ENERGY REQUIREMENTS OF GREY WHALES

by

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Abstract

Eastern North Pacific grey whales (*Eschrichtius robustus*) rely on energy reserves obtained on their northern feeding grounds to complete their annual 17,000 km round-trip migration between the Arctic and Mexico. However, estimates of how much food is required to complete the annual migration is limited to adult whales of average size, and is not readily available across all age classes of males and females. I constructed an age-structured bioenergetics model using detailed information on the grey whale life cycle and migration timings to predict the energy requirements of different cohorts of grey whales. Results show that nursing calves require 24–35 L of milk daily in their first 9 to 10 months. Once weaned, juveniles require ~345 kg day^{-1} of benthic invertebrates (4.5% of body weight), while the largest adult whales will need a minimum of ~870 kg day^{-1} (4.3% of body weight) during the ~5 month (154 days) summer foraging season in the Arctic. In contrast, pregnant individuals need 1,630–1,969 kg of prey day^{-1} (9.3–10.3% of body weight) during this same period to support foetal growth and store sufficient energy to produce milk once the calves are born in Mexico. Lactating whales returning to the Arctic with their calves will require 1,360–1,960 kg of prey day^{-1} (8.2–8.9% of body weight) over the next 4.5 months to continue producing milk. My results can be combined with measured densities of benthic prey in the Arctic to assess and anticipate the likelihood of climate change or conspecific competition causing starvation-related mortality of grey whales in the future. My age-structured bioenergetics model is simple and flexible enough to adapt to any migratory species of interest, including rare, endangered species that may otherwise be considered data deficient.

Lay Summary

Grey whales have the longest migration among marine mammals, covering a distance of 17,000 km, travelling back and forth between the Arctic and Mexico each year. They feed in the Arctic during the summer, storing enough energy for the rest of the year to travel south and overwinter in Mexico. However, there are few estimates for how much individual whales (male/female, young/old) need to eat to complete their annual migrations. I combined detailed information on the grey whale life cycle and migration timings with data on body growth and energy use to estimate how much prey male and female grey whales of various ages need to consume during the 4 to 5 months that they feed each year. This information can be used to assess whether decreases in available prey in the feeding grounds might affect the survival of grey whales during their migration. My model is simple and flexible enough to adapt to predict the energy requirements of other migratory species, including rare and endangered species for which limited information is available.

Preface

The research presented here is my original work. Under the guidance of Dr. Andrew Trites, I conducted the literature search, compiled data from the literature, parametrized the models, performed the analyses, and summarized my results in this thesis. Chapter 1 summarizes the current state of the literature to set the context for my work. In Chapter 2, I describe the bioenergetics model for grey whales, which was based on various models developed for other marine mammals. This data chapter is formatted as a manuscript for submission to a peer-reviewed journal, and contains some repetition of information. In Chapter 3, I summarize the results of the model, discuss its strengths and weaknesses, and identify opportunities for future research.

As part of a directed studies course for my Master's Program requirements, I developed a model on the growth and development of grey whales. The final report describing that work was published in the Journal of Mammalogy in collaboration with Dr. Andrew Trites and Dr. Sarah Fortune (Agbayani et al. 2020), and is cited as a foundational dataset in the bioenergetics modelling work described here.

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List of Abbreviations

$\%O_2$	Percentage of oxygen absorbed with every breath
A	Activity index or activity cost
BMR	Basal Metabolic Rate
CG	Calving grounds
CG_L	Lactating whales in calving grounds
CG_P	Pregnant whales in calving grounds
CI	Confidence Interval
C_L	Cost of lactation
COSEWIC	The Committee on the Status of Endangered Wildlife in Canada
C_P	Cost of pregnancy
ED_{milk}	Energetic Density of grey whale milk
ED_{lip}	Energetic Density of lipids
ED_{prey}	Energetic Density of benthic invertebrate prey
ED_{pro}	Energetic Density of proteins
E_{F+U}	Digestive efficiency (urinary and fecal)
E_{HIF}	Energy expended as heat increment of feeding
ENP	Eastern North Pacific
E_s	Total energetic expenditure
FG	Foraging grounds
FG_N	Nursing whales in foraging grounds
FG_P	Pregnant whales in foraging grounds
FMR	Field Metabolic Rates
GER	Gross Energy Requirements
GER_{lact}	Gross Energy Requirements of lactating grey whales
GER_{preg}	Gross Energy Requirements of pregnant grey whales
H_g	Heat increment of gestation
L	Litres
M	Mass
MJ	Megajoules
M_{nb}	Mass of newborn

mos.	Months
mt	Metric tons
NB	Northbound
NB_L	Northbound lactating grey whales
NB_P	Northbound pregnant grey whales
No.	Number
NOAA	National Oceanic and Atmospheric Administration
P	Production Cost
P_{calf}	Production Cost of calves
PCFG	Pacific Coastal Feeding Group
P_{lip}	Fraction (or proportion) of lipid mass
P_{nb}	Production Cost of newborn
P_{pro}	Fraction (or proportion) of protein mass
R_s	Respiration rates
SB	Southbound
SB_{LP}	Southbound late pregnant whales
SB_{PW}	Southbound post-weaning whales
SB_{RP}	Southbound recently pregnant whales
SD	Standard Deviation
T_s	Number of days per activity stage
UME	Unusual Mortality Events
V_t	Tidal Volume
wk	Week

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For Mama and Papa

Chapter 1: General Introduction

1.1 Grey whales (*Eschrichtius robustus*)

The grey whale (*Eschrichtius robustus*) of the family Eschrichtiidae is considered the most primitive of the modern-day baleen whales as they have remained structurally similar to cetotheres, a common ancestor of all baleen whales (Rice and Wolman 1971). Historically hunted across its range (Figure 1), only two populations remain: (i) the western North Pacific (Korean-Okhotsk) population, and (ii) the eastern North Pacific (California-Chukchi) population (Swartz et al. 2006).

Grey whales have been extinct from the North Atlantic since the 1700s (Carretta et al. 2016), although there were isolated sightings in Namibia in 2013 (Elwen and Gridley 2012) and the Mediterranean Sea in 2010 (Scheinin et al. 2011). The western North Pacific population has not recovered from commercial whaling, and is listed as 'Critically Endangered' by the International Union for Conservation of Nature (IUCN) (Bradford et al. 2008). Only the eastern North Pacific population has recovered since being listed as “Endangered” in the United States in 1973. In Canada, grey whales were listed as “Not At Risk” in 1987, but were later re-listed as “Special Concern” (COSEWIC 2004).

1.2 The longest mammalian migration

Grey whales have the longest migration of any mammal. The eastern North Pacific population spends winters in the warm breeding lagoons in Baja California, Mexico (Rice and Wolman 1971; Urban et al. 2003). Grey whales will travel north along the coast of North America to their

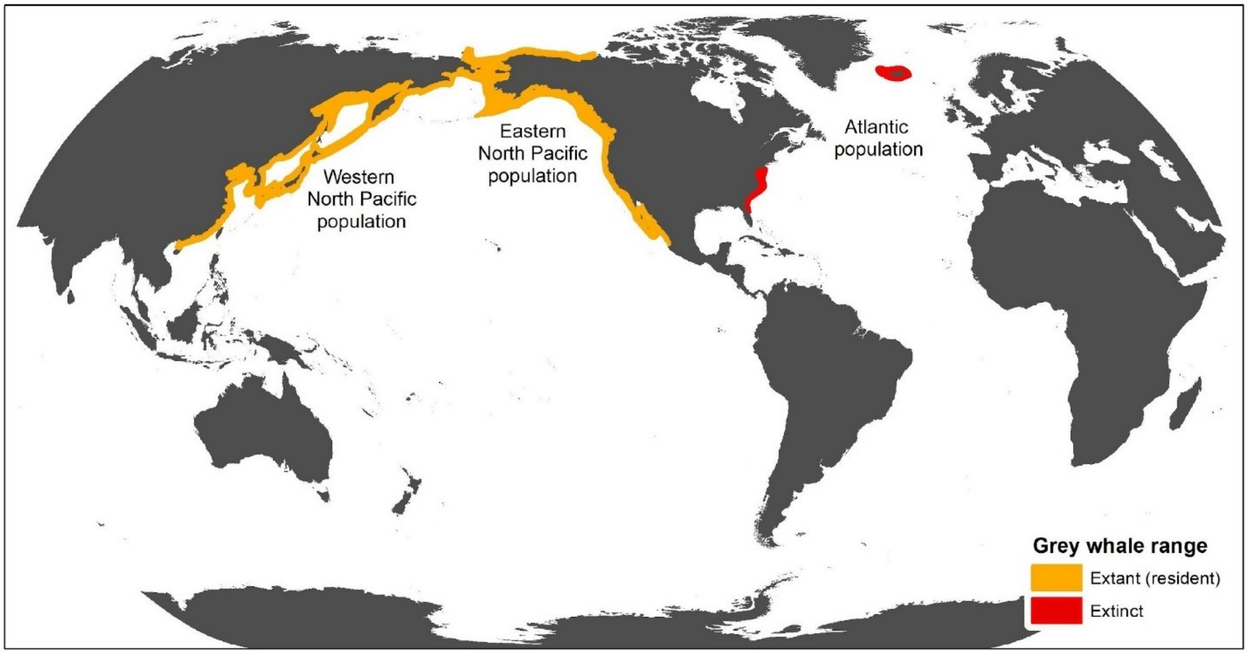

Figure 1. Global grey whale range as published on the IUCN Red List (Cooke 2018a).

summer feeding grounds in the Chukchi and Bering Seas beginning in March (Rice and Wolman 1971; Le Boeuf et al. 2000), and will arrive in these cold, productive northern waters in May, coinciding with the beginning of the Arctic spring melt. Grey whales have evolved to feed only during the summer in northern waters when their prey are accessible and sea ice has melted. They will begin returning south again for the winter between late September and mid-October (Le Boeuf et al. 2000; Rugh et al. 2001).

The western North Pacific population spends the summer feeding in the Okhotsk Sea (Pike 1962), but their winter breeding grounds are largely unknown (Lang 2010). The eastern and western populations are genetically distinct, and their distributions do not generally overlap (LeDuc et al. 2002). However, the level of genetic differentiation between populations is low, and recent observations of grey whales feeding in the western North Pacific travelling to the

Mexican breeding grounds for the winter show what appears to be some male-biased dispersal between the two populations (Lang 2010; Mate et al. 2015; Cooke 2018).

Grey whales remain close to the coast as they travel between their northern feeding grounds and the southern breeding lagoons (Pike 1962; Rice and Wolman 1971). The journey leaves them exposed to various anthropogenic threats, such as ship strikes and entanglement in fishing gear. Increased interest in developing oil and gas leases along with associated requirements for conducting environmental assessments (Bluhm et al. 2007), and the ease with which grey whales can be accessed, has resulted in them being one of the most studied of the great whales. Much is therefore known about their population size and general migration routes, as well as their foraging ecology and preferred prey species (Rice and Wolman 1971; Highsmith et al. 2007; Feyrer and Duffus 2015). However, recent unusual mortality events (UME) have given rise to questions around what may be affecting the grey whales' ability to survive the annual migration.

1.3 Unusual mortality events evoke new questions

The eastern North Pacific grey whale population is considered one of the best examples of successful recovery from the pressures of commercial whaling (Jones and Swartz 2002). The population increased significantly following protections from commercial whaling, but has more recently experienced brief periods of unusually high numbers of whales stranding along the migration route—first in 1999 and 2000 (Le Boeuf et al. 2000; Gulland et al. 2005), and again 20 years later, in 2019 and 2020 (NOAA Fisheries 2020a; Christiansen et al. 2021). The numbers of whales stranding during these periods were significantly higher than previous years, and several of the dead whales were emaciated and carried medium to high loads of whale lice (NOAA Fisheries 2020b).

The reasons behind the unusually high mortality rates during these periods are likely the result of a combination of factors. Climate change and ecosystem shifts in the northern Bering Sea (Grebmeier et al. 2006) may have negatively affected prey availability in the Arctic foraging grounds, thereby decreasing the carrying capacity of the system and the amount of food available to grey whales during summer (Le Boeuf et al. 2000). In addition, the recovering eastern North Pacific population may have reached or overshot the carrying capacity of their northern feeding grounds (Moore et al. 2001; Alter et al. 2007).

1.4 Grey whale foraging ecology: what and how they eat

Grey whales are unique in that they are the only baleen whale that are primarily bottom feeders (Thomson and Martin 1986; Filatova et al. 2022). They forage for infaunal and epifaunal invertebrates by swimming on one side (most often on their right) along the soft shallow bottoms up to 50 m in depth, suctioning up soft mud and sand (Bogoslovskaya et al. 1982; Nerini 1984; Highsmith and Coyle 1992). Substrate and water is then expelled from the other side of the mouth, while prey is filtered out by the baleen (Nerini 1984; Highsmith and Coyle 1992). This method of feeding has been coined “suction sieving” (Weitkamp et al. 1992). The sedentary nature of their benthic prey contributes to their high site fidelity for foraging areas (Filatova et al. 2022), but grey whales have also been observed to seemingly shift or expand their foraging areas when population pressures have affected prey availability (Moore et al. 2003).

The majority of the population undertakes the full migration from the lagoons in Baja California, Mexico, to the Arctic feeding grounds in the Bering and Chukchi Seas (Moore et al.

2003; Brower et al. 2017). This migration is critical because the majority of grey whale prey are primarily found in Arctic waters that are otherwise bound by sea ice in winter months. Grey whales have evolved the ability to feed only during the summer and fast during the rest of the year. In the Arctic feeding grounds, the primary prey are benthic amphipods (Highsmith and Coyle 1990; Moore et al. 2003; Heide-Jørgensen et al. 2012). However, there is a small portion of the population (~230 whales) that remains along the coast of Washington, Oregon, British Columbia, and Alaska for the duration of the summer (Feyrer and Duffus 2011; Carretta et al. 2016; Lagerquist et al. 2019). These whales are considered generalist feeders, and have been observed to shift between feeding on benthic, epi-benthic, and pelagic prey (Scordino et al. 2011). Their diets consist of ampeliscid amphipods (Darling et al. 1998; Dunham and Duffus 2002; Burnham and Duffus 2016), epibenthic or pelagic prey such as swarms of mysid shrimp (Family Mysidae), cumaceans, ghost shrimp (*Callianassa californiensis*), and various species of crab larvae (Weitkamp et al. 1992; Dunham and Duffus 2002; Feyrer and Duffus 2011; Burnham and Duffus 2018; Hildebrand et al. 2021). This group, named the Pacific Coastal Feeding Group (PCFG), has been recognized as a distinct feeding aggregation that warrants consideration as a separate management unit (COSEWIC 2004; Scordino et al. 2011; Carretta et al. 2016). Although the PCFG has been identified as a management unit of concern, my thesis focuses on the vast majority of grey whales that undertake the full migration as permitted by data availability.

1.5 Modeling energy requirements

Estimates of energy requirements are useful for assessing the minimum prey biomass needed to sustain healthy populations, and for informing management decisions that may help the recovery of threatened and endangered species (Winship et al. 2002; Fortune et al. 2013; Rechsteiner et al. 2013a). Estimates of energetic requirements are also useful for evaluating the effects of disturbance on foraging and reproductive success (Christiansen et al. 2014; Villegas-Amtmann et al. 2015, 2017).

Several energetics models have been developed for cetaceans and other marine mammals—some of which are based on an energy balance equation that takes into account growth, body composition, digestive efficiency, metabolism, and activity costs—e.g., North Atlantic Right whales (*Eubalaena glacialis*; Fortune et al. 2013), Pacific white-sided dolphins (*Lagenorhynchus obliquidens*; Rechsteiner et al. 2013a), and Steller sea lions (*Eumetopias jubatus*; Winship et al. 2002). In these models, activity costs are often included in the model as an activity budget, and used as a scalar for basal metabolic rate modeled using Kleiber's (1975) mouse-to-elephant curve (Winship et al. 2002; Fortune et al. 2013) or from resting metabolic rates of captive animals (Rechsteiner et al. 2013a). These methods of parameterizing activity costs are generally used in situations where limited information is available on activity budgets and associated heart rates or metabolic measures.

When observations of respiration rates are available, other methods can be used to estimate activity costs. Some studies have used estimates of energy expenditure by modeling field metabolic rates using field observations of respiration rates—e.g., minke whales (*Balaenoptera acutorostrata*; Christiansen et al. 2014), and grey whales (*Eschrichtius robustus*; Sumich 1983, 2021; Villegas-Amtmann et al. 2015, 2017). In these cases, estimates for energy expenditure are considered approximations of total energy requirements and do not consider digestive efficiency and energetic waste.

A third approach to estimate energy expenditure combines these two strategies by incorporating activity costs into the energy balance model as energetic expenditure estimates using respiration rates—e.g., bottlenose dolphins (*Tursiops truncatus*; Bejarano et al. 2017). The benefit of using the third approach is the ability to incorporate energy expenditure estimates from field observations into the complete energy balance equation that considers digestive efficiency and energetic waste.

Grey whales have been studied extensively. However, most estimates of energy requirements of grey whales have been based on estimates of metabolic rates from respiration data and reported as average annual requirements based on general estimates of population size (Highsmith & Coyle 1992). Each of the available estimates of metabolism have been based on whales of different sizes, between 14 and 23 metric tons (Rice & Wolman 1971, Sumich 1983, Thomson & Martin 1986, Highsmith & Coyle 1992). Others have modeled the energy requirements of female grey whales and calves during the reproductive cycle which spans approximately two years (Villegas-Amtmann et al. (2015, 2017). However, comprehensive estimates for energetic requirements across all ages, sex, and reproductive stages are unavailable.

1.6 Research Goals

The underlying cause of the unusually high mortalities of grey whales due to prey shortages cannot be effectively assessed without knowing how much energy grey whales need to consume to complete their annual migrations. My goal was to use an energy-balance-based bioenergetics model to estimate how much energy (in MJ day^{-1})—and therefore how much food (in kg of prey)—grey whales of various ages and sizes need per day to complete their annual migration. The model I constructed incorporates field observations of respiration rates to capture total energetic expenditure. The model was run as Monte Carlo simulations to capture variation and uncertainty across different ages, sizes, and different life stages, including pregnancy and lactation. My modelling results can be combined with estimates of prey availability within the Arctic feeding grounds to assess the effects of climate variability on foraging success. The model can also be used to understand the energetic requirements of the different groups of grey whales, such as the PCFG and the endangered western population.

Chapter 2: Annual energy requirements for grey whales

2.1 Introduction

Eastern North Pacific grey whales (*Eschrichtius robustus*) forage heavily during the summer to accumulate energy reserves for the 17,000 km round trip migration between the Arctic and Mexico (Lemos et al. 2020). Grey whale body condition improves as the 4–5 month feeding season progresses, but can differ considerably between years by the time the season has ended (Lemos et al. 2020). This inter-annual variability in body condition may be a carry-over effect from past years of poor foraging (Lockyer and Waters 1986; Harrison et al. 2011; Lemos et al. 2020). One unproductive season may have little consequence for a whale with energy reserves from past years, but multiple years of consistently low prey availability or foraging success may negatively affect individual fitness and the ability to survive the annual migration (New et al. 2013).

Energy and food requirements of grey whales have been estimated using respiration and census data (Highsmith & Coyle 1992) for whales ranging from 14–23 mt (Rice & Wolman 1971, Sumich 1983, Thomson & Martin 1986, Highsmith & Coyle 1992). However, minimum energy requirements needed to complete the annual grey whale migration have been limited to adult whales within this size range, and are not readily available across all age classes of males and females. Estimates of energy requirements have also been made for pregnant females and calves (Villegas-Amtmann et al. 2015, 2017), but are not age specific.

I constructed an energy balance bioenergetics model to predict the age-specific minimum annual energy requirements for calves, juveniles, and adult grey whales, as well as for pregnant

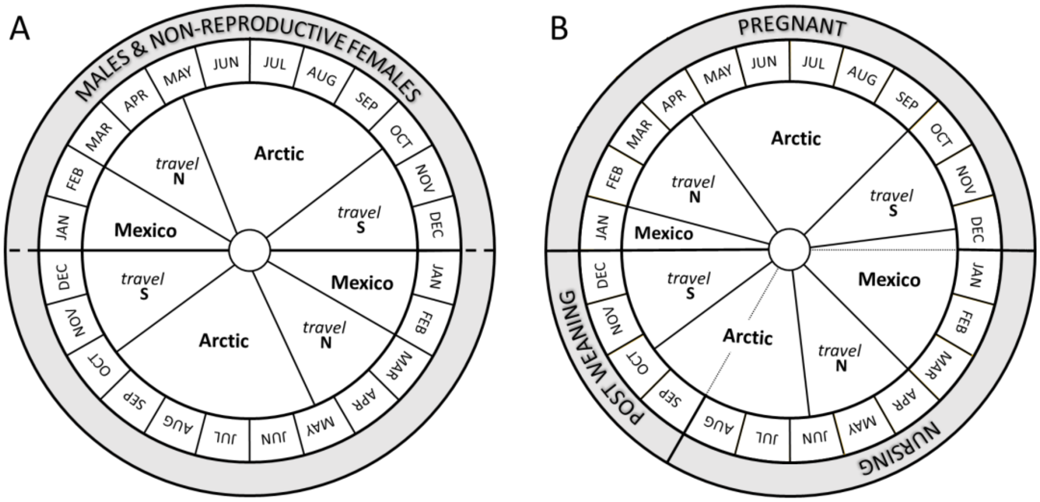

Figure 2. Grey whale life cycle, showing the approximate times of year for different stages in the migration over two years. Panel A shows the migration for males and non-reproductive females, including weaned juveniles. Panel B shows the approximate 2-year cycle for pregnant and lactating females, including nursing calves. These charts show the differences in migration timing between the mother/calf pairs and other whales. Estimates and associated sources for number of days in each activity stage are listed in Table 2, and additional details are listed in Appendix C. Adapted from Villegas-Amtmann et al. (2015).

and lactating females. The model reflects the life cycle of the grey whales, and the specific activities each age cohort undergoes throughout the year. Pregnant females arrive in the Arctic feeding grounds earlier in the season compared to other whales, while nursing mothers remain in the breeding lagoons in Mexico longer than other whales (Figure 2). My results can be used in conjunction with observed prey densities and general population estimates to assess mortality rates in given a year, particularly for years when mortality rates are unusually high. This energy balance method of modeling energy requirements is simple and flexible enough to adapt to any migratory species of interest, including rare, endangered species that may otherwise be considered data-deficient.

2.2 Methods

I used an energy balance equation (e.g., Winship et al. 2002; Fortune et al. 2013; Rechsteiner et al. 2013a) to calculate the gross amount of energy that different cohorts of grey whales must consume during summer to complete their annual migrations. Cohorts were grouped under different growth phases within the model based on growth rates. Phase 1 included nursing calves (≤9 months), and Phase 2 included weaned juveniles (<8 years), single adults (male and female; ≥ 8 years), and reproductive females (pregnant and lactating, ≥8 years).

My model parameters include the energy required for production and growth, total energetic expenditure from activity, and energy lost via fecal and urinary waste. I determined the biomass of prey that would need to be consumed to meet the estimated energy requirements by dividing the gross energy requirements (GER) by the mean energetic densities of grey whale prey available in the Arctic feeding grounds of the Bering and Chukchi Seas. For nursing calves, I calculated milk requirements by dividing calf energy requirements with the energetic density of grey whale milk.

I incorporated uncertainty into all model estimates wherever possible by generating 10,000 Monte Carlo bootstrap estimates of model parameters from the distributions of possible values at every step of the analysis (details presented in Table 1). I assessed the sensitivity of the model to the inputs by running scenarios where single variables were varied and compared the resulting range of uncertainty from each scenario to the scenario where all variables were varied across 10,000 Monte Carlo simulations.

2.2.1 Modeling Gross Energy Requirements (GER)

I used a simple energy balance equation to model gross energy requirements similar to that used by Winship et al. (2002) and Fortune et al. (2013). The model accounts for production (or growth), maintenance (energy required at rest and during activity or movement), and digestion (fecal and urinary energy loss). The values used for each model parameter are shown in Table 1. Gross energetic requirements were calculated as:

$$GER = \left(\frac{P + E_s}{E_{F+U}}\right) \qquad [1]$$

where GER is gross energetic requirement by sex, age and reproductive class, P is production costs (i.e. body growth), E_{F+U} is digestive efficiency (fecal and urinary), and E_s is the total energetic expenditure at different activity states estimated from field measurements of respiration rates and is assumed to include the metabolic costs of activity, basal metabolism, the heat increment of feeding, and growth inefficiencies such that $E_s = \frac{A \times BMR}{1-E_{HIF}}$ where A is the metabolic cost of activity, BMR is the basal metabolic rate, and E_{HIF} is the heat increment of feeding.

For pregnant and lactating females, I modified the base GER equation (Eq. 1) to include the total cost of gestation (C_{preg}) and lactation (C_{lact}):

$$GER_{Preg} = \left(\frac{P + E_s + C_{preg}}{E_{F+U}}\right) \qquad [2]$$

$$GER_{Lact} = \left(\frac{P + E_s + C_{lact}}{E_{F+U}}\right) \qquad [3]$$

Table 1. Parameters and sources used to estimate Gross Energy Requirements (GER). The age and reproductive cohorts considered include newborns (0 years), nursing calves (<0.8 years), juveniles (weaned and <8 years), single adults (> 8 years), and pregnant and lactating females (≥ 8 years). Uncertainty values reported in SD, or estimates are provided as ranges of values.

Parameter	Life stage	Value	Details (and sources)
Production costs (P) – Eq. 4			
ED_{lip}	All ages	39.7 MJ kg^{-1}	Energetic density of lipids (Lockyer 1984; Sumich 1986)
ED_{pro}	All ages	23.7 MJ kg^{-1}	Energetic density of proteins (Lockyer 1984; Sumich 1986)
p_{lip}	All ages	0.33–0.39	Fraction of lipid mass in grey whale adults were sampled from a uniform distribution, where the minimum value (0.34) was from Villegas-Amtmann (2017) and the maximum value (0.39) was from Sumich (1986)
p_{pro}	Newborns	0.126	Fraction of protein mass for grey whale neonates (Villegas-Amtmann et al. 2015, 2017)
	Calves (up to 7 months)	0.0972	Fraction of protein mass for grey whales at 7 months (Villegas-Amtmann et al. 2015, 2017)
	Calves older than 7 months up to adults	0.18	Fraction of muscle mass for grey whales (Sumich 1986; Villegas-Amtmann et al. 2015, 2017)
ΔM	All ages	See Table 6, Table 7, and Appendix B	Change in mass per time step ± SD calculated from growth models by Agbayani et al. (2020)
Total energetic expenditure at different activity states (E_s) – Eq. 5			
$\%O_2$	Calves	10.5 ± 3.0%	Percent of oxygen extracted with every breath, based on direct measurement (n = 66 expirations) of grey whale calves 1-5 months old (Sumich et al. 2001; Villegas-Amtmann et al. 2015, 2017)
	Juveniles/single adults	11 ± 2.7%	Percent of oxygen extracted with every breath, based on observations (n = 136 expirations) of an older grey whale calf from 1-10 months old (Sumich et al. 2001; Villegas-Amtmann et al. 2015, 2017). Measured values for grey whales > 10 months were not available.
T_s	Calves, juveniles/single adults, pregnant females, and lactating females	See Table 2	No. of days per activity stage, estimated based on grey whale migration distances, travel speed, sighting information reported in various field studies, cited in Table 2.

Parameter	Life stage	Value	Details (and sources)
R_s	Calves, juveniles/single adults Pregnant and lactating females	See Table 2	Grey whale respiration rates (breaths per minute) for each activity state, by life stage as reported in various field studies, cited in Table 2.
V_t	Calves Weaned juveniles and adults	See Table 6 See Table 7	Tidal volume (*L*) calculated for each age, estimated monthly for grey whale calves, and yearly for weaned juveniles and adult grey whales (Sumich 1986).
Digestive Efficiency – Eqs. 1, 2, and 3			
E_{F+U}	All ages	0.740–0.858	Conservative range based on fecal and urinary efficiency of right whales (Swaim et al. 2009; Fortune et al. 2013); values encompass the 0.8 fecal and urinary efficiency estimated for grey whales (Thomson and Martin 1986). Values were sampled from a uniform distribution.
Reproduction costs – Eqs. 2, 3, and 6			
M_{nb}	Newborns	983 ± 26.7 kg	Mass of newborn ± SD calculated from growth models by Agbayani et al. (2020)
P_{nb}	Newborns	16,611 ± 715 MJ	Production cost (± SD) from conception to birth (Eq. 3)
P_{calf}	Nursing calves	1,845 ± 556 MJ	Production cost (± SD) from birth to first year (Eq. 3).
H_g	Reproductive females	70,836 ± 1.4 MJ	Heat increment of gestation (Eq. 8)
Food / milk requirements			
ED_{prey}		2.90 ± 0.408 MJ kg^{-1}	Mean energetic density of benthic invertebrate prey available in the Arctic foraging grounds (see Table 3)
ED_{milk}		22.33 MJ kg^{-1}	Energetic density of grey whale milk, at 53% lipid content—average of values reported by Zenkovich (1938) and Tomilin (1946) as cited by Lockyer (1984).

Given that grey whales do not feed throughout the year, I determined the amount of energy they must consume and store during the four summer months they feed in the Arctic to meet their annual requirements. Thus, I divided the daily total gross energetic requirement for a full year by the number of days that grey whales feed each year to determine the increased amount of food they must consume during each day of feeding. For pregnant and lactating females, I calculated the average daily gross energy requirements over the reproductive cycle, which is just under 2 years.

2.2.2 Incorporating growth rates and production costs

I calculated the cost of growth from mass-at-age estimates (Agbayani et al. 2020) and body composition for each age group, using:

$$P = \Delta M \times \left[\left(p_{lip} \times ED_{lip}\right) + \left(p_{pro} \times ED_{pro}\right)\right] \qquad [4]$$

where P is the cost of production or growth (MJ), ΔM is the increase in mass (kg) per year, p_{lip} is the proportion of new body mass that is lipid, ED_{lip} is the energetic density of lipid, p_{pro} is the proportion of lean tissue that is protein, and ED_{pro} is the energetic density of protein. Values and sources used for each parameter are summarised in Table 1.

2.2.3 Incorporating total energetic expenditure per activity stage

To account for energetic cost of activity, I estimated total energetic expenditure (E_s) for a given life stage and activity state as applied by Sumich (1986) and Villegas-Amtmann et al. (2015, 2017):

$$E_s = 0.02 \times \%O_2 \times T_s \times R_s \times V_t \qquad [5]$$

where E_s is total energetic expenditure per life stage and activity state in MJ, 0.02 is the amount of heat produced in MJ L^{-1} of oxygen consumed (Kleiber 1961), $\%O_2$ is the percent of oxygen extracted with every breath (i.e., extraction efficiency), T_s is the time spent at each activity and life stage in number of days, R_s is the respiration rate per minute at each life stage (Table 2), and V_t is the tidal lung volume in L (Sumich 1986).

The $\%O_2$ for calves was 10.5 ± 3.0 % (± *SD*) based on direct measurements (n = 66 expirations) of calves 1-5 months old. In contrast, $\%O_2$ for older juveniles and adults were assumed to be 11 ± 2.7 % based on 136 expirations of an older calf, aged 1-10 months old (Sumich et al. 2001; Villegas-Amtmann et al. 2015, 2017).

I estimated the number of days spent in each activity (T_s) by calves, juveniles, adults, and reproductive females based on migration distances, travel speed, and sighting information reported in field studies (sources are listed in Table 2 with additional details in Appendix C). I updated the T_s values using estimates of age at weaning at 9.6 months derived from an analysis of body growth (Table 2; Agbayani et al. 2020) and field observations of mothers nursing calves in the feeding grounds as late as September 25 (Sychenko 2011).

For the two remaining parameters needed to estimate total energetic expenditure, I used respiration rates (R_s) as reported in various field studies (see Table 2), and estimated tidal volume (V_t) using a formula adapted by Sumich (1986) for grey whales:

$$V_t = 0.014 \times M^{1.04} \tag{6}$$

The mass-at-age estimates were calculated using age-length-mass growth models from Agbayani et al. (2020), and the respiration rates were calculated using 10,000 bootstrap samples drawn from lognormally distributed field respiration rates as reported by others (Table 2). Additional details on the growth model parameters I used are contained in Appendix A.

Table 2. Observed grey whale respiration rates (R_s) and standard deviations (in breaths per minute) for each life stage and associated activity, and no. of days at each stage (T_s). R_s and T_s were used as inputs in Eq. 5, the model for total energetic expenditure (E_s).

Life & activity stage	Approx. time of year	No of days per life stage (T_s)*	Breaths min^{-1} ($R_s \pm SE$)	Source for T_s	Source for R_s
Calf					
Lagoon 1st mo.	Jan	31	2.14 ± 0.5	(Pike 1962; Sumich 1986; Findley and Vidal 2002)	(Sumich 1986; as cited in Villegas-Amtmann et al. 2017)
Lagoon 2nd mo.	Feb	28	1.56 ± 0.4	(Pike 1962; Sumich 1986; Findley and Vidal 2002)	(Sumich 1986; as cited in Villegas-Amtmann et al. 2017)
Lagoon 3rd mo.	Mar	15	1.39 ± 0.3	(Rice and Wolman 1971; Sumich 1986; Findley and Vidal 2002)	(Sumich 1986; as cited in Villegas-Amtmann et al. 2017)
Northbound 3rd–6th mo.	mid-Mar to last wk of Jun	100	0.70 ± 0.1	(Rice and Wolman 1971; Leatherwood 1974; Hessing 1981 as cited in Braham 1984; Braham 1984; Poole 1984; Rodríguez de la Gala-Hernández et al. 2008; Perryman et al. 2010)	(Rodríguez de la Gala-Hernández et al. 2008)
Nursing at foraging grounds 6th–10th mo.	last wk of Jun to mid-Oct	119	1.22 ± 0.3	(Weller et al. 2003; Sychenko 2011; Bradford et al. 2012; for approximate date of weaning: Agbayani et al. 2020)	(Sychenko 2011)
Southbound post-weaning	mid-Oct to Dec	72	0.72 ± 0.2	(Braham 1984; Sumich 1986; Rugh et al. 2001; Laake et al. 2012)	(Sumich 1983; Schwarz 2002; as cited in Villegas-Amtmann et al. 2017)
Juvenile / Adult					
Lagoon solo	mid-Jan to mid-Feb	30	0.62 ± 0.2	(Rice and Wolman 1971; Sumich 1986; Rugh et al. 2001; Findley and Vidal 2002; Urbán R et al. 2021)	(Harvey and Mate 1984; Sumich 1986)
Northbound solo	Mar to mid-May	90	0.50 ± 0.03	(Pike 1962; Rice and Wolman 1971; Leatherwood 1974; Braham 1984; Poole 1984; Rodríguez de la Gala-Hernández et al. 2008; Urbán R et al. 2021)	(Rodríguez de la Gala-Hernández et al. 2008)
Foraging solo	mid-May to mid-Oct	154	1.04 ± 0.2	(Pike 1962; Kim and Oliver 1989; Bradford et al. 2012; Heide-Jørgensen et al. 2012; Urbán R et al. 2021)	(O. Sychenko (unpubl.) as cited in Villegas-Amtmann et al. 2017)
Southbound solo	mid-Oct to mid-Jan	91	0.72 ± 0.2	(Pike 1962; Leatherwood 1974; Braham 1984; Sumich 1986; Rugh et al. 2001; Rodríguez de la Gala-Hernández et al. 2008; Laake et al. 2012)	(Sumich 1983; Schwarz 2002; as cited in Villegas-Amtmann et al. 2017)

Life & activity stage	Approx. time of year	No of days per life stage (T_s)*	Breaths min^{-1} ($R_s \pm SE$)	Source for T_s	Source for R_s
Pregnant					
Southbound recently pregnant	Dec	31	0.72 ± 0.2	(Rice and Wolman 1971; Rice 1983)	(Sumich 1983; Schwarz 2002; as cited in Villegas-Amtmann et al. 2017)
Lagoon breeding	Jan to last wk of Feb	51	0.62 ± 0.2	(Rice 1983)	(Harvey and Mate 1984; Sumich 1986)
Northbound pregnant (solo)	last wk of Feb to May	100	0.50 ± 0.2	(Rice and Wolman 1971; Rice 1983)	(Rodríguez de la Gala-Hernández et al. 2008)
Foraging pregnant	Jun to Oct	153	1.34 ± 0.1	(Rice and Wolman 1971; Rice 1983)	(O. Sychenko (unpubl.) as cited in Villegas-Amtmann et al. 2017)
Southbound pregnant	Nov to Dec	61	0.72 ± 0.2	(Rice and Wolman 1971; Braham 1984; Sumich 1986)	(Sumich 1983; Schwarz 2002; as cited in Villegas-Amtmann et al. 2017)
Lactating					
Lagoon lactating	Jan to mid-Mar	74	0.62 ± 0.2	(Pike 1962; Rice 1983; Sumich 1986; Findley and Vidal 2002)	(Harvey and Mate 1984; Sumich 1986)
Northbound with calf	Mid-Mar to last wk of Jun	100	0.50 ± 0.1	(Rice and Wolman 1971; Leatherwood 1974; Hessing 1981 as cited in Braham 1984; Braham 1984; Poole 1984; Rodríguez de la Gala-Hernández et al. 2008; Perryman et al. 2010)	(Rodríguez de la Gala-Hernández et al. 2008)
Foraging lactating	last wk of Jun to last wk of Oct	119	1.04 ± 0.2	(Weller et al. 2003; Sychenko 2011; Bradford et al. 2012; for approximate date of weaning: Agbayani et al. 2020)	(O. Sychenko (unpubl.) as cited in Villegas-Amtmann et al. 2017)
Southbound post-weaning	Last wk of Oct to Dec	72	0.72 ± 0.2	(Pike 1962; Braham 1984; Sumich 1986; Rugh et al. 2001; Rodríguez de la Gala-Hernández et al. 2008)	(Sumich 1983; Schwarz 2002; as cited in Villegas-Amtmann et al. 2017)

**No. of days per stage (T_s) were based on migration distances, travel speed, and sighting information reported in field studies. Details broken down by month are available in Appendix C.*

2.2.4 Considering digestive efficiency

Direct measurements for digestive efficiency (E_{F+U}) values for grey whales were not available. I therefore I assumed that the digestive efficiency for grey whales was similar to that of North Atlantic right whales. However, right whales that consume mature (Stage 5) *Calanus finmarchicus* (their primary prey) assimilate only ~6% of available energy because its lipid content consists primarily of wax esters that are difficult for mammals to digest (Mayo and Marx 1990; Swaim et al. 2009). In contrast, grey whales primarily consume lipid-rich Arctic amphipods that are dominated by triacylglycerols with little to no wax ester content (Lee 1975; Legeżyńska et al. 2012). While digestive efficiencies could approach 90–100% because grey whale prey do not have waxy esters, I conservatively estimated grey whales to have a digestive efficiency of 74–88% based on the estimated digestive efficiency of North Atlantic right whales when consuming amphipods (Swaim et al. 2009; Fortune et al. 2013). These estimates encompass the capture and digestive efficiency of 80% as assumed by Thomson and Martin (1986) for grey whales. I also assumed that urinary loss is proportional to the nitrogen content of the prey—i.e., ~90% of the nitrogen content of organisms consumed (Worthy 1990).

2.2.5 Incorporating reproductive costs

I added the cost of pregnancy and lactation to the GER calculation for adult females to represent the energy requirements throughout a reproductive cycle (Figure 2). The equation for cost of pregnancy (C_{preg}) was:

$$C_{preg} = H_g + P_{nb} + GER_{calf6mo} \qquad [7]$$

where H_g is the heat increment of gestation in MJ, P_{nb} is the cost of growth to produce the newborn calf, and $GER_{calf6mo}$ is the minimum energy required for lactation to support a nursing calf in the first 6 months of life. I estimated the heat increment of gestation (H_g) using a mass-dependent relationship (Brody 1964; Villegas-Amtmann et al. 2015, 2017):

$$H_g = 18.41 \times M_{nb}^{1.2} \qquad [8]$$

where the mass of the newborn calf (M_{nb}) was calculated using growth models (Agbayani et al. 2020). H_g accounts for the energy required to maintain the pregnancy, including the growth of the uterus and the foetus, and any other tissue growth associated with pregnancy (Lockyer 2007; Fortune et al. 2013). The equation for cost of lactation (C_{lact}) was:

$$C_{lact} = GER_{calf3.6mo} \qquad [9]$$

where $GER_{calf3.6mo}$ is the total energy required for lactation to support a nursing calf in the last 3.6 months of nursing until the calf is weaned (seventh to tenth month), assuming that calves are fully weaned by ~9.6 months (Agbayani et al. 2020).

2.2.6 Calculating food requirements

Grey whales forage on assemblages of prey rather than on a single species (Darling et al. 1998), and do not appear to have dietary differences between males and females, or between older and younger whales (Budnikova and Blokhin 2012). However, caloric content of grey whale prey varies by species and season (Highsmith and Coyle 1990). I used the mean energetic density of common prey species consumed by grey whales to calculate their minimum food requirements (Table 3). I then calculated prey requirements for adults and weaned juveniles by dividing the estimated mean daily energy requirements (mean GER) by a mean energetic density value for

Table 3. Dry (ED_{dry}) and calculated wet weight (ED_{wet}) energetic densities for amphipods in the Arctic feeding grounds. These values were used to calculate food requirements by dividing gross energy requirements by the wet weight energetic density of prey (*ED_{wet}*).

Area sampled	Year sampled	Season	ED_{dry} (kcal g^{-1})	Dry/wet wt conversion factor*	ED_{wet}		Source
					(kcal g^{-1})	(MJ kg^{-1})	
Chirikov Basin, Bering Sea	1986–88	May–Nov	4.12	0.146†	0.60	2.51	Coyle et al. (2007)
Chirikov Basin, Bering Sea	2002–03	Jun/Sept	4.28	0.146†	0.62	2.61	Coyle et al. (2007)
Chirikov Basin, Bering Sea	1982	Jul/Sep	5.20	0.150	0.78	3.26	Thomson and Martin (1986)
Bering and Chukchi Shelf	1970-74	Jan–Sep	5.22	0.156	0.81	3.41	Stoker (1978)
Chukchi Sea	2010	Jul–Aug	4.92	0.131	0.64	2.70	Wilt (2012)
			4.75	**0.146**	**0.69**	**2.90**	**Average**
						0.408	**SD**

**Dry weight conversion factors ratios of reported dry weights to wet weights, except Coyle et al. (2007).* †*Samples collected by Coyle et al. (2007) were fixed in formalin, which may have desiccated them. Therefore, the dry/weight conversion factor used to calculate energetic density for wet weight of samples from Coyle et al. (2007) was an average of the dry/wet weight conversion factors of samples from other studies.*

benthic amphipods in the Arctic feeding grounds (calculated from reported values of dry weight caloric densities as reported in various studies; see Table 3). I multiplied dry weight energetic density values by the ratio of dry weights to wet weights to obtain wet weight energetic densities, and converted the values from kcal g^{-1} to MJ kg^{-1} (where 1 kcal = 0.004184 MJ).

2.2.7 Calculating milk requirements

For nursing calves, I calculated the volume of milk they required by dividing the mean daily energetic requirements (GER_{calf}) by the energy density of grey whale milk, at a 53% lipid content (Zenkovich 1938; Lockyer 1984), assuming that the energy equivalent for lipid is 39.3 MJ kg^{-1}, and protein is 24.5 MJ kg^{-1} (Oftedal 1997). I calculated the energy density of grey whale milk as the average of values from Zenkovich (1938) and Tomilin (1946) cited in Lockyer (1984). I multiplied the percentage wet weight of each component of grey whale milk reported by

Table 4. Calculations for energetic density of grey whale milk from composition values reported by Zenkovich (1938). These values were averaged with values reported by Lockyer (1984) to calculate milk requirements for grey whale calves (see Table 5). *Total percentage of protein, ash, and lactose, where ash and lactose were assumed to be negligible.

	(Zenkovich 1938)		
	Energy composition of grey whale milk (MJ kg^{-1})	% Wet wt.	Energetic density of components (MJ kg^{-1})
Fat (lipid)	20.84	53.04	39.30
Protein*	1.56	6.38	24.50
Water		40.58	0.00
Total	**22.41**	**100.00**	

Table 5. Energetic density of grey whale milk (ED_{milk}). as calculated from values as cited by Lockyer (1984). Milk requirements for calves were calculated by dividing gross energy requirements of calves by the average value of the energetic density of grey whale milk. *Unit conversion: 1 kcal = 0.004184 MJ.

Source	ED_{milk} (kcal g^{-1})	ED_{milk} (MJ kg^{-1})
(Tomilin 1946)	5.32	22.26*
(Zenkovich 1938)		22.41
Average		**22.33**

Zenkovich (1938) with the energetic density to determine the energy values in MJ kg^{-1} (Table 4) and summed the values to get a value for the energy density of grey whale milk. I converted the value reported by Tomilin (1946) using a conversion of 1 kcal = 0.004184 MJ, and calculated the energy density of grey whale milk as the average of the values from Tomilin (1946) and Zenkovich (1938) at 22.33 MJ kg^{-1} (Table 5).

2.2.8 Assessing model uncertainty and sensitivity

I assessed model uncertainty and sensitivity using a series of model runs that determined the contribution of each input parameter to the overall model uncertainty. I ran the model comparisons for each life stage under different scenarios, where parameters with assigned sampling distributions (assumed or taken from field observations) were varied within its range of uncertainty, while the other parameters were assigned a nominal value (i.e., their mean values). I assumed that most of the parameters had normal sampling distributions, except where otherwise identified in the literature or where only minimum and maximum values were available. I assumed that parameters with only minimum and maximum values had uniform distributions (Table 1). I calculated the standard deviation around the mean for 10,000 Monte Carlo simulations per scenario to identify which parameter contributed the widest range of uncertainty to the overall model results.

For the gross energy requirement (GER) calculations for Phase 1 and 2 growth, I ran a total of four scenarios: 1) all variables were varied, 2) only production cost (P) was varied, 3) only total energetic expenditure (E_s) was varied, and 4) only digestive efficiency (E_{F+U}) was varied. For the GER calculation for pregnant females, I ran a total of seven scenarios. In addition to the three variables that were varied for Phase 1 and Phase 2, the variables contributing towards the cost of pregnancy (C_{preg}) and cost of lactation (C_{lact}) were varied. I ran three additional scenarios for pregnant females: 1) only the heat increment of gestation (H_g) was varied, 2) only the production cost of an average newborn (P_{nb}) was varied, and 3) only the total energy requirement for a calf from birth to 6 months of age ($GER_{calf6mo}$) was varied. For lactating females, I ran only one additional scenario, where only the total energy requirement for a calf for the last few months of nursing ($GER_{calf3.6mo}$) was varied.

Based on exploratory analyses showing the large contribution of total energetic expenditure (E_s) to uncertainty in estimated gross energy requirements, I ran another set of scenarios to determine which variables contributed the greatest uncertainty in E_s. For all life stages (Phase 1, Phase 2, pregnant, and lactating), four scenarios were run: 1) all variables were varied, 2) only tidal volume (V_t) was varied, 3) only respiration rates (R_s) were varied, and 4) only percentage of oxygen assimilated ($\%O_2$) was varied. This allowed me to compare the GER estimates between life stages, as well as identify parameters that contributed the highest levels of uncertainty in the model. The method also facilitated validating the GER estimates for each life stage by assessing the consistency in GER estimates across uncertainty scenarios.

2.3 Results

2.3.1 Growth rates and production costs

Grey whales grow fastest in their first year of life while supported by energy-rich mothers' milk, gaining an average of 515 ± 11 kg in the first month, with the highest growth spurt of approximately 577 ± 18 kg (ΔMass ± *SD*) occurring in the 3rd month (Table 6). Associated production costs (*P*) are 8,725 ± 396 MJ for the first month, and peak at 9,568 ± 491 MJ in the third month (Table 6). Production cost drops abruptly after the 9th month, to 2,233 ± 119 MJ for the 11th month and 2,308 ± 127 MJ for the 12th month, indicating that calves would be completely weaned by this time. This drop in production cost coincides with the drop in growth rates at 0.8 years (~9.6 months) that was reported by Agbayani et al. (2020). The equivalent values of production cost per day in MJ day^{-1} for each month is shown alongside mean mass (kg) in Figure 3.

Table 6. Estimated mean change in body mass (ΔM) in kg and mean production cost (P) in MJ per month of growth in the first year. Mean mass change for neonatal (i.e., at age 0 mos.) represents the mass change from conception to birth; mean mass change for the other rows represent growth over the full year (i.e., the 1st month represents the mass change from birth to the end of January). Uncertainty values represent the standard deviation (± *SD*) around the mean of 10,000 Monte Carlo estimates.

Phase 1 - Calves		
Age (mos.)	Mean ΔMass (kg) ± *SD*	Mean P per month (MJ) ± *SD*
neonatal	983 ± 27	16981 ± 821
1	515 ± 11	8725 ± 396
2	505 ± 16	8388 ± 440
3	577 ± 18	9568 ± 491
4	554 ± 12	9190 ± 431
5	551 ± 8	9152 ± 402
6	503 ± 2	8349 ± 345
7	482 ± 1	7995 ± 330
8	440 ± 1	7345 ± 301
9	385 ± 3	6469 ± 269
10	306 ± 120	5151 ± 2023
11	133 ± 5	2233 ± 119
12	137 ± 5	2308 ± 127

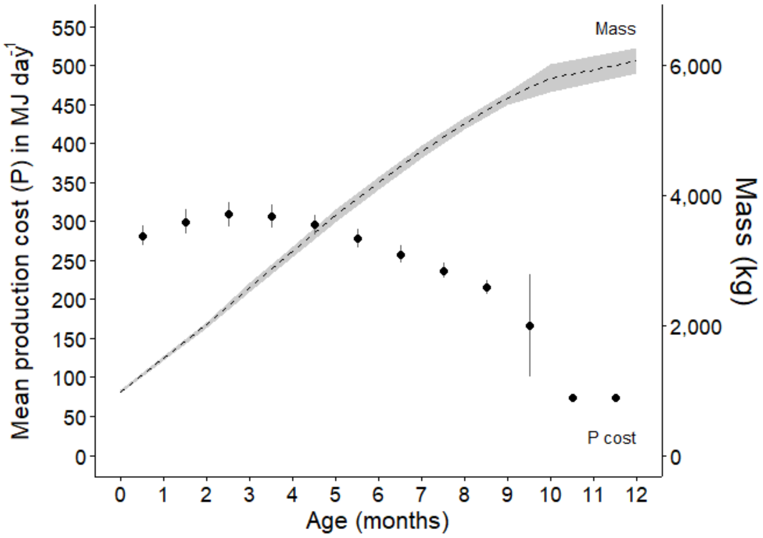

Figure 3. Production cost per day and mass growth curves for calves. Average production cost (MJ) per day on the primary axis, represented as a dotted line, and total mass (kg) shown on the secondary axis, as modelled by Agbayani et al. (2020) represented as a dashed line. Grey shading represents the standard deviation (±SD) around the mean of 10,000 Monte Carlo estimates.

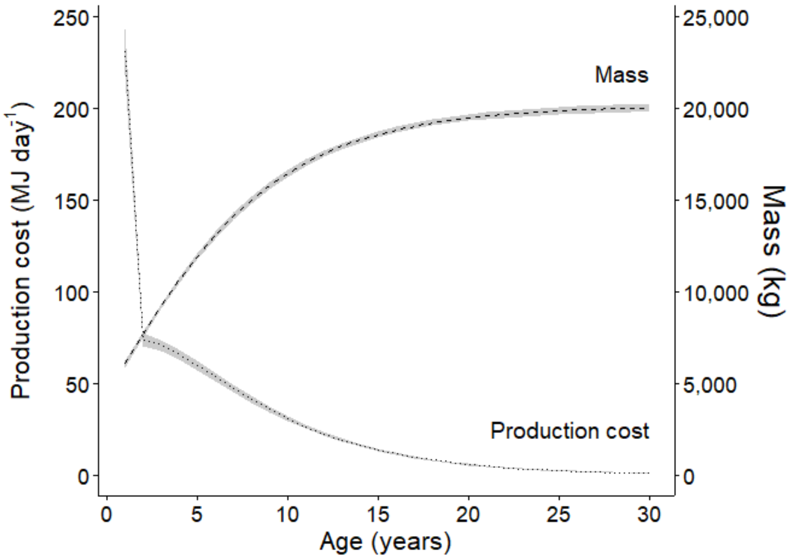

Figure 4. Production cost per day and mass growth curves for juveniles and adult grey whales. Average production cost (MJ) per day on the primary axis, represented as a dotted line, and total mass (kg) shown on the secondary axis, as modelled by Agbayani et al. (2020) represented as a dashed line. Grey shading represents the standard deviation (±SD) around the mean of 10,000 Monte Carlo estimates.

Over the first year of growth, grey whale calves gained 5,234 ± 178 kg of mass, which translated into mean production costs of 86,903 ± 4,649 MJ (Table 7). Growth rates decreased with increasing age, dropping to an average annual mass change of 799 ± 3 kg (P = 13,467 ± 550 MJ year^{-1}) once they have reached sexual maturity in the ninth year (Table 7). Equivalent values of production cost per day (MJ day^{-1}) are shown in Figure 4. Growth rates and production costs then continue to decrease as they reach asymptotic sizes as mature adults (e.g., mass ~20,000 ± 230 kg at ~30 years; Figure 4). Production cost values for other life stages such as pregnant and lactating are comparable to non-reproductive adults (see Appendix B.1 for additional information).

Table 7. Estimated mean change in mass (ΔM) in kg and mean production cost (P) in MJ per year of growth for juveniles and adults. Values shown here represents mean mass attained and production cost over the full year of growth (i.e., the first year represents the time from birth to 1 year of age). Mean mass change begins to approach 0 at ~50 y. Uncertainty values represent the standard deviation (± *SD*) around the mean of 10,000 Monte Carlo estimates.

Phase 2 - Juveniles and non-reproductive adults		
Age (y)	Mean ΔMass (kg) ± *SD*	Mean P per year (MJ) ± *SD*
1	5089 ± 178	84496 ± 4573
2	1603 ± 40	26999 ± 1293
3	1536 ± 14	25873 ± 1080
4	1428 ± 9	24066 ± 989
5	1300 ± 19	21896 ± 947
6	1163 ± 17	19586 ± 848
7	1026 ± 6	17291 ± 709
8	897 ± 4	15109 ± 617
9	777 ± 3	13094 ± 535
10	669 ± 7	11272 ± 472
11	573 ± 9	9652 ± 419
12	488 ± 9	8230 ± 366
13	415 ± 8	6992 ± 314
14	352 ± 6	5923 ± 261
15	297 ± 2	5005 ± 207
16	251 ± 1	4221 ± 172
17	211 ± 3	3555 ± 151
18	177 ± 4	2989 ± 140
19	149 ± 6	2511 ± 143
20	125 ± 6	2107 ± 139
21	105 ± 6	1767 ± 130
22	88 ± 7	1480 ± 133
23	74 ± 7	1240 ± 122
24	62 ± 7	1038 ± 121
25	52 ± 6	869 ± 104
26	43 ± 5	727 ± 94
27	36 ± 5	608 ± 85
28	30 ± 5	508 ± 80
29	25 ± 4	425 ± 68
30	21 ± 4	425 ± 68

2.3.2 Total energetic expenditure across activity stages

My estimates of total energetic expenditure across all activity stages (E_S) fluctuated monthly in the first year, depending on the breathing rates associated with each activity stage (Table 4). In the 6th month, as the mother-calf pairs arrive at the northern feeding grounds in the Arctic (see Figure 2), calves transition from traveling northbound with their mother expending an average of 140 ± 40 MJ day^{-1} to 170 ± 42 MJ day^{-1} while nursing in the foraging grounds. Calf daily energy expenditure is highest in the ninth month (405 ± 98 MJ day^{-1}) as calves approach the end of their weaning period and increasing to 434 ± 105 MJ day^{-1} as they transition from nursing to feeding on their own. As calves continue traveling southward on their own in the tenth month (see Figure 2), their daily energy expenditures begin to decline.

Assuming juveniles and single adults (male and female) generally follow similar migratory timings, calves expend an average of 75,334 ± 12,574 MJ in their first year, while individuals entering sexual maturity at ~8 years expend 276,151 ± 44,701 MJ per year (Table 9, Figure 6). Pregnant females (~8 years old) expend 358,806 ± 61,389 MJ over 396 days of pregnancy (906 ± 155 MJ day^{-1}), whereas lactating females are expected to expend 276,036 ± 42,448 MJ over the span of 365 days (756 ± 116 MJ day^{-1}; Table 9, Figure 6).

Table 8. Monthly estimated energetic expenditure (E_s) from activity. Calculated from observations of respiration rates of grey whale calves from (Sumich 1986). Activity stages include CG – nursing at calving grounds; NB – northbound migration; FG_N – nursing at foraging grounds; SB – weaned on southbound migration. Values represent the energetic expenditure for the whole month, e.g., the 1st month represents the time from birth to the end of January. Uncertainty values (± *SD*) show the standard deviation around the mean of 10,000 Monte Carlo simulations.

Age (mos.)	Tidal Volume at mid-month ± *SD* (L)	Activity stages	No. of days per stage	Daily E_s ± *SD* (MJ day^{-1})	Monthly E_s ± *SD* (MJ $mo.^{-1}$)
1	22.9 ± 0.60	CG	31	148 ± 42	4588 ± 1302
2	33.0 ± 0.87	CG	28	156 ± 44	4358 ± 1237
3	43.8 ± 1.19	CG	31	184 ± 52	2760 ± 784
4	55.0 ± 1.57	NB	30	93 ± 26	1483 ± 421
5	66.0 ± 1.53	NB	31	116 ± 33	3492 ± 992
6	76.8 ± 1.85	NB	23	140 ± 40	4331 ± 1228
		FG_N	7	170 ± 42	3914 ± 955
7	86.8 ± 2.05	FG_N	31	297 ± 72	2076 ± 507
8	96.2 ± 1.83	FG_N	31	335 ± 82	10397 ± 2537
9	104.8 ± 1.91	FG_N	30	371 ± 90	11516 ± 2804
10	112.2 ± 2.01	FG_N	20	405 ± 98	12140 ± 2955
		SB	11	434 ± 105	8670 ± 2110
11	116.0 ± 4.02	SB	30	256 ± 62	2814 ± 685
12	119.1 ± 4.52	SB	31	265 ± 65	7937 ± 1949

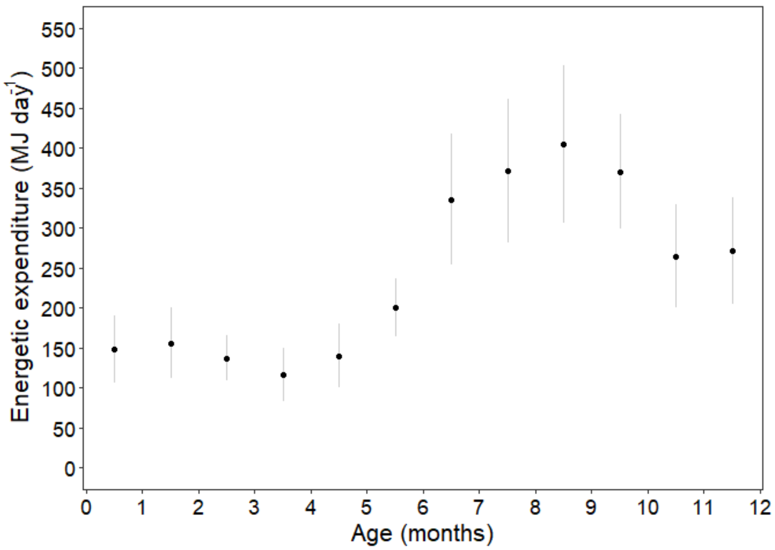

Figure 5. Estimates of average daily energetic expenditure from activity (MJ day^{-1}) for each month in the first year (Phase 1). Values are plotted at the midpoint of each month. Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations. Note: E_s values for the 6th and 10th months represent energetic expenditures across two activity stages.

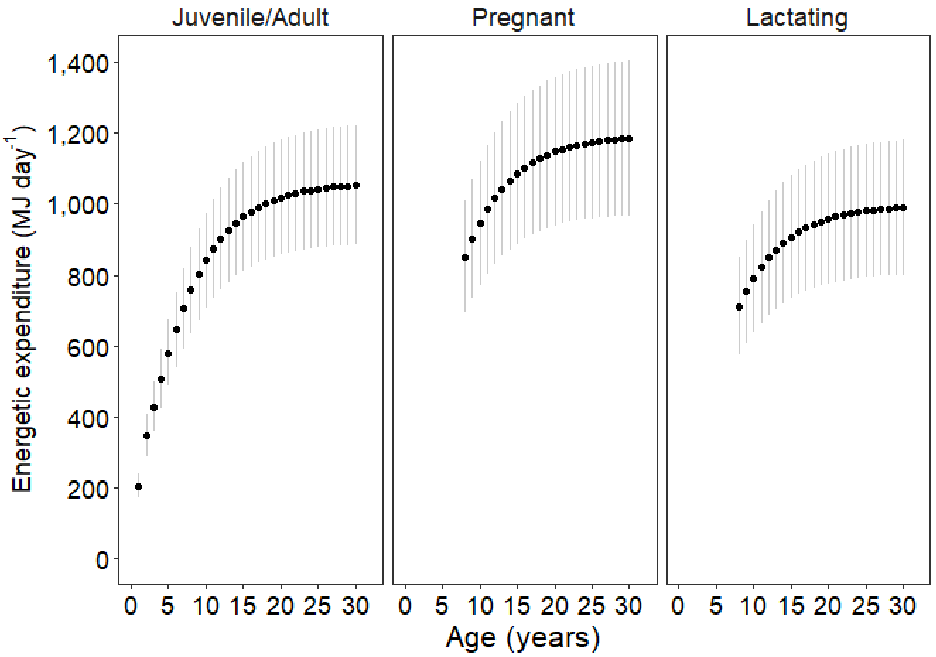

Figure 6. Estimates of daily average energetic expenditure from activity (MJ day^{-1}) for juveniles and single adults, pregnant and lactating females per year. Values are plotted at the midpoint of each year. Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations.

Table 9. Estimated energetic expenditure at each activity stage (E_s) per Sumich (1986). Activity stages include CG – at calving grounds; CG_P – at calving grounds, pregnant; CG_L – lactating at calving grounds; NB – northbound migration; NB_P – pregnant during northbound migration; FG – at foraging grounds, FG_P – pregnant at foraging grounds; FG_L – lactating at foraging grounds; SB – southbound migration; SB_{RP} – southbound migration, recently pregnant; SB_{LP} – southbound migration, late pregnant; SB_{PW} – southbound migration, post-weaning. Values represent energy expenditure for the whole year, i.e., the 1st year represents the time from birth to the end of the 1st year.

Age (y)	Tidal Volume at mid-year ± *SD* (L)	Activity stages	No. of days per stage	E_s ± *SD* (MJ day^{-1})	Total E_s ± *SD* (MJ) per activity stage
Juveniles and single adults					
1	81.7 ± 2.03	CG	30	161 ± 43	4844 ± 1301
		NB	90	130 ± 35	11719 ± 3148
		FG	154	271 ± 73	41709 ± 11203
		SB	91	188 ± 50	17063 ± 4583
8	300.2 ± 4.83	CG	30	592 ± 154	17756 ± 4625
		NB	90	477 ± 124	42958 ± 11190
		FG	154	993 ± 259	152891 ± 39826
		SB	91	687 ± 179	62546 ± 16293
Pregnant females					
8	309.1 ± 4.84	SB_{RP}	31	732 ± 204	22694 ± 6336
		CG_P	51	630 ± 177	32149 ± 9018
		NB_P	100	508 ± 144	50834 ± 14390
		FG_P	153	1363 ± 375	208472 ± 57311
		SB_{LP}	61	732 ± 204	44656 ± 12468
Lactating females					
8	309.1 ± 4.84	CG_L	74	630 ± 177	46648 ± 13085
		NB_L	100	508 ± 141	50840 ± 14094
		FG_L	119	1057 ± 293	125839 ± 34863
		SB_{PW}	72	732 ± 204	52709 ± 14716

2.3.3 Predicted gross energy requirements

The predicted Gross Energy Requirements (GER) for calves (Figure 5) followed the same general trend as total energetic expenditure (E_s). It peaked around the ninth month (at 778 ± 139 MJ day^{-1}), and had the highest standard deviation around GER in the tenth month (where GER =

673 ± 198 MJ day^{-1}) as calf growth rates transitioned from Growth Phase 1 to Growth Phase 2 (Agbayani et al. 2020).

The estimates for the gross energetic requirement to complete an annual migration (Figure 7) range from 528 ± 82 MJ day^{-1} for typical weaned juveniles in the 2nd year to approximately 1,329 ± 222 MJ day^{-1} for single adults. However, grey whales tend to focus their feeding in the summer foraging season, and would need to consume between 1,004 ± 156 MJ day^{-1} for typical weaned juveniles in the second year and 2,526 ± 422 MJ day^{-1} for the largest adults to meet their annual requirements (Figure 8).

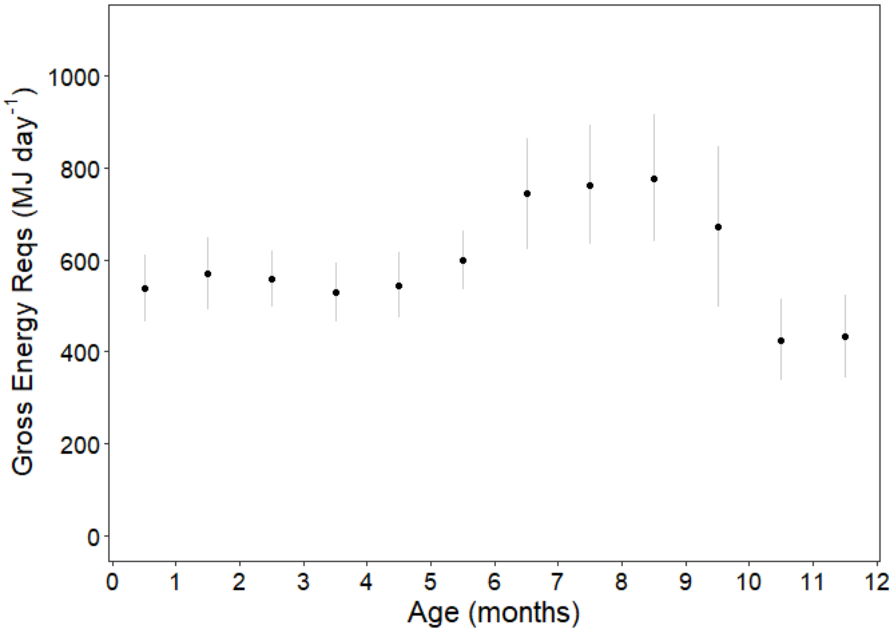

Figure 7. Daily average gross energy requirements for calves in the first year in MJ day^{-1}. Values are plotted at the midpoint of each month. Error bars represent the *SD* of 10,000 Monte Carlo estimates.

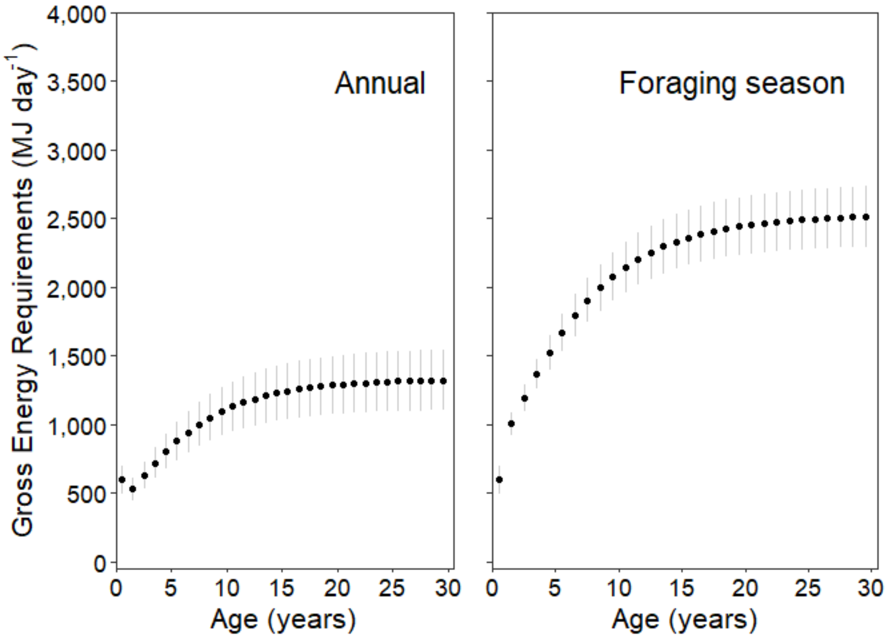

Figure 8. Daily average gross energy requirements over the year compared to gross daily requirements when foraging is limited to the summer season. Foraging season spans ~154 days for juveniles and adults. Values are plotted at the midpoint of each year. Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations.

Pregnant and lactating females have the greatest energetic needs compared to other single adult whales (Figure 9). Annual gross energy requirements for pregnant females range from 1,814 ± 211 MJ day^{-1} to 2,191 ± 288 MJ day^{-1}, and lactating females require 1,603 ± 205 MJ day^{-1} to 1,991 ± 268 MJ day^{-1}. Considering that energy consumption occurs primarily in the summer, pregnant females would need to consume between 4,726 ± 550 MJ day^{-1} and 5,708 ± 750 MJ day^{-1} during the foraging season while lactating females require slightly less, ranging from 3,946 ± 505 MJ day^{-1} to 4,902 ± 660 MJ day^{-1}.

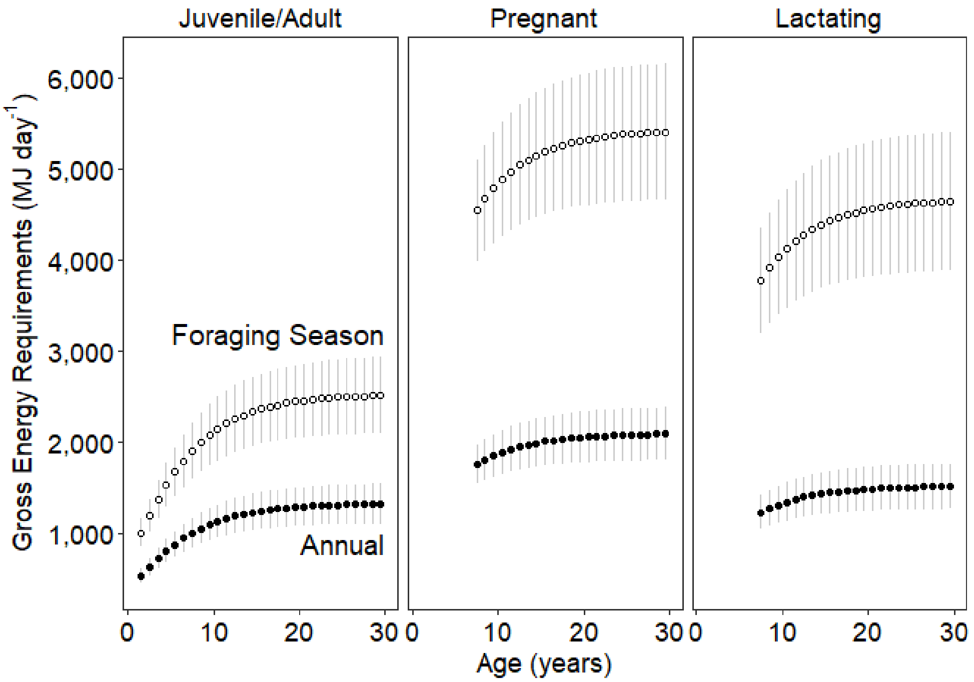

Figure 9. Estimates for gross energy requirements for pregnant, lactating females, and others (juvenile and other adult grey whales). Daily gross energy requirements for a full year (annual) are represented with black circles. White circles represent daily gross energy requirements for when feeding is limited during the foraging season. Foraging season is assumed to be ~154 days for single juveniles (1-7 y) and adults (>8 y), ~153 days for pregnant females, and ~119 days for lactating females. Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations.

2.3.4 Predicted milk/food requirements for grey whale calves

Milk requirements for calves range from 24 ± 3 L in the first month, to 35 ± 6 L of milk day^{-1} at the peak of nursing in the ninth month (Figure 10). Young grey whales weaning in their tenth and eleventh month would need to consume 146 ± 29 kg of prey day^{-1} (2.4 ± 0.40% body weight) in the eleventh month and 149 ± 29 kg of benthic invertebrate prey day^{-1} (2.4 ± 0.41% body weight) in the twelfth month to meet their energetic requirements.

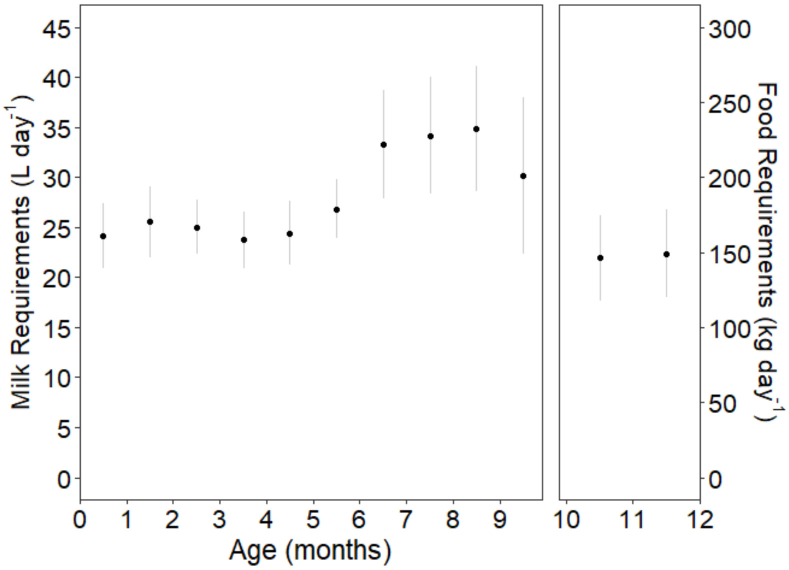

Figure 10. Average daily milk requirements for calves. The left panel represents milk requirements (L day^{-1}) for calves up to 9 months (left panel), and the right panel represents food requirements (kg of benthic invertebrate prey day^{-1}) for weaned calves over 9 months. Values are plotted at the midpoint of each month. Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations.

2.3.5 Predicted daily food requirements for weaned juveniles and adult grey whales

Food requirements for weaned juveniles and other adults plateau as they attain their asymptotic body lengths. Weaned juveniles in the second year require 347 ± 49 kg of prey day^{-1} during foraging season, corresponding to 4.4 ± 0.54% of their body weight (Figure 11). Food requirements increase to 869 ± 134 kg prey day^{-1} (4.2 ± 0.6% of body weight) for fully grown adults weighing 20,726 kg, as estimated using the grey whale body growth model (Agbayani et al. 2020). Foraging pregnant females require between 1,630 ± 191 kg day^{-1} (10.3 ± 0.97% of body weight) for 8-year-old whales, and 1,969 ± 260 kg day^{-1} (9.3 ± 1.03% of body weight) for the largest pregnant whales weighing 21,119 ± 510 kg (i.e., the sum of the asymptotic female mass and 40% of an average newborn calf). Having stored large amounts of energy during their pregnancy, lactating females' daily foraging needs are slightly less than their pregnant

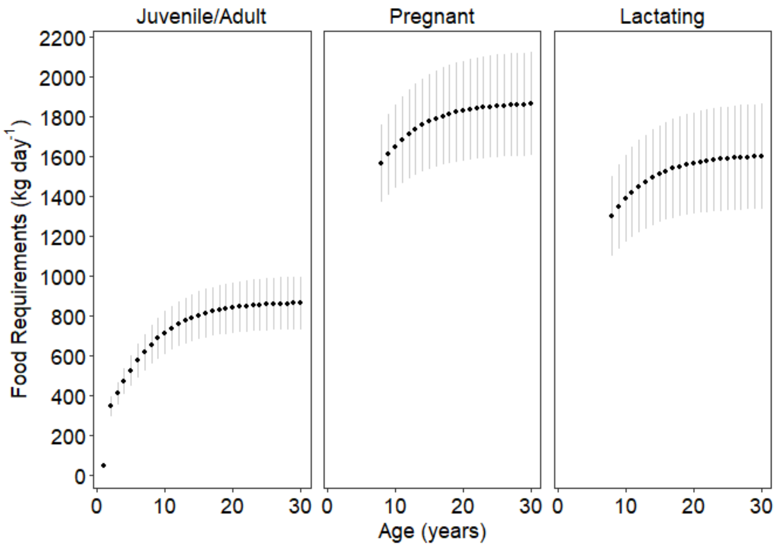

Figure 11. Average daily food requirements (kg day^{-1}) of benthic invertebrate prey for pregnant females, lactating females, and others (juveniles and other adult grey whales) during foraging season. Foraging season is assumed to be ~154 days for single juveniles (1–7 y) and adults (>8 y), ~153 days for pregnant females, and ~119 days for lactating females. Values are plotted at the midpoint of each year. Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations.

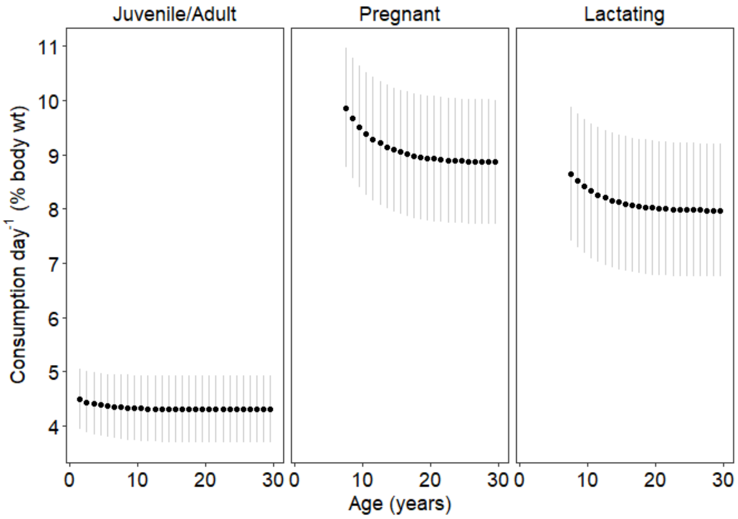

Figure 12. Average percentage of body weight consumed per day during the foraging season for juveniles and other adults, pregnant females, and lactating females. Foraging season is assumed to be ~154 days for single juveniles (1-7 y) and adults (>8 y), ~153 days for pregnant females, and ~119 days for lactating females. Note that the y-axis does not start at 0. Values are plotted at the midpoint of each year. Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations.

counterparts averaging 1,361 ± 176 kg of prey day^{-1} (8.8 ± 1.03% of body weight) for individuals 8 years of age and up to 1,691 ± 229 kg of prey day^{-1} (8.2 ± 1.01% of body weight) for the oldest and largest whales (Figure 12).

2.3.6 Model uncertainty and sensitivity

The scenario analyses exploring model uncertainty and sensitivity show that the parameter contributing the highest range of uncertainty (±SD) to the gross energy requirements was total energetic expenditure (*E_s*; Figure 13), and that the variable contributing the highest range of uncertainty within the E_s calculations was the percentage of oxygen absorbed (*$\%O_2$*; Figure 14). The pattern holds for Phase 2, pregnant, and lactating life stages, even when additional parameters are examined for the pregnant and lactating stages (see Figure 21 in Appendix D).

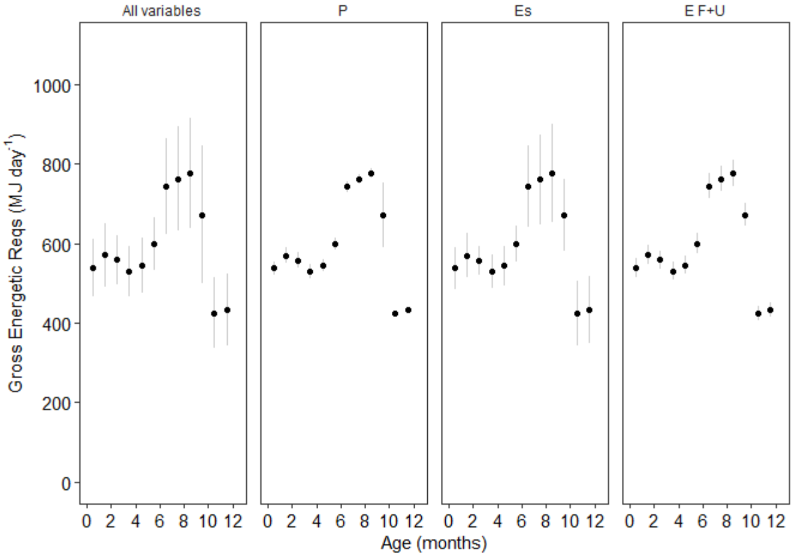

Figure 13. Comparison of uncertainty analyses on GER model outputs for grey whale calves (Phase 1). Panels shown represent scenarios where single parameters were varied while the remaining parameters were kept constant. P – Production cost; Es – Total energetic expenditure; E F+U – Digestive efficiency (fecal and urinary). Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations for each scenario.

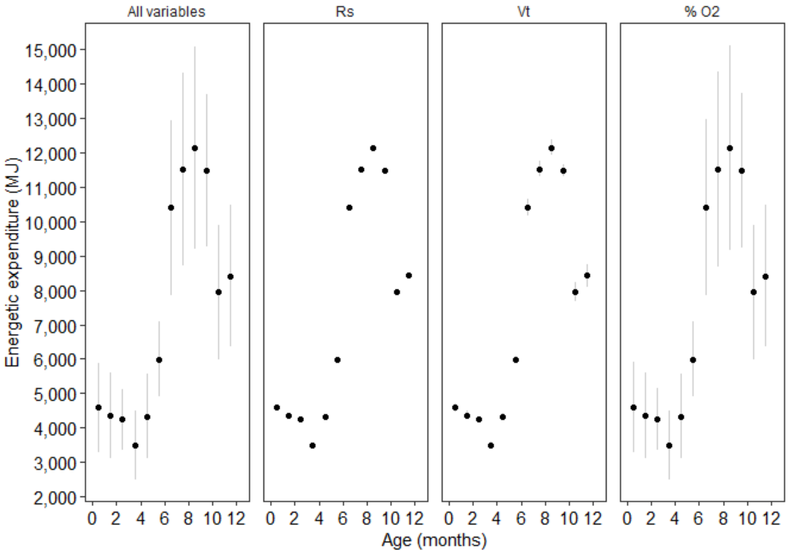

Figure 14. Comparison of uncertainty analyses on E_s model outputs for grey whale juveniles and non-reproductive adults (Phase 2). Panels shown represent scenarios where single parameters were varied while the remaining parameters were kept constant. R_s – Respiration rates; Vt – Tidal volume; $\%O_2$ – Percentage of oxygen absorbed. Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations for each scenario.

2.4 Discussion

The bioenergetics model shows the minimum daily energy requirements needed by grey whales to complete an annual migration. The model is simple and flexible because it is based on an energy balance equation, and it can be adapted and parametrized to other populations of grey whales or other species of interest, including rare or endangered species that may otherwise be considered data deficient. Model assumptions, limitations, and sources of uncertainty are broadly related to the restricted feeding season of the grey whales, data available for the parametrization of activity cost, and the nuances around the parametrization for pregnancy and lactation. Monte Carlo simulations allowed uncertainty to be incorporated within the model estimates. The model produced results that were consistent across each uncertainty scenario, and yielded predictions of energy requirements that are comparable to other published values. My estimates represent the minimum amount of energy and food consumption required for grey whales to survive an annual migration and are therefore conservative. The model provides insight into the requirements of grey whales across their life cycle, the differences between newborns, juveniles, non-reproductive adults, and pregnant and lactating females.

2.4.1 Model uncertainty and sensitivity driven by oxygen absorption parameter

The results of my sensitivity analysis show that oxygen absorption ($\%O_2$) contributed more to overall uncertainty in predicted food requirements compared to any other parameter. The values I used for percent oxygen absorbed were measured in young grey whales, and applied across all ages. Total energetic expenditure (E_s) can vary substantially because it directly depends on the fraction of oxygen absorbed into the lungs, which depends on both the size of the lungs and the length of time each breath is held (Sumich 1983; Fahlman et al. 2016). Early investigations reported grey whales used 10–12% of the oxygen in inspired air for breath holds of between 20–25 seconds, and that breath-hold durations of 20–30 seconds were most commonly observed presumably because this duration allowed for maximum oxygen absorption (Sumich 1983). More recent models of the grey whale ventilatory cycle suggest that oxygen absorption is highly variable even when breath-hold durations remain consistent (Sumich 2021). Incorporating better estimates of oxygen uptake into the grey whale bioenergetic model through a better understanding of grey whale respiration (e.g., Sumich 2021) would contribute to increasing confidence in the predictions of energy requirements of grey whales.

I did not further test the sensitivity of parameters by increasing or decreasing values by set percentages as has been done for other models (e.g., Bejarano et al. 2017). However, during early model development, I did note how preliminary model predictions changed as additional data became available and the migration timeline evolved—particularly for respiration rates and the number of days associated with different activity stages. I assessed the effect of varying respiration rates here, but decided to not include the number of days per activity stage in my assessment of uncertainty because these were represented by single values (rather than a distribution of values). Future research comparing the energy requirements of the PCFG with those of the larger Northeast Pacific grey whale population would be informative in demonstrating the effect that different migration timelines would have on the predicted energy requirements of grey whales.

2.4.2 Daily food requirements driven by the restricted feeding season

My model assumed that grey whales feed primarily in the summer foraging grounds in the Arctic, and that they generally do not feed along the migration route or during the winter in the breeding lagoons. This is likely the case for most grey whales in the eastern North Pacific population but there are notable exceptions. The PCFG have drawn research attention in recent years, and observations of grey whales feeding along the migration route have increased (Braham 1984; Mallonée 1991; Dunham and Duffus 2001, 2002; Urbán R et al. 2021). These whales have a different migration timetable and tend to feed on a different range of prey along the migration route as opposed to what they would normally feed on in the Arctic feeding grounds (Dunham and Duffus 2001, 2002; Hildebrand 2020; Hildebrand et al. 2021). As such, while the energy requirements for the PCFG are likely similar to those of a typical grey whale from the main population, the model could be parametrized specifically for PCFG migration timings and prey species to better estimate their energy requirements. Grey whales feed on at least two prey species off the coast of Oregon (i.e., Dungeness crab megalopae and a mysid

Neomysis rayii) that have a higher calorie content compared to *Ampelisca macrocephala*, i.e. the ampeliscid amphipods found in abundance the Arctic foraging grounds (Hildebrand et al. 2021). My model can be used to assess the effect of factors such as shorter migration distances, an extended foraging season, higher caloric content in prey species, lower prey densities, and patchier prey distribution along the coast of North America on their daily energy requirements during the foraging season. This combination of factors may allow for lower daily consumption rates for PCFG whales compared to the whales that travel the full migration distance to the Arctic foraging grounds.

2.4.3 Refining activity cost estimates by modeling total energetic expenditure

I adapted my bioenergetics model for grey whales from models used for right whales (Fortune et al. 2013), Steller sea lions (Winship et al. 2002) and Pacific white-sided dolphins (Rechsteiner et al. 2013a). These prior efforts modelled activity costs as a multiplier of resting metabolic rates measured in captive individuals (Rechsteiner et al. 2013b) or as a multiplier of basal metabolic rates derived from Kleiber's (1975) mouse-to-elephant curve in the absence of actual measurements (Winship et al. 2002; Fortune et al. 2013). However, some marine mammals have been found to have a higher basal metabolic rate than predicted by the Kleiber curve (Williams et al. 2001). In my model, I used observed rates of respiration during different stages of the grey whale life cycle to estimate total energy expenditure (Table 2). I assumed that total energy expenditure modeled from respiration rates encompassed all maintenance costs, including heat increment of feeding (Maresh et al. 2015). As such, the variables previously associated with activity (A), basal metabolic rate (BMR or BM), and heat increment of feeding ($1-E_{HIF}$) or energetic costs of resting metabolism and thermoregulation (E_m) in prior bioenergetic models

(Winship et al. 2002; Fortune et al. 2013; Rechsteiner et al. 2013a) were incorporated into total energy expenditure (E_s) in my model.

Total energetic expenditure from activity for grey whales were estimated from respiration rates (Sumich 1983, 1986; Villegas-Amtmann et al. 2015, 2017). This method has been used to estimate energy expenditure for other species, including minke whales (*Balaenoptera acutorostrata*; Christiansen et al. 2014), killer whales (*Orcinus orca*; Roos et al. 2016), and bottlenose dolphins (*Tursiops truncatus*; Yazdi et al. 1999). However, estimates of energy expenditure generated from respiration rates depend on the assumption that the vital capacity of cetaceans is high (~80–90% of total lung capacity), and that tidal volume (V_t) and the oxygen exchange fraction (ΔO_2) are constant over time, which is not necessarily true (Fahlman et al. 2016). Breath-by-breath variation was not taken into account, and any estimates of energy expenditure relied on the premise that these values represent an average over time (Fahlman et al. 2016). Recent modeling of tidal volume, oxygen consumption, and field metabolic rates of calves have begun considering how these factors vary at finer scales (Sumich and May 2009; Sumich 2021). However, my analysis used rates of respiration averaged across monthly time scales for calves, and annual time scales for juveniles and adults—similar to that of Villegas-Amtmann et al. (2015, 2017).

2.4.4 Validating grey whale energy requirements and associated rates of consumption

Prior studies have estimated grey whale energy requirements using respiration data and general estimates of population size (Highsmith and Coyle 1992) for whales ranging from 14–23 metric tons (Rice and Wolman 1971; Sumich 1983; Thomson and Martin 1986; Highsmith and Coyle 1992). While these are useful as a general benchmark for the ‘typical’ whale, there is considerable variability in energy requirements across different ages and life stages. A typical calf will have different requirements compared to a typical weaned juvenile, and a pregnant or nursing female will have significantly different energetic requirements compared to a non-pregnant, non-lactating adult female of similar age and size.

Daily energy requirements of grey whales (standardized to a 19.6 mt whale) have been previously estimated to range from 1,088 to 2,176 MJ day^{-1} (Table 10), which encompasses my estimate of 1,291 ± 213 MJ day^{-1}. When the restricted feeding season is taken into account, my model shows that whales feeding for 6.5 months will need to consume a minimum of 2,455 ± 404 MJ day^{-1}, which is less than the 3,182 MJ day^{-1} that Highsmith and Coyle (1992) predicted grey whales consume during 6 months of feeding.

My estimates for food requirements (869 ± 134 kg of prey day^{-1}) fall within the range of prior estimates for the amount of food that an average grey whale consumes per day—from ~400 kg (Nerini 1984) to 1,000–1,200 kg day^{-1} (Zimushko and Lenskaya 1970; Rice and Wolman 1971; Brodie 1975). My estimates for grey whale prey consumption are based on an average energetic density of prey available to grey whales in the Arctic feeding grounds—the Chukchi and Bering Seas. The amount of prey that each whale needs to consume will likely differ from these estimates depending on different prey species that may be most abundant in their chosen feeding areas. The dominant prey species ingested in the Arctic feeding grounds are Ampeliscid amphipods (Coyle et al. 2007), whereas the dominant prey species ingested by the PCFG along the migration route are more varied.

Table 10. Comparisons of estimates for energetic requirements.

Source	Whale weight (mt)	Energy requirement ($\times 10^5$ kcal day^{-1})	Standardized to 19.6 mt whale ($\times 10^5$ kcal day^{-1})	(MJ day^{-1})
Rice and Wolman (1971)	14.0	2.7	3.7	1,548
Sumich (1983)	13.6	2.9	3.7	1,548
Thomson and Martin (1986)	23.0	3.0	2.6	1,088
Highsmith and Coyle (1992)	19.6	5.2	5.2	2,176
This paper	**19.6**	**3.0**	**3.0**	**1,291**

The energy and food requirements presented here are minimum estimates of energy each individual grey whale requires to complete an annual migration from the birthing lagoons in Mexico to the Arctic feeding grounds in the Chukchi and Bering Seas, and back. It is possible and very likely that grey whales consume more energy per day in terms of prey mass compared to the estimates presented here, depending on the amount of prey available to them at any given time.

2.4.5 Separating reproductive costs into pregnancy and lactation

Reproduction is the most energy intensive biological process a female whale can undergo, and each stage of the reproductive cycle has differing energy needs. I calculated the costs of each reproductive stage by separating the reproductive cycle into pregnancy and lactation. Gestation in grey whales can occur over the span of 13 months, and the overall reproductive cycle occurs over a period of just under 2 years (Rice 1983; Villegas-Amtmann et al. 2015). Observed dates of birth for grey whale calves range from January 5 to February 15 (Rice 1983).

Adult and juvenile grey whales do not generally feed during the northward migration, and opportunities for lactating mothers to forage for prey while migrating north with their nursing calf are limited. I therefore assumed that the energy required to support lactation for a nursing calf during the first 6 months needed to be acquired during pregnancy, and that the energy required for the latter 4 months of lactation would come from prey consumed on the Arctic feeding grounds. I therefore assumed that the cost of milk production from birth to weaning equalled the sum of the energy required for the calf to grow (production cost) and the total energetic expenditure of calves at each activity stage. I also assumed that the cost of milk production beyond these considerations were negligible (Villegas-Amtmann et al. 2015).

There is limited information available on the nutritional composition of grey whale milk (Zenkovich 1938; Tomilin 1946), and no available empirical measures for milk assimilation efficiency of grey whale calves. Other bioenergetic models (Villegas-Amtmann et al. 2015) have assumed that milk assimilation efficiency for grey whale calves are similar to values reported for six northern elephant seals, ranging from 80% to 100% milk assimilation efficiency (Costa et al. 1986). Given that northern elephant seals tend to have a compressed lactation period of 2.5 months, characterized by abrupt weaning (Costa et al. 1986), a high rate of milk assimilation efficiency would benefit elephant seal pups. Grey whales on the other hand, have a longer period of lactation, and no evidence of abrupt cessation of nursing. I therefore assumed a more conservative estimate of milk assimilation efficiency at around 80%, similar to prey digestive efficiencies reported by Thomson and Martin (1986).

2.4.6 Daily energy requirements higher for pregnant than lactating females

Energetic costs for mammals to produce milk are generally higher than the costs of pregnancy (Lockyer 2007; Rosen and Worthy 2018). However, grey whales need to consume significantly more prey during pregnancy compared to females nursing calves on the foraging grounds (Figure 11 and Figure 12) because pregnant females must cover the cost of foetal growth, plus store enough energy to produce 6 months of milk needed to feed the calf in Mexico. Increasing energy intake while pregnant on the Arctic feeding grounds while food is abundantly available (Le Boeuf et al. 2000; Villegas-Amtmann et al. 2015, 2017) is a strategy that reduces dependence on environmental conditions at the time and place that calves are born, which is different from the strategy used by income breeders that feed throughout the reproductive cycle (Stephens et al. 2014).

Mysticetes are known to fast or consume minimal food during lactation (Oftedal 1997, 2000; Rosen and Worthy 2018). In the case of grey whales, lactation begins in the breeding lagoons in Mexico and continues during northbound migration when little if any feeding occurs (Perryman and Lynn 2002; Villegas-Amtmann et al. 2015). As such, pregnant grey whales need to consume and store sufficient energy to support (i) herself and her growing foetus during the southbound migration, (ii) parturition (the process of giving birth) and nursing in the lagoons, and (iii) daily maintenance and lactation during the northbound migration (Rice and Wolman 1971). These energy needs are reflected in the 35% average weight gain noted by Rice and Wolman (1971) in pregnant females compared to whales that had recently ovulated or recently weaned a calf. Approximately 1,000–2,000 kg of the increased weight can be attributed to the foetus and associated membranes and fluids, and the remaining amount corresponds to increases in fat stores (Rice and Wolman 1971).

Northbound grey whales passing San Francisco, have been estimated to weigh ~11–29% less than southbound whales travelling past the same area (Rice and Wolman 1971). Among these whales, lactating females travelling north were observed to have the narrowest girth to length ratios compared to other cohorts (Perryman and Lynn 2002). These decreases in body size reflect the high energetic costs of lactation.

2.4.7 Weaning likely occurs over a period of 2 to 3 months

Grey whales are believed to begin weaning at ~7 months old (Rice and Wolman 1971; Sumich et al. 2013; Villegas-Amtmann et al. 2015, 2017) based on benthic prey being in the stomachs of young whales (8.5–9 m long) harvested in August, September and October (Rice and Wolman 1971). However, the presence of solid food is insufficient to confirm when weaning ends because of the difficulty of detecting small amounts of milk when stomach contents also contain remains of prey (Best et al. 1984; Oftedal 1997). Therefore, relying on stomach contents alone can underestimate age at weaning.

Weaning is likely to also be accompanied by decreases in growth rates as calves stop receiving energy-rich milk and learn how to forage on less nutritious benthic invertebrates. Calves grow rapidly until ~9.6 months, after which growth rates slow (Agbayani et al. 2020). I therefore assumed that grey whales begin supplementing their milk diet with solid food at around 7 months and are fully weaned by ~9.6 months of age (Costa and Williams 1999; Bradford et al. 2012; Agbayani et al. 2020).

2.4.8 Future directions

The estimated energy requirements I derived are valid for the eastern North Pacific population of grey whales, but are not applicable to the PCFG which do not travel as far north to feed. The PCFG have a different migration timeline and activity budget, and also feed on different prey species. Prey availability along the coast of North America differs from the Arctic feeding grounds in terms of caloric content and patchiness (Hildebrand 2020). Further work to apply this model to estimate the energy requirements for the Pacific Coastal Feeding Group (PCFG) would require PCFG-specific migration timings and estimates for the energetic density of region-specific prey.

Prey availability in the Arctic feeding grounds are likely to be affected by changing environmental conditions associated with climate change. Changes in grey whale foraging behaviour such as shifts in foraging areas and changes in targeted prey species have been attributed to climate change (Moore et al. 2003, 2022; Salvadeo et al. 2013). Further work on linking prey hotspots with annual and seasonal environmental patterns will be useful for predicting prey availability in the face of climate change (Grebmeier et al. 2015; Moore et al. 2022). My results can be combined with estimates of prey availability within summer foraging grounds to evaluate the effects of climate change on the probability of foraging and migration success.

My estimates of energy requirements used data from respiration rates to characterize total energetic expenditure to better represent activity costs in the model. The search for the 'perfect' model is arguably futile, but the goal of a model is to get as close to representing reality as possible (Box 1976; Posada and Buckley 2004). While adding parameters to a model may help to effectively capture real life complexity, Occam's Razor (i.e., William of Occam's principle of parsimony) states that the simplest model is likely to be the best one (Posada and Buckley 2004). Added parameters may have less data or higher uncertainty associated with them (Posada and Buckley 2004), possibly rendering model results less useful. It may be valuable to compare my estimates for gross energy requirements with estimates calculated using a simple activity index, where the parameter A is the proportion of time spent in each activity stage (Winship et al. 2002; Fortune et al. 2013; Rechsteiner et al. 2013a). It would be an interesting exercise to examine how grey whale energy requirement estimates would differ between activity index methods used in other studies and this method using observed respiration rates (e.g., Bejarano et al. 2017) .

Refinements to the model can be made over time, as new information becomes available from continued research on the migration, behaviour, diets, and physiology of grey whales. Future model updates and applications can incorporate new information as it becomes available, and additional sensitivity analyses can also be done (i.e. increasing/decreasing parameters incrementally by various percentages) to further examine the sensitivity of the model results to the input parameters.

2.4.9 Conclusion

My results represent estimates of energy requirements (in MJ day^{-1}) and food requirements (in kg of prey) for grey whales of various ages, sizes, and reproductive status (pregnant and lactating) to complete an annual migration. My results can be combined with estimates of prey availability within summer foraging grounds to evaluate the effects of climate change on the probability of foraging success. The energetics model can also be used to explore the unique energy needs of the different groups of grey whales, such as the Pacific Coastal Feeding Group (PCFG) and the endangered western population. Where sufficient data is available, models similar to the one I developed for grey whales can also be developed for other rare or endangered migratory species to inform management decisions and recovery efforts.

Chapter 3: Research Conclusions

3.1 Summary of findings

Estimating the food requirements of grey whales contributes towards understanding the impacts of reduced food availability on the survival of grey whales in the Eastern North Pacific. In recent years, the recovering eastern North Pacific population of grey whales have experienced unusually high mortality events. Various possible reasons have been brought forward to try and explain what may have caused these high mortality events, including (i) decreased prey availability due to changes in climate, (ii) increased population numbers putting pressure on the prey resources to the point where prey resources can no longer support the entire whale population, or (iii) a combination of the two.

Chapter 2 used a mathematical model to estimate the energy requirements of grey whales of all ages and reproductive stages. My estimates are consistent with existing estimates of energy requirements for a grey whale weighing 19,600 kg. The approach I used went further than others have done to date by providing a more complete overview of the relationship between grey whales and their prey. Most notably, I estimated the energy requirements for grey whales of various ages throughout their lifespan. Breaking down the components of the grey whale life history allows for more detailed and in-depth analyses for individuals at different life stages.

The importance of analyzing energy requirements for each life stage is highlighted for reproductive females. As expected, my results indicated that pregnant and lactating females require more energy during the reproductive cycle compared to non-reproducing adults. However, pregnant whales need to consume more food per day during their pregnancy compared to the lactation period, which was contrary to my expectations that lactating whales would need to consume the most food on a daily basis compared to other cohorts. Upon closer examination of the results, the higher energy requirement for pregnant whales is due to grey whale mothers fasting during the first 6 months of lactation. They therefore need to consume the energy required in advance by increasing their feeding rates during pregnancy. My estimates by life stage also highlighted that rapid growth rates of juveniles lead to higher food and energy requirements per body mass compared to adults.

3.2 Summary of strengths and weaknesses

The bioenergetic model I presented here improves the understanding of energy requirements of grey whales because it uses a comprehensive growth model that takes into account a comprehensive set of age-length-mass data and provides age specific mass values for the model rather than a stage based model (Agbayani et al. 2020). This allowed me to estimate the energy requirements of grey whales from birth to maturity, based on their estimated increases in body mass as they grow. Prior estimates of energy requirements have been based on the mass of a typical or average whale at 19.6 mt (Highsmith and Coyle 1992), and present only a snapshot of what the whales might need to consume in their lifetime. The results I present are conservative and represent only the minimum energy required for a typical grey whale of a certain age or size at a given life stage to complete an annual migration. Typical consumption rates of healthy whales will likely be greater than the values I present here.

One of the strengths of my model is that it is based on an explicit migration timeline (Figure 2; Table 2). I reviewed existing literature on grey whale sightings at various points along the migration and estimated the average amount of time each cohort would spend within each activity stage. I combined these estimates with information on the length of gestation in grey whales (~13 months), approximate range of birth dates (Jan 5–Feb 13; Rice 1983), and the average amount of time it takes for a grey whale to undergo a complete reproductive cycle of just under two years (Rice 1983; Villegas-Amtmann et al. 2015). The result is a detailed and comprehensive description of the migration timeline for every grey whale cohort, which has not been previously done. This information allowed me to account for sex- and season-specific behavioural differences in my model in a way that may not be entirely captured by other models (Bejarano et al. 2017). This modular method of accounting for the migration is useful for making comparisons between groups of whales that may follow slightly different migration timelines and have different activity budgets (e.g., comparing the Pacific Coastal Feeding Group (PCFG) with the rest of the Eastern grey whale population). Data sources and information on decision points for the migration timeline are available in Appendix C.

Another strength of my model is the integration of total energetic expenditure. Bioenergetic models developed for other species (e.g., North Atlantic Right whales; Fortune et al. 2013) have been based on limited information for field metabolic rates. Estimates of respiration rates for species such as North Atlantic Right whales were not available, and metabolic costs of activity were estimated using a coarse activity index (A) from activity budgets, and Kleiber's (1961) predictive equation for basal metabolic rate (BMR) as a function of body mass. However, for grey whales, field observations of breathing rates for various activity states are available and estimates for total energetic expenditure have been modelled based on this data. Various assumptions contributed to uncertainty in model predictions as a result of using respiration rates to estimate metabolism (Fahlman et al. 2016). Nevertheless, my model is an improvement over prior models.

While data refinements have contributed to more detailed estimates of energy requirements for grey whales, there remain logistical challenges in obtaining empirical observation data for free swimming whales engaged in various activity states. These logistical challenges translate into data gaps that are filled by using model estimates that cannot easily be validated with field observations and data. For example, I estimated the approximate time when a calf would be fully weaned based on a growth model (Agbayani et al. 2020) derived from historical observations of hunted whales. Similar measurements are unavailable for contemporary whales since whaling has been restricted. Such historical observations may not be representative of contemporary whales because possible changes in the population since hunting ceased have not been effectively captured. I therefore assumed that the time of weaning has not significantly changed for contemporary whales. I also calculated milk requirements using limited information on the nutritional composition of grey whale milk (Zenkovich 1938; Tomilin 1946), and had no empirical measures for milk assimilation efficiency of grey whale calves. I therefore assumed a conservative assimilation efficiency of 80%, matching the assimilation efficiencies for prey (Thomson and Martin 1986).

3.3 Future directions

In the future, my model can be adapted to other grey whale populations (e.g. the Western Grey Whales) and to unique subsets of the population, such as the PCFG. My model assumes that grey whales feed during the summer in the Arctic foraging grounds and fast along the migration route and in the breeding lagoons. While most whales in the eastern North Pacific population likely follow this pattern, the PCFG have a different migration timetable and suite of preferred prey. This bioenergetics model could be parametrized specifically for PCFG migration timings and caloric content of specific prey species to better estimate their energy requirements. This can be similarly done with Western Grey whales assuming that they are indeed morphometrically and behaviourally similar to the Eastern North Pacific population (Yablokov and Bogoslovskaya 1984). Beyond grey whales, my model can be further adapted for other migratory species of concern where sufficient information for input parameters are available.

3.4 Conclusion

I have estimated the minimum energy and food requirements that every age cohort of grey whales would need to complete an annual migration. If prey availability does not meet the minimum energy needs of individual grey whales, mortality rates are likely to increase in a given year. Factors that may affect prey availability include decreases in prey abundance caused by climate related events (e.g., increased temperatures or acidification of the ocean) or non-sustainable consumption (e.g., should the grey whale population exceed the carrying capacity of the system), or a combination of both. My results can be used in conjunction with information on prey density and availability in the Arctic foraging grounds (Wilt et al. 2014) and along the migration route (Hildebrand et al. 2021) to assess and anticipate high stress years with increased likelihood of starvation-related mortality events occurring, be it due to competition from increased population numbers, or lack of access to prey in the feeding grounds due to environmental variability (e.g., delayed ice melt or increased acidification of ocean waters), or a combination of both. Predictive models coupling environmental factors and benthic prey hotspots can be used to anticipate these potentially high stress years, and steps can be taken to protect grey whales in key foraging areas both in the Arctic foraging grounds and along the migration route from increased anthropogenic activity during those periods.

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Appendices

Appendix A Grey whale growth models

A.1 Age-Length relationship

Putter growth models fit to grey whale data for size (*S*) at age (*t*) data.

$$S_t = A\left(1 - e^{-k(t-t_0)}\right)$$

Size is measured as standard length (in meters), and age is measured in decimal years. *A* represents asymptotic size, t_0 is time at which size is zero, and *k* is a fitted parameter indicative of growth rate (Agbayani et al. 2020).

```
## Putter Growth Curve Phase 1
## -----------------------------------------------------------------
## Formula: length_m ~ A * (1 - (exp(-k * (age_yrs - t0))))
##
## Parameters:
##    Estimate Std. Error t value Pr(>|t|)
## A   9.47498    0.18885   50.17   <2e-16 ***
## k   1.84657    0.15072   12.25   <2e-16 ***
## t0 -0.36038    0.02095  -17.20   <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 0.3841 on 217 degrees of freedom
##
## Number of iterations to convergence: 15
## Achieved convergence tolerance: 1.607e-06
```

```
## Putter Growth Curve Phase 2
## -----------------------------------------------------------------
## Formula: length_m ~ A * (1 - (exp(-k * (age_yrs - t0))))
##
## Parameters:
##    Estimate Std. Error t value Pr(>|t|)
## A  12.81614    0.05562  230.42   <2e-16 ***
## k   0.18010    0.01019   17.67   <2e-16 ***
## t0 -5.08708    0.40030  -12.71   <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 0.6128 on 428 degrees of freedom
##
## Number of iterations to convergence: 7
## Achieved convergence tolerance: 2.504e-06
```

A.2 Length-Mass relationship

Body mass was estimated using an allometric length–mass relationship ($W = aL^b$), which was linearized in logarithmic form:

$$log_{10}W = log_{10}a + b \cdot log_{10}L$$

where W represents mass in kg, L represents length in meters, a is a constant factor, and b is an exponential constant (Agbayani et al. 2020).

```
## Length vs. Mass
## Call:
## lm(formula = log10_mass_kg ~ log10_length_m)
##
## Residuals:
##      Min       1Q   Median       3Q      Max
## -0.11144 -0.05568  0.00425  0.04750  0.12669
##
## Coefficients:
##                Estimate Std. Error t value Pr(>|t|)
## (Intercept)      1.0354     0.1590   6.511 1.97e-05 ***
## log10_length_m   2.9509     0.1693  17.427 2.14e-10 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 0.07205 on 13 degrees of freedom
## Multiple R-squared:  0.9589, Adjusted R-squared:  0.9558
## F-statistic: 303.7 on 1 and 13 DF,  p-value: 2.143e-10
```

Appendix B Parameter values by age

B.1 Mass change and Production Cost

Table 11. Estimates for mean change in mass (ΔM) in kg and mean production cost (P) in MJ per month of growth in the first year. Mean mass change for neonatal represents the mass change from conception to birth; mean mass change for the other rows represent growth over the full year (i.e., the 1st month represents the mass change from birth to the end of January). Uncertainty values represent the standard deviation (± *SD*) around the mean of 10,000 Monte Carlo estimates.

Phase 1 - Calves		
Age (mos.)	Mean ΔMass (kg) ± *SD*	Mean P (MJ) ± *SD*
neonatal	983 ± 27	16981 ± 821
1	515 ± 11	8725 ± 396
2	505 ± 16	8388 ± 440
3	577 ± 18	9568 ± 491
4	554 ± 12	9190 ± 431
5	551 ± 8	9152 ± 402
6	503 ± 2	8349 ± 345
7	482 ± 1	7995 ± 330
8	440 ± 1	7345 ± 301
9	385 ± 3	6469 ± 269
10	306 ± 120	5151 ± 2023
11	133 ± 5	2233 ± 119
12	137 ± 5	2308 ± 127

Table 12. Estimates for mean change in mass (ΔM) in kg and mean production cost (P) in MJ per year of growth for juveniles and adults. Values shown here represents mean mass attained and production cost over the full year of growth (i.e., the first year represents the time from birth to 1 year of age). Mean mass change begins to approach 0 at ~50 y. Uncertainty values represent the standard deviation (± *SD*) around the mean of 10,000 Monte Carlo estimates.

Phase 2 - Juveniles and non-reproductive adults		
Age (y)	Mean ΔMass (kg) ± *SD*	Mean P (MJ) ± *SD*
1	5089 ± 178	84496 ± 4573
2	1603 ± 40	26999 ± 1293
3	1536 ± 14	25873 ± 1080
4	1428 ± 9	24066 ± 989
5	1300 ± 19	21896 ± 947
6	1163 ± 17	19586 ± 848
7	1026 ± 6	17291 ± 709
8	897 ± 4	15109 ± 617
9	777 ± 3	13094 ± 535
10	669 ± 7	11272 ± 472
11	573 ± 9	9652 ± 419
12	488 ± 9	8230 ± 366
13	415 ± 8	6992 ± 314
14	352 ± 6	5923 ± 261
15	297 ± 2	5005 ± 207
16	251 ± 1	4221 ± 172
17	211 ± 3	3555 ± 151
18	177 ± 4	2989 ± 140
19	149 ± 6	2511 ± 143
20	125 ± 6	2107 ± 139
21	105 ± 6	1767 ± 130
22	88 ± 7	1480 ± 133
23	74 ± 7	1240 ± 122
24	62 ± 7	1038 ± 121
25	52 ± 6	869 ± 104
26	43 ± 5	727 ± 94
27	36 ± 5	608 ± 85
28	30 ± 5	508 ± 80
29	25 ± 4	425 ± 68
30	21 ± 4	425 ± 68

Table 13. Estimates for mean change in mass (ΔM) in kg and mean production cost (P) in MJ per year of growth for pregnant females. Mean mass change for each year represents the mass attained over the full year of growth (i.e., the values for age 8 y represents the time between 7 and 8 years of age), not including the mass of the foetus (production cost of a newborn grey whale is calculated separately from the mother). Mean mass change begins to approach 0 at ~50 y. Uncertainty values represent the standard deviation (± *SD*) around the mean of 10,000 Monte Carlo estimates.

Pregnant females		
Age (y)	Mean ΔMass (kg) ± *SD*	Mean P (MJ) ± *SD*
8	922 ± 4	24695 ± 232
9	799 ± 3	21401 ± 202
10	688 ± 7	18424 ± 238
11	589 ± 9	15776 ± 267
12	502 ± 9	13451 ± 261
13	427 ± 8	11427 ± 230
14	362 ± 6	9680 ± 179
15	306 ± 2	8181 ± 94
16	258 ± 1	6900 ± 61
17	217 ± 3	5810 ± 84
18	182 ± 4	4885 ± 117
19	153 ± 6	4103 ± 163
20	129 ± 6	3443 ± 175
21	108 ± 6	2887 ± 174
22	90 ± 7	2420 ± 188
23	76 ± 7	2026 ± 177
24	63 ± 7	1696 ± 180
25	53 ± 6	1420 ± 155
26	44 ± 5	1188 ± 141
27	37 ± 5	993 ± 129
28	31 ± 5	831 ± 123
29	26 ± 4	694 ± 105
30	22 ± 4	580 ± 96

Table 14. Estimates for mean change in mass (ΔM) in kg and mean production cost (P) in MJ per year of growth for lactating females. Mean mass change for each year represents the mass the mass attained over the full year of growth (i.e., the values for age 8 y represents the time between 7 and 8 years of age), not including mass gained from pregnancy. Mean mass change begins to approach 0 at ~50 y. Uncertainty values represent the standard deviation (± *SD*) around the mean of 10,000 Monte Carlo estimates.

	Lactating females	
Age (y)	Mean ΔMass (kg) ± *SD*	Mean P (MJ) ± *SD*
8	922 ± 4	19849 ± 2576
9	799 ± 3	17201 ± 2232
10	688 ± 7	14808 ± 1926
11	589 ± 9	12680 ± 1654
12	502 ± 9	10811 ± 1414
13	427 ± 8	9185 ± 1202
14	362 ± 6	7780 ± 1017
15	306 ± 2	6575 ± 854
16	258 ± 1	5546 ± 720
17	217 ± 3	4670 ± 608
18	182 ± 4	3926 ± 516
19	153 ± 6	3298 ± 446
20	129 ± 6	2768 ± 384
21	108 ± 6	2321 ± 331
22	90 ± 7	1945 ± 293
23	76 ± 7	1629 ± 254
24	63 ± 7	1363 ± 228
25	53 ± 6	1141 ± 193
26	44 ± 5	954 ± 168
27	37 ± 5	798 ± 146
28	31 ± 5	667 ± 131
29	26 ± 4	558 ± 111
30	22 ± 4	466 ± 98

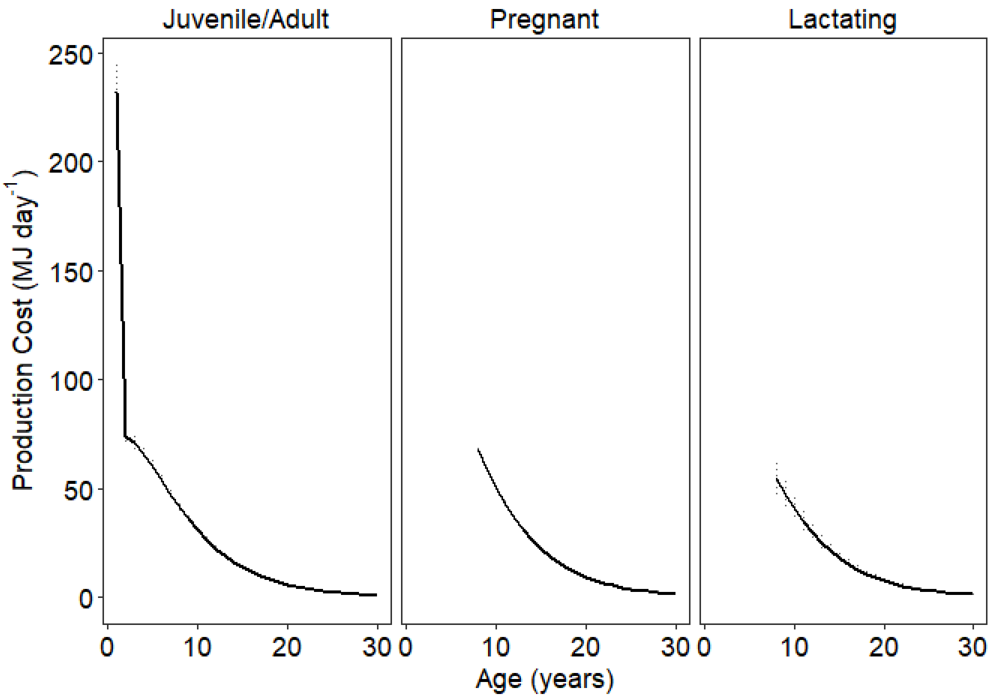

Figure 15. Estimates for mean production cost (P) in MJ per year of growth for grey whales. Uncertainty values represent the standard deviation (± *SD*) around the mean of 10,000 Monte Carlo estimates.

B.2 Gross Energy Requirements and Food Requirements

Table 15. Estimates for daily gross energy requirements and milk/food requirements for grey whale calves. Milk requirements were calculated using the mean energetic density of mother's milk at 53% lipid content. Food requirements were calculated using the mean energetic density of benthic invertebrate prey available in the Arctic feeding grounds. Estimates represent the energy/food requirements over the full month (i.e., the 1st month represents the time from birth to the end of January). Uncertainty values represent the standard deviation (± *SD*) around the mean of 10,000 Monte Carlo estimates.

Phase 1 – Calves		
Age (mo.)	Daily GER (MJ day^{-1}) ± SD	Milk/Food requirements (day^{-1}) ± SD
1	538 ± 73	24 ± 3 L milk
2	571 ± 79	26 ± 4 L milk
3	618 ± 90	28 ± 4 L milk
4	530 ± 64	24 ± 3 L milk
5	545 ± 70	25 ± 3 L milk
6	599 ± 80	27 ± 4 L milk
7	744 ± 121	34 ± 5 L milk
8	763 ± 130	34 ± 6 L milk
9	778 ± 139	35 ± 6 L milk
10	713 ± 208	245 ± 68 kg prey
11	572 ± 125	197 ± 41 kg prey
12	585 ± 129	201 ± 42 kg prey

Table 16. Estimates for daily gross energy requirements and food requirements for juveniles and non-reproductive adult grey whales per year. Food requirements were calculated using the mean energetic density of benthic invertebrate prey available in the Arctic feeding grounds. Estimates represent the energy/food requirements over the full year (i.e., the 1st year represents requirements from birth to the end of the first year). Uncertainty values represent the standard deviation (± *SD*) around the mean of 10,000 Monte Carlo estimates. *See Table 15 for energy and food/milk requirements for the 1st year.

Phase 2 – Juveniles and non-reproductive adults				
Age (y)	Daily GER (MJ day^{-1}) ± SD	Daily GER –foraging season (MJ day^{-1}) ± SD	Food Requirements (kg benthic inverts)	% Body weight consumed
1	656 ± 128	656 ± 128	*	
2	527 ± 81	1003 ± 153	345 ± 48	4.5 ± 0.54
3	626 ± 95	1190 ± 180	409 ± 57	4.4 ± 0.55
4	718 ± 110	1364 ± 209	470 ± 66	4.4 ± 0.56
5	801 ± 124	1523 ± 236	524 ± 75	4.4 ± 0.56
6	876 ± 138	1666 ± 262	573 ± 83	4.4 ± 0.57
7	942 ± 149	1791 ± 284	616 ± 90	4.4 ± 0.58
8	999 ± 159	1900 ± 303	654 ± 96	4.3 ± 0.58
9	1048 ± 168	1993 ± 319	686 ± 101	4.3 ± 0.59
10	1091 ± 175	2074 ± 332	714 ± 105	4.3 ± 0.59
11	1127 ± 181	2142 ± 344	737 ± 109	4.3 ± 0.59
12	1157 ± 186	2200 ± 353	757 ± 112	4.3 ± 0.6
13	1183 ± 190	2250 ± 361	774 ± 114	4.3 ± 0.6
14	1206 ± 193	2292 ± 368	789 ± 116	4.3 ± 0.6
15	1224 ± 196	2327 ± 373	801 ± 118	4.3 ± 0.6
16	1240 ± 199	2357 ± 379	811 ± 120	4.3 ± 0.6
17	1254 ± 202	2383 ± 383	820 ± 121	4.3 ± 0.6
18	1265 ± 204	2405 ± 387	828 ± 122	4.3 ± 0.6
19	1275 ± 206	2423 ± 391	834 ± 124	4.3 ± 0.6
20	1283 ± 207	2439 ± 394	839 ± 125	4.3 ± 0.6
21	1290 ± 209	2452 ± 397	844 ± 126	4.3 ± 0.6
22	1296 ± 210	2463 ± 400	848 ± 126	4.3 ± 0.6
23	1301 ± 211	2472 ± 402	851 ± 127	4.3 ± 0.6
24	1305 ± 212	2480 ± 404	854 ± 128	4.3 ± 0.6
25	1308 ± 213	2487 ± 405	856 ± 128	4.3 ± 0.6
26	1311 ± 214	2493 ± 407	858 ± 129	4.3 ± 0.6
27	1314 ± 215	2497 ± 408	859 ± 129	4.3 ± 0.6
28	1316 ± 215	2502 ± 409	861 ± 129	4.3 ± 0.6
29	1318 ± 216	2505 ± 410	862 ± 130	4.3 ± 0.6
30	1319 ± 216	2508 ± 411	863 ± 130	4.3 ± 0.6

Table 17. Estimates for daily gross energy requirements and food requirements for pregnant grey whales per year. Food requirements were calculated using the mean energetic density of benthic invertebrate prey available in the Arctic feeding grounds. Estimates represent the energy/food requirements over the full year (i.e., 8th year represents the time between 7 and 8 years of age). Uncertainty values represent the standard deviation (± *SD*) around the mean of 10,000 Monte Carlo estimates.

Pregnant females				
Age (y)	Daily GER (MJ day^{-1}) ± SD	Daily GER–foraging season (MJ day^{-1}) ± SD	Food Requirements (kg benthic inverts)	% Body weight consumed
8	1821 ± 211	4713 ± 546	1625 ± 190	10.25 ± 1.08
9	1877 ± 222	4857 ± 574	1675 ± 200	10.05 ± 1.09
10	1924 ± 231	4980 ± 599	1718 ± 208	9.90 ± 1.10
11	1964 ± 239	5085 ± 619	1754 ± 215	9.77 ± 1.11
12	1999 ± 245	5173 ± 635	1784 ± 221	9.67 ± 1.11
13	2028 ± 251	5248 ± 649	1810 ± 226	9.59 ± 1.12
14	2052 ± 255	5312 ± 661	1832 ± 230	9.53 ± 1.12
15	2073 ± 259	5365 ± 670	1851 ± 233	9.47 ± 1.12
16	2091 ± 262	5411 ± 679	1866 ± 236	9.43 ± 1.12
17	2106 ± 266	5450 ± 688	1880 ± 239	9.39 ± 1.13
18	2119 ± 269	5483 ± 695	1891 ± 242	9.37 ± 1.13
19	2130 ± 271	5512 ± 702	1901 ± 244	9.34 ± 1.13
20	2139 ± 273	5536 ± 708	1909 ± 246	9.32 ± 1.13
21	2147 ± 275	5557 ± 713	1916 ± 248	9.31 ± 1.13
22	2154 ± 277	5574 ± 717	1922 ± 249	9.30 ± 1.13
23	2159 ± 279	5589 ± 721	1928 ± 251	9.29 ± 1.13
24	2164 ± 280	5601 ± 725	1932 ± 252	9.28 ± 1.13
25	2168 ± 281	5612 ± 728	1936 ± 253	9.27 ± 1.13
26	2172 ± 282	5621 ± 730	1939 ± 254	9.27 ± 1.13
27	2175 ± 283	5629 ± 732	1941 ± 254	9.26 ± 1.13
28	2177 ± 284	5635 ± 734	1944 ± 255	9.26 ± 1.13
29	2179 ± 284	5641 ± 736	1946 ± 256	9.26 ± 1.12
30	2181 ± 285	5645 ± 737	1947 ± 256	9.26 ± 1.12

Table 18. Estimates for daily gross energy requirements and food requirements for lactating grey whales per year. Food requirements were calculated using the mean energetic density of benthic invertebrate prey available in the Arctic feeding grounds. Estimates represent average requirements per year (i.e., the 8th year represents the time between 7 and 8 years of age). Uncertainty values represent the standard deviation (± *SD*) around the mean of 10,000 Monte Carlo estimates.

Lactating females				
Age (y)	Daily GER (MJ day^{-1}) ± SD	Daily GER–foraging season (MJ day^{-1}) ± SD	Food Requirements (kg benthic inverts)	% Body weight consumed
8	1821 ± 211	4713 ± 546	1625 ± 190	10.25 ± 1.08
9	1877 ± 222	4857 ± 574	1675 ± 200	10.05 ± 1.09
10	1924 ± 231	4980 ± 599	1718 ± 208	9.90 ± 1.10
11	1964 ± 239	5085 ± 619	1754 ± 215	9.77 ± 1.11
12	1999 ± 245	5173 ± 635	1784 ± 221	9.67 ± 1.11
13	2028 ± 251	5248 ± 649	1810 ± 226	9.59 ± 1.12
14	2052 ± 255	5312 ± 661	1832 ± 230	9.53 ± 1.12
15	2073 ± 259	5365 ± 670	1851 ± 233	9.47 ± 1.12
16	2091 ± 262	5411 ± 679	1866 ± 236	9.43 ± 1.12
17	2106 ± 266	5450 ± 688	1880 ± 239	9.39 ± 1.13
18	2119 ± 269	5483 ± 695	1891 ± 242	9.37 ± 1.13
19	2130 ± 271	5512 ± 702	1901 ± 244	9.34 ± 1.13
20	2139 ± 273	5536 ± 708	1909 ± 246	9.32 ± 1.13
21	2147 ± 275	5557 ± 713	1916 ± 248	9.31 ± 1.13
22	2154 ± 277	5574 ± 717	1922 ± 249	9.30 ± 1.13
23	2159 ± 279	5589 ± 721	1928 ± 251	9.29 ± 1.13
24	2164 ± 280	5601 ± 725	1932 ± 252	9.28 ± 1.13
25	2168 ± 281	5612 ± 728	1936 ± 253	9.27 ± 1.13
26	2172 ± 282	5621 ± 730	1939 ± 254	9.27 ± 1.13
27	2175 ± 283	5629 ± 732	1941 ± 254	9.26 ± 1.13
28	2177 ± 284	5635 ± 734	1944 ± 255	9.26 ± 1.13
29	2179 ± 284	5641 ± 736	1946 ± 256	9.26 ± 1.12
30	2181 ± 285	5645 ± 737	1947 ± 256	9.26 ± 1.12

Appendix C Grey whale migration timeline

C.1 Migration timings and respiration rates (breaths per minute) for all life stages.

Table 19. Details on migratory timings and respiration rates for all grey whale life stages, broken down by month. Direct quotes from sources are provided where available; alternate spellings for species names (e.g., gray vs. grey) are preserved. ****Decision points and assumptions used in the model are noted.*

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
1	Calf	Lagoon 0-1 mths (Jan)	calving grounds	31	"The earliest births are reported in early January and newborn calves are not seen after mid-February (Jones and Swartz, 1984). Most births occur in the last half of January, with variations in the mean date of birth of no more than two weeks from one year to the next (Rice et al, 1981)." – pg 84, Sumich (Sumich 1986) "Rice et al. (1981) reported that in Laguna Ojo de Liebre most births occur until around 15 February, and estimated 27 January as the mean date for births." Pg 35 – Findley & Vidal (2002) "Reconstruction of the migration from all available data shou's that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December." Pike (1962)	2.14 ± 0.5	From Sumich (1986) (0 mo: 2.14 ± 0.5, 1 mo:1.56 ± 0.4, 2 mo: 1.39 ± 0.3 breaths min−1) cited in Villegas-Amtmann et al. (2017) **I assume breath rates for 0 mo applies to time period between birth to end of Jan, breath rates for 1 mo applies to Jan-Feb, and breath rates for 2 mo applies to Feb-Mar.*
2	Calf	Lagoon 2 mth (Feb)	calving grounds	28	"Calves occupy these lagoons with their mothers until late March or early April when they commence their northward migration." – pg 84, Sumich (1986) "Reconstruction of the migration from all available data shou's that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June	1.56 ± 0.4	From Sumich (1986) (0 mo: 2.14 ± 0.5, 1 mo:1.56 ± 0.4, 2 mo: 1.39 ± 0.3 breaths min−1) cited in Villegas-Amtmann et al. (2017) **I assume breath rates for 0 mo applies to time period*

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					through October, and migrates southward in November and December.” Pike (1962) “during the 61 days spent at Tojahui, a total of only two cow/calf pairs and a solitary adult were seen (Table 1). The presence of these whales off Tojahui was often sporadic during the 36-day period between initial and final sightings (21 January and 25 February), with the cow/calf pairs and the solitary adult moving seemingly independently into and out of the observational area. During 16 days of this 36-day period, at least one cow/calf pair (probably the same pair) was present, but only occasionally along with the other pair and/or the lone adult. […] For 1984, the maximum number of whales observed for one day was six (3 cow/calf pairs) on 29 January. Again, presence of the whales off Tojahui was sporadic between the initial and final sightings (20 January and 12 February), with at least one of the cow/calf pairs seen during a non-consecutive eight-day period. […]For the 1985-1987 seasons, numbers of gray whales (all from reports by informants) were (Table 1): for 1985, two unaccompanied ‘adults’ off Tojahui on ca 11 January, and an ‘adult’ (one of the previously sighted two?) off Bajerobeta on 15 January; for 1986, one ‘adult’ off Bajerobeta in early January and ‘some cow/calf pairs’ during February; for 1987, ‘some whales’ (including at least one cow/calf pair) in late January and early February.” – pg 30, Findley & Vidal (2002)		*between birth to end of Jan, breath rates for 1 mo applies to Jan-Feb, and breath rates for 2 mo applies to Feb-Mar.*
3	Calf	Lagoon 3 mths (Mar)	calving grounds	15	“Calves occupy these lagoons with their mothers until late March or early April when they commence their northward migration.” – pg 84, Sumich (1986) “Table 2 (see p. 39ff.) presents counts of gray whales in Bahía Santa María. The counts for this study began in 1982, and the (combined daily) maximum number observed was 20-22 individuals (10-11 cow/calf pairs) on 22 and 23 February, and 8 March of that year, all at or near the northern entrance of the lagoon. In 1983, the (combined daily) maximum was less, 12 (6 cow/calf	1.39 ± 0.3	From Sumich (1986) (0 mo: 2.14 ± 0.5, 1 mo:1.56 ± 0.4, 2 mo: 1.39 ± 0.3 breaths min−1) cited in Villegas-Amtmann et al. (2017) **I assume breath rates for 0 mo applies to time period between birth to end of Jan, breath rates for 1 mo applies to Jan-Feb, and*

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					pairs) on 19 and 20 February, and 5 March; again all at the northern mouth." – pg 34, Findley & Vidal (2002) "Calves must remain in warm protected waters until they have grown sufficiently to face the rigors of the long north- ward migration." Pg 22 – Rice and Wolman (1971) **I assume others leave lagoons by mid-Feb, while mom/calf pairs leave the lagoons later in mid-March*		*breath rates for 2 mo applies to Feb-Mar.*
4	Calf	Northbound 3 mths (Mar)	northbound	16	"Finally, a second group of the northbound migration (mother–calf pairs) passes Costa Azul from the first days of March until the third week of May." Rodriguez de la Gala Hernandez 2008 Shore Based Surveys (2001-2009) off Piedras Blancas light station (California): "Shore-based survey effort began in mid to late March each year and effort continued until counts of northbound gray whale calves fell to insignificant numbers (Table 1; Figure 4)." **end dates 22-31 May, latest June* 5- Perryman et al. (2010) Central California: Northbound cow/calf pairs sighted mid-March to mid-May 1980 (open bars in Figure 3) and April to late-May 1981 (open bars in Figure 4) - Poole (1984). "The route taken by females with calves during the spring migration is unknown. During this study, the catcher-boat crews saw only one female with a calf—near Point Reyes on 15 March 1969." pg 14, Rice and Wolman (1971) Southern California: "Twenty-three northward migrating groups containing mothers with calves were observed during the aerial surveys (Figure 6) . The earliest was sighted 18 February . the latest on 18 May." – Leatherwood (1974)	0.7 ± 0.1	"northbound calves 0.7 ± 0.1 breaths/min" n = 25, Table 1 - Rodriguez de la Gala-Hernandez et al. (2008)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
5	Calf	Northbound 4 mths (Apr)	northbound	30	Central California: Northbound cow/calf pairs sighted mid-March to mid-May 1980 (open bars in Figure 3) and April to late-May 1981 (open bars in Figure 4) Poole (1984). "Finally, a second group of the northbound migration (mother–calf pairs) passes Costa Azul from the first days of March until the third week of May." Rodriguez de la Gala Hernandez 2008 Shore Based Surveys (2001-2009) off Piedras Blancas light station (California): "Shore-based survey effort began in mid to late March each year and effort continued until counts of northbound gray whale calves fell to insignificant numbers (Table 1; Figure 4)." **end dates 22-31 May, latest June* 5- Perryman et al. (2010) Southern California: "Twenty-three northward migrating groups containing mothers with calves were observed during the aerial surveys (Figure 6) . The earliest was sighted 18 February . the latest on 18 May." – Leatherwood (1974)	0.7 ± 0.1	"northbound calves 0.7 ± 0.1 breaths/min" ; n = 25, Table 1 - Rodriguez de la Gala-Hernandez et al. (2008)
6	Calf	Northbound 5 mths (May)	northbound	31	Central California: Northbound cow/calf pairs sighted mid-March to mid-May 1980 (open bars in Figure 3) and April to late-May 1981 (open bars in Figure 4) Poole (1984). "Finally, a second group of the northbound migration (mother–calf pairs) passes Costa Azul from the first days of March until the third week of May." Rodriguez de la Gala Hernandez 2008 Shore Based Surveys (2001-2009) off Piedras Blancas light station (California): "Shore-based survey effort began in mid to late March each year and effort continued until counts of northbound gray whale calves fell to insignificant numbers (Table 1; Figure 4)." **end dates 22-31 May, latest June* 5- Perryman et al. (2010)	0.7 ± 0.1	"northbound calves 0.7 ± 0.1 breaths/min" ; n = 25, Table 1 - Rodriguez de la Gala-Hernandez et al. (2008)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					"Morejohn (1968) reported a female with a calf at Moss Landing, northeast of Monterey, California, on 2 May 1967." pg 14, Rice and Wolman (1971) Alaska: "Hessing (1981), working at Unimak Pass from March 23 to June 17,1981, observed two phases, and although all sizes of whales were observed throughout the study, cows with calves were not seen until May, continuing to increase to mid-June when the study ended." – Braham (1984) Southern California: "Twenty-three northward migrating groups containing mothers with calves were observed during the aerial surveys (Figure 6) . The earliest was sighted 18 February . the latest on 18 May." – Leatherwood (1974)		
7	Calf	Northbound 6 mths (June)	northbound	23	Alaska: "Hessing (1981), working at Unimak Pass from March 23 to June 17,1981, observed two phases, and although all sizes of whales were observed throughout the study, cows with calves were not seen until May, continuing to increase to mid-June when the study ended." – Braham (1984)	0.7 ± 0.1	"northbound calves 0.7 ± 0.1 breaths/min" ; n = 25, Table 1 - Rodriguez de la Gala-Hernandez et al. (2008)
8	Calf	Nursing at Foraging grounds 6 mths (June)	nursing at foraging grounds	7	Northeastern Sakhalin Island: Survey of behaviour of mother-calf pairs between 20 June -30 Sep (variable dates, 2002-2009). Table 3, Sychenko (2011) Survey data in foraging grounds Sakhalin Island, Russia - Whale sighting data from 1995 to 2007, during months ranging from June to October, we conducted 336 small-boat photo-identification surveys. "These surveys produced 5,159 sightings of 169 individual western gray whales, which include 24 known reproductive females, 72 whales 1st identified as calves, and 142 individuals of known sex (59 females and 83 males). We considered a given female to be reproductive overall and lactating for the field season when genetic or behavioral observations, or both, linked her to a calf of the year" – Bradford et al. 2012	1.22 ± 0.3	Calves Dive-Surface Blow rate (blows/min) Mean 1.22 SD 0.3, n = 28, Table 7, Sychenko (2011)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					**I assume that mother/calf behaviours and migratory timings are similar between Western and Eastern North Pacific grey whales.*		
9	Calf	Nursing at Foraging grounds 7 mths (July)	nursing at foraging grounds	31	Northeastern Sakhalin Island: Survey of behaviour of mother-calf pairs between 20 June -30 Sep (variable dates, 2002-2009). Table 3, Sychenko (2011) Sakhalin Island M/C pairs observed Jul/Aug/Sep 2001 – Weller et al. 2003 Survey data in foraging grounds Sakhalin Island, Russia – Lactating females, calves and others observed between Jul, Aug, Sep. Table 1, Bradford et al. (2012) **I assume that mother/calf behaviours and migratory timings are similar between Western and Eastern North Pacific grey whales.*	1.22 ± 0.3	Calves Dive-Surface Blow rate (blows/min) Mean 1.22 SD 0.3, n = 28, Table 7, Sychenko (2011)
10	Calf	Nursing at foraging grounds 8 mths (Aug)	nursing at foraging grounds	31	Northeastern Sakhalin Island: Survey of behaviour of mother-calf pairs between 20 June -30 Sep (variable dates, 2002-2009). Table 3, Sychenko (2011) Sakhalin Island M/C pairs observed Jul/Aug/Sep 2001 – Weller et al. 2003 Survey data in foraging grounds Sakhalin Island, Russia – Lactating females, calves and others observed between Jul, Aug, Sep. Table 1, Bradford et al. (2012) **I assume that mother/calf behaviours and migratory timings are similar between Western and Eastern North Pacific grey whales.*	1.22 ± 0.3	Calves Dive-Surface Blow rate (blows/min) Mean 1.22 SD 0.3, n = 28, Table 7, Sychenko (2011)
11	Calf	Nursing at foraging grounds (Sep)	nursing at foraging grounds	30	Northeastern Sakhalin Island: Survey of behaviour of mother-calf pairs between 20 June -30 Sep (variable dates, 2002-2009). Table 3, Sychenko (2011) Sakhalin Island M/C pairs observed Jul/Aug/Sep 2001 – Weller et al. (2003)	1.22 ± 0.3	Calves Dive-Surface Blow rate (blows/min) Mean 1.22 SD 0.3, n = 28, Table 7, Sychenko (2011)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					Survey data in foraging grounds Sakhalin Island, Russia – Lactating females, calves and others observed between Jul, Aug, Sep. Table 1, Bradford et al. (2012) **I assume that mother/calf behaviours and migratory timings are similar between Western and Eastern North Pacific grey whales.*		
12	Calf	nursing at foraging grounds (Oct)	nursing at foraging grounds	20	Growth model indicates decreased rate of growth at ~9.6 mths, indicating approx date of weaning - Agbayani et al. 2020 “Calves are weaned and become independent by seven to nine months old while on the summer feeding ground.” Weller 2009 *white paper	1.22 ± 0.3	Calves Dive-Surface Blow rate (blows/min) Mean 1.22 SD 0.3, n = 28, Table 7, Sychenko (2011)
13	Calf	Southbound post-weaning (Oct)	southbound	11	Cape Sarichef, Alaska: “Peak sighting dates were recorded on 23 November 1977 (high count), 3 December 1978 (median) and 7 December 1979 (median).” Rugh et al. 2001 “Generally, then, most gray whales are migrating out of northern seas sometime between mid-October and November, but some have been seen near the Chukotka Peninsula as late as mid-December (reviewed in Yablokov and Bogoslovskaya, 1984).” Rugh et al 2001. Alaska: “From September 1975 to October 1981 gray whales were observed from air, land, and at sea during their annual migrations and on their northern feeding grounds. […] October and November sightings of gray whales are plotted in Fig. 4B as reported by local residents or scientists working on land or along the coast.” Braham (1984)	0.72 ± 0.2	Sumich (1983); Schwarz (2002); Villegas-Amtmann 2017 *The mean (±SE) breathing rate for southbound whales was 0.8 ± 0.1 breaths/min *based on n= 32. (Table 1, Rodriguez de la Gala-Hernandez et al. 2008).* *“Breathing rate for southbound migrating whales in this work (0.8 breaths/min) is similar to the 0.72 breaths/min obtained by Sumich (1983).” (Rodriguez de la Gala-Hernandez et al. 2008).*

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
							*I decided to use the values from Sumich (1983) and Schwarz (2002)
14	Calf	Southbound post-weaning (Nov)	southbound	30	Immature gray whales: “Other immature gray whales must have similar girth measurements at the commencement of their southward fasting migration in November, for their mean girth is reduced to O.56L by the time they reach central California a month later.” Sumich (1986) Cape Sarichef, Alaska: “Peak sighting dates were recorded on 23 November 1977 (high count), 3 December 1978 (median) and 7 December 1979 (median).” Rugh et al. 2001 “Generally, then, most gray whales are migrating out of northern seas sometime between mid-October and November, but some have been seen near the Chukotka Peninsula as late as mid-December (reviewed in Yablokov and Bogoslovskaya, 1984).” Rugh et al 2001.	0.72 ± 0.2	Sumich (1983); Schwarz (2002); Villegas-Amtmann 2017 _The mean (±SE) breathing rate for southbound whales was 0.8 ± 0.1 breaths/min *based on n= 32. (Table 1, Rodriguez de la Gala-Hernandez et al. 2008)._ _“Breathing rate for southbound migrating whales in this work (0.8 breaths/min) is similar to the 0.72 breaths/min obtained by Sumich (1983).” (Rodriguez de la Gala-Hernandez et al. 2008)._ _*I decided to use the values from Sumich (1983) and Schwarz (2002)_
15	Calf	Southbound post-weaning (Dec)	southbound	31	Immature gray whales: “Other immature gray whales must have similar girth measurements at the commencement of their southward fasting migration in November, for their mean girth is reduced to O.56L by the time they reach central California a month later.” Sumich (1986) Cape Sarichef, Alaska: “Peak sighting dates were recorded on 23 November 1977 (high count), 3 December 1978 (median) and 7 December 1979 (median).” Rugh et al. 2001	0.72 ± 0.2	Sumich (1983); Schwarz (2002); Villegas-Amtmann 2017 _The mean (±SE) breathing rate for southbound whales was 0.8 ± 0.1 breaths/min *based on n= 32. (Table 1, Rodriguez de la Gala-Hernandez et al. 2008)._ _“Breathing rate for southbound migrating_

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					“Generally, then, most gray whales are migrating out of northern seas sometime between mid-October and November, but some have been seen near the Chukotka Peninsula as late as mid-December (reviewed in Yablokov and Bogoslovskaya, 1984).” Rugh et al 2001. California – southbound migration surveys. Observations from Dec – Feb, peaking mid-January. Figure 1, Laake et al. (2012)		_whales in this work (0.8 breaths/min) is similar to the 0.72 breaths/min obtained by Sumich (1983).” (Rodriguez de la Gala-Hernandez et al. 2008)._ _*I decided to use the values from Sumich (1983) and Schwarz (2002)_
16	Pregnant	Southbound newly pregnant (Dec)	Southbound recently pregnant	31	Time frame of life stages indicated in Figure 1 from Rice (1983) “A mean conception date of about 5 December was estimated by Rice and Wolman (1971) on the basis of the developmental state of embryos and early fetuses from females collected during the northward migration” - pg. 539, Rice (1983) “The mean conception date calculated from the fetal growth curve (see below) is 5 December.” – pg 74, Rice and Wolman (1971) “As noted above, the timing of the southward migration of pregnant females depends on the stage of gestation. Because late pregnant females pass San Francisco for at least 38 days, we may assume that the calving season lasts about that many days. Therefore, we estimate that calving occupies a period of 5 or 6 weeks from late December to early February.” – pg 81, Rice and Wolman (1971) “Most conceptions occur within a 3-week period during southward migration, with a peak about 5 December.” – pg 129 Rice and Wolman (1971)	0.72 ± 0.2	Sumich (1983); Schwarz (2002); Villegas-Amtmann 2017 _The mean (±SE) breathing rate for southbound whales was 0.8 ± 0.1 breaths/min *based on n= 32. (Table 1, Rodriguez de la Gala-Hernandez et al. 2008)._ _“Breathing rate for southbound migrating whales in this work (0.8 breaths/min) is similar to the 0.72 breaths/min obtained by Sumich (1983).” (Rodriguez de la Gala-Hernandez et al. 2008)._ _*I decided to use the values from Sumich (1983) and Schwarz (2002)_
17	Pregnant	Lagoon breeding (Jan)	calving grounds	31	Time frame of life stages indicated in Figure 1 from Rice (1983)	0.62 ± 0.2	Lagoon lactating, and lagoon breeding: (0.62 ±

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
			recently pregnant				0.2 breaths min^{-1}) from Harvey & Mate (1984) Cited in Table 1, Villegas-Amtmann et al. (2017)
18	Pregnant	Lagoon breeding (Feb)	calving grounds recently pregnant	20	Time frame of life stages indicated in Figure 1 from Rice (1983)	0.62 ± 0.2	Lagoon lactating, and lagoon breeding: (0.62 ± 0.2 breaths min^{-1}) from Harvey & Mate (1984) Cited in Table 1, Villegas-Amtmann et al. (2017)
19	Pregnant	Northbound solo pregnant (Feb)	northbound pregnant	8	Time frame of life stages indicated in Figure 1 from Rice (1983) “During the northward migration, the first to pass are the newly pregnant females, which comprised the recently ovulated class of the preceding southward migration. Most of them pass within a limited period of about 15 days. We took them only between 21 February and 7 March in 1967, and between 26 February and 10 March in 1968.” Rice & Wolman (1971)	0.5 ± 0.03	"Northbound whales without calves showed a breathing rate of 0.5 ± 0.03 breaths/min”, n = 36 - Table 1, Rodriguez de la Gala-Hernandez et al. (2008)
20	Pregnant	Northbound solo pregnant (Mar)	northbound pregnant	31	Time frame of life stages indicated in Figure 1 from Rice (1983) “During the northward migration, the first to pass are the newly pregnant females, which comprised the recently ovulated class of the preceding southward migration. Most of them pass within a limited period of about 15 days. We took them only between 21 February and 7 March in 1967, and between 26 February and 10 March in 1968.” Rice & Wolman (1971)	0.5 ± 0.03	"Northbound whales without calves showed a breathing rate of 0.5 ± 0.03 breaths/min”, n = 36 - Table 1, Rodriguez de la Gala-Hernandez et al. (2008)
21	Pregnant	Northbound solo pregnant (Apr)	northbound pregnant	30	Time frame of life stages indicated in Figure 1 from Rice (1983)	0.5 ± 0.03	"Northbound whales without calves showed a breathing rate of 0.5 ± 0.03 breaths/min”, n = 36 - Table 1, Rodriguez de la Gala-Hernandez et al. (2008)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
22	Pregnant	Northbound pregnant (May)	northbound pregnant	31	Time frame of life stages indicated in Figure 1 from Rice (1983)	0.5 ± 0.03	"Northbound whales without calves showed a breathing rate of 0.5 ± 0.03 breaths/min", n = 36 - Table 1, Rodriguez de la Gala-Hernandez et al. (2008)
23	Pregnant	Foraging pregnant (June)	foraging pregnant	30	Time frame of life stages indicated in Figure 1 from Rice (1983) "Pregnant females apparently are the first to arrive on the summer feeding grounds and spend more time there than lactating females." Rice and Wolman (1971)	1.34 ± 0.1	Respiration rates for pregnant females in foraging grounds = 1.34 ± 0.1 breaths min^{-1}) - O. Sychenko (unpubl.) cited in Villegas-Amtmann (2017)
24	Pregnant	Foraging pregnant (July)	foraging pregnant	31	Time frame of life stages indicated in Figure 1 from Rice (1983)	1.34 ± 0.1	Respiration rates for pregnant females in foraging grounds = 1.34 ± 0.1 breaths min^{-1}) - O. Sychenko (unpubl.) cited in Villegas-Amtmann (2017)
25	Pregnant	Foraging pregnant (Aug)	foraging pregnant	31	Time frame of life stages indicated in Figure 1 from Rice (1983)	1.34 ± 0.1	Respiration rates for pregnant females in foraging grounds = 1.34 ± 0.1 breaths min^{-1}) - O. Sychenko (unpubl.) cited in Villegas-Amtmann (2017)
26	Pregnant	Foraging pregnant (Sep)	foraging pregnant	30	Time frame of life stages indicated in Figure 1 from Rice (1983)	1.34 ± 0.1	Respiration rates for pregnant females in foraging grounds = 1.34 ± 0.1 breaths min^{-1}) - O. Sychenko (unpubl.) cited in Villegas-Amtmann (2017)
27	Pregnant	Foraging pregnant (Oct)	foraging pregnant	31	Time frame of life stages indicated in Figure 1 from Rice (1983)	1.34 ± 0.1	Respiration rates for pregnant females in foraging grounds = 1.34 ± 0.1 breaths min^{-1}) - O. Sychenko (unpubl.) cited in Villegas-Amtmann (2017)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
28	Pregnant	Southbound pregnant (Nov)	southbound pregnant	30	Time frame of life stages indicated in Figure 1 from Rice (1983) San Diego, California: "By this time [*Dec-Jan*], most late pregnant whales were presumed to have passed the study site on their way to Mexican calving lagoons (Rice and Wolman, 1971), leaving immature whales and nonpregnant adults as the principal subjects for observation." pg. 20, Sumich (1986)	0.72 ± 0.2	Sumich (1983) "The results of 74 whales monitored over 354 whale km yielded a mean velocity of 2.0 rn/s and a mean breathing rate of 0.72 breaths/mm." – Chapter 2 Abstract pg. 17 Schwarz (2002)
29	Pregnant	Southbound pregnant (Dec)	southbound pregnant	31	Time frame of life stages indicated in Figure 1 from Rice (1983) San Diego, California: "By this time [*Dec-Jan*], most late pregnant whales were presumed to have passed the study site on their way to Mexican calving lagoons (Rice and Wolman, 1971), leaving immature whales and nonpregnant adults as the principal subjects for observation." pg. 20, Sumich (1986)	0.72 ± 0.2	Sumich (1983) "The results of 74 whales monitored over 354 whale km yielded a mean velocity of 2.0 rn/s and a mean breathing rate of 0.72 breaths/mm." – Chapter 2 Abstract pg. 17 Schwarz (2002)
30	Lactating	Lagoon lactating (Jan)	calving grounds lactating	31	Time frame of life stages indicated in Figure 1 from Rice (1983) "Pregnant and non-pregnant whales arrive 2 weeks apart" […] "Pregnant whales arrive first in January" […] "Soon after lagoon arrival, pregnant females give birth"– Sumich (1986). "Reconstruction of the migration from all available data shou's that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December." Pike (1962) "Rice et al. (1981) reported that in Laguna Ojo de Liebre most births occur until around 15 February, and estimated 27 January as the mean date for births." Pg 35 – Findley & Vidal (2002)	0.62 ± 0.2	"The average surfacing rates for tagged adult whales indicated a breathing rate of approximately 36 breaths per hr. […] our large sample size of surfacings and the certainty of detection of tagged whale signals suggests that a breathing rate of 36 breaths/hr is representative of gray whale activities in the lagoon." (Harvey and Mate 1984) On lactating females in lagoons - "Harvey and Mate (1984) reported long-term monitoring of breath

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
							holds of 7 radio-tagged lactating females (minimum breath holds/whale = 342; mean = 1465 breath holds/whale) in Laguna San Ignacio, and found mean breathing rates of 0.62 breaths/mm.” (cited in Sumich 1986, pg 161.)
31	Lactating	Lagoon lactating (Feb)	calving grounds lactating	28	Time frame of life stages indicated in Figure 1 from Rice (1983) “Despite the general conclusion that lactating females do little or no foraging in winter lagoons, they remain there with their calves for 1-2 months after other gray whales have departed for northern feeding grounds.” Sumich (1986) “Reconstruction of the migration from all available data shou's that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December.” Pike (1962) “Jones and Swartz (1984) conducted an intense study further south in Laguna San Ignacio in 1978-82 and reported maximum counts of single whales on 9 February (Table 2) and maximum counts of cow/calf pairs in late March or early April. The other lagoons had similar dates for single whales (1-10 February), but counts of cow/calf pairs were highest between 4 and 12 February (instead of March or April), depending on the lagoon” Rugh et al. (2001). “Table 2 (see p. 39ff.) presents counts of gray whales in Bahía Santa María. The counts for this study began in 1982, and the (combined daily) maximum number observed was 20-22 individuals (10-11 cow/calf pairs) on	0.62 ± 0.2	On lactating females in lagoons - “Harvey and Mate (1984) reported long-term monitoring of breath holds of 7 radio-tagged lactating females (minimum breath holds/whale = 342; mean = 1465 breath holds/whale) in Laguna San Ignacio, and found mean breathing rates of 0.62 breaths/mm.” (cited in Sumich 1986, pg 161.) “The average surfacing rates for tagged adult whales indicated a breathing rate of approximately 36 breaths per hr. […] our large sample size of surfacings and the certainty of detection of tagged whale signals suggests that a breathing rate of 36 breaths/hr is representative of gray whale activities in the lagoon.” (Harvey and Mate 1984)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					22 and 23 February, and 8 March of that year, all at or near the northern entrance of the lagoon. In 1983, the (combined daily) maximum was less, 12 (6 cow/calf pairs) on 19 and 20 February, and 5 March; again all at the northern mouth." – pg 34, Findley &Vidal (2002)		
32	Lactating	Lagoon lactating (March)	calving grounds lactating	15	(coincides with NB calves) "Despite the general conclusion that lactating females do little or no foraging in winter lagoons, they remain there with their calves for 1-2 months after other gray whales have departed for northern feeding grounds." Sumich (1986) "Table 2 (see p. 39ff.) presents counts of gray whales in Bahía Santa María. The counts for this study began in 1982, and the (combined daily) maximum number observed was 20-22 individuals (10-11 cow/calf pairs) on 22 and 23 February, and 8 March of that year, all at or near the northern entrance of the lagoon. In 1983, the (combined daily) maximum was less, 12 (6 cow/calf pairs) on 19 and 20 February, and 5 March; again all at the northern mouth." – pg 34, Findley &Vidal (2002) "Jones and Swartz (1984) conducted an intense study further south in Laguna San Ignacio in 1978-82 and reported maximum counts of single whales on 9 February (Table 2) and maximum counts of cow/calf pairs in late March or early April. The other lagoons had similar dates for single whales (1-10 February), but counts of cow/calf pairs were highest between 4 and 12 February (instead of March or April), depending on the lagoon" Rugh et al. (2001). "Finally, a second group of the northbound migration (mother–calf pairs) passes Costa Azul from the first days of March until the third week of May." Rodriguez de la Gala Hernandez 2008	0.62 ± 0.2	Lagoon lactating, and lagoon breeding: (0.62 ± 0.2 breaths min^{-1}) from Harvey & Mate (1984) Cited in Table 1, Villegas-Amtmann et al. (2017) On lactating females in lagoons - "Harvey and Mate (1984) reported long-term monitoring of breath holds of 7 radio-tagged lactating females (minimum breath holds/whale = 342; mean = 1465 breath holds/whale) in Laguna San Ignacio, and found mean breathing rates of 0.62 breaths/mm." (cited in Sumich 1986, pg 161.) "The average surfacing rates for tagged adult whales indicated a breathing rate of approximately 36 breaths per hr. […] our large sample size of surfacings and the certainty of detection of tagged whale signals suggests that a breathing rate of 36 breaths/hr is representative of gray whale activities in

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
							the lagoon." (Harvey and Mate 1984)
33	Lactating	Northbound with calf (March)	northbound lactating	16	"Finally, a second group of the northbound migration (mother–calf pairs) passes Costa Azul from the first days of March until the third week of May." Rodriguez de la Gala Hernandez et al. (2008) Central California: Northbound cow/calf pairs sighted mid-March to mid-May 1980 (open bars in Figure 3) and April to late-May 1981 (open bars in Figure 4) - Poole (1984). Shore Based Surveys (2001-2009) off Piedras Blancas light station (California): "Shore-based survey effort began in mid to late March each year and effort continued until counts of northbound gray whale calves fell to insignificant numbers (Table 1; Figure 4)." **end dates 22-31 May, latest June* 5- Perryman et al. (2010) Southern California: "Twenty-three northward migrating groups containing mothers with calves were observed during the aerial surveys (Figure 6) . The earliest was sighted 18 February . the latest on 18 May." – Leatherwood (1974)	0.5 ± 0.1	"northbound mothers 0.5 ± 0.1 breaths/min" n = 26, Table 1 - Rodriguez de la Gala-Hernandez et al. (2008)
34	Lactating	Northbound with calf (April)	northbound lactating	30	Central California: Northbound cow/calf pairs sighted mid-March to mid-May 1980 (open bars in Figure 3) and April to late-May 1981 (open bars in Figure 4) - Poole (1984). "Finally, a second group of the northbound migration (mother–calf pairs) passes Costa Azul from the first days of March until the third week of May." Rodriguez de la Gala Hernandez et al. (2008)	0.5 ± 0.1	"northbound mothers 0.5 ± 0.1 breaths/min" n = 26, Table 1 - Rodriguez de la Gala-Hernandez et al. (2008)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					Shore Based Surveys (2001-2009) off Piedras Blancas light station (California): “Shore-based survey effort began in mid to late March each year and effort continued until counts of northbound gray whale calves fell to insignificant numbers (Table 1; Figure 4).” _*end dates 22-31 May, latest June_ 5- Perryman et al. (2010) Southern California: “Twenty-three northward migrating groups containing mothers with calves were observed during the aerial surveys (Figure 6) . The earliest was sighted 18 February . the latest on 18 May.” – Leatherwood (1974) "On whale marking cruises in 1965, 1966, 1967, and 1969, we traveled north during late February, March, and early April, by which time most females with calves had already left the calving lagoons.” Rice and Wolman (1971)		
35	Lactating	Northbound with calf (May)	northbound lactating	31	Central California: Northbound cow/calf pairs sighted mid-March to mid-May 1980 (open bars in Figure 3) and April to late-May 1981 (open bars in Figure 4) Poole (1984). “Finally, a second group of the northbound migration (mother–calf pairs) passes Costa Azul from the first days of March until the third week of May.” Rodriguez de la Gala Hernandez et al. (2008) Shore Based Surveys (2001-2009) off Piedras Blancas light station (California): “Shore-based survey effort began in mid to late March each year and effort continued until counts of northbound gray whale calves fell to insignificant numbers (Table 1; Figure 4).” _*end dates 22-31 May, latest June_ 5- Perryman et al. (2010) Alaska: “Hessing (1981), working at Unimak Pass from March 23 to June 17,1981, observed two phases, and although all sizes of whales were observed throughout the study, cows with calves were not seen until May,	0.5 ± 0.1	"northbound mothers 0.5 ± 0.1 breaths/min"; n = 26, Table 1 - Rodriguez de la Gala-Hernandez et al. (2008)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					continuing to increase to mid-June when the study ended." – Braham (1984) Southern California: "Twenty-three northward migrating groups containing mothers with calves were observed during the aerial surveys (Figure 6) . The earliest was sighted 18 February . the latest on 18 May." – Leatherwood (1974)		
36	Lactating	Northbound with Calf (June)	northbound lactating	23	"Hessing (1981), working at Unimak Pass from March 23 to June 17,1981, observed two phases, and although all sizes of whales were observed throughout the study, cows with calves were not seen until May, continuing to increase to mid-June when the study ended." – Braham (1984) **I was unable to obtain a copy of Hessing (1981)*	0.5 ± 0.1	"northbound mothers 0.5 ± 0.1 breaths/min" n = 26, Table 1 - Rodriguez de la Gala-Hernandez et al. (2008)
37	Lactating	Foraging lactating (June)	foraging lactating	7	Northeastern Sakhalin Island: Survey of behaviour of mother-calf pairs between 20 June -30 Sep (variable dates, 2002-2009). Table 3, Sychenko (2011) **I assume that mother/calf behaviours and migratory timings are similar between Western and Eastern North Pacific grey whales.*	1.04 ± 0.2	Respiration rates for single females in foraging grounds, non-pregnant/lactating = 1.04 ± 0.2 breaths min^{-1}) - O. Sychenko (unpubl.) cited in Villegas-Amtmann (2017)
38	Lactating	Foraging lactating (July)	foraging lactating	31	Northeastern Sakhalin Island: Survey of behaviour of mother-calf pairs between 20 June -30 Sep (variable dates, 2002-2009). Table 3, Sychenko (2011) Survey data in foraging grounds Sakhalin Island, Russia – Lactating females, calves and others observed between Jul, Aug, Sep. Table 1, Bradford et al. (2012) **I assume that mother/calf behaviours and migratory timings are similar between Western and Eastern North Pacific grey whales.*	1.04 ± 0.2	Respiration rates for single females in foraging grounds, non-pregnant/lactating = 1.04 ± 0.2 breaths min^{-1}) - O. Sychenko (unpubl.) cited in Villegas-Amtmann (2017)
39	Lactating	Foraging lactating (Aug)	foraging lactating	31	Northeastern Sakhalin Island: Survey of behaviour of mother-calf pairs between 20 June -30 Sep (variable dates, 2002-2009). Table 3, Sychenko (2011)	1.04 ± 0.2	Respiration rates for single females in foraging grounds, non-

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					Survey data in foraging grounds Sakhalin Island, Russia – Lactating females, calves and others observed between Jul, Aug, Sep. Table 1, Bradford et al. (2012) **I assume that mother/calf behaviours and migratory timings are similar between Western and Eastern North Pacific grey whales.*		pregnant/lactating = 1.04 ± 0.2 breaths min^{-1}) - O. Sychenko (unpubl.) cited in Villegas-Amtmann (2017)
40	Lactating	Foraging lactating (Sep)	foraging lactating	30	Northeastern Sakhalin Island: Survey of behaviour of mother-calf pairs between 20 June -30 Sep (variable dates, 2002-2009). Table 3, Sychenko (2011) Survey data in foraging grounds Sakhalin Island, Russia – Lactating females, calves and others observed between Jul, Aug, Sep. Table 1, Bradford et al. (2012) **I assume that mother/calf behaviours and migratory timings are similar between Western and Eastern North Pacific grey whales.*	1.04 ± 0.2	Respiration rates for single females in foraging grounds, non-pregnant/lactating = 1.04 ± 0.2 breaths min^{-1}) - O. Sychenko (unpubl.) cited in Villegas-Amtmann (2017)
41	Lactating	Foraging lactating (Oct)	foraging lactating	20	Growth model indicates decreased rate of growth at ~9.6 mths, indicating approx date of weaning - Agbayani et al. 2020 “Calves are weaned and become independent by seven to nine months old while on the summer feeding ground.” Weller 2009 *white paper	1.04 ± 0.2	Respiration rates for single females in foraging grounds, non-pregnant/lactating = 1.04 ± 0.2 breaths min^{-1}) - O. Sychenko (unpubl.) cited in Villegas-Amtmann (2017)
42	Lactating	Southbound postweaning (Oct)	soutbound postweaning	11	Cape Sarichef, Alaska: “Peak sighting dates were recorded on 23 November 1977 (high count), 3 December 1978 (median) and 7 December 1979 (median).” Rugh et al. 2001 “Generally, then, most gray whales are migrating out of northern seas sometime between mid-October and November, but some have been seen near the Chukotka Peninsula as late as mid-December (reviewed in Yablokov and Bogoslovskaya, 1984).” Rugh et al 2001.	0.72 ± 0.2	Sumich (1983); Schwarz (2002); as cited in Villegas-Amtmann 2017 *The mean (±SE) breathing rate for southbound whales was 0.8 ± 0.1 breaths/min *based on n= 32. (Table 1, Rodriguez de la Gala-Hernandez et al. 2008).*

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					“The southbound migration probably begins by early October when the whales travel from the northern to the southeastern Bering Sea and intersect the southwest end of the Alaska Peninsula before leaving the Bering Sea through Unimak Pass, from late October to January.” Braham (1984) “The southbound migration starts in October, and whales are observed off Ensenada, Baja California, from the beginning of December until mid-February (Heckel et al. 2001).” Rodriguez de la Gala-Hernandez (2008) “Advance of the ice through Bering Strait in October initiates the southern migration for most of the herd.” Pike (1962)		*“Breathing rate for southbound migrating whales in this work (0.8 breaths/min) is similar to the 0.72 breaths/min obtained by Sumich (1983).” (Rodriguez de la Gala-Hernandez et al. 2008).* **I decided to use the values from Sumich (1983) and Schwarz (2002)*
43	Lactating	Southbound postweaning (Nov)	southbound postweaning	30	Cape Sarichef, Alaska: “Peak sighting dates were recorded on 23 November 1977 (high count), 3 December 1978 (median) and 7 December 1979 (median).” Rugh et al. 2001 “Generally, then, most gray whales are migrating out of northern seas sometime between mid-October and November, but some have been seen near the Chukotka Peninsula as late as mid-December (reviewed in Yablokov and Bogoslovskaya, 1984).” Rugh et al 2001. “The southbound migration probably begins by early October when the whales travel from the northern to the southeastern Bering Sea and intersect the southwest end of the Alaska Peninsula before leaving the Bering Sea through Unimak Pass, from late October to January.” Braham (1984) “The southbound migration starts in October, and whales are observed off Ensenada, Baja California, from the beginning of December until mid-February (Heckel et al. 2001).” Rodriguez de la Gala-Hernandez (2008)	0.72 ± 0.2	Sumich (1983); Schwarz (2002); as cited in Villegas-Amtmann 2017 *The mean (±SE) breathing rate for southbound whales was 0.8 ± 0.1 breaths/min *based on n= 32. (Table 1, Rodriguez de la Gala-Hernandez et al. 2008).* *“Breathing rate for southbound migrating whales in this work (0.8 breaths/min) is similar to the 0.72 breaths/min obtained by Sumich (1983).” (Rodriguez de la Gala-Hernandez et al. 2008).*

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
							**I decided to use the values from Sumich (1983) and Schwarz (2002)*
44	Lactating	Southbound postweaning (Dec)	southbound postweaning	31	San Diego, California - "Southbound gray whales in large numbers can be easily observed from shore at numerous sites, particularly in California, during late December and January, as they swim steadily on courses generally parallel to shore." Sumich (1986) Cape Sarichef, Alaska: "Peak sighting dates were recorded on 23 November 1977 (high count), 3 December 1978 (median) and 7 December 1979 (median)." Rugh et al. 2001 "Generally, then, most gray whales are migrating out of northern seas sometime between mid-October and November, but some have been seen near the Chukotka Peninsula as late as mid-December (reviewed in Yablokov and Bogoslovskaya, 1984)." Rugh et al 2001. "The southbound migration probably begins by early October when the whales travel from the northern to the southeastern Bering Sea and intersect the southwest end of the Alaska Peninsula before leaving the Bering Sea through Unimak Pass, from late October to January." Braham (1984) "The southbound migration starts in October, and whales are observed off Ensenada, Baja California, from the beginning of December until mid-February (Heckel et al. 2001)." Rodriguez de la Gala-Hernandez (2008)	0.72 ± 0.2	Sumich (1983); Schwarz (2002); as cited in Villegas-Amtmann 2017 *The mean (±SE) breathing rate for southbound whales was 0.8 ± 0.1 breaths/min *based on n= 32. (Table 1, Rodriguez de la Gala-Hernandez et al. 2008).* *"Breathing rate for southbound migrating whales in this work (0.8 breaths/min) is similar to the 0.72 breaths/min obtained by Sumich (1983)." (Rodriguez de la Gala-Hernandez et al. 2008).* **I decided to use the values from Sumich (1983) and Schwarz (2002)*
	Juvenile/ Adult	Southbound (Jan)	southbound	15	San Diego, California - "Southbound gray whales in large numbers can be easily observed from shore at numerous sites, particularly in California, during late December and January, as they swim steadily on courses generally parallel to shore." Sumich (1986)	0.72 ± 0.2	Sumich (1983); Schwarz (2002); as cited in Villegas-Amtmann 2017 *The mean (±SE) breathing rate for southbound whales was 0.8 ± 0.1 breaths/min*

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					"The southbound migration starts in October, and whales are observed off Ensenada, Baja California, from the beginning of December until mid-February (Heckel et al. 2001)." Rodriguez de la Gala-Hernandez (2008)		_*based on n= 32. (Table 1, Rodriguez de la Gala-Hernandez et al. 2008)._ _"Breathing rate for southbound migrating whales in this work (0.8 breaths/min) is similar to the 0.72 breaths/min obtained by Sumich (1983)." (Rodriguez de la Gala-Hernandez et al. 2008)._ _*I decided to use the values from Sumich (1983) and Schwarz (2002)_
45	Juvenile/ Adult	Lagoon solo (Jan)	calving grounds	16	"Pregnant and non-pregnant whales arrive 2 weeks apart" – and "pregnant whales arrive first in January" – Sumich (1986). "Gray whales arrive in Baja California in late December or early January and apparently move from lagoon to lagoon until almost all have left the area 9-11 weeks later in March (Jones and Swartz, 1984)." Rugh et al. 2001. "In January and February most gray whales of the eastern Pacific population are in warm temperate or tropical waters on the west coast of Baja California and the southern Gulf of California." Rice and Wolman (1971) "Local fishermen reported that gray whales formerly arrived at the northern part of the lagoon in January-February and departed in March-April". Findley & Vidal (2002) _*I assume that the whales arriving in Jan-Feb also include solo Juv/Adults_	0.62 ± 0.2	Lagoon lactating, and lagoon breeding: (0.62 ± 0.2 breaths min^{-1}) from Harvey & Mate (1984) cited in Table 1, Villegas-Amtmann et al. (2017) _*I assume "lagoon breeding" whales are observed as solo whales._ "The average surfacing rates for tagged adult whales indicated a breathing rate of approximately 36 breaths per hr. […] our large sample size of surfacings and the certainty of detection of tagged whale signals suggests that a breathing rate of 36

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
							breaths/hr is representative of gray whale activities in the lagoon." (Harvey and Mate 1984)
46	Juvenile/ Adult	Lagoon solo (Feb)	calving grounds	14	"In January and February most gray whales of the eastern Pacific population are in warm temperate or tropical waters on the west coast of Baja California and the southern Gulf of California." Rice and Wolman (1971) "Local fishermen reported that gray whales formerly arrived at the northern part of the lagoon in January-February and departed in March-April". Findley & Vidal (2002) **I assume that the whales arriving in Jan-Feb also include solo Juv/Adults* Maria satellite tracking signal indicate location in calving grounds, not yet migrating. Urban et al. 2021 "Jones and Swartz (1984) conducted an intense study further south in Laguna San Ignacio in 1978-82 and reported maximum counts of single whales on 9 February (Table 2) and maximum counts of cow/calf pairs in late March or early April. The other lagoons had similar dates for single whales (1-10 February), but counts of cow/calf pairs were highest between 4 and 12 February (instead of March or April), depending on the lagoon" Rugh et al. (2001).	0.62 ± 0.2	Lagoon lactating, and lagoon breeding: (0.62 ± 0.2 breaths min^{-1}) from Harvey & Mate (1984) cited in Table 1, Villegas-Amtmann et al. (2017) **I assume "lagoon breeding" whales are observed as solo whales.* "The average surfacing rates for tagged adult whales indicated a breathing rate of approximately 36 breaths per hr. […] our large sample size of surfacings and the certainty of detection of tagged whale signals suggests that a breathing rate of 36 breaths/hr is representative of gray whale activities in the lagoon." (Harvey and Mate 1984)
47	Juvenile/ Adult	Northbound solo (Feb)	northbound	14	136 northbound whales taken in Feb and March off central California – Rice and Wolman (1971) Central California: Northbound single whales sighted mid-March to mid-May 1980 (solid bars in Figure 3) and mid-February to end of March and a few more up to mid-May 1981 (solid bars in Figure 4) - Poole (1984).	0.5 ± 0.03	"Northbound whales without calves showed a breathing rate of 0.5 ± 0.03 breaths/min", n = 36 - Table 1, Rodriguez de la Gala-Hernandez et al. (2008)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					“Off Washington and British Columbia the northward migration begins in February, ends in May, and is at a peak during the first two weeks in April; the southward migration occurs in December and January, and is at a peak in late December.” Pike (1962) "Following southbound migrating whales, a first group of north- bound migrating individuals (whales without calves: adults and juveniles of both sexes) can be seen from the coastal lo- cation of Costa Azul from February to May.” - Rodriguez de la Gala Hernandez et al. (2008) “Pregnant and non-pregnant whales arrive 2 weeks apart” […] “Pregnant whales arrive first in January” […] “Nonpregnant females usually remain for about one month, and are the first to depart on the northward migration (Rice and Wolman, 1971).” Sumich (1986)		
48	Juvenile/ Adult	Northbound solo (March)	northbound	31	136 northbound whales taken in Feb and March off central California – Rice and Wolman (1971) Central California: Northbound single whales sighted mid-March to mid-May 1980 (solid bars in Figure 3) and mid-February to end of March and a few more up to mid-May 1981 (solid bars in Figure 4) – Poole (1984). “Off Washington and British Columbia the northward migration begins in February, ends in May, and is at a peak during the first two weeks in April; the southward migration occurs in December and January, and is at a peak in late December.” Pike (1962) “Reconstruction of the migration from all available data shows that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December.” Pike (1962)	0.5 ± 0.03	"Northbound whales without calves showed a breathing rate of 0.5 ± 0.03 breaths/min”, n = 36 - Table 1, Rodriguez de la Gala-Hernandez et al. (2008)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					“The northbound migration occurs from March through June and is roughly divided into two phases or "waves." The first phase apparently includes nonparturient adults and immatures, followed in about 1 month mainly by cows and young-of-the-year calves.” Braham (1984) Maria tracking signal indicated start of northward migration on March 9. Urban et al. 2021 "Following southbound migrating whales, a first group of north- bound migrating individuals (whales without calves: adults and juveniles of both sexes) can be seen from the coastal lo- cation of Costa Azul from February to May.” - Rodriguez de la Gala Hernandez et al. (2008) Southern California Migration peaks: “Peak densities were observed in January for the southward and in March for the northward migration.” Leatherwood (1974)		
49	Juvenile/ Adult	Northbound solo (April)	northbound	30	136 northbound whales taken in Feb and March off central California – Rice and Wolman (1971) *data ends in April; Central California: Northbound single whales sighted mid-March to mid-May 1980 (solid bars in Figure 3) and mid-February to end of March and a few more up to mid-May 1981 (solid bars in Figure 4) Poole (1984). “Off Washington and British Columbia the northward migration begins in February, ends in May, and is at a peak during the first two weeks in April; the southward migration occurs in December and January, and is at a peak in late December.” Pike (1962) “Reconstruction of the migration from all available data shou's that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December.” Pike (1962)	0.5 ± 0.03	"Northbound whales without calves showed a breathing rate of 0.5 ± 0.03 breaths/min”, n = 36 - Table 1, Rodriguez de la Gala-Hernandez et al. (2008)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					“The northbound migration occurs from March through June and is roughly divided into two phases or "waves." The first phase apparently includes nonparturient adults and immatures, followed in about 1 month mainly by cows and young-of-the-year calves.” Braham (1984) Maria tracking signal showing northbound migration - Urban et al. 2021 "Following southbound migrating whales, a first group of north- bound migrating individuals (whales without calves: adults and juveniles of both sexes) can be seen from the coastal lo- cation of Costa Azul from February to May.” - Rodriguez de la Gala Hernandez et al. (2008)		
50	Juvenile/ Adult	Northbound solo (May)	northbound	15	Central California: Northbound single whales sighted mid-March to mid-May 1980 (solid bars in Figure 3) and mid-February to end of March and a few more up to mid-May 1981 (solid bars in Figure 4) Poole (1984). “Off Washington and British Columbia the northward migration begins in February, ends in May, and is at a peak during the first two weeks in April; the southward migration occurs in December and January, and is at a peak in late December.” Pike (1962) “Reconstruction of the migration from all available data shou's that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December.” Pike (1962) “The northbound migration occurs from March through June* and is roughly divided into two phases or "waves." The first phase apparently includes nonparturient adults and immatures, followed in about 1 month mainly by cows and young-of-the-year calves.” Braham (1984)	0.5 ± 0.03	"Northbound whales without calves showed a breathing rate of 0.5 ± 0.03 breaths/min”, n = 36 - Table 1, Rodriguez de la Gala-Hernandez et al. (2008)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					**I assume that any individuals migrating through June are a minority group arriving at the foraging grounds late in the season, or remaining in PCFG foraging grounds.* Urban et al. 2021 (Maria stopped migrating May 24) "Following southbound migrating whales, a first group of north- bound migrating individuals (whales without calves: adults and juveniles of both sexes) can be seen from the coastal lo- cation of Costa Azul from February to May." - Rodriguez de la Gala Hernandez et al. (2008)		
51	Juvenile/ Adult	Foraging solo (May)	foraging	16	Feeding whales observed in foraging grounds of Bering and Chukchi seas in May, June, July – Kim and Oliver (1989) Maria tracking signal indicating Area Restricted Search (ARS; assumed to be feeding) - Urban et al. 2021 "An individual gray whale is estimated to gain 16–30% of its body mass during a 5-month stay feeding in the Arctic (Nerini 1984)…" Heide-Jorgensen et al. 2012 **I assume that if the whales arrive in the foraging grounds in mid-May, they likely leave mid-Oct*	1.04 ± 0.2	Respiration rates for single females in foraging grounds, non-pregnant/lactating = 1.04 ± 0.2 breaths min^{-1}) - O. Sychenko (unpubl.) as cited in Villegas-Amtmann (2017)
52	Juvenile/ Adult	Foraging solo (June)	foraging	30	Feeding whales observed in foraging grounds of Bering and Chukchi seas in May, June, July – Kim and Oliver (1989) "Reconstruction of the migration from all available data shou's that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December." Pike (1962) Maria tracking signal indicating Area Restricted Search (ARS; assumed to be feeding) - Urban et al. 2021	1.04 ± 0.2	Respiration rates for single females in foraging grounds, non-pregnant/lactating = 1.04 ± 0.2 breaths min^{-1}) - O. Sychenko (unpubl.) as cited in Villegas-Amtmann (2017)

ID	**Life stage**	**Description**	**Activity stages**	**No of days**	**Source for approx. time of year and no. of days**	**Respiration rates (bpm ± SE)**	**Source for respiration rates**
					"An individual gray whale is estimated to gain 16–30% of its body mass during a 5-month stay feeding in the Arctic (Nerini 1984)…" Heide-Jorgensen et al. 2012 **I assume that if the whales arrive in the foraging grounds in mid-May, they likely leave mid-Oct*		
53	Juvenile/ Adult	Foraging solo (July)	foraging	31	"Reconstruction of the migration from all available data shou's that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December." Pike (1962) Maria tracking signal indicating Area Restricted Search (ARS; assumed to be feeding), signal stopped July 11- Urban et al. 2021 Survey data in foraging grounds Sakhalin Island, Russia - Whale sighting data from 1995 to 2007, during months ranging from June to October, we conducted 336 small-boat photo-identification surveys [for body condition study] – Bradford et al. 2012 Feeding whales observed in foraging grounds of Bering and Chukchi seas in May, June, July – Kim and Oliver (1989) "An individual gray whale is estimated to gain 16–30% of its body mass during a 5-month stay feeding in the Arctic (Nerini 1984)…" Heide-Jorgensen et al. 2012 **I assumed that if the whales arrive in the foraging grounds in mid-May, they likely leave mid-Oct*	1.04 ± 0.2	Respiration rates for single females in foraging grounds, non-pregnant/lactating = 1.04 ± 0.2 breaths min^{-1}) - O. Sychenko (unpubl.) as cited in Villegas-Amtmann (2017)
54	Juvenile/ Adult	Foraging solo (Aug)	foraging	31	"Reconstruction of the migration from all available data shows that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June	1.04 ± 0.2	Respiration rates for single females in foraging grounds, non-pregnant/lactating = 1.04 ± 0.2 breaths min^{-1}) - O.

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					through October, and migrates southward in November and December.” Pike (1962) Survey data in foraging grounds Sakhalin Island, Russia - Whale sighting data from 1995 to 2007, during months ranging from June to October, we conducted 336 small-boat photo-identification surveys [for body condition study] – Bradford et al. 2012 “An individual gray whale is estimated to gain 16–30% of its body mass during a 5-month stay feeding in the Arctic (Nerini 1984)…” Heide-Jorgensen et al. 2012 **I assume that if the whales arrive in the foraging grounds in mid-May, they likely leave mid-Oct*		Sychenko (unpubl.) as cited in Villegas-Amtmann (2017)
55	Juvenile/ Adult	Foraging solo (Sep)	foraging	30	“Reconstruction of the migration from all available data shows that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December.” Pike (1962) “Gray whales feed in the waters of the Chukchi Sea along the Siberian and Alaskan coasts in July, August and September.” Pike (1962) Survey data in foraging grounds Sakhalin Island, Russia - Whale sighting data from 1995 to 2007, during months ranging from June to October, we conducted 336 small-boat photo-identification surveys [for body condition study] – Bradford et al. (2012) Chukotka peninsula: Tagged whales remained in foraging grounds – Sep, Oct, Nov 2006 (Figure 3, Heide-Jorgensen et al. (2012). “An individual gray whale is estimated to gain 16–30% of its body mass during a 5-month stay feeding in the Arctic (Nerini 1984)…” Heide-Jorgensen et al. 2012	1.04 ± 0.2	Respiration rates for single females in foraging grounds, non-pregnant/lactating = 1.04 ± 0.2 breaths min^{-1}) - O. Sychenko (unpubl.) as cited in Villegas-Amtmann (2017)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					**I assume that if the whales arrive in the foraging grounds in mid-May, they likely leave mid-Oct*		
56	Juvenile/ Adult	Foraging solo (Oct)	foraging	16	Feeding whales observed in foraging grounds of Bering and Chukchi seas in May, June, July – Kim and Oliver (1989) "An individual gray whale is estimated to gain 16–30% of its body mass during a 5-month stay feeding in the Arctic (Nerini 1984)…" Heide-Jorgensen et al. 2012 **I assume that if the whales arrive in the foraging grounds in mid-May, they likely leave mid-Oct* Chukotka peninsula: Tagged whales remained in foraging grounds – Sep, Oct, Nov 2006 (Figure 3, Heide-Jorgensen et al. (2012). "Reconstruction of the migration from all available data shou's that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December." Pike (1962) Survey data in foraging grounds Sakhalin Island, Russia - Whale sighting data from 1995 to 2007, during months ranging from June to October, we conducted 336 small-boat photo-identification surveys [for body condition study] – Bradford et al. 2012 "The last sightings in the Bering Strait region were in early October to late November, and the last whales near the coast of the northern Bering Sea were seen in late October to late November. Yablokov and Bogoslovskaya (1984) provided a review of Russian studies of gray whales and concluded that this stock departs from northern seas beginning in the middle of October or November, depending on the year, and some whales are	1.04 ± 0.2	Respiration rates for single females in foraging grounds, non-pregnant/lactating = 1.04 ± 0.2 breaths min^{-1}) - O. Sychenko (unpubl.) as cited in Villegas-Amtmann (2017)

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					still in the area (the southern tip of the Chukotka Peninsula) as late as mid-November or mid-December." Rugh et al. 2001		
57	Juvenile/ Adult	Southbound (Oct)	southbound	15	"Advance of the ice through Bering Strait in October initiates the southern migration for most of the herd." Pike (1962) "Generally, then, most gray whales are migrating out of northern seas sometime between mid-October and November, but some have been seen near the Chukotka Peninsula as late as mid-December (reviewed in Yablokov and Bogoslovskaya, 1984)." Rugh et al 2001. "The southbound migration probably begins by early October when the whales travel from the northern to the southeastern Bering Sea and intersect the southwest end of the Alaska Peninsula before leaving the Bering Sea through Unimak Pass, from late October to January." Braham (1984) "The southbound migration starts in October, and whales are observed off Ensenada, Baja California, from the beginning of December until mid-February (Heckel et al. 2001)." Rodriguez de la Gala-Hernandez (2008)	0.72 ± 0.2	Sumich (1983); Schwarz (2002); as cited in Villegas-Amtmann 2017 *The mean (±SE) breathing rate for southbound whales was 0.8 ± 0.1 breaths/min *based on n= 32. (Table 1, Rodriguez de la Gala-Hernandez et al. 2008).* *"Breathing rate for southbound migrating whales in this work (0.8 breaths/min) is similar to the 0.72 breaths/min obtained by Sumich (1983)." (Rodriguez de la Gala-Hernandez et al. 2008).* **I decided to use the values from Sumich (1983) and Schwarz (2002)*
58	Juvenile/ Adult	Southbound (Nov)	southbound	30	Immature gray whales: "Other immature gray whales must have similar girth measurements at the commencement of their southward fasting migration in November, for their mean girth is reduced to O.56L by the time they reach central California a month later." Sumich (1986) "Reconstruction of the migration from all available data shou's that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June	0.72 ± 0.2	Sumich (1983); Schwarz (2002); as cited in Villegas-Amtmann 2017 *The mean (±SE) breathing rate for southbound whales was 0.8 ± 0.1 breaths/min *based on n= 32. (Table 1, Rodriguez de la Gala-Hernandez et al. 2008).*

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					through October, and migrates southward in November and December." Pike (1962) "The southbound migration probably begins by early October when the whales travel from the northern to the southeastern Bering Sea and intersect the southwest end of the Alaska Peninsula before leaving the Bering Sea through Unimak Pass, from late October to January." Braham (1984) Cape Sarichef, Alaska: "Peak sighting dates were recorded on 23 November 1977 (high count), 3 December 1978 (median) and 7 December 1979 (median)." Rugh et al. 2001 "Generally, then, most gray whales are migrating out of northern seas sometime between mid-October and November, but some have been seen near the Chukotka Peninsula as late as mid-December (reviewed in Yablokov and Bogoslovskaya, 1984)." Rugh et al 2001.		*"Breathing rate for southbound migrating whales in this work (0.8 breaths/min) is similar to the 0.72 breaths/min obtained by Sumich (1983)." (Rodriguez de la Gala-Hernandez et al. 2008).* _*I decided to use the values from Sumich (1983) and Schwarz (2002)_
59	Juvenile/ Adult	Southbound (Dec)	southbound	31	San Diego, California "Southbound gray whales in large numbers can be easily observed from shore at numerous sites, particularly in California, during late December and January, as they swim steadily on courses generally parallel to shore." – Sumich (1986) California – southbound migration surveys. Observations from Dec – Feb, peaking mid-January. Figure 1, Laake et al. (2012) "Off Washington and British Columbia the northward migration begins in February, ends in May, and is at a peak during the first two weeks in April; the southward migration occurs in December and January, and is at a peak in late December". Pike (1962) "Reconstruction of the migration from all available data shou's that most of the American	0.72 ± 0.2	Sumich (1983); Schwarz (2002); as cited in Villegas-Amtmann 2017 _The mean (±SE) breathing rate for southbound whales was 0.8 ± 0.1 breaths/min *based on n= 32. (Table 1, Rodriguez de la Gala-Hernandez et al. 2008)._ *"Breathing rate for southbound migrating whales in this work (0.8 breaths/min) is similar to the 0.72 breaths/min obtained by Sumich (1983)." (Rodriguez de la*

ID	Life stage	Description	Activity stages	No of days	Source for approx. time of year and no. of days	Respiration rates (bpm ± SE)	Source for respiration rates
					herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December." Pike (1962) "Based on available observations and calculations using a travel rate of 147km/day, current median (peak) sighting dates of the southbound migration should be: 1 December in the north central Bering Sea (here considered the theoretical starting point for the migration); 12 December at Unimak Pass, Alaska; 18 December for Kodiak Island, Alaska; 5 January for Washington State; 7 January for Oregon; 15 January for central California; 18 January in southern California; and 24 January at the northern lagoons in Baja California (considered here to be the terminus of the migration)." Rugh et al. 2001 "The southbound migration probably begins by early October when the whales travel from the northern to the southeastern Bering Sea and intersect the southwest end of the Alaska Peninsula before leaving the Bering Sea through Unimak Pass, from late October to January." Braham (1984) Southern California Migration peaks: "Peak densities were observed in January for the southward and in March for the northward migration." Leatherwood (1974)		*Gala-Hernandez et al. 2008).* **I decided to use the values from Sumich (1983) and Schwarz (2002)*

Appendix D Uncertainty and model sensitivity – scenario results

D.1 Gross Energy Requirements (GER)

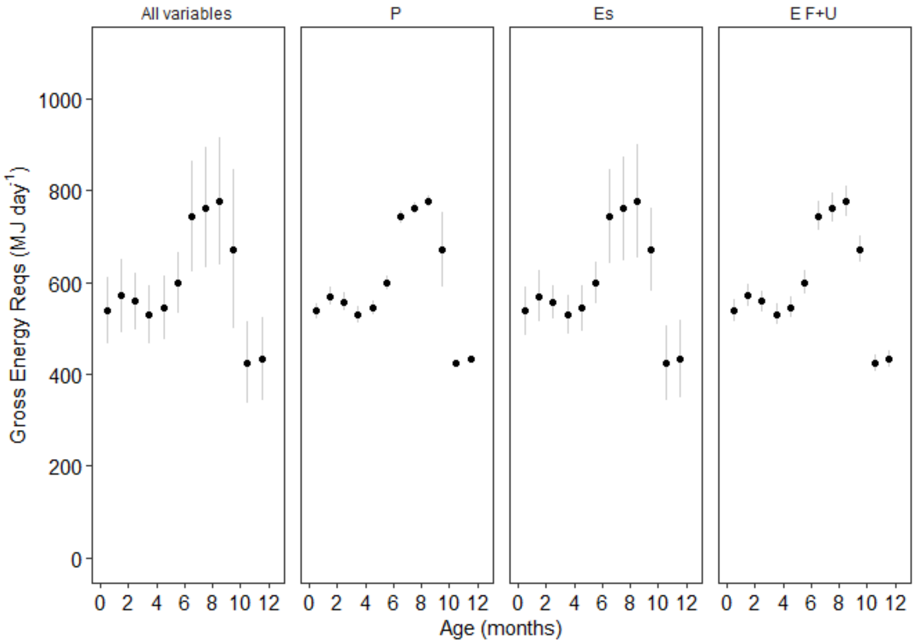

Figure 16. Comparison of uncertainty contributed by parameters towards GER model outputs for grey whale calves (Phase 1). Panels shown represent scenarios where single parameters were varied while the remaining parameters were kept constant (P – Production cost, Es – Total energetic expenditure, E F+U – Digestive efficiency: fecal and urinary). Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations for each scenario.

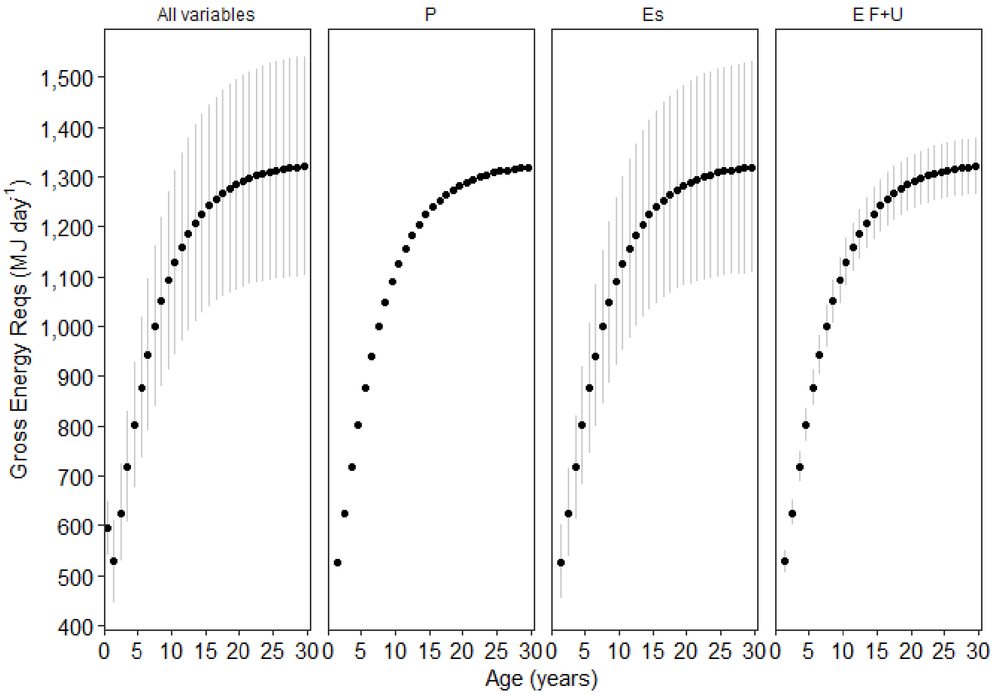

Figure 17. Comparison of uncertainty contributed by parameters towards GER model outputs for grey whale juveniles and non-reproductive adults (Phase 2). Panels shown represent scenarios where single parameters were varied while the remaining parameters were kept constant (P – Production cost, Es – Total energetic expenditure, E F+U – Digestive efficiency: fecal and urinary). Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations for each scenario.

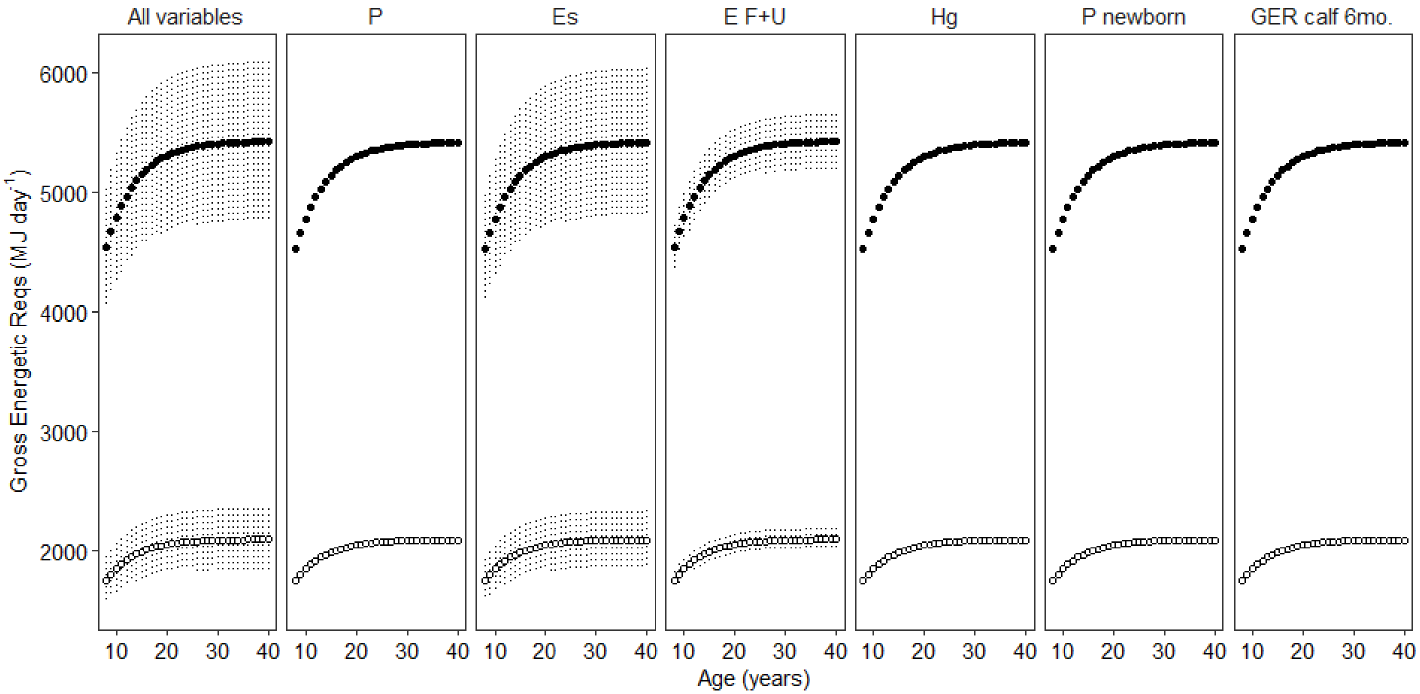

Figure 18. Comparison of uncertainty contributed by parameters towards GER model outputs for pregnant grey whales. Panels shown represent scenarios where single parameters were varied while the remaining parameters were kept constant (P – Production cost, Es – Total energetic expenditure, E F+U – Digestive efficiency: fecal and urinary, Hg – Heat increment of gestation, P newborn – Production cost of a newborn, GER calf 6mo. – gross energy requirements for a calf over a period of 6 months). Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations for each scenario.

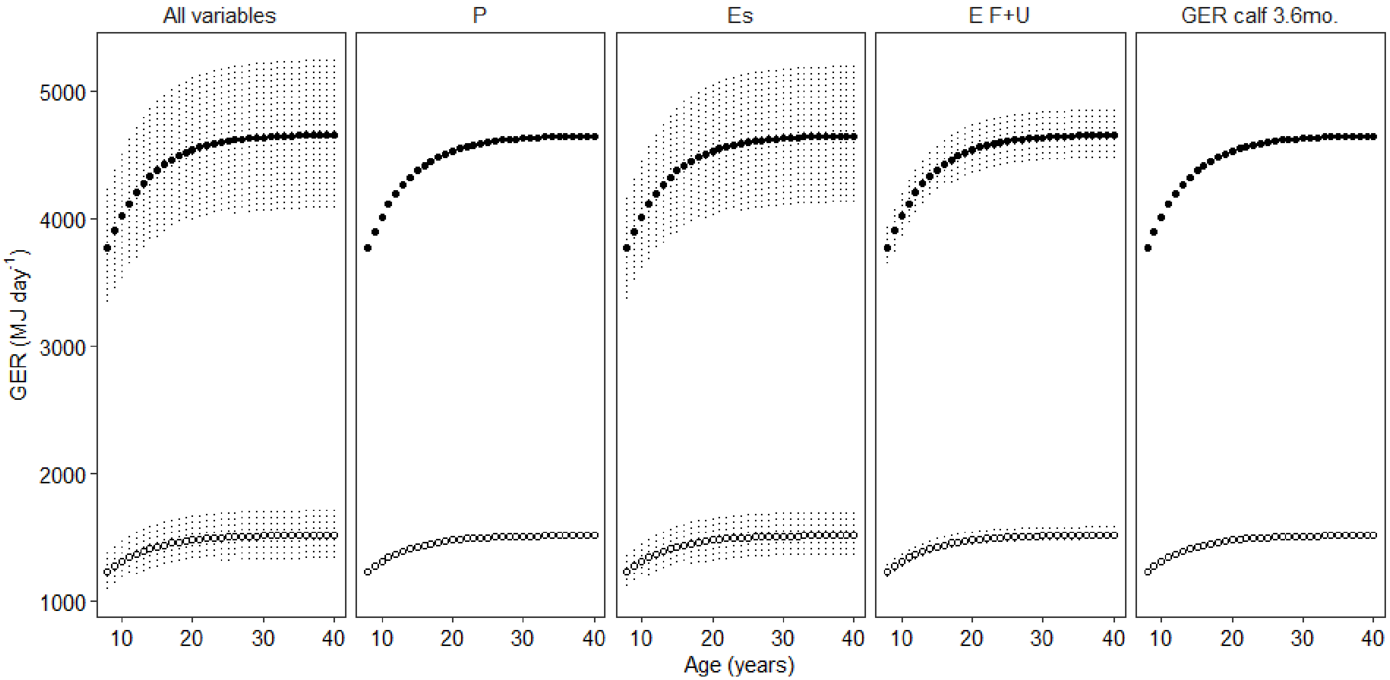

Figure 19. Comparison of uncertainty contributed by parameters towards GER model outputs for lactating grey whales. Panels shown represent scenarios where single parameters were varied while the remaining parameters were kept constant (P – Production cost, Es – Total energetic expenditure, E F+U – Digestive efficiency: fecal and urinary, GER calf 3.6mo. – gross energy requirements for a calf over a period of 3.6 months). Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations for each scenario.

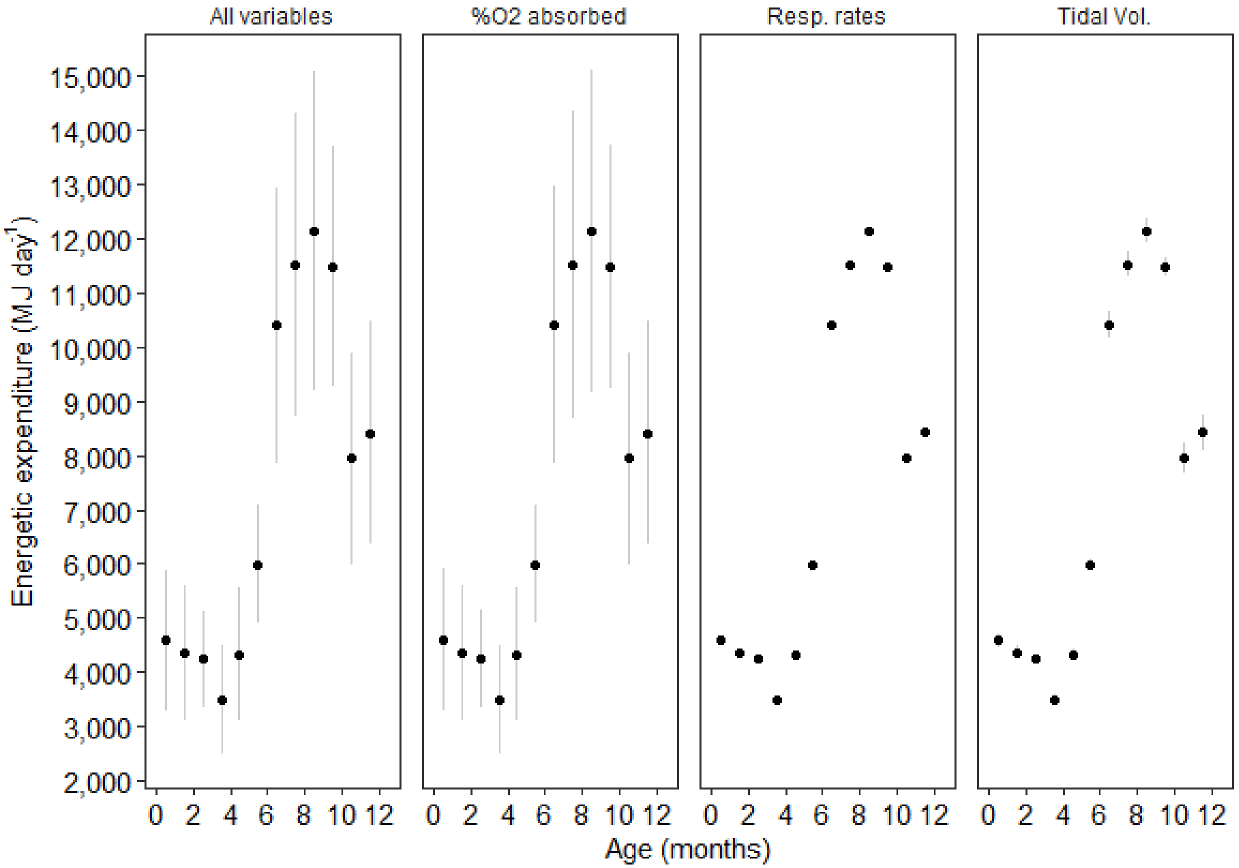

Figure 20. Comparison of uncertainty contributed by parameters towards E_s model outputs for grey whale juveniles and non-reproductive adults (Phase 2). Panels shown represent scenarios where single parameters were varied (i.e., percentage of oxygen absorbed, respiration rates, and tidal volume) while the remaining parameters were kept constant. Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations for each scenario.

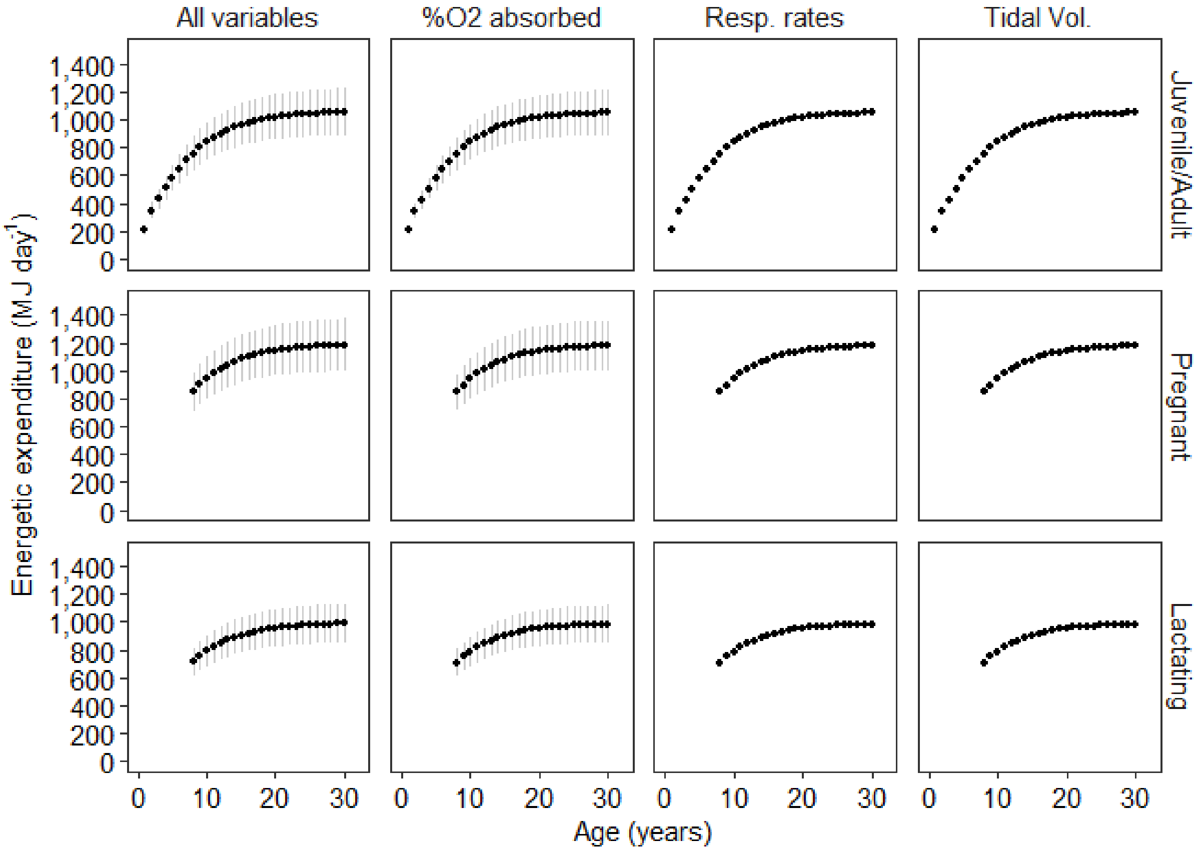

Figure 21. Comparison of uncertainty contributed by parameters towards GER model outputs for grey whale juveniles and adults, including pregnant and lactating females. Panels shown represent scenarios where single parameters were varied (i.e., percentage of oxygen absorbed, respiration rates, and tidal volume) while the remaining parameters were kept constant. Error bars show the standard deviation around the mean of 10,000 Monte Carlo simulations for each scenario.