NORTH ATLANTIC RIGHT WHALE GROWTH AND ENERGETICS

by

Sarah Marie Elizabeth Fortune

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Abstract

Management plans for North Atlantic right whales (*Eubalaena glacialis*) focus on preventing mortality from ship strikes and fishing gear entanglement. However, population recovery may also be limited by nutritional stress. I derived growth curves and quantified the food requirements of North Atlantic right whales by age, sex and reproductive state. I also compared their predicted needs with field estimates of prey consumption to evaluate the model predictions and consider whether different demographic groups of right whales might be nutritionally stressed. Energy requirements were estimated using a bioenergetics model that incorporated uncertainty in energy inputs and outputs. Consumption was estimated with prey samples taken near feeding whales in two critical feeding habitats—Cape Cod Bay (n=28 net collections) and the Bay of Fundy (n=19 optical plankton counts). Model predictions indicate that mothers invest heavily in their calves, which effectively double in size and attain ~73% of their mother's length by weaning at one year of age. Calves gained an average of ~1.7 cm and ~34 kg per day while nursing during this rapid growth phase. Body growth was best described using a two-phased Gompertz model and could not be fit using any of the single continuous growth models commonly used for other mammals. Energetically, calves required the least energy (~1129 MJ/day) and lactating females required the most (~2934 MJ/day). Adult males and non-reproductive females fell in between at ~1140 and ~1217 MJ/day respectively. Estimates of energy requirements for juveniles, adult males, pregnant and non-reproductive females compared favorably with estimates of actual prey consumption in their winter habitat (i.e., they differed by ≤15%), suggesting that the model was reliable. However, lactating females appear to obtain considerably less (~45%) of their predicted daily energy requirements in Cape Cod Bay, and almost met their needs in the Bay of Fundy (obtaining ~87% of daily requirements). This suggests that lactating females may be experiencing an energy deficit, which may affect reproductive rates and slow population recovery. Nutritional stress may thus be limiting the recovery of North Atlantic right whales.

Preface

Various collaborators provided the data that I analyzed. The North Atlantic Right Whale Consortium provided identification and necropsy data. These data are curated by P. Hamilton (New England Aquarium) and M. Moore (Woods Hole Oceanographic Institution). Photogrammetric measurements of North Atlantic right whales were provided by W. Perryman (Southwest Fisheries Science Center). Zooplankton data came from C. Mayo (Provincetown Center for Coastal Studies) and Baumgartner & Mate (2003).

I received statistical advice from R. Ahrens B. Battaile, T. Jeanniard du Dot, D. Schluter, and B. Young.

Two papers (Chapters 2 and 3) have been prepared for peer-reviewed scientific journals, which were edited by my supervisor (A. Trites), committee members (C. Mayo, R. Shadwick and D. Rosen) and coauthors (W. Perryman, M. Moore, H. Pettis, M. Lynn, C. Mayo and A. Trites). Additional reviews were provided by B. Perrin, S. Chivers, O. Nichols E. Taylor and T. Webster and one anonymous reviewer.

Chapter 2 working title: Growth and Rapid Early Development of North Atlantic Right Whales (*Eubalaena glacialis*).

Chapter 3 working title: Energetic requirements of North Atlantic right whales and implications for species recovery.

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Chapter 1: Introduction

North Atlantic right whales (*Eubalaena glacialis*) are one of the rarest species of large whales in the world (Brownell *et al.* 1986, Kraus *et al.* 2005, Caswell *et al.* 1999). Recent estimates (2010) suggest that a minimum of 449 right whales remain in the western North Atlantic (Hamilton & Knowlton 2010) compared to 6,787 southern right whales (off South Africa, Australia and Argentina) (IWC 2001), and fewer than 40 (between 28 and 31 individuals) North Pacific right whales (Wade *et al.* 2010). North Atlantic right whales are recovering slowly from over-exploitation since being protected from commercial whaling in 1935 (Kraus *et al.* 2001). Changes in numbers have varied between -0.02 and 2.5% per year (Fujiwara & Caswell 2001, Knowlton *et al.* 1994), which is considerably lower than southern right whales (increasing by 7.2% per year off South Africa which numbered 3,104 individuals in 1997, 8.2% off Australia n=1,197 whales, and 7.1% off Argentina n=2,577 whales) (IWC 2001). It is widely accepted that anthropogenic mortality from ship strikes and entanglement in fishing gear have limited the recovery of North Atlantic right whales (Caswell et al. 1999), but recent observations of poor body condition suggest that nutritional factors may also be impeding recovery as well (Miller *et al.* 2011, Pettis *et al.* 2004).

Signs of compromised health were first observed in North Atlantic right whales in the mid-to-late 1990s when emaciated individuals began appearing in the Bay of Fundy with various forms of skin lesions (Rolland *et al.* 2007a, Pettis et al. 2004). Blubber thickness of juvenile and adult males was particularly thin in 1998, and was associated with a low abundance of prey, especially *Calanus finmarchicus,* in the Gulf of Maine (Miller et al. 2011, Pershing *et al.* 2005). Just over half of the population observed at that time (n=439) had white lesions on their bodies (Rolland et al. 2007a, Hamilton & Marx 2005), which was consistent with starvation or disease according to Pettis *et al.* (2004). Others noted that the changes in health corresponded with changes in oceanographic conditions (Rolland et al. 2007a, Greene *et al.* 2003, Greene & Pershing 2004) thought to have adversely affected the availability of prey.

The numbers of calves born each year has also varied overtime from 1 to 39 individuals (2000 – 2009) and also appears to correspond with changes in resource availability (Kraus *et al.* 2007, Waring *et al.* 2011, Greene & Pershing 2004) associated with changes in ocean conditions (Greene & Pershing 2004). The mean calving interval (time between individual birthing events) has also oscillated overtime (increasing from ~3 years to over 5 years between 1993 and 1998, and decreasing to just over 3 years in 2004 and 2005) (Kraus et al. 2001, Kraus et al. 2007). Years of low reproductive success appear to follow times of reduced prey availability suggesting that North Atlantic right whales may experience periods of nutritional stress.

Individuals that do not acquire sufficient quantity or quality of prey to meet their daily needs are said to be nutritionally stressed (Trites & Donnelly 2003). Nutritional stress can manifest in various ways, including reduced blubber thickness, reduced birth rates, increased perinatal and neonatal mortality, reduced body size and behavioural changes (Rosen 2009, Lockyer 2007, Lockyer 1981b, Lockyer 1981a, Lockyer 1978, Trites & Donnelly 2003). Several symptoms of nutritional stress appear to have been manifested in the North Atlantic right whale population. However, the role of nutritional stress and the validity of this hypothesis in the poor recovery of North Atlantic right whales have not been tested.

1.1 Research

Although empirical evidence regarding changes in health and reproduction suggests that right whales are experiencing periods of nutritional stress, knowledge regarding the nutritional requirements and energetic intake of the species is poor. Thus, the primary goal of my research was to quantify the food requirements of different demographic groups of North Atlantic right whales. The energy needs of specific life-stages, sexes and reproductive states of North Atlantic right whales, which are necessary to evaluate the nutritional status of the species, have not been previously quantified.

Energy expenditure can be directly estimated for mammals in captivity (e.g. respirometry) or indirectly in the wild from various proxies of energy expenditure (e.g. doubly-labeled water and overall body dynamic acceleration). However, it has been impractical to date to employ such methods for large cetaceans because of the invasiveness of attaching long-term data archiving tags to calculate remotely collected proxies of energy expenditure, and because individual whales cannot be manipulated in the wild. Bioenergetic modeling thus serves as the only viable method to quantify food needs of large whales (e.g. Lockyer 1981b, Williams *et al.* 2011, Noren 2011, Lockyer 2007).

The energy requirements of animals are a function of body size, but current knowledge of North Atlantic right growth is limited to a small sample (n=23) of morphological measurements taken from stranded animals (Moore *et al.* 2004). I therefore attempted to derive a better model of right whale growth by combining a large set of morphometric measurements from dead (necropsy) and living whales (photogrammetry) for different sexes and age-classes (Chapter 2) (n=154). I also examined growth in fluke width and maximum body width.

To consider nutritional status, I quantitatively estimated the food requirements of different demographic groups of North Atlantic right whales and compared model predictions with estimates of prey consumption (Chapter 3). My primary research questions were: 1) how do energy needs vary according to age, sex and reproductive state; 2) how do the predicted energy needs compare to estimates of prey consumption; and 3) is a nutritional imbalance likely, given what is known about the food resource and the anticipated energy needs of North Atlantic right whales?

1.2 Thesis Structure

My thesis is organized into four units: a general introduction (Chapter 1), analysis of North Atlantic right whale growth (Chapter 2), analysis of North Atlantic right whale energetics and prey consumption (Chapter 3) and a general conclusion (Chapter 4). Data Chapters 2 and 3 are written as manuscripts and contain some repetition of information.

Chapter 2: North Atlantic Right Whale Growth

2.1 Summary

Body growth of North Atlantic right whales (*Eubalaena glacialis*) was described from measurements of known-age live and dead individuals to gain insights into the nutritional needs and life history strategies of this endangered species. Body lengths from 154 individuals revealed that calves more than doubled in size and attained three-quarters of asymptotic adult size by the time they had weaned at 12 months. Calves gained on average ~1.7 cm and ~34 kg per day while nursing during this extremely rapid growth phase. Mean predicted lengths and weights were 4.2 m and 1.1 metric tons (mt) at birth, 10.3 m and 13.5 mt at weaning, and 13.6 m and 29.6 mt when fully grown. Growth of right whales was best described using a 2-phased Gompertz growth model and could not be fit using any of the single continuous growth models commonly used for other mammals. Rapid growth during dependency may minimize the risk of predation and maximize calf survival. Rapid calf growth may also maximize development of the mouth and baleen to optimize foraging efficiency of juveniles at the time of weaning, as well as improve reproductive fitness by reducing the age at which sexual maturity is attained. However, transferring the amount of energy needed to support the rapid postnatal growth of North Atlantic right whales may ultimately affect the intervals between pregnancies (>3 years) of mature females.

2.2 Introduction

Growth models that describe body size have been widely applied to address questions pertaining to species biology, ecology, physiology and conservation. They have been integrated into bioenergetic models to determine the total energetic requirements of fish species (e.g., Juncos *et al.* 2011, Thomas *et al.* 2011, Hufnagl & Peck 2011), as well as into multi-species (e.g., Rochet *et al.* 2011) and ecosystem models (e.g., Xu *et al.* 2011) to determine the flow of energy through predator-prey interactions. Growth models have also been used to compare changes in body size over time to make inferences about the nutritional and reproductive status of populations (e.g., Fearnbach *et al.* 2011, Perryman &

Lynn 2002, Calkins *et al.* 1998). They have even been used to establish appropriate drug dosages for sedatives and antibiotics of animals of different sizes and consequently of different ages (e.g., Woods *et al.* 1989).

Various techniques have been used to obtain the data needed to describe body growth. Growth of small aquatic animals can be easily studied with field and laboratory studies. For example, fish can be easily live captured for weighing and measuring (e.g., Koch *et al.* 2011, Beamish & McFarlane 1983, Brouwer & Griffiths 2004, Barkman & Bengtson 1987), or sampled and aged using dead individuals (e.g., Mercier *et al.* 2011). Data from larger species, such as marine mammals, have traditionally come from dead animals (e.g., Trites & Bigg 1996, Winship *et al.* 2001) and sometimes from live-caught (e.g., Crawley 1975, Iverson *et al.* 1993) or captive animals (e.g., Jones *et al.* 2011, Liu *et al.* 2011). However, large aquatic animals such as cetaceans present logistical challenges and have typically been measured after being harvested (e.g., Lockyer 1981b, Frazer & Huggett 1973, George *et al.* 1999, Markussen *et al.* 1992, Lockyer & Waters 1986), stranded, or unintentionally caught in fishing gear (e.g., Read & Tolley 1997, Agusa *et al.* 2011, Perrin *et al.* 1976). Growth models for cetaceans have therefore been typically constructed from few measurements.

The majority of data available to describe the size-at-age of cetaceans have been collected from whaling ships and whaling stations, and were collected to assist in the management of exploited and depleted stocks. These historic studies (e.g., Mackintosh & Wheeler 1929, Nishiwaki & Hayashi 1950, Laws 1959) laid the foundation for what is presently known about cetacean growth. More recently, growth studies have been conducted using datasets from stranding events and fisheries by-catch (e.g., Read & Tolley 1997, Agusa et al. 2011). Growth models thus exist for many commercially exploited and by-caught species, but are largely unavailable for species such as North Atlantic right whales that were commercially extinct (Reeves *et al.* 2007) before standardized data collection and aging procedures were implemented (e.g., Norris 1961).

In 1935, North Atlantic right whales (*Eubalaena glacialis*) were deemed over-exploited and placed under international legal protection by the League of Nations (Kraus & Rolland 2007). Unfortunately, the few morphometric measurements taken during the historical right whale hunt were inaccurate (weights) or inconsistent (lengths) according to the Smithsonian National Museum of Natural History (Potter 2009). Growth of right whales thus remained undescribed until morphometric measurements from beached carcasses (1970–2002, n=23 individuals) were analyzed (Moore et al. 2004). This small data set from beach cast whales included animals that were pulled onto the shore and likely stretched prior to measurement. It also contained calves of uncertain ages (estimated in decimal years), which prevented modeling the growth of dependent young.

One means of improving the existing crude model of North Atlantic right whale growth (Moore et al. 2004) is to increase the sample size of morphometric measurements. This can be done using measurements of living animals estimated by aerial photogrammetry (e.g., Perryman & Lynn 2002). Photogrammetric techniques have been widely established to collect non-invasive morphological measurements of various cetacean species (Webster *et al.* 2010, Fearnbach et al. 2011).

Refining the existing body growth model for North Atlantic right whales can allow questions to be better answered about food requirements, age at sexual maturation and appropriate doses of medications. Researchers have long hypothesized that the poor recovery of North Atlantic right whales is partially attributed to nutritional stress (Kraus et al. 2007, Reeves *et al.* 2001, Rolland et al. 2007a, Miller et al. 2011) and direct anthropogenic mortality from ship strikes and entanglement in fishing gear (Caswell et al. 1999, Moore et al. 2004, Kraus et al. 2005). Researchers have also hypothesized that delayed ages at sexual maturation (5-21 years) may reflect reproductive failure through neonatal and perinatal loss, but are uncertain about the age at sexual maturation (Browning *et al.* 2010). A growth model would contribute to testing the nutritional stress hypothesis (e.g., by constructing a bioenergetics model), and could be used to confirm or refine present estimates of the mean age at sexual maturation (9 years). It could even be used to assist in determining effective doses of antibiotics to administer to wounded animals, and doses of sedatives to entangled animals of different sizes (Moore *et al.* 2010).

The goal of my study was to describe North Atlantic right whale growth using linear and non-linear models fit to measurements from live (remotely measured through photogrammetry) and dead whales (physically measured during necropsy). I modeled growth in length and mass using standard growth functions that have been previously applied to fish and mammals, and tested the use of 2-phased models to account for differential growth of immature and mature right whales. I also described growth in maximum body width and fluke width with linear mixed-effects models to enable field biologists to determine the relative age and length of stranded animals that cannot be accurately measured due to decomposition. My results describe the body growth of North Atlantic right whales and provide new insights into the reproductive strategy and energetic investment employed by this endangered species.

2.3 Materials and Methods

2.3.1 Length

I modeled length-at-age relationships using measurements from dead North Atlantic right whales and from live animals photographed during aerial surveys. Photogrammetric measurements (n=133) were taken of 94 unique individuals in the Bay of Fundy between 2000 and 2002, following the methods of Perryman and Lynn (2002). Some of these 94 individuals (n=17 calves, n=39 juveniles, n=38 adults) were seen and measured in more than one year. This included 9 juveniles and 10 adults that were measured twice, and 8 juveniles and 2 adults that were measured in three different years. Calves represented individuals between 0 and 1 year; juveniles consisted of individuals >1 and < 9 year; and adults included those ≥ 9 year. I further increased the sample size of measurements by including 21 necropsy length measurements collected from known individuals between 1970 and 2009. Age classes of all measured animals were determined for individual whales by matching photographs of their unique callosity patterns (dry patches of dead skin; Kraus *et al.* 1986) using the North Atlantic Right Whale Consortium Identification Database (Right Whale Consortium 2010).

The aerial photographs were taken by the National Oceanic and Atmospheric Association's Southwest Fisheries Science Centre using a KA-76A US military reconnaissance camera mounted over an 18" camera port in the hull of a Twin Otter aircraft. The camera had a fixed focal length 126 mm lens and used Kodak Aerial Ektachrome film

(SO-397) for the majority of the images. Cycle rate for the camera was determined based on a combination of aircraft altitude and ground speed to ensure that adjacent frames overlapped by 60 – 80%. This rapid cycle rate allowed each animal to be captured on 3-4 frames during each photo pass. Position (based on GPS) and altitude (radar altimeter; Honeywell AA-300 series) were recorded automatically each time the camera fired. Bias in radar altimetry data was estimated each field season from regression analysis of a photographed series of floating targets. This calculated bias was used to correct recorded altitude for each frame from which length measurements were made. More detailed explanation of these techniques can be found in Perryman and Lynn (2002).

Necropsy length measurements (n=21) consisted of a straight-line distance from the tip of the snout to the fluke notch. The straight-line distance is usually measured by laying the tape measure on the beach parallel to the body, and measuring from the tip of the rostrum to the fluke notch. However, there is some degree of variation associated with the person making the measurement, and from the difficulty of placing the tape measure at the exact spot that is perpendicular to the rostrum tip and fluke notch. Necropsy measurements were adjusted to correct for the assumed effects of stretching (while animals were mechanically maneuvered on the beach) by subtracting 9% of the total body length for individuals that were hauled before they were measured. In the absence of pre-and post-hauling length measurements for North Atlantic right whales, I assumed that length was overestimated by 9% based on the finding by George (2004) that bowhead whales (*Balaena mysticetus*) stretched by this amount during the post-harvest hauling process.

2.3.2 Age

Lengths were available for calves of unknown ages (≤1y) and for juveniles and adults of known ages. I estimated the ages of the dead calves based on when they stranded and the estimated median date of birth for North Atlantic right whales, which I assumed was the median day of first sighting of 154 individual calves on the calving grounds off the southeastern United States using identification data from 1991–2007 (Right Whale Consortium 2010). All juveniles and adults were observed within their first year of life and were aged in decimal years using the assumed median birth date and the year and day they were measured. I compared calculated ages with length measurements for 78 females and 73 males (3 measurements were of unknown sex) and between datasets (133 photogrammetric and 21 necropsy measurements) to identify outliers or possible errors in measurements and estimates.

2.3.3 Growth Curves

I attempted to fit four commonly used growth functions to the length-at-age data. These included the Putter (Eq.1, von Bertalanffy 1938, Ricker 1979), von Bertalanffy (Eq.2, Ricker 1979, von Bertalanffy 1938), Gompertz (Eq.4, Zach *et al.* 1984, Gompertz 1825) and logistic equation (Eq. 4, Ricker 1979):

$$S_t = A(1 - e^{-k(t-t_0)}) \qquad \text{Eq. 1.}$$

$$S_t = A(1 - e^{-k(t-t_0)})^3 \qquad \text{Eq. 2.}$$

$$S_t = Ae^{-ce^{-kt}} \qquad \text{Eq. 3.}$$

$$S_t = \frac{A}{1 + e^{-k(t-t_0)}} \qquad \text{Eq. 4.}$$

where S is size at age t for males and females, A is asymptotic size, t_0 is time at which size is zero, c is the constant of integration (Zach et al. 1984) and k is indicative of growth rate (Ricker 1979). These parameters have slightly different properties between models, but are generally comparable within models.

I fit the growth models using a 2-phased approach with non-linear, least squares regression (nls package) in the statistical program R (R Development Core Team 2009), and was unable to apply non-linear mixed-effects models to the limited duplicate measurements (i.e., few animals were measured three times). Phase 1 represented calves that experienced a rapid growth period and Phase 2 represented both juvenile and adult animals that experienced decelerated growth. The inflection point between Phase 1 and Phase 2 was defined as the age at which the difference between the predicted length of the Phase 1 and Phase 2 models was zero. I used the Akaike information criterion (AIC) to measure the relative fit of each model and selected the model with the smallest AIC value as having the lowest relative expected Kullback-Leibler distance and maximized log-likelihood (Burnham & Anderson 2002). To account for repeated measures (i.e., some whales were seen in more than one year and were photogrammetrically measured as many as 3 times), I generated a set of 10,000 datasets from the 154 measurements with randomly selected duplicate length measurements removed. I then bootstrapped these samples with replacement and fit the growth function to the data. I extracted mean model parameters from the bootstrap replicates and defined these coefficients as the ‘best model’. I then generated confidence intervals by sorting the bootstrap replicates into 95% quartiles (by ordering bootstrap replicates into the 2.5% and 97.5% quartiles).

I tested for sexual dimorphism by comparing mean length-at-age measurements for males and females aged 9 to 22 years using a repeated measures analysis of variance (*ANOVA*). I then fit sex-specific growth curves to the data using the above methods.

2.3.4 Mass

Growth in mass-at-age was modeled using the allometric relationship of length and weight derived from dead whales (Table 2; Right Whale Consortium 2010, Moore et al. 2004) to predict mass-at-age from the length-at-age models. Body weights from the 15 individuals were collected by using either 1) a vessel travel lift while the animal was removed from the water, 2) individually weighing dismantled body parts (flesh and bones) and adding 6.8% to account for fluid loss (Lockyer 1976), or 3) weighing the individual at a weigh station on a flatbed truck (McLellan *et al.* 2002, Moore et al. 2004). Additionally, 16 length and weight measurements from North Pacific right whale (*Eubalaena japonica*) whaling records (Omura *et al.* 1969) were compared to the North Atlantic measurements for possible inclusion in length and weight models to increase the sample size.

Body mass was estimated using Schultz's (1938) allometric model to predict weight based on body length:

$$W = aL^b \qquad \text{Eq. 5.}$$

where W is weight in kilograms, L is length in centimeters, a is a constant factor and b is an exponential constant. This length and weight model may be expressed in its logarithmic form as:

$$\log_{10} W = b\log_{10} L + \log_{10} a \qquad \text{Eq. 6.}$$

I fit linear regressions to both North Atlantic and North Pacific right whale data. A two-tailed student's *t*-test (Zar 1996) compared the allometric regressions for North Atlantic and Pacific right whales by testing for significance in the difference of the slopes.

I generated weight-at-age estimates by substituting predicted lengths-at-age into the allometric model once I had solved for the a and b parameters. Uncertainty was incorporated into the weight-at-age estimates by first bootstrapping the allometric model and generating 10,000 fitted parameters, and then by using predicted length-at-age estimates from 10,000 bootstrap replicates.

2.3.5 Width

I used photogrammetric measurements of fluke and maximum body width to model the relationship between width and total body length. The analysis of fluke width included 130 measurements of both sexes of 83 unique individuals, and 94 measurements of 65 unique individuals for maximum body width. The relationship between width (maximum body and fluke width) and total body length was tested with linear mixed-effects models using the lme statistical package in R (R Development Core Team 2009) to address violations of independence (Pinheiro & Bates 2000). These models accounted for repeated measures and were fit by maximum likelihood (Pinheiro & Bates 2000). Multiple linear regressions were fit to the data to test for differences between sexes and age classes and were compared using *ANOVA*. Because body width is likely to be confounded by body length, I

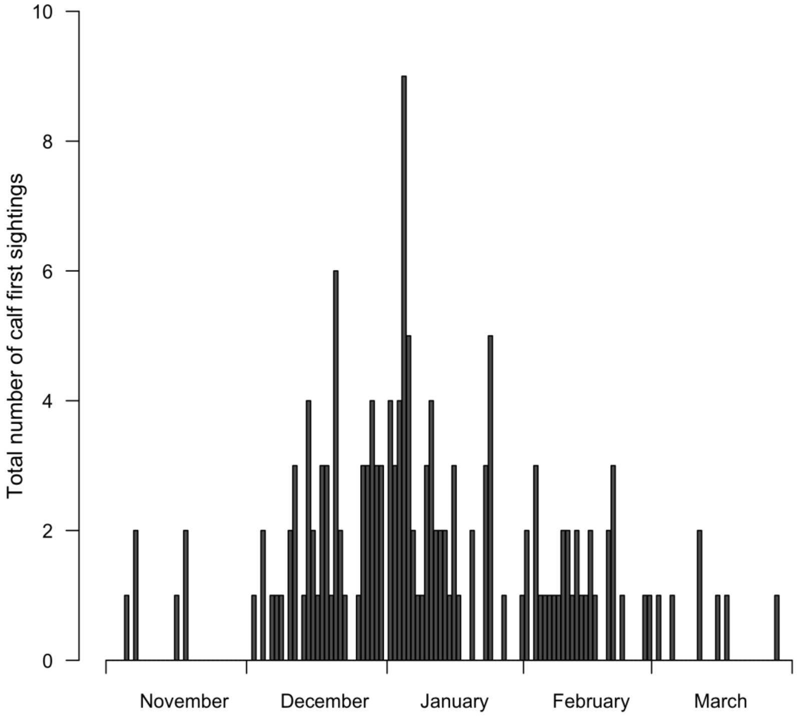

Figure 2-1. Frequency distribution of first sightings of uniquely identified North Atlantic right whale calves in the Southeast United States (Florida and Georgia) collected between November and March for 1991 to 2007. Each tick mark represents the first day of each month, and 5 January represents the median day of first sighting.

tested for significant adult width-to-length ratio differences between sexes using a repeated measures *ANOVA*.

2.4 Results

2.4.1 Age

Half of all North Atlantic right whale calves observed on the calving grounds during intensive aerial surveys (1991-2007) were seen for the first time by January 5 (Fig. 2-1). January 5 was also the day with the greatest number of first sightings—9 calves (Fig. 2-1). First sightings of right whale calves were most frequent between November and March, thereby suggesting that the estimated median birth date of January 5 had an associated uncertainty of approximately ± 2 months.

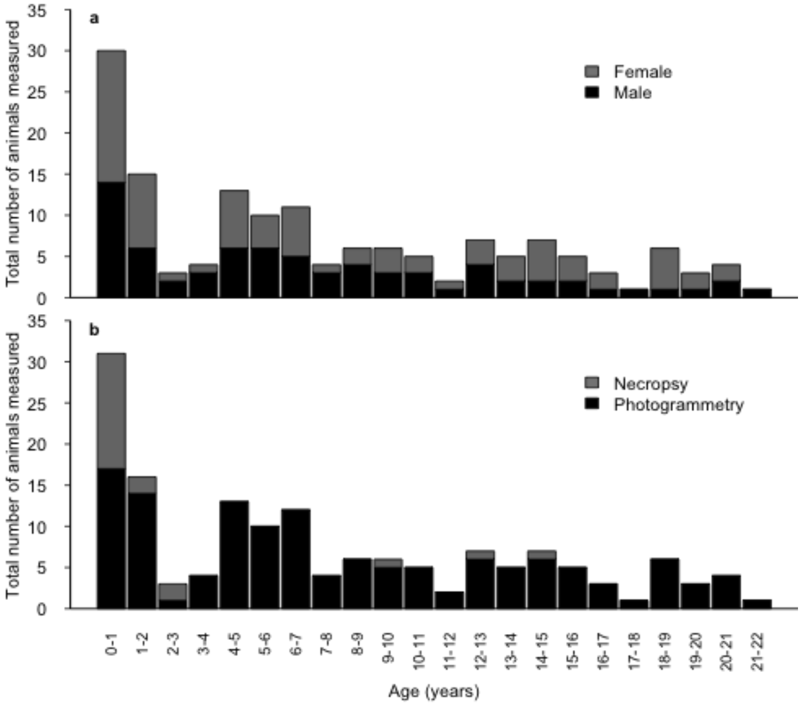

Figure 2-2. Age-frequency distributions of body lengths of North Atlantic right whales from the necropsy and photogrammetry databases categorized by a. sex and b. data type.

I used the January 5th birth date to estimate the decimal ages of all animals. Individuals less than 1 year old represented 25% of the total sampled body-length measurements (Fig. 2-2a), suggesting that the data were skewed towards immature animals. In comparison, 40% of female and 33% of male body-length measurements were from animals aged 9 –22 years old (Fig. 2-2a). As a general trend, the frequency of measurements decreased with age for both sexes. Comparisons of age-frequency data by category (Fig. 2-2b) also showed that the majority of necropsy measurements (67%) were from individuals aged 0–1 year, and that relatively few were from non-calves (33%).

2.4.2 Length

Of the four growth models I tested (Eqs. 1-4), the 2-phased Gompertz curve yielded the lowest AIC scores and was judged to be the best descriptor of growth for males and females combined (Fig. 2-3; Table 2-1). However, AIC scores for the von Bertalanffy model were considerably small as well. I ultimately selected the Gompetz model over the von Bertalanffy model for biological reasons because the Gompertz model accounts for somatic and reproductive development whereas the von Bertalanffy model assumes perfect allocation of resources and only accounts for somatic growth (Neuenhoff *et al.* 2011). The mean Gompertz model parameters derived from 10,000 bootstrap replicates for Phase 1 were 1082.04 ± 13.719 for A, 0.95 ± 0.096 for c, and -3.02 ± 0.280 for k. Phase 2 model coefficients were 1390.87 ± 30.737 for A, 0.33 ± 0.021 for c, and -0.13 ± 0.273 for k. Fitting two curves was the only way to account for the rapid growth of individuals between ages 0 and 1.05 years old (Phase 1; Fig. 2-3), and the decelerated growth of older animals (1.06-22.00 years old; Phase 2; Fig. 2-3). I found that calves gained an average of 621 cm (± 62 *SD*) from birth to weaning. This translates into 1.70 cm per day (± 0.17 *SD*), assuming a constant growth rate. Predicted asymptotic length (~95% of maximum length) occurred at ~12 years of age.

Length measurements differed significantly between adult males and females (repeated measures *ANOVA*, $F_{1,38}=13.22$, $P<0.001$). Mean lengths at sexual maturity were 1344 cm (± 61 *SD*) for females and 1287 cm (± 48 *SD*) for males, suggesting slight sexual dimorphism (females were 71 cm longer on average than males at maturity).

Table 2-1 2-phased parameter estimates (*A, k, c ,*t_o) (± SE) for growth models (Putter, von Bertalanffy, Gompertz and logistic; Eqs.1-4) where *A* is asymptotic size, *k* is indicative of growth rate, *c* is the constant of integration and t_0 is time at which size is zero. Length measurements were in cm and age was measured in decimal years. Model selection was conducted using the Akaike information criterion (AIC). AIC values are provided along with the difference in AIC values between fitted models, the likelihood of each model and the weight of each model (i.e., the weight of evidence in favor of each model). The model with the greatest weight was considered to be the "best" model.

Model	*a*	*k*	*c*	t_0	AIC Values	AIC Differences	Likelihoods	AIC Weights
Phase one:								
Putter	1658.98 ± 1246.921	0.74 ± 0.183	~	0.87 ± 1.171	357.839	0.536	0.765	0.282
von Bertalanffy	1277.00 ± 405.700	0.30 ± 0.063	~	1.83 ± 1.221	357.480	0.177	0.915	0.337
Gompertz	1193.13 ± 283.420	2.33 ± 1.252	-1.02 ± 0.195	~	357.303	0.000	1.000	0.368
Logistic	966.77 ± 70.157	~	~	4.44 ± 1.789	363.914	6.612	0.037	0.013
Phase two:								
Putter	1392.00 ± 32.35	0.29 ± 0.01	~	0.11 ± 0.02	1368.597	0.348	0.840	0.302
von Bertalanffy	1386.00 ± 29.57	0.10 ± 0.01	~	0.12 ± 0.03	1368.362	0.113	0.945	0.339
Gompertz	1382.87 ± 28.37	0.13 ± 0.03	-0.33 ± 0.02	~	1368.249	0.000	1.000	0.359
Logistic	1269.00 ± 9.45	~	~	0.79 ± 0.06	1461.731	93.481	0.000	0.000

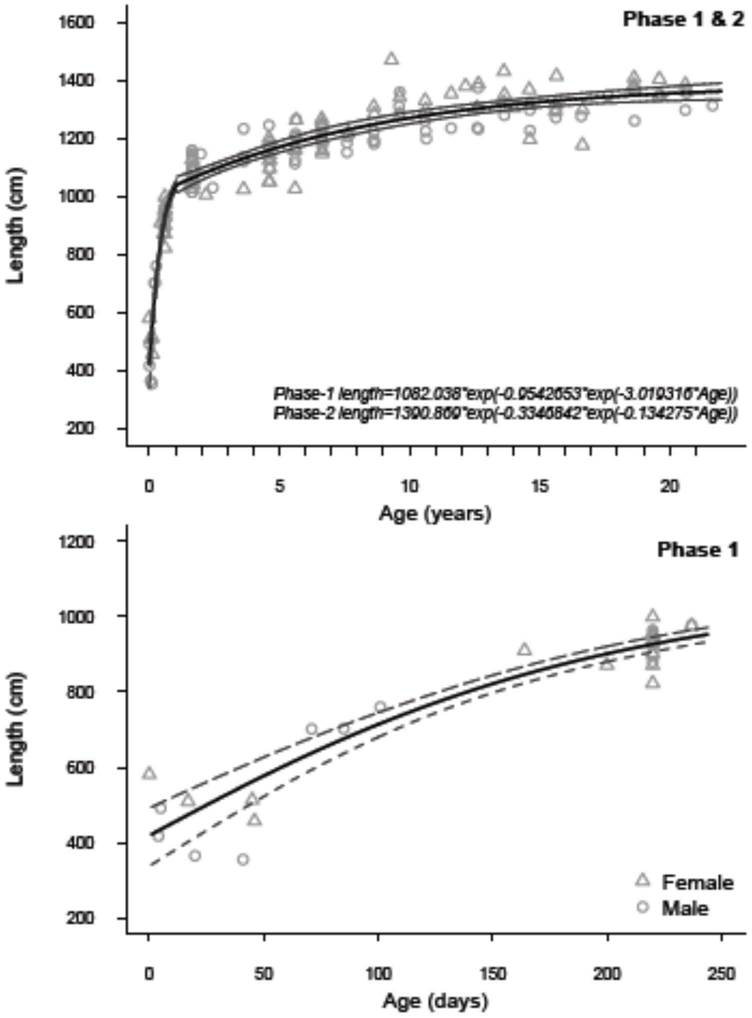

Figure 2-3. Mean two-phase Gompertz growth curve for North Atlantic right whales. Body lengths of necropsied individuals were corrected for potential stretching (~9% body length) and 95% confidence intervals (dashed lines) were derived from 10,000 bootstrap replicates (panel a). Mean Gompertz growth curve describing the growth of North Atlantic right whales during Phase-One. Necropsy measurements were corrected for stretching, and the 95% confidence intervals (dashed lines) were derived from 10,000 bootstrap replicates (panel b).

2.4.3 Mass

The weight-to-length relationship differed significantly between North Atlantic and Pacific right whales (*two-tailed t-test*, t_{28}= 3.04, P<0.01), and showed North Pacific right whales to be heavier for a given length than North Atlantic right whales (Fig. 2-4, Table 2-2). I thus only used North Atlantic right whale data to estimate weight-at-age. I was unable to make additional comparisons between the two right whale species due to small sample sizes and missing age information for North Pacific right whales.

North Atlantic right whale calves gained considerable mass during the 12 months that they were assumed to have nursed. Based on the growth curves, the average calf grew ~34 kg/day and had gained ~12.4 mt by the time it had weaned (based on the mean birth weight of 1101 ± 311 kg and mean weaning weight of 13460 ± 1848 kg; Table 2-3). Remarkably, calves were ~12 times their birth weight at the assumed onset of independence, and had attained ~40% of their weight at sexual maturity. However, mass accretion decelerated considerably between independence and sexual maturity (~2.8 kg/day).

2.4.4 Width

I found a positive, linear relationship between maximum body width and body length. The slope (*ANOVA*, $F_{1,28}$=319.30, P<0.001) and intercept (*ANOVA*, $F_{1,64}$=28007.69, P<0.001) were highly significant for the null model, where both sexes and all age classes were combined (Fig. 2-5). No significant differences were found between the null model and those that accounted for potential differences between sexes (*ANOVA*, $F_{1,63}$=0.002, P = 0.96) and age classes (*ANOVA*, $F_{2,24}$= 0.06, P=0.94). I thus pooled the data due to the similarity among all categories. Similarly, the slope (*ANOVA*, $F_{1,46}$=360.01, P<0.0001) and intercept (*ANOVA*, $F_{1,82}$=38201.77, P<0.0001) were significant for the fluke width and body length model (Fig. 2-5), and sex (*ANOVA*, $F_{2,80}$=2.86, P=0.06) and age-class (*ANOVA*, $F_{2,42}$=0.45, P=0.64) were found to be insignificant. Furthermore, the width-to-length ratio was not significantly different between sexes (repeated measures *ANOVA*, $F_{1,25}$=3.80, P=0.062).

Table 2-2. North Atlantic right whale necropsy and Pacific right whale whaling data used in allometric weight models. One case (no. 14) was excluded from analysis because the recorded values were estimates rather than direct measurements and were considerably lower than what would be predicted based on the individuals' age.

Species	Sex	Length (cm)	Weight (kg)	Case no.
Atlantic	U	600	700	14
Atlantic	F	455	1130	42
Atlantic	F	473	1134	29
Atlantic	F	478	1151	34
Atlantic	M	412	1227	21
Atlantic	M	495	1586	80
Atlantic	M	417	2000	40
Atlantic	M	581	2041	28
Atlantic	M	1030	9055	32
Atlantic	F	910	11045	49
Atlantic	F	1005	15000	26
Atlantic	F	1360	29700	27
Atlantic	F	1370	52640	44
Atlantic	M	365	749	73
Atlantic	F	1229	14785	45
Pacific	M	1470	52870	~
Pacific	M	1510	55250	~
Pacific	M	1520	48250	~
Pacific	M	1610	67770	~
Pacific	M	1640	78500	~
Pacific	M	1700	65760	~
Pacific	M	1710	67240	~
Pacific	M	1240	22250	~
Pacific	M	1710	63490	~
Pacific	F	1170	22870	~
Pacific	F	1630	58590	~
Pacific	F	1660	63130	~
Pacific	F	1710	63490	~
Pacific	F	1740	106500	~
Pacific	F	1260	28920	~
Pacific	M	1410	47560	~

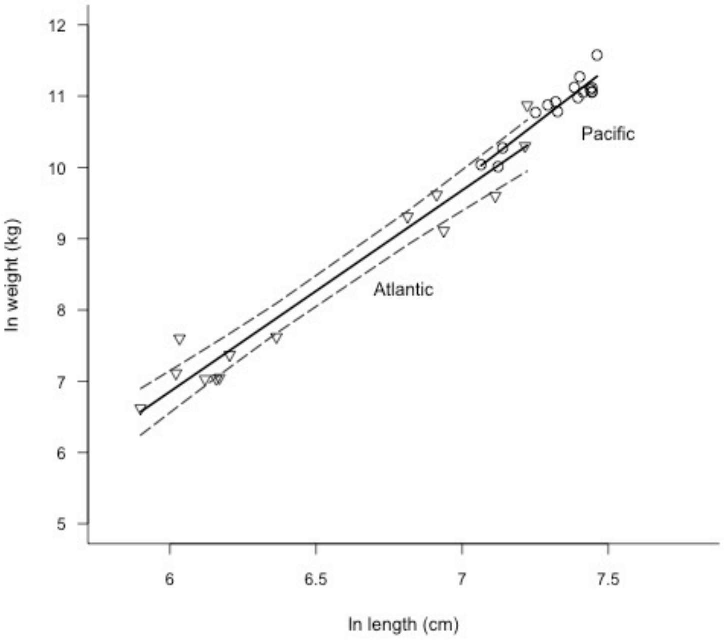

Figure 2-4. Mass – length relationships for North Atlantic (Δ) and North Pacific (o) right whale data. The logged data were fit separately with linear regressions: North Atlantic, y = -10.095x + 2.825, r^2=0.94, p<0.001; North Pacific, y = -12.286x + 3.158, r^2=0.88, p<0.001. Fitted parameters for North Atlantic (a= 0.000041298, b=2.825) and North Pacific (a=0.000004616, b=3.158) right whales were used to model mass.

Table 2-3. Predicted mean weight and length measurements (± *SD*) for North Atlantic right whales. Mean allometric model coefficients for Phase 2 growth were $a = -10.072 \pm 1.368$ and $b = 2.820 \pm 0.211$. Mean parameter estimates for Phase 1 were $a = -10.085 \pm 1.358$ and $b = 2.822 \pm 0.210$.

Age (years)	Weight (kg)	Length (cm)
0	1101 ± 311	422 ± 40
0.25	4332 ± 506	691 ± 18
0.5	8449 ± 996	876 ± 11
0.75	11582 ± 1510	978 ± 9
1	13460 ± 1848	1032 ± 9
2	15147 ± 2168	1076 ± 11
3	16577 ± 2445	1111 ± 9
4	17936 ± 2729	1142 ± 10
5	19213 ± 3005	1170 ± 10
6	20402 ± 3268	1195 ± 11
7	21501 ± 3513	1217 ± 11
8	22510 ± 3738	1237 ± 11
9	23430 ± 3943	1254 ± 11
10	24267 ± 4131	1270 ± 10
11	25025 ± 4301	1284 ± 10
12	25708 ± 4456	1296 ± 9
13	26324 ± 4598	1307 ± 9
14	26876 ± 4726	1316 ± 9
15	27372 ± 4844	1325 ± 9
16	27815 ± 4131	1332 ± 9
17	28212 ± 5051	1339 ± 10
18	28566 ± 5142	1345 ± 11
19	28882 ± 5225	1350 ± 12
20	29163 ± 5302	1354 ± 13
21	29415 ± 5372	1358 ± 14
22	29639 ± 5438	1362 ± 15

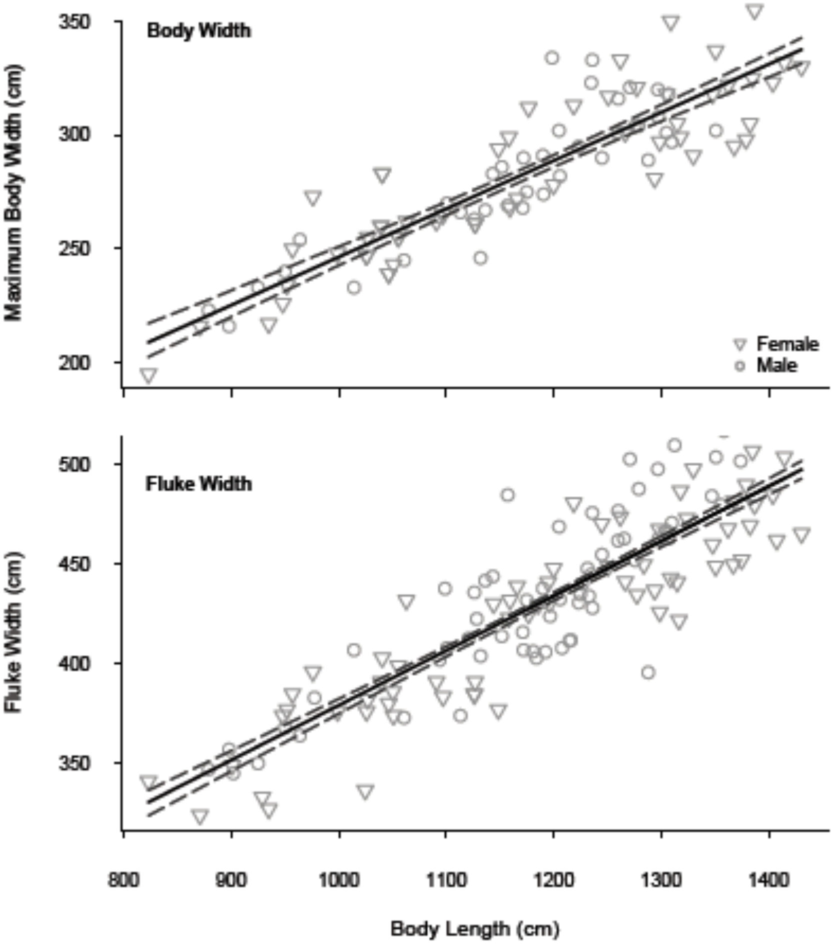

Figure 2-5. Linear mixed effects models fit to maximum body width, fluke width and length data for North Atlantic right whale calves, juveniles and adults of both sexes. 95% confidence intervals (dashed lines) were estimated by bootstrapping the residuals 1,000, times fit to width and length data for calves, juveniles and adults of both sexes. Body width is predicted by y=38.63194x+0.20826, $P=0.006$, and the fluke width is predicted by y=103.964x+0.28, $P<0.0001$ where x is body length in cm.

2.4.5 Data Error and Model Uncertainty

Combining morphometric measurements collected directly from a dead animal or indirectly using photogrammetry increased the sample sizes but could have introduced unintended errors that biased model predictions. Addressing uncertainty by examining necropsy and photogrammetry data for unusually large or small individuals resulted in removing 1 of 15 mass measurements from necropsied individuals (because it was incorrectly measured).

Measurement precision is nearly impossible to estimate for necropsied animals because individuals are generally only measured once while lying in a single position. However, precision can be estimated from photogrammetric measurements where three or more photographs were taken of the same individual. Multiple photogrammetric measurements from individual right whales taken between sampling years suggest that photogrammetry estimates have relatively small coefficients of variation whereby mean *CV* values for length are 0.0236 (range from 0.009-0.047), and 0.022 (0.007-0.0515) for fluke width. *CV* values were not calculable for body width because few duplicate measurements exist. Precision of the photogrammetric measurements are comparable to gray whale measurements, whereby *CV* values are 0.020 for body length, and 0.030 for fluke width (Perryman & Lynn 2002).

Body mass is far more difficult to measure than body length of large cetaceans. Consequently, wide confidence intervals resulting from a small sample size reduced the reliability of my mass estimate. Other studies, however, seem to ignore the uncertainty of length-at-age and weight-at-length predictions when generating confidence intervals for mass-at-age models and thus likely underestimate error in body mass predictions (e.g., Lockyer 1981b, George 2009). The inclusion of unhealthy animals (emaciated animals due to fishing gear entanglement and suckling calves in poor nutritive condition) may have also resulted in mass being underestimated relative to age. The growth curves likely underestimated body mass and should be refined as more data become available. Veterinarians wishing to apply the growth curves should adjust dose levels of antibiotics and sedatives for chronically entangled individuals that are likely to be underweight relative to their body length.

Body mass is also related to girth, and body width can be used as a proxy for girth. My maximum width analysis complements a detailed study of right whale dorsal body shape changes in relation to nutritional condition of North Atlantic right whale calves and mature females (Miller *et al.* 2012). However, I found no significant difference between the widths and width-to-length ratios of males and females, and therefore did not generate sex-specific mass estimates. This lack of difference in widths may reflect my small sample size, lower statistical power and the underrepresentation of pregnant females — therefore warranting further investigation into body width differences.

Errors in aging can also bias the descriptions of growth and are particularly challenging to estimate for large cetaceans. My median birth date method used to estimate age in decimal years introduced ± 0.16 years of uncertainty. Using measurements taken from identified individuals with a known birth year greatly reduced the uncertainty of my estimated ages. Growth studies of other species with unidentifiable individuals often use less accurate techniques to age individuals, such as using aspartic acid racemization (e.g., ± 6-35 years uncertainty in age) to age bowhead whales (George et al. 1999).

Unequal size representation within age classes may also have biased the length-at-age estimates, which were positively skewed towards animals between 0 and 1 year. Consequently, model uncertainty was greater in the juvenile and adult model. The lack of data for animals beyond 22 years limits the predictability of my model for older age classes (the oldest known North Atlantic right whale is just over 70 years old; Right Whale Consortium 2010). However, this is unlikely to have any meaningful consequence because the growth rate of adult animals is small and asymptotic length is likely achieved by ~12 years of age. Overall, I consider any biases in age estimation to be minimal, and have similar confidence in the estimates of body length.

2.5 Discussion

The large data set that resulted from combining measurements of dead and living whales revealed several interesting aspects about right whale growth. Most notably, the morphological measurements showed that right whale calves grow extremely fast compared to other cetacean species as they attain over three-quarters of their asymptotic size upon weaning. Furthermore, the growth rate decreased sharply following the onset of independence.

2.5.1 Single vs. 2-Phased Growth

Commonly used continuous growth equations yielded poor model fits because the growth rates of young right whales differed markedly before and after weaning. Had I fit a continuous growth function, I would have overestimated juvenile growth and underestimated the asymptotic length of adults. Growth functions (Eqs. 1-4) commonly used to describe increases in animal lengths and masses were developed for fish and other species that have different life history strategies and growth patterns. All growth functions have fixed inflection points that are a proportion of adult length (Ricker 1979) which when fit to the right whale data would have resulted in calves reaching the point of inflection at ~37 % of their maximum adult length prenatally. However, right whale calves are only ~31% of their maximum length at birth. Applying a continuous Gompertz model would have incorrectly assumed that a larger proportion of growth was achieved prenatally.

To my knowledge, baleen whale growth has never been described using this 2-phased approach. However, there is evidence that cetacean growth in general is poorly described by continuous functions and that applying single-equation growth models may result in poor model predictions and confound interspecies comparisons. Dolphin and porpoise growth, for example, appears to slow after weaning and increase near sexual maturation, and has been mathematically described using 2-phased Laird's models to account for secondary growth spurts (Danil & Chivers 2007, Larese & Chivers 2009, Perrin et al. 1976). Consequently, future cetacean growth studies should consider using 2-phased models instead of continuous growth functions.

2.5.2 Calf Growth

Overall, the 2-phased model captured the precocious exponential growth of calves. Applying the 2-phased growth model showed that right whales more than double in length and are ~12 times heavier upon weaning. Furthermore, right whales are predicted to be 422 ± 40 cm at birth, which is similar to the mean length of perinatal (near-birth) animals measured in the field (i.e., 446 ± 31 cm, n=3). By the time they wean at 1 year, right whales are 1032 ± 9 cm long and 76% of their asymptotic length. However, in terms of weaned mass, yearlings attain a mere 47% of their asymptotic mass suggesting that a large increase in mass occurs later in life.

The rapid growth of dependent young is consistent with what has been described for other baleen species. For example, the daily growth rate of nursing blue (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) was estimated to be 3.45 cm, and 2.40 cm (over a 7 month nursing period; Lockyer 1981b). However, North Atlantic right whales attain a greater proportion of their maximum size at weaning (~76%) compared to the ~70% attained by blue and fin whales (estimated from Lockyer 1981b). Furthermore, right whales grow an average of ~ 2.6 cm per day when only the first 7 months of nursing are considered. Some of the apparent difference been calf growth rates of blue, fin and right whale species may be explained by the duration of the lactation period (which is 5 months longer for right whales) and length-based whaling regulations that may have led to falsified measurements such as these that were made on whaling vessels (Gilpatrick & Perryman 2008). However, neither possibility of erroneous measurements or different ages at weaning negates the fact that baleen whales appear to employ a similar growth strategy that invests heavily in the physical development of calves.

The length-at-age model predicts that North Atlantic right whale calves grow faster than the closely related bowhead whale. Although both species have a similar weaning age of

12 months (Nerini *et al.* 1984), bowhead whale calves gain a mere 1.1 cm per day while nursing (George 2009), which is slower than the estimate for right whales (at 1.7 cm per day). Furthermore, bowhead calves attain a smaller proportion of their maximum body length after 1 year (52%, estimated from George 2009) compared to 76% for right whales. This faster postnatal growth suggests that right whales may be more precocial than bowheads and that maternal investment is likely greater for right whales (Pontier *et al.* 1993, Gaillard *et al.* 1997).

2.5.3 Juvenile and Adult Growth Model

The 2-phased model shows an apparent pause or deceleration of growth at weaning. This decreased growth rate of yearlings corresponds with the 12-month nursing period, and may reflect reduced energy acquisition during the transition from dependency to independency. Although uncertainty exists in the age of weaning (age of weaning has varied from 8 months to >12 months), 12 months appears to be the most reasonable estimate given visual observations of mother-calf association times (Hamilton *et al.* 1995, Hamilton & Cooper 2010). Whether the reduced growth reflects decreased caloric intake associated with the transition from milk to zooplankton or foraging inexperience is unknown. However, delayed growth at weaning is consistent with current understanding of North Atlantic right whale life history and also agrees with what has been reported for other precocious mammals, including other cetacean species (e.g., Lockyer 1981b).

North Atlantic right whale growth slowed markedly after sexual maturity. My growth model shows that right whales attain ~92% of their maximum length at the mean age at sexual maturation (mean age = 9 year and range = 5-21 year) and ~95% at 12 years. However, cetaceans are generally thought to reach sexual maturity after attaining 86% of their maximum length (Laws 1956), which would have occurred for right whales when 5 years old. The early attainment of maximum length agrees with observations of first parturition in females beginning as early as 5 years (Kraus et al. 2007), and supports the hypothesis of Browning et al. (2010) that extended age at which right whales are believed to first give birth may simply be a function of reproductive dysfunction (i.e., undetected perinatal and neonatal mortality). The adult and juvenile growth model is thus consistent with the current understanding of right whale reproduction and conforms to assumptions about the importance of size in determining the age of first parturition.

Counter to expectations, the growth models did not detect a statistical difference in the growth rates of male and female right whales, although mean lengths of adult females (≥ 9 years old) were significantly greater than those of males (by ~4% on average). Although slight sexual dimorphism was detected in mean lengths, small sample sizes may have prevented differentiating sex-specific growth curves. The difference between mean lengths of adults was consistent with what has been observed for other baleen species (e.g., George et al. 1999, Lockyer 1981b). Greater female size may equate with greater energy reserves that could increase reproductive fitness by partially offsetting the physiological costs of reproduction and reducing offspring mortality (Gittleman & Thompson 1988, Gordon 1989, Blanckenhorn 2005).

2.5.4 Why Rapid Calf Growth?

The rapid growth of calves implies that females invest heavily in the growth of their offspring (Hall *et al.* 2001, Huang *et al.* 2009, McMahon *et al.* 2000). North Atlantic right whales provision their young using energy from stored blubber, and are known to have significantly more blubber than other species (Lockyer 1976). Right whales are thus only likely to be able to meet the high costs of lactation by catabolizing their stored lipid. Trade-offs between maternal investment, offspring mortality and adult survival expectancy are common among mammals (Oftedal 1997, Gittleman & Thompson 1988, Huang et al. 2009, Gordon 1989, Pontier et al. 1993, Glazier 1999). Consequently, the potential benefits of rapid postnatal growth in right whales may include reduced starvation and predation of offspring, and improved foraging efficiency and reproductive fitness of progeny.

Right whale mothers may disproportionately transfer energy to maximize the body condition, growth and survival of their offspring. Such a strategy could offset the challenges that an otherwise recently weaned and inexperienced right whale calf would have in locating sufficient prey patches, which are highly spatially and temporally variable (Baumgartner & Mate 2003, Hlista *et al.* 2009, Jiang *et al.* 2007, Baumgartner *et al.* 2003b, Greene et al. 2003, DeLorenzo Costa *et al.* 2006b, Greene & Pershing 2000, Kenney 2001). Yearlings are known to catabolize a significant proportion of their energy stores shortly after independence (1.7 cm reduction in blubber from calf to yearling; Miller et al. 2011), and are known to be significantly thinner during years of low prey availability compared to years of improved prey availability (Miller et al. 2011). Rapid growth while nursing may thus be an evolutionary adaptation to maximize an offspring's energy stores and enable inexperienced yearlings to better cope with nutritional stress and the ephemeral nature of their prey.

Fast postnatal growth may also optimize foraging success by maximizing baleen development and mouth size. In other words, right whales may need to attain a critical size at weaning if they are to optimally feed. Morphological studies have found that cetaceans invest the greatest growth in expansion of the head and that larger jaws can accommodate a bigger feeding apparatus (Armfield *et al.* 2011, Lockyer 1981b). This pattern of growth may thus reflect the high energy needs of independent whales (Lockyer 1981b). Furthermore, baleen growth is rapid during the first year of life and slows during adulthood for bowhead whales (George 2009). Although little is known about North Atlantic right whale baleen and head development in relation to body length, it is possible that rapid growth maximizes the efficiency of the filter-feeding apparatus to capture prey. Rapid growth may thus be used to improve offspring foraging efficiency and survival.

Increased body size at time of weaning may also reduce the probability of being eaten by a killer whale (*Orcinus orca*) or white shark (*Carcharodon carcharias*) (Huang *et al.* 2011). Right whales are thought to employ active physical defense while in the presence of predators because they are slow swimmers and are unable to flee their predator (Ford & Reeves 2008). As such, right whales have evolved to fight with their strong tailstock and dry accretions of dead skin (callosities) (Ford & Reeves 2008). Killer whale predation, however, does not appear to be a significant threat to the population today as only 9% of North Atlantic right whales have scars from predatory attacks from killer whales and few attacks have been confirmed (Kraus 1990, Hamilton & Knowlton 2010). However, recent observations of white shark attacks on right whale calves have been made (Hamilton &

Knowlton 2010). Thus the evolutionary presence of predators may be enough to warrant such adaptations (Sih 1985, Ford & Reeves 2008, Lima & Dill 1990, Lima 1998).

The heavy investment made by lactating females may increase the probability of their offspring reproducing at younger ages (i.e., increased reproductive fitness; Read & Gaskin 1990, Lockyer 1981b) given that faster growing mammals mature earlier than slower growing species (Ferrero & Walker 1999, Greene & Rothstein 1991). This is consistent with North Atlantic right whales attaining a comparatively larger size at weaning and a younger age at maturity compared with bowhead whales (George 2009). High maternal investment may therefore maximize fitness by optimizing the size at weaning, juvenile survival rate and lowering the age of first birth (Pontier et al. 1993).

Adults may exhibit a reduced lifespan through long-lasting phenotypic effects (Metcalfe & Monaghan 2003) as a consequence of rapid postnatal growth. Reduced life spans may result from increased investment in growth and decreased investment in prevention or repair of molecular damage (Metcalfe & Monaghan 2003, Cichon 1997). However, little is known about the longevity of right whales (Hamilton *et al.* 1998). Calves may thus undergo rapid growth while nursing to minimize the time to reach sexual maturity, but adults may incur long-term consequences.

The reproductive rate of North Atlantic right whales may be adversely affected by the high maternal investment required to support rapid postnatal growth. Mammals with rapid growth trajectories are often not food limited. However, they are susceptible to starvation during food shortages (Metcalfe & Monaghan 2003, Blanckenhorn 2000). Species that undergo rapid growth are generally considered to have high metabolic rates and are poorly equipped to adapt to prey shortages (Arendt 1997). Birth rates of right whales are known to fluctuate wildly from one year to the next (from 1 to 39 calves born per year; Kraus et al. 2007, Waring et al. 2011), and have been correlated with oceanographic anomalies thought to influence the quality and quantity of prey (Greene & Pershing 2004, Hlista et al. 2009). This suggests that reproductively mature females may forgo reproduction during years of sparse prey abundance because they cannot meet the rapid postnatal growth strategy. In this way, females may have evolved to physiologically select offspring quality over quantity (Greene & Rothstein 1991).

2.6 Conclusions

North Atlantic right whales employ a growth strategy that favors rapid development of dependent animals and decelerated growth of larger juveniles. Such a growth trajectory does not conform to continuous growth functions, and is mathematically best described using a 2-phased approach. Rapid growth may increase reproductive fitness by maximizing foraging efficiency and minimizing predation risk at the time of weaning, and could result in right whales reaching sexual maturity at younger ages than other species of baleen whales. However, this growth strategy likely comes at a cost (i.e., variability in calving interval). The possible costs and benefits of mothers investing so heavily in the growth of their calves have significant implications for the ecology, population dynamics and management of North Atlantic right whales.

Chapter 3: North Atlantic Right Whale Energetics

3.1 Summary

Management plans for North Atlantic right whales (*Eubalaena glacialis*) focus on preventing mortality from ship strikes and fishing gear entanglement. However, recovery may also be limited by nutritional stress. I quantified the food requirements of North Atlantic right whales by age, sex and reproductive state—and compared their predicted needs with field estimates of prey consumption to assess whether any demographic group of right whales might be nutritionally stressed. Energy requirements were estimated using a bioenergetics model that accounted for uncertainty in energy inputs and outputs—and consumption was estimated with prey samples taken near feeding whales in Cape Cod Bay (n=28 net collections) and the Bay of Fundy (n=19 optical plankton recordings). I found that calves required the least energy (~1129 MJ/day) and that lactating females required the most (~2934 MJ/day). Juveniles required considerably more energy then adult males and non-reproductive females ~1200 MJ/day. My estimates of energy requirements for juveniles, adult males (~1140 MJ/day), and non-reproductive females (~1217 MJ/day) compared favorably with estimates of actual consumption in their winter habitat (i.e., they differed by ≤15%), suggesting that my model was reliable. However, lactating females appear to obtain considerably less than their predicted energy requirements in Cape Cod Bay (i.e., they obtain ~45% of daily needs), and almost met their needs in the Bay of Fundy (obtaining ~87% of daily requirements). This suggests that lactating females may be experiencing an energy deficit, which may affect reproductive rates and slow population recovery. Nutritional stress may thus be limiting the recovery of North Atlantic right whales.

3.2 Introduction

Anthropogenic mortality from ship strikes and entanglement in fishing gear is widely believed to be delaying the recovery of North Atlantic right whales (*Eubalaena glacialis*) (Caswell et al. 1999). However, such direct anthropogenic mortality may not be the only factor slowing the recovery of right whales (Fujiwara & Caswell 2001, Knowlton et al.

1994). Recent studies have found biotoxins, contaminants, and parasites in right whale blubber and feces (Rolland *et al.* 2007b), which could compromise reproduction. There is also mounting evidence that the North Atlantic population might also be experiencing periods of prey shortage, which could similarly impair calving rates (Reeves et al. 2001, Pettis et al. 2004, Greene & Pershing 2004). Significantly fewer calves were observed between 1993-1995 and 1998-2000, when decreases in prey availability were detected, than would have been expected by chance alone (Kraus et al. 2007, Greene & Pershing 2004).

North Atlantic right whales exhibited signs suggestive of pronounced periods of physiological stress and poor overall health during the late 1990's. While residing in the Bay of Fundy (Canadian feeding ground), they appeared thin and had various forms of skin lesions on their bodies (Pettis et al. 2004). They also had longer intervals than usual between births, and consequently had low reproductive rates (Kraus et al. 2007). Such negative physiological states are consistent with nutritional stress (e.g., Lockyer 2007, Trites & Donnelly 2003, King & Murphy 1985, Lockyer 1986), and might reflect the apparent scarcity of their primary prey during the 1990s (Greene & Pershing 2000, Greene & Pershing 2004). These negative changes during the late 1990's were relatively short lived, and suggest that North Atlantic right whales periodically experience times when they are unable to meet their daily energy needs. Future oscillations in the environmental conditions thought to affect the quality and quantity of right whale prey are expected to increase with greater frequency in parallel with increases in greenhouse gas emissions (Greene & Pershing 2004), which may adversely affect the recovery of the species.

Determining the conditions under which right whales might be nutritionally compromised requires knowing how much food they need and how much they consume. Estimates of energetic consumption can be obtained by observing foraging times and by collecting prey samples near feeding whales — but estimating how much food large whales require is more difficult. For most small species, energy needs can be estimated using well-established captive (e.g. respirometry) and field study techniques (e.g. doubly-labeled water and overall dynamic body acceleration). Data derived from wild studies are often limited to a few demographic groups and a small number of individual measurements. Furthermore, wild studies only provide a single estimate of field metabolic rate relative to a specific set of environmental conditions. However, for a large whale that cannot be kept in captivity, and cannot be physically restrained in the wild or monitored using invasive tags, mathematical modeling can be used to estimate energy needs (Winship *et al.* 2002, Williams et al. 2011, Kenney *et al.* 1986, Lockyer 1981b, Noren 2011).

Only one quantitative bioenergetics model has been constructed to date to estimate the daily food requirements of North Atlantic right whales. This model (Kenney et al. 1986) was parameterized using estimates for average body mass, metabolic rate, assimilation efficiency, time spent feeding, mouth size and swimming speed. An underlying assumption of this model was that the food requirements of North Atlantic right whales could be determined for an average whale and extrapolated to the entire population without accounting for the needs of different sexes, age-classes and reproductive states. Thus, this model did not account for the significant age-specific costs of basal metabolism, activity and feeding rates. Kenney et al. (1986) provided the first quantitative estimate of food requirements, but would benefit from expansion to account for the costs of growth and reproduction, and the age and sex-specific energy needs of the population.

The response of individual animals to changes in the quality and quantity of prey available to them will differ between young and old, pregnant and non-pregnant, and lactating and non-lactating whales. This in turn will, in part, determine whether the overall population will increase, remain stable or decline. In terms of nutrition, species recovery is probably most tightly tied to the nutritional condition of sexually mature females who bear the costs of pregnancy and lactation, and may forgo reproduction to conserve energy during lean years (e.g. Miller et al. 2011, Lockyer 2007, Lockyer 1986). Recovery is also likely tied to the ability of the newly independent and relatively inexperienced juveniles to survive by finding sufficient prey to meet their daily needs. Thus, determining the food requirements of different age-classes, sexes and reproductive states is essential for assessing the nutritional status of the species relative to their potential recovery.

In this study, I predicted the food requirements of different demographic groups of North Atlantic right whales using a generalized bioenergetics model that was parameterized using current information about right whale growth, body composition, digestive efficiency, metabolism, and costs of activity. I incorporated uncertainty into each model parameter and ran a sensitivity analysis to assess the reliability of the model predictions. I then estimated the amount of food North Atlantic right whales actually consumed using observations of feeding behaviour and the energy density of prey sampled in two critical habitats (Bay of Fundy and Cape Cod Bay). Finally, I compared the predicted energy needs of different demographic groups of right whales with the observed amounts of prey consumed in the two habitats to evaluate the model predictions. Model error or an energy imbalance was assumed to occur if the model predictions greatly exceeded the field observations.

3.3 Materials and Methods

3.3.1 Bioenergetics Model

The bioenergetics model for right whales was essentially a simple energy balance equation that was parameterized using both pre-existing species-specific data and estimates to express how gross energy translates into metabolizable energy (e.g., remaining energy after fecal and urinary energy loss), and how it is partitioned among various aspects of production (e.g., growth and reproductive costs) and maintenance parameters (e.g., basal metabolism and costs of locomotion). Parameter values for each demographic group of right whales in the model were not deterministic, but were chosen from distributions of possible values by incorporating uncertainty into each model parameter using Monte Carlo methods that randomly drew values based on probability distributions of each parameter (i.e., normal, uniform, triangular, gamma). This meant that I generated thousands of possible estimates of the daily energy needs for each demographic group of North Atlantic right whales—from which I calculated a mean estimate of energy requirements and standard deviation. This Monte Carlo modeling approach also allowed me to assess the relative influence and uncertainty of each parameter group (metabolism, growth, digestion, fasting and reproduction) on the model outputs.

I calculated mean daily gross energy requirements (*GER*) by sex for three age classes (calf, 0 to 1 years; juvenile, >1 and <9 years; and adult, >9 years) (Hamilton et al. 1998), and for three reproductive states of adult females (pregnant, lactating and resting) using:

$$GER = \frac{\left(\left(\frac{P + (A \times BM)}{E_{HIF} \times E_{F+U}}\right) + R_{G+L}\right) \times 365}{365 - (T_m + T_r)} \qquad \text{Eq. 1}$$

where *GER* is gross energy requirement parameterized by sex, age and reproductive class, and E_{F+U} is fecal and urinary digestive efficiency, E_{HIF} is the efficiency with which metabolizable energy is used (or 1 minus the heat increment of feeding as a proportion of metabolizable energy), *P* is production or energy deposition, *BM* is basal metabolism (or resting metabolism for actively growing and reproductive animals) and *A* is an activity multiplier (Winship et al. 2002). R_{G+L} is the cost of gestation and lactation individually. T_m and T_r capture the time in days individuals spend fasting while residing in the southern calving grounds and while migrating north to the foraging grounds.

To estimate the basic daily energy needs of North Atlantic right whales, and assess whether different demographic groups may be able to meet their energetic needs, I also predicted mean daily *GER* without accounting for the energetic cost of fasting for different demographic groups.

3.3.2 Model Parameters

I estimated digestive efficiency (E_{F+U}) by incorporating existing values of fecal efficiency and predicted values of urinary digestive efficiency. I first assumed that the digestive efficiency of right whales varied according to the species and life-stages of calanoid copepods consumed given that the amount of digestible material (i.e., wax esters) fluctuates between life stages. It was previously estimated that 6% of ingested energy (Swaim *et al.* 2009) would be lost through feces when a right whale consumes an exclusive diet of stage 5 (CV) *Calanus finmarchicus,* which is their primary prey (Mayo & Marx 1990, Baumgartner *et al.* 2003a, Baumgartner et al. 2003b, Beardsley *et al.* 1996). Energy loss through urine is unknown, but is presumably proportional to the nitrogen content of prey (Worthy 1990). I thus assumed that ~8% of ingested energy was lost through urine (based on a mixed diet of all life stages of *Calanus finmarchicus*, *Centropages hamatus* and *typicus* and *Pseudocalanus* spp). I accounted for energy lost from consuming a mixed diet because these are the primary prey consumed in Cape Cod Bay (Mayo & Marx 1990, DeLorenzo Costa *et al.* 2006a). Making these assumptions yielded a combined fecal and urinary loss of 14% (or a digestive efficiency of ~86%) for a mixed diet, but a combined loss of ~26% (digestive efficiency of 74%) if the diet consists only of CV *Calanus finmarchicus.*

Ingested energy is also lost through the heat increment of feeding (E_{HIF}) which represents an increase in heat production associated with digesting food (Smith *et al.* 1978). As much as 10-15% of energy ingested by pinnipeds may be expended during the digestion process (Costa & Williams 1999, Markussen *et al.* 1994), but information on cetacean heat increment of feeding is unavailable (Worthy 1990). Assuming that the heat increment of feeding is partially dictated by nutritional state (Winship et al. 2002, Rosen & Trites 1999, Ryg & ØRitsland 1991), I estimated the efficiency of utilization of metabolizable energy (E_{HIF}) (1-heat increment of feeding) for right whales using normally distributed values derived for Steller sea lions for the energetic costs of digestion associated with maintenance and growth (protein and lipid) (Rosen & Trites 1999, Winship et al. 2002), and assigned the maintenance E_{HIF} parameter to adult right whales, and the weighted proportions of protein and lipid E_{HIF} to juveniles and calves based on the percentage of fat and protein reported for these age classes in commercial whaling data (Lockyer *et al.* 1985, Lockyer 1976) (Tables 3-1 and 3-2). E_{HIF} parameter estimates thus include the inefficiencies of lipid and protein anabolism.

Table 3-1. Digestive efficiency estimates that correspond to maintenance and growth estimates from Winship *et al.* (2002) used to approximate E_{HIF} for right whale calves, juveniles and adults.

	Low	High	Mean	*SD*
Maintenance	0.850	0.900	0.875	0.035
Growth - Fat	0.750	0.950	0.850	0.141
Growth - Protein	0.450	0.560	0.505	0.077

Table 3-2. E_{HIF} values generated according to demographic unit by running 500 Monte Carlo simulations (randomly selecting a parameter value from a normal distribution) (E_{HIF} *Mean* ± *SD*) (Table 3-1).

	Fat	Protein	E_{HIF} Mean	*SD*
Calves	0.210	0.346	0.741	0.042
Juveniles	0.396	0.347	0.739	0.064
Adults	~	~	0.875	0.036

Production costs (*P*) were estimated using growth curves to calculate the increase of body mass from one age to the next, and also included corresponding information about the body composition of each age group. I estimated mass-at-age by first predicting length-at-age using a two-phased Gompertz growth model and then using an allometric weight-at-length model (Chapter 2). I estimated the energetic cost of growth for each age class with growth data for individuals aged 0-22 years using the following (Winship et al. 2002):

$$P = \Delta M \times \left[(plip \times EDlip) + (1 - plip)(1 - pw) \times EDpro \right] \qquad \text{Eq.2}$$

where *P* is production (kJ), Δ*M* is the body mass growth increment (kg), *plip* is the proportion of new body mass that is lipid, *EDlip* is the energetic density of lipid (39330 kJ/kg; Schmidt-Nielsen 1990), *pw* is the proportion of lean tissue that is water, and *EDpro* is the energetic density of protein (17991 kJ/kg; Schmidt-Nielsen 1990, Winship et al. 2002). I assumed that body mass was either lipid or lean tissue, and that lean tissue was either protein or water (Winship et al. 2002). The proportion of total body mass that is blubber varied with age and the proportion of lipid in blubber was 90% for all groups (Weisbrod et al. 2000). Whaling data from other baleen whales provided estimates for the proportion lean tissue that was protein and the proportion of lean tissue that was water (Lockyer et al. 1985).

I estimated basal metabolic rate using an allometric model because it has never been directly measured for right whales. The model I used,

$$Q = 292.88M^{0.75} \qquad \text{Eq.3}$$

was derived from captive studies of terrestrial mammals, where the basal metabolism (Q) is kJ per day and M is body mass in kg (Kleiber 1975, Lockyer 2007). I allowed Q to vary by

drawing estimates of body mass from a distribution of possible values for each age class (from within the 95% confidence limits of the growth curves derived for right whales in Chapter 2).

This general relationship between body mass and metabolism has been broadly used to describe the basal metabolic rate of various species of baleen whales (e.g. Lockyer 2007). Although marine mammals are generally believed to have an elevated metabolic rate compared to terrestrial animals of a similar size (e.g., Irving *et al.* 1935, Scholander *et al.* 1942), the basal metabolic rate of the closely related bowhead whale is estimated to only be about one-third of that predicted by Kleiber using a heat-flux model (George 2009). This low metabolic rate might reflect having a disproportionately greater amount of fat (similar to bowheads) and a low relative proportion of bone and adipose tissue compared to lean tissue (Kleiber 1975, Costa & Williams 1999). Given the uncertainty in whether the basal metabolic rate of North Atlantic right whales is higher or lower than Kleiber, I chose to assume that basal metabolism was best described using Kleiber's equation.

I accounted for the elevated metabolic rate of immature animals that are actively growing (e.g. Worthy 1990, Brody 1945, Hansen *et al.* 1994, Worthy 1987) by multiplying the *BM* of calves by 1.4 and the *BM* of juveniles by 1.2 (decreased *BM* scalar because rate of growth in mass is ~50% less that of calves). Although the scalars were less than twice Kleiber (which is a common assumption), the multiplicative effects of the costs of activity ultimately elevated the metabolic rate to ~1.8 times Kleiber.

Costs of activity were estimated by combining information about the daily activity budget of right whales with the physical forces they need to exert to overcome the swimming drag associated with undertaking each of the dominant behaviours. I began by assuming a simplified activity budget whereby individuals partitioned their time into only feeding and traveling, and incorporated the costs of these activities using a metabolic scalar. I then used activity specific drag coefficients to estimate the costs (*A*) associated with each behaviour (McGregor 2010) and the proportion of time that individuals spent per day engaged in each behaviour (*P*):

$$A = P_{travel} \times A_{travel} + (1 - P_{travel}) \times A_{forage} \quad \text{Eq. 4.}$$

For pregnant females, I increased costs by 3-4% to account for increased drag (McGregor 2010). I also incorporated uncertainty into all parameters in Eq. 4 by varying the proportion of time individuals spent foraging (52-93%), assuming that whales were merely traveling when they were not foraging (Goodyear 1996).

The foraging season of mysticete whales is highly seasonal compared to odontocetes that forage almost continuously throughout the year. I assumed that fasting occurred while individuals were traveling from their calving grounds in the southeastern United States (Florida and Georgia) and while they occupied these calving grounds. I used the North Atlantic Right Whale Consortium Identification Database to estimate the minimum residency time for all demographic groups on the calving grounds by subtracting the first day an individual was observed in the habitat from the last day observed (Right Whale Consortium 2010). I used migration times of 24-26 days (Firestone *et al.* 2008) and assumed that lactating females spent a minimum of 7 days on the calving grounds and excluded any estimates below this threshold. I incorporated the estimates of fasting into the bioenergetics model by reducing the total number of days available for foraging per year (365 days – number of fasting days). To include uncertainty in the predictions, I assumed that the migration parameter had a normal distribution for all demographic groups and that the probability distribution for the residency parameter varied among demographic groups (normal and gamma).

Costs of gestation for mammals in general are commonly estimated by modeling fetal growth. Unfortunately, I had to rely on allometric models because fetal data are too sparse to directly model fetal growth (mass) of North Atlantic right whales. I used two methods to estimate the costs of gestation. First I calculated the heat of gestation, which required calf mass measurements and was estimated using:

$$QG = 18,421.9M^{1.2} \qquad \text{Eq. 5.}$$

where QG is in kJ and M is the mass of the fetus in kg (Brody 1968, Lockyer 2007). This method includes the energy expense of maintaining the pregnant uterus, work of fetal and maternal growth of pregnancy and the increased work of the maternal physiological load (e.g. circulation, excretion, respiration, maternal hormone influences of pregnancy and fetal metabolism) (Lockyer 2007). I also assumed that the cost of pregnancy was equivalent to ~1% of the adult female's basal metabolic cost (Blueweiss *et al.* 1978, Michaud 2005). Employing both methods enabled me to incorporate uncertainty into the model predictions.

I incorporated information about calf energy needs and estimates of female milk production to account for the elevated costs of lactation. First, I added the daily *GER* estimate for the calf to the daily *GER* estimate for the lactating female assuming 90% efficiency of energy transfer between the mother and offspring (resulted in lactating females providing 110% of the predicted energy needs of the calf) (Lockyer 1981b). I then estimated the energetic cost of lactation by accounting for the quantity of milk produced, the duration of the nursing period and the caloric content of milk (Lockyer 1981b). Information from other baleen whales (quantity and quality of milk) was then combined with information on the estimated age of weaning for right whales (Lockyer 1981b). Thus I again employed two different methods to incorporate a range of predictions for the cost of lactation.

3.3.3 Parameter Uncertainty and Model Evaluation

Uncertainties in model predictions were evaluated using Monte Carlo simulations that selected different combinations of parameters from a wide range of possible values. I assigned a probability distribution for each model parameter (e.g. uniform, normal, triangular and gamma) based on available information or assumed a uniform distribution in the absence of adequate information. I then conducted a Monte Carlo simulation by varying all parameter inputs assuming a probability distribution with a range above and below the mean value for a normal distribution, a minimum and maximum value for a uniform distribution, an upper, lower and mode estimate for a triangular distribution, and a shape, rate and scale estimate for the gamma distribution. Ten thousand iterations were completed by simultaneously varying all model inputs (Tables 3-3 and 3-5). Parameters with greater uncertainty were expected to have the largest range in predicted values, which in turn would affect the accuracy of the model predictions.

I conducted a sensitivity analysis of the model predictions to understand whether the model outputs were sensitive to specific input parameters, and whether more accurate values would improve the applicability of the model. I thus sought to determine the sensitivity of model outputs to variability (or uncertainty) of an input parameter, and whether they were correlated with an input parameter to the degree that small changes in the input value caused significant changes in the output (Hamby 1994). Model sensitivity was analyzed by separately varying each parameter group (production, metabolism, digestion, fasting and reproduction) while holding the others constant. Comparisons of the coefficient of variation for each parameter group revealed which parameters introduced the greatest uncertainty into my model predictions. Sensitivity analyses are important for model refinement and for highlighting areas of data deficiency and can thus be used to determine where future research should be focused to derive better estimates of food requirements.

3.3.4 Consumption Estimates

I evaluated the model predictions by comparing the *GER* estimates for different demographic groups with estimates of caloric consumption in two feeding habitats. My general method was to combine estimates of prey energy density (combining prey quality and prey density) from field samples with consumption estimates calculated from foraging behaviour and biomechanics. Prey density was calculated using 19 samples from the Bay of Fundy (Collected by: Baumgartner & Mate 2003) collected at depth from an optical plankton counter, and 28 samples from Cape Cod Bay collected by the Provincetown Center for Coastal Studies at the surface with conical net (60-cm diameter ring net with 333 μm mesh) samples taken from the path of feeding right whales (within 50 m of the skim feeding animal). Consumption rates were calculated by assuming a foraging speed of 0.64 m/s in Cape Cod Bay (Mayo & Marx 1990) and 0.986 m/s in the Bay of Fundy (McGregor 2010), a mouth gape of 1.21 m (Mayo *et al.* 2001), and a proportion of time spent feeding that ranged from 52% to 93% (Goodyear 1996). Varying the time spent feeding allowed me to generate low, medium and high estimates of energy consumption. Since the foraging behaviour differed between habitats (deep diving in Bay of Fundy and surface or near-surface feeding in Cape Cod Bay), the proportion of time individuals spent ingesting prey would likely differ between habitats.

I accounted for ascent, descent, bottom phase (where prey consumption likely occurs), and surface recovery times using results from three tagging studies conducted on North Atlantic right whales in the Bay of Fundy (Goodyear 1996, Baumgartner & Mate 2003, McGregor 2010). According to these studies, right whales spend ~53% of their entire dive cycle (i.e., ascent, descent, bottom phase and surface recovery) near the ocean floor where they are assumed to ingest prey. Thus 47% of the time that right whales spent foraging in the Bay of Fundy was lost due to ascent and descent and respiratory recovery at the surface. I also assumed that prey densities and species composition remained constant over the foraging period, and corrected for the inefficiencies of right whale baleen to capture prey by applying filtration efficiencies (Mayo & Fortune Unpublished data, Mayo et al. 2001).

Table 3-3. Bioenergetic model parameter values (Eq. 1). See text for details.

Parameter	Symbol	Equation	Value	Probability Distribution	Details
Activity	A	(4)	1.773-2.027, 1.900	Triangular	Pregnant
			1.713-1.959, 1.836	Triangular	Calf, juvenile, adult, lactating
Basal metabolism	BM	(3)	2.655 ± 0.799	Normal	All
Fecal and urinary digestive efficiency	E_{F+U}	(1)	0.740 - 0.858	Uniform	All
Heat increment of feeding	E_{HIF}	(1)	0.875 ± 0.036	Normal	Adult, pregnant, lactating
			0.739 ± 0.065	Normal	Juvenile
			0.742 ± 0.042	Normal	Calf
Proportion of body growth that is lipid	P_{lip}	(2)	0.369 ± 0.016	Normal	Pregnant, lactating
			0.358 ± 0.027	Normal	Adult
			0.356 ± 0.043	Normal	Juvenile
			0.189 ± 0.043	Normal	Calf
Proportion of lean body growth that is water	P_w	(2)	0.642-0.702	Uniform	All
Energy deposited during gestation (fetus)	R_G	(5)	4.3-225.5	Uniform	Pregnant (MJ)
Energy transferred during lactation (calf)	R_L	(1)	1233.1-1391.4	Uniform	Lactating (MJ)
Days spent fasting while migrating	T_M	(1)	22.5 ± 1.291	Normal	All (except calves)
Days spent fasting on calving grounds	T_R	(1)	1.638, 0.035, 14.495	Gamma	Resting, pregnant
			46.410 ± 14.540	Normal	Lactating
			0.973, 11.164, 3.388	Gamma	Male
			16.331 ± 8.480	Normal	Juvenile

3.4 Results

3.4.1 Energy Requirements

Mean daily energy requirements (averaged over 1 year for calves, 8 years for juveniles and 13 years for adults) differed between demographic groups. Calves (1130 ± 155.6 *SD* MJ) and adult males required the least total energy 1140 MJ (± 180.0 *SD*) per day and lactating females required the most (2934 ± 254.1 MJ) (Fig. 3-1 and Table 3-5). Pregnant females (1384 ± 220.1 MJ) and juveniles (1337 ± 224.1 MJ) required marginally more energy each day than resting females (1217 ± 210.0 MJ) (Fig. 3-1 and Table 3-5). However, daily energy needs as a proportion of mean body size (Fig. 3-2) shows calves required the most energy per unit mass (0.145 MJ/kg), followed by lactating females (0.108 MJ/kg), juveniles (0.071 MJ/kg), pregnant females (0.051 MJ/kg), resting females (0.045 MJ/kg) and males (0.042 MJ/kg).

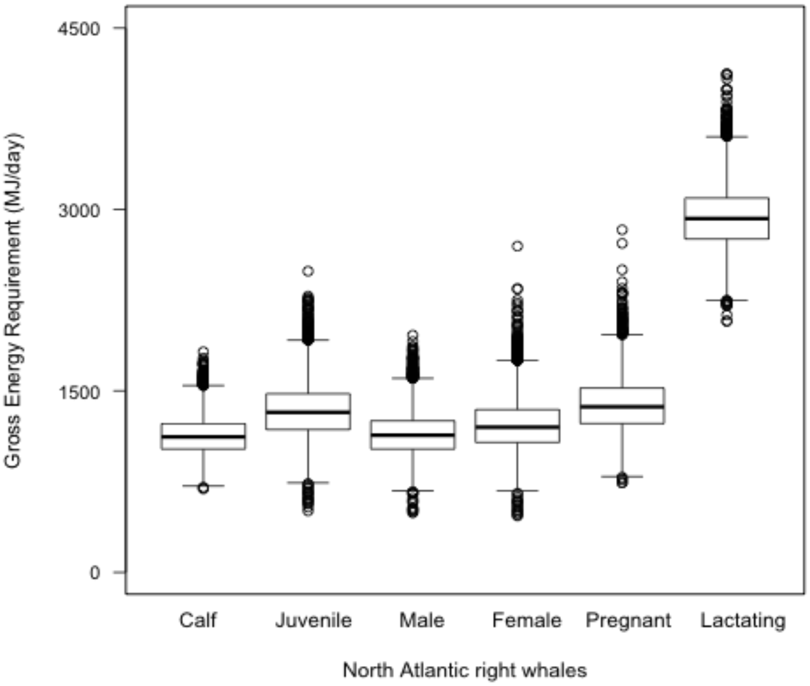

Figure 3-1. Mean daily gross energy requirements for different demographic groups of North Atlantic right whales predicted using the generalized bioenergetics model. Daily requirements were calculated as annual energy requirements or number of available foraging days per year. Males consisted of reproductively mature adults (≥ 9 years) and females consisted of adults that were not pregnant or lactating. Calves consisted of animals' aged 0 to 1 year and juveniles represented animals between >1 and <9 years of age. These estimates were derived from 10,000 Monte Carlo simulations that incorporated uncertainty assuming a model parameter probability distribution of either normal, uniform, triangular or gamma as described in the methods.

The amount of food required by North Atlantic right whales, expressed as a proportion of their own body mass varied across demographic groups. Assuming 1 gram of prey contains 4.186 kJ of energy (Kenney et al. 1986, Lockyer 1981b, Mauchline 1998), calves required the greatest biomass (3.5 % ± 0.48 *SD*) followed by lactating females (2.6 ± 0.22 %) (Table 3-4). Conversely, non-reproductive adults only needed to consume the equivalent of 1.0 ± 0.16 % for males and 1.1 ± 0.18 % of their body mass per day for resting females to meet their food requirements (Table 3-4).

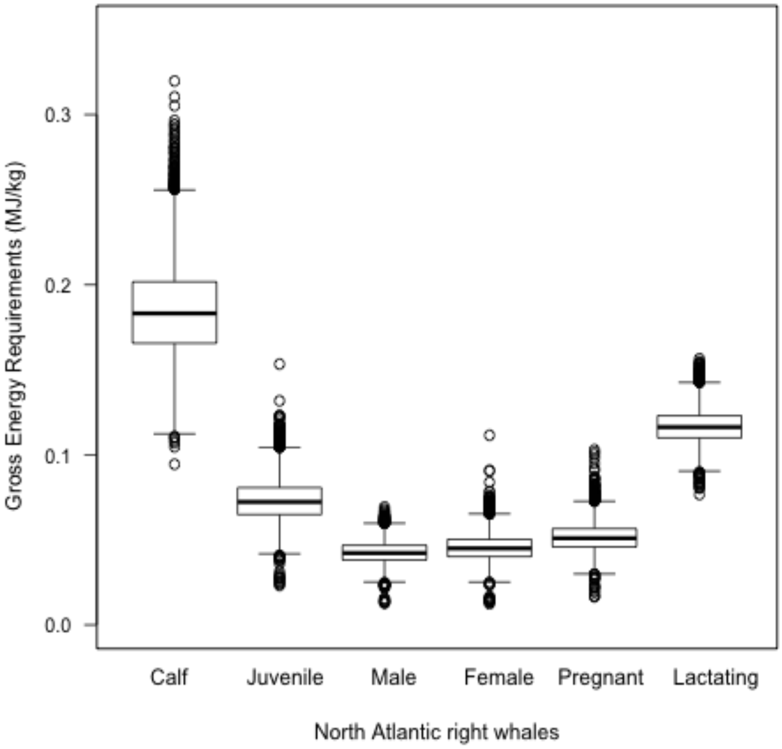

Figure 3-2. Mean daily energy needs for different demographic groups of North Atlantic right whales expressed as a proportion of mean body mass (Chapter 2).

3.4.2 Residency Time

Of all the demographic groups of North Atlantic right whales analyzed (lactating, non-lactating, juvenile and adult male), I found that lactating females (46.32 days ± 14.60 *SD*) spent the longest time on the calving grounds off Florida and Georgia, and that males spent the least time (3.11 ± 3.33 days) (Fig. 3-3). This difference between residency times of males and females is consistent with what I anticipated given the reproductive biology of North Atlantic right whales. Residency times for non-lactating adult female (23.75 ± 18.60 days) and juvenile (16.33 ± 8.50 days) (Fig. 3-3) right whales were similar to each other, but significantly shorter than for the lactating females.

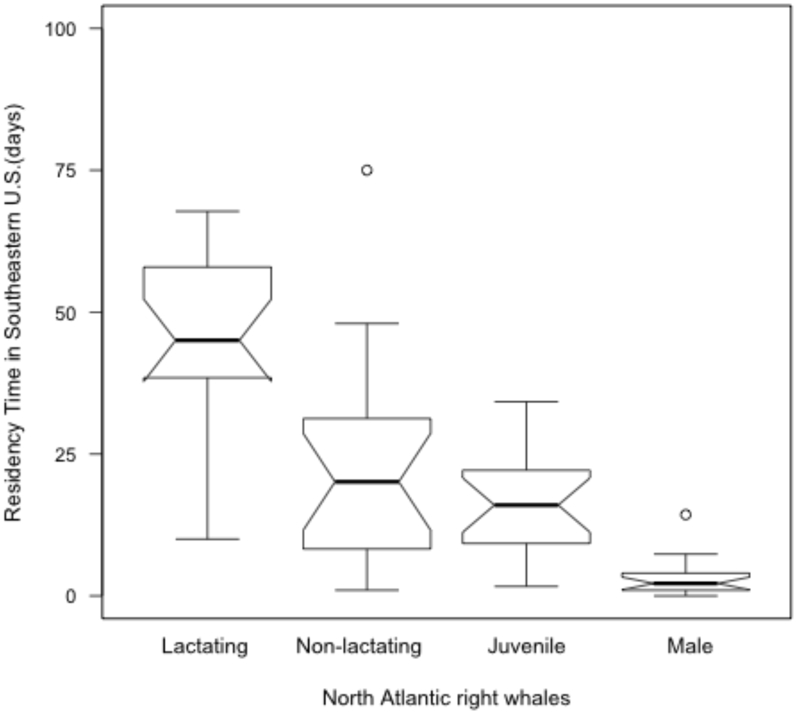

Figure 3-3. Southeastern U.S. mean residency times for different demographic groups of North Atlantic right whales calculated by subtracting the last day seen on the calving grounds (Florida and Georgia) from the first day seen using identification data from the North Atlantic Right Whale Consortium from 1991 to 2009 (n=18 years). Adult males were absent from the calving grounds in 1991 and thus received a residency time of zero days for this year. Each boxplot shows the distribution of 18 annual mean residency times.

Table 3-4. Predicted food requirements expressed as a proportion of mean body mass (Chapter 2) that each demographic group will need to consume to meet there predicted daily energy needs, assuming 1 gram of prey is equivalent to 4.186 kJ.

Demographic Group	Mean % Body Mass	*SD*
Calf	3.5	0.48
Juvenile	1.7	0.28
Adult Male	1.0	0.16
Adult Female	1.1	0.18
Pregnant	1.2	0.19
Lactating	2.6	0.22

3.4.3 Sensitivity Analysis

Systematically incorporating uncertainty into different model parameter groups (i.e., production, digestion, metabolism, time fasting and reproduction) showed that overall the model predictions were most sensitive to uncertainties in the energetic costs of digestion and fasting. For example, digestion introduced the greatest uncertainty into the predicted energy requirements of calves (mean *CV* 13.71, range 11.36-13.71) and juvenile right whales (*CV* 16.33, 12.75-16.33) (Fig. 3-4 and Table 3-5). Digestion also had the greatest effect on the predictions of energy requirements for adult males (*CV* 15.16, 14.12-15.16) (Fig. 3-4 and Table 3-5) due to the short time males spent on the calving grounds, and the considerable uncertainty in estimated fecal and urinary digestive efficiency associated with consuming a mixed diet and the inefficiency of utilization of metabolizable energy. The predicted energy needs of non-reproductive females were most sensitive to estimates of the numbers of days spent fasting (*CV* 15.79, 14.08-15.79), but digestion also introduced considerable uncertainty into the model predictions (*CV* 15.36, 14.08-15.79) (Fig. 3-4 and Table 3-5). The predicted energy needs of pregnant (*CV* 15.27, 13.43-15.27) and lactating females (*CV* 8.39, 6.26-8.39) (Fig. 3-4 and Table 3-5) were most sensitive to fasting due to the greater time they spent on the calving grounds.

3.4.4 Prey Consumption

Particle densities of prey differed between the two feeding habitats. In the Bay of Fundy, prey samples taken near feeding right whales (6618 ± 3481 SD; Baumgartner & Mate 2003) had a mean particle density that was ~56% lower than in Cape Cod Bay (14778 ± 18594 organisms/m^3) (Fig. 3-5). However, the range in particle densities in the two habitats was greater in Cape Cod Bay (740-58742 organisms/m^3) compared to the Bay of Fundy (3020-14945 organisms/m^3) (Fig. 3-5) suggesting that prey consumption was more variable in Cape Cod Bay.

Table 3-5. Sensitivity analysis of bioenergetic model *GER* predictions for North Atlantic right whales where uncertainty was incorporated into each parameter group by running 10,000 Monte Carlo simulations. Results from a Kolmogorov-Smirnov test (using Nortest 1.0 package in R) for normality suggested that all probability distributions were significantly different from a normal distribution (*P*-value <0.05).

Parameter Group	Demographic Group	Mean	SD	CV	Median	Minimum	Maximum	Skew	Kurtosis
Production	Calf	1055	132.7	12.58	1050	643	1590	0.24	3.02
Digestion	Calf	1084	148.6	13.71	1075	632	1762	0.29	3.17
Metabolism	Calf	1104	125.4	11.36	1102	711	1551	0.12	2.94
All	Calf	1126	160.5	14.26	1117	668	1860	0.31	3.08
Production	Juvenile	1160	147.9	12.75	1159	429	1627	-0.11	3.82
Digestion	Juvenile	1263	206.3	16.33	1253	414	2260	0.28	3.55
Metabolism	Juvenile	1243	163.5	13.15	1241	437	1812	-0.10	3.90
Fasting	Juvenile	1162	152.0	13.08	1159	417	1707	-0.03	3.69
All	Juvenile	1352	227.6	16.84	1338	431	2608	0.33	3.67
Production	Adult Male	996	140.7	14.12	997	343	1426	0.07	3.60
Digestion	Adult Male	1079	163.6	15.16	1075	335	1706	0.09	3.64
Metabolism	Adult Male	1064	153.2	14.40	1062	359	1604	0.04	3.63
Fasting	Adult Male	995	144.1	14.48	996	340	1466	-0.04	3.79
All	Adult Male	1154	178.7	15.48	1149	365	1847	0.15	3.49
Production	Adult Female	1062	149.5	14.08	1062	366	1519	0.00	4.00
Digestion	Adult Female	1147	176.1	15.36	1142	381	1147	0.14	3.52
Metabolism	Adult Female	1135	161.8	14.26	1134	370	1678	-0.01	3.81
Fasting	Adult Female	1064	168.1	15.79	1056	349	2202	0.31	4.32
All	Adult Female	1231	209.1	16.99	1217	363	2427	0.30	3.79
Production	Pregnant	1060	142.4	13.43	1053	674	1522	0.27	3.02
Digestion	Pregnant	1142	168.3	14.75	1131	676	1905	0.34	3.18
Metabolism	Pregnant	1157	157.7	13.62	1150	714	1745	0.26	3.01
Fasting	Pregnant	1062	162.3	15.27	1051	638	2089	0.54	3.93
Gestation	Pregnant	1150	155.2	13.50	1146	662	1704	0.20	2.96
All	Pregnant	1384	222.9	16.11	1371	730	2750	0.53	3.77
Production	Lactating	2413	162.2	6.72	2414	1663	2903	0.02	3.68
Digestion	Lactating	2507	190.1	7.58	2501	1662	3210	0.09	3.58
Metabolism	Lactating	2491	178.0	7.15	2490	1676	3069	-0.06	3.84
Fasting	Lactating	2414	202.5	8.39	2405	1563	3293	0.22	3.35
Lactation	Lactating	2758	172.7	6.26	2758	1921	3346	-0.04	3.58
All	Lactating	2933	257.4	8.78	2921	2084	4215	0.32	3.22

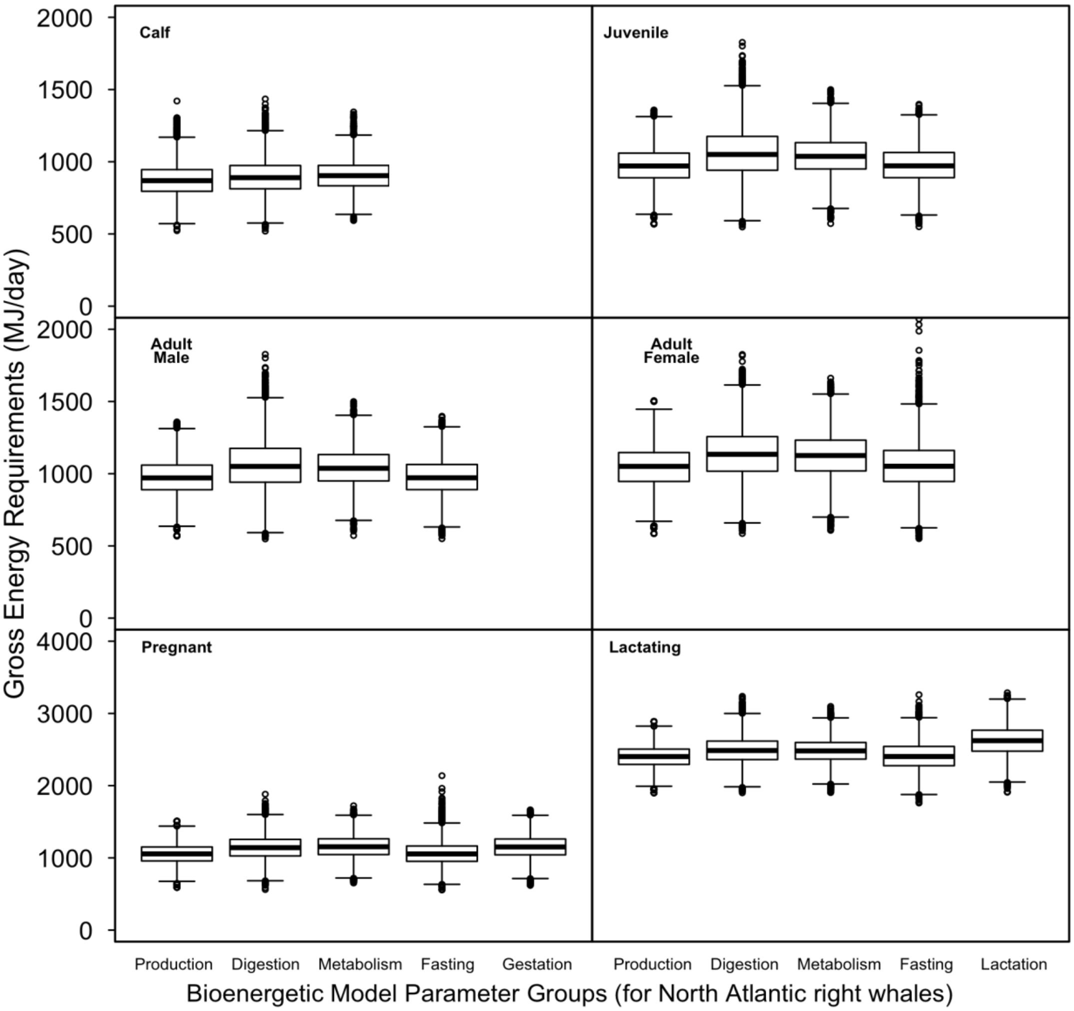

Figure 3-4. Sensitivity analysis results for each demographic group derived from 10,000 Monte Carlo simulations that incorporated uncertainty into each parameter group (i.e., production, digestion, metabolism, fasting and reproduction) separately, while holding the other parameter values constant. Parameter groups with the greatest influence on the bioenergetic model predictions are those with the greatest range in predicted values.

Bay of Fundy prey samples were dominated by late stage *Calanus finmarchicus* (Baumgartner & Mate 2003) and Cape Cod Bay samples contained a mixture of different species and life stages of copepods. Calculating energetic densities (kJ/m^3) of prey sampled near feeding whales showed higher energy densities on average in the Bay of Fundy (52 ± 27 kJ/m^3 *SD*) compared to Cape Cod Bay (20 ± 22 kJ/m^3 *SD*) (Fig. 3-5). Minimum and maximum energetic densities varied from 24 – 116 kJ/m^3 in the Bay of Fundy and 1 – 87 kJ/m^3 in Cape Cod Bay (Fig. 3-5). This suggests that the nutritional value of prey found near the North Atlantic right whales was better on average in the Bay of Fundy.

The mean amounts of food I estimate that right whales consumed in the Bay of Fundy and Cape Cod Bay differed significantly between habitats. Assuming minimum, mean and maximum foraging distances (i.e., distance traveled while foraging) of 29, 35 and 51 kilometers, I predicted that North Atlantic right whales consumed a minimum of 727 MJ/day (± 757 *SD*) a mean of 943 MJ/day (± 969 *SD*), and a maximum of 1311 MJ/day (± 1348 *SD*) (Fig. 3-6) in Cape Cod Bay. Although foraging speeds were greater in the Bay of Fundy (Baumgartner & Mate 2003) during the bottom phase of deep dives when whales were assumed to be feeding at depth, the area covered while foraging was less compared to skim feeding whales in Cape Cod Bay (Mayo & Marx 1990). Average energetic consumption in the Bay of Fundy was predicted to be a minimum of 1429 MJ/day (± 751.69 *SD*) for a right whale swimming a minimum of 20 kilometers per day while ingesting prey, a mean of 1726 MJ/day (± 907.81 *SD*) for a mean of 25 km, and a maximum of 2559 MJ/day (± 1345.82 *SD*) (Fig. 3-6) for a maximum swimming distance of 36 km. Foraging right whales thus obtained more energy while foraging in the Bay of Fundy than those foraging in Cape Cod Bay.

The bioenergetic model estimates of mean daily energy needs showed some disparity with the field derived estimates of energetic consumption for Cape Cod Bay and Bay of Fundy. For example, lactating females foraging at their maximum rates would obtain ~87% of their predicted energy needs from the Bay of Fundy, but only ~45% of their food requirements by foraging in Cape Cod Bay (Table 3-6). Comparatively, lactating females could obtain ~55% of their needs in Cape Cod Bay and ~118% in the Bay of Fundy when

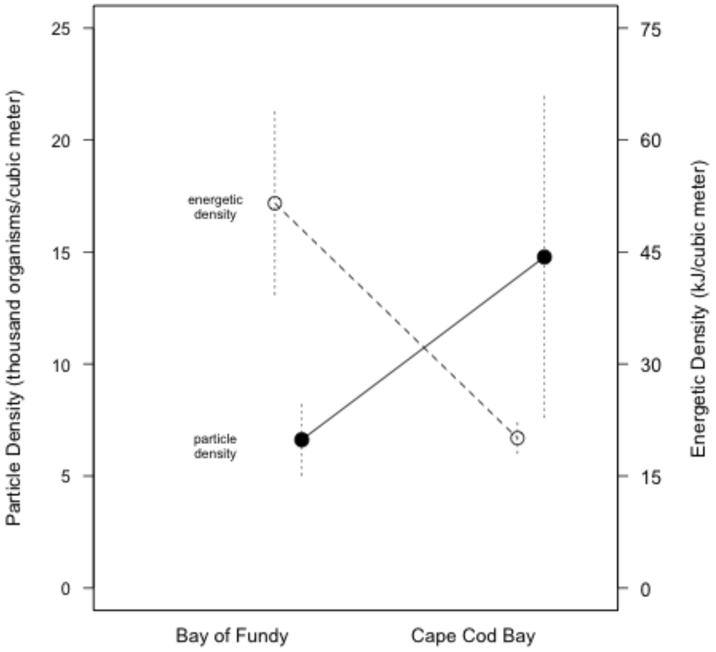

Figure 3-5. Comparison of particle and energetic densities of prey samples taken from Cape Cod Bay and Bay of Fundy. Mean densities are represented by the circles and the dotted lines illustrate the range in values (minimum and maximum estimates). Particle densities for both habitats are connected by a solid line and energetic density is connected by a dotted line.

fasting costs are not accounted for (~19% decrease in mean daily *GER*). However, adult males easily exceeded their needs in Cape Cod Bay (~114%) and the Bay of Fundy (~223%) under the same foraging scenario (Table 3-6). Foraging success (in terms of meeting daily energy requirements) appears to differ between demographic groups, and may be higher in the Bay of Fundy compared to Cape Cod Bay.

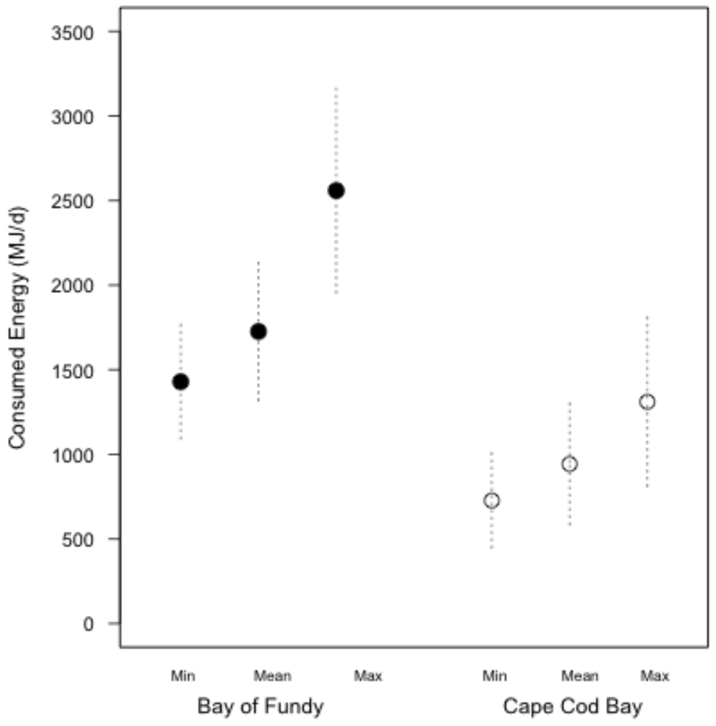

Figure 3-6. North Atlantic right whale energetic consumption predicted for two foraging habitats, Cape Cod Bay (CCB, n=28) and Bay of Fundy (BOF, n=19) where mean energetic consumption are circles and the 95% confidence limits are dotted lines. These estimates were created assuming three foraging scenarios (when individuals are actively consuming prey) of 12.5 (min), 15.1 (mean), and 22.3 (max) hours per day for Cape Cod Bay and 6.6 (min), 8.0 (mean), and 11.8 (max) for Bay of Fundy. Although the time spent foraging is assumed to be the same for both habitats, the time individuals are assumed to be consuming prey is different. Differences between min, mean and max prey ingestion for CCB and BOF are based on observed disparities between the dominant feeding techniques (deep diving in BOF and skim feeding in CCB) employed in both habitats. The consumption estimates were also corrected for imperfect filtration

Table 3-6. Comparisons of empirical prey data and model predictions of daily energy needs for different demographic groups of North Atlantic right whales in Cape Cod Bay (CCB) and the Bay of Fundy (BOF) under three feeding scenarios. The percent of predicted daily energy needs met after foraging in each habitat are shown for periods of 12.5, 15.1 and 22.3 hours per day. Instances when the predicted daily energy needs were within ± 15% of the energy consumed are indicated in bold.

	Cape Cod Bay			Bay of Fundy		
Demographic Group	Min Energy Consumed (12 hr) (727 MJ)	Mean Energy Consumed (15 hr) (943 MJ)	Max Energy Consumed (22 hr) (1311 MJ)	Min Energy Consumed (12 hr) (1429 MJ)	Mean Energy Consumed (15 hr) (1726 MJ)	Max Energy Consumed (22 hr) (2559 MJ)
Juvenile	54%	70%	**97%**	**106%**	128%	190%
Adult Male	63%	82%	**114%**	125%	151%	223%
Ault Female	59%	77%	**106%**	116%	140%	208%
Pregnant	53%	68%	**95%**	**103%**	125%	185%
Lactating	25%	32%	45%	49%	59%	**87%**

3.5 Discussion

Calculating the energy needs of North Atlantic right whales by demographic groups provides a perspective on the nutritional status and recovery of right whales that previous models failed to capture. Most notably, the model shows that lactating females had the highest energy needs of any group, and that they may experience an energy deficit when foraging in Cape Cod Bay. This discrepancy found between the predictions of daily energy needs and estimates of actual energy consumed in Cape Cod Bay suggests that lactating females are more susceptible to experiencing periods of nutritional stress than any other demographic group. This has implications for the recovery of right whales.

3.5.1 Model Predictions

With the exception of lactating females, the daily energy needs of most demographic groups of North Atlantic right whales appear to be relatively similar to one another (Fig. 3-1). The model suggests that mean daily intake ranges from 1141 to 1384 MJ for juveniles, adult males, and adult females (pregnant and non-pregnant). This equates to ~272-331 kg of copepods per day per individual assuming that copepods contain ~4.186 kJ per gram wet weight (Mauchline 1998, Lockyer 2007, Kenney et al. 1986). However, expressing daily energy needs of right whales in terms of mean body size shows that calves (0.145 MJ/kg) require ~50% more energy than juveniles (0.071 MJ/kg), and more than twice that of adults (i.e., an adult female requires 0.045 MJ/kg).

The higher relative energy needs of young animals compared to adults reflect the high energy costs associated with body growth and associated elevated metabolic requirements. North Atlantic right whales attain 76% of their maximum length, but only ~46% of their weight within the first year of life (Chapter 2). However, juvenile right whales obtain ~76% of their maximum mass by 8 years of age (Chapter 2) and thus their basal metabolic rate was estimated to be elevated by 20%. Thus the difference in the daily energy requirements of juveniles compared to adult males is relatively small (i.e., juveniles required only ~15% more energy than adult males) compared with the energetic requirements of calves.

Adult males require ~6% less energy (MJ/day) than non-reproductive adult females due in part to differences in body composition. However, most of the difference between adults reflects the smaller portion of time that adult males spend fasting on the calving rounds—and hence the greater amount of energy that adult females have to make up for when they begin feeding again. Pregnant females also spend longer on the calving grounds than males and require ~17% more energy than males, and 12% more energy than non-reproductive females. This suggests that the energetic cost of carrying a fetus to term is relatively low. These estimates of fasting times by demographic groups are the first to be calculated for North Atlantic right whales and had a significant effect on the amounts of food that right whales were predicted to require during the rest of the year.

While the daily cost of pregnancy alone may be low (0.051 MJ/kg), the costs of lactation are considerably higher (0.108 MJ/kg). Lactating females required more than twice as much total energy per day compared to pregnant females (2934 ± 254.1 MJ/day vs. 1384 ± 221.0 MJ/day), and had the highest demands compared to other groups (Fig. 3-2). The high food requirements of lactating North Atlantic right whales presumably reflect the energy required to support rapid postnatal growth over the 12 month nursing period (Chapter 2). Lactating females also spend ~23 days more than non-lactating females fasting on the calving grounds. Thus, lactating females have a shorter foraging season compared to other demographic groups.

The model predictions for North Atlantic right whales are consistent with estimates of daily energy and biomass needs that have been calculated for other baleen species. For example, analysis of stomach contents and predictions of feeding rates for other cetaceans suggest that large baleen whales consume 1.5-2.0% of their body weight per day in food (Lockyer 1981b) and that fin whales (*Balaenoptera physalus*) consume 1.6-3.3% (Lockyer 2007, Vikingsson 1997). These estimates are all within the range of the model predictions for North Atlantic right whales.

In terms of lactation and gestation, studies of other large whales have also found the costs of gestation to be minimal compared to those of lactation. Such differences have been found for lactating baleen whales, which are predicted to require double the energy of pregnant females (Lockyer 1984). I found that the mean daily energy needs were 53% higher for lactating North Atlantic right whales compared to pregnant females. Furthermore, the costs of lactation alone are predicted to be ~14-15 higher than gestation for fin (*Balaenoptera physalus*) and Antarctic blue whales (*Balaenoptera musculus*) (Lockyer 1981b). My model predicts that right whales would require ~15 times more energy to meet the costs of nursing alone, which is comparable to that predicted by Lockyer (1981b). Additional bioenergetic models that incorporate fetal growth models have also found that baleen and odontocete species incur marginal costs to support gestation (Lockyer 2007).

3.5.2 Model Validation

The consistency between the model predictions and those from other bioenergetic models of large baleen whales suggests that the estimates are reasonable. However, such a comparison alone is insufficient to validate the results given that all of the existing bioenergetic models for baleen whales are simplifications of complex systems that have tended to rely on a common set of assumptions and model parameter values.

Comparing the predictions of energy requirements with empirical data used to estimate prey consumption is another means to evaluate the model. A percent difference between the model predictions and estimates of prey consumption of >15% is considered to be unacceptable and would imply that the model is not supported and should be re-parameterized (Chipps & Wahl 2008, Berkson *et al.* 2002). This calculation showed close agreement (i.e., ≤ 15% for all demographic groups except lactating females) between the mean estimates of consumed and required energy when individuals foraged in Cape Cod Bay for 22 hours per day (Table 3-6). The field data suggest that a lactating female foraging for 22 hours per day only obtains ~45% of her daily energy needs in Cape Cod Bay, but would obtain 87% of her needs by foraging further north for the same length of time in the Bay of Fundy (Table 3-6).

The apparent discrepancy between observations and predictions in Cape Cod Bay may reflect an error in model parameterization or could be due to an error in sampling prey in the field. However, given the observed signs of nutritional stress observed in mature females, this discrepancy may also reflect a real phenomenon of food shortage for lactating females. Few of the model parameters were drawn from direct measurements of right whales because commercial whaling was banned before standard data collection techniques were implemented (e.g. fetal length and weight recording) and because of the inherent logistical constraints involved in studying the energetics of wild cetaceans. Therefore, I relied on model parameters taken from other species (e.g. lactation, heat increment of feeding), which may have overestimated energy needs. Other parameters in the bioenergetics model were estimated using allometric relationships derived from captive studies or studies conducted on harvested baleen species (e.g. basal metabolic rate, and gestation), which could bias model results.

The other possible explanation for the discrepancy between the model predictions and field observations is that observed rates of prey consumption by right whales were underestimated in Cape Cod Bay due to sampling limitations. Differences in the vertical distribution of prey and right whale foraging behaviour resulted in different sampling methods being used to collect zooplankton in Cape Cod Bay and the Bay of Fundy (Mayo & Marx 1990, Parks *et al.* 2011, Baumgartner et al. 2003a, Baumgartner et al. 2003b, Baumgartner & Mate 2003). As a result, surface-net sampling in Cape Cod Bay may have underestimated prey consumption compared with deep-water sampling occurring in the Bay of Fundy where vessel turbulence was less likely to affect prey densities sampled. However, prey densities in the Bay of Fundy may be imprecise as well because collection occurred at specified locations and depths where the whales were assumed to be feeding (compared to Cape Cod Bay where the animals were confirmed to be feeding) (Baumgartner & Mate 2003). Therefore, prey densities sampled near feeding whales in Cape Cod Bay and Bay of Fundy may be lower than actual densities consumed because of sampling error, and should be considered minimum estimates.

Overall I feel that the model parameters used were reasonable and yielded realistic estimates of energy requirements for right whales. I included all of the important parameters that significantly influence energy requirements, and addressed uncertainty in their values (and on model predictions) by assigning error terms for each input value. The model predictions thus consist of a range of values that reflect the relative uncertainty surrounding the parameters used to generate the estimates of energy requirements. The predictions also compare favorably with field estimates of consumption in the Bay of Fundy, but not as well with those from Cape Cod Bay due perhaps to underestimating prey densities in the surface waters. It is noteworthy however that the model suggests that North Atlantic right whales need to feed for long hours in Cape Cod Bay to make ends meet (up to 22 hours per day). This prediction is consistent with limited field observations showing continuous feeding for over 8 hours by right whales that were individually followed in Cape Cod Bay (Jaquet *et al.* 2007).

3.5.3 Habitat Quality

Some of the discrepancy between the estimated energy requirements and estimated prey consumption by right whales in Cape Cod Bay may be explained by sampling methodology. However, it seems unlikely that prey abundance could have been underestimated by so much in this location, or that I overestimated the energy needs of right whales. This raises the possibility that Cape Cod Bay is in fact a marginal habitat for some right whales that have elevated energy needs, such as lactating females. It may also explain why so few calves are observed in Cape Cod Bay compared to the Bay of Fundy.

Lactating females typically arrive in Cape Cod Bay towards the end of the time when zooplankton sampling and systematic aerial surveys are usually conducted in April or May (Jaquet et al. 2007). Their arrival corresponds to a time when prey densities are at their maximum, and the dominant species is *Calanus finmarchicus* (DeLorenzo Costa et al. 2006b). However, only ~10-31% of annually identified mother and calf pairs are found during this time in Cape Cod Bay (Jaquet et al. 2007). Furthermore, only 3 of 19 prey samples taken in Cape Cod Bay between April and May agreed with the predicted energy needs of lactating females. Consequently, Cape Cod Bay may be more suitable for other demographic groups (such as resting adults and juveniles) that have lower daily energy needs.

North Atlantic right whales make a living by foraging on different taxa, life-stages and sexes of calanoid copepods that differ in energetic value. These primary prey taxa include *Calanus finmarchicus*, *Pseudocalanus* spp. and *Centropages hamatus* and *Centropages typicus* (Mayo & Marx 1990, Beardsley et al. 1996, Baumgartner & Mate 2003, DeLorenzo Costa et al. 2006a, Durbin *et al.* 1995), of which *Calanus finmarchicus* appears to form the largest proportion of the whales diet (Kenney *et al.* 2001) throughout most of the feeding range of the species. Some feeding habitats are dominated by *Calanus finmarchicus,* particularly stage-five (CV), which are of high caloric value (DeLorenzo Costa et al. 2006a). CV is the second most energetically dense life stage (adult male is the highest) because they maximize their lipid stores before entering a diapause period when the food supply is low (Michaud & Taggart 2007). The ability of North Atlantic right whales to optimally forage requires them to locate prey patches of adequate size and caloric value and efficiently consume the prey.

As migratory species, right whales utilize various foraging habitats in the western North Atlantic such as Cape Cod Bay, Great South Channel, Roseway Basin and Bay of Fundy. Movements of whales between these habitats appears to coincide with seasonal cycles in the quantities and energetic qualities of calanoid copepods in the Gulf of Maine (particularly *Calanus finmarchicus*) (Baumgartner et al. 2003a). Most whales typically begin foraging in Cape Cod Bay on such species as *Centropages typicus* and *Pseudocalanus* spp. which are dominant but not energetically rich (DeLorenzo Costa et al. 2006a). Maximum abundance of right whales in Cape Cod Bay coincides with the emergence of a more energy rich prey species— *Calanus finmarchicus* (typically early stages) (Jiang et al. 2007). In late spring and early summer, the whales feed in the Great South Channel on dense aggregations of *Calanus finmarchicus* (Pendleton *et al.* 2009), move northward at the start of the summer to the deep habitats such as Roseway Basin and the Bay of Fundy to exploit diapausing CV copepods (*Calanus finmarchicus*) that are high in lipids.

Right whales that forage in the Bay of Fundy may obtain higher energetic returns than those that feed in Cape Cod Bay because of the higher quality of prey rather than the sheer quantities of prey. Despite considerably lower prey densities in the Bay of Fundy, the energetic density of prey patches averaged ~2.6 times more energy than in Cape Cod Bay. This higher energetic density in the Bay of Fundy likely reflected the dominance of lipid rich CV *Calanus finmarchicus* (Michaud & Taggart 2007) compared to various taxa (e.g. *Centropages typicus* and *Centropages typicus*) and developmental stages of calanoid copepods with differing levels of lipid content in Cape Cod Bay (DeLorenzo Costa et al. 2006a, Mayo & Marx 1990). Improved prey quality suggests that North Atlantic right whales can more easily meet their predicted energy needs in the Bay of Fundy. For example, adult males would require ~10 times as many *Centropages typicus* and ~6 times as many *Pseudocalanus* spp. than *Calanus finmarchicus* to meet their predicted energy needs (using average values of copepod calories across all life-stages from: DeLorenzo Costa et al. 2006a). This suggests that foraging success is lower in Cape Cod Bay because individuals need to spend more time locating and consuming prey than in the Bay of Fundy. Consequently, foraging success and thus habitat quality may be more dependent upon prey quality (i.e., calories per organism) than quantity.

If foraging success is compromised in Cape Cod Bay, North Atlantic right whales may exploit other habitats to recoup their energetic losses. Cape Cod Bay is a seasonally important winter foraging ground for North Atlantic right whales and is likely the first foraging habitat visited after fasting on the calving grounds (Watkins & Schevill 1979, Schevill 1986, Hamilton & Mayo 1990, Mayo & Marx 1990, Kraus & Kenney 1991). However, if individuals do not consume sufficient energy to meet their daily needs, they may travel to adjacent habitats where feeding conditions are better (e.g. Massachusetts Bay, the back-side of Cape Cod, the Great South Channel) and may subsequently re-enter Cape Cod Bay at a later date. For example, ~44% (n=59) of the individual right whales that are observed more than once in Cape Cod Bay would have entered and left the habitat 1-3 times in 2007 (Jaquet et al. 2007) assuming that an individual left Cape Cod Bay when it was not sighted during ≥ 3 consecutive aerial surveys. Alternatively, individuals may be able to offset an energy deficit later in the season while occupying habitats with energy rich prey such as the Bay of Fundy (where most demographic groups appear capable of greatly exceeding their predicted daily energy needs). Given these scenarios, it seems unlikely that poor prey availability or quality resulting in daily energy imbalances in Cape Cod Bay would be sufficient to cause an overall deficit in an individual's annual energy budget — but changes in habitat quality outside of Cape Cod Bay could have significant implications for North Atlantic right whale health and reproduction.

3.5.4 Nutritionally Stressed?

Right whales that migrate northwards in the spring may demonstrate signs of nutritional stress if they are unable to recoup their energetic losses in Cape Cod Bay or in other foraging habitats such as the Bay of Fundy. Pronounced shifts in environmental conditions thought to influence prey availability may reduce foraging opportunities and result in an energy imbalance (Greene & Pershing 2004, Miller et al. 2011). Consequently, individuals may further catabolize their fat stores to supplement their daily needs (Miller et al. 2011). Lactating females are likely to show the greatest decrease in blubber reserves because of the increased time spent fasting on the calving grounds and the high costs of lactation. Extensive catabolism would result in apparent emaciation of individuals (Pettis et al. 2004) and lowered reproductive fitness such that adult females may forgo pregnancy if a critical proportion of their body fat is lost (Miller et al. 2011). Without sufficient energy reserves, North Atlantic right whales may experience periods of prolonged anoestrus (Lockyer 1986) because blubber is a lipid rich energy store that is thought to support reproductive costs. For example, blubber is thickest in females before pregnancy (3-6 months), thinnest during lactation and thicker during recovery from lactation (Miller et al. 2011). Therefore, the time between pregnancies may be a function of the time needed to restore their blubber, which may ultimately drive calving intervals and rates of birth.

Signs of compromised health have been observed since the mid-to-late 1990s when North Atlantic right whales appeared emaciated in the Bay of Fundy with various forms of skin lesions (Rolland et al. 2007a, Pettis et al. 2004). Blubber thickness of juveniles and adult males was significantly thinner in 1998 when abundance of prey (especially *Calanus finmarchicus*) was low in the Gulf of Maine (Miller et al. 2011, Pershing et al. 2005), and 52% of the sampled population (n=439 whales) had white lesions on their bodies (Rolland et al. 2007a, Hamilton & Marx 2005). These observed changes in health coincided with a change in the North Atlantic Oscillation (Rolland et al. 2007a, Greene et al. 2003) that may have adversely affected the availability of prey and nutritionally compromised the reproductive success of the right whale population (Greene & Pershing 2004). Reproduction has ranged from 1 to 39 calves born in recent years with a mean calving interval (time between individual birthing events) that has oscillated between ~3 years to over 5 years (Kraus et al. 2001, Kraus et al. 2007, Waring et al. 2011).

Compared to other species of right whales, North Atlantic right whales appear to be in poorer condition and have lower reproductive success, suggesting that they are indeed nutritionally stressed. Blubber layers are significantly thinner in North Atlantic right whales than in South African right whales, which are presumed to have a more favorable nutritional regime (Miller et al. 2011). Similarly, calving rates of North Atlantic right whales are on average one-third to one-half that of the southern populations (Kraus et al. 2007, Browning et al. 2010), which also have a lower and more stable calving interval of 3 years (Cooke *et al.* 2001, Best 2001, Burnell 2001). Superior foraging opportunities and decreased fasting times (females forage on large, late-stage calanids while nursing in Peninsula Valdes, Argentina; Hoffmeyer *et al.* 2010) may account for the better condition and higher reproductive success of southern right whales, while greater interannual variability in quantities and qualities of prey may explain the lower performance of North Atlantic right whales.

Lactating female North Atlantic right whales and to a lesser extent pregnant females may experience periods of nutritional stress because of their elevated energy needs. They are also likely to be more vulnerable to fluctuations in prey abundance and need to allocate more time per day to foraging than other demographic groups to meet their daily energy needs. The models suggest that lactating females cannot obtain enough energy in Cape Cod Bay and have to forage for almost an entire day in the Bay of Fundy where feeding conditions appear to be the best. Pregnant and lactating right whales may thus be living on the ‘edge’. All told, the bioenergetics model in combination with field data on prey densities and feeding behaviour suggest that the recovery of North Atlantic right whales is tied to the nutritional and physiological status of mature females. This and observations of thin right whales further suggest that the slow recovery of North Atlantic right whales may be attributable in part to nutritional stress.

Chapter 4: Conclusion

4.1 Research Summary

The objective of my research was to describe the growth and energy needs of different demographic groups of North Atlantic right whales. Body growth was modeled using morphometric measurements of live (photogrammetry n=133) and dead (necropsy n=21) whales. Standard growth equations were fit to these data to predict age-specific changes in length, and allometric models were used to estimate age-specific changes in mass from length. I later used these predictions in a generalized bioenergetics model to predict mean daily energy requirements. My model incorporated functions to express how gross energy translates into metabolizable energy (e.g., remaining energy after fecal and urinary energy loss), and how it is partitioned among various aspects of production (e.g., growth and reproductive costs) and maintenance parameters (e.g., basal metabolism and costs of locomotion). The model output was evaluated by comparing estimates of prey consumption in two critical foraging habitats (Cape Cod Bay and Bay of Fundy) with predictions of daily energy needs.

The comprehensive analysis of North Atlantic right whale body size revealed that right whales have a rapid growth strategy—whereby calves more than double in size and attain three-quarters of asymptotic adult size by the time they wean at 12 months. Calves gain ~1.7 cm and ~34 kg per day while nursing during this the rapid growth phase. Mean predicted lengths and weights were 4.2 m and 1.1 mt at birth, 10.3 m and 13.5 mt at weaning, and 13.6 m and 29.6 mt when fully grown. Rapid growth during dependency may minimize the risk of predation and maximize survival of calves. Quick calf growth may also maximize development of the mouth and baleen to optimize foraging efficiency of juveniles at the time of weaning, as well as improve reproductive fitness by reducing the age at which sexual maturity is attained. However, rapid post-natal growth likely requires high maternal investment and may increase the species' vulnerability to nutritional stress during periods of prey shortage.

Predictions from the bioenergetic model suggest that, like most mammals, the energy needs of lactating females are considerably higher than for all other demographic groups (i.e., 2934 ± 254.1 MJ compared to 1384 ± 220.1 MJ for pregnant females and 1217 ± 210.0 MJ for resting females). Increased daily energy needs are attributed to the increased costs of supporting the rapid post-natal growth of dependent young and a reduced foraging season. Nursing females spend prolonged periods fasting (46.32 ± 14.60 days; 15 times longer than fasting adult males) and likely have to recoup their losses by catabolizing their energy stores on the calving grounds and augmenting their daily caloric intake once they return to their northern foraging grounds.

Lactating females may be more likely to experience energy deficits than other demographic groups returning to the foraging grounds because of their elevated food needs. Consequently, a large deficit (~45% of daily needs) was observed between prey consumption estimates and model predictions of daily energy needs for lactating females feeding for 22 hours per day in Cape Cod Bay. However, all other demographic groups were able to meet their predicted needs given the same feeding conditions. The model suggests that lactating females may almost obtain their daily needs (~87% of daily needs) in the Bay of Fundy when foraging for the same time. Comparatively, lactating females could obtain ~55% of their needs in Cape Cod Bay and ~118% in the Bay of Fundy when fasting costs are not accounted for (~19% decrease in mean daily *GER*). This suggests that lactating females may be able to meet their immediate energy requirements on the Bay of Fundy feeding grounds. The model results also indicate that all other demographic groups greatly exceed their needs (i.e., they can consume ~1.3-2.2 times more energy than they need to meet their daily needs). The discrepancy in prey consumption between foraging habitats may be attributed to differences in prey quality and quantity.

Although the density of organisms consumed may be greater in Cape Cod Bay, the energetic density of prey appears to be higher in the Bay of Fundy. Mean particle densities in Cape Cod Bay (14778 copepods/m^3 ± 18594 SD) were more than twice those sampled in the Bay of Fundy (6618 ± 3481 SD; Baumgartner & Mate 2003). However, prey densities were much more variable in Cape Cod Bay, which may reflect temporal variability because sampling occurred over 10 years (February-May) in Cape Cod Bay and for only 2 years (July and August) in the Bay of Fundy. Despite high prey densities, the mean energetic density of prey was ~2.6 times higher in the Bay of Fundy. The higher energetic return in the Bay of

Fundy likely reflects North Atlantic right whales primarily ingesting lipid-rich CV *Calanus finmarchicus* (Baumgartner & Mate 2003) compared to a mixed diet in Cape Cod Bay that includes less energetically rich prey (DeLorenzo Costa et al. 2006a). The divergent estimates of energy consumption suggest that foraging conditions are unequal between the two habitats and that North Atlantic right whales may periodically experience periods of energy imbalance in Cape Cod Bay.

Energy imbalances may adversely affect North Atlantic right whale recovery. In particular, lactating females may not be able to recoup all of the energetic losses they experienced while fasting and nursing, and may require a longer time to replenish their blubber reserves post-lactation (Miller et al. 2011). Consequently, the number of years between individual birthing events may be extended (i.e. the calving interval), thus resulting in a lower overall birth rate (Reeves et al. 2001, Kraus et al. 2007). Furthermore, reproductively mature females may forgo reproducing if they have not acquired sufficient energy stores (Miller et al. 2011). Thus, changes in the nutritional regime of adult females, particularly lactating females, may slow the rate of population growth.

4.2 Study Limitation

4.2.1 Growth

Combining morphometric measurements from dead and living whales increased the sample size but may have introduced unintended errors and biased model predictions. However, inspecting the datasets for outliers showed none for the photogrammetry measurements, and resulted in excluding only one of the necropsy measurements (sample no. 14) because the individual's recorded mass was incorrectly measured (mass was estimated without using standardized techniques).

Precision of measurements is difficult to estimate for necropsied animals because they are generally only measured once while lying in the same position. However, precision can be estimated for photogrammetry measurements where three or more measurements were taken of the same individual. Photogrammetric measurements taken of the same individual over multiple years resulted in relatively small coefficients of variation, whereby the mean *CV* values for length was 0.0236 (range from 0.009-0.047), and 0.022 (0.007-0.0515) for fluke width. *CV* values are unavailable for body width because few duplicate measurements exist.

Predicting changes in body mass relative to age was particularly challenging because such data are particularly sparse. The reliability of the mass estimates were reduced because of logistical challenges that resulted in a small sample size and the inclusion of unhealthy animals (emaciated animals due to fishing gear entanglement and suckling calves in poor nutritive condition). Consequently, mass may have been underestimated relative to age.

Growth model predictions are particularly sensitivity to errors in aging. The median birth date method I used to estimate age introduced ±2 months of uncertainty. However, unequal sample sizes within age classes may also have biased the length-at-age estimates, which were positively skewed towards animals between 0 and 1 year. The greater numbers of calves may have increased uncertainty in the assumed ages of older animals in the model. The lack of data for animals beyond 22 years limits the predictability of the model for older age classes (the oldest known North Atlantic right whale is just over 70; North Atlantic Right Whale Consortium 2009). However, this is unlikely to have any meaningful consequence for the predictions given that the growth rate of adult animals is so small.

4.2.2 Energetics and Prey Consumption

Poor agreement between empirical prey data and predictions of energy needs suggest that lactating females may experience food shortages in Cape Cod Bay. However, the discrepancy may also simply reflect an error in model parameterization or could be due to an error in prey sampling. Many model parameters had to be indirectly estimated, because standard data collection techniques were not in place (e.g. to record fetal length and weight) before commercial whaling was banned and because of the logistical constraints involved in studying the energetics of wild cetaceans. The estimates of energy requirements could also be overestimated because I used model parameters from other species (e.g. costs of lactation and heat increment of feeding). Other parameters in the bioenergetics model were estimated using allometric relationships derived from captive studies or studies conducted on harvested baleen species (e.g. basal metabolic rate, and gestation).

Alternatively, prey consumption may have been underestimated in Cape Cod Bay due to sampling limitations. North Atlantic right whales are frequently observed feeding in the upper few meters of the water column in Cape Cod Bay, whereas foraging occurs at considerable depth (~150 m) in the Bay of Fundy (Mayo & Marx 1990, Parks et al. 2011, Baumgartner & Mate 2003, Baumgartner et al. 2003b, Baumgartner et al. 2003a). Different sampling techniques with different biases were employed in the habitats. Most notably, surface-net sampling in Cape Cod Bay may have underestimated prey consumption compared with deep-water sampling in the Bay of Fundy where vessel turbulence was less likely to affect prey densities sampled. However, prey densities in the Bay of Fundy may be imprecise as well because collection occurred at depths where the whales were assumed to be feeding (compared to Cape Cod Bay where the animals were confirmed to be feeding) (Baumgartner & Mate 2003). Therefore, prey densities sampled near feeding whales in both habitats may be lower than actual densities consumed because of sampling error, and should be considered minimum estimates.

Small samples size prevented the assessment of seasonal trends in energy consumption. The energetic density of primary prey (*Centropages typicus*, *Centropages hamatus*, *Pseudocalanus* spp. and *Calanus finmarchicus*) is known to vary over the foraging season (January-May), which would affect estimates of consumed energy. Changes in the chemical composition of zooplankton occur largely because of their life strategies and fluctuations in environmental conditions (DeLorenzo Costa et al. 2006a). For example, herbivorous copepods adapt to prey scarcity (phytoplankton availability varies seasonally) by storing energy, but omnivorous copepods are more opportunistic foragers and generally have small lipid reserves (DeLorenzo Costa et al. 2006a). Consequently, high resource availability results in an increase in the structural, store weights and lipids of *Calanus finmarchicus* (Hygum *et al.* 2000). For example, the carbon content of CV *Calanus finmarchicus* fluctuated by almost 40% over two months in Cape Cod Bay (DeLorenzo Costa et al. 2006a). This suggests that actual caloric consumption varies across the sampling season.

Predicted energy deficits may have occurred more easily in Cape Cod Bay because in-path prey samples were taken from individuals of unknown identity. Individual whales were not identified using photo-identification techniques in the field during prey sampling and thus lactating females may have been poorly represented. The samples may have been biased towards other demographic groups with lower daily energy needs (e.g. juveniles and adult males) and thus the energy deficit observed for lactating females may reflect this sampling bias (although it is un-testable). However, during the time that lactating females are most likely present in Cape Cod Bay (April and May), 3 of 19 prey samples exceeded the predicted energy needs of lactating females—and the remaining 16 samples were all well below predicted daily energy needs.

Overall, the model parameters used were considered to be reasonable and yielded realistic estimates of energy requirements for right whales. All-important parameters known to significantly influence energy requirements were included, and uncertainty in parameter values were assessed by assigning error terms to each input value. The model predictions thus consisted of a range of values that reflected the relative uncertainty surrounding the parameters used to generate the estimates of energy requirements. Furthermore, the model predictions compared favorably with field estimates of consumption in the Bay of Fundy, but not as well with those from Cape Cod Bay due perhaps to underestimating prey densities in the surface waters. It is noteworthy however that the model suggests that North Atlantic right whales need to feed for long hours in Cape Cod Bay to make ends meet (up to 22 hours per day). This prediction is consistent with limited field observations showing continuous feeding for over 8 hours by right whales that were individually followed in Cape Cod Bay (Jaquet et al. 2007).

4.3 Research Applications

Future environmental conditions thought to influence the quality and quantity of North Atlantic right whale prey are predicted to oscillate with increasing frequency (Greene & Pershing 2004). The results of this research may be used to quantitatively evaluate changes in the nutritive regime of North Atlantic right whales in response to environmental changes. Furthermore, the results may be qualitatively used to make linkages between observed changes in body condition and reproductive success to demonstrate nutritional stress.

The slow recovery of North Atlantic right whales can be partially attributed to anthropogenic mortality from ship strikes and entanglement in fishing gear (Caswell et al. 1999). An estimated 2.6 animals of a total population of at least ~449, die or incur serious injury (likely resulting in death) each year from vessel strikes and fishing gear entanglement (Waring et al. 2011). Comprehensive knowledge of North Atlantic right whale growth could assist in determining effective doses of antibiotics to administer to wounded animals, and doses of sedatives to entangled animals of different sizes (Moore et al. 2010). Administration of these treatments may improve the success of disentanglement efforts and the recovery of injured animals. However, some adjustments to dose levels will need to be made for chronically entangled individuals, as they are likely to be underweight relative to their body length. The growth model for North Atlantic right whales can thus be used to assist in medical treatment.

4.4 Future Research

This study was the first to estimate the energy needs of different demographic groups of North Atlantic right whales and to compare them with field estimates of prey consumption within two important habitats. The results of my study provide insight into the significant differences in quality and quantity of prey available to right whales in their core feeding habitats, and the potential for these two factors to create an energy imbalance. However, further quantitative assessments of the nutritional status of North Atlantic right whales will require continuous sampling of prey over the course of the year. Prey samples should also be collected in the presence of recognizable individuals (i.e. for animals of known age, sex and reproductive state); and the quality of prey consumed should also be frequently estimated to account for seasonal and temporal changes in prey quality.

The sensitivity analysis results highlighted several important areas for future research. For example, the sensitivity analysis demonstrated that estimates of digestive efficiency and residency time have large effects on the predicted energy needs of species. However, fecal digestive efficiency is unknown for right whales consuming a mixed diet and urinary efficiency is entirely unknown. There are also no estimates of the heat increment of feeding for right whales (or any other baleen whale). Another influential parameter was metabolism (basal metabolism and activity), which is largely a function of mass. Consequently, the bioenergetics model would benefit from having field estimates of metabolic rates (particularly for lactating females) as well as mass-at-age estimates. Obtaining such data will require developing novel techniques, but will ultimately improve the predictions of bioenergetics models and further contribute to the conservation and management of North Atlantic right whales.

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