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A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales

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Abstract. While sophisticated tools are used to monitor behavioral changes of large marine vertebrates, determining whether these changes are meaningful for management and conservation is challenging. The Population Consequences of Disturbance model proposed a bioenergetics model to detect biologically meaningful population responses, where disturbance costs are linked to lost energy. The model assumes that changes in behavior, caused by disturbance, compromise maternal condition, reducing energy delivery to offspring, leading to reduced reproduction, increased offspring mortality, and eventually increased adult mortality. Given its coastal habits and past whaling history, gray whales' (*Eschrichtius robustus*) life history and ecology are better known than for many other baleen whales. However, their preference for coastal habitat increases their exposure to human disturbance. We created a female gray whale bioenergetics model to determine energy requirements for a two-year reproductive cycle and determined the consequences of lost energy under three possible disturbance scenarios. An annual energetic loss of 4% during the year in which she is pregnant, would prevent a female from successfully producing/weaning a calf. For this reason, gray whale reproduction is particularly sensitive to disturbance during pregnancy. During the year in which she is lactating, she would wean her calf at a lower mass with a 37% energetic loss. A female would lack the energy to become pregnant during a year with a 30–35% energetic loss, and female mortality would likely occur at 40–42% annual energetic loss. Our model can be used for assessing disturbance costs or other effects associated with climate change and/or anthropogenic activities and can be applied to other species with similar life histories.

Key words: Bayesian analysis; cetacean; energetic cost; *Eschrichtius robustus*; lost foraging opportunity; metabolic rate; mysticete; reproductive costs.

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INTRODUCTION

While sophisticated tools and approaches to monitor behavioral changes of large marine vertebrates have been developed (Block 2005, Costa et al. 2012), we are faced with the challenge of determining whether these changes are meaningful in terms of management and conservation. This is especially critical as we attempt to interpret animals' responses to anthropogenic activities and changing climate (Tyack 2008, 2009, Costa et al. 2010, Doney et al. 2012, Hazen et al. 2013). In the context of conservation and management, a biologically meaningful response is one where a sufficient number of individuals are affected that there is a change in the population. Therefore, understanding the response of animals to different stressors will

require an approach that integrates behavior, physiology, ecology, and population dynamics (Cooke et al. 2014).

The National Research Council Committee on Population Consequences of Acoustic Disturbance (PCAD), developed a framework that detailed how behavioral responses to sound may affect life functions (survival, migration, feeding, breeding), how life functions are linked to vital rates, and how changes in vital rates cause population change through a series of transfer functions (NRC 2005). While logistical limitations in data acquisition preclude assessment of these transfer functions for most marine mammals, there are a few species where data are available to parameterize these functions, such as the gray whale (*Eschrichtius robustus* (Lilljeborg 1861)). Given its coastal habits, gray whales are easily observed from shore. As a result of that and its past whaling history, many facets of their life history and ecology, such as distribution, migration, and behavior, are better known than for other baleen whales (Rice and Wolman 1971, Jones et al. 1984).

The PCAD model has recently been reformulated by the ONR (Office of Naval Research) PCoD (Population Consequences of Disturbance) working group. The new framework allows for a variety of approaches to detect a biologically meaningful response, including a bioenergetics model where costs associated with disturbance are linked to reductions in foraging success (Costa 2012, New et al. 2013, 2014). Bioenergetics models are used to understand life history requirements (Costa 2001, 2008, Molnar et al. 2009, Christiansen et al. 2013*b*, Fortune et al. 2013, Stephens et al. 2014) and quantitatively assess the effort animals spend acquiring resources, and how they allocate those resources. In a reproductive female, the ability to reproduce is tied to her ability to acquire prey for her and her offspring's metabolic requirements. In long-lived organisms, reproductive individuals typically terminate offspring care or pregnancy, rather than jeopardize their own survival (Goodman 1974), which buffers the species against environmental variability (Goodman 1981, 1984, Costa 1993, 2008, Forcada et al. 2008). The PCoD model therefore assumes that changes in behavior, caused by disturbance, compromise maternal condition by reducing energy gain (interrupting foraging behavior) and increasing energy expenditure (cost of avoidance). This could compromise adult condition and reduce energy delivery to offspring. In turn, reduced energy gain would lead to reduced natality, increase offspring mortality rates, and at the extreme, increase adult mortality (Costa 2012, Christiansen et al. 2013*a*, New et al. 2013). Population growth in long-lived species is usually most sensitive to reproductive females. Therefore, we created a female gray whale bioenergetics model to determine energy requirements for self-maintenance and costs of reproduction over a female's two-year reproductive cycle (Fig. 1). We used the bioenergetics model to develop disturbance scenarios to predict the magnitude of reduced energetic intake that would result in lost reproduction, reduced offspring care, and ultimately death of female gray whales.

Intense commercial whaling through the first half of the 1900s brought most baleen species to near extinction. Gray whales recovered quickly once whaling ended in the mid-1900s. They are extant only in the North Pacific with two stocks that may represent distinct populations, the eastern stock with 15,000–22,000 individuals (Laake et al. 2009) and the western stock with ~140 non-calf individuals in 2012 (Cooke et al. 2013). Eastern gray whales exhibit one of the longest annual migrations, traveling ~8,000 km for approximately two months, from their summer feeding grounds in the Chuckchi and Bering Sea to their winter breeding grounds in Baja California, Mexico. The western gray whale migration routes are not well known, however, some animals travel ~10,000 km from summer feeding grounds around Sakhalin Island, Russia to Baja California (Mate et al. 2011, Weller et al. 2012). While there is some indirect evidence for minimal feeding during the migration (Sanchez-Pacheco et al. 2001), as capital breeders eastern gray whales acquire almost all their energy during a relatively short period of their annual cycle (mainly from ampeliscid amphipods; Rice and Wolman 1971, Bogoslovskaya et al. 1981, Nerini 1984, Blokhin 1986), relying on stored energy to sustain their migration and most of the reproductive cycle.

Gray whales potentially give birth every other winter, and rarely in successive years if the first calf is lost early (Jones 1990). Gestation is roughly

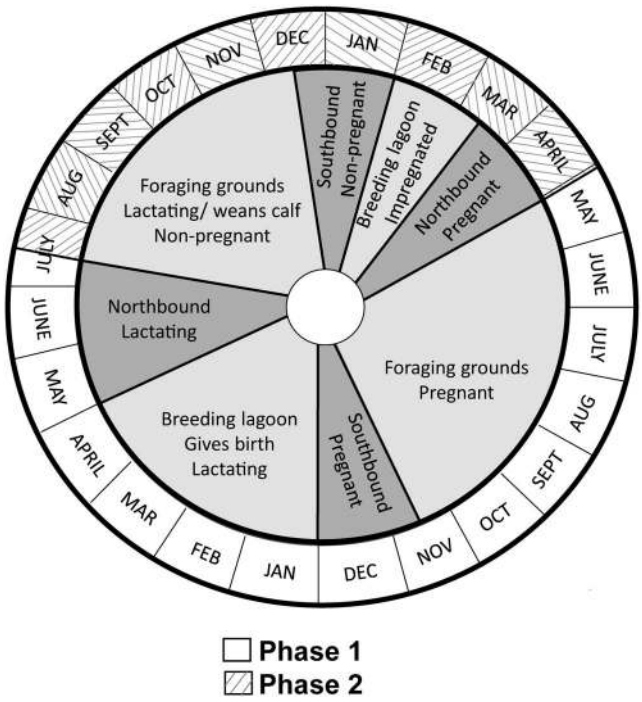

Fig. 1. Female gray whale timing and duration of life stages on a two-year cycle.

13 months, and weaning occurs at approximately seven months of age (Rice and Wolman 1971). Lactation is one of the most energetically expensive physiological processes in mammals (Hanwell and Peaker 1977, Williams et al. 2007) and, for gray whales, occurs mostly during their fasting period. Therefore, the energy a female can acquire during a limited foraging period has consequences for her and her offspring. A reduction in the energy acquired could potentially reduce the calf weaning mass, which may affect its survival. Additionally, if a female cannot recover the energy expended during nursing, the female's health and future reproductive events could be compromised or at least delayed, increasing the inter-birth interval to three or more years. A number of western gray whale adult females that were observed with a calf at the foraging grounds, have also been observed without a calf during two or more consecutive years (Sychenko 2011). Both inter-birth interval and calf survival are important determinants of population growth rate, the basic metric for population consequences of disturbance. Energy losses in foraging opportunities and during migration may lead to changes in vital rates (i.e., reproduction). If these changes are severe enough and sufficient number of females are affected will result in population-level effects. Gray whales' preference for coastal habitat increases their exposure to human activities, and therefore the risk of disturbance. The Scientific Committee of the IWC (International Whaling Commission) and IWC/IUCN (International Union for Conservation of Nature) Western Gray Whale Conservation plan have acknowledged that coastal development and industrial activity pose real threats to their survival (Jones et al. 1984). Consequently, it becomes crucial to understand how this species responds to disturbances.

Methods

Since energy acquisition for reproductive females affects current and future reproductive output, our model estimates the total energetic requirements for an adult female gray whale to survive and successfully accomplish all stages of its life history, such as migration and reproduction. With such estimates we predicted how reduced foraging due to three different distur-

bance scenarios would affect reproduction, offspring care and survival. Gray whale female energetic demands can be parsed into three categories: (1) field metabolic rate (FMR), reflecting energy requirements for maintenance at different activity levels and reproductive stages; (2) pregnancy costs; and (3) lactation costs, consisting of calf maintenance or metabolic rate and calf growth costs from 0-7 months of age (weaning age). We identified eight gray whale female stages with different energy requirements based on a two-year reproductive cycle divided into two phases: Phase 1: (i) foraging grounds (pregnant), (ii) southbound migration (pregnant), (iii) breeding lagoons (lactating), (iv) northbound migration (lactating), Phase 2: (v) foraging grounds (lactating, weaning), (vi) southbound migration (non-pregnant), (vii) breeding lagoons (in estrus), (viii) northbound migration (newly pregnant; Fig. 1). Data to calculate gray whale female energetic demands were obtained from an extensive literature review and evaluation.

Most morphometric data for our model is based on direct measurements obtained from gray whales ($n = 316$) harvested along the coast of Central California between Half Moon Bay (37°30′ N lat.) and Point Reyes (38°00′ N lat.) during their southward and northward migrations from 1959 to 1969 (Rice and Wolman 1971).

Incorporating uncertainty

In contrast to previous bioenergetics models of gray whales, most of the variables used in our model were obtained and reworked from original data. We used Monte Carlo sampling to build distributions around each variable using measurement and process uncertainty, instead of using a mean or other point value. Therefore, our model provides a more realistic picture of the variability and uncertainty in energetic requirements, allowing us to present results with 95% intervals. We accounted for uncertainty in model parameters whenever possible. Variability for most parameters was found in the literature. Estimates and uncertainty of tidal volume for calves were based on a Bayesian reanalysis of original data, regressing tidal volume as a function of mass or expiration duration and length (Appendix C). Via Monte Carlo sampling ($N = 150000$, to produce a representative distribution), we incorporated uncertainty into resulting metabolic requirements. Subsequently, we determined the proportion of energy needed for each phase of a successful two-year migration cycle with weaning of a calf. We were then able to quantify the proportion of lost energy that would lead to an unsuccessful cycle.

The following sections provide details on the various components of the model, reflecting the three categories of gray whale female energetic demands, and the model assumptions.

Gray whale female energetic demands

Field metabolic rate (FMR).—FMR in megajoules (MJ) was estimated from respiration rates obtained by visual observation of females during all phases of the two-year cycle (Sumich 1986). Ventilation rates are mediated mainly by breathing rates; therefore, breathing rates alone provide reasonable relative indices of metabolic rates (Sumich 1986). FMR of calves was similarly estimated for each of three pre-weaning calf stages (used to estimate lactation costs), assuming a mean birth date of Jan. 27 (breeding lagoons: 0–2 months old, northbound migration: 3–5 months old, and foraging grounds: 5.7–7 months old; Rice et al. 1981, Withrow 1983, Jones and Swartz 1986).

Total metabolic energy expenditure for a given stage (E_s) in MJ was calculated using the following relationship:

$$E_s = 0.0200 \cdot \%O_2 \cdot T_s \cdot R_s \cdot V_t \qquad (1)$$

where 0.0200 is the amount of heat produced in MJ/L O_2 consumed, from Kleiber (1961). Other parameters are O_2 extraction efficiency per breath ($\%O_2$), the number of days in that stage (T_s), respiration rate (R_s in breaths/day), and tidal lung volume (V_t in L).

O_2 extraction efficiency ($\%O_2$).—Calf $\%O_2$ was based on direct measurements (66 expirations) from young calves (1–5 months old) in captivity and at the lagoons (10.5% ± 3.0%). Percent O_2 data are not available for adult gray whales. Therefore, we calculated the mean and standard deviation (SD) from plotted data (136 expirations) presented in Sumich (2001) to determine $\%O_2$ for a captive calf from 1–10 months old at 11% ± 2.7%, and we used this value for adult females.

Duration of female stages (T_s).—We determined

Table 1. Mean parameters used to estimate tidal volume and total energetic costs for adult females and calves.

Age class	Length (m)	Girth (m)	Mass (kg × 10^3)	Expiration duration (s)	Tidal vol. (V_t) (L)
Adult females	12.7 (0.6)	7.6 (0.4)	26 (17.4, 36.6)	...	550 (360, 780)
Calf 0 months	4.6 (0.5)	2.3 (1.8, 2.8)	1 (0.5, 1.8)	0.4 (0.02)	14 (6, 29)
Calf 1 months	5.6 (4.6, 6.5)	2.4 (2.5, 3.6)	2.1 (1.2, 3.3)	0.5 (0.01)	29 (13, 56)
Calf 2 months	6.3 (5.3, 7.2)	3.2 (2.9, 4.0)	3 (1.8, 4.4)	0.6 (0.04)	46 (21, 89)
Calf 3 months	6.9 (5.9, 7.8)	3.7 (3.2, 4.3)	3.8 (2.4, 5.5)	...	90 (11, 300)
Calf 4 months	7.3 (6.4, 8.3)	4.0 (3.5, 4.6)	4.6 (3, 6.5)	...	120 (14, 390)
Calf 5 months	7.7 (6.7, 8.6)	4.2 (3.7, 4.7)	5.3 (3.6, 7.3)	...	140 (18, 450)
Calf 5.75 months	7.9 (6.9, 8.8)	4.3 (3.8, 4.8)	5.7 (3.9, 7.8)	...	150 (19, 450)
Calf 6.5 months	8.0 (7.0, 8.9)	4.4 (3.9, 4.9)	5.9 (4, 8)	...	160 (20, 460)
Calf 7 months†	8.2 (7.2, 9.1)	4.5 (4.0, 5.0)	6.3 (4.3, 8.6)	...	170 (23, 490)

Note: Single numbers in parentheses (standard deviation, SD) are taken from published direct measurements. Estimates with two numbers in parentheses (95% posterior intervals) were calculated. Expiration duration was only used and available for 0–2 month calves (from source 2). Female length and girth, and calf 0 month length were measured from source 1, 2 and 1-4 respectively. All other values (except expiration duration) were calculated. Sources are (1) Rice and Wolman (1971); (2) Sumich (1986); (3) Rice (1983); (4) Perryman and Lynn (2002).

† Data only used for calf growth costs-lactation costs, not total energy requirements; calves are weaned at 7 months.

adult T_s based on migration distance, travel speed and sighting information (Pike 1962, Rice and Wolman 1971, Sumich 1983, Braham 1984, Jones and Swartz 1986, Sumich 1986, Rodriguez de la Gala-Hernandez et al. 2008; Fig. 1). The duration a calf spent in each stage was simply the age range for that stage (Appendix A).

Respiration rate (R_s).—To determine R_s in breaths/day for calves and adult females, direct measurements of breaths/minute with means and S.D. were obtained from the literature (Sumich 1983, Harvey and Mate 1984, Sumich 1986, Wursig et al. 1986, Sumich 2001, Schwarz 2002, Rodriguez de la Gala-Hernandez et al. 2008; Appendix B). To translate to breaths/day, we sampled from a lognormal distribution of breaths per minute and inverted the value to get breath-hold time. Then, we added up breath-hold times and number of breaths until reaching 24 hours, and reiterating as a Monte Carlo simulation 20,000 times to adequately sample uncertainty. The method greatly reduced uncertainty and provided a more realistic distribution of respiration rate compared to simply multiplying the distribution of breaths/min by 1440 min/day.

Tidal lung volume (V_t).—V_t for calves younger than three months old was estimated using a Bayesian regression analysis of V_t as a function of expiration duration (E_d in s) and body length (L in m) using published data (Sumich 1986; Appendix C)

$$\ln V_t = \beta_0 + \beta_1 \ln L + \beta_2 \ln E_d. \quad (2)$$

Since the above relationship has not been established for older calves, V_t of calves three months old and older were estimated using a Bayesian regression analysis of V_t as a function of mass (M in kg) from published data (Sumich 1986). V_t uncertainty was high, particularly for older calves. Therefore, we set a conditional upper bound on calf V_t, not allowing a calf's sampled V_t to exceed the sampled V_t of the adult female (Appendix C)

$$\ln V_t = \beta_0 + \beta_1 \ln M. \quad (3)$$

V_t of adult females was estimated using Eq. 3, but instead of uncertainty in parameters, we used maximum likelihood values of β_0, β_1, and the error variance since such exponential uncertainty led to almost no resolution in tidal volume for larger animals (Appendix C).

Mass (M).—Adult female mass (kg) was estimated based on L (m) (Table 1) as $M = bL^3$ (Rice and Wolman 1971; Appendix D). Uncertainty in the parameter b was calculated from original data, predominantly from harvested gray whales taken along the Central California coast (Rice and Wolman 1971). Variability in adult female length was also incorporated into total energy estimates as the standard deviation of published lengths data (Appendix D).

Mass of calves was estimated from the relationship between M, girth (G in meters), and L

$$M = 28.5 \cdot G^{1.17} \cdot L^{1.73}. \quad (4)$$

This relationship was not re-analyzed since it accounted for a very high proportion of the

variance ($R^2 = 0.997$; Sumich et al. 2013). The girth-to-length ratio for newborn calves was assumed to be $0.5 \pm 0.02L$ (Norris and Gentry 1974, Sumich 1986).The girth-to-length ratio for older calves was assumed to be 0.55 (Sumich 1986; Appendix D). Parameter L for newborn calves was based on late term fetuses and neonates measurements (Rice and Wolman 1971, Rice 1983, Sumich 1986). L for older calves was estimated using the Gompertz equation from Sumich et al. (2013), $L = 8.85e^{-e^{(-0.47-0.068t)}}$, $R^2 = 0.911$, where t is age in weeks. Although we did not estimate uncertainty for this relationship, we assumed length at age varied the same as when calves are born (SD = 0.5; Appendix D).

Pregnancy costs.—Pregnancy costs were calculated as the sum of the heat increment of gestation (H_g) in MJ combined with the energy contained in the newborn calf (C_{nb}) in MJ and associated tissues. H_g was estimated using the relationship between mass and energy developed by Brody (1945) without uncertainty

$$H_g = 18.41 \times 10^6 \cdot M_{nb}^{1.2}. \quad (5)$$

Variance in newborn mass (M_{nb}) in kg was determined from Eq. 4 using distributions of length and girth from late term fetuses and neonates (Rice and Wolman 1971, Norris and Gentry 1974, Rice 1983, Sumich 1986, Perryman and Lynn 2002; Table 1; Appendices C and D). C_{nb} was calculated from the relative contribution of lipid and protein to its mass

$$C_{nb} = (M_{nb} \times F_{lipid} \times E_{lipid}) + (M_{nb} \times F_{prot} \times E_{prot}). \quad (6)$$

The energy density of lipid $E_{lipid} = 39.7$ MJ/kg and protein $E_{prot} = 23.8$ MJ/kg were obtained from Kleiber (1961). Lipid content of neonatal mammals is generally low. We used a percent lipid mass estimate of 5% ($F_{lipid} = 0.05$) based on fraction lipid mass found in ringed seal neonates (*Pusa hispida* (Schreber, 1775)) (mean = 4.7%; Lydersen et al. 1992). Our estimate of F_{lipid} is higher than that measured in fetal fin whale (*Balaenoptera physalus* (Linnaeus, 1758)) blubber (Lockyer et al. 1984) and higher than that measured for other mammalian neonates (1–5%) (Hatai 1917, Bailey et al. 1960, Wood and Groves 1965). Fraction newborn protein mass (F_{prot}) was based on the proportion of muscle ($F_{muscle} = 0.12$) from 26 harvested lean gray whales (Rice and Wolman 1971, Sumich 1986) and the fraction of protein in muscle ($F_{pm} = 0.22$; Arai and Sakai 1952) and other tissue ($F_{po} = 0.12$; Sumich 1986). Accordingly final $F_{prot} = 0.126$.

$$F_{prot} = (1.0 - F_{muscle} - F_{lipid}) \times F_{po} + (F_{muscle} \times F_{pm}). \quad (7)$$

The energy contained in the placenta and tissues associated with pregnancy (excluding the fetus) was estimated assuming the full-term fetus was 80.7% ± 2.5% of the total cost of reproductive tissue (Anderson and Fedak 1987, Kurta and Kunz 1987, Blaxter 1989).

Lactation costs (calf metabolic rate and calf growth costs).—Total lactation costs are the sum of calf *FMR* (see *Field metabolic rate*) and calf growth costs from 0–7 months old (until weaned). Based on capital-breeding northern elephant seals (Costa et al. 1986), we assumed production of milk had a negligible cost (in addition to the calf's metabolic rate and growth costs) and assimilation efficiency of milk by the calf was 100%. To determine growth costs, we also assumed calves begin with a very low percent lipid (5%) (Lydersen et al. 1992) and that calves reached the same mass fraction lipid and muscle as fat adults by the age of seven months when they are weaned (Appendix E). Evidence suggests calves reach those proportions as early as three months of age (Sumich 1986), but the age at which they reach those values does not change the total calf growth cost value. Energy needed for total calf growth 0–7 months old, was the difference between calf caloric value at birth (Eq. 6 main text) and at seven months old. The caloric value for seven months old was estimated using Eqs. 6 and 7 with age-estimated masses from Eq. 4 and a F_{lipid} and F_{muscle} determined for adult whales ($F_{lipid} = 0.34$, $F_{muscle} = 0.18$), so $F_{prot7mo.} = 0.0972$ (Sumich 1986; Appendix E).

Metabolic rate comparison

We compared our estimated adult female *FMR* for the entire two-year period with estimates made by other authors, specifically for gray whales (Rice and Wolman 1971, Sumich 1983, Thomson and Martin 1986, Highsmith and Coyle 1992) as well as the more general equation by Lockyer (1976; $FMR = 110 \times M^{0.783}$) for large baleen whales. Additionally, we assumed our minimum adult female metabolic rate (using the

lowest respiration rate during non-foraging periods) was equivalent to a resting metabolic rate (*RMR*) for the entire two-year period. We compared our *RMR* estimates with basal metabolic rate (*BMR*) equations from three different authors. Assuming *RMR* is 1.18 times *BMR* (Brody 1968, Lockyer 1981*c*): $RMR = 1.18{\cdot}70{\cdot}M^{0.75}$ (Kleiber 1961), $RMR = 1.18{\cdot}115.5{\cdot}M^{0.75}$ (Kleiber 1961) adjusted for cost of movement through the water as in Lockyer (1981*b*), and $RMR = 1.18{\cdot}70.5{\cdot}M^{0.7325}$ (Brody 1968). The Brody and Kleiber equations appear to be very similar. Indeed, within the range of animal masses measured for their studies (0.02 kg mouse to 600 kg cow), *BMR* estimates vary at most by 10%. However, when scaling up to large whales, the Brody estimate can be 16% lower than the Kleiber estimate. Therefore, we report both results. When calculating *BMR* and *FMR* as a function of mass, we used our estimates of adult female mass with uncertainty based on the distribution of length and the length-mass relationship (Eq. 4 and Table 1).

Model assumptions

The predicted consequences of lost foraging opportunity are based on a two-year reproductive cycle for an adult female gray whale. Based on available literature we made the following model assumptions. (1) Females can acquire all the energy necessary for most of pregnancy and all of lactation (7 months) during the foraging period in which they are pregnant (when females with calves arrive at the foraging grounds the following year, they still have enough stored energy to support their calf an additional 1.3 months). The lack of differences in girth/length values between southbound males and non-pregnant females indicates that fattening for pregnancy occurs only during the summer preceding parturition (Sumich 1986). (2) Calves must reach the foraging grounds to survive (at least 5.7 months of lactation), based on the lack of observations of single calves migrating northward (L. K. Schwarz, *unpublished manuscript*). (3) If females lack sufficient energy reserves to complete the southward migration (poor body condition), they will also lack the resources necessary to come into estrous and will not copulate that year. Furthermore, if they fail to copulate then they should be able to acquire the necessary resources to achieve good body condition, migrate southwards to the breeding ground and become pregnant the following year. (4) There is no feeding outside of foraging grounds. (5) Females can overwinter somewhere other than breeding lagoons. (6) Female gray whales will prioritize resource allocation to their own survival and maintenance (metabolic rate) over calf maintenance and growth (lactation), and lastly fetus maintenance and growth (pregnancy). (7) Females are capable of acquiring energy at the same rate during both foraging periods.

Disturbance predictions

Considering our model assumptions, we predicted consequences of lost foraging opportunity for three disturbance scenarios using the bioenergetics model. Each scenario was based on a two-year reproductive cycle (most energetically demanding) with different energy acquisition and allocation requirements (Phase 1: females are pregnant at foraging grounds; Phase 2: females are lactating, non-pregnant and her calf gets weaned at foraging grounds) (Fig. 1). The three disturbance scenarios we considered were: Prediction 1: Disturbance during Phase 1 when females are pregnant; Prediction 2: Disturbance during Phase 2, when females are lactating, with no previous disturbance during Phase 1 when they were pregnant; and Prediction 3: Disturbance during Phase 2 with additional disturbance during Phase 1.

Prediction 1: disturbance during Phase 1.—For estimating consequences of disturbance during Phase 1 when females are pregnant, we calculated a female's total energetic requirement for Phase 1 (RC_{P1}) as the sum of the energy utilized at foraging grounds (E_{Fg}), while southbound (E_{Sb}), at the breeding lagoon (E_{Bl}), while northbound (E_{Nb}), pregnancy costs (PC) and lactation costs (LC; 7 months).

We calculated female minimum maintenance costs for Phase 1 (MC_{P1}) using the lowest measured R_s of 0.31 breaths/minute (determined by calculating breaths/day from original value and back to breaths/min to reduce uncertainty; see *Field metabolic rate* and Appendix B), measured during the northbound migration, for periods outside the foraging grounds (Rodriguez de la Gala-Hernandez et al. 2008). There are no significant energetic costs associated with migra-

tion. Migration has no considerable additional cost to that of the whale's own maintenance since the mean migration speeds of southbound gray whales is nearly identical to the speed at which the cost of transport is minimum (Sumich 1983, 1986). The lowest measured R_s was used to estimate female's maintenance costs when she is not pregnant and spends the winter outside the foraging grounds and breeding lagoons. This was used to calculate the minimum amount of energy needed for a female to survive a year. Female MC_{P1} was calculated as $E_{Fg} + (E_{Nb} \times$ no. days outside foraging grounds in Phase 1). Then, considering a female is disturbed, so she has reduced energy reserves, we calculated the proportion of energy necessary for a female's own maintenance for Phase 1, below which a female would not survive, as MC_{P1}/RC_{P1}.

Lastly, we calculated the proportion of energy necessary to give birth to and wean a calf during Phase 1. We assumed that if a female is disturbed and do not acquire enough resources for a minimum lactation of 5.7 months (when female and calf reach the foraging grounds), the calf will not survive. For this purpose, we estimated female reproductive costs for a 5.7 months lactation ($RC_{5.7mo.}$) as $RC_{P1} - (LC \times propL_{Fg})$, where $propL_{Fg}$ is the proportion of lactation time at the foraging grounds (0.2). Proportion of energy for calf production during Phase 1 was then calculated as $RC_{5.7mo.}/RC_{P1}$.

Prediction 2: disturbance during Phase 2 with no disturbance in Phase 1.—We calculated the proportion of energy needed for female survival and reproduction (energy needed to migrate and become pregnant) during Phase 2, when females are lactating and become pregnant again. Female maintenance and migration costs for Phase 2 (MMC_{P2}) were calculated as $E_{Fg} + E_{Sb} + E_{Bl} + E_{Nb}$. Following prediction 1; we calculated the minimum female maintenance costs for Phase 2 (MC_{P2}) using northbound breathing rates. During Phase 2, the amount of time spent at the foraging grounds is shorter ($D_{Fg2} = 137$ days) than during Phase 1 ($D_{Fg1} = 248$). Then, considering females are disturbed, so they have reduced energy reserves, we calculated the proportion of energy for a female's own maintenance for Phase 2, below which a female would not survive, as MC_{P2} /[$(RC_{P1} \times D_{Fg2})/D_{Fg1}$]. We also calculated the proportion of energy necessary for calf production during Phase 2, below which a female would not be able to migrate and become pregnant, as MMC_{P2} /[$(RC_{P1} \times D_{Fg2})/D_{Fg1}$].

Prediction 3: disturbance during Phase 2 (Phase 2b) with disturbance in Phase 1.—We calculated the proportion of energy needed for female survival, reproduction (energy required for 7 months of lactation) and breeding (energy required to migrate and become pregnant) during Phase 2 when females are lactating and become pregnant. Considering females were disturbed during the previous phase, females do not have the energy necessary for the last portion of lactation at the foraging grounds during Phase 2b (20% of total lactation time) and need to acquire that energy during that phase. We estimated consequences of disturbance at the foraging grounds during Phase 2b by calculating female maintenance, migration and lactation costs for Phase 2b ($MMLC_{P2b}$) as $E_{Fg} + E_{Sb} + E_{Bl} + E_{Nb} + (LC \times propL_{Fg})$. We calculated the proportion of energy necessary for calf production during Phase 2b (below which a female would not reproduce or get pregnant) as MMC_{P2b} /[$(RC_{P1} \times D_{Fg2})/D_{Fg1}$], assuming females prioritize successful weaning of their current calf over breeding again (migrating and becoming pregnant). For estimating the proportion of energy necessary to wean a calf at seven months during Phase 2b (below which the calf is weaned at a lower mass), we calculated female maintenance and lactation costs in Phase 2b as (MLC_{P2b}) as $MC_{P2} + (LC \times propL_{Fg})$. The proportion of energy necessary to wean a calf at seven months during Phase 2b was then calculated as MLC_{P2b} /[$(RC_{P1} \times D_{Fg2})/D_{Fg1}$]. The proportion of energy necessary for female maintenance during Phase 2b (below which a female would not survive) is the same as in prediction 2.

Linking lost foraging opportunities to reproduction and survival

Based on results from the predictions calculations (above and see *Model disturbance predictions* in the following *Results* section) and from the proportion of foraging energy not consumed when females are disturbed, we estimated the probability of a female falling into three possible categories for prediction 1 and 2: (1) female survives and produces a calf/breeds, (2) female survives but loses the calf/does not breed and (3)

female dies. For prediction 3 we added a fourth category: (4) female does not breed and weans a calf at a lower mass. Using our Monte Carlo simulation results ($N = 150{,}000$), we determined the proportion of simulations falling into each category given the proportion of energy lost. We sampled the proportion of energy lost at a 0.001 increment and scored each simulation based on whether or not it had reached its energy proportion threshold for producing a calf and then its threshold for survival.

Results

Gray whale female energetic demands

Gray whale female energetic demands based on our model parameters (obtained from the literature) and assuming no disturbance are as follows. As calves age, their tidal volume (V_t) increased, along with the uncertainty (Table 1; Appendix C). Respiration rates (R_s) and thus metabolic rates were lowest for females with calves during the northbound migration, and highest for females on the foraging grounds. The metabolic rate of calves increased with age, except for a temporary decrease at three months (Table 2). Females expend the most energy on the feeding grounds while pregnant, not because pregnancy is more costly than lactation, but because females spend the most time of their two-year cycle in that stage (Table 2). Total female gray whale energy required for a two year period (successfully weaning a calf) is 118.2×10^4 MJ (95% range: 61.3×10^4–191.2×10^4). The overall daily metabolic rate for the entire two year cycle is 1.3×10^3 MJ/day (0.55×10^3–2.3×10^3). Total energy females require for the first phase of their two year reproductive cycle is 78.6×10^4 MJ (44.5×10^4–122.2×10^4) and the minimum amount of energy to survive is 48.4×10^4 MJ (20.2×10^4–84.9×10^4). Total energy females require for the second phase of their reproductive cycle is 39.5×10^4 MJ (16.5×10^4–69.3×10^4) and a minimum of 35.0×10^4 MJ (14.6×10^4–61.3×10^4) to survive. Total pregnancy cost is 8.7×10^4 MJ (3.7×10^4–16.2×10^4), lower than total lactation cost: 13.3×10^4 MJ (9.0×10^4–18.7×10^4; Table 3).

Model disturbance predictions consequences of lost foraging opportunities

Prediction 1: disturbance during Phase 1.—During the first phase of the reproductive cycle, when a female is pregnant, a 3.6% (1.9–6.1%) reduction in energy intake will result in a female having insufficient energy to nurse the calf to the foraging grounds, resulting in either abortion of the fetus or pre-mature weaning and subsequent calf loss. A female would not be able to survive the winter non-feeding period if there was a 40.0% (28.6–56.5%) reduction in energy intake during the first phase of the two-year reproductive cycle (assuming there are no extra energy stores to compensate for this decrease in energy intake; Fig. 2A).

Prediction 2: disturbance during Phase 2 with no disturbance in Phase 1.—Given a female who acquired enough energy for lactation during her pregnancy (Phase 1), if there is a 34.6% (22.5–52.8%) reduction in foraging energy during Phase 2, (non-pregnant period at foraging grounds), when a female is lactating and weans her calf, she will not successfully become pregnant the following breeding season (Fig. 2B). During Phase 2, a female will not survive the breeding period once energetic losses exceed 42.1% (31.4–58.2%) of the total energy she can acquire during the non-pregnant foraging period (Fig. 2A, B).

Prediction 3: disturbance during Phase 2 with disturbance in Phase 1.—A female that does not have enough stored energy to complete lactation but successfully brings her calf to the foraging grounds, must acquire additional energy while at the foraging grounds to provide for her calf until seven months old. Since a female will provision her existing calf before storing additional energy for future reproduction, breeding will not be successful in Phase 2b, once she loses 30.0% (19.6–45.3%) of the energy she can acquire while foraging during the non-pregnant foraging period. A female will wean her calf at a lower mass when energetic loss is between 37.3-42.1% (28.5–58.2%) during Phase 2b (Fig. 2C).

Discussion

Gray whale female energetic demands

Tidal volume (Vt) and O_2 extraction efficiency (%O_2).—V_t estimated in our model as a function of body mass (M) falls within other estimates for gray whales and other cetacean species (Table 1, Fig. 3). The %O_2 used in our model, 10.5% ± 3.0

Table 2. Mean parameters required to estimate total metabolic energy for a female during different phases of a two-year reproductive cycle and a calf (from birth to weaning age).

Age class/life stage	Respiration rate (R_s) (breaths/day)	Source	Metabolic rate (MJ/day)	Duration (T_s) (days)	Total metabolic energy (MJ $\times$ 10^3)
Adult females					
Southbound	964.9 (7.7)	1, 2	1167 (489, 2039)	48	56 (23.5, 97.9)
Lagoon, lactating	809.2 (9.2)	3	979 (410, 1709)	120	117.5 (49.2, 205.1)
Lagoon, breeding	809.2 (9.2)	3	979 (410, 1709)	36	35.2 (14.8, 61.5)
Northbound, with calf	445.6 (14.3)	4	539 (225, 944)	80	43.1 (18, 75.6)
Northbound, no calf	638.0 (9.1)	4	772 (323, 1349)	53	40.9 (17.1, 71.5)
Foraging grounds, not pregnant, lactating	1488.0 (50.5)	5	1800 (752, 3150)	148	266.4 (111.2, 466.2)
Foraging grounds, pregnant	1488.0 (50.5)	5	1800 (752, 3150)	197	354.6 (148.1, 620.6)
Calves					
Lagoon (0 months)	2897.5 (13.6)	6	88 (29, 196)	31	2.7 (0.9, 6.1)
Lagoon (1 month)	2127.3 (11.0)	6	131 (45, 280)	31	4.1 (1.4, 8.7)
Lagoon (2 months)	1924.0 (8.8)	6	187 (64, 406)	31	5.8 (2.0, 12.6)
Northbound (3 months)	668.1 (18.5)	4	127 (13, 447)	31	3.9 (0.4, 13.9)
Northbound (4 months)	668.1 (18.5)	4	168 (18, 578)	30	5.0 (0.5, 17.3)
Northbound (5 months)	668.1 (18.5)	4	203 (22, 673)	19	3.9 (0.4, 12.8)
Foraging grounds (5.75 months)	827.3 (36.1)	7	262 (29, 844)	12	3.1 (0.3, 10.1)
Foraging grounds (6.5 months)	827.3 (36.1)	7	275 (31, 876)	31	8.5 (1.0, 27.2)

Note: Values in parentheses are as in Table 1. Respiration rates were calculated by sampling from a lognormal distribution of published breaths/min, obtaining breath-hold time and adding breath-hold times and number of breaths until reaching 24 hours. Sources are (1) Sumich (1983); (2) Schwarz (2002); (3) Harvey and Mate (1984); (4) Rodriguez de la Gala-Hernandez et al. (2008); (5) Wursig et al. (1986); (6) Sumich (1986); (7) Sumich (2001).

for calves (data obtained from 1-5 month old calves) and 11% ± 2.7% for adult females (data obtained from 1-10 month old calves; Sumich 2001) is within the range of $\%O_2$ values reported for other cetacean species. Wahrenbrock et al. (1974) reported $\%O_2$ of 8.5–12.5% for a 2–3 month old gray whale in captivity. Sumich (1986) reported values between 4.5% and 12.5% for 10 gray whales at the breeding lagoons at 6–10 weeks of age, as well as a range of $\%O_2$ of 2.5–12% in two quiescent bottlenose dolphins (*Tursiops truncatus* (Montagu, 1821)). Sumich (2001) reported values between 4.8-18.2% for a 0–14 month old captive gray whale. Ridgeway et al. (1969) reported a range of 8–17.5% for smaller bottlenose dolphins at the water surface, and Spencer (1970) measured a range of 6–8% for killer whales (*Orcinus orca* (Linnaeus, 1758)).

Table 3. Mean costs of reproduction.

Reproductive stage	Reproductive cost (MJ $\times$ 10^3)
Pregnancy	
Fetal tissue	5.3 (2.6, 9.0)
Other tissue	1.3 (0.6, 2.3)
Heat increment of gestation	80.6 (33.8, 149.9)
Total	87.3 (36.9, 161.7)
Lactation	
Calf maintenance from birth to 5.75 months	25.4 (8.3, 58.4)
Calf maintenance from 5.75 months to weaning	11.7 (1.4, 36.2)
Calf growth from birth to 5.75 months	75.6 (50.7, 104.6)
Calf growth from 5.75 months to weaning	18.8 (12.6, 26.0)
Total	132.8 (90.1, 186.9)

Note: Numbers in parentheses are 95% posterior intervals. Calves reach foraging grounds at age 5.7 months (calf possibly survives if weaned at this age).

Calf metabolic rate.—The observed temporary decrease in calves' metabolic rate at three months old resulted from different functions used to calculate calf V_t at the different ages. V_t for 0–2 month old calves were estimated using results from a Bayesian analysis of V_t as a function of expiration duration (E_d) and body length (L; Eq. 2; Appendix C; Sumich 1986). E_d was directly measured in calves from birth to lagoon departure (Sumich 1986). E_d for older calves is lacking, therefore, V_t for calves 3–7 months old, was estimated using results from a Bayesian analysis of V_t as a function of mass from published data (Eq. 3 and Appendix C; Sumich 1986). Expiration duration is a direct measurement from which V_t can be more accurately determined. While we would have preferred to estimate calf V_t from a single model, V_t as a function of mass is currently the best method available to determine V_t for 3–7 months old because E_d for older calves is lacking. Additionally, uncertainty (SD) around metabolic

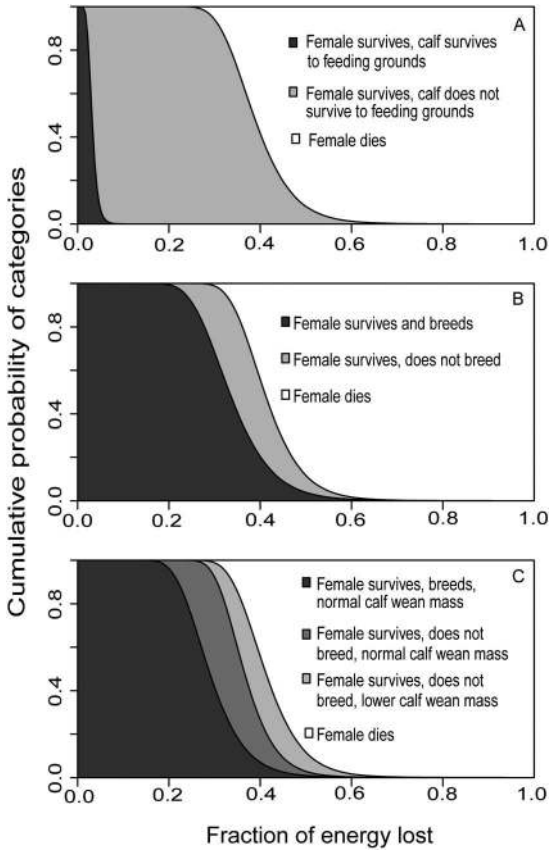

Fig. 2. Cumulative probabilities of females falling into different categories dependent on fraction of lost energy. (A) During the year she is pregnant, gives birth, and migrates to foraging grounds with her calf. (B) and (C) During the year she weans her calf and potentially becomes pregnant again. If the female needs additional energy for lactation in the second year, she will forgo breeding and allocate additional resources to her almost-weaned calf (C).

rate values was incorporated in our model and SD values around three and four month old calves are greater than those for two months old (Table 2). Furthermore, total calf metabolic costs constitute a small percentage (around 2%) of estimated total energy costs for an adult female; therefore, such differences would produce minimal changes in the final analysis.

Reproductive costs: pregnancy and lactation costs.—Lactation costs for gray whales have been previously estimated by Sumich (1986) as 3.2×10^4 MJ (7,714 Mcal), but only for the period at the breeding lagoon, assuming calves have reached the same proportion of lipid and muscle as an adult female by the time they leave the lagoons (3 months). We made no assumption about the age at which calves reached adult lipid and muscle proportions. We only considered that calves have reached these proportions some time before they are weaned (7 months). Sumich's estimate was based on the energy value of postnatal tissue growth in the mass added by the calf plus the calf metabolic rate at the lagoon. He estimated metabolic rate based on the kg of lipid/L of O_2 consumed based on respiration rates and lipid energy density. His results are lower compared to our lactation costs of 4.4×10^4 MJ (2.7×10^4–6.5×10^4) estimated for the time portion at the breeding lagoon based on calf growth cost and calf metabolic rate. In our model we used an improved equation to estimate mass (Eq. 4), therefore calf masses are greater than those estimated by Sumich (1986), resulting in greater lactation costs. Assuming a linear change in fraction of blubber and muscle with age, lactation costs estimates at the lagoons based on data from our model were higher than Sumich's (1986) previous estimates. However, Sumich's estimates fall within our 95% interval. In addition, we calculated lactation costs for the period at the breeding lagoon with data from our model following Sumich's method. These results were higher (6.9×10^4 MJ) than those produced following our model methods.

Our mean percent of energy a female gray whale will allocate to reproduction over a two-year period is similar to that estimated for several Balaenoptera species (Fig. 4; Lockyer 1981*c*, *b*). In all cases, lactation costs are higher than pregnancy costs (Fig. 4). Lockyer (1984) also states that 19–26% of total energy cost in a two year cycle goes to pregnancy and lactation in baleen whales. While uncertainty was high, we estimated the percent allocated to reproduction in a two-year cycle as 20.0% (10.5–36.2%) for gray whales (pregnancy costs + lactation costs/total energy costs for a two-year breeding cycle) (Fig. 4 and Table 3).

Milk production efficiency and milk assimilation efficiency were different in our analyses compared to Lockyer (1981*b*, *c*). While our lactation percentage was higher than other whale species, we still may be underestimating lactation costs since we assumed mammary gland effi-

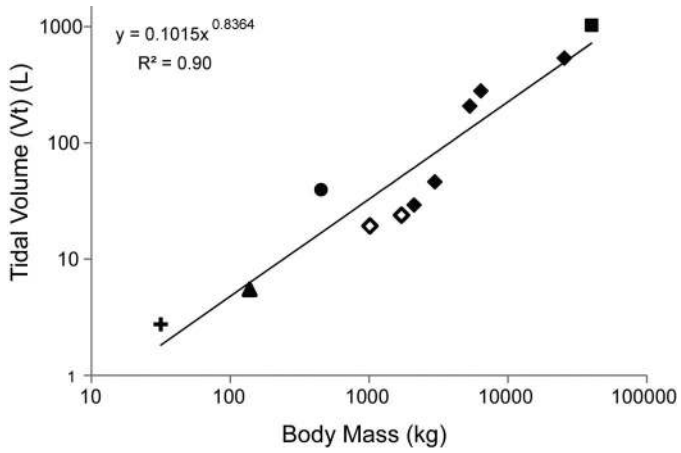

Fig. 3. Tidal volume (V_t) (L) of different cetacean species as a function of body mass (kg). Regression equation for line is indicated. Data obtained from the literature and this study as follows. *Phocoena* (cross): Kooyman and Sinnett (1979); *tursiops* (triangle): Ridgeway et al. (1969); pilot whale (circle): Olsen et al. (1969); gray whale calf (open diamonds, 1 and 2 month old): Sumich (1986); gray whales (closed diamonds, 1, 2, 5 and 7 month old calves and adult female): this study; and fin whale (square): Lafortuna et al. (2003).

ciency and milk assimilation efficiency were equal to that measured in fasting northern elephant seals (*Mirounga angustirostris* (Gill, 1866); Costa et al. 1986). Others have assumed milk assimilation efficiency between 0.8 and 0.95 for baleen whales and larger toothed whales such as pilot (*Globicephala macrorhynchus* (Gray, 1846)) and sperm whales (*Physeter macrocephalus* (Linnaeus, 1758); Lockyer 1981*a*, *b*, *c*, 1987, 1993). Brody (1968) estimated a mammary gland efficiency of 0.9 across species. Given that measurements of assimilation efficiency for other marine mammals feeding on fish range between 88% and 97.9% the assimilation of milk with its

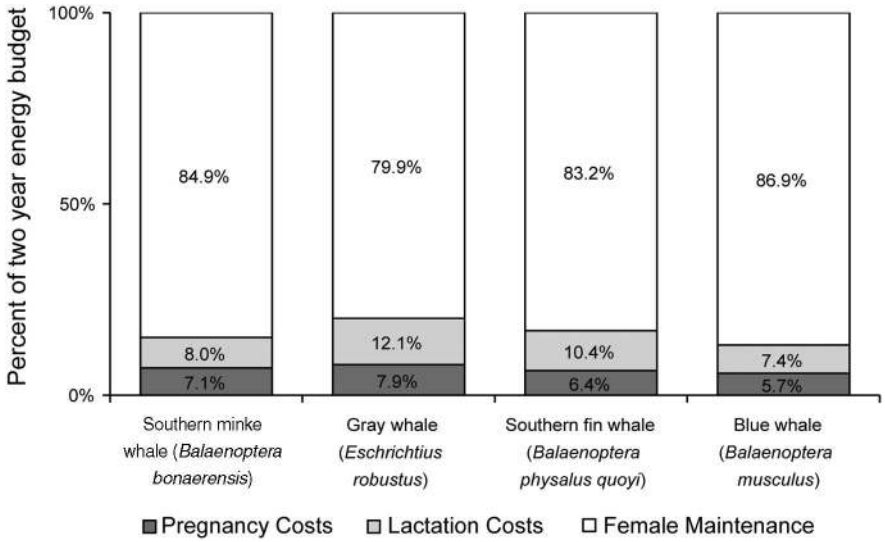

Fig. 4. Percentage of a two-year energy budget allocated to pregnancy, lactation, and female maintenance by species. Northern minke whale: Lockyer (1981*b*); gray whale: this study; Southern fin whale: Lockyer (1981*c*, 1987); blue whale: Lockyer (1981).

high lipid and low ash contents should certainly approach 100% assimilation (Costa 2009).

Uncertainty

We were not able to incorporate process uncertainty in several parameters because those relationships were calculated using data from smaller animals (adult V_t and heat increment of gestation (H_g)). Those functions were extrapolated from juvenile gray whales (V_t) or smaller terrestrial animals (H_g) and include an exponent term, so uncertainty expands considerably when extrapolated beyond the original data. That high level of uncertainty is demonstrated in the large intervals around V_t for older calves (Table 1), estimated from the Bayesian re-analysis of data in Eq. 4. In general, uncertainty in calf V_t does not create high uncertainty in overall costs compared to high uncertainty in V_t of adult females because maternal metabolism makes up the majority of costs (Fig. 4).

Metabolic rate comparison

Estimates of field metabolic rate (*FMR)* and resting metabolic rate (*RMR)* from other studies and using other methods fell within our quantified 95% posterior intervals. Our *FMR* was closest to Lockyer's (Lockyer 1976) estimate, and our *RMR* was closest to Kleiber's (Kleiber 1961) estimate adjusted for the cost of movement through water (Lockyer 1981*b*). Uncertainty is lower for all other estimates not because they are methods with less uncertainty. Rather, four studies reported no uncertainty, and the other five equation estimates only accounted for uncertainty in mass, not in the relationships (Table 4).

Our model estimated a lower *FMR* over a two-year period, comparable to Rice and Wolman (1971). They used a lower mass (20 metric tons (MT), compared to 26 MT used in our model), a larger lung volume (based on fin whales) and a single breathing rate of 1 breath/min. Sumich (1983) and Thomson and Martin (1986) estimated a lower *FMR* . Sumich (1983) used a lower mass (15 MT) and a single breathing rate of 0.72 breaths/min based on a migrating whale. Highsmith and Coyle (1992) reported a higher estimate, and used a significantly lower mass (19.6 MT) based on the population average mass, the relationship between gray whale body weight and oxygen consumption and population estimates (Table 4). However, their goal was to determine the maximum prey biomass gray whales could remove from their environment, so a high metabolic rate was appropriate in their study.

Model assumptions

We assumed that female gray whales do not feed outside the foraging grounds. Very little feeding is believed to occur outside the northern feeding grounds, as gray whale stomachs are generally empty along the migration route (Scammon 1874, Andrews 1914, Pike 1962, Rice and Wolman 1971), and in the southern lagoons (Scammon 1874). However, feeding has been suggested (Gilmore 1961, Pike 1962, Sund 1975) or documented (Howell and Huey 1930, Mizue 1951, Rice and Wolman 1971) outside the northern feeding grounds on several occasions. Gray whale feeding is not common in Baja California; however, many whales apparently feed along Vancouver Island during the northward migration, and some individuals spend the entire summer there (Darling 1977, Oliver et al. 1983). Sumich (1986) reported that over 50% of the whales along the central coast of Oregon during summer were thought to be feeding, and the majority of these whales were sub-adults, calves, and yearlings (body lengths determined photogrammetrically). Oregon summer whales are predominantly immature or atypically small mature animals (Sumich 1986). While these observations document gray whale feeding behavior outside foraging grounds, this opportunistic feeding is not likely to provide much nourishment (Oliver et al. 1983). Furthermore, our assumption is conservative, as any prey consumption outside of the foraging grounds would buffer the female, making her less sensitive to disturbance and any associated time lost on the foraging grounds.

We also assume that gray whales can overwinter somewhere other than the breeding lagoons if they do not acquire the energy necessary for migration. They have recently been documented feeding year-round off Kodiak Island, Alaska (Moore et al. 2007). Their calls were detected in the western Beaufort Sea throughout the winter of 2003–2004 (Moore et al. 2006). However, these may not be reproduc-

Table 4. Field metabolic rate (FMR) and resting metabolic rate (RMR) calculated in this and other studies.

Metabolic rate (MJ × 10^3/day)	Reference
FMR	
1.3 (0.6, 2.3)	This study
1.3 (0.9, 1.7)	Lockyer (1976)
1.6	Rice and Wolman (1971)
1.2	Sumich (1983)
1.3	Thomas and Martin (1986)
2.2	Highsmith and Coyle (1992)
RMR	
1.1 (0.5, 2.0)	This study
0.6 (0.5, 0.9)	Kleiber (1961)
1.0 (0.8, 1.5)	Kleiber (1961); adjusted for swimming
0.6 (0.5, 0.9)	Brody (1968)

Note: Numbers in parentheses are 95% posterior intervals.

tive females. It is possible that females generally migrate south because the energetic cost of overwintering at colder climates is higher than migrating to the warmer lagoons (Rice and Wolman 1971). However, the minimum maintenance costs estimated by our model for a female overwintering at the lagoons were higher than the minimum costs estimated for females overwintering at higher latitudes. Therefore, if our assumption about overwintering (which assumes lower metabolic costs and no energy intake during that period) is incorrect, adult females would need a higher proportion of the estimated energy for their own survival, and their survival would be more sensitive to lost foraging opportunities.

If we relax the assumption that females must procure all the necessary energy for lactation and most energy for pregnancy during the year in which they are pregnant, females may be able to amortize the cost of reproduction over multiple years. In such cases, reproductive rates would be less sensitive to lost energy. However, calf production (as indicated by northbound calf counts) is most correlated with environmental fluctuations occurring in the foraging grounds during the year of calf production (Perryman et al. 2002*a*, *b*). Such a result could indicate that the population is nearing carrying capacity, and reproduction is still dependent on immediate conditions. If females only acquire the energy needed for pregnancy and lactation during their pregnancy year, the species would not have survived prolonged periods of poor foraging. However, the gray whale is among the longest enduring baleen species, and has survived at least through one ice age (Jones et al. 1984), indicating extreme resilience to long term environmental fluctuations. Therefore, while the two-year cycle represents a worst-case scenario, an amortization scenario where the female produces a calf every three or more years may be more realistic.

Model disturbance predictions and population level effects

While our model predicted that a 4% loss in foraging energy intake would reduce a female's ability to successfully bring a calf to the foraging grounds (lower reproductive rate), population growth is not strongly affected by this short-term reproductive loss. Demographic rates are not available for the eastern gray whale stock; however, survival rates for the western stock indicate that non-calf females (1.5 years and older) are very long-lived with a median annual survival rate of 0.985 (90% Bayesian confidence interval 0.977–0.991; Cooke 2010).

If the eastern gray whale stock survival is similar, this would indicate that the survival rate is relatively insensitive to environmental variability, and population growth is more sensitive to females' mortality than to annual reproductive rates. Furthermore, estimating the Leslie matrix dominant eigenvalue as in Cooke (2010), with all other rates kept stable, the population growth rate would not fall below one until the annual reproductive rate declined to 0.1 (females reproducing every 10 years). In addition, a 50% probability of population decline does not occur until the reproductive rate is 0.06 (females reproduce every 16.6 years). In contrast, a decline in non-calf survival rate from 0.985 to just 0.938 (with all other rates kept stable) would also produce a 50% probability of negative population growth. Demographic rates often do not decline independently of one another. Given our results, the large energetic buffer between losing a calf and female death implies that increased adult female mortality as a result of lost energy would also indicate reduced calf production. Therefore, if there is lower adult female survival, other demographic rates will most likely also be in decline.

Gray whales may be the oldest extant baleen

whale species (Barnes and McLeod 1984) and are one of the most adaptable and versatile of the mysticetes (Moore and Huntington 2008). Gray whales have adapted to multiple habitat changes over thousands of years. The eastern North Pacific gray whale population has shown behavioral responses to shorter-term environmental variability. They shifted their southbound migration timing one week later, coincident with the late 1970s warm regime shift in the North Pacific Ocean (Rugh et al. 2001) and may have also shifted their foraging range in the Chirikov Basin coincident with a decline in benthic infauna (Moore et al. 2003, 2006, Moore and Huntington 2008). However, our population level effects estimates showed that population growth is more sensitive to female adult survival than reproductive rates. Therefore, the mean range of 40–42% (29–58%) energy loss predicted by our model, that could increase female mortality, should be taken carefully into consideration for possible disturbance scenarios.

While our model focuses on the potential effects of lost foraging opportunities, it is also applicable for assessing disturbance costs or other effects associated with climate change and/or anthropogenic activities. These could either increase the cost of any of the female's life stages previously described or expose larger feeding areas for a longer period of time, reducing those costs. For example, a disturbance along the migratory corridor due to increased human activities; or increased migration distance due to foraging habitat movement in response to changing environmental conditions; might increase migration costs. Such an increase, without compensation of the energy consumed at the foraging grounds, would be considered "lost energy." Alternatively, exposure of larger feeding areas due to ice melting as a consequence of warmer climate; might decrease migration costs. However, it is not clear how reduced ice for prolonged periods will affect the ecosystem and the biomass that gray whales might consume. Additionally, energy loss from our model can be translated to days of disturbance via various foraging reductions scenarios. For example, assuming one day of disturbance equals one day of lost foraging and females forage the entire time at the foraging grounds, 10 days of disturbance equals a loss of 5% of the energy required to successfully complete Phase 1 (pregnancy). In this case, 10 days of lost foraging would result in an unsuccessful pregnancy.

We have estimated female gray whale energy requirements for a two-year reproductive cycle and determined the consequences of lost energy under three possible disturbance scenarios. We determined the percentage of energy lost that would result in a female losing its calf (pregnancy; 4%), not being able to reproduce (30–35%), weaning its calf at a lower mass (37%) and ultimately female's survival (40–42%). Demographic rates for the western stock demonstrate that population growth is more sensitive to female adult survival than reproductive rates. Disturbance during the year of pregnancy has potentially the most impact on the reproductive cycle of gray whales. Finally, our model can be applied for assessing disturbance costs or other effects associated with climate change and/or anthropogenic activities and can be applied to other species with similar life histories.

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Supplemental Material

Ecological Archives

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