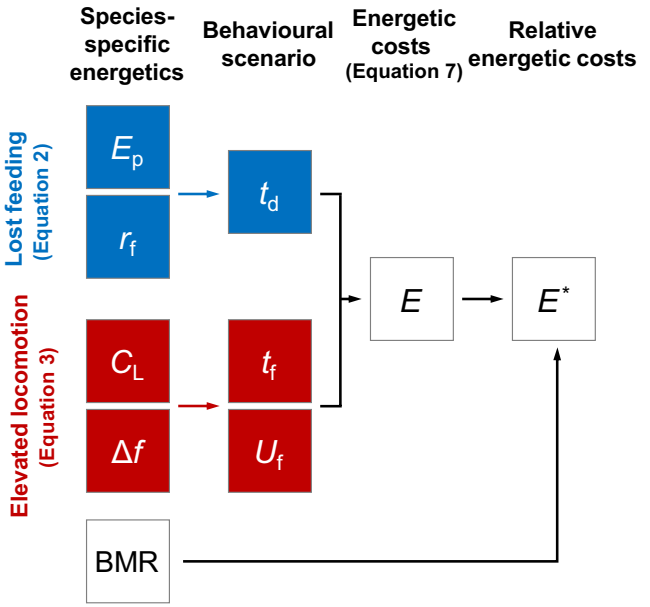

FIGURE 1 Flowchart explaining model components. Each species' energy intake (blue) and expenditure (red) parameters (first column) were estimated from empirical evidence or scaling relationships. The behavioural scenario (second column) quantifies the magnitude of the response to sonar. The energetic cost of the response (third column) is a function of the species-specific energetics mediated by the behavioural scenario. The costs from a long feeding cessation (t_d) depend on the energy content in prey (E_p) and the feeding rate (r_f), whereas the costs of a long (t_f) or fast (U_f) flight response depend on locomotor costs (C_L) and the change in fluking frequency (Δf). The relative energetic cost (E^*, fourth column) of a behavioural scenario is defined as the ratio of the energetic cost to the daily basal metabolic rate. Since energy budgets increase with body size, E^* facilitates interspecific comparisons

are species-specific parameters based on empirical data and scaling relationships.

2.1 | Lost energy acquisition

The undisturbed rate of energy acquisition was modelled as the product of feeding rate and energy acquired per feeding event.

$$P_a = r_f E_p, \quad (2)$$

where:

r_f is the feeding rate in prey capture events/hr.

E_p is the energy acquired per prey capture event in kJ.

Feeding rates were estimated using kinematic and acoustic data from animal-borne bio-logging devices (Goldbogen et al., 2019). We excluded deployments involving controlled exposure experiments to get a best estimate of undisturbed feeding rates. Harbour porpoises were temporarily lifted from the water to deploy bio-loggers, so the first hour following deployment was excluded to remove deployment response behaviours (Rojano-Doñate et al., 2018; Wisniewska et al., 2018). Each deployment was divided into hourly bins, excluding the first fraction of an hour, to generate species-specific empirical distributions. For example, a 1.5-hr deployment would yield one hourly feeding rate, counting all feeding events from 0.5 to 1.5 hr after deployment. Excluding the first fractional hour was intended to reduce the influence of potential changes in behaviour associated with tag deployment. Although data are sparse, available evidence suggests cetaceans have extremely high feeding success rates (Wisniewska et al., 2016), so we assumed all feeding events resulted in prey capture.

Energy acquired per feeding event (E_p) was modelled as a log-normal variable to match the distribution of resources in patchy environments (Benoit-Bird et al., 2019; Pagel et al., 1991; Sims et al., 2008; Sugihara, 1980). For odontocetes, the lognormal was parameterized using prey size and energy density data from the literature (Goldbogen et al., 2019, Tables S1–S9). Specifically, the lognormal mean and variance of E_p for each species were estimated as the

mean and variance of the logged product of prey size (in kg) and prey energy density (in kJ/kg), weighted by diet composition. We used acoustic prey mapping spatially and temporally linked with feeding whales to measure biomass densities available to rorquals (Goldbogen et al., 2019). Biomass density was modelled as a lognormal distribution and the energy per feeding event was then calculated as the product of biomass density (kg/m^3; Cade et al., 2021), engulfment capacity (m^3) and prey energy density (kJ/kg). Engulfment capacity was estimated from a morphological model (Goldbogen et al., 2010; Kahane-Rapport and Goldbogen, 2018; Potvin et al., 2012). We used krill energy density values based on *Thysanoessa spinifera* krill (3,800 kJ/kg) for all rorqual species except *B. bonaerensis*, which feeds on *Euphausia superba* (4,575 kJ/kg; Chenoweth, 2018; Färber-Lorda et al., 2009). Although rorquals feed on a variety of prey, we focused on krill-feeding individuals for two reasons. First, krill is the most common diet across species (Kawamura, 1980; Nemoto, 1970). Second, fish-feeding rorquals feed at lower and more variable rates and longer datasets are needed to properly quantify patterns in undisturbed feeding behaviour (Cade et al., 2016, 2020).

2.2 | Increased energy expenditure

The increase in energy expenditure due to the flight response was modelled as the additional locomotor costs from swimming at an elevated speed.

$$\Delta P_e\left(U_f\right) = \Delta f\left(U_f\right) C_L m, \tag{3}$$

where:

Δf is the increase in stroke frequency from cruising to flight speed in stroke/hr, a function of swim speed.

C_L is the mass-specific locomotor cost of a stroke in kJ stroke^{-1} kg^{-1}.

m is the mass of the animal in kg.

The mass-specific locomotor cost of a stroke for cetaceans at cruising speed is estimated to be (Williams et al., 2017):

$$C_L = 1.46 \times 10^{-3} + 5.0 \times 10^{-7}\,\text{m}. \tag{4}$$

This relationship was derived using data from odontocete species massing 42 kg to 2,700 kg, and is therefore a source of uncertainty for larger odontocetes and mysticetes. Williams et al. (2017) also derived a locomotor cost relationship for maximum aerobic performance; however, the relationship had low explanatory power and produced unrealistic results when extrapolated to rorqual body sizes. We estimated the increase in stroke frequency by assuming cetaceans cruise at 1.5 m/s and swim efficiently by maintaining a Strouhal number of 0.3 (Rohr & Fish, 2004; Sato et al., 2007). The Strouhal number is a dimensionless ratio relating swimming speed to stroke amplitude and frequency ($St = \frac{Af}{U}$). Assuming a stroke amplitude of 1/5 body length (Bainbridge, 1958; Fish, 1998; Gough et al., 2019), a Strouhal number of 0.3 can be used to estimate stroke frequency as:

$$f = \frac{1.5U}{L} \times 3600, \tag{5}$$

where:

St is the Strouhal number (unitless).

A is the stroke amplitude in m.

f is the stroke frequency in strokes/s.

U is the swimming speed in m/s.

L is the length of the animal in m.

Substituting a cruising speed of 1.5 m/s (Gough et al., 2019; Sato et al., 2007; Watanabe et al., 2011) into Equation (5) gives the increase in stroke frequency (in strokes/hr) as:

$$\Delta f\left(U_f\right) = \frac{5400}{L}\left(U_f - 1.5\right). \tag{6}$$

There is considerable uncertainty associated with the values of many of the parameters in Equations 4 and 6. The slope of the scaling relationship for C_L (Equation 4) was not significant in the original study, likely due to small sample sizes, and the estimate for the change in fluking frequency depends on assumptions of a fixed cruising speed and Strouhal number (Equation 6). To account for this uncertainty, Equations 4 and 6 were treated as best estimates and C_L and Δf were drawn from gamma distributions with means equal to the best estimates. See the next section, *Sensitivity analysis*, for more details.

Combining Equations (1–3 and 6) yields the final, expanded model:

$$E = r_f E_p t_d + \frac{5400}{L}\left(U_f - 1.5\right) C_L m t_f. \tag{7}$$

2.3 | Sensitivity analysis

We conducted a sensitivity analysis using a global approach (i.e. one that samples all parameters simultaneously) to understand how altering one energetic parameter (r_f, E_p, Δf and C_L) changes the model result (E) across the full range of the other parameters. We generated a matrix of input values using Latin hypercube sampling (which produces random combinations of inputs evenly distributed throughout the parameter space), then calculated a vector of model outputs. A multiple linear regression of the outputs with respect to the inputs quantified the global sensitivity of the model to each parameter; that is, each coefficient describes the change in the output with respect to a change in one parameter after controlling for all other parameters. However, the four parameters considered in our sensitivity analysis are of greatly different magnitudes and in different units, so a standardization step is necessary for the regression coefficients to be comparable. We standardized the input matrix and the output vector by z-score, that is, the difference of the parameter value from the parameter mean divided by the standard deviation. Conducting the sensitivity analysis in this way allowed us to, for example, understand how changes in locomotor costs (C_L) affect model output (E) across all combinations of feeding rates (r_f), energy obtained per feeding event (E_p) and change in fluking frequency (Δf). This global approach is opposed to local sensitivity analyses where all other parameters are held at a fixed value (typically the mean) and

each parameter is varied individually, which describes sensitivity in a more limited context (Marino et al., 2008).

The distribution of hourly feeding rates (r_f) for each species was generated empirically by counting the number of feeding events (lunges in rorquals and buzzes in toothed whales) in each hour of each deployment, discarding the leading incomplete hour (see *Lost energy acquisition* above). The mean and standard deviation of the rorqual E_p distributions were based on prey mapping data from two California locations in the years 2011–2018 (Goldbogen et al., 2019). For odontocete *Ep* distributions, we fit a lognormal distribution to available prey data in the literature (Goldbogen et al., 2019). Both Δf and C_L were treated as gamma distributions with a mean equal to the parameter's best estimate (Equations 4 and 5). We sampled parameter values using Latin hypercube sampling with the pse R package (Chalom & de Prado 2017).

The model's sensitivity to energetic parameters is conditional on the behavioural response, for example, E will be more sensitive to r_f and E_p when t_d is very long relative to t_f. Therefore, we assessed model sensitivity for two different behavioural response scenarios that emphasize energy acquisition (i.e. greater t_d, lesser t_f and U_f) and energy expenditure (i.e. greater t_f and U_f, lesser t_d; Table 3). The magnitude of the behavioural parameters in these scenarios was constrained to responses observed in controlled exposure experiments, and though they are not representative of the full spectrum of potential responses they provide a basis for comparing the sensitivity of energetic costs to lost feeding opportunities versus elevated locomotor effort. For each behavioural scenario and species, we generated a matrix of input values via Latin hypercube sampling and calculated a vector of model results. Inputs and outputs were standardized by *z*-score and we fit a linear regression to calculate a standardized coefficient for each parameter and species $\left[z(E) \sim z\left(r_f\right) + z\left(E_p\right) + z(\Delta f) + z\left(C_L\right)\right]$ using the lm function in base R (R Core Team, 2018). Each coefficient, then, represents the change in model output if the parameter was increased by one standard deviation, after controlling for the other parameters.

2.4 | Relative energetic costs

As energy budgets increase with body size, a size-corrected metric is necessary for interspecific comparisons of energetic costs for a clade covering three orders of magnitude of body size. We used our model to estimate the absolute energetic costs associated with three behavioural scenarios corresponding to observed mild, strong and extreme responses to sonar (Table 4). These costs were divided by daily basal metabolic demands, as predicted by allometric relationships between size and basal metabolic rate ($\text{BMR} = 293.1 \times [\text{mass (kg)}]^{0.75}$; Kleiber, 1975). The resulting metric, E^*, represents the relative energetic costs of a behavioural response with respect to body size and is only applicable to interspecific comparisons; it is not a meaningful metric for comparing intraspecific relative energetic costs for individuals differing in size or metabolic rates. E^* calculations for additional metabolic scaling relationships are reported in Supporting Information Appendix 1 (see Figures S5–S7; Maresh, 2014; Nagy et al., 1999; White & Seymour, 2003). All computational details (code, session information) are also available in Supporting Information Appendix 1.

TABLE 3 Behavioural scenarios used to test model sensitivity to energetic parameters. t_d, duration of feeding cessation; t_f, duration of flight response; U_f, swimming speed of flight response

Scenario	t_d (hr)	t_f (hr)	U_f (m/s)
Energy acquisition	4.0	0.25	3.0
Energy expenditure	1.0	1.0	5.0

3 | RESULTS

3.1 | Lost energy acquisition

Baseline rate of energy acquisition (P_a) was calculated as the product of the hourly feeding rate (r_f) and energy per feeding event (E_p; Equation 2). r_f was zero-inflated and we modelled E_p with a lognormal distribution; therefore, P_a was zero-inflated and right-skewed (Figure 2). Rorquals and harbour porpoises had the greatest mass-specific energy acquisition rates while beaked whales and sperm whales had the lowest (Table 5). Hourly feeding rates were highly variable. Mean r_f ranged from 2.44 (first and third quartile, Q1–Q3: 0–3, short-finned pilot whale) to 110 feeding events per hour (Q1–Q3 19–169, harbour porpoise; Figure 3a). The first quartile of feeding rates was 0 for all but two species: harbour porpoises and sperm whales. E_p increased with body size such that bulk filter-feeding rorquals consumed multiple orders of magnitude more energy per feeding event than odontocetes (Table 5). However, the Q1–Q3 range of mass-specific energy acquired per feeding event overlapped among delphinids and balaenopterids, with substantially lower values for ziphiids and physeterids (Figure 3b).

3.2 | Sensitivity analysis

Parameters associated with lost energy acquisition (r_f, E_p) were more influential than the energy expenditure parameters (Δf, C_L) across species groups in both behavioural scenarios. In the scenario

TABLE 4 Behavioural scenarios used to model relative energetic costs. t_d, duration of feeding cessation; t_f, duration of flight response; U_f, swimming speed of flight response

Scenario	t_d (hr)	t_f (hr)	U_f (m/s)
Mild response	1	0.25	2.5
Strong response	2	0.5	3.5
Extreme response	8	2	5

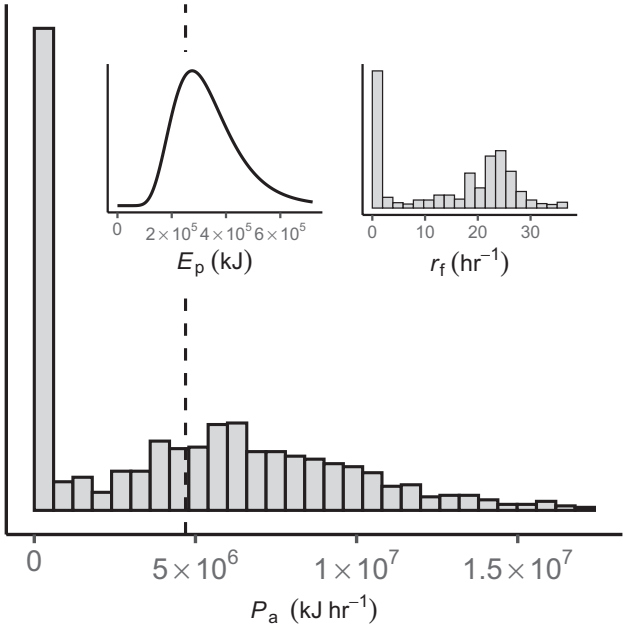

FIGURE 2 Example of baseline rate of energy acquisition (ΔE_a, main plot) for a blue whale as the product of lognormally distributed prey energy content (E_p) and empirically measured hourly feeding rates (r_f; inset plots). Mean P_a indicated with dashed line. Similar distributions were calculated for all species in the study (see Supporting Information)

emphasizing feeding cessation (t_d = 4 hr, t_f = 0.25 hr, U_f = 3.0 m/s), sensitivity coefficients were greater for r_f and E_p than Δf and C_L with no overlap in the 95% confidence intervals (Figure 4a). Model sensitivity to energy expenditure parameters increased in the elevated flight scenario (t_d = 1 hr, t_f = 1 hr, U_f = 5.0 m/s), but did not fully exceed sensitivity to energy acquisition parameters (Figure 4b). In this scenario, E_p was the most sensitive parameter for most species followed by C_L and r_f. Rorquals were most sensitive to E_p (95% CI 0.524–0.593) followed by C_L (95% CI 0.389–0.456) and r_f (95% CI 0.165–0.220). Similarly, porpoises and dolphins were most sensitive to E_p (95% CI 0.499–0.575) followed by C_L (95% CI 0.175–0.247) and r_f (95% CI 0.065–0.144). Only the beaked and sperm whales were most sensitive to an energy expenditure parameter, C_L (95% CI 0.743–0.798), followed by E_p (95% CI 0.254–0.308) and Δf (95% CI 0.103–0.155).

3.3 | Relative energetic costs

Relative energetic costs (E^*) were concave upward with respect to body size, indicating that the smallest and largest species face greater short-term relative energetic costs (Figure 5). Within each scenario, the greatest median E^* values were associated with humpback and blue whales and the lowest with short-finned pilot whales

TABLE 5 Energy acquisition parameters (feeding rate in events/hr: r_f, energy acquired per prey capture event: E_p, baseline energy intake rate: P_a, and mass-specific rate: P_a/m) presented as mean and Q1–Q3. Species ordered by size, mysticetes in bold.

Species (n individuals, hours)	r_f (hr^{-1})	E_p (kJ)	P_a (kJ/hr)	P_a/m (kJ hr^{-1} kg^{-1})
P. phocoena (8, 161)	110 (19–169)	14.9 (8.20–27.2)	2.40×10^3 (186–2.86×10^3)	74.5
G. griseus (11, 39)	11.7 (0–17.5)	282.0 (215.0–369.0)	3.26×10^3 (0.0–4.31×10^3)	8.57
M. densirostris (14, 105)	12.8 (0–23)	218.0 (152.0–313.0)	2.97×10^3 (0.0–4.81×10^3)	3.95
G. macrorhynchus (2, 9)	2.44 (0–3)	1.31×10^3 (732.0–2.33×10^3)	3.34×10^3 (0.0–2.74×10^3)	3.80
G. melas (9, 101)	7.37 (0–13)	1.31×10^3 (732.0–2.33×10^3)	1.25×10^4 (0.0–1.52×10^4)	11.1
Z. cavirostris (3, 53)	10.8 (0–21)	419.0 (223.0–786.0)	6.89×10^3 (0.0–7.31×10^3)	2.41
***B. bonaerensis* (6, 121)**	48.4 (0–62)	2.82×10^3 (2.28×10^3–3.50×10^3)	1.53×10^5 (2.25×10^3–1.97×10^5)	20.6
P. macrocephalus (29, 237)	11.4 (4–17)	2.70×10^3 (1.57×10^3–4.64×10^3)	4.19×10^4 (8.94×10^3–5.61×10^4)	2.83
***M. novaeangliae* (28, 229)**	17.0 (0–26)	9.29×10^4 (7.42×10^4–1.16×10^5)	1.68×10^6 (0.0–2.68×10^6)	45.4
***B. physalus* (4, 39)**	14.8 (0–26)	1.44×10^5 (1.16×10^5–1.78×10^5)	2.07×10^6 (0.0–3.63×10^6)	42.0
***B. musculus* (21, 243)**	14.3 (0–24)	3.13×10^5 (2.46×10^5–3.98×10^5)	4.98×10^6 (0.0–7.86×10^6)	51.4

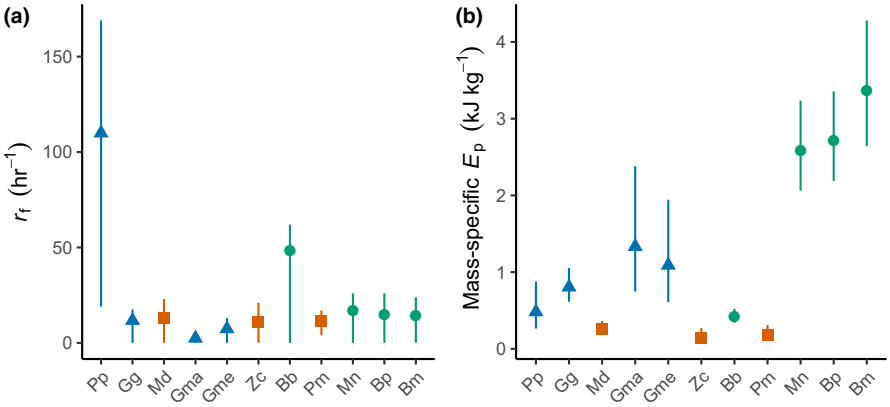

FIGURE 3 (A) hourly feeding rates (r_f, mean and Q1–Q3) were greatest for the smallest odontocete (harbour porpoise) and mysticetes (minke whale). (b) Mass-specific energy acquired per feeding event (mass-specific E_p, mean and Q1–Q3) increased with body size with the exception of beaked and sperm whales. Families Phocoenidae and Delphinidae in blue triangles, Ziphiidae and Physeteridae in orange squares, and Balaenopteridae in green circles. Species ordered by size; see Table 2 for abbreviations

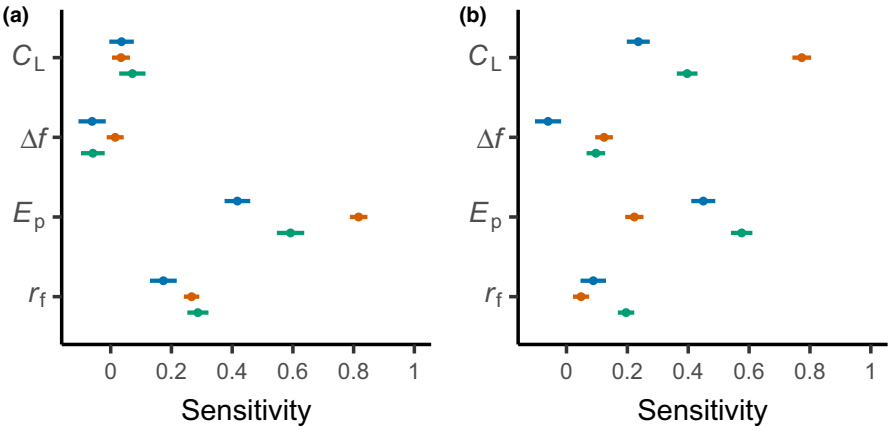

FIGURE 4 Sensitivity analyses indicated parameters associated with energy acquisition (energy from prey, E_p; feeding rate, r_f) were more influential than energy expenditure parameters (locomotor cost, C_L; change in stroke frequency, Δf) in behavioural scenarios emphasizing both energy acquisition (a) and energy expenditure (b; Table 3). Families Phocoenidae and Delphinidae in blue, Ziphiidae and Physeteridae in orange, and Balaenopteridae in green. See text for details

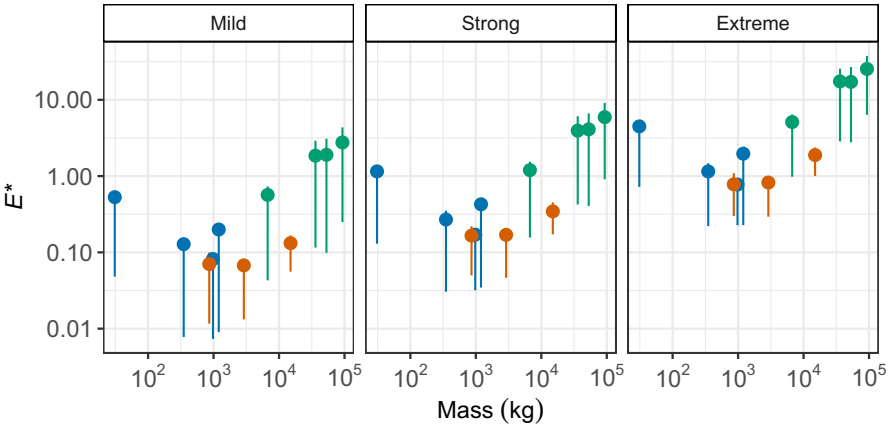

FIGURE 5 The relative energetic costs (E^*) of three behavioural responses (Table 4) with respect to body size (points and lines: median and Q1–Q3). The concave pattern indicates very large and small cetaceans face greater immediate energetic costs relative to their size for a given behavioural response than intermediate-sized species. The relative energetic costs of a mild response by large rorquals exceeded those of an extreme response by short-finned pilot whales and beaked whales. Families Phocoenidae and Delphinidae in blue, Ziphiidae and Physeteridae in orange, and Balaenopteridae in green

and the beaked whales. Across behavioural scenarios, the relative energetic cost of a mild behavioural response by a blue whale (t_d = 1 hr, t_f = 0.25 hr, U_f = 2.5 m/s) was significantly greater than an extreme behavioural response (t_d = 8 hr, t_f = 2.0 hr, U_f = 5.0 m/s) by a Cuvier's beaked whale (*t* test, $p < 0.001$).

4 | DISCUSSION

We modelled the energetic costs of sonar disturbance to cetaceans using measurements of undisturbed feeding rates, empirical prey characteristics and energetic costs from changes in locomotion based on metabolic allometry and biomechanical constraints. Lost feeding opportunities generally had a greater impact on energetic costs than elevated locomotion. The importance of feeding cessation relative to increased locomotor costs during disturbances was previously identified for minke and killer whales (Christiansen et al., 2013; Noren et al., 2016; Williams et al., 2006). This work generalizes those findings, as energetic costs were more sensitive to lost feeding opportunities for most species and behavioural response scenarios. The only exceptions were the two beaked whales and the sperm whale in a scenario emphasizing elevated locomotion. Considering the model's sensitivity to locomotor costs for those species and the magnitude of flight responses observed in Cuvier's beaked whale during controlled exposure experiments (DeRuiter et al., 2013), cost of transport for large, deep-diving odontocetes is a critical data gap. The harbour porpoise and rorquals faced the greatest immediate relative energetic costs (E^*) due to their high energy intake potential. As such, the relative energetic costs incurred by a blue whale exhibiting a 'mild' behavioural response exceed those of an 'extreme' response by a Cuvier's beaked whale (Figure 5).

There is an apparent correlation between species' relative energetic costs from disturbance (E^*) and their life history, behaviour and physiology (i.e. their 'pace of life'). The pace of life syndrome concept describes a slow–fast continuum based on covarying biological traits (Réale et al., 2010). Traits of fast-paced species include short life spans, high reproductive output and lower sociability. Concordantly, the high E^* species, porpoises and rorquals, have reduced longevity

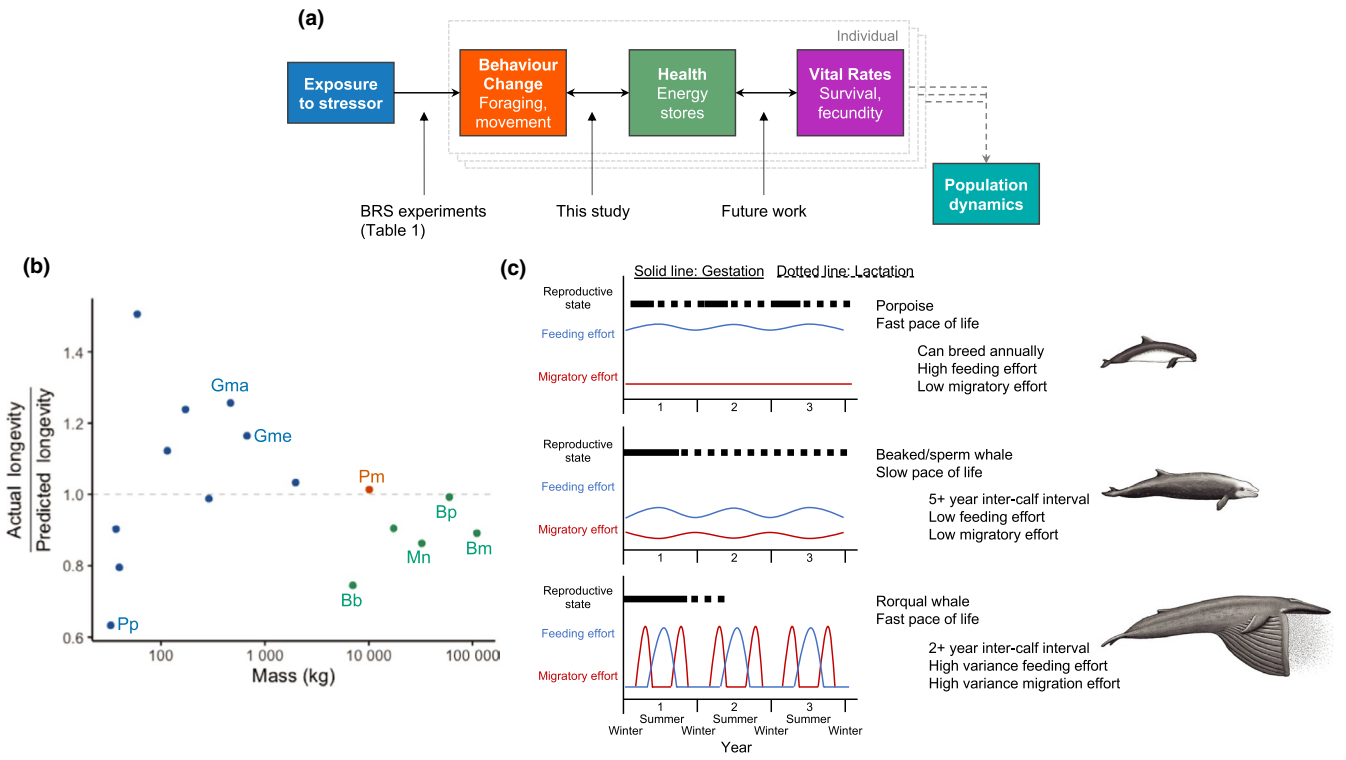

FIGURE 6 (a) The energetic models presented here fill a gap in the PCoD framework along the behavioural-energetic pathway. Earlier behavioural response studies quantified the relationships, and uncertainty, between the exposure to a stressor (sonar) and the subsequent behaviour changes (feeding cessation and elevated locomotion). The present study predicts the energetic costs of these responses, connecting behavioural changes to health. Future empirical work is needed to comprehensively understand how reduced energy stores affect vital rates. (b) Species with the greatest relative energetic costs from disturbance (porpoises, rorquals) have low longevity for their size while those with lower relative energetic costs (larger odontocetes, such as pilot whales and sperm whales) have greater longevity for their size. The *y*-axis shows the ratio of female cetaceans' longevity (Trites & Pauly, 1998) to allometrically predicted longevity (Speakman, 2005). Species included in the present study are labelled; see table 2 in Trites and Pauly (1998) for complete list of species. Families Phocoenidae and Delphinidae in blue, Physeteridae in orange, and Balaenopteridae in green. (c) In addition to longevity, rorquals and porpoises exhibit fast pace of life traits such as rapid reproduction and high feeding effort. Larger odontocetes, such as beaked and sperm whales, reproduce more slowly and exhibit greater sociality, typical of a slow pace of life. Population sizes of species with a fast pace of life are often more sensitive to reduced reproductive success, whereas survival is a greater concern for those with a slow pace of life. Illustrations by Alex Boersma

for their size (Figure 6b) and rapid reproductive cycles (Figure 6c; Speakman, 2005; Trites & Pauly, 1998). Conversely, low E^* species, such as delphinids and sperm whales, form complex social networks and their parental care extends for years longer than rorquals (Lockyer, 2007; May-Collado et al., 2007). Overall, species with high relative energetic costs from disturbance have a fast pace of life and vice versa. This has conservation implications because pace-of-life correlates with population dynamics. Specifically, population growth of fast-paced species is more sensitive to changes in fecundity, whereas slow-paced species are more sensitive to changes in survival (Oli, 2004; Stahl & Oli, 2006).

Our model can be applied in the Population Consequences of Disturbance (PCoD) framework to predict the immediate energetic costs for behavioural responses. Table 6 illustrates how resource managers could use the model for a variety of species and contexts. These energetic costs impact individuals' energy stores and body condition if they cannot behaviourally or physiologically compensate. Future research specific to species' foraging ecology and life history is therefore critically needed (Booth, 2020; Pirotta et al., 2021). For example, blue whales face enormous immediate energetic costs from disturbance due to their remarkable foraging efficiency. However, that efficiency could also facilitate rapid compensation, depending on their time budgets (can they make up feeding later?) and the distribution of their prey (can they find another prey patch?). These unresolved questions may be answered by longer duration, high-resolution tags (Calambokidis et al., 2019, 2020) and prey mapping at spatial scales relevant to foraging whales (Cade et al., 2021). As a species with a fast pace of life, their population growth is likely more sensitive to changes in reproduction than survival. Therefore, research on the transfer function linking energy stores to reproductive success should be prioritized.

Our model was designed to be broadly applicable to other species and sources of disturbance. Cetaceans' behavioural responses to disturbance are highly variable and context-dependent (Ellison et al., 2012). By parameterizing the behavioural response as time displaced from feeding (t_d), time fleeing the sound source (t_f), and swimming speed (U_f), resource managers can draw on expertise in their system to predict short-term energetic costs from disturbance, regardless of the sound source. Our model is equally applicable to whale-watching (Senigaglia et al., 2016) and underwater pile driving (Thompson et al., 2010) as it is to sonar, allowing resource managers to understand the energetic costs of anticipated behavioural responses. Furthermore, our scaling approach facilitates assessments of understudied species for which empirical energetic data are unavailable. For example, PCoD models for Cook Inlet belugas *Delphinapterus leucas* face data deficiencies that necessitate expert solicitation to estimate the magnitude of energetic costs of disturbance (Tollit et al., 2016). Our model predictions for similarly sized species complement expert opinion and serve as an additional input for conservation planning.

Here, we have added to the PCoD framework by connecting behaviour to health using empirical foraging data. Specifically, we build on the behavioural-energetic pathway. Other pathways may be triggered by direct physiological responses and/or affect other aspects of health than body condition, such as stress levels, immune status and organ condition (Schwacke et al., 2014). Along the behavioural-energetic pathway, earlier behavioural response studies used controlled field experiments to evaluate altered foraging and movement behaviours (Table 1). Downstream, further research is needed to quantify the connections between health (i.e. body condition) and vital rates, most critically survival and fecundity (Christiansen & Lusseau, 2015; Christiansen et al., 2018). Our model applies an extensive dataset to address the gap between foraging behaviour and vital rates. In the absence of these data, previous work was limited by unknown energy intake rates in undisturbed conditions. Although the capacity to compensate for these energetic costs remains unknown, we uncover a correlation between the magnitude of short-term (minutes to hours) energetic costs with species' pace of life. At time-scales relevant to population dynamics (months to years), the chronic energetic effects of disturbance depend not only on

TABLE 6 Example applications of the present model to humpback whales in Hawaii and blue whales and Cuvier's beaked whale in California. Behaviour parameters (first column) may be drawn from behavioural response studies when available, otherwise from expert opinion. The 0 hr displacement from feeding (t_d) for the Hawaii humpback whale reflects its capital breeding strategy and the behaviour parameters for the blue whale (Southall et al., 2019) and Cuvier's beaked whale (DeRuiter et al., 2013) are based on behavioural response studies. The immediate energy costs (second column) establish the magnitude of compensation necessary to avoid body condition deterioration. Options for compensation (third column) depend on foraging ecology and reproductive strategy. The species' pace of life (fast for humpback and blue whales, slow for Cuvier's beaked whale) suggests the most sensitive vital rate (fourth column) for consideration in full PCoD models

	Behaviour parameters	Energy costs (kJ)	Compensation options	Key vital rate
Humpback whale (HI)	$t_d = 0$ hr $t_f = 0.3$ hr $U_f = 2.8$ m/s	8.17×10^4 (5.07×10^4–1.40×10^5)	Terminate lactation	Calf survival
Blue whale (CA)	$t_d = 0.25$ hr $t_f = 0.2$ hr $U_f = 3.0$ m/s	1.25×10^6 (4.20×10^5–2.01×10^6)	Additional feeding, delay migration	Gestation termination
Cuvier's beaked whale (CA)	$t_d = 7.6$ hr $t_f = 1.7$ hr $U_f = 3.1$ m/s	3.30×10^4 (1.48×10^4–6.69×10^4)	Additional feeding, terminate gestation/lactation	Adult survival

the frequency and magnitude of these costs but also on individuals' ability to compensate. Fast-paced species (porpoises, rorquals) face relatively greater short-term costs, but whether that translates to long-term deficits remains unknown and warrants future work. Using empirical data to quantify short-term energetic costs allows improved prediction of the tipping points where chronic disturbance leads to population declines.

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AUTHORS' CONTRIBUTIONS

M.F.C., M.S.S. and J.A.G. conceived the study; All authors contributed to study design and provided critical feedback on the manuscript; M.F.C. was responsible for writing the manuscript and data analyses.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.pvmcvdnkq (Czapanskiy et al., 2021a). An R Markdown file with all computational details for running the analysis and producing the figures and tables is archived on Zenodo https://doi.org/10.5281/zenodo.4646110 (Czapanskiy et al., 2021b).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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