A Theoretical Approach To Assessing Annual Energy Balance In Gray Whales (eschrichtius Robustus)

2005

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A THEORETICAL APPROACH TO ASSESSING ANNUAL ENERGY BALANCE IN GRAY WHALES (ESCHRICHTIUS ROBUSTUS)

by

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B.S. Texas A&M University at Galveston, 2000

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in the Department of Biology in the College of Arts and Sciences at the University of Central Florida Orlando, Florida

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2005
ABSTRACT

While direct measurements of energetic demands are nearly impossible to collect on large cetaceans, comprehensive bioenergetic models can give insights on such parameters by combining physiological and ecological knowledge. This model was developed to estimate necessary food intake of gray whales, *Eschrichtius robustus*, of the Eastern North Pacific stock. Field Metabolic Rates (FMR) for gray whales were first estimated based on various assumptions (e.g. volumetric representation of gray whales, extent of their feeding season, and blubber depth distribution) using morphometric data, energetic costs, and food assimilation according to age and gender specific requirements. Food intake rates for gray whales of varying maturity and gender were then estimated based on FMR and caloric value of prey and compared to food intake rates of previous studies. Monte Carlo simulations and sensitivity analysis were performed to assess the model’s predictions compared to observed field data from previous studies. Predicted average food intakes for adult male, pregnant/lactating female, and immature whales were 475 ± 300, 525 ± 300 and 600 ± 300 kg d$^{-1}$, respectively. Estimated blubber depths resulting from these food intakes were comparable to field data obtained from whaling data. Sensitivity analysis indicated food intake, from all parameters, as having the highest impact on the percent change in ending mass from a simulation. These food intake estimates are similar to those found in a previous study and fall within the range of food intake per body mass observed in other species of cetaceans. Though thermoregulation can be a factor in some cetaceans, it appears not to be an additional cost for gray whales as the present
model’s predicted lower critical temperatures for the whales ($T_{LC}$) were below ambient
temperatures. With temperatures increasing in the Bering Sea, the main prey of gray whales,
ampeliscid amphipods, could be adversely affected, possibly resulting in increased food
shortages leading to a surge in gray whale strandings.
This work is dedicated to Dr. S. Jonathan Stern, without whom I would have never started this project, and to Dr. Pedro F. Quintana-Ascencio, without whom I would have never finished this project.
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This research would have been impossible without the help of many people. I thank the University of Central Florida Biology Department and Dr. Graham A. J. Worthy for providing instrumental funding for my research.

Foremost, I thank my family and loved ones for always supporting me in following my dreams. My parents, Lewis and Sylvette Greenwald, helped and guided me throughout every bump in my life and I would not be the person I am today without them. My brother, Scott Greenwald, has always been there to support and help me in every way possible. I also thank Michael Faulk, a very important person in my life, who has supported and guided me throughout this journey.

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This research is greatly due to several scientists who were so kind as to allow the usage of their data. I thank Dr. James Sumich for providing morphometric data and the migration map. Dr. Dale Rice and Sally Mizroch entered in all of Dr. Rice and Dr. Wolman’s data from their gray
whales studies and provided them for this research. John Calambokidis kindly provided additional morphometric data.

There were additional scientists who were always ready to help. Dr. Bernd Würsig gave me guidance and support since my undergraduate years. Dr. “Paco” Ollervides provided great advice in the initial set-up of this project. I want to thank Dr. Jonathan Leason and colleagues for their help at the last minute. Dr. Patrick Miller very kindly supplied a reference I needed at the last second, when we had never spoken before.

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INTRODUCTION

While energetic demands of terrestrial mammals have been extensively researched, such measurements are restricted in marine mammals, especially free-ranging baleen whales, mainly due to their large size and limited accessibility in their habitat. By compiling known allometric and physiological parameters of marine mammals into a simulation model, it may be possible to better understand how these factors interact and possibly predict impacts that environmental changes could have on the animals themselves. In order to further understand energetic demands in the wild, it may also be necessary to use a model to determine the areas that have not yet been extensively examined.

Techniques for Measuring Energetic Demands

Doubly labeled water is a methodology commonly used for measuring energetic demands. This procedure consists of dosing an animal with a precisely known quantity of water composed of the heavier isotopes of hydrogen and oxygen, and later collecting blood samples to determine the dilution of the isotopes over a measured time period (e.g. Bevan et al. 1995, Garcia et al. 2004, Hernandez et al. 2004, Shaffer et al. 2004). There are limitations to this method, however, including the high monetary cost of dosing and the logistical considerations of using this approach with an animal the size of a baleen whale (Suborder Mysticeti) in the field.
Another methodology that has been frequently used is open/closed respirometry. This approach involves placing an animal in an enclosed chamber with a known flow rate and measuring the oxygen concentration of the air exiting the chamber, allowing for the calculation of the animal’s metabolic rate (e.g. Worthy et al. 1987, Haim et al. 1992, Bustamante et al. 2002). Though this technique has been used on smaller marine mammals (e.g. Worthy et al. 1987, Webb et al. 1998, Mcphee et al. 2003), it would be difficult if not impossible to confine larger marine mammals, such as mysticetes, inside a chamber.

Simulation models have been used in place of direct measurements when such logistical constraints prevent direct measurements. For example, Winship et al. (2002) calculated the food requirements of Steller sea lions, Eumetopias jubatus, by estimating energy requirements based on the bioenergetic scheme and population size as well as age structure. Markussen et al. (1992) were able to estimate food consumption for the entire northeast Atlantic minke whale, Balaenoptera acutorostrata, population consisting of 2.2 million tons of prey over a feeding period of five months. With actual energetic measurements being virtually impossible to collect in the field, modeling is a practical solution to estimate the energetic requirements for large marine mammals.

**Energetic Demands**

Basal metabolic rate (BMR) is the minimum operating metabolism for an organism to survive (Worthy 2001) and is a function of mass and age (Kleiber 1975). There has been a great deal of debate in the literature as to whether marine mammals follow the Kleiber (1975) relationship. There is good evidence that at least some groups of marine mammals, specifically phocid seals, follow Kleiber’s (1975) relationship of BMR and body mass (Lavigne et al. 1986,
Costa and Williams 1999, Worthy 2001), however there is inadequate information in the literature for cetaceans (Lavigne et al. 1986). To be truly comparable, BMR must be measured under certain prescribed conditions. Animals must be adult, at rest, thermally neutral, and postabsorptive (Kleiber 1975). For juveniles, BMR is generally double that estimated for an adult of similar mass, to compensate for the additional energetic expenditures of growth (Brody 1945, Kleiber 1975, Worthy 2001).

Consumed prey ultimately provides the energy needed to compensate for all energetic costs. Ingested energy (IE) is processed through a series of steps described as the bioenergetic scheme (Figure 1). There is a loss of energy in the form of feces, with apparent digestible energy remaining. Additional energy is lost as urine, leaving metabolizable energy, which includes that used for heat production (BMR, heat increment of feeding, work and activity) and recovered energy used for somatic growth, reproduction, and energy storage (Costa and Williams 1999, Worthy 2001). In order to store energy, ingested energy must exceed energy requirements and the surplus is stored in the form of fat, generally blubber in the case of marine mammals (Costa and Williams 1999, Worthy 2001).

To calculate amount of energy available for storage, additional costs must also be incorporated into this scheme. These costs include foraging, locomotion, and reproduction, and are difficult to measure. This total energy expenditure is known as Field Metabolic Rate (FMR) and is the sum of BMR, cost of locomotion, cost of thermoregulation, and cost of pregnancy/lactation (Costa and Williams 1999, Worthy 2001). Once FMR is calculated, daily food intake for an animal can be estimated by following the bioenergetic scheme backwards. Modeling is currently the only available technique that allows the estimation of food intakes and energetic requirements for large marine mammals.
Figure 1. Diagrammatic representation of the flow of energy in mammals (Costa and Williams 1999, Worthy 2001).
Gray whales, *Eschrichtius robustus*, are the only extant members of the Family Eschrichtiidae. There are two stocks remaining, the Eastern North Pacific (ENP) and the Western North Pacific (WNP) (Rice and Wolman 1971, Rice 1998). The WNP stock possibly numbers less than 100 whales and little is known of it. However, the ENP stock has approximately 26,000 animals and has been examined in greater detail (Marine Mammal Commission 2001). Whales from the ENP stock can migrate over 18,000 km per year, from the northernmost parts of the Chukchi Sea to the southeast corner of the Gulf of California (Figure 2). Some gray whales follow a shorter migration route from the waters off Vancouver Island to those of Central California (Rice 1998), while a few immature gray whales do not migrate to Baja California and remain off the coast of British Columbia (Rice and Wolman 1971).

Prior to leaving the feeding grounds, gray whales must ingest and store enough energy to maintain themselves for the next six to seven months while they migrate to their wintering grounds. Summer feeding grounds consist of the northern and western Bering Sea, the Chukchi Sea, and the western Beaufort Sea (Rice and Wolman 1971, Reed *et al*. 1988) which sustain benthic communities of ampeliscid amphipods on which gray whales feed (Oliver *et al*. 1983, Oliver *et al*. 1984, Oliver and Kvitek 1984, Kvitek and Oliver 1986, Kim and Oliver 1989). Based on stomach content analyses, Rice and Wolman (1971) showed that *Ampelisca macrocephala* was the major prey species and estimated an average intake of 1100 kg of prey per day during their feeding season to sustain themselves during their migration.
Figure 2. Map of migration route of gray whales (Sumich personal communication). The stripped region indicates the feeding grounds.
Gray whales are segregated by age, gender, and reproductive status as they depart the
feeding grounds to begin their migration to the breeding grounds off Baja California, Mexico.
The first whales to migrate are generally adult, pregnant or ovulating female whales, followed by
adult male whales (Rice and Wolman 1971). Later, immature male and female whales leave
the feeding grounds (Rice and Wolman 1971). During migration, gray whales have an average
swimming speed of 6.3 km h\(^{-1}\) over the full 24-hour cycle (Perryman et al. 1999). This speed is
relatively constant from the Chukchi Sea (0 ° – 8 °C) to the coastal waters off of Baja California
(18 ° – 22 °C) (Rice and Wolman 1971). Cost of thermoregulation may be a factor for adult
whales if they experience low food availability resulting in low blubber depths or may be an
issue for young-of-the-year.

The sharp increase in the number of strandings of dead gray whales that occurred
during their northern migration in 1999 and 2000 has been hypothesized to be due to insufficient
energetic reserves. Out of an estimated stock of 26,000 whales in 2000 (Perryman et al. 2002),
there were 284 strandings in 1999 and 377 in 2000 (Marine Mammal Commission 2001). Prior
to this phenomenon, strandings averaged less than 40 whales per year, with a record high of
only 87 prior to 1999 (Marine Mammal Commission 2001). In recent studies, it has been
postulated that food availability for gray whales could have been affected by an increase in
water temperatures in the Bering Sea, part of the summer feeding grounds for the whales
(Coyle and Highsmith 1994, Moore et al. 2003, Tynan 2004). However, if whales were unable
to consume and store enough energy to support their energetic demands for the migration, it is
conceivable that these mortalities could have been due to starvation. While it is generally
believed that gray whales do not eat during their migration, sightings of gray whales feeding
along the migration route (Rice and Wolman 1971) and on the breeding grounds have increased
(Sánchez-Pacheco et al. 2001). The energetic significance of these occasional feedings, if any,
is unknown.
Objectives

The main goal of this study was to develop a model that allows for a better understanding of the energetic costs to which gray whales are subjected during migration. Based on allometric and physiological parameters, this study estimated energy requirements and growth of gray whales of varying life history stages (adult male, pregnant/lactating female, and immature whales) throughout their annual migration and period of summer feeding. Additionally, energy expenditures and mass changes that could occur over the course of several years on different levels of food intake were simulated using gray whales of known mass and linear measurements.
MATERIALS AND METHODS

A model was written to simulate expenditures of gray whales (Matlab Version 6.5, Mathworks). Whales were represented using a cylinder with an interlocking cone at each end, allowing the estimation of body volume and mass. Blubber depth was assumed to be uniform over the mid-body (cylinder) and tail region (posterior cone) and absent on the head region (anterior cone) (Figure 3). Adult whale length was held constant through time, whereas immature gray whales were assumed to grow at an average rate of 1.1 m per year. Core volume was assumed to remain constant in all adult simulations even with increasing/decreasing energy stores. Core lipid reserves comprised an assumed 20% of core mass, based on data for body composition of other marine mammal species (Worthy 1985). Feeding was limited to May 16 through October 31 of each year. Migration took place from November 1 to May 15 when the whales returned to the feeding grounds.

Initial morphometrics, energetic costs, food assimilation, modification of morphometrics, and fetal growth for pregnant female whales were calculated. Food intake (kg d\(^{-1}\)), mass (kg), girth (m), blubber depth (cm), length (m), gender, stage of maturity (adult versus juvenile), and number of days initialized the beginning of each simulation (Table 1). These same initial parameters were used for each of the three life history categories of whales (Table 2). Monte Carlo simulations were run using 500 replicates of whales, each lasting three years (1095 days) except in the case where female animals were modeled with two consecutive pregnancies that resulted in simulations lasting four years (1461 days). A median of the 500 replicates was determined for each set of runs as well as a 95% confidence interval. On the first day of each
Figure 3. Diagrammatic representation of a gray whale using a cylinder with an interlocking cone at each end compared to a picture of a gray whale as reference (Rice and Wolman 1971). “Head” refers to the region from the snout to the occipital condyles, the “body” is from the occipital condyles to the anus, and the “tail” region is from the anus to the fluke. The hashed region indicates blubber.
Table 1. List of symbols used in the main model for gray whales, the parameters they represent, and the units of measurement.

<table>
<thead>
<tr>
<th>Model Matrix^</th>
<th>Symbol~</th>
<th>Parameter</th>
<th>Unit of measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>whalea (1/ i, …)</td>
<td>1</td>
<td>Mass*</td>
<td>kg</td>
</tr>
<tr>
<td>2</td>
<td>Girth*</td>
<td>m</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Blubber depth*</td>
<td>m</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Blubber mass</td>
<td>kg</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>CG (cm to g) ratio</td>
<td>m kg^-1</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Basal Metabolic Rate</td>
<td>MJ d^-1</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Cost of Locomotion</td>
<td>MJ d^-1</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Field Metabolic Rate</td>
<td>MJ d^-1</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Blubber used</td>
<td>kg</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Core energy used</td>
<td>kg</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>Blubber remaining</td>
<td>kg</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>Core energy remaining</td>
<td>kg</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>Heat Increment of Feeding</td>
<td>MJ d^-1</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>Energy</td>
<td>MJ d^-1</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>Energy stored</td>
<td>MJ d^-1</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>New blubber depth</td>
<td>m</td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>New mass</td>
<td>kg</td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>New Lower Critical Temperature</td>
<td>ºC</td>
<td></td>
</tr>
<tr>
<td>whaleb (1/ i, …)</td>
<td>1</td>
<td>Gender* (0 = immature; 1 = mature male; 2 = mature female; 3 = pregnant/ lactating female</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>Length*</td>
<td>m</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Radius</td>
<td>m</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Volume</td>
<td>m^3</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Core radius</td>
<td>m</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Core volume</td>
<td>m^3</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Blubber volume</td>
<td>m^3</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Core mass</td>
<td>kg</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Core energy available</td>
<td>kg</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Assimilation Energy</td>
<td>MJ d^-1</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>Gross Energy</td>
<td>MJ d^-1</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>New radius</td>
<td>m</td>
<td></td>
</tr>
<tr>
<td>whalec (1/ i, …)</td>
<td>1</td>
<td>Fetal length</td>
<td>m</td>
</tr>
<tr>
<td>2</td>
<td>Fetal radius</td>
<td>m</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Fetal volume</td>
<td>m^3</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Fetal mass</td>
<td>kg</td>
<td></td>
</tr>
</tbody>
</table>

^ Parameters separated into three matrices due to limitation of program.
~ Each assigned symbol corresponds to the variables in the models (see Appendices A – E).
* Initial input parameters needed to run the model.
Table 2. Values of initial input parameters used in all of the simulations for an adult male, a pregnant/lactating female and an immature gray whale (based on Rice and Wolman 1971).

<table>
<thead>
<tr>
<th>Whale Type</th>
<th>Initial Input Parameters</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult male</td>
<td>Mass</td>
<td>16000.0 kg</td>
</tr>
<tr>
<td></td>
<td>Girth</td>
<td>6.0 m</td>
</tr>
<tr>
<td></td>
<td>Blubber Depth</td>
<td>13.0 cm</td>
</tr>
<tr>
<td></td>
<td>Length</td>
<td>11.7 m</td>
</tr>
<tr>
<td>Pregnant/ lactating female</td>
<td>Mass</td>
<td>16000.0 kg</td>
</tr>
<tr>
<td></td>
<td>Girth</td>
<td>6.0 m</td>
</tr>
<tr>
<td></td>
<td>Blubber Depth</td>
<td>14.0 cm</td>
</tr>
<tr>
<td></td>
<td>Length</td>
<td>12.7 m</td>
</tr>
<tr>
<td>Immature</td>
<td>Mass</td>
<td>8700.0 kg</td>
</tr>
<tr>
<td></td>
<td>Girth</td>
<td>4.7 m</td>
</tr>
<tr>
<td></td>
<td>Blubber Depth</td>
<td>12.0 cm</td>
</tr>
<tr>
<td></td>
<td>Length</td>
<td>9.14 m</td>
</tr>
</tbody>
</table>
run, the whale was considered to not be feeding and female whales were not pregnant or lactating.

**Morphometrics**

Proportions of total length associated with the head region, main body region, and tail region were estimated for different age categories of whales based on stranding and whaling data (Rice and Wolman 1971, Calambokidis unpublished data, Rice unpublished data). The estimated percentages of total length representing each body region (head, body, and tail) were used to define the dimensions of the cone-cylinder-cone volumetric representation of whales (Figure 3) in each age category.

For immature whales, the percentages of total length (snout to fluke) were 22.6%, 46.0%, and 31.4% for the head, body, and tail regions, respectively (Calambokidis unpublished data, Rice unpublished data). Proportions for mature whales were estimated at 22.9 %, 46.6%, and 30.5%, and fetal length proportions were 23.0%, 49.0%, and 28.0%, respectively (Calambokidis unpublished data, Rice unpublished data).

Growth rate of immature whales was estimated using whaling data (Rice unpublished data). Growth in length was linearly modeled ($r^2 = 0.921$, $p < 0.001$):

$$L_i = 9.143 + 0.0018^*t$$

(1)

where $L_i$ is length of immature whale (m) and $t$ is simulated time of model (days) (Figure 4).
Figure 4. Growth rate of immature gray whales (Equation 1) ($r^2 = 0.921$, $p < 0.001$) based on data collected from commercial whaling over a three-year period (circles) (Rice and Wolman 1971, Rice unpublished data).
Initial radius of each whale was calculated based on girth (Figure 5). Core radius was defined as total radius minus blubber depth. Total volume and core volume were calculated using their respective radii and the equations appropriate for the assessment of the volume of cones and cylinders. Core volume was subtracted from total volume to calculate blubber volume. Blubber volume was subsequently converted into blubber mass using an average cetacean blubber density of 0.94 g cm\(^{-3}\) (Worthy, personal communication). Core mass was calculated as the difference between blubber mass and total mass.

From subsequent days of the simulation, the final blubber depth of each day was used as the initial blubber depth for the next day. Blubber depth was then related to blubber mass using a ratio of depth and mass (CG ratio - Worthy 1985) and depth recalculated after mass changes:

\[
\text{CG ratio} = \frac{BD}{B_{\text{mass}}} \quad (2)
\]

where CG is the cm to g ratio, BD is blubber depth (m) and \(B_{\text{mass}}\) is blubber mass (kg).

**Energetics**

Gray whale basal metabolic rate was estimated using Kleiber’s equation (1975) as suggested by Lavigne *et al.* (1990):

\[
\text{BMR} = 3.4 M^{0.75} \quad (3)
\]

where BMR is basal metabolic rate (J s\(^{-1}\)) and M is total body mass (kg) of the whale (Figure 6). For immature whales, BMR was estimated to be twice that described above to account for
Figure 5. Diagrammatic representation of an algorithm describing the flow of morphometric parameters in the model: circles are variables; double circles are initial input parameters; shaded boxes indicate parameters affected by life history stage; and open boxes indicate where values are subsequently used in the model. CG ratio represents cm to g ratio. Whalea and whaleb refer to membership of these variables in model matrices and respective symbols (Table 1).
the increased metabolism found in juvenile whales to accommodate growth (Lavigne et al. 1990).

Cost of locomotion was estimated, based on Lockyer (1981) and an average swimming speed of 6.3 km h\(^{-1}\) for gray whales (Perryman et al. 1999):

\[
C_T = 0.248 V M^{0.7}
\]  \hspace{1cm} (4)

where \(C_T\) is the cost of locomotion (MJ d\(^{-1}\)), \(V\) is velocity (m s\(^{-1}\)), and \(M\) is whale mass (N).

Pregnant and lactating female whales incurred additional energetic costs. Cost of pregnancy was calculated by adding the mass of the growing fetus to the mother’s mass and using this combined mass to estimate a total BMR. Cost of lactation was estimated using a relationship derived for minke whales by multiplying BMR by a factor of 1.75 (Lockyer 1981, Worthy 2001). For pregnant and lactating female whales, FMR was the sum of BMR, cost of locomotion, and their respective reproductive costs.

During the feeding season, daily energy requirements were subtracted from metabolizable energy and any excess was stored as fat (15\% of energy in the blubber and 85\% of energy in the core). Maximum core fat content was assumed to be 20\% of core mass based upon measurements from other marine mammals (Worthy 1985). Once core reserves were full, all surplus energy was stored in the blubber.

During migration, energy needs were assumed to be met by initially deriving 15\% of total daily needs from blubber reserves and 85\% from core reserves, until the core reserves were exhausted, at which point 100\% of energy needs were derived from blubber (Worthy 1985). It is assumed that a gray whale in the wild would deplete core fat stores first in order to maintain the blubber layer that is critical for hydrodynamics and thermoregulation.
Figure 6. Diagrammatic representation of an algorithm describing the flow of energetic parameters in the model: circles are variables; double circles are initial input parameters; shaded boxes indicate parameters affected by life history stage; trapezoid represents a constant; and open box indicates where value is subsequently used in the model. Energy is represented as E and basal metabolic rate as BMR. Whalea and whaleb refer to membership of these variables in model matrices and respective symbols (Table 1).
Assimilation Efficiency

Gray whales primarily feed on amphiliscid amphipods (Rice and Wolman 1971) and for this model, it was assumed that their energy content is comparable to other invertebrates (1 kcal g\(^{-1}\)) (Tyler 1973, Lowry and Frost 1984). Fecal energy losses are assumed to be 20% of ingested energy (IE) (Costa and Williams 1999) and an additional 10% of assimilated energy lost as urine (Costa and Williams 1999, Figure 7). Remaining energy was gross energy available for use by the whale, with the exception of energy lost as the heat increment of feeding (HIF), which accounts for an added loss of 10% of IE (Costa and Williams 1999).

Modified Morphometrics

Body morphometrics were recalculated at the end of every day to account for changes that had occurred as a result of energy intake and/or expenditures. Morphometric estimates from the end of the day were used as the starting morphometric parameters for the following day. New blubber and core masses were calculated depending on depletion or addition of energy (Figure 8). Using the CG ratio (eqn 2), the resulting new blubber mass (after energy deposit or withdrawal) was converted to a new blubber depth.

Lower critical temperature (T\(_{LC}\)) was estimated at the beginning of each day to determine if thermoregulation was a cost experienced by the whales (Figure 9). Estimates of the T\(_{LC}\) were calculated as suggested for blue whales (Lavigne et al. 1990) using the formula:
Figure 7. Diagrammatic representation of an algorithm describing the flow of food assimilation parameters in the model: circles are variables; trapezoid represents a constant; and open box indicates where value is subsequently used in the model. Energy is represented as E and heat increment of feeding as HIF. Whalea and whaleb refer to membership of these variables in model matrices and respective symbols (Table 1).
Figure 8. Diagrammatic representation of an algorithm of parameters describing the condition of the whale at the end of the daily cycle in the model: circles are variables; double circles are initial input parameters; and open boxes indicate where values are subsequently used in the model. Energy is represented as E. Whalea and whaleb refer to membership of these variables in model matrices and respective symbols (Table 1). The cm to g (CG) ratio is used to convert blubber depth to blubber mass (Worthy 1985).
Figure 9. Diagrammatic representation of an algorithm representing the flow of lower critical temperature parameters in the model: circles are variables; and double circles are initial input parameters. Basal metabolic rate is represented as BMR and lower critical temperature as $T_{LC}$. Whalea and whaleb refer to membership of these variables in model matrices and respective symbol (Table 1).
\[ T_{LC} = T_{MB} - 0.5 \cdot \frac{Q_{CY}}{2 \cdot \pi \cdot k \cdot L} \cdot \log_e \left( \frac{M}{M_C} \right) \] (5)

where \( T_{LC} \) is lower critical temperature (°C), \( T_{MB} \) is mean body temperature (37 °C), \( Q_{CY} \) is metabolic rate (J s\(^{-1}\)), \( M \) is total mass (kg), \( M_C \) is core mass (kg), \( L \) is length (m), and \( k \) is thermal conductivity (assumed to be 0.2 J s\(^{-1}\) m\(^{-1}\) °C\(^{-1}\)) (Worthy 1985, Kvadsheim et al. 1994, Kvadsheim et al. 1996).

**Fetal Growth**

Gestation was assumed to begin on December 5 and end 13 month later on January 10. Lactation was assumed to last seven months, ending on August 10 (Rice and Wolman 1971). The model assumed that if a female became pregnant in year one, she lactated through year two, and could then potentially become pregnant again that following December (year three). The impact of carrying a fetus on the energetic needs of the female continually increased through gestation as a function of estimated fetal mass (Figure 10).

As mentioned previously, energy needs of pregnant female whales were estimated by incorporating the increasing mass of the fetus into total female whale mass to calculate the cost of pregnancy. Given the lack of available data on fetal masses, a power model was developed using lengths of fetuses from two months to thirteen months of gestational age collected through as a result of commercial whaling (Rice and Wolman 1971; \( r^2 = 0.999, p = 0.017 \)):

\[ L_F = 4.1 \cdot 10^{-7} a^{2.3329} \] (6)
Figure 10. Diagrammatic representation of an algorithm describing fetal development in the model: circles are variables; trapezoid represents a constant; and open box indicates where value is subsequently used in the model. Whalea and whaleb refer to membership of these variables in model matrices (Table 1).
where \( L_F \) is fetal length (m) and \( a \) is fetal age (days). Using a photo of a gray whale fetus of known length from Rice and Wolman (1971), the diameter of the fetus was estimated and girth calculated. With these measurements, fetal volume was calculated in the same manner as for mature and immature whales. This volume was then converted to mass (1 g cm\(^{-3}\)).

Estimated fetal growth in length and mass are depicted in Figure 11. Total lengths of fetuses at 2-3, 8-9, and 12-13 months of age were 0.096 ± 0.006 m, 2.05 ± 0.06 m, 4.62 ± 0.05 m, respectively (Rice and Wolman 1971, Figure 11). Fetal mass remained fairly linear for the first seven months and then curved sharply, ending with a mass of approximately 1440 kg and length of about 4.85 m.

**Modeling of Food Intake**

For all simulations, food intake was allowed to vary by ± 300 kg d\(^{-1}\). With varying food intakes, changes in blubber depths, masses, and lower critical temperatures (\( T_{LC} \)) were estimated for each category of whale. Estimated blubber depth medians were compared to mean (± SE) depths obtained from healthy gray whales collected from the Western North Pacific (WNP) stock and from the Eastern North Pacific (ENP) stock (Tables 3 & 4). Predictions were considered significantly different from field data if estimated blubber depth medians were outside the range of field blubber depth means (± SE).

Immature whales were simulated to grow during the three years. Due to limitations of the linear model and the whaling data, immature whales measured 9.14 m in length at the beginning of each simulation and reached 11.11 m at the end of three years, classifying it as an adult if the model was to simulate a fourth year.
Figure 11. Power model (Eqn. 5, $r^2 = 0.999$, $p = 0.017$) representing prenatal growth curve (solid lines) for gray whale fetuses, from conception to parturition, based on mean length of gray whale fetuses from two months to twelve months old (circles, Rice and Wolman 1971) (A). Using a picture of a near-term gray whale fetus of known length (Rice and Wolman 1971), a girth to length comparison was used to estimate girth, radius and volume during the entire pregnancy. Volume of the fetus was then converted to mass (B).
Table 3. Morphometrics (mean ± SE) of healthy gray whales from the Eastern North Pacific stock taken as part of commercial whaling operations off the coast of California (from 1959 to 1969; Rice and Wolman 1971, Rice unpublished data).

<table>
<thead>
<tr>
<th>Whale Category</th>
<th>Parameter</th>
<th>Mean</th>
<th>Low range</th>
<th>High range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>Length</td>
<td>11.9 (± 0.0)</td>
<td>11.1</td>
<td>13.3</td>
</tr>
<tr>
<td></td>
<td>Girth</td>
<td>6.3 (± 0.1)</td>
<td>4.8</td>
<td>9.5</td>
</tr>
<tr>
<td></td>
<td>Blubber Depth</td>
<td>13.3 (± 0.1)</td>
<td>9.5</td>
<td>18.0</td>
</tr>
<tr>
<td>Female</td>
<td>Length</td>
<td>12.5 (± 0.1)</td>
<td>12.5</td>
<td>12.8</td>
</tr>
<tr>
<td></td>
<td>Girth</td>
<td>6.9 (± 0.1)</td>
<td>6.9</td>
<td>8.0</td>
</tr>
<tr>
<td></td>
<td>Blubber Depth</td>
<td>15.2 (± 0.3)</td>
<td>10.5</td>
<td>20.0</td>
</tr>
<tr>
<td>Pregnant Female</td>
<td>Length</td>
<td>12.8 (± 0.1)</td>
<td>11.6</td>
<td>14.1</td>
</tr>
<tr>
<td></td>
<td>Girth</td>
<td>8.0 (± 0.1)</td>
<td>5.5</td>
<td>9.5</td>
</tr>
<tr>
<td></td>
<td>Blubber Depth</td>
<td>15.5 (± 0.2)</td>
<td>10.0</td>
<td>19.0</td>
</tr>
<tr>
<td>Immature</td>
<td>Length</td>
<td>10.5 (± 0.1)</td>
<td>8.6</td>
<td>11.7</td>
</tr>
<tr>
<td></td>
<td>Girth</td>
<td>5.5 (± 0.1)</td>
<td>3.4</td>
<td>7.8</td>
</tr>
<tr>
<td></td>
<td>Blubber Depth</td>
<td>12.9 (± 0.2)</td>
<td>8.0</td>
<td>17.5</td>
</tr>
<tr>
<td>Fetus</td>
<td>Length</td>
<td>3.42 (± 0.23)</td>
<td>0.04</td>
<td>5.31</td>
</tr>
</tbody>
</table>

* Length in m, Girth in m, Blubber Depth in cm.
^ Fetuses measured in more precise manner.
Table 4. Mean blubber depths (cm ± SE) measured on healthy gray whales taken as part of aboriginal whaling of the Western North Pacific Stock (June to November of 1980 to 1991; Sumich et al. unpublished data) and scientific collections of the Eastern North Pacific Stock (December to April of 1959 to 1969; Rice unpublished data).

<table>
<thead>
<tr>
<th>Month</th>
<th>Adult Male</th>
<th>Pregnant Female</th>
<th>Immature</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>-</td>
<td>15.5 (1)</td>
<td>9.0 (1)</td>
</tr>
<tr>
<td>July</td>
<td>11.3 ± 1.9 (6)</td>
<td>13.0 (2)</td>
<td>11.0 ± 0.4 (4)</td>
</tr>
<tr>
<td>August</td>
<td>11.8 ± 0.3 (50)</td>
<td>13.7 ± 0.3 (28)</td>
<td>11.1 ± 0.2 (38)</td>
</tr>
<tr>
<td>September</td>
<td>11.4 ± 0.2 (65)</td>
<td>14.5 ± 0.3 (35)</td>
<td>11.0 ± 0.1 (82)</td>
</tr>
<tr>
<td>October</td>
<td>12.1 ± 0.2 (51)</td>
<td>14.4 ± 0.3 (31)</td>
<td>11.0 ± 0.2 (66)</td>
</tr>
<tr>
<td>November</td>
<td>14.0 (1)</td>
<td>14.2 ± 1.2 (3)</td>
<td>11.4 ± 0.8 (4)</td>
</tr>
<tr>
<td>December</td>
<td>12.7 ± 0.5 (10)</td>
<td>15.8 ± 0.3 (28)</td>
<td>14.5 (1)</td>
</tr>
<tr>
<td>January</td>
<td>13.6 ± 0.2 (58)</td>
<td>15.6 ± 0.3 (24)</td>
<td>13.6 ± 0.3 (27)</td>
</tr>
<tr>
<td>February</td>
<td>13.6 ± 0.5 (5)</td>
<td>15.0 ± 0.7 (11)</td>
<td>14.5 (1)</td>
</tr>
<tr>
<td>March</td>
<td>13.0 ± 0.2 (49)</td>
<td>15.4 ± 0.3 (11)</td>
<td>12.6 ± 0.3 (32)</td>
</tr>
<tr>
<td>April</td>
<td>-</td>
<td>-</td>
<td>11.8 ± 0.4 (5)</td>
</tr>
</tbody>
</table>

*Sample sizes are in parentheses*
RESULTS

Necessary Food Intake for Growth and Energetic Costs

Gray whale energetic requirements for different age classes and genders (adult male, pregnant and lactating female, immature whales) were estimated and the impact of varying food intakes was modeled. Food intakes of 250 kg d$^{-1}$ and 1100 kg d$^{-1}$ were simulated first to test estimations from other studies (Rice and Wolman 1971, Nerini 1984, Wolman 1985, Wells et al. 1999, and Jones and Swartz 2000). Additional simulations were run to estimate average food intakes for each class of whale which best fit field observational data from previous studies (Rice and Wolman 1971, Sumich et al. unpublished data). In all simulations, blubber depth followed the same pattern of decreasing during the migration and increasing during the feeding season, as expected.

Low Range Food Intake

Adult male gray whales consuming 250 kg d$^{-1}$ showed a decrease in blubber depth from 13.0 to 11.4 cm during the first migration (Figure 12A). Blubber depth then increased to 11.8 cm while on the feeding grounds. If this yearly energy intake continued, blubber depth declined to 10.3 cm at the end of the second year migration, increasing to 10.8 cm during the summer feeding period. Blubber depths continued to decline in year three, reaching a minimum of 9.5 cm, ending at 10.2 cm. By the end of year three, these estimates of blubber depth were
Figure 12. Median blubber depth (solid lines) (+ 95% CI) (dashed lines) of an adult male (A), pregnant/lactating female (B), and immature gray whale (C) at food intakes of 250 ± 300 kg d⁻¹ for three years. Circles represent mean field blubber depths (± SE) of healthy gray whales (Sumich et al. unpublished data). Triangles represent mean field blubber depths (± SE) of healthy gray whales (Rice unpublished data). Migration occurs from Nov. 1 to May 14 with feeding lasting from May 15 to Oct. 31 each year. Conception was assumed to happen on Dec. 5 of the first and third year, and birth occurring on Jan. 10 of the second year.
significantly different from observed mean blubber depths based upon both the WNP and the ENP (Figure 12A).

Blubber depth predictions of pregnant and lactating female whales deviated significantly from the observed mean blubber depths at the same food intake for the entire three-year period (Figure 12B). Blubber depths declined from 14.0 to 12.5 cm during the migration and then increased to 12.8 cm on the feeding grounds. By the end of migration in year two, blubber depths decreased to 11.5 cm and then increased to 12.0 cm during the summer feeding period. In year three, blubber depths continued to decline, reaching a minimum of 10.7 cm, ending at 11.3 cm (Figure 12B).

An immature whale feeding at a rate of 250 kg d\(^{-1}\) showed a decrease in blubber depths from 12.0 cm to 9.5 cm during the entire migration, followed by an increase to 10.4 cm, prior to the southward migration (Figure 12C). Upon return to the feeding grounds, blubber depth declined to 8.8 cm and increased to 9.7 cm during the summer feeding period. Depths continued to decline in year three, reaching a low of 8.5 cm, ending at 9.4 cm. These predictions were also significantly different from field observation means during the entire three year period, except for June in year two (Figure 12C).

**High Range Food Intake**

When food intake was increased to 1100 kg d\(^{-1}\) for the three-year period, blubber depth simulations showed the same annual trend of decreasing during the migration and increasing during the feeding months but got increasingly deeper over the entire period (Figure 13). Blubber depth predictions for adult male whales showed a steady increase annually from the initial 13.0 cm to 16.7 cm at the first summer, 19.5 cm (year two) and finally 21.6 cm at the end of year three (Figure 13A). At the end of migration for year one, two, and three, blubber depths
Figure 13. Median blubber depth (solid lines) (+ 95 % CI) (dashed lines) of an adult male (A), pregnant/lactating female (B), and immature gray whale (C) at food intakes of 1100 ± 300 kg d\(^{-1}\) for three years. Circles represent mean field blubber depths (± SE) of healthy gray whales (Sumich et al. unpublished data). Triangles represent mean field blubber depths (± SE) of healthy gray whales (Rice unpublished data). Migration occurs from Nov. 1 to May 14 with feeding lasting from May 15 to Oct. 31 each year. Conception was assumed to happen on Dec. 5 of the first and third year, and birth occurring on Jan. 10 of the second year.
had declined to 11.4 cm, 14.7 cm, and 17.2 cm, respectively. Field observation means were significantly different from the predictions for the three years, except for December of year one (Figure 13A).

At the start of the southward migration for pregnant and lactating female whales with the same food intake, blubber depth predictions increased annually from the initial 14.0 cm to 17.4 cm at the first summer, 20.0 cm (year two) and finally 22.0 cm (year three) (Figure 13B). At the end of the migration of years one, two and three, blubber depths were predicted to reach 12.5 cm, 15.6 cm, and 18.0 cm, respectively, significantly different from observed means during the entire simulated period (Figure 13B).

Immature whales’ blubber depths increased from 12.0 cm to 16.6 cm by the start of the first southward migration and ending with 9.5 cm upon return to the feeding grounds (Figure 13C). An increase to 18.8 cm is estimated upon migration in year two, followed by another decline to 13.6 cm. In year three, blubber depth increased to 19.9 cm and ended at 15.6 cm. When compared to mean field observations, these predictions were significantly different except for July of year one (Figure 13C).

**Best Fit Food Intake According to Model**

With a food intake of 475 kg d⁻¹, predicted blubber depths of adult male whales at commencement of the southward migration equaled the initial blubber depth of 13.0 cm and 11.4 cm at end of southward migration annually, suggesting no overall change in blubber depth over the three year period (Figure 14A). These predictions were not significantly different from the observed field mean blubber depths, except for the months of January, February, March and November of each year (Figure 14A).
Figure 14. Median blubber depth (A), mass (B), and $T_{LC}$ (C) (solid lines) ($\pm$ 95% CI) (dashed lines) of an adult male gray whale at food intake of 475 ± 300 kg d$^{-1}$ for three years. Circles represent observed mean field blubber depths ($\pm$ SE) of adult male gray whales (Sumich et al. unpublished data). Triangles represent mean field blubber depths ($\pm$ SE) of adult male gray whales (Rice unpublished data). Migration occurs from Nov. 1 to May 14 with feeding lasting from May 15 to Oct. 31 each year.
Since blubber depths with this food consumption rate showed no overall variation over the three-year period and compared favorably with field data, a more detailed examination of changes in masses and $T_{LC}$ was undertaken (Figure 14). As would be expected, mass decreased during migration and then increased during the feeding period of each year, with an estimated mass of approximately 16,000 kg at the beginning of migration each year indicating no overall change in mass over three years (Figure 14B). Predicted $T_{LC}$ increased during the migration and then decreased during feeding each year. At the beginning of the southward migration each year, $T_{LC}$ was approximately -17.9 ºC, and showed no change over the three-year period (Figure 14C).

For pregnant and lactating female whales with a food intake of 525 kg d$^{-1}$, initial blubber depth was 14.0 cm, declined to 12.5 cm after year one migration, and increased slightly to 14.3 cm at the end of year one (Figure 15A). After the migration of year two, blubber depth reached a minimum of 12.8 cm and increased to 14.5 cm by the end of the feeding period. Blubber depth decreased to 13.0 cm after the third migration, ending at 14.6 cm for year three, suggesting a change of less than 1.0 cm in blubber depth over the three-year period. These predictions were not significantly different from mean field observations with the exceptions of December through March and June of each year (Figure 15A).

With less than 1 cm change over the three year period and favorable comparison with field data, change in masses and $T_{LC}$ were also examined at the food intake of 525 kg d$^{-1}$ (Figure 15). To compare masses, fetal mass must be taken into account if applicable and be subtracted from the female’s mass (Figure 11). Within year one, the female gained close to 500 kg, 400 kg in year two and 300 kg in year three, indicating an overall increase of 1200 kg in three years (Figure 15B). A sharp decline of about 1400 kg occurred on January 10, indicating birth of the fetus at a mass of approximately 1400 kg. A slight decrease in predicted $T_{LC}$
Figure 15. Median blubber depth (A), mass (B), and T_{LC} (C) (solid lines) (+ 95% CI) (dashed lines) of a pregnant/ lactating female gray whale at food intake of 525 ± 300 kg d^{-1} for three years. Circles represent observed mean field blubber depths (± SE) of pregnant female gray whales (Sumich et al. unpublished data). Triangles represent mean field blubber depths (± SE) of pregnant female gray whales (Rice unpublished data). Migration occurs from Nov 1 to May 14 with feeding lasting from May 15 to Oct. 31 each year. Conception was assumed to happen on Dec. 5 of the first and third year, and birth occurring on Jan. 10 of the second year (portrayed as a sharp decline in mass and T_{LC}).
occurred for the beginning of the migration of year one and two, from -23.6 °C to -23.8 °C, respectively (Figure 15C). However, at the beginning of year three, \( T_{LC} \) decreased to -25.0 °C and increased slightly to -24.8 °C by the end of the simulation. A sharp decline of 2.4 °C in \( T_{LC} \) occurred on January 10 of year two, again due to mass changes associated with parturition (Figure 15C).

If immature gray whales, with a BMR twice that of an adult whale of similar mass, consumed 600 kg d\(^{-1}\), a repeatable annual cycle was calculated that fit observed field data (Figure 16A). Overall, blubber depth at the commencement of the southward migration varied from 12.6 cm in year one, 12.8 cm in year two, and ending at 12.9 cm, indicating an overall change in blubber depth of less than 1 cm over the three year period. Following the migrations, on the feeding grounds, blubber depths also experienced a slight increase over the three years from 9.5 cm to 10.5 cm and ending at 11.0 cm. These blubber depth estimates were significantly different from September, October, and December to March and June of every year. They were also significantly different from April in year one and two, as well as, August and November in year three (Figure 16A).

By the end of the simulated three years, immature whales reached maturity (according to length), indicating their metabolism, initially assumed at twice BMR, had slowed to BMR; the point at which this occurred was not known. Therefore, simulations with food intakes of 300 kg d\(^{-1}\) at BMR were also run (Figure 16A). Blubber depth at the beginning of each migration equaled the initial blubber depth of 12.0 cm, thereby predicting no net change in blubber depth in three years. Blubber depths at the end of each migration showed an increase of 0.5 cm over the three years from 10.4 cm to 10.7 cm to 10.9 cm. These predictions, when compared to the mean field blubber depths, were significantly different during the months of December to March, June, September, and October of every year. In addition, predictions for April were also significantly different in year one and two (Figure 16A).
Figure 16. Median blubber depth (A), mass (B), and $T_{LC}$ (C) (solid lines) (± 95% CI) (dashed lines) of an immature gray whale at food intakes of 600 (twice BMR, solid lines) and 300 (BMR, dotted lines) ± 300 kg d$^{-1}$ for three years. Circles represent mean field blubber depths (± SE) of immature gray whales (Sumich et al. unpublished data). Triangles represent mean field blubber depths (± SE) of immature gray whales (Rice unpublished data). Migration occurs from Nov. 1 to May 14 with feeding lasting from May 15 to Oct. 31 each year.
Since estimated blubber depths given a food intake of 600 kg d$^{-1}$ showed little overall change over the three year period and compared favorably with field data, change in mass and $T_{LC}$ were also examined (Figure 16). As the immature whale grew in length during the three years, an increase in mass was also predicted. Initial mass was 8700 kg, increased to 9900 kg at the end of year one, raised to 10600 kg at the end of year two and finally reached 11000 kg at the end of year three (Figure 16B). $T_{LC}$ decreased slightly during the first migration (-54.1 °C to -54.9 °C), followed by an expected sharper decrease during the feeding months to -77.7 °C (Figure 16C). This pattern was repeated in year two, decreasing to -88.3 °C to -97.5 °C. However in year three, $T_{LC}$ declined to -118.8 °C by the end of the migration and ended at -116.6 °C (Figure 16C). Simulations, with food intakes of 300 kg d$^{-1}$ at one times BMR, predicted similar trends to those with food intakes of 600 kg d$^{-1}$ at twice BMR. $T_{LC}$ declined in the first migration from -54.1 °C to – 59.1 °C, followed a sharp decrease during the feeding months down to -76.2 °C (Figure 16C). In the second year, temperature decreased to -88.3 °C at the end of the migration and reached a maximum of -98.1 °C. During year three, $T_{LC}$ declined to -118.7 °C during the migration and ended at -120.8 °C (Figure 16C).

Additional food intake variance was added by varying the first day of the feeding season for the remaining simulations resulting in longer or shorter overall feeding seasons. Simulations of 500 replicates for an adult male, pregnant and lactating female, and an immature whale were run with respective estimated average food intakes to see if this additional variance significantly altered the predictions compared to field observations (Figure 17). Even with the added variability to the model, predictions followed the same trend of significant differences as seen in previous simulations with only food intake as a variance.
Figure 17. Median blubber depth (dotted lines) (± 95% CI) (dashed-dotted lines) of an adult male at food intake of 475 (A), pregnant and lactating female at 525 (B), and immature gray whale at 600 at 2 x BMR (C) ± 300 kg d⁻¹ for three years. Median blubber depths (solid lines) (± 95% CI) (dashed lines) of the same whale categories represent simulations where the feeding seasons fluctuated in duration, as a form of additional variance. Circles represent mean field blubber depths (± SE) of healthy gray whales (Sumich et al. unpublished data). Triangles represent mean field blubber depths (± SE) of healthy gray whales (Rice unpublished data). Migration occurs from Nov. 1 to May 14 with feeding lasting from ~ May 15 to ~ Oct. 31 each year. Conception was assumed to happen on Dec. 5 of the first and third year, and birth occurring on Jan. 10 of the second year.
Energetic Impact of Low Food Availability for Multiple Years

Simulations were run for all life history categories of whales to predict the possible impact of continuing low food availability for a three-year period. All simulations assumed a food intake of 300 ± 300 kg d⁻¹.

For adult male whales, blubber depth predictions decreased during the first migration from a starting value of 13.0 cm to 11.4 cm and increased during the feeding period to 12.0 cm (Figure 18A). During year two, blubber depth decreased to 10.5 cm and increased during feeding to 11.3 cm. In year three, blubber depth declined again during migration reaching a low of 9.9 cm at the end of migration and ending at 10.7 cm prior to the migration of the following year. By the end of the three-year period, estimated blubber depths were significantly different from mean field observations (Figure 18A).

Pregnant and lactating female gray whales followed the same trend, with a decline in blubber depth from initial 14.0 cm to 12.5 cm during the first migration and increased to 13.1 cm (Figure 18B). Another decrease in blubber depth by the end of the second migration resulted in a decline to 11.7 cm, followed by an increase to 12.4 cm on the feeding grounds. At the end of migration in year three, blubber depth reached a low of 11.1 cm and ended at 11.9 cm (Figure 18B).

Immature whale blubber depths decreased during the first migration from a starting value of 12.0 cm to 9.5 cm and increased during the feeding period to 10.4 cm (Figure 18C). Blubber depth decreased to 8.7 cm during the second migration and increased during the feeding months to 9.7 cm. In year three, blubber depth decreased reaching a low of 8.5 cm at the end of migration and ending at 9.3 cm at the end of the feeding season (Figure 18C).
Figure 18. Median blubber depth (solid lines) (± 95% CI) (dashed lines) of an adult male (A), pregnant and lactating female (B), and immature gray whale (C) at food intakes of 300 ± 300 kg d⁻¹ for three years to simulate multiple years of low food availability. Circles represent mean field blubber depths (± SE) of healthy gray whales (Sumich et al. unpublished data). Triangles represent mean field blubber depths (± SE) of healthy gray whales (Rice unpublished data). Migration occurs from Nov. 1 to May 14 with feeding lasting from May 15 to Oct. 31 each year. Conception was assumed to happen on Dec. 5 of the first and third year, and birth occurring on Jan. 10 of the second year.
As expected, with a food intake of 300 kg d\(^{-1}\), \(T_{\text{LC}}\) increased during the migration and decreased during feeding. An increase in \(T_{\text{LC}}\) at the beginning of migration was predicted with each consecutive year. For adult male whales, at the end of year one, \(T_{\text{LC}}\) increased from the initial value of -17.9 °C to -14.6 °C (Figure 19A). \(T_{\text{LC}}\) further increased to -12.1 °C at the end of year two and finally \(T_{\text{LC}}\) was -10.2 °C at the end of the third migration, with a maximum of -7.3 °C.

Pregnant and lactating female whales experienced an increase in \(T_{\text{LC}}\) from the initial value of -23.6 °C to -20.3 °C at the end of year one (Figure 19B). By the end of year two, \(T_{\text{LC}}\) further increased to -19.0 °C and ended at -16.8 °C at the end of the third migration, with a maximum of -15.5 °C. A sharp decrease of 2.8 °C in \(T_{\text{LC}}\) occurred on January 10 of year two, indicating parturition. Despite these significant increases in \(T_{\text{LC}}\), these temperatures never exceeded the coldest temperatures to which whales would be exposed (Figure 19B).

Immature whales experienced the same decrease of \(T_{\text{LC}}\) at an irregular rate from the beginning of year one to the end of the third migration, at which point, it increases at a rapid rate. At the end of year one, \(T_{\text{LC}}\) declined from -54.1 °C to -69.8 °C (Figure 19C). \(T_{\text{LC}}\) further decreased to -98.1 °C at the end of year two and finally ended at -139.6 °C, with a minimum of -183.8 °C.

**Energetic Impact of Multiple Consecutive Pregnancies**

By extending the duration of simulations to four years, energetic costs of two pregnancies were modeled from conception to parturition. Conception occurred in years one and three on December 5, while parturition was set on January 10 of years two and four.
Figure 19. $T_{LC}$ (solid lines) ± 95% CI (dashed lines) of an adult male (A), pregnant and lactating female (B), and immature gray whale (C) at food intakes of 300 ± 300 kg d$^{-1}$ for three years to simulate multiple years of low food availability. Migration occurs from Nov. 1 to May 14 with feeding lasting from May 15 to Oct. 31 each year. Conception was assumed to happen on Dec. 5 of the first and third year, and birth occurring on Jan. 10 of the second year.
Low food availability was simulated by allowing an intake of 300 ± 300 kg d\(^{-1}\) during the feeding periods of all four years. A decrease in blubber depth at the beginning of each migration was observed, from an initial 14.0 cm to 13.1 cm at the end of year one and 12.4 cm at the end of year two (Figure 20A). Blubber depth only lost an additional 0.5 cm in year three and ended at 11.6 cm by year four. These predictions deviated significantly from the observed mean blubber depths during the months of June to November and December to March for every year (Figure 20A).

Median \(T_{LC}\) rose during the migration and dropped during the feeding season (Figure 20B). This trend was repeated every year, with two exceptions, occurring on January 10 of both year two and year four, where sharp declines were correlated with parturition. \(T_{LC}\) began at -23.6 °C and increased to -20.3 °C by the end of year one (Figure 20B). Within a year, \(T_{LC}\) increased an additional 1.2 °C and reached -16.8 °C by year three, reaching a final \(T_{LC}\) of -16.7 °C.

When daily food intake was 525 ± 300 kg d\(^{-1}\), blubber depth at the beginning of the southward migration increased from an initial 14.0 cm to 14.3 cm by the end of year one and 14.5 cm by year two (Figure 21A). An additional 0.1 cm was gained in year three and ended at 14.8 cm by year four. These predictions were not significantly different from mean field observations, except for December to March and June of every year, in addition to September of year one and July of year two and three (Figure 21A).

High food availability was simulated with an intake of 750 kg d\(^{-1}\) (Figure 21B). Median predicted blubber depths followed the earlier trend, experiencing a sharp increase in blubber depth at the beginning of each migration, from an initial 14.0 cm to 15.5 cm by the end of year one to 16.7 cm by year two. Blubber depth increased to 17.5 cm and ended with an additional 0.7 cm by year four. By the end of the three-year period, the predictions were significantly different from all field observations (Figure 21B).
Figure 20. Median blubber depth (A) and $T_{LC}$ (B) (solid lines) (+ 95% CI) (dashed lines) of a pregnant female gray whale at food intakes of 300 ± 300 kg d$^{-1}$ for four years, simulating two consecutive pregnancies and births. Circles represent observed mean field blubber depths (± SE) of pregnant female gray whales (Sumich et al., unpublished data). Triangles represent mean field blubber depths (± SE) of immature gray whales (Rice unpublished data). Migration occurs from Nov. 1 to May 14 with feeding lasting from May 15 to Oct. 31 each year. Conception was assumed to happen on Dec. 5 of the first and third year, with birth occurring on Jan. 10 of the second and fourth year (portrayed as a sharp decline in TLC).
Figure 21. Median blubber depths (solid lines) (+ 95% CI) (dashed lines) of a pregnant female gray whale at food intakes of 525 (A), 750 (B), and alternating food intakes per year (525/300/750/525) (C) ± 300 kg d⁻¹ for four years, simulating two consecutive pregnancies and births. Circles represent observed mean field blubber depths (± SE) of pregnant female gray whales (Sumich et al. unpublished data). Triangles represent mean field blubber depths (± SE) of pregnant female gray whales (Rice unpublished data). Migration occurs from Nov. 1 to May 14 with feeding lasting from May 15 to Oct. 31 each year. Conception was assumed to happen on Dec. 5 of the first and third year, with birth occurring on Jan. 10 of the second and fourth year.
To simulate a combination of low, average and high food availability likely experienced in the field, food intake was simulated using $525 \pm 300$ kg d$^{-1}$ in year one, $300 \pm 300$ kg d$^{-1}$ in year two, $750 \pm 300$ kg d$^{-1}$ in year three and $525 \pm 300$ kg d$^{-1}$ in year four. Median predicted blubber depths, increased at varying daily feeding rates during the feeding seasons (Figure 21C). Blubber depth at the beginning of the southward migration increased from an initial 14.0 cm to 14.4 cm after year one, then decreasing to 13.3 cm at the end of year two when food intake was reduced. When food intake was increased, blubber depth increased to 13.8 cm in year three, and ended at 14.1 cm after year four. These simulations resulted in blubber depths significantly different from observed field mean blubber depths, except for July, August, October and November in year one, July and August in year two, and July, August, and October in year four (Figure 21C).

**Energetic Impact of Varying Food Intakes with Variances**

Simulations were run with multiple combinations of food intakes and variances to predict possible consequences if the whales were to experience such fluctuations in food availability in actuality. Subsequently, 200 replicates with varying food intakes and daily variance in food intake were simulated. Food intake rates began at 100 kg d$^{-1}$ increasing to 900 kg d$^{-1}$ in increments of 200 kg d$^{-1}$, with variance ranging from 0% to 50% (increments of 10%) and 100% to 500% (increments of 100%).

Ratios of ending mass and initial mass after three years, of each category of gray whale, were calculated, resulting from varying food intakes and percent variance. These ratios were then represented in Figures 22, 23 & 24 for each life history category of whale.
Figure 22. Ratio of ending and initial masses, after three years, for an adult male gray whale experiencing varying food intakes and their percent variance. Any combination resulting in a response of 1.000 indicates the adult male received sufficient food for energetic cost without any loss in mass, indicating neither loss nor gain. Combinations estimating responses greater than 1.000 imply a gain in mass, while responses less than 1.000 imply a loss in mass. Circles indicate combinations of food intake with variance closest to 1.000.
Figure 23. Ratio of ending and initial masses, after three years, for a pregnant female gray whale experiencing varying food intakes and their percent variance. With the added mass of the fetus at the end of the three years, any combination resulting in a response of 1.080 indicates the adult female received sufficient food for maintaining energetic, pregnancy and lactation costs. Combinations estimating responses greater than 1.080 imply an excessive gain in mass, while responses less than 1.080 imply an insufficient gain in mass. Circles indicate combinations of food intake with variance closest to 1.080.
Figure 24. Ratio of ending and initial masses, after three years, for an immature gray whale experiencing varying food intakes and their percent variance. Ending mass includes added mass of growth by the end of three years, any combination resulting in a response of 1.840 indicates the immature received sufficient food for maintaining energetic cost and growth. Combinations estimating responses greater than 1.840 imply an excessive gain in mass, while responses less than 1.840 imply an insufficient gain in mass. Circles indicate combinations of food intake with variance closest to 1.840.
Any combination resulting in a response of 1.000 indicates an adult male whale received sufficient food intake to meet energetic costs without any change in mass (Figure 22). Combinations resulting in responses greater than 1.000 imply a net gain in mass, while responses less than 1.000 imply a net loss in mass. Food intakes of 500 kg d\(^{-1}\) with either a 200 kg d\(^{-1}\) (± 40%) or 250 kg d\(^{-1}\) (± 50%) variance were the combinations whose responses were closest to 1.000 (1.023 and 1.021, respectively, Figure 22).

With the added mass of the fetus at the end of the three years, any combination of food intake with variance resulting in a response of 1.080 indicated that the pregnant and lactating female whale received sufficient food for maintaining energetic, pregnancy and lactation costs (Figure 23). Combinations estimating responses greater than 1.080 represented net gain in mass, while responses less than 1.080 implied a net loss in mass. Food intakes of 300 ± 900 kg d\(^{-1}\) (±300%) and 500 ± 500 kg d\(^{-1}\) (±100%) were the combinations whose responses were closest to 1.080 (1.085 and 1.098, respectively, Figure 23).

For a growing immature whale, with the gained mass over the three-year period, any combination resulting in a response of 1.840 indicated that the immature whale received sufficient food for maintaining energetic cost and growth (Figure 24). Combinations estimating responses greater than 1.840 implied a net gain in mass, while responses less than 1.84 represented a net loss in mass. Food intakes of 700 ± 1400 kg d\(^{-1}\) (±200%) and 900 ± 0, 90 (10%), 180 (20%), 900 kg d\(^{-1}\) (100%) were the combinations whose responses were closest to 1.840 (1.911, 1.784, 1.785, 1.780 and 1.907, respectively, Figure 24).
Sensitivity Analysis

With 34 parameters potentially included in the model, the sensitivity of some of these parameters was explored by increasing and decreasing their values by 10%. Impact was assessed by the percent change in ending mass from a simulation with no variance compared to a simulation with parameter(s) altered. When the five initial input parameters were tested, mass and food intake had the highest impacts. BMR and cost of locomotion also had high impacts, while energy distribution had almost no impact. Of these, the parameter with the highest influence was placed in combination with the two initial parameters with highest impact and were in turn assessed (Table 5).

The ending mass for an adult male with a food intake of 475 kg d$^{-1}$ is 16292 kg (a net gain of 292 kg). A pregnant female with a food intake of 525 kg d$^{-1}$ would have a predicted final mass of 17913 kg (a net gain of 1538 kg). Finally, an immature, with 600 kg d$^{-1}$, was estimated at 11294 kg after 3 years (a net gain of 2594 kg).

For all three categories of whales, combination of mass and food intake had the highest effect, followed by food intake, then BMR, and finally mass. Girth, blubber depth, and length, when varied by 10%, did not impact the final mass in any of the categories of whales (Table 5).
Table 5. Sensitivity analyses of eight parameters and four combinations of these for male (a), pregnant/ lactating female (b), and immature (c) gray whales. The normal ending mass for a male, a pregnant/ lactating female, and an immature gray whale are ~16000 kg, ~18000 kg, and ~11000 kg, respectively.

### a) Male Gray Whale

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<th>Initial Parameters</th>
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<th>Modified Parameters</th>
<th>% Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mass</td>
<td>16000.0 kg</td>
<td>17600.0 kg</td>
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<tr>
<td></td>
<td>14400.0 kg</td>
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<tr>
<td>Girth</td>
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</tr>
<tr>
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<tr>
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<td></td>
<td>427.5 kg d(^{-1})</td>
<td>-7.5%</td>
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<tr>
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<tr>
<td></td>
<td></td>
<td>Eqn 2 * 0.9</td>
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<td>Eqn 3 * 0.9</td>
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<tr>
<td>Energy distribution</td>
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<td>16.5 % blubber</td>
<td>0.0%</td>
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<td></td>
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<td>13.5% blubber</td>
<td>-0.0%</td>
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<tr>
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<td>17600.0 kg &amp; Eqn 2 * 1.1</td>
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<tr>
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<td>Eqn 2</td>
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<td>17600.0 kg &amp; 522.5 kg d(^{-1})</td>
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<td>Eqn 2</td>
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<td>-11.7%</td>
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<td>Food intake &amp; BMR</td>
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<td>Eqn 2</td>
<td>427.5 kg d(^{-1}) &amp; Eqn 2 * 0.9</td>
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<td>BMR</td>
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### b) Pregnant/ Lactating Female Gray Whale

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<tr>
<td>Girth</td>
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<tr>
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<tr>
<td>Blubber depth</td>
<td>14.0 cm</td>
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<td>0.0%</td>
</tr>
<tr>
<td></td>
<td>12.6 cm</td>
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<td>0.0%</td>
</tr>
<tr>
<td>Length</td>
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<td>Food intake</td>
<td>525.0 kg d(^{-1})</td>
<td>577.5 kg d(^{-1})</td>
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<tr>
<td></td>
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<td>472.5 kg d(^{-1})</td>
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<td>BMR</td>
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<td>Eqn 2 * 0.9</td>
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Table 5 (continued).

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<tr>
<td>Cost of Locomotion</td>
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<td>-1.9%</td>
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<tr>
<td>Energy distribution</td>
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<td>Mass &amp; BMR</td>
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<td>Mass, Food intake</td>
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<td>17600.0 kg &amp; 577.5 kg d(^{-1}) &amp; Eqn 2 * 1.1</td>
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<tr>
<td>Mass &amp; BMR</td>
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<td>BMR</td>
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**c) Immature Gray Whale**

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<td>Mass</td>
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<td>Girth</td>
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<td>10.7%</td>
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<tr>
<td>BMR</td>
<td>Eqn 2</td>
<td>Eqn 2 * 1.1</td>
<td>-6.5%</td>
</tr>
<tr>
<td>Mass &amp; BMR &amp; Food Intake, BMR</td>
<td>Eqn 2 &amp; Eqn 2</td>
<td>7830.0 kg &amp; Eqn 2 * 1.1</td>
<td>5.5%</td>
</tr>
<tr>
<td>Mass &amp; BMR &amp; Food Intake, BMR</td>
<td>8700.0 kg &amp; 600.0 kg d(^{-1})</td>
<td>9570.0 kg &amp; 660.0 kg d(^{-1}) &amp; Eqn 2 * 1.1</td>
<td>5.1%</td>
</tr>
</tbody>
</table>

55
DISCUSSION

Food Intake and Energetic Cost of Migration

Accurate information on rates of food consumption is critical to understanding animal performance and to assess the consequences of environmental changes on species persistence. Gray whales of the ENP stock migrate over 18,000 km per year, tracking the eastern side of the Bering Sea, passing through the Unimak Pass in the Fox Islands, then following the western coast of North America to the breeding lagoons of the Gulf of California (Rice and Wolman 1971). The energetic demands necessary to survive the migration must be met prior to departure from the feeding grounds. Due to the size and habitat of gray whales, direct measurements of energetic needs and food consumption are not easy to obtain. A promising approach is using models based on allometric and physiological parameters to estimate these energetic needs. The results of computer simulations based on such parameters presented in this study suggest an average food intake of 475 – 600 ± 300 kg d\(^{-1}\) during the feeding season (lasting from May 15 to October 31) would be the minimum requirement for gray whales to avoid a long term decline in mass.

The minimum food intake for long-term survival estimated in the present study (3.0% food intake per body mass for male, 3.3% for pregnant female, and 6.9% for immature whales) is consistent with data based on direct food consumption observations of odontocetes in captivity. Food intake evaluated from odontocetes in aquaria ranged from 4.0% food intake in
Globicephala scammoni and 4.05% Orcinus orca to 10.0% Phocoena phocoena and 12.7% in Globicephala macrorhynchus (Sergeant 1969). The estimated food intake for the gray whales in this study also fit within the general negative relationship between body mass and daily food consumption found for these captive animals (Sergeant 1969).

Results from the current study were slightly higher than estimates of comparable simulations of energy requirements of the North East Atlantic minke whale (277 kg\(^{-1}\) daily food intake, approximately 3.0% food consumption for female whales, and 204 kg d\(^{-1}\), approximately 2.1% for male whales, Markussen et al. 1992). Similar to gray whales, minke whales have a seasonal feeding period acquiring 90.0% of their yearly energy requirements during summer, but differ from the former by including higher energy density fish together with krill in their diets (Markussen et al. 1992). This difference in diet may explain the lower percent food intake in minke whales compared to gray whales. In seals, available gross energy varies from 60.9% of intake when eating shrimp (Pandalus borealis) to 88.0% when eating herring (Keiver 1982). With ampeliscid amphipods lacking an outer carapace (Ruppert and Barnes 1994), unlike shrimp, the present study’s estimate of 80.0% of intake available as gross energy seems appropriate.

Food intake estimates from simulations of the present study were larger than food intake values based on indirect estimates of prey consumption. Oliver et al. (1984) estimated a food intake for an adult gray whale to be 552 kg of infaunal prey per 12-h day (1104 kg d\(^{-1}\)) assuming they consume prey 24 h d\(^{-1}\), five excavations per dive, 13.6 dives h\(^{-1}\), 0.72 m\(^2\) average excavation size, and 197 g m\(^{-2}\) faunal biomass. However, Oliver et al. (1984) recognized that their estimates could be subject to error, since the variation of the average duration of feeding and the average number of excavations per dive was unknown.

Food intake based on estimates of energy supplied by the diet and of daily energy requirements differed from the results of the present study. Rice and Wolman (1971) showed that Ampelisca macrocephala was the major prey species of the gray whale in waters off the
coast of California. Assuming that amphipods provide 500 kcal kg\(^{-1}\) and the daily energy requirements are 5.3 x 10\(^5\) kcal, Rice and Wolman (1971) estimated an average intake of 1100 kg of prey d\(^{-1}\) whale\(^{-1}\) would be necessary to sustain the whales during the migration. Energy content for ampeliscid amphipods used by Rice and Wolman (1971) is actually half the value assumed in the present study (1000 kcal kg\(^{-1}\)). By compensating for this difference, Rice and Wolman’s estimated average food intake is reduced to 550 kg d\(^{-1}\), similar to present findings.

Based on the simulations of the present study, the estimated food intake from Rice and Wolman (1971) predicted blubber depths (21.6 cm for adult male, 18.0 cm pregnant and lactating female whales) that are outside the observed stock’s range (14.0 cm for adult male, 14.5 cm pregnant and lactating female whales; Rice unpublished data, Sumich unpublished data). With the present model, simulations considering three years at a low food intake of 250 kg d\(^{-1}\) predicted a general decrease on low blubber depth and body mass, and a final median blubber depth of 10.2 cm. These blubber depths were associated with gray whales stranded off the coast of California between May and July 2000 (blubber depths ranging from 8.1 cm to 15.0 cm; Gulland unpublished data). Therefore, the necessary food intakes for all categories of gray whales was probably somewhere between 250 kg d\(^{-1}\) and 1100 kg d\(^{-1}\).

Estimates of food intake based on energy supplied (lipid content of benthic amphipods), associated energy transfer, and time spent on feeding grounds were consistent with the results of our study (Nerini 1984). Estimated food intake based on these assumptions of 36821 kg yr\(^{-1}\) (~409 kg d\(^{-1}\)) closely matches the predicted value by the simulations in the present study (minimum average food intake for the long term persistence of adult male, pregnant and lactating female, and immature whales were 475 kg d\(^{-1}\), 525 kg d\(^{-1}\) and 600 kg d\(^{-1}\), respectively).
Assumptions

The model presented in this study was based on available information on allometric and physiological parameters of whales. Assumptions on volumetric representation of gray whales, the extent of their feeding season, blubber depth distribution and variation, and metabolic rate of immature whales were among the more uncertain parameters in the model and may have a greater impact on the outcomes of the simulations.

Similar to Guldberg (1907) and Lockyer (1976), a first approximation for this model assumed an initial volumetric representation of a gray whale in the shape of two cones. Although this representation worked apparently well for many balaenopterids (Lockyer 1976), all gray whale parameters in the present study with simulations over three years did not match those observed in the field. A better representation for gray whales for this model was designed with the use of a cylinder with an interlocking cone at each end, producing ending parameters closer to field observations from previous studies.

Although feeding was assumed to occur during their non-breeding and non-migrating season (from May 16 to October 31), gray whales have been observed feeding on their breeding grounds (Sánchez-Pacheco et al. 2001) and evidence of yellow or orange colored blubber could be indicative of the ingestion of the larval stage of red crab, Pleuroncodes planipes, along the migration path (Rice and Wolman 1971). The energetic importance of this occasional feeding is unknown, therefore, in an attempt to take into account this additional energy, length of feeding periods were extended varyingly. The additional variance in the duration of feeding seasons did not significantly modify the minimum food intake estimates obtained in this study.

Unlike the assumption of this model, blubber depth is not evenly distributed throughout the body in marine mammals, but rather is thickest at the posterior dorsal area (Lockyer et al.)
1984, Doidge 1990, Kvadsheim et al. 1996). To compensate for the assumption of uniform blubber depth, blubber depths from the dorsal mid-lateral region were used, an area that falls between the posterior dorsal region (highest blubber depth) and anterior dorsal region (lowest blubber depth) in thickness (Lockyer et al. 1984, Doidge 1990, Kvadsheim et al. 1996). This minimized potential over estimates of available energy reserves.

Simulations for immature whales were also run over a period of three years during which time whales potentially reached physical maturity. During this maturation, a change in metabolic rate would occur decreasing from the elevated common in juveniles (i.e. twice the predicted BMR) to the rate estimated for an adult (Kleiber 1975). The first set of simulations for immature whales were run at twice BMR with a food intake of $600 \pm 300$ kg d$^{-1}$, producing continuously decreasing $T_{LC}$ values until the last feeding season, contrary to the cyclic pattern observed in adults, and reaching a low of -119.0 °C. The second set of simulations was run at BMR (assuming maturity was reached) with a food intake of $300 \pm 300$ kg d$^{-1}$, estimating a continuous decrease in $T_{LC}$ values with an exception in late May, where values reached a plateau, and reaching a low of -120.8 °C. Both of these simulations predict $T_{LC}$ values that demonstrate a change in their patterns that occur during the feeding period of year three possibly indicating when immature gray whales undergo a change in metabolic rate.

**Sensitivity Analysis**

The model's sensitivity to parameter variation provides an estimate of the potential impact of the parameters' uncertainty in the model. Twelve different combinations of values were simulated for each type of whale and the ending masses of the simulations were compared to the few known masses of gray whales from the ENP stock. Known adult gray
whale masses range from 15700 kg to 16600 kg (n=2; 16400 kg to 33800 kg for pregnant female whales, n=3) and from 6600 kg to 8900 kg for immature gray whales (n=3; Rice and Wolman 1971). Variances in girth, blubber depth, and length were not significant enough to create any change in the ending mass for each category of whale. Simulations of adult male gray whales resulted in 2/3 of the predicted percent changes of ending mass being greater or less than known masses of adult male gray whales (-3.6% to 1.9%; Rice and Wolman 1971). These percent changes in ending masses were only compared to the restricted sample size of the known masses of two adult gray whales, which could explain why such a high number of simulations resulted in percent changes of ending mass outside the known range. For the pregnant and lactating female gray whales, only the ten percent increase in the combination of mass and food intake estimated a percent change in ending mass outside the known range of adult pregnant female whales (-8.5% to 88.7%; Rice and Wolman 1971). Known masses of immature gray whales were beyond the percent changes in mass resulting from all the simulations for immature gray whales (~41.6% to -21.2%; Rice and Wolman 1971). This is most likely due to immature gray whales of known masses are shorter (8.5 to 9.9 m) and, by definition, likely younger than the simulated immature gray whales (11.1 m), indicating that the latter were almost of length to be labeled as adults, consequently having greater masses than whales distinctly labeled immature whales (Rice and Wolman 1971).

With food intake having the most effect on the model, additional research needs to be carried out on this parameter. A similar finding occurred when a bioenergetics model for Steller sea lions was created (Winship et al. 2002). With gray whales relying on the Bering Sea and its surrounding waters for most of its prey, any changes could have an extremely negative impact on the gray whale stock in less than five years.
Impacts on Bering Sea

The Bering Sea is the second largest and considered one of the most productive shelf systems in the world (Walsh & McRoy 1986, Tynan 2004). Over the past 30 years, certain abnormalities have occurred indicating a possible shift in the Bering Sea’s ecosystem, such as decreased availability of nutrients (Tanaka et al. 2004) and increased water temperatures (Reed 2003). These factors, possibly due to global warming, may have impacted additional anomalies such as declining sea herring (Naumenko 1996), sea walleye pollock (Balykin 1996), and Pacific cod (Vinnikov 1996) stocks.

However, such decreases in abundance are not limited to fishes. Highsmith and Coyle (1992) observed a 30% decline in production of ampeliscid amphipods in the northern Bering Sea from 1986 to 1988. If gray whales experience limited prey availability of ampeliscid amphipods for an extended period of time, a possible result is an abnormally high rate of gray whale strandings, perhaps similar to those from 1999 and 2000.

Validation of Model

In order to analyze the validity of the model, predicted values were compared to field observations from other studies. The two available sets of field blubber depth data were obtained in different seasons and from different gray whale stocks (Table 4; Rice and Wolman 1971, Sumich et al. in press). Rice and Wolman’s (1971) observations were taken from 1959 to 1969 along the migration path of gray whales from the ENP stock. The median blubber depths from these observations were above the predictions from this present study for all categories of whales yet followed the same trend. Sumich et al. (in press) collected blubber depths on the
feeding grounds of gray whales from the Western North Pacific (WNP) stock from 1980 to 1991. These values overlapped with the predicted ones from the present study. This dissimilarity could be an indication that the body condition of gray whales was lower during the 1960’s than in more recent decades.

**Future Studies**

By examining the gray whale literature and placing the parameters in a model, this study was able to identify areas where additional research is needed to gain a better understanding of the energetic demands of migration on gray whales. In addition, this study has again demonstrated that modeling gives insight on parameters that scientists do not possess the technology to access and tests assumptions made on previous attempts to estimate some of these parameters.

In the field, measuring the mass of live gray whales, which could weigh up to 34 metric tons (Rice and Wolman 1971), is presently impossible. An alternate indicator of body condition is blubber depth, which according to the model undergoes the most variability, following mass. Multiple, accurate measurements of individuals’ blubber depths could be taken at different seasons over several years, with the use of ultrasound. By taking individual morphometric measurements of tagged whales at several points during their migration, more accurate costs of migration could be estimated, as opposed to having only a single measurement taken at death.

Additionally, masses of fetuses at different times of the gestation could be taken when available from aboriginal whaling. With this added information, actual fetal mass could be compared to a mass estimated using conversions from diameter to girth and length to volume to mass.
The predicted $T_{LC}$ for all three categories of gray whales did not exceed the ambient temperatures to which the whales would experience in nature, indicating that cost of thermoregulation was not a factor for the whales under the various simulated conditions. However, the predicted $T_{LC}$ for the immature whales did not follow the same cyclic pattern as observed for the adults and reached a $T_{LC}$ of -183.8 °C, much lower than -111.5 °C predicted for a 10000 kg blue whale calf using the same equation (Lavigne et al. 1990). This equation may need to be reexamined for immature gray whales.

In essence, the model created in this study can easily be used for any animal and carried out to the population level. In order to use this model for another species, certain assumptions made would have to undoubtedly be changed as necessary, however, the basic concepts of energy intake, distribution, usage and loss are the same in all organisms. By using estimated food intakes for specific categories of whales and knowing the population’s percent composition, it would be possible to predict annual necessary prey availability for an entire population, such as gray whales, and prepare for potential strandings during subsequent years of low food availability.
APPENDIX A START MODEL
This model allows the user to easily change parameters without having to go through the main model (TM9abc).

The separation of the parameters into whalea and whaleb is simply due to the limitation of the software with matrices of up to 37 x 1461 (37 being the number of parameters and 1461 the number of days).

We discovered this limitation at the attempt of a matrix 33 x 365.

The sex and maturity of the whale is redefined for simplicity and separation in the main model.

In parentheses, the x-value represents which day of the run and the y-value is which parameter (whaleb tells the model which matrix to choose from).

It is necessary to randomize parameters requiring variability.

The model will run for the length of time in days instructed here.

days=366;

For whalea, the mass of the whale is represented in kg as the first number in the matrix, followed by girth (meters), and finally, blubber depth (meters).

whalea=zeros(days,18);
whalea(1,1)=8700;
whalea(1,2)=4.7;
whalea(1,3)=0.12; %0.13

For whaleb, the first number tells the model the sex and maturity of the whale and length in meters is the second.

whaleb=zeros(days,12);
whaleb(1,1)=0;
whaleb(1,2)=9.14; %11.7

These parameters set up the model for food intake during the feeding months, while making sure the model does not represent an increase in weight from feeding during migrating months.

foodintake=0;
var=0;

For the feeding months (May 16 to October 31), food intake is identified as food (kg d\(^{-1}\)) with a variance (var, kg d\(^{-1}\)) to represent the non-consistent source of food experienced by whales in reality.

food=600;

Change is by how much food is varied (kg d\(^{-1}\)) between the three types of food availability years.

change=300;
To look at the impact of varying levels of food availability from year to year, a low food
availability year is identified by lowyear, a high one with highyear, and a normal one with
normyear.

lowyear=1;
highyear=2;
normyear=3;

% Variance for onset of feeding
vtime1=0; %1+0.03*randn;

% Variance for onset of pregnancy
vtime2=0;

% This code is a warning created to prevent an immature being run for too long of a duration
% with this model, resulting in a mature whale that the model would still be considering as an
% immature.

% This warning will only be displayed in the command window if the semi-colon is removed from
% the end of the line.
if (days > 1461 & sex==0)
say='For immatures, this program cannot be run for more than 1461 days'
% keyboard
quit
end
This model contains all parameters and their relations to one another to represent a gray whale modeled using a cylinder with an interlocking cone at each end.

The separation of the parameters into whalea and whaleb is simply due to the limitation of the software with matrices of up to 37 x 1461 (37 being the number of parameters and 1461 the number of days).

We discovered this limitation at the attempt of a matrix 33 x 365.

For whalea, the first parameter in the matrix is mass (kg), followed by girth (meters) and blubber depth (meters). Next, blubber mass is represented in kg. CG ratio is blubber depth (meters) divided by blubber mass (kg) and has no units. Basal metabolic rate (BMR) and cost of locomotion have units of MJ d\(^{-1}\). Field Metabolic Rate (FMR) is the addition of BMR and cost of locomotion, with the same units of MJ d\(^{-1}\). Blubber used is the amount of FMR times the percentage of energy coming from blubber in kg. Core energy used is the FMR times the percentage of energy coming from the core fat reserves in kg. Blubber remaining (kg) is the blubber mass minus blubber used, while Core energy remaining is the core mass (kg, whaleb) minus the core energy used. Heat increment of feeding (HIF, MJ d\(^{-1}\)) is only a factor during feeding months. Energy is the assimilation of food (MJ d\(^{-1}\), only pertaining to feeding months, and Energy stored (MJ d\(^{-1}\)) is Energy minus DEC. Lower critical temperature (T\(_{LC}\), °C) is the temperature at which the whale's BMR increases due to thermoregulatory problems.

The parameters for the whale will be different at the end of the day than they were at the beginning. The animal's mass, for example will be less, at the end of a migrating day. So, certain parameters must be recalculated at the end of every day. These parameters are referred to as new blubber depth (meters), new mass (kg), and new lower critical temperature percentage (%(T\(_{LC}\), °C)).

Whaleb has much fewer parameters, beginning with the gender and maturity of the animal. Immature gray whales are designated the number 0, 1 is for mature male whales, 2 for mature female whales, and 3 is for pregnant, lactating female whales). Length is simply the total length (from snout to notch). The radius (meters) is calculated using the girth, then used in conjunction with length to estimate the whale's volume (m\(^{3}\)). By subtracting the blubber depth from the radius, a core radius is calculated (meters). The same method is used to determine the core volume (m\(^{3}\)). By subtracting the core volume from the total volume, a blubber volume is estimated (m\(^{3}\)). The blubber volume is converted to blubber mass and subtracted from total mass, estimating a core mass. The core mass has a percentage composed of fat storage and is referred to as core energy (E) available (kg). Assimilation energy (AE) and Gross energy (GE) are only pertinent during feeding months (MJ d\(^{-1}\)). Again, some of the parameters change between the beginning and the end of each day, creating the need for recalculation of new radius (m).

Whaleb = [sex(0=immature, 1=male, 2=female, 3=pregnant and lactating), length,
Whale’s matrix is composed of parameters dealing only with the fetus when a whale is pregnant. The fetal length is the first parameter measured in meters, followed by fetal radius (meters). Using the radius and proportions of the length of the fetus, its volume is estimated (m^3). From there, the volume is converted to mass (kg).

\[
\text{whalec} = [\text{fetal length, fetal radius, fetal volume, fetal mass}]
\]

The model starts every run on November first, a non-feeding, non-pregnant, non-lactating day.

It is necessary to randomize parameters requiring variability.

\[
\text{randn}('state',\text{sum}(100*\text{clock}));
\]

The beginning values for certain parameters needed in this model are found in the model TM9abc_start.

\[
\text{TM9abc}_\text{start};
\]

These values help set up the time for pregnancy and feeding periods.

c=1;
d=1;

This code informs the model that female whales are not pregnant at the onset of the simulation.

\[
p\text{regnant}=0;
\]

Values of parameters from the end of the previous day are equal to the parameters at the beginning of that day.

\[
\text{for } i=1:\text{days}
\]

\[
\text{if } i>1
\]

\[
\text{whaleb}(i,1)=\text{whaleb}(i-1,1);
\]

\[
\text{whaleb}(i,2)=\text{whaleb}(i-1,2);
\]

\[
\text{end}
\]

\[
\text{whaleb}(i,3)=\text{whaleb}(i,2)/(2*\pi);
\]

\[
\text{whaleb}(i,5)=\text{whaleb}(i,3)-\text{whaleb}(i,3);
\]

\[
\text{if } \text{whaleb}(i,1)==0
\]

\[
\text{whaleb}(i,4)=\pi*\text{whaleb}(i,2)*(\text{whaleb}(i,3)^2)*(((1/3)*0.226)+0.460+((1/3)*0.314));
\]

\[
\text{if } i==1
\]

\[
\text{whaleb}(i,6)=\pi*\text{whaleb}(i,2)*((\text{whaleb}(i,3)^2)*((1/3)*0.226)+((\text{whaleb}(i,5)^2)*0.460+((1/3)*0.314)));
\]
else
    whaleb(i,6)=whaleb(1,6);
end
else
    % Volume calculations for mature whales with respective percentages of lengths.
    whaleb(i,4)=pi*whaleb(i,2)*(whaleb(i,3)^2)*(((1/3)*0.229)+0.466+((1/3)*0.305));

    % Core volume calculation needed for the first day and following days for mature
    % whales.
    if i==1
        whaleb(i,6)=pi*whaleb(i,2)*((whaleb(i,3)^2)*((1/3)*0.229)+(whaleb(i,5)^2)*(0.466+
        ((1/3)*0.305));
    else
        whaleb(i,6)=whaleb(1,6);
    end
end

% Conversions of volume to energy available to energy used.
whaleb(i,7)=whaleb(i,4)-whaleb(i,6);
whalea(i,4)=whaleb(i,7)*0.94*(10.^3);
whalea(i,5)=whalea(i,3)/whalea(i,4);
whalea(i,6)=(3.4*(whalea(i,1).^0.75)*0.0864);
whalea(i,7)=((0.248*1.75*((whalea(i,1)*9.81).^0.7)*0.0864)*1.1);
whalea(i,9)=whalea(i,6)+whalea(i,7);

% These commands indicate to the model how to calculate BMR and increasing length for
% immature whales.
if whaleb(i,1)==0
    whalea(i,6)=whalea(i,6)*2;
    whaleb(i,2)=9.143+0.0018*i;
end

% The division of energy sources between core and blubber sources.
perener1=0.15;
perener2=1-perener1;

% Timing of pregnancy for female whales.
time1=365;
time2=730;
if (i==time2*d-695)
    pregnant=1;
end

% The impact of pregnancy on female whales and growth of fetuses.
if whaleb(i,1)==3 & (i>=time2*d-695) & i<=(time2*d-295) & pregnant==1
    age= i-(time2*d-695)-1;
    whalec(age,1)=0.0000041*(age)^2.3329;
    whalec(age,2)=whalec(age,1)*0.078;
    whalec(age,3)=pi*whalec(age,1)*whalec(age,2)^2)*(((1/3)*0.23)+0.49+((1/3)*0.28));
    whalec(age,4)=whalec(age,3)*(10^3);
    if age ==1;
whalea(i,1)=whalea(i,1)+ whalec(age,4); %conception
else
    whalea(i,1)=whalea(i,1)+ (whalec(age,4)-whalec(age-1,4)); %fetus growth + female
end
whalea(i,6)=3.4*(whalea(i,1).^0.75)*0.0864;
say='pregnant';
elseif whaleb(i,1)==3 & (i>=(time2*d-294) & i<=(time2*d-82));
    if i ==time2*d-294
        whalea(i,1)=whalea(i,1)-whalec(age,4); %parturition
        say='delivery';
    else
        cost_of_lactation = whalea(i,6)*1.75;
        whalea(i,9)=whalea(i,6)+whalea(i,7)+cost_of_lactation;
        say='lactating';
    end
end
if i== time2*d-80
    pregnant=0;
end
%Timing of multiple pregnancies.
if i>time1*c
    c=c+1;
end
if i>time2*d
    d=d+1;
end

%Feeding occurs during the time frames indicated and is modeled as follows.
if (i>=time1*c-168)& (i<=time1*c)
    foodintake=food+var*randn;
    if foodintake < 0
        foodintake=0;
    end
    whalea(i,10)=0;
    whalea(i,11)=0;
else
    foodintake=0;
end
whaleb(i,8)=whalea(i,1)-whalea(i,4);
whaleb(i,9)=whaleb(i,8)*0.2;
whaleb(i,10)=(foodintake*4.184)*0.8;
whaleb(i,11)=whaleb(i,10)*0.9;

%During feeding months, energy needed is first removed from the available energy from the
%food intake.
whalea(i,10)=(whalea(i,9)*perener1)/(4.184*7.05);
whalea(i,11)=(whalea(i,9)*perener2)/(4.184*9.4);
whalea(i,12)=whalea(i,4)-whalea(i,10);
whalea(i,13)=whaleb(i,9)-whalea(i,11);
if whalea(i,13)<whalea(i,11)
perener2=0;
perener1=1;
end
whalea(i,14)=(foodintake*4.184)*0.1;
whalea(i,15)=(foodintake*4.184)-(foodintake*4.184)*0.2-whaleb(i,10)*0.1-whalea(i,14);
if whalea(i,15)>whalea(i,9)
    whalea(i,16)=whalea(i,15);
    whalea(i,12)=whalea(i,12)+((whalea(i,16)*perener1)/(4.184*7.05));
    whalea(i,13)=whalea(i,13)+((whalea(i,16)*perener2)/(4.184*9.4));
else
    whalea(i,16)=0;
end

These parameters are the new morphometrics at end of day
whalea(i,17)=whalea(i,12)*whalea(i,5);
whaleb(i,12)=pi*2*(whaleb(i,5)+whalea(i,17));
whaleb(i,13)=whaleb(i,12)-(whale(i,10)+whalea(i,11))+(whale(i,16)*perener1)/(4.184*7.05)+((whale(i,16)*perener2)/(4.184*9.4));

These commands are to create graphs of variables indicated (ex: time, mass) and must
be turned off when replication models are run (ex: Montecarlo)
subplot(3,1,1), plot(time,mass);
hold on
subplot(3,1,2), plot(time,temperature)
subplot(3,1,3), plot(time,test)

This command indicates to the model to keep values of parameters so that they can be
sorted and displayed in replication models (ex: Montecarlo).
hold on
whalea(days,1)
keyboard

Matlab must be cleared from the matrices prior to running the models again.
clear all
APPENDIX C  REPLICATION MODEL FOR MATURE MALE AND IMMATURE GRAY WHALES
Montecarlo was created by Nathalie Greenwald and Pedro Quintana-Ascencio.
University of Central Florida, Department of Biology
February 2004

This model will run the main model (TM9abc) as many times as is indicated (r, from 1:?)..

The separation of the parameters into whalea and whaleb is simply due to the limitation of the software with matrices of up to 37 x 1461 (37 being the number of parameters and 1461 the number of days).

We discovered this limitation at the attempt of a matrix 33 x 365.

The parameters we want to analyze are separated and renamed (from "whalea(j,1)" to "final1(j,r)).

Once all the runs are completed each of the parameters are sorted for statistical purposes.

Length of whalea is the number of days TM9abc_start has been set to run for.
for r=1:200

The model will use parameters from another model (T9abc) while being run.
TM9abc
  for j=1:length(whalea)
    final1(j,r)=whalea(j,1);
    final2(j,r)=whalea(j,3);
    final3(j,r)=whalea(j,6);
    final4(j,r)=whalea(j,18);
    final5(j,r)=whaleb(j,2);
  end
%keyboard
clear whalea;
clear whaleb;
end

The parameters are transposed (final1') and sorted ("sort(final1)").
final1=final1';
final1=sort(final1,1);

Due to the limitations of how many columns Excel can have, the columns representing each day must be separated. This separation is altered when the model is run for a different number of days than the 1095 here.
final1a=final1(:,1:200);
final1b=final1(:,201:400);
final1c=final1(:,401:600);
final1d=final1(:,601:800);
final1e=final1(:,801:1000);
final1f=final1(:,1001:1095);

The model is told to save the parameter separately by intervals of days, name the file("data1a.wk1"), and its location ('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1a.wk1').
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1a.wk1',final1a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1b.wk1',final1b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1c.wk1',final1c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1d.wk1',final1d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1e.wk1',final1e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1f.wk1',final1f)

final2=final2';
final2=sort(final2,1);
final2a=final2(:,1:200);
final2b=final2(:,201:400);
final2c=final2(:,401:600);
final2d=final2(:,601:800);
final2e=final2(:,801:1000);
final2f=final2(:,1001:1095);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2a.wk1',final2a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2b.wk1',final2b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2c.wk1',final2c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2d.wk1',final2d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2e.wk1',final2e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2f.wk1',final2f)

final3=final3';
final3=sort(final3,1);
final3a=final3(:,1:200);
final3b=final3(:,201:400);
final3c=final3(:,401:600);
final3d=final3(:,601:800);
final3e=final3(:,801:1000);
final3f=final3(:,1001:1095);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3a.wk1',final3a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3b.wk1',final3b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3c.wk1',final3c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3d.wk1',final3d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3e.wk1',final3e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3f.wk1',final3f)

final4=final4';
final4=sort(final4,1);
final4a=final4(:,1:200);
final4b=final4(:,201:400);
final4c=final4(:,401:600);
final4d=final4(:,601:800);
final4e=final4(:,801:1000);
final4f=final4(:,1001:1095);
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4a.wk1',final4a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4b.wk1',final4b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4c.wk1',final4c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4d.wk1',final4d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4e.wk1',final4e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4f.wk1',final4f)

final5=final5;
final5=sort(final5,1);

final5a=final5(:,1:200);
final5b=final5(:,201:400);
final5c=final5(:,401:600);
final5d=final5(:,601:800);
final5e=final5(:,801:1000);
final5f=final5(:,1001:1095);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5a.wk1',final5a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5b.wk1',final5b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5c.wk1',final5c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5d.wk1',final5d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5e.wk1',final5e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5f.wk1',final5f)

% Matlab must be cleared from the matrices prior to running the models again.
clear all
APPENDIX D  REPLICATION MODEL FOR PREGNANT FEMALE GRAY WHALES OVER THREE YEARS
MontecarloPreg was created by Nathalie Greenwald and Pedro Quintana-Ascencio.
University of Central Florida, Department of Biology
February 2004

This model will run the main model (TM9abc) for mature, pregnant and lactating females as many times as is indicated (r, from 1:?).

The separation of the parameters into whalea, whaleb, and whalec is simply due to the limitation of the software with matrices of up to 37 x 1461 (37 being the number of parameters and 1461 the number of days).

We discovered this limitation at the attempt of a matrix 33 x 365.

The parameters we want to analyze are separated and renamed (from "whalea(j,1)" to "final1(j,r)).

Once all the runs are completed each of the parameters are sorted for statistical purposes.

Length of whalea is the number of days TM9abc_start has been set to run for.
for r=1:500

The model will use parameters from another model (TM9abc) while being run.
TM9abc
for j=1:length(whalea)
    final1(j,r)=whalea(j,1);
    final2(j,r)=whalea(j,3);
    final3(j,r)=whalea(j,6);
    final4(j,r)=whalea(j,18);
    final5(j,r)=whaleb(j,2);
end

Whalec matrix consists of parameters on the fetus.
for k=1:length(whalec)
    final6(k,r)=whalec(k,1);
    final7(k,r)=whalec(k,4);
end
%keyboard
clear whalea;
clear whaleb;
clear whalec;
end

The parameters are transposed (final1') and sorted ("sort(final1)").
final1=final1';
final1=sort(final1,1);

Due to the limitations of how many columns Excel can have, the columns representing each day must be separated. This separation is altered when the model is run for a different number of days than the 1095 here.
final1a=final1(:,1:200);
final1b=final1(:,201:400);
% The model is told to save the parameter separately by intervals of days, name the file
  % ("data1a.wk1"), and its location ('D:\My Documents\Master Work\Thesis\Matlab\Work with
  % Pedro\data1a.wk1').
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1a.wk1', final1a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1b.wk1', final1b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1c.wk1', final1c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1d.wk1', final1d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1e.wk1', final1e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1f.wk1', final1f)

final2=final2';
final2=sort(final2,1);

final2a=final2(:,1:200);
final2b=final2(:,201:400);
final2c=final2(:,401:600);
final2d=final2(:,601:800);
final2e=final2(:,801:1000);
final2f=final2(:,1001:1095);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2a.wk1', final2a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2b.wk1', final2b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2c.wk1', final2c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2d.wk1', final2d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2e.wk1', final2e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2f.wk1', final2f)

final3=final3';
final3=sort(final3,1);

final3a=final3(:,1:200);
final3b=final3(:,201:400);
final3c=final3(:,401:600);
final3d=final3(:,601:800);
final3e=final3(:,801:1000);
final3f=final3(:,1001:1095);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3a.wk1', final3a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3b.wk1', final3b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3c.wk1', final3c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3d.wk1', final3d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3e.wk1', final3e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3f.wk1', final3f)

final4=final4';
final4=sort(final4,1);
final4a=final4(:,1:200);
final4b=final4(:,201:400);
final4c=final4(:,401:600);
final4d=final4(:,601:800);
final4e=final4(:,801:1000);
final4f=final4(:,1001:1095);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4a.wk1',final4a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4b.wk1',final4b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4c.wk1',final4c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4d.wk1',final4d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4e.wk1',final4e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4f.wk1',final4f)

final5=final5';
final5=sort(final5,1);

final5a=final5(:,1:200);
final5b=final5(:,201:400);
final5c=final5(:,401:600);
final5d=final5(:,601:800);
final5e=final5(:,801:1000);
final5f=final5(:,1001:1095);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5a.wk1',final5a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5b.wk1',final5b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5c.wk1',final5c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5d.wk1',final5d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5e.wk1',final5e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5f.wk1',final5f)

final6=final6';
final6=sort(final6,1);

final6a=final6(:,1:200);
final6b=final6(:,201:401);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data6a.wk1',final6a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data6b.wk1',final6b)

final7=final7';
final7=sort(final7,1);

final7a=final7(:,1:200);
final7b=final7(:,201:401);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data7a.wk1',final7a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data7b.wk1',final7b)

%Matlab must be cleared from the matrices prior to running the models again.
clear all
APPENDIX E  REPLICATION MODEL FOR PREGNANT FEMALE GRAY WHALES OVER FOUR YEARS
%MontecarloPreg4yrs was created by Nathalie Greenwald and Pedro Quintana-Ascencio.
%University of Central Florida, Department of Biology
%February 2004

%This model will run the main model (TM9abc) for mature, pregnant and lactating females as
%many times as is indicated (r, from 1:?).

%The separation of the parameters into whalea, whaleb, and whalec is simply due to the
%limitation of the software with matrices of up to 37 x 1461 (37 being the number of parameters
%and 1461 the number of days).

%We discovered this limitation at the attempt of a matrix 33 x 365.

%The parameters we want to analyze are separated and renamed (from "whalea(j,1)" to
%"final1(j,r)).

%Once all the runs are completed each of the parameters are sorted for statistical purposes.

%Length of whalea is the number of days TM9abc_start has been set to run for.
for r=1:500

%The model will use parameters from another model (TM9abc) while being run.
TM9abc
  for j=1:length(whalea)
    final1(j,r)=whalea(j,1);
    final2(j,r)=whalea(j,3);
    final3(j,r)=whalea(j,6);
    final4(j,r)=whalea(j,18);
    final5(j,r)=whaleb(j,2);
  end

%Whalec matrix concerns parameters on the fetus.
  for k=1:length(whalec)
    final6(k,r)=whalec(k,1);
    final7(k,r)=whalec(k,4);
  end
%keyboard
clear whalea;
clear whaleb;
clear whalec;
end

%The parameters are transposed (final1') and sorted ("sort(final1)").
final1=final1';
final1=sort(final1,1);

%Due to the limitations of how many columns Excel can have, the columns representing each
%day must be separated. This separation is altered when the model is run for a different
%number of days than the 1461 here.
final1a=final1(:,1:200);
final1b=final1(:,201:400);
final1c=final1(:,401:600);
final1d=final1(:,601:800);
final1e=final1(:,801:1000);
final1f=final1(:,1001:1220);
final1g=final1(:,1221:1461);

% The model is told to save the parameter separately by intervals of days, name the file
% ("data1a.wk1"), and its location ('D:\My Documents\Master Work\Thesis\Matlab\Work with
% Pedro\data1a.wk1').
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1a.wk1',final1a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1b.wk1',final1b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1c.wk1',final1c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1d.wk1',final1d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1e.wk1',final1e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1f.wk1',final1f)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data1g.wk1',final1g)

final2=final2';
final2=sort(final2,1);
final2a=final2(:,1:200);
final2b=final2(:,201:400);
final2c=final2(:,401:600);
final2d=final2(:,601:800);
final2e=final2(:,801:1000);
final2f=final2(:,1001:1220);
final2g=final2(:,1221:1461);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2a.wk1',final2a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2b.wk1',final2b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2c.wk1',final2c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2d.wk1',final2d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2e.wk1',final2e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2f.wk1',final2f)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data2g.wk1',final2g)

final3=final3';
final3=sort(final3,1);
final3a=final3(:,1:200);
final3b=final3(:,201:400);
final3c=final3(:,401:600);
final3d=final3(:,601:800);
final3e=final3(:,801:1000);
final3f=final3(:,1001:1220);
final3g=final3(:,1221:1461);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3a.wk1',final3a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3b.wk1',final3b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3c.wk1',final3c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3d.wk1',final3d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3e.wk1',final3e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3f.wk1',final3f)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data3g.wk1',final3g)

final4=final4';
final4=sort(final4,1);

final4a=final4(:,1:200);
final4b=final4(:,201:400);
final4c=final4(:,401:600);
final4d=final4(:,601:800);
final4e=final4(:,801:1000);
final4f=final4(:,1001:1220);
final4g=final4(:,1221:1461);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4a.wk1',final4a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4b.wk1',final4b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4c.wk1',final4c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4d.wk1',final4d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4e.wk1',final4e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4f.wk1',final4f)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data4g.wk1',final4g)

final5=final5';
final5=sort(final5,1);

final5a=final5(:,1:200);
final5b=final5(:,201:400);
final5c=final5(:,401:600);
final5d=final5(:,601:800);
final5e=final5(:,801:1000);
final5f=final5(:,1001:1220);
final5g=final5(:,1221:1461);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5a.wk1',final5a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5b.wk1',final5b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5c.wk1',final5c)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5d.wk1',final5d)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5e.wk1',final5e)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5f.wk1',final5f)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data5g.wk1',final5g)

final6=final6';
final6=sort(final6,1);

final6a=final6(:,1:200);
final6b=final6(:,201:400);
final6c=final6(:,401:403);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data6a.wk1',final6a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data6b.wk1',final6b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data6c.wk1',final6c)

final7=final7';
final7=sort(final7,1);

final7a=final7(:,1:200);
final7b=final7(:,201:400);
final7c=final7(:,401:403);

wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data7a.wk1',final7a)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data7b.wk1',final7b)
wk1write('D:\My Documents\Master Work\Thesis\Matlab\Work with Pedro\data7c.wk1',final7c)

%Matlab must be cleared from the matrices prior to running the models again.
clear all
APPENDIX F LIST OF SYMBOLS
<table>
<thead>
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<th>Symbols</th>
<th>Definitions</th>
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<tbody>
<tr>
<td>°C</td>
<td>Degree Celcius</td>
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<td>a</td>
<td>Fetal age</td>
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<td>BD</td>
<td>Blubber depth</td>
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<tr>
<td>$B_{\text{mass}}$</td>
<td>Blubber mass</td>
</tr>
<tr>
<td>BMR</td>
<td>Basal metabolic rate</td>
</tr>
<tr>
<td>CI</td>
<td>Confidence interval</td>
</tr>
<tr>
<td>CG</td>
<td>Centimeters to grams ratio</td>
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<tr>
<td>cm</td>
<td>Centimeters</td>
</tr>
<tr>
<td>$C_T$</td>
<td>Cost of locomotion</td>
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<tr>
<td>d</td>
<td>Day</td>
</tr>
<tr>
<td>E</td>
<td>Energy</td>
</tr>
<tr>
<td>ENP</td>
<td>Eastern North Pacific stock</td>
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<tr>
<td>FMR</td>
<td>Field metabolic rate</td>
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<td>Hour</td>
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<td>Heat increment of feeding</td>
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<td>Ingested energy</td>
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<td>Length</td>
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<td>Fetal length</td>
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<td>$L_I$</td>
<td>Immature length</td>
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<td>Megajoules</td>
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<tr>
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<td>Metabolic rate</td>
</tr>
<tr>
<td>s</td>
<td>Seconds</td>
</tr>
<tr>
<td>SE</td>
<td>Standard error</td>
</tr>
<tr>
<td>t</td>
<td>Time</td>
</tr>
<tr>
<td>$T_{\text{LC}}$</td>
<td>Lower critical temperature</td>
</tr>
<tr>
<td>Symbols</td>
<td>Definitions</td>
</tr>
<tr>
<td>---------</td>
<td>---------------------</td>
</tr>
<tr>
<td>$T_{MB}$</td>
<td>Mean body temperature</td>
</tr>
<tr>
<td>V</td>
<td>Velocity</td>
</tr>
<tr>
<td>WNP</td>
<td>Western North Pacific</td>
</tr>
</tbody>
</table>
APPENDIX G CONVERSIONS USED IN MODEL
<table>
<thead>
<tr>
<th>Variables</th>
<th>Formulas</th>
<th>Units with Conversions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radius</td>
<td>Girth / 2\pi</td>
<td>m</td>
</tr>
<tr>
<td>Core radius</td>
<td>Radius – blubber depth</td>
<td>m</td>
</tr>
</tbody>
</table>
| Volume                  | \[\frac{1}{3} \text{radius}^2 \times \% \text{of total length for cone } 1\] + \[
\text{radius}^2 \times \% \text{of total length for cone } 1\] + \[
\frac{1}{3} \text{radius}^2 \times \% \text{of total length for cone } 1\] | m$^3$                   |
| Core volume             | \[\frac{1}{3} \text{radius}^2 \times \% \text{of total length for cone } 1\] + \[
\text{core radius}^2 \times \% \text{of total length for cone } 1\] + \[
\frac{1}{3} \text{core radius}^2 \times \% \text{of total length for cone } 1\] | m$^3$                   |
<p>| Blubber volume          | Volume – core volume                                                     | m$^3$                  |
| Blubber mass            | Blubber volume * density of blubber                                       | m$^3$ * $10^6$ cm$^3$/ m$^3$ * 0.94g/cm$^3$ * kg/10$^3$g = kg |
| Core mass               | Mass – blubber mass                                                      | kg                     |
| BMR                     | 3.4 * mass$^{0.75}$                                                     | J/ s * MJ/ 10$^6$ J * 86400 s/ d = MJ d$^{-1}$ |
| Cost of locomotion      | 0.248 * velocity * (mass<em>9.81)$^{0.7}$                                   | J/ s * MJ/ 10$^6$ J * 86400 s/ d = MJ d$^{-1}$ |
| Daily energetic cost    | BMR + cost of locomotion                                                 | MJ d$^{-1}$            |
| Core energy available   | Core mass * 0.2                                                         | kg                     |
| Assimilation energy     | (Food intake</em>4.184) * 0.8                                                | kg/d * 10$^3$g/ kg * kcal/ g * 4.184kJ/ kcal * MJ/ 10$^3$kJ = MJ d$^{-1}$ |
| Heat increment of feeding (HIF) | (Food intake<em>4.184) * 0.1                                           | kg/d * 10$^3$g/ kg * kcal/ g * 4.184kJ/ kcal * MJ/ 10$^3$kJ = MJ d$^{-1}$ |
| Gross energy            | Assimilation energy * 0.9                                               | MJ d$^{-1}$            |
| Energy                  | (Food intake</em>4.184) – assimilation energy – [(Food intake<em>4.184) * 0.2] – HIF | MJ d$^{-1}$            |
| Energy stored           | Energy (if energy &gt; daily energetic cost)                               | MJ d$^{-1}$            |
| Core energy used        | Daily energetic cost * 0.85 (until core energy available &lt; core energy used which then = 0) | MJ $^</em>$ 10$^3$kJ/ MJ * kcal/ 4.184kJ * g/ 9.4kcal * kg/10$^3$g = kg |
| Core energy remaining   | Core energy available – core energy used + [(energy stored<em>0.85) / (4.184</em>9.4)] | MJ $^*$ 10$^3$kJ/ MJ * kcal/ 4.184kJ * g/ 9.4kcal * kg/10$^3$g = kg |</p>
<table>
<thead>
<tr>
<th>Variables</th>
<th>Formulas</th>
<th>Units with Conversions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blubber used</td>
<td>Daily energetic cost * 0.15 (until core energy available &lt; core energy used which then = 1)</td>
<td>MJ * $10^4$kJ/ MJ * kcal/ 4.184kJ * g/ 7.05kcal * kg/ $10^3$g = kg</td>
</tr>
<tr>
<td>Blubber remaining</td>
<td>Blubber mass – blubber used + ((stored energy<em>0.15) / (4.184</em>7.05))</td>
<td>MJ * $10^3$kJ/ MJ * kcal/ 4.184kJ * g/ 7.05kcal * kg/ $10^3$g = kg</td>
</tr>
<tr>
<td>CG ratio</td>
<td>Blubber depth / blubber mass</td>
<td>m kg$^{-1}$</td>
</tr>
<tr>
<td>New blubber depth</td>
<td>Blubber remaining * CG ratio</td>
<td>kg * m/ kg = m</td>
</tr>
<tr>
<td>New girth</td>
<td>(New blubber depth + Core radius) * 2π</td>
<td>m</td>
</tr>
<tr>
<td>New mass</td>
<td>Mass – (core energy used + blubber used) + ((stored energy<em>0.15) / (4.184</em>7.05)) + ((stored energy<em>0.85) / (4.184</em>9.4))</td>
<td>kg</td>
</tr>
<tr>
<td>Lower critical</td>
<td>$37 – ((0.5*(3.4<em>mass^{0.75})<em>ln(mass/ core mass))/(2π</em>0.2</em>length))</td>
<td>ºC</td>
</tr>
<tr>
<td>temperature</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fetal length</td>
<td>$(4.1*10^{-7}) *$ fetal age$^{2.3329}$</td>
<td>m</td>
</tr>
<tr>
<td>Fetal radius</td>
<td>Fetal length * 0.078</td>
<td>m</td>
</tr>
<tr>
<td>Fetal volume</td>
<td>$(1/3$ fetal radius$^2$ * % of total fetal length for cone 1) + (fetal radius$^2$ * % of total fetal length for cone 1) + (1/3 fetal radius$^2$ * % of total fetal length for cone 1)</td>
<td>m$^3$</td>
</tr>
<tr>
<td>Fetal mass</td>
<td>Fetal volume * $10^3$</td>
<td>m$^3$ * $10^6$cm$^3$/ m$^3$ * 1g/ cm$^3$ * kg/ $10^3$g = kg</td>
</tr>
</tbody>
</table>
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