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Resilience of the endangered sperm whale *Physeter macrocephalus* to foraging disturbance in the Gulf of Mexico, USA: a bioenergetic approach

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ABSTRACT: The endangered sperm whale *Physeter macrocephalus* spends the majority of its time foraging, relying upon echolocation to locate and consume several 100 kg of prey per day. In the northern Gulf of Mexico, sperm whales are exposed to a variety of anthropogenic stressors, including ship strikes, fisheries interactions, habitat loss and degradation due to oil and gas development, and chemical and noise pollution. In particular, they are exposed to high levels of anthropogenic noises related to geological and geophysical surveys for hydrocarbon deposits. The sounds produced by these surveys could reduce sensory volume, increase search effort required to locate resources, and interfere with auditory signal processing critical to foraging success. We developed a stochastic life-stage structured bioenergetic model to evaluate the consequences of reduced foraging efficiency on carbohydrate, lipid, and protein reserves in the blubber, muscle, and viscera. The model indicates that individual resilience to foraging disruptions is primarily a function of size (i.e. reserve capacity) and daily energetic demands. Mothers are the most vulnerable life stage due to the high energy demands associated with pregnancy and lactation. Continuous disruption has a greater impact than intermittent disruption; even minor foraging disruptions may lead to terminal starvation if the whales have no opportunity to replenish reduced reserves. Infrequent, minor disruptions in foraging are unlikely to be fatal, but may result in reduced body reserves that may be associated with reduced reproductive success. Our model provides a bioenergetic framework for evaluating the level, frequency, and consequences of foraging disruptions associated with anthropogenic stressors.

KEY WORDS: Conservation · Disturbance · Foraging ecology · Risk assessment · Odontocete

INTRODUCTION

Cetaceans (whales, dolphins, and porpoises) are exposed to a variety of anthropogenic stressors including direct harvest by whaling operations (IWC statistics 1959–1983, https://iwc.int/index.php?cID=1336&cType=document), resource depletion by fisheries (Williams et al. 2011), pollution (Schwacke et al. 2016), and habitat degradation (Hoyt 2012). Additionally, anthropogenic noise from boats, sonar, acoustic pingers, and seismic airguns may result in behavioral disturbance (Weilgart 2007). Odontocete (toothed ceta-

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ceans) responses to anthropogenic noise and vessel presence include changes in vocal behavior, surface active behavior, dive patterns, swim speed, direction of travel, and behavioral state (Kruse 1991, Williams et al. 2002a,b, 2006, 2009, Holt et al. 2009, Lusseau et al. 2009, Noren et al. 2009, Tyack et al. 2011, DeRuiter et al. 2013, Kastelein et al. 2015, Powell et al. in press). The potential effects of anthropogenic sounds on cetaceans may include trauma and death, temporary and permanent hearing loss, non-auditory health effects, self-stranding, auditory signal masking, reduced availability of prey, and behavioral disturbance (Richardson et al. 1995, Southall et al. 2007). It is possible that anthropogenic sound may reduce sensory volume (Lima & Zollner 1996), increase search effort required to locate resources (Zollner & Lima 1999), and interfere with complex auditory stream signal processing (Fais et al. 2015). There seems to be a ubiquitous response in odontocetes to reduce or cease foraging in response to noise and/or vessel disturbance (Senigaglia et al. 2016, Falcone et al. 2017, Noren et al. 2017). Assessing the energetic costs of behavioral responses is a useful method for quantifying their biological significance. Bioenergetic modeling approaches have been used to evaluate the consequences of disturbance for odontocetes including beaked whales (family Ziphiidae; New et al. 2013) and delphinids (Noren et al. 2012). Bioenergetic modeling approaches can also be used as a transfer function in a PCoD (population consequences of disturbance) theoretical framework to evaluate how changes in individual behavior caused by disturbance may result in population-level effects by impacting reproduction and survival (NRC 2005). In the present study, we develop a flexible life-stage structured bioenergetic framework for odontocetes, and parameterize the model for Gulf of Mexico sperm whales *Physeter macrocephalus*.

Sperm whales are a bioenergetically unique, large-bodied, deep-diving odontocete. There is substantial management interest in quantifying the impacts of disturbance to sperm whales, which are listed as ‘endangered’ under the US Endangered Species Act (ESA) and ‘Vulnerable’ by the IUCN. Sperm whales are found throughout the world’s oceans in deep waters from the tropics to the edge of the ice at both poles (Rice 1989, Whitehead 2002). A predominantly female population is present year-round in continental slope and oceanic habitats of the US Gulf of Mexico (Mullin et al. 1994, Hansen et al. 1996, Mullin & Hoggard 2000, Fulling et al. 2003, Mullin & Fulling 2004, Mullin et al. 2004, Maze-Foley & Mullin 2006). The northern Gulf of Mexico stock is listed as a ‘strategic stock’ under the US Marine Mammal Protection Act (MMPA; NMFS 2013). Blubber is the primary energy source for most marine mammals (Strandberg et al. 2008); however, the physiological properties of sperm whale blubber suggest they are poorly adapted to handle periods of food shortage (Lockyer 1981, Clarke et al. 1988, Koopman 2007). For example, the energy density of sperm whale blubber is much lower than that of other cetaceans (e.g. fin whales, Lockyer 1986, Lockyer 1991), sperm whale blubber thickness does not vary much with body length, nor are there appreciable changes in thickness during lactation (Clarke et al. 1988). These observations all suggest that the sperm whale blubber layer is not heavily utilized during periods of increased energy expenditure.

Sperm whales in the northern Gulf of Mexico face a plethora of direct and indirect anthropogenic stressors, including the population impacts of historical whaling and contemporary ship strikes, fisheries interactions, habitat loss and degradation due to oil and gas development, and chemical and noise pollution (Townsend 1935, NMFS 2013). During the Deepwater Horizon oil spill, over 500 000 kl of oil were released into the Gulf of Mexico for a total of 87 d (DWH-NRDAT 2016). This oil spill exposed approximately 16% of the Gulf of Mexico sperm whale stock to volatile chemicals (Schwacke et al. 2016) and reduced prey populations due to the presence of toxic polycyclic aromatic hydrocarbons in the benthos and subsurface waters (Camilli et al. 2010, Diercks et al. 2010, Montagna et al. 2013). Additionally, sperm whales in the northern Gulf of Mexico are exposed to high levels of airgun and other anthropogenic noises related to geological and geophysical surveys for hydrocarbon deposits in the seabed. The Bureau of Ocean Energy Management (BOEM) has projected over 4 million km of seismic survey lines will be shot in the Gulf of Mexico over the next 10 yr (BOEM 2017).

Few studies on behavioral responses of sperm whales to anthropogenic sound have been conducted. In the Gulf of Mexico, controlled exposure experiments (CEE) conducted with 8 tagged sperm whales over a series of 30 min intervals during pre-exposure, ramp-up, and full-array airgun firing indicated no avoidance behaviors but did suggest reduced foraging behavior (Miller et al. 2009). Sperm whales engage in resting behavior where they maintain a vertical posture near the sea surface; however, the most closely approached whale (1.4–5.7 km) engaged in an unusually long resting bout of 265 min, and began foraging 4 min after the final airgun pulse (Miller et al. 2008, 2009). For comparison, usual inactive periods observed by Miller et al. (2008) were 0.7–31.5 min (mean ± SD; 12.7 ± 8.7 min, N = 70). In addition to this observed potential delay in foraging during exposure, the 7 whales with lower exposure levels exhibited decreases in movements and vocalizations associated with successful foraging (Miller et al. 2009). Bayesian analysis suggested a 20% decrease in foraging activity was more likely than no change in foraging activity, with 1 whale showing a statistically significant decrease in foraging activity of 60% (Jochens et al. 2008).

In CEE off Norway, sperm whales demonstrated avoidance, change in locomotion and/or orientation, change in dive profiles, cessation of foraging, cessation of resting, and changes in vocal behavior in response to naval sonar (Miller et al. 2011, 2012, Sivle et al. 2011, Curé et al. 2016). All changes in foraging activities included alteration or cessation of the production of foraging sounds (i.e. regular clicks and buzzes) and changes in the dive profile (Curé et al. 2016). Changes in coda and slow click production rates were also observed in many exposure sessions (Curé et al. 2016). Sperm whales respond more strongly and at lower sound levels to low frequency active sonar (LFAS; 1–2 kHz) than mid-frequency active sonar (MFAS; 6–7 kHz). Airguns used in seismic surveys produce most of their energy below 200 Hz, but contain significant acoustic energy over a broad band of operational frequencies ranging up to those covered by LFAS (Zeddies et al. 2015).

Cessation of foraging or reduction in foraging efficiency may lead to caloric deficits that must be paid from a sperm whale's body energy reserves. In cetaceans, energy is stored as carbohydrates, lipids, and proteins in various depots throughout the body, including the blubber, muscle, and viscera (Lockyer 1991). In the present study, we apply a flexible life-stage structured bioenergetic framework for Gulf of Mexico sperm whales to evaluate the consequences of reduced foraging efficiency associated with anthropogenic disturbance. We use bootstrapping approaches to account for individual variability in availability and usage of body energy reserves to cover caloric deficits associated with foraging disturbance (Noren et al. 2003, Noren & Mangel 2004, Rea et al. 2007, Verrier et al. 2009). We evaluate maximum continuous disturbance duration until terminal starvation, consequences of continuous versus intermittent disturbance, and consequences of complete versus partial disruption of foraging. Finally, we evaluate changes in relative body condition and potential mortalities associated with reductions in foraging efficiency.

MATERIALS AND METHODS

We developed bioenergetic models in R (R Core Team 2016) and parameterized them for juvenile, mature, pregnant, lactating, and post-breeding females, and juvenile and mature male sperm whales following life-stage definitions in Chiquet et al. (2013) and Lockyer (1981). Some bioenergetic parameters varied based on size within life stages, using Lockyer's (1981) distinctions between sexually mature and physically mature females, and sexually mature, socially mature, and physically mature males (Table 1). Changes in whale body mass and associated energy reserve levels were tracked on a daily basis (Table 2, Fig. 1). Available energy reserves and daily energy requirements, expressed as field metabolic rates (FMR), were dependent on the life stage, size, and reproductive status of the individual. FMR is the total metabolic cost of all physiological processes and activities of an animal in the wild. Daily metabolism for juveniles and adult sperm whales that are not pregnant or lactating was assumed to equate to 5 times Kleiber's (1975) predicted basal metabolic rate (BMR):

$$\mathrm{FMR}_d = 350\, T_d^{0.75} \times \chi_d \tag{1}$$

where T_d is body mass (kg) on day d. Following Lockyer (1981), additional metabolic demands were imposed for pregnant and lactating females as a scalar on FMR (χ_d; Table 1), such that FMRs across the population of sperm whales range from 5 to 6 times Kleiber's (1975) predicted BMR, following Noren (2011).

Energy reserves during periods of impacted foraging were available from carbohydrates (H) in the blubber and muscle; lipids (D) in the blubber, muscle, and viscera; and proteins (R) in the muscle and viscera. Change in total body mass (i.e. growth) was modeled as follows:

$$\begin{aligned} &\text{Natural foraging: } T_d = T_{d-1} + \gamma \times \varphi \\ &\text{Disturbed foraging: } T_d = T_{d-1} - H_d - D_d - R_d \end{aligned} \tag{2}$$

where γ is the growth (kg d^{-1}) observed for a given life stage (Lockyer 1981) and φ is a scalar associated with a potential 'hunger response' (i.e. increased foraging effort to compensate for caloric deficits; Webber & MacDonald 1994), allowing reserves to be replaced at a rate exceeding γ during natural (e.g. undisturbed) days when foraging opportunities become available. As γ for physically mature females and males is negligible (Lockyer 1981), these life stages were assumed to replenish depleted reserves at γ = 1.51 and 2.74 kg d^{-1}, respectively (Table 1).

Table 1 (this and the next 2 pages). Bioenergetic model parameters, their definitions and sources, and the distributions from which parameter values are drawn to categorize uncertainty. *U*: uniform distribution; *N*: normal distribution

Symbol	Description	Juvenile female	Mature female	Mother (lactating female)	Post-breeding female	Juvenile male	Mature male	Source
Ξ	Body length (m)	$U(6, 8.7)$	$N(\mu = 9.55, \sigma = 0.76, a = 8.7, b = 12.25)$			$U(6.0, 12.0)$	$U(9.65, 15.85)$	Lockyer (1981), Jochens et al. (2008)
Ψ	Meristic conversion between length (m) and mass (kg)	$0.0218(l)^{2.74}\times1000$						Lockyer (1981)
γ	Daily growth (kg) under undisturbed foraging conditions	3.01 kg d^{-1}	1.51 kg d^{-1} if under 10.9 m, else 0 kg d^{-1}			3.01 kg d^{-1} if under 9.65 m, else 2.74 kg d^{-1}	2.74 kg d^{-1} if under 13.65 m, else 0 kg d^{-1}	Lockyer (1981)
FMR	Field metabolic rate (kcal)	$350(\Psi)^{0.75}\times\chi$						Noren (2011)
χ	Scalar on daily energy requirement accounting for additional metabolic demands of pregnancy or lactation	1	Not pregnant: 1, pregnant: $U(1.05, 1.1)$	$U(1.32, 1.63)$	1			Lockyer (1981)
δ	Energy value of carbohydrates (kcal g^{-1})	3.99						Lockyer (1991)
Θ	Energy value of lipids (kcal g^{-1})	9.44						Lockyer (1991)
P	Energy value of proteins (kcal g^{-1})	5.64						Lockyer (1991)
θ	Percent lipid reserve use (if available) to cover caloric deficit	0.9						Noren et al. (2009)
ρ	Percent protein reserve use (if available) to cover caloric deficit	0.1						Noren et al. (2009)
β	Blubber mass as a percentage of body mass	$U(0.31, 0.32)$					0.33	Lockyer (1991)

Table 1 (continued)

Symbol	Description	Juvenile female	Mature female	Mother (lactating female)	Post-breeding female	Juvenile male	Mature male	Source
μ	Muscle mass as percentage of body mass	$U(0.225, 0.30)$					0.26	Lockyer (1991)
ν	Viscera mass as percentage of body mass	0.09						Lockyer (1991)
ς_b	Carbohydrate mass as a percentage of blubber mass	$1/3 \times U(0.08, 0.30) + 1/3 \times 0.06 \times 1/3 \times 0.01$						Lockyer (1991): carbohydrates make up 8–30% of the blubber in the middle and posterior sections, but only 6% in the anterior dorsal and <1% in the anterior ventral regions
ς_m	Carbohydrate mass as a percentage of muscle mass	$N(\mu = 0.0097, \sigma = 0.0198, a = 0, b = 0.05)$						Lockyer (1991)
Π_m	Protein mass as percentage of muscle mass	0.267						Worthy et al. (1992), Iverson et al. (1993)
Π_v	Protein mass as percentage of viscera mass	$U(0.0161, 0.0167)$						Lockyer (1991)
π	Protein available until terminal starvation is reached	U(0.30, 0.50)						Castellini & Rea (1992)
Λ_b	Lipid mass as a percentage of blubber mass	$N(\mu = 0.568, \sigma = 0.278, a = 0.247, b = 0.732)$	Under 10.9 m: $N(\mu = 0.548, \sigma = 0.194, a = 0.451, b = 0.893)$; over 10.9 m: $N(\mu = 0.488, \sigma = 0.183, a = 0.162, b = 0.86)$	$N(\mu = 0.418, \sigma = 0.1, a = 0.348, b = 0.489)$	Under 10.9 m: $N(\mu = 0.548, \sigma = 0.194, a = 0.451, \text{upper} = 0.893)$; over 10.9 m: $N(\text{mean} = 0.488, \sigma = 0.183, a = 0.162, b = 0.86)$	$N(\mu = 0.446, \sigma = 0.269, a = 0.256, b = 0.637)$	$N(\mu = 0.423, \sigma = 0.121, a = 0.338, b = 0.509)$	Lockyer (1981) (sexually mature versus physically mature), Evans et al. (2003)
Λ_m	Lipid mass as a percentage of muscle mass	$N(\mu = 0.0288, \sigma = 0.0342, a = 0.01, b = 0.1)$						Lockyer (1991, their Fig. 7 plus text)
Λ_v	lipid mass as a percentage of viscera mass	$U(0.6944, 0.8043)$						Lockyer (1991)

Table 1 (continued)

Symbol	Description	Juvenile female	Mature female	Mother (lactating female)	Post-breeding female	Juvenile male	Mature male	Source
ω_b	Wax ester mass as a percentage of blubber lipid mass	$U(0.613, 1.0)$						Lockyer (1991; their Table 8), Koopman (2007)
ω_m	Wax ester mass as a percentage of muscle lipid mass	0.154						Lockyer (1991, their Table 5)
ω_v	Wax ester mass as a percentage of viscera lipid mass	0.4508						Lockyer (1991)
τ	Triacylglycerol (TAG) mass as a percentage of lipid mass	$1\text{-}\omega$						Lockyer (1991, their Table 8), Koopman (2007)
λ_b	Percentage of blubber lipids available as energy reserves	$\tau \times U(50\%, 67\%) + \omega_b \times U(0\%, 50\%)$						Struntz et al. (2004) (33–67%), Dunkin et al. (2005) (48%), Koopman et al. (2002) (50% blubber thickness, evaluated by Struntz et al. 2004 as 57% lipid), Koopman (2007), Lockyer (1991), pers. comm. with W.A. Pabst, H. Koopman, E. Fougeres, D. Noren
λ_m	Percentage of muscle lipids available as energy reserves	$\tau \times U(50\%, 67\%) + \omega_m \times U(0\%, 50\%)$						
λ_v	Percentage of viscera lipids available as energy reserves	$\tau + \omega_v \times U(0\%, 50\%)$						
g	Duration of gestation (d)		456					Chiquet et al. (2013)
n	Duration of nursing (d)			730				Chiquet et al. (2013)
r	Interbirth interval (d)		1460					Chiquet et al. (2013)
HR	Kernel utilization distribution 50% core home range	$N(\mu = 8258, \sigma = 6836, a = 324, b = 100600)$					$N(\mu = 41285, \sigma = 40604, a = 324, b = 101600)$	Jochens et al. (2008)
$T_{\text{transition}}$	Size (kg) at transition to different life stages/sub-stages	Sexually mature female: 5760.623	Physically mature female: 12246.99			Sexually mature male: 16329.3	Socially mature male: 24856.86; physically mature male: 39553.25	Lockyer (1981)

Table 2. Bioenergetic model daily step parameters utilized to track whale life stage, reproductive status, and body energy reserves through time

Symbol	Code	Description
T_d	BodyMass	Total body mass (kg)
C_d	CaloricDeficit	Caloric deficit due to impaired foraging (kcal)
c_d	remainingDeficit	Caloric deficit remaining after burning carbohydrates
h	HungerResponse	Hunger response scalar to daily growth
H_d	CarbLoss	Loss of carbohydrates to cover caloric deficit (kg)
D_d	LipidLoss	Loss of lipids to cover caloric deficit (kg)
R_d	ProteinLoss	Loss of protein to cover caloric deficit (kg)
K_d	CarbMass	Carbohydrate mass (kg)
B_d	BlubberMass	Blubber mass (kg)
M_d	MuscleMass	Muscle mass (kg)
V_d	VisceraMass	Viscera mass (kg)
$L_{\mathrm{b},d}$	BlubberLipidMass	Blubber lipid mass (kg)
$l_{\mathrm{b},d}$	BlubberLipidReserveMass	Metabolically active blubber lipid mass (kg)
$L_{\mathrm{m},d}$	MuscleLipidMass	Muscle lipid mass (kg)
$l_{\mathrm{m},d}$	MuscleLipidReserveMass	Metabolically active muscle lipid mass (kg)
$L_{\mathrm{v},d}$	VisceraLipidMass	Viscera lipid mass (kg)
$l_{\mathrm{v},d}$	VisceraLipidReserveMass	Metabolically active viscera lipid mass (kg)
$P_{\mathrm{m},d}$	MuscleProteinMass	Muscle protein mass (kg)
$p_{\mathrm{m},d}$	MuscleProteinReserveMass	Metabolically active muscle protein mass (kg)
$P_{\mathrm{v},d}$	VisceraProteinMass	Viscera protein mass (kg)
$p_{\mathrm{v},d}$	VisceraProteinReserveMass	Metabolically active viscera protein mass (kg)
l_d	LipidReserveMass	Metabolically active lipid mass (kg)
p_d	ProteinReserveMass	Metabolically active protein mass (kg)
kE_d	CarbEnergy	Available energy from carbohydrates (calories)
lE_d	LipidReserveEnergy	Available energy from lipids (calories)
pE_d	ProteinReserveEnergy	Available energy from muscle proteins (calories)
tE_d	BodyReserveEnergy	Total available energy reserves (calories)
F_d	ForagingEfficiency	Daily foraging efficiency (%)
$\%_{\mathrm{bl}}$	blubber_lipid_use_pct	Rate of blubber lipid depletion relative to lipids in other tissue
$\%_{\mathrm{ml}}$	muscle_lipid_use_pct	Rate of muscle lipid depletion relative to lipids in other tissue
$\%_{\mathrm{vl}}$	viscera_lipid_use_pct	Rate of viscera lipid depletion relative to lipids in other tissue
$\%_{\mathrm{mp}}$	muscle_protein_use_pct	Rate of muscle protein depletion relative to proteins in other tissue

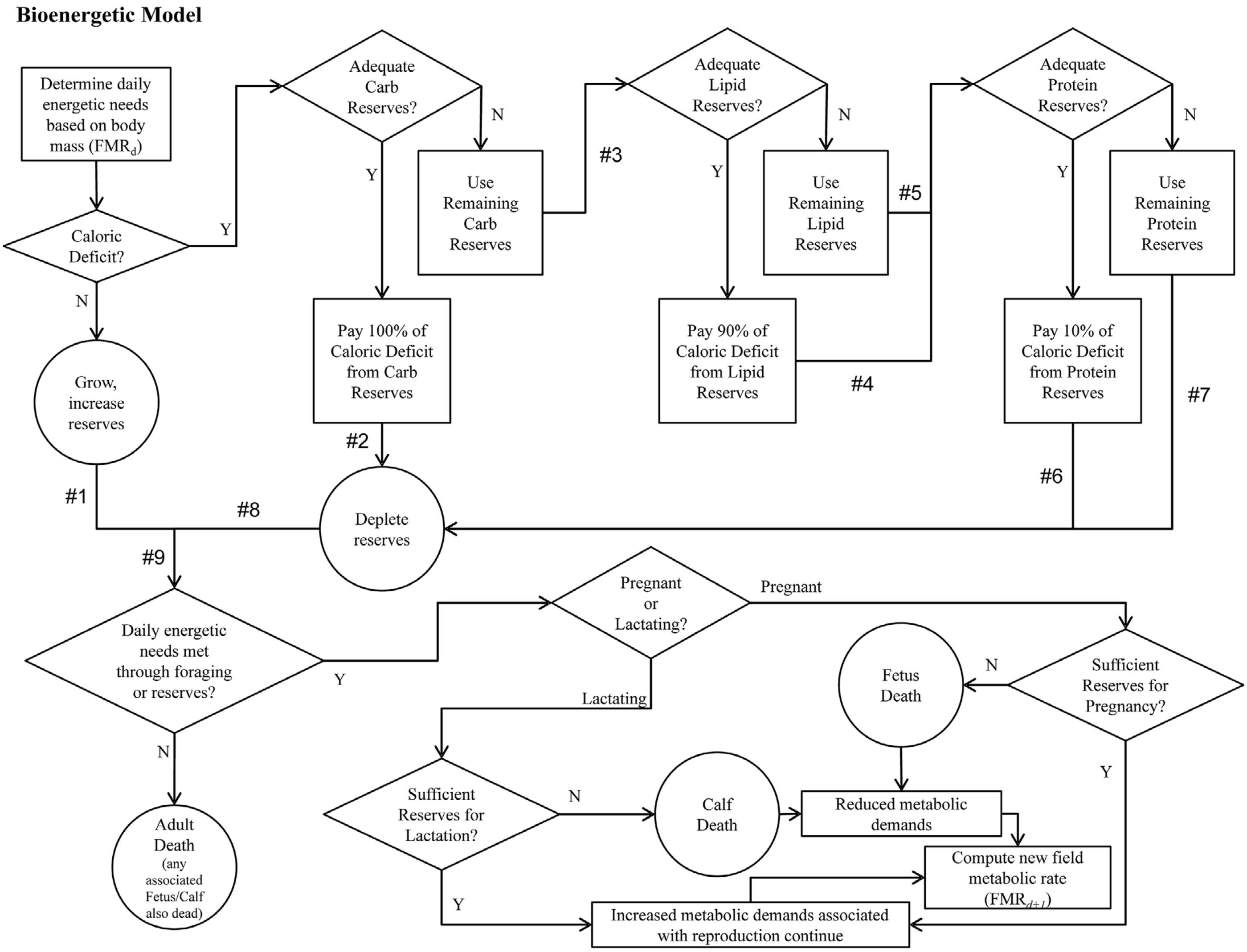
The approach described in Eq. (2) assumes that, on average, undisturbed whales will grow as empirically observed by Lockyer (1981), whereas disturbed whales will incur a caloric deficit proportional to the amount of lost foraging opportunities, and this caloric deficit will be paid out of body reserves.

To allow longer simulations, the bioenergetic model incorporated growth, a reproductive cycle, and transitions to different life stages. At the beginning of each model year, whales were able to transition from juvenile to sexually mature females, from sexually mature females to physically mature females, from sexually mature to socially mature males, or from socially mature males to physically mature males following growth. Sizes at different life stages are from Lockyer (1981). When whales transitioned to different life stages, all associated bioenergetic metrics were also updated, following Table 1.

Gestation length was set at 15 mo, nursing duration was set at 2 yr, and interbirth intervals were set at 4 yr, with 25.28% of 'mature females' considered pregnant at the beginning of the simulation (Chiquet et al. 2013). Following Chiquet et al. (2013), pregnant females transitioned to lactating 'mothers' upon reaching the end of the gestation interval. Lactating mothers transitioned to 'post-breeding' females (i.e. post-calving females in the interbirth interval) following the nursing duration, then became pregnant again once they reached the end of the interbirth interval. To initialize the simulation, days since previous birth for 'post-breeding' females was set randomly between 1 and 1460 d (4 yr).

Natural foraging

During natural foraging (e.g. no anthropogenic disturbance), body tissues and associated reserve levels grew in proportion to the overall increase in body mass. Growth in blubber (B_d), muscle (M_d), and viscera (V_d) mass during natural foraging was proportional to total body growth:



#1

$H_d=0,\ D_d=0,\ R_d=0$

$T_d=T_{d-1}+\gamma*\varphi$

$K_d=K_{d-1}+\gamma*\beta*\varsigma_b+\gamma*\mu*\varsigma_m$

$B_d=B_{d-1}+\gamma*\beta$

$M_d=M_{d-1}+\gamma*\mu$

$V_d=V_{d-1}+\gamma*\nu$

$L_{b,d}=L_{b,d-1}+\gamma*\beta*\Lambda_b$

$l_{b,d}=l_{b,d-1}+\gamma*\beta*\Lambda_b*\lambda_b$

$L_{m,d}=L_{m,d-1}+\gamma*\mu*\Lambda_m$

$l_{m,d}=l_{m,d-1}+\gamma*\mu*\Lambda_m*\lambda_m$

$L_{v,d}=L_{v,d-1}+\gamma*\nu*\Lambda_v$

$l_{v,d}=l_{v,d-1}+\gamma*\nu*\Lambda_v*\lambda_v$

$P_{m,d}=P_{m,d-1}+\gamma*\mu*\Pi_m$

$p_{m,d}=p_{m,d-1}+\gamma*\mu*\Pi_m*\pi$

$P_{v,d}=P_{v,d-1}+\gamma*\mu*\Pi_v$

$p_{v,d}=p_{v,d-1}+\gamma*\mu*\Pi_v*\pi$

#2

$c_d=0$

$K_d=K_{d-1}-(C_d)/(10^3*\delta)$

$H_d=K_{d-1}-K_d$

$D_d=0,\ R_d=0$

$\theta=0.9,\ \rho=1-\theta$

#3

$c_d=(C_d- K_{d-1}*10^3*\delta)$

#4

$D_d=(c_d*\theta)/(10^3*\Theta)$

$\theta=0.9,\ \rho=1-\theta$

#5

$l_d=0$

$D_d=l_{d-1}$

$\theta=l_{d-1}*[(10^3*\Theta)/c_d],\ \rho=1-\theta$

#6

$R_d=(c_d*\rho)/(10^3*P)$

$\rho=0.1,\ \theta=1-\rho$

#7

$p_d=0$

$R_d=p_{d-1}$

$\rho=p_{d-1}*[(10^3*P)/c_d],\ \theta=1-\rho$

#9

$p_d=p_{m,d}+p_{v,d}$

$l_d=l_{b,d}+l_{m,d}+l_{v,d}$

$kE_d=K_d*10^3*\Theta$

$lE_d=(l_{b,d}+l_{m,d}+l_{v,d})*10^3*\Theta$

$pE_d=(p_{m,d}+p_{v,d})*10^3*P$

$tE_d=kE_d+lE_d+pE_d$

#8

$T_d=T_{d-1}-H_d-D_d-R_d$

$l_{b,d}=l_{b,d-1}-\%_{bl}*D_d$

$l_{m,d}=l_{m,d-1}-\%_{ml}*D_d$

$l_{v,d}=l_{v,d-1}-\%_{vl}*D_d$

$p_{m,d}=p_{m,d-1}-\%_{mp}*R_d$

$p_{v,d}=p_{v,d-1}-(1-\%_{vp})*R_d$

$L_{b,d}=L_{b,d-1}-(l_{b,d-1}-l_{b,d})$

$L_{m,d}=L_{m,d-1}-(l_{m,d-1}-l_{m,d})$

$L_{v,d}=L_{v,d-1}-(l_{v,d-1}-l_{v,d})$

$P_{m,d}=P_{m,d-1}-(p_{m,d-1}-p_{m,d})$

$P_{v,d}=P_{v,d-1}-(p_{v,d-1}-p_{v,d})$

$B_d=B_{d-1}-(l_{b,d-1}-l_{b,d})$

$M_d=M_{d-1}-(l_{m,d-1}-l_{m,d})-(p_{m,d-1}-p_{m,d})$

$V_d=V_{d-1}-(l_{v,d-1}-l_{v,d})-(p_{v,d-1}-p_{v,d})$

Fig. 1. Bioenergetic model. A decision tree representing one time step (1 d) in bioenergetic model simulations for the energy budget of an individual sperm whale. Individuals with reduced foraging efficiency repay caloric debts from body energy reserves in the blubber, muscle, and viscera. Squares represent computations, diamonds represent decision points, and circles represent possible outcomes. Y = yes; N = no. See Tables 1 & 2 for definitions of variables

$$B_d = B_{d-1} + \gamma \times \beta \quad (3)$$

$$M_d = M_{d-1} + \gamma \times \mu \quad (4)$$

$$V_d = V_{d-1} + \gamma \times \nu \quad (5)$$

where β, μ, and ν are blubber, muscle, and viscera mass as a percentage of total body mass, respectively. Similarly, growth in carbohydrate mass (K_d) during natural foraging was proportional to growth in blubber and muscle mass:

$$K_d = K_{d-1} + \gamma \times \beta \times \varsigma_b + \gamma \times \mu \times \varsigma_m \quad (6)$$

where ς_b and ς_m are carbohydrate mass as a percentage of blubber and muscle mass, respectively.

Increases in lipid mass in the blubber (L_b), muscle (L_m), and viscera (L_v) were computed as follows:

$$L_{b,d} = L_{b,d-1} + \gamma \times \beta \times \Lambda_b \quad (7)$$

$$L_{m,d} = L_{m,d-1} + \gamma \times \mu \times \Lambda_m \quad (8)$$

$$L_{v,d} = L_{v,d-1} + \gamma \times \nu \times \Lambda_v \quad (9)$$

where Λ_b, Λ_m, and Λ_v are lipid mass as a percentage of blubber, muscle, and viscera mass, respectively. Similarly, increases in protein mass in the muscle ($P_{m,d}$) and viscera ($P_{v,d}$) were computed as follows:

$$P_{m,d} = P_{m,d-1} + \gamma \times \mu \times \Pi_m \quad (10)$$

$$P_{v,d} = P_{v,d-1} + \gamma \times \mu \times \Pi_v \quad (11)$$

where Π_m and Π_v are protein mass as a percentage of muscle and viscera mass, respectively.

Observations of starved animals suggest that not all body lipids and proteins are available for metabolism during a starvation event. Most cetaceans store the majority of lipids in their blubber as triacylglycerols (TAGs), and draw upon these TAGs as an energy reserve (Koopman 2007). Evidence from stranded cetaceans suggests that not all TAGs are available for metabolism during a starvation event; some may be structural or otherwise unavailable to the animal. Based on studies of reductions in blubber TAGs in emaciated stranded cetaceans, we modeled between 50 and 67% of TAGs as available in sperm whale blubber, muscle, and viscera (Koopman et al. 2002, Struntz et al. 2004, Dunkin et al. 2005, H. Koopman & W. A. Pabst, UNCW, pers. comm.). Sperm whales (and beaked whales) seem unique amongst odontocetes in that they store the vast majority of their blubber lipids as wax esters (WEs) instead of TAGs (Lockyer 1991, Koopman 2007, Pabst et al. 2016). WEs may have reduced demands on oxygen metabolism relative to TAGs, which may explain their prevalence in deep-diving whales. However, evidence from *in vitro* and *in vivo* studies indicates most animals are inefficient at metabolizing WEs, hydrolyzing WEs at around one-tenth the rate of TAG (Savary 1971, Patton & Benson 1975, Sargent et al. 1976, Place 1992, Pond 1998). Because substantial uncertainty exists with regards to the amount of WEs available for metabolism during a starvation event, we modeled between 0 and 50% of WE lipids as metabolically available (H. Koopman & W. A. Pabst pers. comm). Increases in metabolically available lipids in the blubber (l_b), muscle (l_m), and viscera (l_v) were computed as follows:

$$l_{b,d} = l_{b,d-1} + \gamma \times \beta \times \Lambda_b \times \lambda_b \quad (12)$$

$$l_{m,d} = l_{m,d-1} + \gamma \times \mu \times \Lambda_m \times \lambda_m \quad (13)$$

$$l_{v,d} = l_{v,d-1} + \gamma \times \nu \times \Lambda_v \times \lambda_v \quad (14)$$

where λ_b, λ_m, and λ_v are the percentages of metabolically available lipids within blubber, muscle, and viscera tissue, respectively. Similarly, increases in metabolically available protein in the muscle (p_m) and viscera (p_v) were computed as follows:

$$p_{m,d} = p_{m,d-1} + \gamma \times \mu \times \Pi_m \times \pi \quad (15)$$

$$p_{v,d} = p_{v,d-1} + \gamma \times \mu \times \Pi_v \times \pi \quad (16)$$

where π is the percentage of muscle protein available for metabolism prior to terminal starvation following Castellini & Rea (1992).

Disturbed foraging

Bioenergetic responses to foraging disturbance were based on Castellini & Rea (1992). Reductions in foraging efficiency due to anthropogenic disturbance create a caloric deficit (C_d):

$$C_d = \mathrm{FMR}_{d-1} \times \chi_{d-1} \times (1 - F_{d-1}) \quad (17)$$

where F_{d-1} is the reduction in foraging efficiency in the previous day. If sufficient carbohydrate reserves were available to cover C_d, they are depleted as follows:

$$K_d = K_{d-1} - (C_d) / (10^3 \times \delta) \quad (18)$$

where δ is the caloric value of carbohydrates (kcal g^{-1}). If insufficient carbohydrate reserves are available, the carbohydrate reserves are completely depleted (i.e. $K_d = 0$) and any remaining daily caloric deficit (c_d) is covered by lipid and protein reserves. If sufficient lipid and protein reserves were available, 90% of the remaining caloric deficit was covered from lipid reserves and 10% from protein reserves (Noren et al. 2009):

$$D_d = (c_d \times \theta) / (10^3 \times \Theta) \quad (19)$$

$$R_d = (c_d \times \rho) / (10^3 \times P) \quad (20)$$

where D is lipid loss, R is protein loss, θ is the percent of c_d met by lipid oxidation, ρ is the percent of c_d met by protein oxidation, and Θ and P are the caloric value of lipids and proteins, respectively. If lipid reserves are inadequate to cover 90% of the c_d, then >10% of the c_d is covered from protein reserves (Fig. 1). Similarly, if protein reserves are inadequate to cover 10% of the c_d, then >90% of the c_d is covered from lipid reserves. In all cases, lipid and protein reserves in the various body tissues are depleted proportional to their availability (Fig. 1).

Payments of caloric deficits reduce body mass (Eq. 2) and available lipid (l) and protein (p) reserves in the blubber (b), muscle (m), and viscera (v) as follows:

$$l_{t,d} = l_{t,d-1} - \%_{tl} \times D_d \tag{21}$$

$$p_{t,d} = p_{t,d-1} - \%_{tp} \times R_d \tag{22}$$

where t is a general subscript for the different body tissue types (b, m, v) and $\%_t$ is the relative depletion rate specific to each tissue.

Total energy reserves at the end of each day (TE_d) are the sum of the masses of available carbohydrate, lipid, and protein in the blubber, muscle, and viscera multiplied by their respective oxidative coefficients:

$$\mathrm{TE}_d = (K_d \times 10^3 \times \delta) + [(l_{\mathrm{b},d} + l_{\mathrm{m},d} + l_{\mathrm{v},d}) \times 10^3 \times \Theta] + [(p_{\mathrm{m},d} + p_{\mathrm{v},d}) \times 10^3 \times P] \tag{23}$$

If total available energy reserves were depleted to zero, the individual reached terminal starvation. At terminal starvation, protein stores are greatly depleted, lipid utilization falls, circulating ketones decline, and cardiac tissue and other organs are compromised (Castellini & Rea 1992). Recovery by refeeding at terminal starvation is a long and difficult process that may take up to a year in humans, even under close medical supervision (Burton 1976). It is unlikely that animals in the wild could recover from terminal starvation. Following New et al. (2013), we assumed pregnant or lactating adult females prioritize their own survival and might abort their fetus or abandon their calf if their energy stores hit critical levels (Table 1).

Replacement of lost reserves

How sperm whales allocate body growth on natural foraging days following a disturbance is an important consideration for their resilience. We captured the uncertainty in how growth might be allocated by allowing sperm whales on a daily basis to replace lost reserves in a uniform range between somatic growth levels (e.g. Eqs. 6, 12–16) and perfect proportional replacement of lost reserves. For perfect replacement, the daily growth rate (γ) was apportioned between metabolically available carbohydrate, lipid, and protein reserves in the blubber, muscle, and viscera proportional to their loss during prior disturbances.

Model runs

Bioenergetic model evaluations were performed on 500 simulated individuals for each life stage, with bootstrapping used to capture the variability in the bioenergetic parameters presented in Table 1. To evaluate the consequences of WE energy storage on the ability to survive disturbance events, the maximum continuous disturbance duration until terminal starvation for modeled sperm whales storing the majority of their lipids as WEs was compared to maximum continuous disturbance duration until terminal starvation for hypothetical sperm whales storing all of their lipids as TAGs. To evaluate the consequences of complete versus partial disturbance, complete foraging disruptions (i.e. starvation events) were modeled along with 25, 50, and 75% foraging disruptions over 24 h periods. To evaluate the impacts of consecutive versus intermittent disturbance, complete foraging disruptions were evaluated as daily, every other day, or weekly events. To evaluate the impacts of intermittent disturbance on body condition, the reserve levels of undisturbed individuals were compared to those of individuals with random 5% foraging disruptions. To evaluate the impacts of a 'hunger response,' time to terminal starvation was compared for identically sized females at different compensatory foraging levels expressed as a scalar (h) on daily growth rate (γ) (see Eq. 2). For this simulation, h was allowed to exceed 1 so long as the individual's reserve levels were lower than those of an undisturbed individual with identical physiological parameters. Deterministic comparisons evaluated the level of compensatory foraging the whale would require in order to survive a decade of weekly disturbance.

RESULTS

The bootstrapping approach applied in this modeling process allowed a broad range of sperm whale sizes to be evaluated in order to develop general conclusions about resilience to foraging disturbance. In general, mature male sperm whales have greater

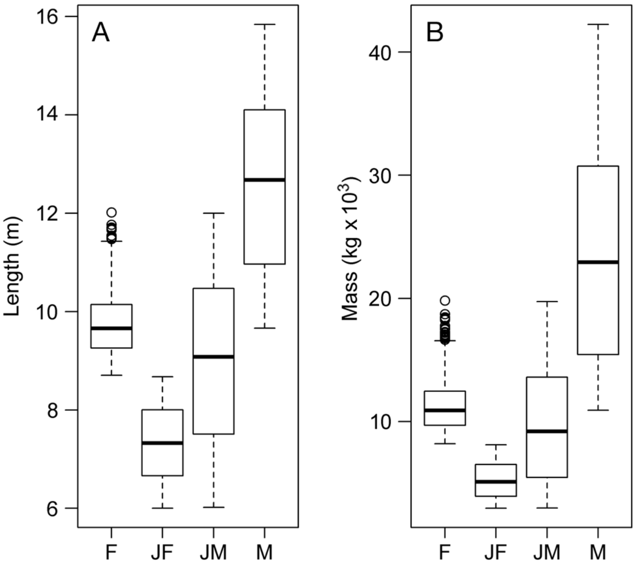


Fig. 2. Whale size by sex and maturity. Boxplots of (A) length in m and (B) body mass in kg for 500 simulated sperm whales of each sex and stage of maturity (F: mature female; JF: juvenile female; JM: juvenile male; M: mature male). Boxes show medium (thick line) with upper and lower quartiles, whiskers, and outliers

reserve capacity than females owing to their larger size (Fig. 2) and higher blubber content as a percentage of body mass (Fig. 3). With the exception of lipid concentration as a percentage of blubber mass, differences in bioenergetics parameters between life stages are relatively minor (Fig. 3E). Lactating mothers and mature males have the lowest percentage of lipids per unit blubber mass.

Individual resilience to starvation events is primarily a function of size (i.e. reserve capacity) and daily energetic demands (i.e. FMR). An undisturbed sperm

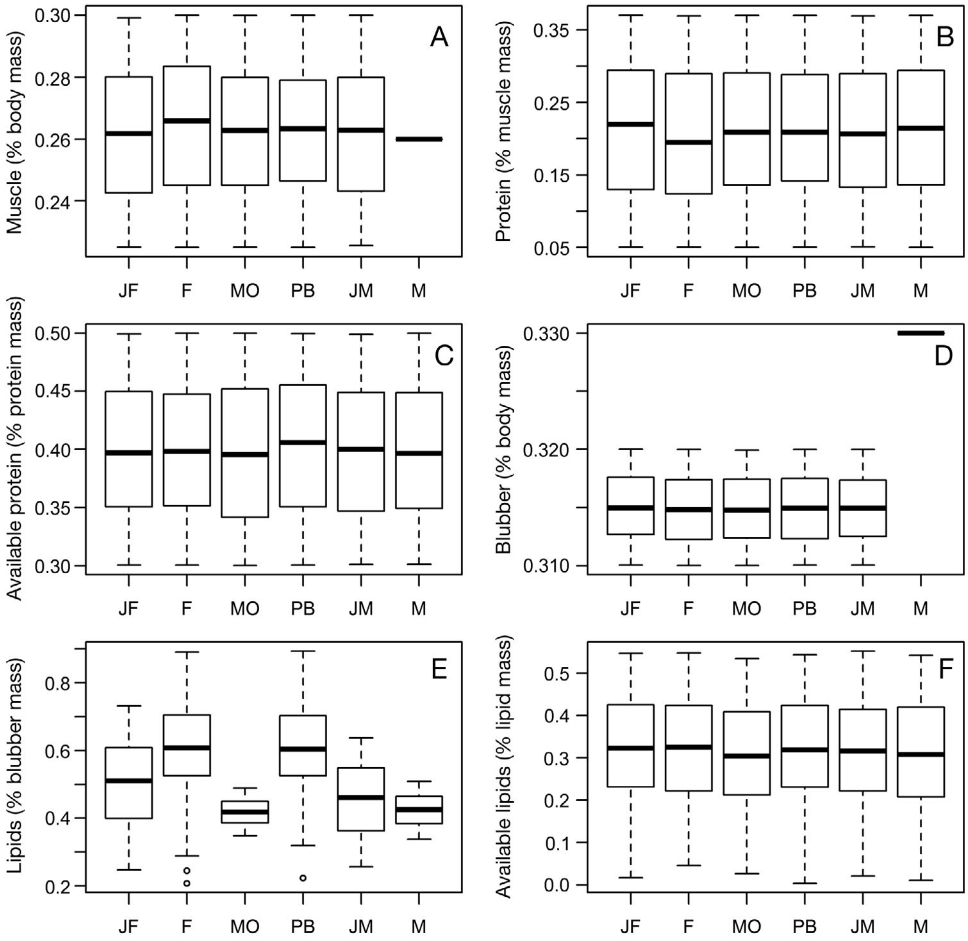


Fig. 3. Bioenergetic parameters. Boxplots of bioenergetic model parameters including (A) muscle mass as % body mass, (B) protein mass as % muscle mass, (C) metabolically available protein as % protein mass, (D) blubber mass as % body mass, (E) lipid mass as % blubber mass, and (F) metabolically available lipid mass as % lipid mass for 500 simulated sperm whales in each life stage (JF: juvenile female; F: mature female; MO: mother with calf; PB: post-breeding female; JM: juvenile male; M: mature male). Note the lack of uncertainty for some male parameters is an artifact of low sample size (n = 1) in Lockyer (1991)

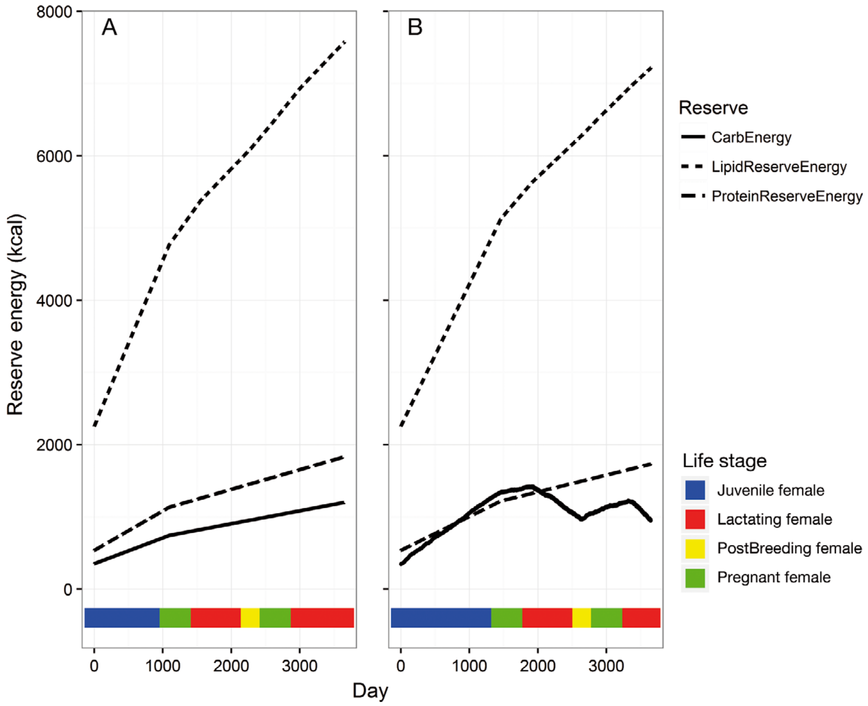


Fig. 4. Impacts of disturbance on total reserves. Available energy in lipid, protein, and carbohydrate reserves through time for (A) a simulated undisturbed female sperm whale versus (B) the same whale exposed to a minor disturbance (95% foraging efficiency) once per week over a 10 yr period. Note that the whale begins as a juvenile and progresses through maturation and the reproductive cycle during the simulation

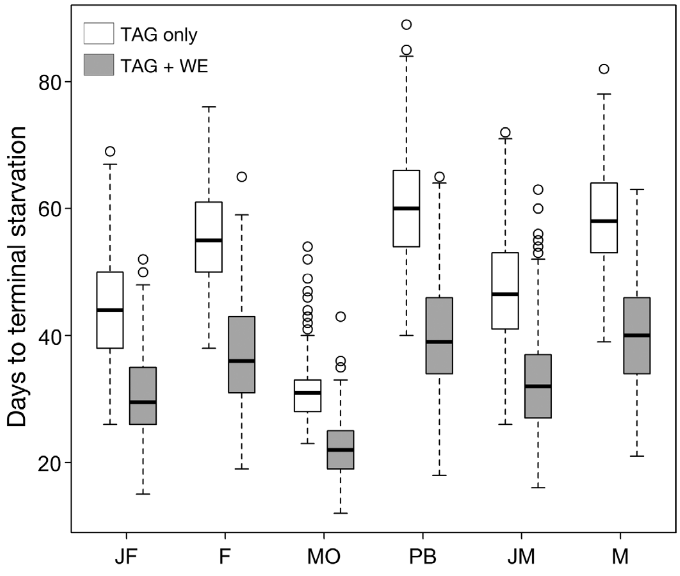


Fig. 5. Wax esters (WEs) versus triacylglycerols (TAGs). Boxplots of maximum continuous disturbance duration until terminal starvation with lipid energy stored as a combination of WEs and TAGs as observed in nature (gray fill) versus storing all lipid energy as TAGs (white fill) for 500 simulated sperm whales in each life stage (JF: juvenile female; F: mature female; MO: mother with calf; PB: post-breeding female; JM: juvenile male; M: mature male)

whale makes substantial gains in reserves through time; the rate of these gains in reserves varies with life stage and reproductive status (Fig. 4A). Model runs suggest that infrequent, minor disruptions in foraging are not fatal, but may result in reduced body reserves, relative to an undisturbed individual, and delays in sexual maturation (Fig. 4B). Carbohydrate reserves, in particular, are rapidly depleted because they are drawn upon first to cover the recurring caloric deficits.

Model outputs suggest that sperm whale lipid energy storage as a combination of WEs and TAGs reduces their ability to withstand starvation events by around 30% (Fig. 5). Our simulation results illustrate that sperm whales can endure partial foraging disruptions for much longer time periods than full foraging disruptions (i.e. starvation), largely because partial foraging results in smaller daily caloric deficits (Fig. 6). For example, whales foraging at 75% efficiency took approximately 3.5 times longer to reach terminal starvation than whales unable to forage (e.g. 0% efficiency). However, model runs suggested that frequent disruption of foraging, even at low levels, can be fatal for sperm whales, because they are unable to replenish their reserves without an undisrupted foraging day.

Sperm whale mothers and juveniles are the life stages most vulnerable to foraging disturbance (Fig. 7). Postbreeding females endured >60% more days of fasting than lactating females. Frequency of fasting events is a major determinant for how long a sperm whale can survive foraging disturbances, as natural foraging periods of several days to weeks allow them to grow and replenish some of their lost reserves (Fig. 7). Days to terminal starvation was roughly inversely proportional to the frequency of disturbance; however, less frequent disturbances allowed whales to rebuild reserves, extending time to terminal starvation. Across life stages, time to terminal starvation for whales with disturbances every other day, weekly, and monthly was approximately 1.6, 7.0, and 33.5 times longer than time to terminal starvation with continuously (e.g. daily) disrupted foraging, respectively. Model runs suggested that males were most resilient to foraging disturbance, and many males were able to survive monthly foraging disturbances.

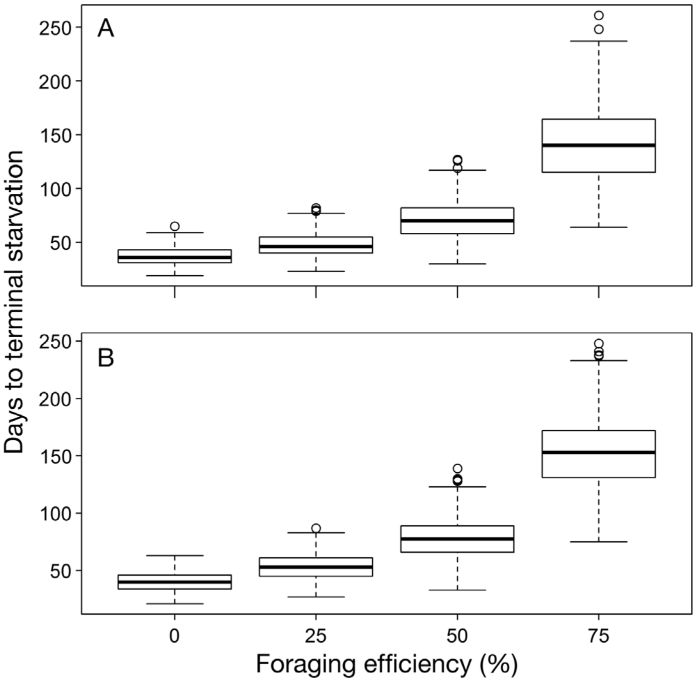


Fig. 6. Foraging efficiency and starvation. Boxplots of maximum disturbance duration until terminal starvation for 500 simulated mature (A) female and (B) male sperm whales at different foraging efficiencies

The increases in viability are less substantial for reproductively active females (e.g. mature female, mother with calf, post-breeding female) due to the dampening influence of the additional energetic demands of the reproductive cycle.

Increases in a whale's ability to replace body reserves above observed daily growth (γ) are required to survive routine weekly disturbances over a 10-yr simulation period (Fig. 8). A doubling in daily growth capacity (e.g. $\varphi = 2$) is required on undisturbed foraging days for a female whale to avoid terminal starvation with a weekly 25% disturbance (Fig. 8, circles). A 6-fold increase in daily growth capacity is required for a female whale to avoid terminal starvation with a weekly 50% disturbance (Fig. 8, triangles). A 14-fold increase in daily growth capacity was inadequate for a female whale to avoid terminal starvation with a weekly 75% disturbance (Fig. 8, squares).

A day of starvation for an 8179 kg mature female sperm whale results in a caloric deficit of approximately 300 000 kcal, equivalent to approximately either 75 kg of carbohydrate reserves (if available) or 28 kg of lipid and 5 kg of protein reserves. By contrast, without a 'hunger response' (e.g. $\varphi = 1$), the daily growth of a mature female sperm whale is only 1.51 kg d^{-1} (Table 1). If this growth is distributed

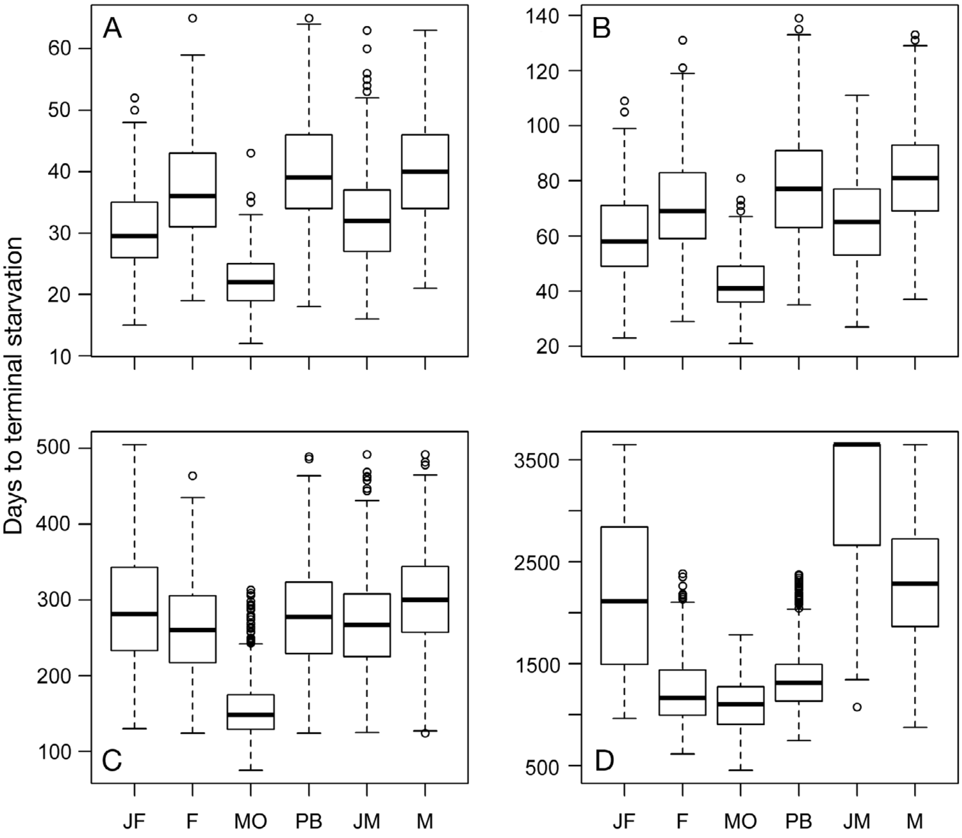


Fig. 7. Resilience to starvation events. Boxplots of maximum disturbance duration until terminal starvation for different frequencies of starvation events: (A) daily; (B) every other day; (C) once per week; and (D) once per month, for 500 simulated sperm whales in each life stage (JF: juvenile female; F: mature female; MO: mother with calf; PB: post-breeding female; JM: juvenile male; M: mature male)

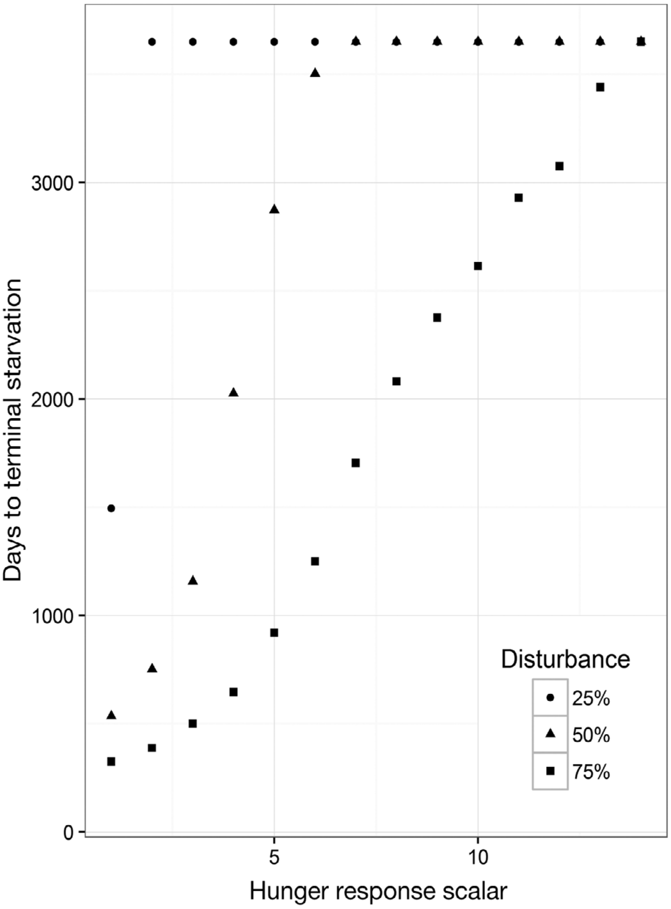


Fig. 8. Hunger response. Days to terminal starvation over a 10 yr period with weekly foraging disturbances of 25, 5, and 75% given different 'hunger responses', expressed as a scalar on daily growth rate during days of natural foraging

amongst body tissues proportional to standard somatic growth, a female whale can only replace approximately 0.04, 0.12, and 0.05 kg of metabolically available carbohydrate, lipid, and protein reserves, respectively. This equates to only approximately 0.5% of FMR. If growth is distributed amongst body tissues with imperfect allocation between somatic growth and proportional replacement of lost reserves, mean replacement is approximately 2% of FMR. A 'hunger response' increases this replacement rate, providing added metabolic benefits to undisturbed foraging days, yet the physiological capacity of 'hunger responses' in wild sperm whales remains unknown.

DISCUSSION

For approximately 23 million years, sperm whales have used sound to pursue prey in the deep ocean, one of the most stable environments on the planet. Sperm whales use echolocation (Miller et al. 2004a) to capture several hundred kilograms of various deep-water prey (Berzin & Yablokov 1972, Best 1979, Kawakami 1980, Clarke et al. 1993) on a daily basis. Under typical ambient conditions, they may be able to acoustically locate prey at distances up to 1000 m (Møhl et al. 2003, Madsen et al. 2007). Sperm whale decisions about where to forage may be based on prior foraging success, echo information gathered during ascent (Fais et al. 2015), and eavesdropping on conspecifics foraging nearby (Madsen et al. 2002). Sperm whales appear to perform complex auditory processing, tracking multiple prey targets simultaneously (Fais et al. 2015). This complex information gathering allows sperm whales to efficiently locate and access prey resources in a dark, patchy, and vast environment (Fais et al. 2015). Sperm whales in the Gulf of Mexico have been exposed to high levels of anthropogenic noise from seismic testing for decades. Although habituation may be possible, it is likely that increased anthropogenic noise impairs or inhibits their use of sound to acquire prey (Lima & Zollner 1996, Zollner & Lima 1999, Fais et al. 2015). Our bioenergetic simulations suggest that frequent disruptions in foraging can have potentially severe fitness consequences for sperm whales. Anthropogenic disturbance may lead to caloric deficits that must be paid through body reserves. If disturbance is frequent and severe, it may lead to terminal starvation. Frequent partial disturbances of foraging may lead to lower body condition, with potential indirect effects of delayed sexual maturation or reduced reproductive fitness.

To maximize individual survival and reproduction, organisms must optimize how they acquire and allocate resources (Stearns 1989). Optimal foraging theory predicts that animals should maximize energy intake rate and minimize the time spent obtaining food (Schoener 1971). Physiological constraints play an important role in determining the foraging behavior of marine mammals (Rosen et al. 2007). To meet their energy needs, marine mammals must balance the time required to capture prey (limited by foraging time, diving capabilities, and thermoregulatory costs) and process that prey (limited by maximum digestive capacity and time required for digestion). Deep-diving marine mammals have a substantial incentive for efficient foraging, as they must access 2 vital but spatially separated resources: air at the surface and food at depth (Kramer 1988). Recent field studies involving southern elephant seals *Mirounga leonina* have suggested that their deep-dive foraging behavior is consistent with optimal foraging theory (Thums et al. 2013). If anthropogenic disturbance interferes with sperm whale acoustic signal processing, they may cease or reduce foraging effort (Miller et al. 2009, 2011, 2012, Sivle et al. 2011, Curé et al. 2016).

Sperm whales may be less resilient to reduced foraging efficiency than other similar sized whales due to their income breeding strategy and their unique body composition. The income breeding strategy (use of concurrent intake to pay for a reproductive attempt) used by sperm whales requires stable or predictable environments that enable continuous energy acquisition throughout the year (Oftedal 1997, Irvine et al. 2017). The vast majority of sperm whale blubber lipids are stored as WEs, which conserve oxygen during metabolism but are less accessible as a source of mobilizable energy (Lockyer 1981, Koopman 2007). The dominance of WEs, rather than TAGs, in the blubber of sperm whales has led several authors to suggest that sperm whales may not use blubber lipids as an energy reserve and may be reliant upon stable foraging environments (Lockyer 1991, Koopman 2007, Pabst et al. 2016). Although sperm whales are extremely large animals, our simulations suggest the prevalence of WEs in their blubber may reduce their resilience to terminal starvation by approximately 30%.

We attempted to capture the uncertainty in sperm whale bioenergetic modeling through bootstrap Monte Carlo sampling. The metabolic dynamics of starvation are complex, and our model has its limitations. The fasting response includes a suite of energy-conserving adaptations that limit tissue loss and delay death by starvation. These adaptations include decreased locomotion, increased sleep, and metabolic depression (Keys et al. 1950). In our model, FMR is reduced as a function of changes in body mass as reserves are expended, but metabolic depression is not explicitly modeled. Metabolic depression is a rapid response to fasting that drops metabolism below levels that would be predicted by losses in body mass, and is most clearly demonstrated by animals that undergo natural fasting (Hudson 1973, Mrosovsky & Sherry 1980, Merkt & Taylor 1994). In Steller sea lions *Eumetopias jubatus* subjected to 9 to 14 d fasts, resting metabolic rates decreased on average by 31%; however, metabolic depression did not occur during 28-d food restriction trials despite substantial decreases in body mass (Rosen & Trites 2002). Metabolic depression has been observed in fasting weaned northern elephant seal pups (*Mirounga angustirostris*; Rea & Costa 1992). However, for northern elephant seals (Noren 2002) and fur seals (*Arctocephalus tropicalis*; Verrier et al. 2009), the strongest predictor of resting metabolic rate during extended fasts is body mass, including lean mass and lipid mass (e.g. body condition). Decreases in metabolism may be limited or precluded by potential conflicts with thermoregulatory abilities, buoyancy, or water balance (Aschoff & Pohl 1970, Fuglei & Øritsland 1999, Miller et al. 2004b, Svärd et al. 2009). Given these somewhat equivocal results for fasting species, it is unclear whether sperm whales would demonstrate metabolic depression, as they do not typically undergo extended periods of fasting during their life cycle. If metabolic depression occurs in sperm whales, evidence from other marine mammals suggests that this response is less likely during a period of impaired foraging than during an extended starvation event (Rosen & Trites 2002).

During a period of impaired foraging, where additional resources may be perceived as available, animals may demonstrate a 'hunger response' where they increase foraging effort to compensate for caloric deficits (Cornish & Mrosovsky 1965, Collier 1969, Rosen & Trites 2002). The total daily energy gain on undisturbed foraging days without a 'hunger response' equates to approximately 0.5–2% of FMR when $\chi = 1$ (i.e. no additional demands from pregnancy or lactation). The 'hunger response' is accompanied by an increase in metabolism (Webber & MacDonald 1994). We simulated 'hunger responses' as the animal's ability to acquire sufficient food on days of natural foraging to replace lost reserves as a scalar on observed daily growth rates from Lockyer (1981). The substantial increase in daily growth required to compensate for foraging disruptions suggests that the costs of maintaining their massive bodies greatly outweigh the costs associated with daily growth for these long-lived, slow-growing predators (Lockyer 1981). A mature female sperm whale loses over 30 kg of metabolically available reserve mass during a day without foraging, but gains less than 2 kg of total body mass on a natural foraging day in the absence of a 'hunger response'. Rosen & Trites (2002) report a 2 kg d^{-1} loss and 1 kg d^{-1} replacement for Steller sea lions that were starved for approximately 2 wk and then re-fed for 2 wk. This 50% replacement ratio would equate to an approximately 10-fold 'hunger response' for a sperm whale. Because body growth scales proportionally to size with a slope of 0.75 (Case 1978), this 50% daily replacement rate may not be attainable in an adult sperm whale that is over 50 times larger than a Steller sea lion. Additionally, the Steller sea lions in the Rosen & Trites (2002) study were re-fed in a captive situation (e.g. no foraging effort and no prey limitations). On average, sperm whales in the Gulf of Mexico spend 72 ± 32.7 % (17.3 ± 7.8 h) of each day in foraging dive cycles, consisting of 45.5 ± 7.4 min dives followed by 8.1 ± 2.6 min surface intervals (Watwood et al. 2006). The substantial daily investment in foraging for Gulf of Mexico sperm whales suggests that the foraging effort required to support substantial increases in daily growth rate may be impossible to achieve in reality, due to limits on food intake associated with constraints on prey acquisition and processing (reviewed in Rosen et al. 2007). Thus, it is likely that any 'hunger response' and associated increases in daily growth rate for sperm whales would be lower than that observed for Steller sea lions by Rosen & Trites (2002).

Our model accounted for reductions in carbohydrate, protein, and lipid reserves, but did not account for several other fasting health impacts that can lead to a downward spiral of increased tissue catabolism to pay for increased energy costs (Rosen et al. 2007). Failure to consume sufficient prey has feedback effects on foraging, thermoregulation, and digestive capacity (Rosen et al. 2007). Depletion of the blubber layer affects buoyancy and gait, increasing the energetic costs of future foraging efforts (Miller et al. 2004b, Rosen et al. 2007). Dehydration and ketosis are associated with the catabolism of energy stores (Castellini & Rea 1992). The release of chemical substances into the bloodstream associated with the breakdown of adipose body reserves may have neurotoxic and immunotoxic effects and has been implicated in marine mammal strandings (Mazzariol et al. 2011). Similarly, our model does not account for increases in the energy required to maintain a stable internal body temperature (Watts et al. 1993) associated with reductions in blubber energy stores (Rosen et al. 2007). Additionally, the circulatory demands of diving, thermoregulation, and digestion may be mutually incompatible, forcing animals to alter time budgets to meet these exclusive demands (Rosen et al. 2007). Finally, we did not model the increased vulnerability to disease associated with malnutrition (Scrimshaw et al. 1968).

With their immense size, exploitation of relatively stable deep ocean environments, and considerable ability to move between food patches, starvation is an unlikely cause of death for sperm whales under natural circumstances. However, terminal starvation may be possible for whales lost or trapped in a novel environment (Mazzariol et al. 2011) or whales repeatedly exposed to anthropogenic stressors that reduce their foraging ability (Miller et al. 2009, 2011, 2012, Sivle et al. 2012, Curé et al. 2016). Our model suggested that mature sperm whales would take between 3 wk and 2 mo to reach terminal starvation. Captive starvation studies of cetaceans have not been performed; however, field observations may be used to ground-truth our simulation results. In general, sperm whales would be expected to endure starvation longer than smaller odontocetes, owing to their larger size and associated reserves. Studies suggest that the harbor porpoise *Phocoena phocnea*, a small odondocete inhabiting the cold temperate waters of the Northern Hemisphere, would starve to death in only 3 to 5 d (Koopman 1994, Kastelein et al. 1997). Medium-sized orcas entrapped in sea ice may survive between 14 and 75 d (Lowry et al. 1987, Higdon & Ferguson 2014). In 2014, 3 transient (e.g. marine mammal eating) orcas, including a late-term pregnant female, that travelled up the Nashagak River near Dillingham, Alaska, presumably died from starvation (and possibly dehydration) after being without food for at least 25 d (K. Savage, NOAA, pers. comm.). Anecdotal information suggests that beluga whales *Delphinapterus leucas* entrapped in sea ice have starved within 60–90 d (Flood 2001). Several of these field observations are confounded by partial foraging, stranding injuries, polar bear attacks, and limited details regarding the actual dates of entrapment or mortality. Records of emaciated animals stranding on beaches are more common because they are more easily observed. However, it is difficult to back-calculate how long the animals have starved, and emaciation is usually implicated as only one among many probable causes of death (Bogomolni et al. 2010). Recently, Mazzariol et al. (2011) suggested a possible concurrent role for starvation in the mass stranding of 7 male sperm whales in the Adriatic Sea, with a minimum starvation period of 3 to 7 d. These various field observations suggest that our estimates of time to starvation for sperm whales are within a reasonable range.

Our analysis suggests that foraging disruptions would have to be relatively frequent to lead to terminal starvation, but continual minor disruptions can cause substantial reductions in available reserves. Reductions in available reserves may be equivalent to a reduction in body condition (Christiansen & Lusseau 2015). Theoretical and empirical studies of other cetaceans suggest that lower body condition in mothers may decrease the probability of calf production (New et al. 2013, 2014, Christiansen et al. 2014) or reduce the size of the calf at birth (Kovacs & Lavigne 1986), which may reduce the probability of calf survival (McMahon et al. 2000). Our model suggests that sperm whale mothers with calves are the life stage most vulnerable to foraging disruptions because of the high additional metabolic demands associated with lactation (see Fig. 5). Reductions in female fitness or female mortalities may be accompanied by the mortality of any associated fetus or calf, or lactating mothers may provide an energetic buffer to their offspring at the expense of their own body condition and future reproductive success (Bradford et al. 2012, Rolland et al. 2016). Juveniles are also vulnerable to starvation events due to their relatively low body reserve levels (see Fig. 5). If anthropogenic disturbance disrupts sperm whale foraging, these findings are cause for concern for the Gulf of Mexico stock.

It is difficult to evaluate the simultaneous impacts of the broad suite of anthropogenic stressors that might reduce sperm whale foraging efficiency; however, the potential consequences are substantial. The estimated annual rate of increase from reproduction for Gulf of Mexico sperm whales ranges from zero (Schwacke et al. 2016) to less than 1 % per year (Chiquet et al. 2013). From 1 January 2000 to 1 September 2017 there were 36 sperm whale strandings recorded in the US Gulf of Mexico (including all of Monroe County, Florida) in the NOAA Marine Mammal Health and Stranding Response Program National Database (data pulled on 5 August 2017; B. Mase, NOAA, pers. comm.). Body condition is not explicitly recorded on the Level A data entered in this database (Level A data include details of each stranding such as species, date, stranding location, carcass condition, sex, length, examiner, signs of human interaction); however, 8 of 36 (22 %) of these strandings noted in comments that animals were thin/underweight (ranging from thin to emaciated). Potential biological removals (PBR) for the gulf population is 1 individual per year (NMFS 2016). PBR is defined by the US Marine Mammal Protection Act as the maximum number of animals, excluding natural mortalities, that may be removed from a marine mammal stock while allowing that stock to reach or maintain its optimum sustainable population. Sperm whale mortalities and reductions in individual fitness associated with anthropogenic stressors in the Gulf of Mexico could lead to population-level effects if PBR exceeds 1 individual per year. Additionally, the ESA recovery plan for sperm whales seeks to minimize or eliminate effects of human activities that are detrimental to the recovery of their global populations, including threats such as competition for resources, loss of prey base due to climate change, and disturbance from anthropogenic noise (NMFS 2010). Our bioenergetic model provides a flexible framework for additional CEE and simulation modeling to evaluate the level, frequency, and consequences of foraging disruptions associated with various anthropogenic stressors. Applying this bioenergetic modeling approach within a PCoD framework that includes a time series for anthropogenic disturbance would allow empirical estimation of individuals reaching terminal starvation and reductions in body condition for survivors.

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