Vol. 478: 253–272, 2013
doi: 10.3354/meps10000

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 25

Energetic requirements of North Atlantic right whales and the implications for species recovery

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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, recovery may also be limited because individuals are under nutritional stress. We 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. 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). We found that calves required the least energy (~1767 MJ d^{-1}) and that lactating females required the most (~4120 MJ d^{-1}). Juveniles required considerably more energy than adult males and non-reproductive females. Our estimates of energy requirements for juveniles (~1906 MJ d^{-1}), adult males (~1793 MJ d^{-1}), and non-reproductive females (~2104 MJ d^{-1}) compared favorably with estimates of actual consumption in Cape Cod Bay and the Bay of Fundy (i.e. they differed by ≤15%), suggesting that our model was reliable. However, lactating females appear to have obtained considerably less than their predicted energy requirements in both habitats. These findings suggest 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.

KEY WORDS: Bioenergetic model · *Eubalaena glacialis* · Nutritional stress · Energetic consumption · Calving rate · Reproductive interval

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 their recovery (Knowlton et al. 1994, Fujiwara & Caswell 2001). Several studies have found biotoxins, contaminants, and parasites in right whale tissue, feces and prey (e.g. Woodley et al. 1991, Weisbrod et al. 2000, Durbin et al. 2002, Doucette et al. 2006, Godard et al. 2006, Rolland et al. 2007b, Wise et al. 2008a,b), which could compromise reproduction. There is also mounting evidence that the North Atlantic population might be experiencing periods of prey shortage, which could similarly impair calving rates (Reeves

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et al. 2001, Greene & Pershing 2004, Pettis et al. 2004). Significantly fewer calves were observed between 1993 to 1995 and 1998 to 2000, when decreases in prey availability were detected (Greene & Pershing 2004), than would have been expected by chance alone (Kraus et al. 2007).

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). Adult females 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. King & Murphy 1985, Lockyer 1986, 2007, Trites & Donnelly 2003) and might reflect the apparent scarcity of their primary prey during the 1990s (Greene & Pershing 2000, 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 further 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 cetacean 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 (Lockyer 1981, Kenney et al. 1986, Winship et al. 2002, Noren 2011, Williams et al. 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. These early estimates of food requirements (Kenney et al. 1986) can be refined by accounting 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 influence 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. Lockyer 1986, 2007, Miller et al. 2011). 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.

We sought to predict 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. We incorporated uncertainty into each model parameter and ran a sensitivity analysis to assess the reliability of the model predictions. We then estimated the amount of food right whales actually consumed using observations of feeding behaviour and the energy density of prey sampled in 2 critical habitats (Bay of Fundy and Cape Cod Bay). Finally, we compared the predicted energy needs of different demographic groups of right whales with the observed amounts of prey consumed in the 2 habitats to evaluate the model predictions and assess the nutritional stress hypothesis.

MATERIALS AND METHODS

Bioenergetics model

The bioenergetics model for right whales was essentially a simple energy balance equation that expressed 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 was parameterized using both pre-existing species-specific data and non-specific estimates from other marine mammal species. 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 (10 000) based on probability distributions of each parameter (i.e. normal, uniform, triangular, gamma). We therefore generated thousands of possible estimates of the daily energy needs for each demographic group of North Atlantic right whales, from which we calculated a mean estimate of energy requirements and a standard deviation. This Monte Carlo modeling approach also allowed us to assess the relative influence and uncertainty of each parameter group (metabolism, growth, digestion, fasting and reproduction) on the model outputs (e.g. Petersen et al. 2008, Winship et al. 2002).

We calculated mean daily gross energy requirements (GER) by sex for 3 age classes (calf, 0 to 1 yr; juvenile, >1 and <9 yr; and adult, >9 yr) (Hamilton et al. 1998), and for 3 reproductive states of adult females (pregnant, lactating and resting) using:

$$\text{GER} = \frac{\left[\left(\dfrac{P + (A \times \text{BMR})}{E_{\text{HIF}} \times E_{\text{F+U}}}\right) + R_{\text{G+L}}\right] \times 365}{365 - (t_{\text{m}} + t_{\text{r}})} \qquad (1)$$

where GER is the gross energy requirement by sex, age and reproductive class, and P is production or body growth, A is activity, BMR is basal metabolic rate or resting metabolic rate for actively growing or reproductive individuals, E_{HIF} is the efficiency with which metabolizable energy is used (or 1 minus the heat increment of feeding expressed as a proportion of metabolizable energy), and $E_{\text{F+U}}$ is digestive efficiency (fecal and urinary) (Winship et al. 2002). $R_{\text{G+L}}$ is the total cost of gestation and lactation. t_{m} and t_{r} represent the time in days individuals spend fasting while migrating and residing in the southern calving grounds and north to the foraging grounds, respectively.

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

Model parameters

We estimated digestive efficiency ($E_{\text{F+U}}$) by incorporating existing values of fecal efficiency from right whales and predicted values of urinary digestive efficiency. We 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. Previous estimations 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, Beardsley et al. 1996, Baumgartner et al. 2003a,b), were used. Energy loss through urine is unknown but is presumably proportional to the nitrogen content of prey (urinary loss represents ~90 % of total nitrogen content per organism; Worthy 1990). We thus assumed that ~8 % of ingested energy was lost through urine. This estimate is based on a mixed diet of all life stages of *C. finmarchicus*, *Centropages hamatus*, *Centropages typicus* and *Pseudocalanus* spp. and was calculated using mean carbon/nitrogen values for different life stages from DeLorenzo Costa et al. (2006a). We accounted for the energy lost when 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 containing equal proportions of all species, but a combined loss of ~26 % (digestive efficiency of 74 %) if the diet consists only of CV *C. finmarchicus.* Overall, the digestive efficiency was estimated to be lower for an exclusive CV *C. finmarchicus* diet compared to a mixed diet because the nitrogen content of CV *C. finmarchicus* is ~80 % higher than for the other taxa (DeLorenzo Costa et al. 2006a).

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 to 15% of energy ingested by pinnipeds may be expended during the digestion process (Markussen et al. 1994, Costa & Williams 1999), 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 (Ryg & Øritsland 1991, Rosen & Trites 1999, Winship et al. 2002), we 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 *Eumetopias jubatus* for the energetic costs of digestion associated with maintenance and growth in protein and lipid (Rosen & Trites 1999, Winship et al. 2002). We 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 records (Lockyer 1976, Lockyer et al. 1985; Tables 1 & 2). E_{HIF} parameter estimates thus included the inefficiencies of lipid and protein anabolism. We used estimates from Steller sea lions because energetic costs associated with the heat increment of feeding are influenced by prey composition (e.g. 6% carbohydrates, 13% fat, and 30% protein; Costa & Williams 1999) and the protein content of Steller sea lion and North Atlantic right whale prey is somewhat similar. For example, Steller sea lion prey (herring *Clupea harengus*) is 15.8% protein (Rosen & Trites 1999) and the nitrogen content of right whale prey, which may be used as a proxy for protein content, ranges from 3.5% (*Centropages typicus* all stages) to 22.2% (*Calanus finmarchicus* CV) (DeLorenzo Costa et al. 2006b).

Production costs (P) were estimated using growth curves to calculate the increase in body mass from one age to the next and also included corresponding information about the body composition of each age group. We estimated mass-at-age by first predicting length-at-age using a 2-phased Gompertz growth model and then using an allometric weight-at-length model (Fortune et al. 2012). We estimated the energetic cost of growth for each age class with growth data for individuals aged 0 to 22 yr using the following (Winship et al. 2002):

$$P = \Delta M \times [(p_{\mathrm{lip}} \times \mathrm{ED}_{\mathrm{lip}}) + (1 - p_{\mathrm{lip}})(1 - p_{\mathrm{w}}) \times \mathrm{ED}_{\mathrm{pro}}] \quad (2)$$

where P is production (kJ), ΔM is the body mass growth increment (kg), p_{lip} is the proportion of new body mass that is lipid, $\mathrm{ED}_{\mathrm{lip}}$ is the energetic density of lipid (~39 300 kJ kg^{-1}; Schmidt-Nielsen 1990), p_{w} is the proportion of lean tissue that is water, and $\mathrm{ED}_{\mathrm{pro}}$ is the energetic density of protein (~18 000 kJ kg^{-1}; Schmidt-Nielsen 1990, Winship et al. 2002). We 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 (Woodley et al. 1991, Miller et al. 2011). Whaling data from other baleen whales provided estimates for the proportion of lean tissue that was protein and the proportion of lean tissue that was water (Lockyer et al. 1985).

Table 1. *Eubalaena glacialis.* Digestive efficiency estimates that correspond to maintenance and growth estimates from Winship et al. (2002) used to approximate the efficiency with which metabolizable energy is used (E_{HIF}) for North Atlantic right whale calves, juveniles and adults

	E_{HIF}			
	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 2. *Eubalaena glacialis.* Values of efficiency with which metabolizable energy is used (E_{HIF}) generated for North Atlantic right whales according to demographic unit by running 500 Monte Carlo simulations (randomly selecting a parameter value from a normal distribution) (Table 1). na: not applicable

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

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

$$\mathrm{BMR} = 292.88M^{0.75} \quad (3)$$

was derived from captive studies of terrestrial mammals, where the basal metabolism (BMR) is kJ d^{-1} and M is body mass in kg (Kleiber 1975, Lockyer 2007). We allowed BMR 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; Fortune et al. 2012).

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 *Balaena mysticetus* is estimated (using a heat-flux model) to only be about one-third of that predicted by Kleiber for terrestrial mammals (George 2009). This low metabolic rate might reflect having a disproportionately greater amount of fat and a low relative proportion of to lean tissue compared bone and adipose 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 the Kleiber allometric prediction, we chose to assume that basal metabolism was best described using Kleiber's equation.

We accounted for the elevated metabolic rate of immature animals that are actively growing (e.g. juvenile metabolic rate is 2 times the rate of adults of the same body mass; Brody 1945, Worthy 1987, 1990, Hansen et al. 1995) by multiplying the BMR of calves by 1.4 and the BMR of juveniles by 1.2 (decreased BMR scalar because rate of growth in mass is ~50 % less than 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 predominant behaviours. We began by assuming a simplified activity budget wherein individuals partitioned their time into either only feeding or traveling and incorporated the costs of these activities using a metabolic scalar. For example, Nousek-McGregor (2010) estimated that the energetic costs of foraging were ~500 MJ d^{-1} and that costs associated with traveling were ~30 % lower. We then used activity-specific drag coefficients to estimate the activity costs (A) associated with each behaviour (Nousek-McGregor 2010) and the proportion of time (PT) that individuals spent per day engaged in each behaviour (travel or foraging):

$$A = PT_{\text{travel}} \times A_{\text{travel}} + (1 - PT_{\text{travel}}) \times A_{\text{forage}} \qquad (4)$$

For pregnant females, we increased costs by 3 to 4 % to account for increased drag (Nousek-McGregor 2010). We also incorporated uncertainty into our estimate of A by varying the proportion of time individuals spent foraging (PT_{forage}) (52 to 93 % or ~12 to 22 h d^{-1}), assuming that whales were only traveling when they were not foraging (Goodyear 1996). Since the energetic costs of foraging are greater than traveling, our upper bound estimate of A assumed the whales foraged for ~22 h d^{-1} and our lower bound estimate assumed only ~12 h d^{-1}.

The foraging season of mysticete whales is highly seasonal compared to odontocetes that forage almost continuously throughout the year. We assumed that fasting occurred while individuals were traveling from their calving grounds in the southern United States (Florida and Georgia) and while they occupied these calving grounds. We 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 sighted (North Atlantic Right Whale Consortium 2010). We used migration times of 21 to 26 d (Firestone et al. 2008) and assumed that lactating females spent a minimum of 7 d on the calving grounds and excluded any estimates below this threshold. We incorporated the estimates of fasting into the bioenergetics model by reducing the total number of days available for foraging per year (365 minus the number of fasting days). To include uncertainty in the predictions, we 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, we had to rely on allometric models because fetal data are too sparse to directly model fetal growth (mass) of North Atlantic right whales. We used 2 methods to estimate the costs of gestation. First we calculated the heat of gestation (R_G), which required calf mass measurements and was estimated using:

$$R_G = 18\,421.9 M_f^{1.2} \qquad (5)$$

where R_G is in kJ and M_f 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). We 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 en-

Table 3. *Eubalaena glacialis.* Bioenergetic model parameter values for North Atlantic right whales (Eq. 1). See 'Materials and methods' for details

Parameter	Symbol	Equation	Demographic groups	Value	Probability distribution
Activity	A	(4)	Pregnant	1.773–2.027, 1.900	Triangular
			Calf, juvenile, adult, lactating	1.713–1.959, 1.836	Triangular
Basal metabolic rate (kJ d^{-1})	BMR	(3)	All	2.655 ± 0.799	Normal
Fecal and urinary digestive efficiency	E_{F+U}	(1)	All	0.740–0.858	Uniform
Heat increment of feeding	E_{HIF}	(1)	Adult, pregnant, lactating	0.875 ± 0.036	Normal
			Juvenile	0.739 ± 0.065	Normal
			Calf	0.742 ± 0.042	Normal
Proportion of body growth that is lipid	p_{lip}	(2)	Pregnant, lactating	0.369 ± 0.016	Normal
			Adult	0.358 ± 0.027	Normal
			Juvenile	0.356 ± 0.043	Normal
			Calf	0.189 ± 0.043	Normal
Proportion of lean body growth that is water	p_w	(2)	All	0.642–0.702	Uniform
Energy deposited during gestation (fetus) (MJ)	R_G	(5)	Pregnant	4.3–225.5	Uniform
Energy transferred during lactation (calf) (MJ)	R_L	(1)	Lactating	1391–1933	Uniform
Time fasting while migrating (d)	t_m	(1)	All (except calves)	22.5 ± 1.291	Normal
Time fasting on calving grounds (d)	t_r	(1)	Resting, pregnant	1.638, 0.035, 14.495	Gamma
			Lactating	46.410 ± 14.540	Normal
			Male	0.973, 11.164, 3.388	Gamma
			Juvenile	16.331 ± 8.480	Normal

abled us to incorporate uncertainty into the model predictions.

We incorporated information about calf energy needs and estimates of female milk production to account for the elevated costs of lactation. First, we 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 1981). We 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 1981). Information on the quantity and quality of milk from other baleen whales was then combined with information on the estimated age of weaning for right whales (Lockyer 1981). Thus, we again employed 2 different methods to incorporate a range of predictions for the cost of lactation.

Parameter uncertainty and model evaluation

Uncertainties in model predictions were evaluated using Monte Carlo simulations that selected different combinations of parameters from a predetermined range of possible values. We assigned a probability distribution for each model parameter (i.e. uniform, normal, triangular and gamma) based on available information or assumed a uniform distribution in the absence of adequate information. We 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 & 4). 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.

We 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. This analysis would determine the sensitivity of model outputs to variability (or uncertainty) of an input parameter and whether model outputs 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

Table 4. *Eubalaena glacialis.* Sensitivity analysis of bioenergetic model gross energy requirement (GER) predictions for North Atlantic right whales by demographic group where uncertainty was incorporated into each parameter group by running 10 000 Monte Carlo simulations. Results from a Kolmogorov-Smirnov test for normality (using Nortest 1.0 package in the statistical program R) suggested that all probability distributions were significantly different from a normal distribution ($p < 0.05$)

Parameter group				GER (MJ d^{-1})				
	Mean	SD	CV	Median	Minimum	Maximum	Skew	Kurtosis
Calf								
Production	1928	250.3	12.98	1910	1091	2955	0.35	3.29
Digestion	1699	238.4	14.03	1685	898	2932	0.37	3.33
Metabolism	2015	237.2	11.77	2002	1193	2897	0.22	3.14
All	1767	261.0	14.77	1750	963	3039	0.41	3.38
Juvenile								
Production	2107	262.2	12.44	2097	1341	3111	0.27	3.18
Digestion	1970	311.4	15.81	1945	1037	3764	0.47	3.47
Metabolism	2254	286.5	12.71	2246	1403	3441	0.26	3.18
Fasting	2108	267.2	12.68	2099	1305	3289	0.26	3.15
All	2104	345.2	16.41	2074	1150	3719	0.52	3.46
Adult male								
Production	1802	248.4	13.78	1782	1088	2691	0.30	3.02
Digestion	1674	252.2	14.57	1660	902	2807	0.31	3.09
Metabolism	1933	273.7	14.16	1916	1112	2974	0.26	3.06
Fasting	1799	250.4	13.92	1783	1081	2732	0.28	3.10
All	1793	261.3	14.57	1778	964	2803	0.31	3.03
Adult female								
Production	1918	264.8	13.81	1902	1158	2859	0.26	3.07
Digestion	1787	266.4	15.89	1774	1044	3070	0.28	3.03
Metabolism	2050	288.2	14.06	2033	1162	3173	0.26	3.12
Fasting	1924	300.1	15.60	1897	1078	3885	0.54	3.76
All	1906	302.9	15.89	1885	1013	3705	0.48	3.57
Pregnant								
Production	1926	266.3	13.82	1905	1164	2868	0.30	3.10
Digestion	1787	268.3	15.01	1769	978	2904	0.32	3.03
Metabolism	2106	298.9	14.19	2090	1220	3250	0.28	3.08
Fasting	1933	293.9	15.27	1906	1100	4000	0.60	4.17
Gestation	1992	266.8	13.39	1973	1163	3024	0.27	3.07
All	2090	329.6	15.77	2068	1124	4232	0.54	4.14
Lactating								
Production	3778	287.6	7.61	3756	2963	4797	0.28	3.05
Digestion	3198	289.2	9.05	3178	2331	4354	0.33	3.09
Metabolism	3477	310.9	8.94	3454	2568	4678	0.29	3.12
Fasting	3344	332.5	9.94	3325	2336	4814	0.32	3.18
Lactation	4112	346.0	8.41	4103	2979	5447	0.16	2.92
All	4120	414.0	10.05	4105	2807	5738	0.24	3.05

of variation for each parameter group revealed which parameters introduced the greatest uncertainty into our 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.

Consumption estimates

We evaluated the model predictions by comparing the GER estimates for different demographic groups with estimates of energetic consumption (EC; see Eq. 6) in 2 feeding habitats. Our general method was to combine estimates of prey energy density (combining prey quality D_{energy} and prey density D_{prey}) from field samples with consumption estimates calculated from foraging behaviour and biomechanics. Prey density was calculated using 17 samples from the Bay of Fundy and 2 samples from the adjacent Roseway Basin habitat. All were collected at depth from an optical plankton counter (Baumgartner & Mate 2003). The 28 samples from Cape Cod Bay were collected at the surface with a conical net (60 cm diameter ring net with 333 µm mesh) by the Provincetown Center for Coastal Studies; samples were taken from the path of feeding right whales (within 50 m of the skim feeding animal). Consumption rates were calculated by estimating the foraging distance ($F_{distance}$) and assuming a foraging speed of 0.64 m s^{-1} in Cape Cod Bay (Mayo & Marx 1990) and 0.986 m s^{-1} in the Bay of Fundy (Nousek-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 (~12, 15 and 22 h d^{-1} according to Goodyear 1996) allowed us 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 capturing prey would likely differ between habitats.

For the deeper diving Bay of Fundy animals we accounted for ascent, descent, and bottom phases (where prey consumption likely occurs), and surface recovery times using results from 3 tagging studies conducted on North Atlantic right whales in the Bay of Fundy (Goodyear 1996, Baumgartner & Mate 2003, Nousek-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. We also assumed that prey densities and species composition remained constant over the foraging period, and we corrected for the inefficiencies of right whale baleen to capture prey by applying filtration efficiencies ($B_{filtration}$) (Mayo et al. 2001, C. A. Mayo & S. M. E. Fortune unpubl. data) to the following energetic consumption (EC) estimate:

$$EC = D_{prey} \times B_{filtration} \times D_{energy} \times F_{distance} \qquad (6)$$

RESULTS

Energy requirements

Mean (±SD) daily energy requirements (averaged over 1 yr for calves, 8 yr for juveniles and 13 yr for adults) differed between demographic groups. Calves (1767 ± 261.0 MJ) and adult males (1793 ± 261.3 MJ) required the least total energy per day and lactating females required the most (4120 ± 414.0 MJ; Fig. 1, Table 4). Pregnant females (2090 ± 329.6 MJ) and juveniles (2104 ± 345.2 MJ) required marginally more energy each day than resting females (1906 ± 302.9 MJ; Fig. 1, Table 4). However, daily energy needs as a proportion of mean body size (Fig. 2) shows calves required the most energy per unit mass (0.227 MJ kg^{-1}), followed by lactating females (0.151 MJ kg^{-1}), juveniles (0.111 MJ kg^{-1}), pregnant females (0.077 MJ kg^{-1}), resting females (0.070 MJ kg^{-1}) and males (0.066 MJ kg^{-1}).

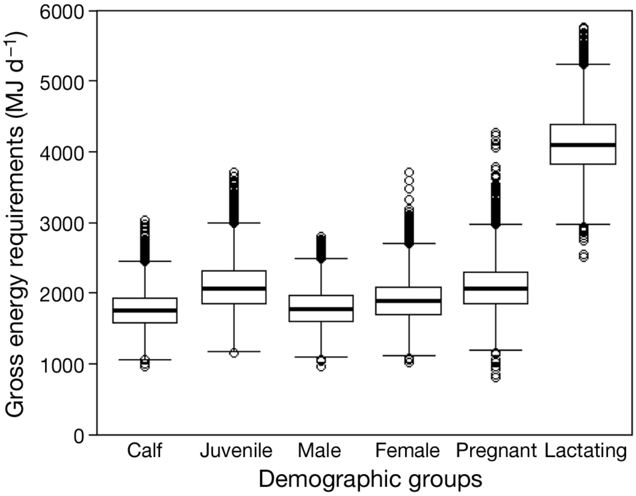

Fig. 1. *Eubalaena glacialis.* Mean daily gross energy requirements for different demographic groups of North Atlantic right whales predicted using the generalized bioenergetics model and calculated as annual energy requirements divided by the number of available foraging days per year. Males: reproductively mature adults (≥9 yr); females: adults ≥9 yr that were not pregnant or lactating; calves: animals aged 0 to 1 yr; juveniles: animals >1 and <9 yr of age. These estimates were derived from 10 000 Monte Carlo simulations that incorporated uncertainty assuming model parameter probability distributions of either normal, uniform, triangular or gamma, as described in Table 3. Bar: median; box: interquartile range; whiskers: max./min. values; dots: outliers

North Atlantic right whales exhibit rapid post-natal growth and consequently, the mean daily energy requirements of immature (calves and juveniles) animals varied considerably overtime (Fig. 3). For example, calves attain ~75% of their maximum size upon weaning and their mean daily energy requirements increase by ~57% between age 0 and 1 (mean daily energy requirements range from 730 to 1700 MJ, Fig. 3). Furthermore, juvenile animals attain 92% of their maximum size before sexual maturity (9 yr) and their energy requirements increase by ~27% between age 1 and 9 (mean daily energy requirements range from 1770 to 2410 MJ; Fig. 3). The predicted energy needs of calves (0.5 to 1.0 yr) is higher than juveniles (2 to 3 yr) because of the high costs associated with post-natal growth (e.g. elevated production and metabolic costs). Upon weaning at 1 yr, the daily growth rate of juveniles decreases considerably (Fortune et al. 2012), thus lowering energetic requirements.

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 g of prey contains 4.186 kJ of energy (Lockyer 1981, Kenney et al. 1986, Mauchline 1998), calves required the greatest relative biomass (5.4 ± 0.76%) followed by lactating females (3.6 ± 0.37%; Table 5). Conversely, non-reproductive adults only needed to consume the equivalent of 1.6 ± 0.24% for males and 1.7 ± 0.27% of their body mass per day for resting females to meet their food requirements (Table 5).

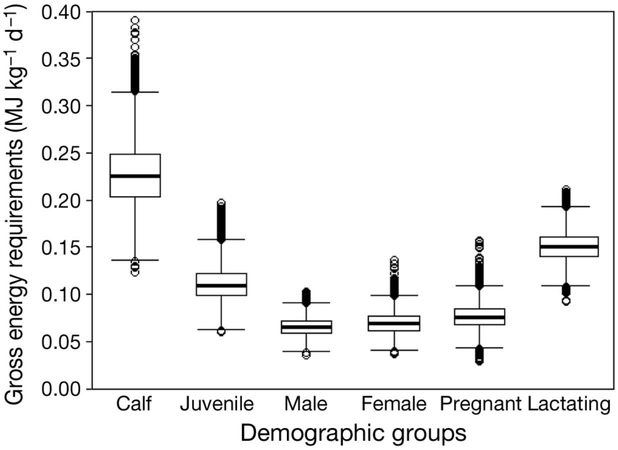

Fig. 2. *Eubalaena glacialis.* Mean daily energy needs for different demographic groups of North Atlantic right whales expressed as a proportion of mean body mass (Fortune et al. 2012). See Fig. 1 legend for definitions of demographic groups. Boxplot limits as in Fig. 1

Residency time

Of all the demographic groups of North Atlantic right whales analyzed (lactating, non-lactating, juvenile and adult male), we found that lactating females spent the longest time (mean ± SD) on the calving grounds off Florida and Georgia (46.32 ± 14.60 d), and that males spent the least time (3.11 ± 3.33 d; Fig. 4). This difference between residency times of males and females is consistent with what we anticipated given the reproductive biology of North Atlantic right whales. Residency times for non-lactating adult female (23.75 ± 18.60 d) and juvenile (16.33 ± 8.50 d) right whales were similar to each other, but significantly shorter than for the lactating females (Fig. 4). This analysis only included data collected from the calving grounds and thus assumes that all demographic groups spend a portion of the year fasting.

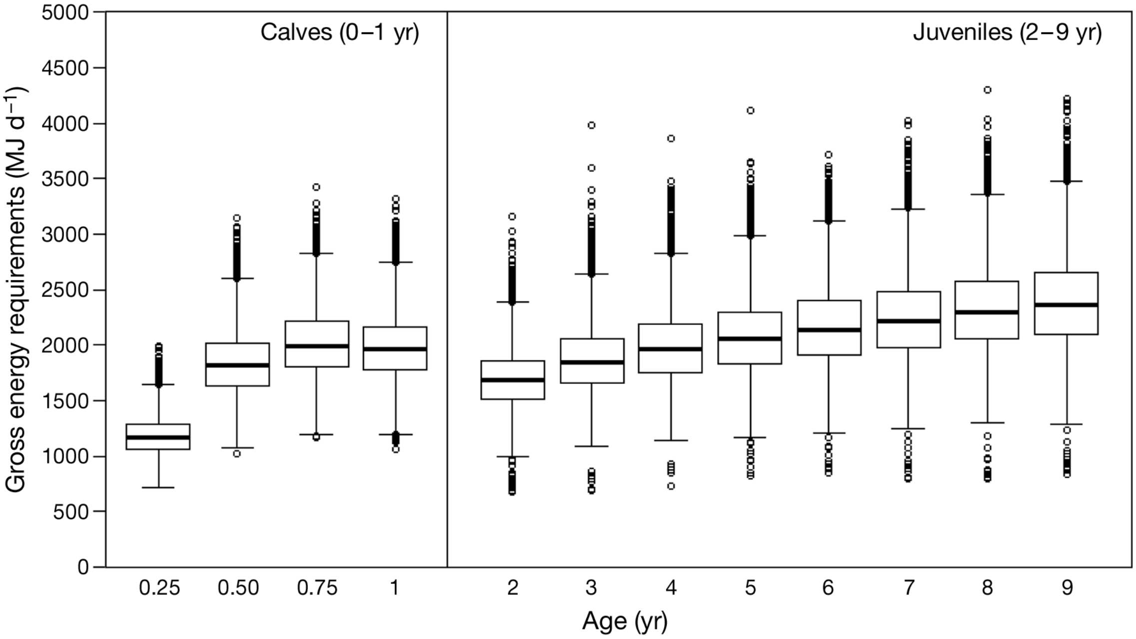

Fig. 3. *Eubalaena glacialis.* Mean daily gross energy requirements for immature North Atlantic right whales predicted using the generalized bioenergetics model, and calculated as annual energy requirements divided by the number of available foraging days per year for juveniles and quarterly energy requirements for calves (i.e. energy required between 0–0.25, 0.25–0.50, 0.50–0.75 and 0.75–1.00 yr). Calves consisted of animals aged 0 to 1 yr and juveniles represented animals >1 and <9 yr of age. These estimates were derived from 10 000 Monte Carlo simulations that incorporated uncertainty into model parameters. The elevated energy needs of calves between 0.50 and 1 yr (compared to juveniles of 2–3 yr) largely reflects the high cost of body growth (of which ~75% occurs during dependency). Boxplot limits as in Fig. 1

Table 5. *Eubalaena glacialis.* Predicted food requirements expressed as a proportion of mean body mass (Fortune et al. 2012) that each demographic group of North Atlantic right whales need to consume to meet their predicted daily energy needs, assuming 1 g of prey is equivalent to 4.186 kJ

Demographic group	Food requirements (% body mass) Mean	SD
Calf	5.4	0.76
Juvenile	2.7	0.31
Adult male	1.6	0.24
Adult female	1.7	0.27
Pregnant	1.8	0.30
Lactating	3.6	0.37

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 14.03, range 11.77 to 14.03) and juvenile right whales (15.81, 12.44 to 15.81; Fig. 5, Table 4). Digestion also had the greatest effect on the predictions of energy requirements for adult males (14.57, 13.78 to 14.57; Fig. 5, Table 4) 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 also most sensitive to estimates of digestion (15.89, 13.81 to 15.89; Fig. 5, Table 4). The predicted energy needs of pregnant (15.27, 13.39 to 15.27) and lactating females (9.94, 7.61 to 9.94; Fig. 5, Table 4) were most sensitive to fasting due to the greater range in time they spent on the calving grounds.

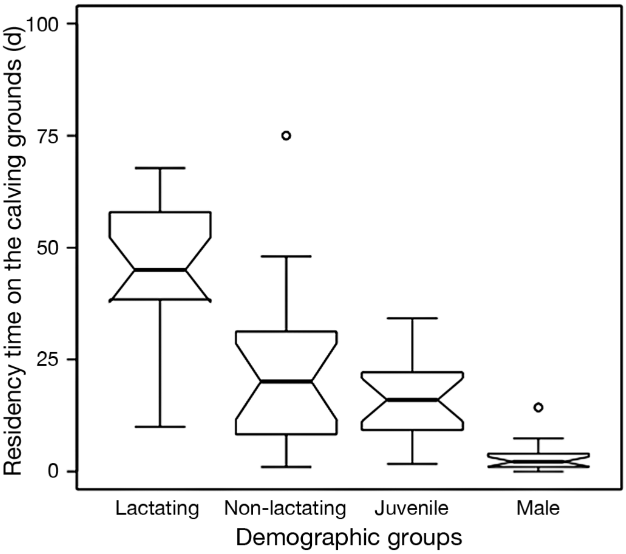

Fig. 4. *Eubalaena glacialis.* Mean residency times on the calving grounds (Florida and Georgia, Southeastern US) for different demographic groups of North Atlantic right whale calculated by subtracting the last day seen on the calving grounds from the first day seen using identification data from the North Atlantic Right Whale Consortium from 1991 to 2009 (n = 18 yr). Adult males were absent from the calving grounds in 1991 and thus received a residency time of 0 d for this year. Each boxplot shows the distribution of 18 annual mean residency times. Boxplot limits as in Fig. 1; notch indicates median uncertainty (confidence interval)

Prey consumption

Particle densities of prey differed between the 2 feeding habitats. In the Bay of Fundy, prey samples taken near feeding right whales (6618 ± 3481 organisms m^{-3}, mean ± SD; Baumgartner & Mate 2003) had a mean particle density that was ~56 % lower than in Cape Cod Bay (14778 ± 18594 organisms m^{-3}; Fig. 6). However, the range in particle densities in the 2 habitats was greater in Cape Cod Bay (740 to 58 742 organisms m^{-3}) compared to the Bay of Fundy (3020 to 14 945 organisms m^{-3}; Fig. 6), suggesting that prey consumption may be more variable in Cape Cod Bay. However, zooplankton patches could also be more spatially disjointed in Cape Cod Bay, and some samples could have been collected from areas where extreme concentrations formed.

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 (mean ± SD) in the Bay of Fundy (52 ± 27 kJ m^{-3}) compared to Cape Cod Bay (20 ± 22 kJ m^{-3}; Fig. 6). Minimum and maximum energetic densities varied from 24 to 116 kJ m^{-3} in the Bay of Fundy and 1 to 87 kJ m^{-3} in Cape Cod Bay (Fig. 6). This suggests that the nutritional value of prey found near the North Atlantic right whales was better on average in the Bay of Fundy.

Our estimates of the mean (±SE) amounts of food 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 forag-

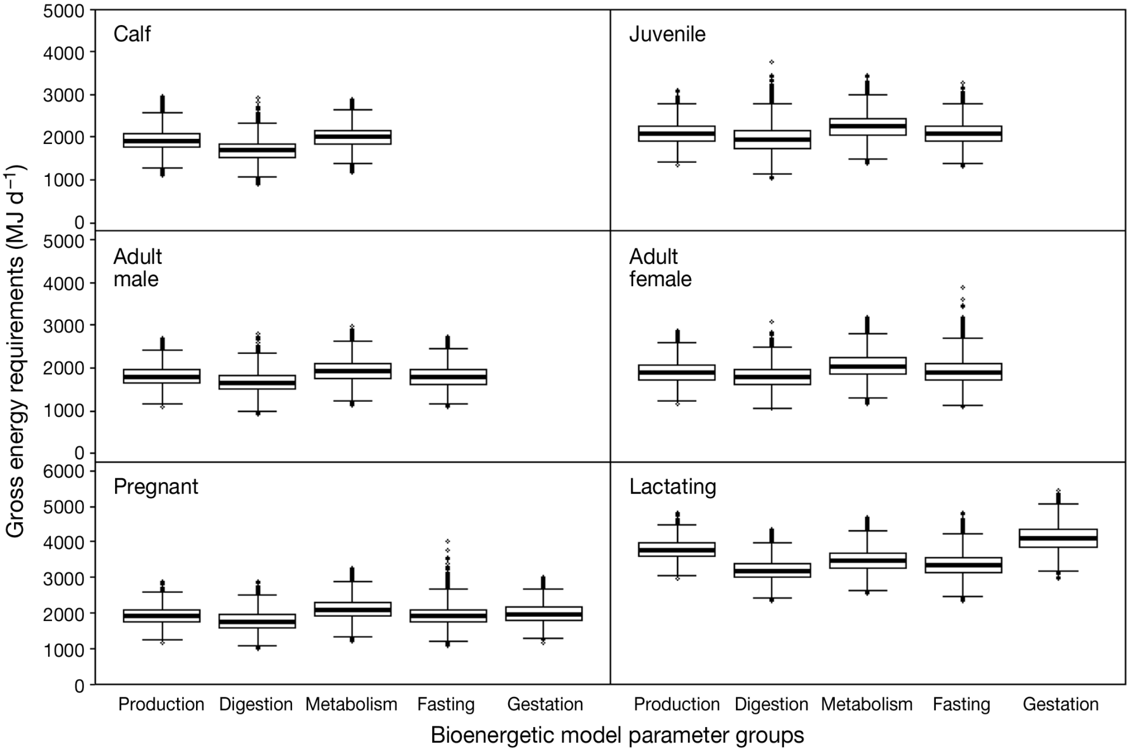

Fig. 5. *Eubalaena glacialis.* Sensitivity analysis results from the bioenergetic model that predicted the daily gross energy requirements for each demographic group of North Atlantic right whales derived from 10 000 Monte Carlo simulations that incorporated uncertainty into each parameter group (i.e. 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. Boxplot limits as in Fig. 1

ing, F_{distance} in Eq. 6) of 29, 35 and 51 km, we predicted that North Atlantic right whales consumed a minimum of 727 ± 757 MJ d^{-1}, a mean of 943 ± 969 MJ d^{-1}, and a maximum of 1311 ± 1348 MJ d^{-1} (Fig. 7) 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 than that for 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 ± 751.69 MJ d^{-1} for a right whale swimming a minimum of 20 km d^{-1} while ingesting prey, a mean of 1726 ± 907.81 MJ d^{-1} for a mean of 25 km d^{-1}, and a maximum of 2559 ± 1345.82 MJ d^{-1} (Fig. 7) for a maximum swimming distance of 36 km d^{-1}. 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 on average ~62% (47–77 95% CI) of their predicted energy needs from the Bay of Fundy, and only ~33% (20–44) of their food requirements by foraging in Cape Cod Bay (Table 6). Comparatively, lactating females could obtain ~39% (29–54) of their needs in Cape Cod Bay and ~77% (59–95) in the Bay of Fundy when fasting costs are not accounted for (~19% decrease in mean daily GER). However, adult males almost met their needs in Cape Cod Bay (~73, 45–101%) and exceeded their needs in the Bay of Fundy (~142, 109–176%) under the same foraging scenario (Table 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.

Based on estimates of average energy consumption derived from the relatively few prey samples (n = 28 in Cape Cod Bay between 2001 and 2010, n = 19 in the Bay of Fundy between 2000 and 2001), right whales in Cape Cod Bay needed to feed for significantly longer to meet their daily needs, and there did not appear to be sufficient energy in either habitat to support lactating females (Table 6). However, a

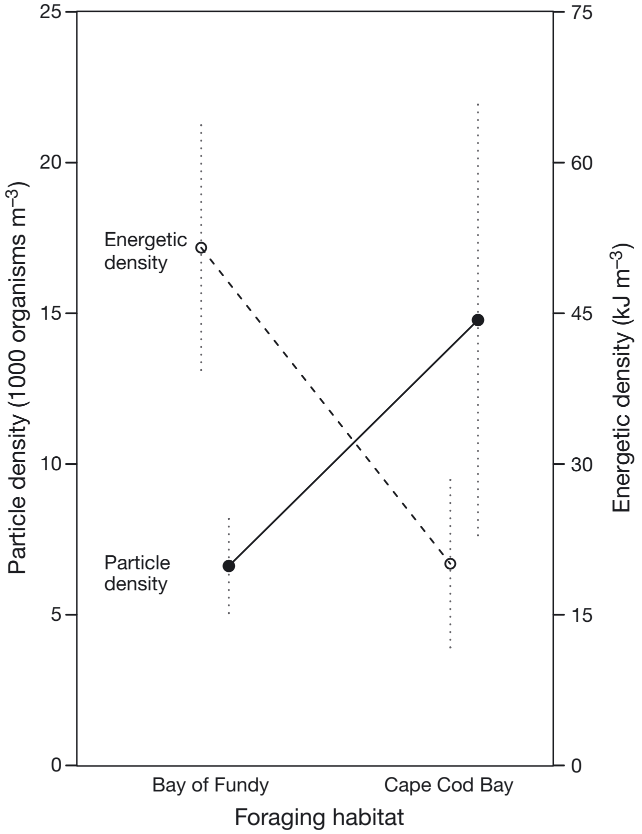

Fig. 6. Comparison of particle (solid line) and energetic densities (dotted line) of prey samples taken from Cape Cod Bay and Bay of Fundy. Data are mean densities ± full range of estimates

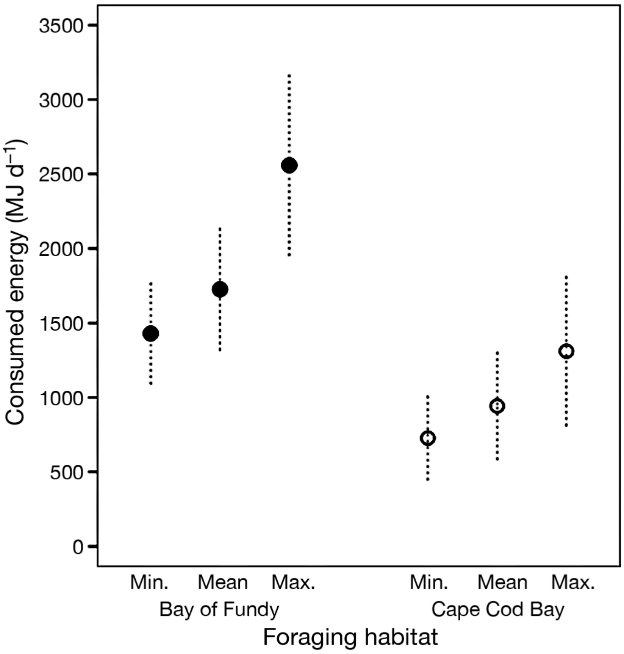

Fig. 7. *Eubalaena glacialis*. North Atlantic right whale mean energetic consumption predicted for 2 foraging habitats, Cape Cod Bay (CCB, n = 28, ○) and the Bay of Fundy (BOF, n = 19, ●) with 95% confidence limits (dotted lines). These estimates were created assuming minimum, mean and maximum foraging scenarios (when individuals are actively consuming prey) of 12.5, 15.1, and 22.3 h d^{-1}, respectively, for CCB and 6.6, 8.0, and 11.8 h d^{-1}, respectively, for BOF. 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 minimum, mean and maximum 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. Consumption estimates were also corrected for imperfect filtration (Eq. 6)

small portion of the prey samples did have sufficient energy to support all demographic groups of right whales. For example, 4% of the prey samples from Cape Cod Bay cointained sufficient energy to meet the energetic needs of all demographic groups foraging for 15 h d^{-1}, and 11–14% of the samples were sufficient to meet their needs under the 22 h d^{-1} feeding scenario (Table 6). In the Bay of Fundy all demographic groups, except lactating females, were able to meet their food needs after foraging for only 12 h d^{-1}, and all demographic groups were able to achieve an energy balance after foraging for 15 and 22 h d^{-1}. Thus, the model predictions of energy requirements are consistent with the field estimates of prey availability assuming that the whales could locate the higher energy-rich patches.

DISCUSSION

Calculating the energy needs of North Atlantic right whales by demographic group provides a perspective on the nutritional status and potential impacts on 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 and the Bay of Fundy. The discrepancy between the predictions of daily energy needs and estimates of actual energy consumed suggests that lactating females are more susceptible to experiencing periods of nutritional stress than any other demographic group. This finding has implications for the recovery of right whales.

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

Table 6. *Eubalaena glacialis.* Estimated energy consumed (MJ d^{-1}) by individual North Atlantic right whales and the percent of mean daily energy requirements that different demographic groups could obtain in Cape Cod Bay (between 2001 and 2010) and the Bay of Fundy (2000 and 2001) under 3 foraging scenarios (feeding either 12.5, 15.1 or 22.3 h d^{-1}). All values are means with 95% confidence limits in brackets, with numbers in **bold** indicating when the predicted daily energy needs were within ± 15% of the energy consumed. Also shown are the percentages of prey samples for each region (n = 28, Cape Cod Bay; n = 19, Bay of Fundy) that contained sufficient energy to meet (within ±15%) or exceed (>15%) the predicted daily energy needs of the right whales. Instances when at least one prey sample yielded an estimate of energy consumption that was within 15% of the predicted energy needs is indicated in **bold**

	Cape Cod Bay scenarios			Bay of Fundy scenarios		
	Minimum	Mean	Maximum	Minimum	Mean	Maximum
Time feeding (h d^{-1})	12.5	15.1	22.3	12.5	15.1	22.3
Energy consumed (MJ d^{-1})	727	943	1311	1429	1726	2559
Energy (95% CIs)	(447–1008)	(584–1303)	(811–1810)	(1091–1767)	(1318–2134)	(1954–3164)
Demographic group	Predicted energy needs met (%)			Predicted energy needs met (%)		
Juvenile (95% CIs)	34 (21–48)	45 (28–62)	**62 (38–86)**	68 (52–84)	**82 (62–101)**	**121 (92-150)**
Adult male	40 (25–56)	52 (32–72)	**73 (45–101)**	**79 (61–98)**	**96 (73–119)**	**142 (109–176)**
Adult female	38 (23–53)	50 (31–68)	**69 (43–95)**	**75 (57–93)**	**91 (69–112)**	**134 (103–166)**
Pregnant	35 (21–48)	45 (28–62)	**63 (39–86)**	68 (52–84)	**82 (63–102)**	**122 (93–151)**
Lactating	18 (11–24)	23 (14–32)	32 (20–44)	35 (26–43)	42 (32–52)	62 (47–77)
Demographic group	Prey samples (%)			Prey samples (%)		
Juvenile	7	**14**	**25**	**26**	**26**	**68**
Adult male	**11**	**14**	**29**	**26**	**42**	**74**
Adult female	**11**	**14**	**25**	**26**	**42**	**68**
Pregnant	7	**14**	**25**	**26**	**26**	**74**
Lactating	0	**4**	7	0	**5**	**21**

to one another (Fig. 1). The model suggests that mean daily intake ranges from 1793 to 2104 MJ for juveniles, adult males, and adult females (pregnant and non-pregnant). This equates to ~427 to 568 kg of copepods d^{-1} for each individual, assuming that copepods contain ~4.186 kJ g^{-1} wet wt (Kenney et al. 1986, Mauchline 1998, Lockyer 2007). However, expressing daily energy needs of right whales in terms of mean body size shows that calves (0.23 MJ kg^{-1}) require ~50% more energy than juveniles (0.11 MJ kg^{-1}) and more than twice that of adults (i.e. an adult female requires 0.07 MJ kg^{-1}).

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 (e.g. Brody 1945, Worthy 1987, 1990, Hansen et al. 1995). North Atlantic right whales attain 76% of their maximum length but only ~46% of their weight within the first year of life (Fortune et al. 2012). However, juvenile right whales obtain ~76% of their maximum mass by 8 yr of age (Fortune et al. 2012) 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 d^{-1}) than non-reproductive adult females due in part to differences in body composition (blubber and lean tissue). However, most of the estimated difference between adults reflects the smaller portion of time that adult males spend fasting on the calving grounds—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 ~14% more energy than males and ~9% 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 substantial 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 (0.077 MJ kg^{-1}), the costs of lactation are considerably higher (0.151 MJ kg^{-1}). Lactating females required almost twice as much total energy per day compared to pregnant females (4120 ± 414.0 vs. 2090 ± 329.6 MJ d^{-1}) and had the highest demands compared to other groups (Fig. 2). The high food requirements of lactating North Atlantic right whales presumably reflect the energy required to support rapid postnatal growth (Fortune et al. 2012) over the ~12 mo nursing period (Hamilton et al. 1995, Hamilton & Cooper 2010). Lactating females also spend ~23 d 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 to 2.0% of their body weight per day in food (Lockyer 1981) and that fin whales *Balaenoptera physalus* consume 1.6 to 3.3% (Vikingsson 1997, Lockyer 2007). Furthermore, Sergeant (1969) suggested that baleen whales would require 4% of their body weight per day in prey during the summer foraging season. These estimates are comparable with the range of the model predictions for North Atlantic right whales (1.6 to 5.4% body weight d^{-1}).

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). We found that the mean daily energy needs were 50% higher for lactating North Atlantic right whales compared to pregnant females. Furthermore, our model predicts that lactating right whales would require ~15 times more energy than pregnant females to meet the costs of nursing alone, which is comparable to the predictions for fin and Antarctic blue whales *Balaenoptera musculus* (Lockyer 1981). Additional bioenergetic models that incorporate fetal growth models have also found that baleen and odontocete species incur marginal costs to support gestation (Lockyer 2007).

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 (Berkson et al. 2002, Chipps & Wahl 2008). We therefore evaluated our model by comparing predictions of mean daily energy requirements with (1) estimates of average energy consumption and (2) individual estimates of energy consumption derived from 28 prey samples in Cape Cod Bay and 19 in the Bay of Fundy.

Our study showed close agreement (i.e. ≤15% for all demographic groups except lactating females) between the (95% CIs) estimates of consumed and required energy when individuals foraged on energy-rich prey patches (i.e. those representing the upper 95% confidence limits in Cape Cod Bay) for 22 h d^{-1} in Cape Cod Bay and between 12 and 22 h d^{-1} in the Bay of Fundy (Table 6). The field data suggest that a lactating female foraging for 22 h d^{-1} only obtains ~33 (20–44)% of her daily energy needs in Cape Cod Bay and 62 (47–72)% of her needs by foraging further north for the same length of time in the Bay of Fundy (Table 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 identified 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, we 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 (e.g. basal metabolic rate, 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, Baumgartner et al. 2003a,b, Baumgartner & Mate 2003, Parks et al. 2012). 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 (Baumgartner & Mate 2003) compared to Cape Cod Bay where the animals were confirmed to be feeding. Therefore, prey densities sampled near feeding whales in Cape Cod Bay and the Bay of Fundy may be lower than actual densities consumed because of sampling error and should be considered minimum estimates.

Overall we feel that the model parameters used were reasonable and yielded realistic estimates of energy requirements for right whales. We 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 and should be applied with this uncertainty in mind. 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. A noteworthy finding, however, is that the model suggests that right whales would need to feed for long hours in Cape Cod Bay to make ends meet (up to 22 h d^{-1}). This prediction is consistent with limited field observations showing continuous feeding for over 8 h by right whales that were individually followed in Cape Cod Bay (Jaquet et al. 2007).

The average energy density of prey patches sampled in Cape Cod Bay and the Bay of Fundy appear to have been insufficient to support lactating females (Table 6). However, some of the individual prey patches sampled were sufficient to meet and exceed the model estimates of energy needs in both habitats (Table 6). For example, 1 of the 28 samples from Cape Cod Bay contained enough energy to fulfill 96% of the nutritional requirements of a lactating female foraging for 15 h d^{-1}, and 2 of the 28 samples exceeded the requirements by 16 and 42% if they foraged for 22 h d^{-1}. Furthermore, in the Bay of Fundy 3 of 19 prey samples yielded estimates of daily energy consumption that comprised 95% (~15 h d^{-1}), 93 and 112% (~22 h d^{-1}) of the energetic needs of lactating females. Thus, lactating females could meet and exceed their food requirements in Cape Cod Bay and the Bay of Fundy provided they could access nutritionally rich prey patches, but would have had difficulty if they relied on average patches. These results suggest that the model predictions are reasonable and that average energetic consumption alone may not be adequate to evaluate the model outputs because of variability in the caloric density of prey patches. Collecting additional prey samples to estimate ingested energy, and specifically targeting prey patches consumed by lactating females, will shed more light on how likely lactating whales are to meet their predicted energy requirements in both habitats and how foraging success is impacted by variability in prey quality and quantity over space and time.

Habitat quality

Some of the discrepancy between the predicted energy requirements and estimated prey consumption by right whales in Cape Cod Bay may be explained by sampling methodology. However, the underestimation of prey abundance by so much in this location or the great overestimation of the energy needs of right whales seem unlikely. 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). The whales' 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 to 31% of annually identified mother and calf pairs are found during this time in Cape Cod Bay (Jaquet et al. 2007). Furthermore, only 2 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., *Centropages hamatus* and *Centropages typicus* (Mayo & Marx 1990, Durbin et al. 1995, Beardsley et al. 1996, Baumgartner & Mate 2003, DeLorenzo Costa et al. 2006a), of which *C. 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 *C. finmarchicus,* particularly Stage 5 (CV), which are of high caloric value (DeLorenzo Costa et al. 2006a). CV *C. finmarchicus* are the second most energetically dense of the life stages because they maximize their lipid stores before entering a diapause period when the food supply is low (Michaud & Taggart 2007). The ability of 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 the Bay of Fundy. Movements of whales among these habitats appear 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 *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 the more energy-rich prey species — *C. finmarchicus* (typically early stages) (Jiang et al. 2007). In late spring and early summer, whales feed in the Great South Channel on dense aggregations of *C. finmarchicus* (Pendleton et al. 2009), then 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 (*C. finmarchicus*) that are high in lipids.

North Atlantic 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 quantity. 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 reflects the dominance of lipid-rich CV *Calanus finmarchicus* (Michaud & Taggart 2007) compared to various taxa (e.g. *Centropages typicus* and *Centropages hamatus*) and developmental stages of calanoid copepods with differing levels of lipid content in Cape Cod Bay (Mayo & Marx 1990, DeLorenzo Costa et al. 2006a). Improved prey quality suggests that 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. as *C. finmarchicus* to meet their predicted energy needs (using average values of copepod calories across all life-stages; 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. kJ organism^{-1}) than prey 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 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 ocean 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 have been estimated to enter and leave the habitat 1 to 3 times in 2007 (Jaquet et al. 2007). 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 exceeding their predicted immediate daily energy needs. Given these scenarios, poor prey availability or quality, resulting in daily energy imbalances in Cape Cod Bay, seems unlikely to 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.

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 to 6 mo), 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 birth rates.

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

Compared to the Southern Hemisphere species of right whale *Eubalaena australis*, North Atlantic right whales appear to be in poorer condition and have lower reproductive success, suggesting that they are indeed nutritionally stressed. For example, 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 yr (Best et al. 2001, Burnell 2001, Cooke et al. 2001). Superior foraging opportunities and decreased fasting times (e.g. 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, and to a lesser extent pregnant, female North Atlantic right whales 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 to meet their predicted energy requirements in either habitat unless they feed on prey patches with higher energy densities than occur on average. 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 right whales is tied to the nutritional and physiological status of mature females. Along with observations of thin right whales, this further suggests that the slow recovery of North Atlantic right whales may be attributable in part to nutritional stress.

Our findings provide insight into the significant differences in quality and quantity of prey available to right whales in their core feeding habitats, and the potential that some demographic groups of right whales in the North Atlantic Ocean are subjected to nutritional stress. However, further quantitative assessments of the nutritional status of right whales will require the application of novel techniques to measure the resting metabolic rate of different demographic groups of right whales and the costs of lactation. Furthermore, continuous sampling of prey over the course of the year is necessary to estimate annual energetic consumption. 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.

Acknowledgements. The identification data we used to estimate the residency time of right whales on the calving grounds are maintained by the New England Aquarium and provided by the North Atlantic Right Whale Consortium. We are grateful to all of the organizations that have contributed to this database. We thank D. Osterberg and K. Stamieszkin for their assistance in the collection of zooplankton samples in Cape Cod Bay. We also appreciate the review and suggestions provided by R. Shadwick, E. Taylor, O. Nichols, P. Corkeron, and 3 anonymous reviewers—and thank R. Ahrens, K. Banack, I. Barzelai, B. Battaile and R. Gu for their modeling support, and B. Larson for contributing right whale baleen filtration estimates. An NSERC Discovery Grant awarded to A.W.T. and the Ruth Hiebert Memorial Fellowship awarded to S.M.E.F. supported this study in part.

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Editorial responsibility: Peter Corkeron,
Woods Hole, Massachusetts, USA

Submitted: April 16, 2012; Accepted: August 12, 2012
Proofs received from author(s): December 4, 2012