



Uncertain bioenergetics of North Atlantic right whales

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ABSTRACT: Without substantive reduction in anthropogenic trauma, Critically Endangered North Atlantic right whales *Eubalaena glacialis* (NARWs) risk extinction. Decreasing population size is attributable to 2 main issues besides vessel collision: entanglement in fishing gear and changes in food availability due to ecosystem changes in the face of climate disruption. Both can affect NARW energetics, leading to reduced body condition, decreased reproductive success of individuals, and deterioration of overall population health. To measure the impact of these stressors and their interaction, energetic costs associated with entanglement and starvation were incorporated in a bioenergetics model, established for a generic female right whale. We compared models for a NARW living now, one from 2 decades ago, when the species' abundance was increasing at approximately 2% yr⁻¹, and a southern right whale (SRW) from a population increasing at approximately 6% yr⁻¹. Parameter uncertainty associated with daily estimates of energy income, basal metabolic rate, and possible influences of baleen rack disruption from entanglement was so great that differences between the 3 generic right whale females were indistinguishable. Therefore, we included a stunted whale in the model. It was also indistinguishable from our first 3 model whales. Further, it made robust predictions of NARW energy budgets, let alone the impact of specific stressors of varying intensity, impossible. The capacity of bioenergetic modeling to inform conservation management of NARWs will be substantially enhanced by resolving these parameter uncertainties.

KEY WORDS: Bioenergetics model · Energy budget · Sublethal stressor · Reproductive success · Entanglement · *Eubalaena glacialis* · Cetacea

1. INTRODUCTION

North Atlantic right whales *Eubalaena glacialis* (NARWs) are one of the most threatened whale species. They are listed as Critically Endangered with a declining population trend on the IUCN Red List (Cooke 2020), assigned as 'endangered' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2013), and listed as 'endangered' under the US Endangered Species Act of 1973. After commercial whaling for right whales ended in 1935, NARWs were at extremely low numbers, but grew to just under 500 individuals in 2010 (Pace et al. 2017).

Since then, they have declined (Pace et al. 2017) to 340 (with a 95% credibility interval of 333–347) in 2022 (Pettis et al. 2023).

NARWs occur in the urbanized and heavily industrialized region along the eastern shores of the USA and Canada (Kraus & Rolland 2007). As a consequence, individuals confront anthropogenic stressors, the most important being entanglement in fishing gear (Knowlton et al. 2012) and vessel collisions (van der Hoop et al. 2015). Climate disruption has led to shifts in prey distribution, abundance, and availability to NARWs (Meyer-Gutbrod et al. 2021). These increasing anthropogenic stressors coincide with a

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decreased body condition of individual NARWs in 2022 when compared with their condition in 2000–2002 (Miller et al. 2012). Calving NARW females are in poorer condition than southern right whales *E. australis* (SRWs) (Christiansen et al. 2020). NARWs born in recent years are stunted in comparison with NARWs born decades ago, and entanglements are the only contributor clearly identified for stunting (Stewart et al. 2021).

Between 1980 and 2009, 83% of all individual NARWs were entangled in fishing gear at least once, and 26% acquired new entanglement scars each year (Knowlton et al. 2012). Individuals carry entangling gear for months to years (van der Hoop et al. 2016, 2017a) while experiencing pain, stress, and debilitation (Moore & van der Hoop 2012). Entanglement events can cause acute mortality, but most cases are chronic (Moore & van der Hoop 2012). A sublethal effect can be emaciation due to higher energy demands as a result of increased drag (van der Hoop et al. 2017b).

Many entanglements include rope wrapped through an individual whale's baleen rack (Sharp et al. 2019). Balaenid whales' buccal anatomy creates hydrodynamic flow while swimming, creating a hydraulic circuit that increases flow over the baleen rack (Werth 2004, Werth & Potvin 2016, Potvin & Werth 2017). The extent to which entangling rope disrupting the baleen rack interferes with this flow has not previously been considered as posing an issue for foraging NARWs; however, oral entanglement has been hypothesized to interfere with a critical hydrostatic oral seal in bowhead and right whales (Lambertsen et al. 2005).

Feeding throughout the water column (Baumgartner et al. 2007), NARWs target calanoid copepods, mainly copepodite Stage 5 (C5) of *Calanus finmarchicus* (Mayo & Marx 1990, Mayo et al. 2001). Prey availability correlates with NARW population health (Rolland et al. 2016) and reproductive success (Klanjscek et al. 2007, Miller et al. 2011, Meyer-Gutbrod et al. 2015). In the past decade, the abundance of *C. finmarchicus* has declined in the Gulf of Maine (Greene 2016, Record et al. 2019).

NARWs are capital breeders. They rely on extensive fat reserves that are accumulated during periods of foraging to provide the energy required for periods of prey shortage (George et al. 2021). Reproducing females have the highest energy needs of all demographic groups (Fortune et al. 2013). Apart from their greater costs of migration, mature females must provide energy for pregnancy and, particularly, lactation from their reserves (Fortune et al. 2013).

The energy balance of a NARW over a specific period is defined by the difference between energy income (food) and expenses (basal metabolic rate = BMR, active metabolism, and reproduction). These have been estimated for large whales (Baumgartner & Mate 2003, Nousek-McGregor 2010, Fortune et al. 2013, van der Hoop et al. 2014, 2019) and included in bioenergetics models (Kenney et al. 1986, Fortune et al. 2013, New et al. 2013, Gavrilchuk et al. 2021). In addition to natural factors, stressors also impact energy balance (van der Hoop et al. 2017b). Both food limitation (Meyer-Gutbrod et al. 2015, Meyer-Gutbrod & Greene 2018) and entanglement (van der Hoop et al. 2017b) are potential explanatory factors contributing to the recent decrease in calving rate (Pettis et al. 2017, Christiansen et al. 2020).

The original aim of this study was to model the energy balance of an unhealthy versus a healthy NARW female over one calving interval, and to include varying levels of both stressors, using published data to inform the model. Our intent was to explore the possible relative influences of entanglement and food limitation on the energy balance, and hence likelihood of calving, of female NARWs. A reviewer of the first draft of our manuscript noted that uncertainty around some model parameters had not been appropriately considered in our initial work. Once we started including parameter uncertainty more fully in our model formulation, the extent to which that uncertainty over-rode other considerations became clear. Therefore, the aim of this manuscript changed, to assessing how the substantial uncertainties around some parameters of bioenergetics models of NARWs impact our capacity to make inference on NARW biology, and therefore management decisions, from these models.

2. METHODS

In traditional bioenergetics models (Nisbet et al. 2012), energetic income (via feeding) and energetic expenses (via BMR, active metabolism, and reproduction) of organisms are opposed over a fixed time period (e.g. a calving interval) to examine the energy budget of an individual, a population, or a species. By then subtracting the expenses from the income, energy balances can be obtained to examine whether the study object experiences an energy deficit.

Here, we began by modeling for one 'generic' individual, representing all sexually mature, female NARWs of a specific population, or rather, represent

the body condition of that population. Average morphological parameters estimated from aerial photographs were taken from Christiansen et al. (2020) (representing the recent NARW population), from Miller et al. (2012) (representing the NARW population from 2000–2002, before the more recent increase in the impacts of anthropogenic stressors), and from Christiansen et al. (2020) (for SRWs). These respectively represent NARWs in decline (Pace et al. 2017), NARWs when they were increasing at ~2% annually (Pace et al. 2017), and a population of SRWs from a population showing relatively rapid increase, approximately 6% annually (Corkeron et al. 2018). As the parameter ranges for these whale classes overlap, we did an additional model run for a stunted whale (whale 3617 from Stewart et al. 2022) to test the sensitivity of our model to body size. Mean values of body length (to calculate swimming speed and baleen length for foraging rate), body volume (to calculate total body mass for BMR), head width (to calculate mouth gape area for foraging rate), and maximum width (to compare body condition) are provided in Table 1. Aerial photogrammetric data of live animals are the best source of such data, because necropsy measurements are biased by unknown intervals between time of death and when measured, allowing for significant but unknown changes in girth and blubber thickness from decomposition and maceration (Moore et al. 2020).

Based on body volume (V), body mass (M) was estimated using the following equation from (Christiansen et al. 2019):

$$M[\text{kg}] = 754.63[\text{kg m}^{-3}] \times V[\text{m}^3] \quad (1)$$

After defining our model organisms, we set up the energy budgets for the 3 generic right whale females. To do so, the values of each parameter integrating into energetic income and expenses were estimated from the literature (Table 2). We also included reported uncertainty, or derived estimates of uncertainty from the published data. These uncertainties soon proved to be so large that we decided to model only daily energetic income and daily energetic expenses of BMR. We did not consider other expenses such as active metabolism or reproduction. Likewise, the even wider uncertainties around aspects of female whales' life history (e.g. migration patterns) that would need to be multiplied further did not allow us to differentiate between different life stages (pregnant, lactating, or resting), nor to extend the model to a full year or calving interval. We did not calculate an energy balance, as the energy budget was modeled only partly. However, we compared daily energetic income to energetic costs of BMR for the 3 right whale females and the stunted NARW.

In addition to natural energetic expenses, unnatural expenses can occur, for example due to entanglement in fishing gear and increased drag while swimming (van der Hoop et al. 2017b). Therefore, we modeled daily entanglement costs relative to daily energy income and daily BMR. In a final scenario, we assumed that ropes wrapped around the head of a whale reduce filtration efficiency by distorting baleen racks and impeding the opening of the gape (Lambertsen et al. 2005, Sharp et al. 2019), and modeled the reduced energy income relative to BMR and entanglement costs accordingly.

As this model is based on resamplings from literature estimates and not on field data, we did not

Table 1. Mean (\pm SD) morphological parameters of a North Atlantic right whale (NARW) living now (measurements of the recent population from 2017, which is in an overall poor body condition), a historical, healthier NARW (measurements of the population in the Bay of Fundy between 2000 and 2002, prior to the occurrence of anthropogenic stressors), a southern right whale (SRW) living now (measurements of the recent population from 2018), and a stunted NARW from 2006 as a measure of sensitivity, which were used to generate generic female right whales. Head width at 10% body length from rostrum, maximum width at 30% body length from rostrum. As width measurements were not available for the stunted NARW, gape area was derived from its body length directly based on Fig. 2 in van der Hoop et al. (2019)

	Length (m)	Body volume (m ³)	Head width (m)	Max. width (m)
Recent NARW (2017) Christiansen et al. (2020)	12.94 (\pm 0.55)	23.2079 (\pm 3.41)	1.80 (\pm 0.20)	2.50 (\pm 0.15)
Historical NARW (2000) Miller et al. (2012)	13.27 (\pm 0.67)	30.04 (\pm 4.57) ^a	2.02 (\pm 0.10)	3.06 (\pm 0.20)
Recent SRW (2018) Christiansen et al. (2020)	13.63 (\pm 1.01)	34.4539 (\pm 11.93)	1.79 (\pm 0.16)	2.86 (\pm 0.29)
Stunted NARW (2006) (Stewart et al. 2022)	10.5	14.845 ^a	–	–

^aCalculated using Eq. (5) in Christiansen et al. (2020)

Table 2. Parameters used to model energetic income, natural energetic expenses through basal metabolic rate (BMR), and unnatural expenses due to entanglement in fishing gear for generic female right whales (a recent and a historical North Atlantic right whale [NARW], a recent southern right whale, and a stunted NARW, as described in Table 1). Most parameter ranges were taken from literature sources, 10 000 uniform random numbers drawn from them, and these distributions taken as a basis. In 2 cases (marked with '#'), available data sets were resampled based on log-normal distributions, and for BMR, single values were applied

Parameter	Definition	Value	Unit	Equation	Source
EFC	Capture efficiency	44.25–150	%	5	Mayo et al. (2001), Werth & Sformo (2021)
FA	Time spent with foraging activities	15.8–22	h d ⁻¹	6	Kenney et al. (1986), Fortune et al. (2013)
#FE	Proportional value of actual feeding	5.1–68.0	%	6	Baumgartner & Mate (2003)
#CD	Plankton density	3020–14945	ind. m ⁻³	8	Baumgartner & Mate (2003)
EV	Energy value	3.4–12.67	J ind. ⁻¹	8	Comita et al. (1966), DeLorenzo Costa et al. (2006)
BMR	Basal metabolic rate	30, 50, 75 and 100	%	9	Kleiber (1975), George et al. (2021)
ET	Entanglement drag	72 × 10 ⁶ –752 × 10 ⁶	J d ⁻¹		van der Hoop et al. (2017b)

conduct null hypothesis significance testing to test differences between the 3 whale classes and the stunted NARW. All calculations were performed in R version 4.2.1 (R Core Team 2022), with the libraries 'ggplot2' (Wickham 2016), 'ggpubr' (Kassambara 2020), 'ggprism' (Dawson 2021), and 'ggdist' (Kay 2022). The script is provided in the Supplement at www.int-res.com/articles/suppl/m725p167_supp.txt.

2.1. Income

There are multiple ways to build the energetic income, and our approach unites a broad range of recent research and provides a simple estimate for a bioenergetic NARW model. Here, an average food composition consisting of late stages of *Calanus finmarchicus* was assumed for all 4 whales, because this constitutes a proxy for food availability (Mayo et al. 2001, Meyer-Gutbrod et al. 2015). There are differences in the species that comprise the diet of NARWs and SRWs, as they do not occur in the same hemisphere. Recent tagging data (e.g. Siguendo Ballenas 2021, Tohorā Voyages 2021) and stable isotope analysis (Valenzuela et al. 2018) give some insights where the main foraging grounds for some SRWs might be. In Tohorā Voyages (2021, 2022) all whales except 2 appear to feed around the Subtropical Convergence, which means they could be consuming copepods, euphausiids, or both. Historically, analysis of stomach contents of SRWs from South Georgia found euphausiids present (Matthews 1938), and behavioral observations suggested they fed on *Munida gregaria* (Matthews 1938), another decapod crustacean. Recently, plankton sampling at a site where SRWs were observed foraging found a zooplankton fauna of cladocerans, copepods, and decapods, in-

cluding euphausiids (D'Agostino et al. 2018). Fecal analysis of SRWs from the same site found only *C. australis* present (D'Agostino et al. 2016). Recent analyses using stable isotopes indicate that SRWs in the western South Atlantic feed on both copepods and euphausiids (Valenzuela et al. 2018).

The data available on the diet of SRWs is insufficient to derive reliable estimates of their diet for comparison with that of NARWs. Also, the data available for the densities of likely SRW prey, and the energy values available for likely prey (see Section 4) are also poor, compared with the data for NARWs. Therefore, we considered the data available on NARWs to be the best current model for SRWs, and assuming copepods as their food as a reasonable first approximation.

Daily energy income (EI) was calculated using the amount of water filtered per day (WF), plankton (*C. finmarchicus*) density (CD), and energy value of *C. finmarchicus* (EV).

For better comparison to other models, species, and scenarios, we further disaggregated the amount of water filtered per day (WF) in filtration rate of ingested nutrition (FRI) and the time NARWs spend feeding per day (FT). Foraging time of SRWs (e.g. Zerbini et al. 2016, their Fig. 9) appears comparable to that of NARWs, although available field data are very sparse. Foraging time is the product of swimming speed (*S*), gape area (*G*), and capture efficiency (EFC). *S* while filtering, and the length of the longest baleen plate (BAL) were estimated from total body length (*L*) using equations of van der Hoop et al. (2019). *G* was then calculated from the length of the longest baleen plate (BAL) and head width (HW) by a third equation from van der Hoop et al. (2019). As width measurements were not available for the stunted NARW, gape area was directly derived from

Fig. 2 in van der Hoop et al. (2019) based on its body length:

$$S \text{ [m s}^{-1}\text{]} = 0.09 (\pm 0.03) \times L \text{ [m]} \quad (2)$$

$$\text{BAL [m]} = 0.2077 \times L \text{ [m]} - 1.095 \quad (3)$$

$$G \text{ [m}^2\text{]} = \frac{\text{HW [m]} \times \text{BAL [m]}}{2} \quad (4)$$

The capture efficiency (EFC) of baleen whales is approximately 88.5% (Mayo et al. 2001, Werth 2012). However, recent studies suggest a pipe effect resulting from the morphology of the gape and the baleen racks during water filtration (Werth 2004, Lambertsen et al. 2005, Werth et al. 2018, Werth & Sformo 2021). This could increase the filtration efficiency to 150%. Therefore, we drew 10 000 uniform random numbers from the range of 88.5 to 150% and used this distribution in the model. Ideally, one would also consider energetic losses through feces and urine, the heat increment of feeding (Fortune et al. 2013), and assimilation efficiency. However, as this would add even more uncertainty, we decided not to include these parameters, but they should be included in future models that are based on enhanced field data.

With these values, the filtration rate of ingested nutrition (FRI) was calculated:

$$\text{FRI [m}^3 \text{ s}^{-1}\text{]} = S \text{ [m s}^{-1}\text{]} \times G \text{ [m}^2\text{]} \times \text{EFC [\%]} \quad (5)$$

The amount of time NARWs spend feeding per day (FT) consists of time spent on foraging activities per day (FA) and the proportion of active feeding during these foraging activities (FE). Baumgartner & Mate (2003) reported 91% of all dives to be foraging dives in feeding periods. This equates to the upper bound of 22 h d⁻¹ assumed by Fortune et al. (2013), while Kenney et al. (1986) used a lower estimate of 15.8 h d⁻¹. From this reported range, again 10 000 uniform random numbers were drawn for FA and the distribution was used in the model. The proportional value of feeding (FE) corresponds to only the bottom time of a foraging dive cycle (Baumgartner et al. 2017, van der Hoop et al. 2019), which was estimated to be 56.3% for resting females (Nousek-McGregor 2010) and 40.4% as an average between all states (Baumgartner & Mate 2003). Here, FE was drawn from Baumgartner & Mate (2003, their Table 3) by resampling this data set with a log-normal distribution. Time spent feeding per day (FT) was calculated as the factor of time spent for foraging activities per day (FA) and the proportion of active feeding during these activities (FE) (for SRWs, these parameters are unknown):

$$\text{FT [s d}^{-1}\text{]} = \text{FA [s d}^{-1}\text{]} \times \text{FE [\%]} \quad (6)$$

From the above follows water filtered per day (WF):

$$\text{WF [m}^3 \text{ d}^{-1}\text{]} = \text{FRI [m}^3 \text{ s}^{-1}\text{]} \times \text{FT [s d}^{-1}\text{]} \quad (7)$$

Patches of *C. finmarchicus* can exceed 10⁶ ind. m⁻³ (Kenney et al. 1986, Baumgartner & Mate 2003, Parks et al. 2012), while NARWs usually do not feed below 1000 ind. m⁻³ (Mayo & Marx 1990). Baumgartner & Mate (2003) measured peak *C. finmarchicus* (C5) densities in NARW feeding paths between 3020 and 14 945 individuals m⁻³, with an average of 6618 ± 3481 (SD) ind. m⁻³. For the model, we took their data set (Baumgartner & Mate 2003, their Table 3) as a basis and resampled it with a log-normal distribution. For estimates of daily food income, we assumed the dry mass of *C. finmarchicus* to be 0.25 mg ind.⁻¹ (Maps et al. 2010, 2011). Conversions to plankton wet mass (Wiebe et al. 1988) are not common and are very uncertain.

Estimates of the energy content of C5 individuals of *C. finmarchicus* (EV) include an average of 3.4–5 J ind.⁻¹ in the Bay of Fundy (Michaud & Taggart 2007), 8.02–12.67 J ind.⁻¹ in the Bay of Fundy (McKinstry et al. 2013), 8.3–9.6 J ind.⁻¹ in Cape Cod Bay (DeLorenzo Costa et al. 2006), and 6.8 J ind.⁻¹ in the Bute Channel (Comita et al. 1966). Here, we drew 10 000 uniform random numbers from a range of 3.4–12.67 J ind.⁻¹.

Finally, total energy income per day (EI) arose from water filtered per day (WF), plankton (*C. finmarchicus*) density (CD), and energy value of *C. finmarchicus* (EV):

$$\text{EI [J d}^{-1}\text{]} = \text{WF [m}^3 \text{ d}^{-1}\text{]} \times \text{CD [ind. m}^{-3}\text{]} \times \text{EV [J ind.}^{-1}\text{]} \quad (8)$$

2.2. Expenses

BMR is defined as a resting metabolic rate, thus ‘the power produced by a fasting, inactive organism’ (Kolokotronis et al. 2010, p. 753). So far, BMR of large marine mammals has been projected only by models. Almost 50 yr ago, Kleiber (1975) found an empirical relationship between BMR and body mass (M):

$$\text{BMR [J d}^{-1}\text{]} = (292.88 \times M \text{ [kg]}^{0.75}) \times 1000 \quad (9)$$

Today, several modern derivatives of this relationship exist (e.g. Kolokotronis et al. 2010, Ballesteros et al. 2018, Kearney 2021). However, BMR of bal-aeid whales could be substantially less than these

equations suggest (George 2009, George et al. 2021). As the true value for BMR most likely lies in the range between 30 and 100 % of Kleiber's (1975) estimate, we conducted model runs for 30, 50, 75, and 100 % of this estimate. This approach also allows for examining the sensitivity of our model to BMR. For comparison, we calculated the fraction of daily energy income (EI) of BMR:

$$EI_{\text{fraction}} \text{BMR} = \frac{EI [\text{J d}^{-1}]}{\text{BMR} [\text{J d}^{-1}]} \quad (10)$$

Entanglement in fishing gear causes additional, unnatural energetic demands due to drag, previously described for several incidents and various gear configurations by van der Hoop et al. (2016). For our model, we considered a cost range for entanglement (ET) of 7.24×10^7 to $7.52 \times 10^8 \text{ J d}^{-1}$ as reported by van der Hoop et al. (2017b), from which we drew 10 000 uniform random numbers as a distribution. For comparison, we calculated the fraction of entanglement (ET) of daily energy income (EI), as well as of BMR:

$$EI_{\text{fraction}} \text{EI} = \frac{ET [\text{J d}^{-1}]}{EI [\text{J d}^{-1}]} \quad (11)$$

$$EI_{\text{fraction}} \text{BMR} = \frac{ET [\text{J d}^{-1}]}{\text{BMR} [\text{J d}^{-1}]} \quad (12)$$

2.3. Effects of entanglement on filtration efficiency

To assess the possible correlation of entanglement in fishing gear and food intake, we examined a scenario in which rope wrapped around a right whale's head reduces filtration efficiency by up to half. Accordingly, we drew 10 000 uniform numbers of a range of filtration efficiency (EFC) between 44.25 and 75 %. From that, we calculated water filtered per day (WF), energy income (EI), and the comparisons of energy income (EI) versus BMR, as well as entanglement drag (ET) versus energy income (EI), as described above. Finally, we examined the total effect of entanglement by subtracting the costs of entanglement drag (ET) from the entanglement-induced, reduced energy income (EI) and calculated the fraction of this value of the energy income when not entangled. This depicts the amount of energy a whale could spend per day when entangled in comparison to a whale that is not entangled:

$$EI_{\text{available}} [\%] = \frac{EI_{\text{entangled}} [\text{J d}^{-1}] - ET [\text{J d}^{-1}]}{EI_{\text{unentangled}} [\text{J d}^{-1}]} \quad (13)$$

3. RESULTS

The following results are at times surprising but are based on available published data (Tables 1 & 2). As they overlap almost completely for the 3 classes of right whales, means with standard deviations and 95 % confidence intervals (CIs) of the 3 whale classes are given in the text below. Detailed results including the stunted NARW are listed in Table 3 and are visualized in Figs. 1–3. Note the high SDs and large CIs, which reveal the substantial uncertainty in model results.

Resampling from estimates suggest that right whales filter a mean of $70\,562 \pm 28\,331 \text{ m}^3$ (95 % CI: 34 269–123 145) of seawater per day (Fig. 1A), with substantial overlap between the 3 classes of right whales. Whales consumed an estimated mean of $117 \pm 81.2 \text{ kg}$ (95 % CI: 33.6–272.5) of *Calanus* per day (dry weight), with almost complete overlap between the 3 classes of right whales (Fig. 1C), resulting in an estimated daily energy income of $3746 \pm 3006.9 \text{ MJ}$ (95 % CI: 855.5–9490.5) (Fig. 1E).

The estimates of daily BMR for the 3 classes range between $158.7 \pm 23.3 \text{ MJ d}^{-1}$ (30 % of Kleiber 1975) and $528.9 \pm 77.6 \text{ MJ d}^{-1}$ (100 % of Kleiber; Fig. 2A). From Eq. (10), this means that estimates of daily energy income range between 23.8 ± 19.1 times daily BMR (30 % of Kleiber) and 7.1 ± 5.7 times daily BMR (100 % of Kleiber) with almost complete overlap between the 3 classes of right whales (Fig. 3A). Resampling from estimates suggests that the energetic costs (alone) of entanglement drag represent approximately $18.7 \pm 19.3\%$ of daily energy income (95 % CI 2.4–54.6, Fig. 3C). The daily energetic cost of entanglement ranged between $262.9 \pm 131\%$ daily BMR (for 30 % of Kleiber) and $78.9 \pm 39.3\%$ daily BMR (for 100 % of Kleiber, Fig. 2B).

If an entanglement that wraps through the baleen rack also reduces filtration efficiency by up to half, estimates of water filtration reduce to $35\,303 \pm 14\,209 \text{ m}^3$ (95 % CI: 17 264–61 758) of seawater per day (Fig. 1B). This would lead such whales to consume an estimated mean of $58 \pm 40.7 \text{ kg}$ (95 % CI: 16.8–135.9) of *Calanus* per day (dry weight), with an almost complete overlap between the 3 classes of right whales (Fig. 1D), giving in an estimated daily energy income of $1872 \pm 1509.9 \text{ MJ}$ (95 % CI: 423.8–4735.8, Fig. 1F), or a range of 11.89 ± 9.58 times daily BMR (30 % of Kleiber) and 3.6 ± 2.9 times daily BMR (100 % of Kleiber, Fig. 3B). In this scenario, the energetic costs of entanglement drag approximate $37.4 \pm 39.1\%$ (95 % CI: 4.8–112.3) of daily energy income (Fig. 3D), which is reduced due to a worse filtration efficiency. There is again an almost complete overlap

Table 3. Main model results given as mean (\pm SD) for the 3 whale classes and the stunted North Atlantic right whale (NARW) (as described in Table 1). The first part assumes no entanglement, the second part assumes that entanglement reduces filtration by up to half. Food income is given in *Calanus* dry mass, assuming the dry mass of *C. finmarchicus* to be 0.25 mg ind.⁻¹ (Maps et al. 2010, 2011). SRW: southern right whale. ‘Kleiber’ refers to Kleiber (1975)

Model	Abbreviation	Unit	Recent NARW	Historical NARW	SRW	Stunted NARW
Without entanglement						
Water filtered	WF	m ³ d ⁻¹	63288 (\pm 24882)	76009 (\pm 29883)	72388 (\pm 28460)	32262 (\pm 12684)
Food income		kg d ⁻¹	105 (\pm 72.2)	126 (\pm 86.7)	120 (\pm 82.6)	54 (\pm 36.8)
Energy income	EI	MJ d ⁻¹	3360 (\pm 2677)	4035 (\pm 3215)	3843 (\pm 3062)	1713 (\pm 1365)
Basal metabolic rate — 30% of Kleiber —	BMR	MJ d ⁻¹	133.7	162.3	179.9	95.7
Basal metabolic rate — 50% of Kleiber —	BMR	MJ d ⁻¹	223	270.5	299.8	159.5
Basal metabolic rate — 75% of Kleiber —	BMR	MJ d ⁻¹	334.4	405.8	449.7	239.2
Basal metabolic rate — 100% of Kleiber —	BMR	MJ d ⁻¹	445.9	541.1	599.6	318.9
Assuming entanglement decreases filtration efficiency						
Water filtered	WF	m ³ d ⁻¹	31664 (\pm 12481)	38028 (\pm 14989)	36217 (\pm 14275)	16141 (\pm 6362)
Food income		kg d ⁻¹	52 (\pm 36.2)	63 (\pm 43.5)	60 (\pm 41.4)	27 (\pm 18.4)
Energy income	EI	MJ d ⁻¹	1679 (\pm 1344.4)	2017 (\pm 1614.7)	1921 (\pm 1537.8)	856 (\pm 685.3)

between the 3 classes of right whales. Consequently, an entangled right whale has an energy income that is 1619 ± 1412 MJ (CI: 305.5–4329) less than when not entangled. Additionally, it needs to spend some of the energy income for the additional drag from the gear. Therefore, an entangled right whale with the exact same life history as an unentangled right whale can spend only 1207 ± 1436 MJ (CI: –184 to 3911.6) of energy for its natural expenses, or $25.9 \pm 28.8\%$ (CI: –24.8 to 47.2) of the amount it could spend when not entangled.

4. DISCUSSION

The original aim of this modeling study was to assess the relative extent to which food availability and entanglements could be contributing to the poor reproductive success currently exhibited by NARWs (Pettis et al. 2023). To achieve that, we also needed to account for uncertainties in estimates used in the model. Uncertainty means that for many parameters, there is a range of possible values known within which the true value lies. For example, this range can result from natural variability, but also from the accuracy of the measurement. Further research and methodical enhancements may reduce the level of uncertainty or the range of possible values. We have included uncertainties reported in the literature for the values that

we used, or derived estimates of uncertainty from data provided in the literature. Before we had finished developing models accounting only for daily energy income and expenditure, it became apparent that the uncertainties in the data were so high as to obscure any differences between our model scenarios. The 95% confidence bounds of most estimates had a spread of approximately an order of magnitude. The substantial uncertainties around aspects of female whales’ life history that would need to be multiplied further such as the time spent migrating, the daily energetic cost of travel during migration, and costs associated with lactation, would only add to the cumulative uncertainty of model results. That being so, we decided to stop further development of our model.

Predictions of bioenergetics models for NARWs differed from field observations in the past. Partly, this might be due to the modeling approach itself, as most models are a simplification. However, we hypothesize that this substantial uncertainty can help explain instances where the predictions of models of NARW energetics are not borne out by field data. For example, Gavrilchuk et al. (2021) published a comprehensive analysis of the density of *Calanus* spp., coupled with a model of NARW energetics. Based on their models, they demonstrate conclusively that female NARWs foraging in the Gulf of St Lawrence (GoSL) since 2014 do not have sufficient prey densities available to them to successfully calve. However, 2 recently

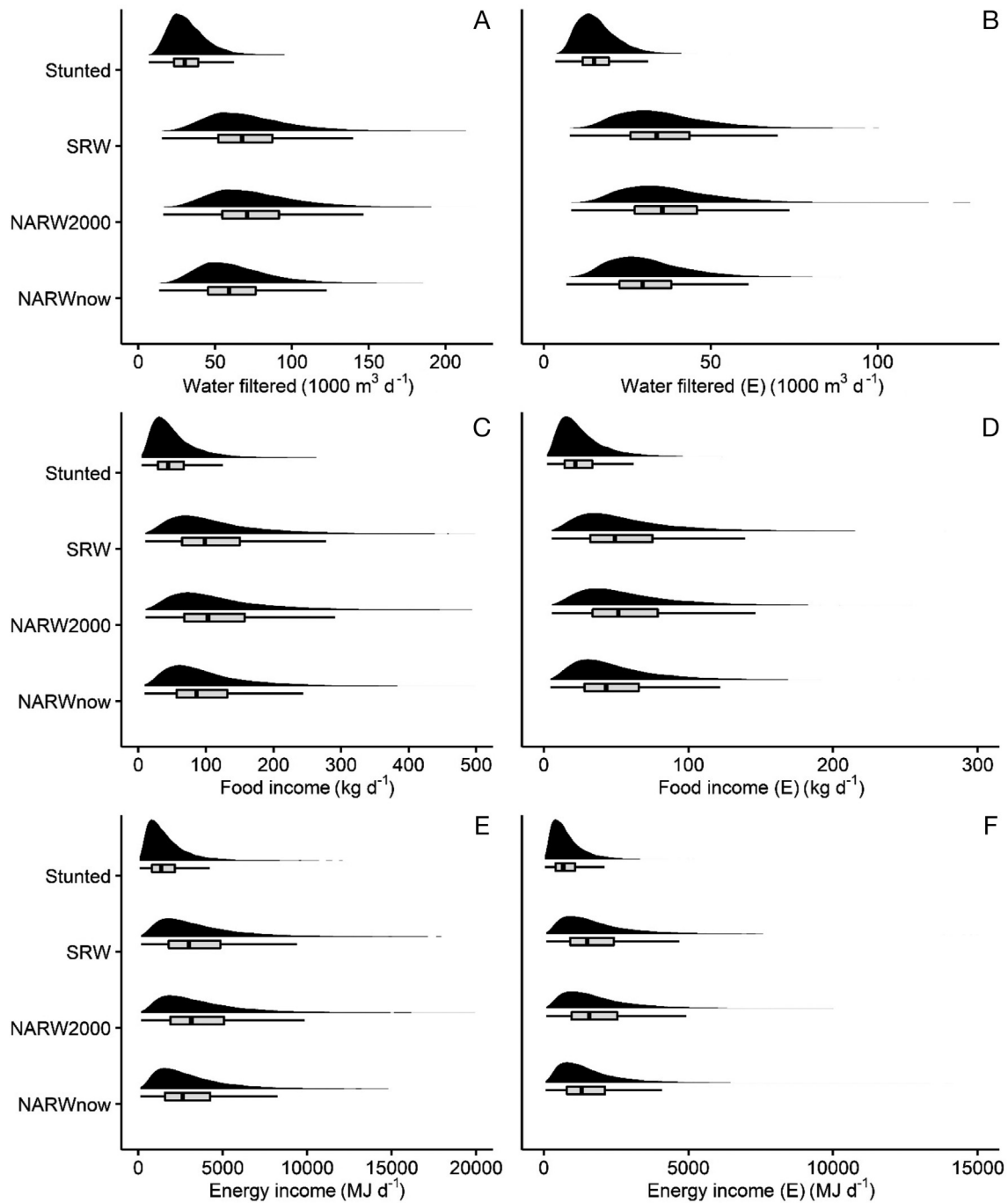


Fig. 1. Modeled estimates of aspects of daily foraging activity of female right whales, *Eubalaena* spp., each from 10 000 realizations, for 3 generic whale classes (a recent North Atlantic right whale [NARW], a historical NARW from 2000, as well as a recent southern right whale [SRW]) and a stunted individual NARW, as described in Table 1. All aspects are modeled for whales not impacted by entanglement (left column) versus a scenario which assumes rope entanglement to reduce whale filtration rates (right column). On the y-axis, counts of resamples are given. The boxplots show the 50th (thick vertical line), 25th and 75th (boxes), and 5th and 95th (whiskers) percentiles. (A,B) Model estimates of the amount of water filtered daily, from Eq. (7). (C,D) Model estimates of the quantities (dry weight) of prey, *Calanus finmarchicus*, consumed in a day. (E,F) Model estimates of the energy content of *C. finmarchicus* consumed in a day, thus daily energy income, from Eq. (8)

published papers, based on field data, demonstrate the opposite. Sexually mature females that have used the GoSL since 2015 were more likely to give birth

over this time period compared to individuals who did not use that habitat (Bishop et al. 2022). Further, the cohort of individual NARWs foraging in the GoSL

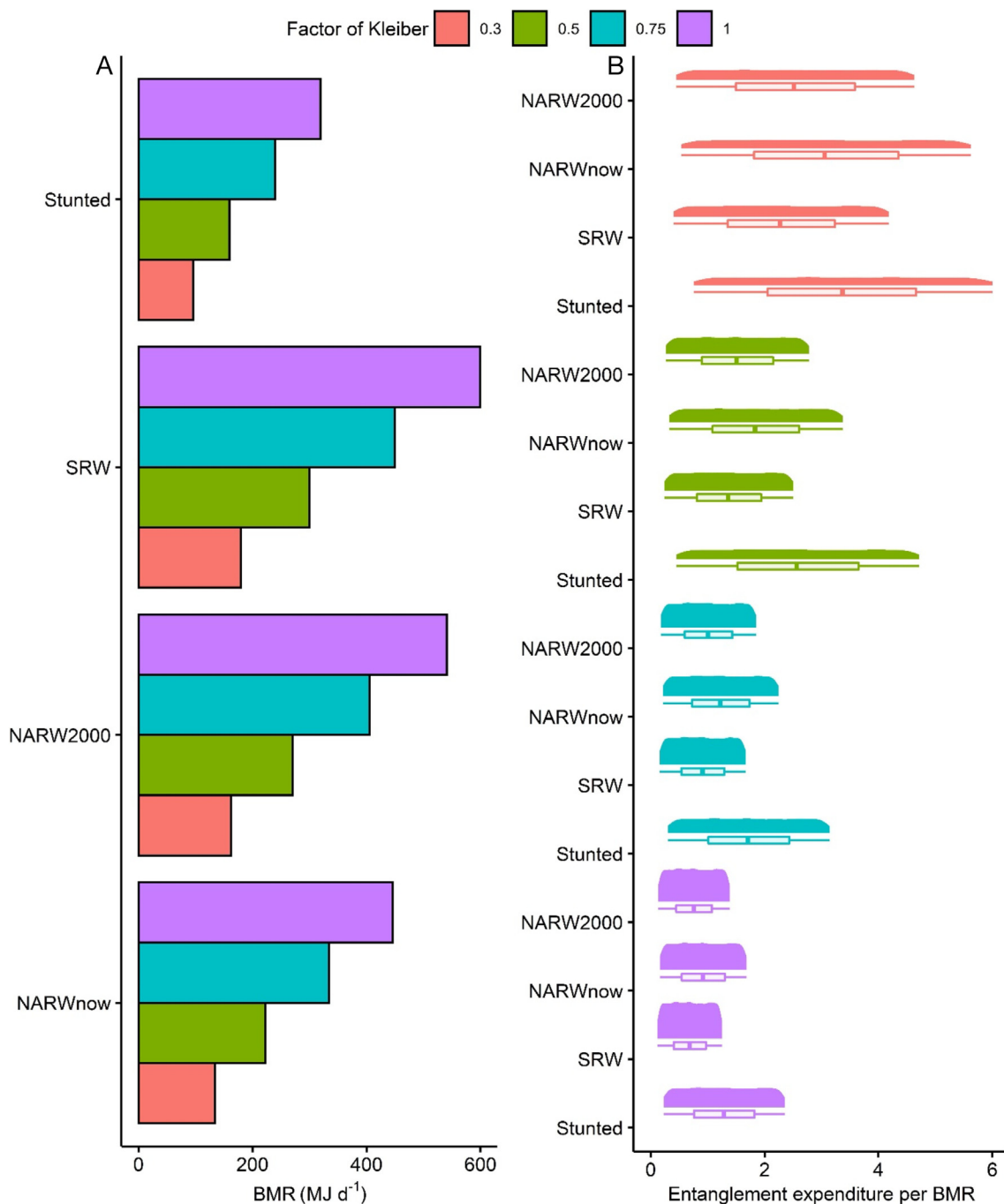


Fig. 2. Modeled estimates of aspects of daily energetic expenses of female right whales, *Eubalaena* spp., for 3 generic whale classes (a recent North Atlantic right whale [NARW], a historical NARW from 2000, as well as a recent southern right whale [SRW]) and a stunted individual NAWR, as described in Table 1. (A) Daily basal metabolic rate (BMR) for 30, 50, 75, and 100% of Kleiber (1975) (Eq. 9). (B) Daily energetic cost of entanglement drag divided by daily BMR, from Eq. (12). A value of 1 indicates that the energetic cost of entanglement drag equals BMR; values >1 indicate that the energetic cost of entanglement drag is greater than BMR. On the y-axis, counts of resamples are given. The boxplots show the 50th (thick vertical line), 25th and 75th (boxes), and 5th and 95th (whiskers) percentiles

since 2014 has consistently been the same individuals (Crowe et al. 2021). Most of these individuals remain in the GoSL throughout the summer, and so obtain much, possibly most, of their food for the year

there (Duff et al. 2013, Simard et al. 2019, Crowe et al. 2021). These females must be obtaining sufficient energy foraging in the GoSL to support gestating and then suckling a calf (Christiansen et al. 2022), raising

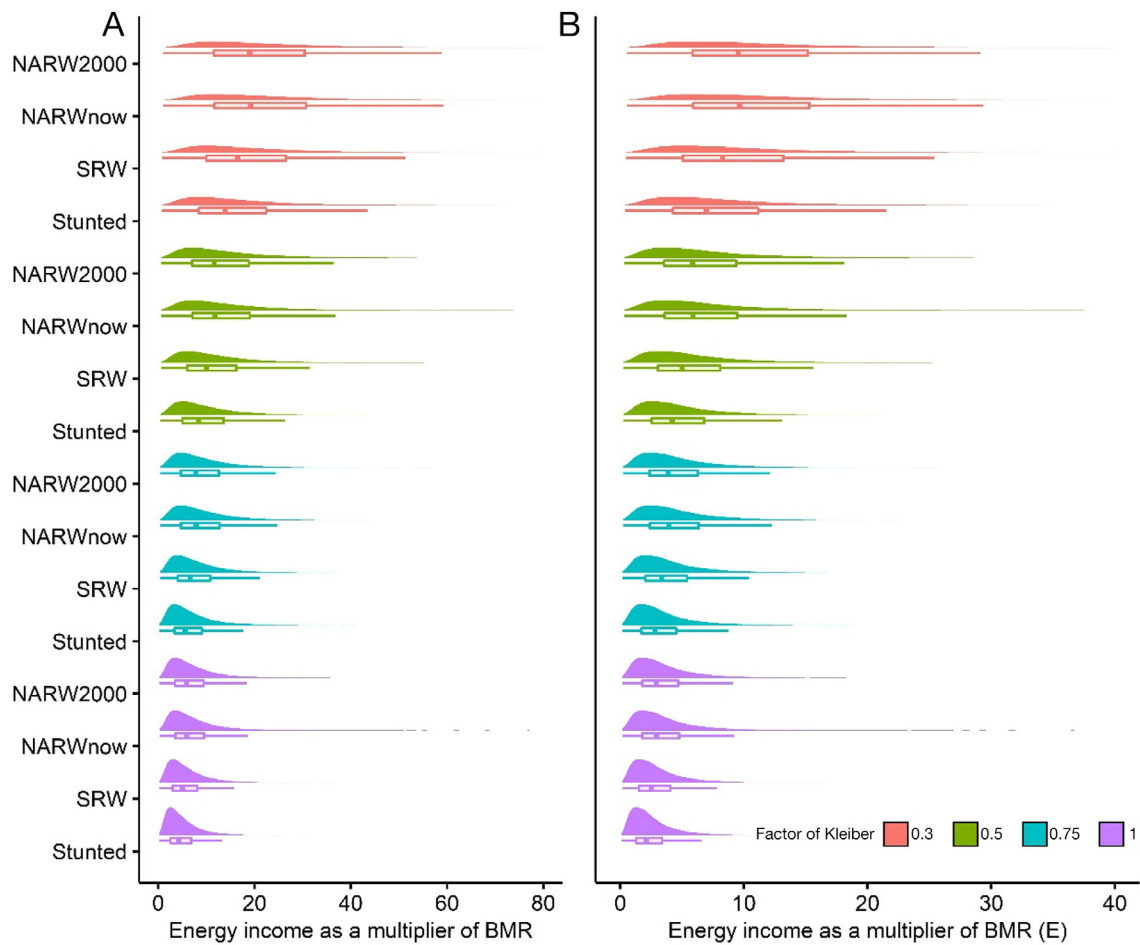


Fig. 3 continued on next page

Fig. 3. Modeled estimates of aspects of daily energy balance of female right whales, *Eubalaena* spp., each from 10 000 realizations, for 3 generic whale classes (a recent North Atlantic right whale [NARW], a historical NARW from 2000, as well as a recent southern right whale [SRW]) and a stunted individual NAWR, as described in Table 1. On the y-axis, counts of resamples are given. The boxplots show the 50th (thick vertical line), 25th and 75th (boxes), and 5th and 95th (whiskers) percentiles. Aspects are modeled for whales (A) not impacted or (C) only impacted by entanglement drag, versus (B,D) scenarios which additionally assume rope entanglement to reduce whale filtration rates. (A,B) Daily energy income divided by BMR, from Eq. (10). (C,D) Daily energetic costs of entanglement drag divided by daily energy income, from Eq. (11)

questions as to the findings of the model reported by Gavrilchuk et al. (2021).

We suggest 2 areas of immediate interest in attempting to resolve the conundrum of why modeling suggests that NARWs are not getting enough energy to calve, when some clearly do. First, NARWs might ingest plankton at a greater rate, regardless of plankton density, than currently assumed in these models. Recent work on the anatomy of balaenid feeding mechanisms suggests that the architecture of their mouth and baleen rack acts to increase the flow rate of surrounding water and prey (Werth 2004, Lambertsen et al. 2005, Werth et al. 2018, Werth & Sformo 2021). While this means that input rates for NARWs need reconsideration, it also has implications for the impact of entanglements on foraging efficiency.

Given the substantial uncertainty that this implies for our understanding of capture efficiency, we modeled a range of values for EFC from 44.25% (assuming that capture efficiency is halved by entangling rope disrupting the baleen rack) to 150% (where the NARW feeding mechanism acts to ingest plankton from more than just their immediate path).

Entangling rope commonly wraps around the heads of NARWs (Sharp et al. 2019), displacing parts of the baleen rack. If the baleen rack needs to be undisturbed for suitably efficient foraging (as anatomical studies imply), then food intake, as well as the energetics of locomotion impeded due to entanglement, require further consideration. This also implies that the impact of entanglement will be greater than previously imagined. Whether a halving of ingestion ef-

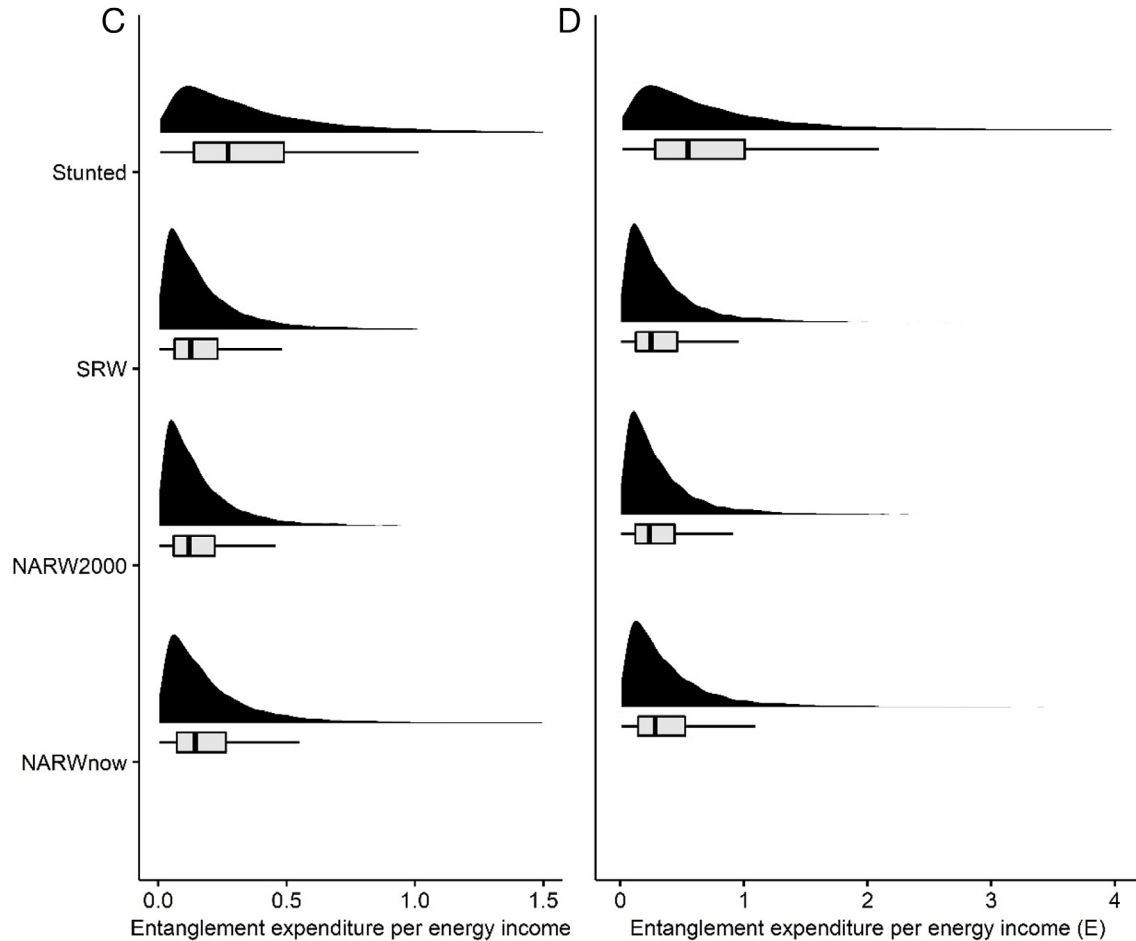


Fig. 3. Continued

efficiency is realistic is currently unknown; we chose the value as a starting point. Field studies of entangled NARWs foraging, using drone-based infra-red video (Lonati et al. 2022), could start to assess the extent to which rope interfering with the baleen rack disrupts filtration efficiency.

Second, all prior models of NARW energetics assume that the BMR of these whales is approximated by the equation of Kleiber (1975) (Fortune et al. 2013) or modern derivations thereof (Gavrilchuk et al. 2021). As Fortune et al. (2013) also noted, bowhead whales *Balaena mysticetus*, the other genus in the Balaenidae, are thought to have a BMR substantially less than that predicted by the Kleiber equation (George 2009, George et al. 2021). Whether the Arctic, pagophilic habitat of bowhead whales make them a poor model for *Eubalaena* is unclear. The other option published to date, such as that taken by Gavrilchuk et al. (2021), is to assume that captive dolphins and seals are the appropriate model for inputting BMR into these models. We consider this to be unrealistic.

Several eutherian mammals' metabolic rates do not fit Kleiber's equation or its derivatives (McNab 1980, 1983, 1988). Captive-based estimates of the metabolic rate of West Indian manatees suggest that in water at their thermoneutral zone, their metabolism is approximately 20% that predicted by the Kleiber equation (Blair Irvine 1983). This is not dissimilar for the lower estimate for bowhead whales: roughly 30% of that predicted by the Kleiber equation (George et al. 2021). If NARW metabolic rates are substantially less than those used in models to date, it will dramatically change their predictions and implications for conservation. Right whales are very fat, and the high proportion of body fat to lean tissue is another indication that they might have a lower BMR relative to their mass in comparison to other marine (and terrestrial) species. At present, we can do little but guess what their BMR is. That being so, we took the range of BMRs recently posited for another balenid, the bowhead whale (George et al. 2021), and tested several values from that range in our model.

McHuron et al. (2022) identified 11 key knowledge

gaps in the field of marine mammal bioenergetics and ranked them by importance, including field metabolic rates (ranked as most important), and prey abundance, distribution, and energy density, which goes along with our findings. In Table 4, we give an overview of data gaps regarding NARW bioenergetics that we encountered in our analysis and make suggestions how they could be addressed.

4.1. Types of uncertainty and analysis of sensitivity

Although we aggregate uncertainties in our model description, these uncertainties differ in type. For instance, the estimates of the range of drag per day from entangling gear encompass the range of directly measured values of drag for gear known to entangle whales. Thus, for entanglement, the upper estimates of possible impacts are impacts known to occur from gear that has been removed from whales (van der Hoop et al. 2017a,b). Likewise, the estimates of plankton density in the vicinity of whales and the energy content of *Calanus finmarchicus* are values taken from the field (Baumgartner & Mate 2003).

Unlike for NARWs, there are few estimates of plankton density available for SRWs. One data point

from a site where SRWs were feeding (D'Agostino et al. 2018) identified a mix of species: cladocerans, copepods, euphausiids, and other decapods, that, when all combined, were at densities within the range used in our models (D'Agostino et al. 2018, their Table 4). Previous work in the same area found a similar plankton species composition, although only relative densities were assessed (Hoffmeyer et al. 2010). These zooplankton species are also found in areas where satellite tracking (Zerbini et al. 2016) has identified foraging areas for SRWs (e.g. Marrari et al. 2004). Other estimates of euphausiid abundances, not necessarily at SRW foraging sites (e.g. Nowacek et al. 2011), suggest that euphausiid densities fall within, or below, the bounds of those used in our models. The energy contents of copepods and euphausiids (in kJ g^{-1} dry weight) are similar (e.g. Harmelin-Vivien et al. 2019). Therefore, rather than add further uncertainty to our models by attempting to model the prey of SRWs as well, we took the simplification of comparing all modeled whales to the well known NARW food, *C. finmarchicus*.

Unlike drag and plankton density estimates, the possible values for BMR or filtration efficiency (with or without entangling rope) are ranges of plausible values either from literature models (BMR) or by

Table 4. Summary of data gaps encountered in our attempt to model parts of North Atlantic right whale (NARW) bioenergetics, and possible approaches how to fill these gaps. Additionally, novel methods should be developed, especially regarding basal metabolic rate (BMR), and differences between NARWs and southern right whales (SRWs) should be examined (first regarding habitat characteristics, food, and way of life)

Data gap	Possible approaches
Plankton - Density - Nutritional value - Species composition - Differences between NARWs and SRWs	Increased sampling efforts in the feeding paths of right whales, both NARWs and SRWs, e.g. with remotely operated vehicles equipped with sampling devices, hydroacoustic devices (Benoit-Bird et al. 2020), and/or video cameras. Establishment of a database that covers different locations and times of the year at a higher resolution, as conditions can vary substantially between a few meters or minutes.
Capture efficiency (baleen hydrodynamics) and impact of entanglement	Analysis of drone-based infra-red video (Lonati et al. 2022), flow measurements of baleen samples from dead whales (Werth & Potvin 2016), investigation of a possible pipe effect (Werth 2004, Lambertsen et al. 2005, Werth et al. 2018, Werth & Sformo 2021), picture analysis of damaged baleen taken at necropsies.
BMRs (measured in the field)	Physiologging (Hawkes et al. 2021), thus biologging sensors worn by animals for e.g. near-infrared spectroscopy to measure oxygenated and deoxygenated hemoglobin concentrations inside tissues such as skin, muscle, and the brain, as well as respiration events and heart rate (Ruesch et al. 2022); lung mechanics, scaling of heart rate and breathing frequency if and when practicable in the field (Fahlman et al. 2015, 2016, Blawas et al. 2021), rates of oxygen consumption (Sumich 2021), double-layered water method, if and when practicable for balaenids in the field (Westerterp 2017, McHuron et al. 2022), development of new methods, e.g. as in Chung et al. (2019).
Life cycle associated parameters (e.g. migration, feeding behavior)	Increased field observations and application of long-term tags.

extrapolation, given information available in the literature (filtration efficiency). Without field-based verification of these values, they will remain uncertain. As discussed above, analysis of drone-based infrared video (Lonati et al. 2022) of foraging whales could help elucidate filtration efficiency. Work by Sumich (2021) on the metabolism of gray whales *Eschrichtius robustus* shows how to collect data that can improve understanding of the metabolism of free-ranging large whales, although that work also relies on measurements of some variables, obtained from young gray whales held in captivity for rehabilitation.

As no empirical data are available for BMR in the field, we applied 4 single BMR values to our model which are based on the model of Kleiber (1975). In this way, we also provide a measure of sensitivity of our model to BMR. The results of this sensitivity test now show how the model results change depending on the single BMR values. We found the model results (energy income as a multiplier of BMR) to vary by a factor of 3.3, which means a rather high sensitivity, and reveals the need to collect data on BMR (corroborating the findings of McHuron et al. 2022) or at least to improve its estimation.

As another measure of sensitivity, we tested the sensitivity of the model to body size by modeling a stunted NARW (Stewart et al. 2021), given that the body mass estimates of our 3 right whale populations overlap. The stunted individual was about 2.8 m (~20%) shorter than the mean and about 2 m shorter than the lower range of the 3 whale populations. Unfortunately, no measurement of the head width was available for the stunted whale, which is why we had to derive its gape area from Fig. 2 in van der Hoop et al. (2019) based on its body length. As expected, when modeling the stunted whale, which is an outlier of its population, the difference between its modeled energy income and the 3 whale classes is more distinctive than within these 3 classes (Fig. 1E). Nevertheless, the uncertainties around the model estimates of the stunted whale still overlap with those of the 3 whale classes, which shows that even when varying the body size estimate by 20%, the effect and thus parameter uncertainties swamp even this substantial difference in body size.

4.2. Implications for conservation and research

Much of the discourse around NARW conservation presupposes that the factors driving their current decline are well understood. Population consequences of disturbance (PCoD) models are a conceptual frame-

work used to assess the potential for population-level consequences following exposure of animals to a disturbance activity or stressor (Harwood et al. 2016). This framework has been used in marine mammal research (e.g. New et al. 2014, Villegas-Amtmann et al. 2015, Dunlop et al. 2021), but no PCoD model has been fully parameterized with empirical data yet (Pirota et al. 2018) because those data are difficult to obtain. However, management agencies request and fund PCoD-style modeling work to support or guide their management decisions. For example, recently a project to assess the likely impact of offshore wind development on NARWs using the PCoD approach has been funded by the Bureau of Ocean Energy Management (Baker 2022), as a very specific example of a management application.

Several studies have attempted to determine which is more important: the energetic cost of entanglement or the cost of not finding/having access to enough food. On the one hand, it has been hypothesized that food shortages, driven by changes in copepod distribution due to climate disruption, are driving the reduction in calving rates (Meyer-Gutbrod & Greene 2018, Gavrilchuk et al. 2021, Meyer-Gutbrod et al. 2021). On the other hand, most individual NARWs have been entangled in fishing gear, often multiple times (Knowlton et al. 2012). Entanglement has been shown to be associated with shorter whales, body lengths in NARWs have been decreasing since 1981 (Stewart et al. 2021), and arrested growth may lead to reduced reproductive success (Christiansen et al. 2018, Stewart et al. 2022). Further, NARWs have been shown to be in poorer body condition than SRWs, which, in comparison to NARWs, do not face sublethal stress from entanglement in fishing gear and vessel strikes (Christiansen et al. 2020). This is a major management issue, because not much can be done directly to increase plankton densities, but with the right management actions, entanglements (and vessel strikes) can be reduced. Models can inform this process, but we find that improved field data are required first to improve the value of these models.

We have a good description of NARW abundance over time (Pace et al. 2017, Pettis et al. 2023) and know that their distribution, at the scale of the east coast of North America, has changed in past decades (Davies et al. 2019). Correlational studies, e.g. Meyer-Gutbrod et al. (2021), offer possible explanations for observed changes in NARW movements. However, the current scientific capacity to provide predictions for conservation is poorer. Quintana-Rizzo et al. (2021) showed that the spatial model of

Pendleton et al. (2012), which indicated suitable foraging habitat for NARWs in the area south of Cape Cod, was the one model that provided a reliable prediction. However, despite decades of research on NARWs, and a recommendation for a protected area in the GoSL (Duff et al. 2013), no published study predicted their move into that area after 2014, as was later described by Simard et al. (2019).

Nevertheless, there are important findings that emerge from our modeling. First, as has been demonstrated previously (van der Hoop et al. 2017a,b), entanglement may impose substantial energetic costs. The upper estimate of the daily cost of entanglement, about 3 times BMR (assuming 50% of Kleiber 1975), demonstrates that entanglements in gear with substantial drag impose costs comparable to the cost of a pregnancy. At the other extreme, the energetic costs of gear with relatively low drag, although an order of magnitude less, are still not negligible, at around 30% of daily BMR. When the possible impact of reduced filtration efficiency from entangling rope disrupting the hydrodynamic flow of the baleen rack is also modeled, the energetic impacts of entanglement from both drag and reduced food intake reinforce the deleterious impact of this anthropogenic stressor. These same points also held true for estimates of the energetic cost of entanglement relative to daily energy income, with or without disruption of the baleen rack.

We attempted to compare the likely impact of entanglements on right whales of 4 different sizes. Larger female SRWs off southern Australia have larger, more robust calves that grow faster than calves of slightly smaller females (Christiansen et al. 2018). At present, calving female NARWs are smaller and less robust than SRWs, and also smaller than NARWs were at the turn of the century (Miller et al. 2012, Stewart et al. 2022). Therefore, we intended to compare these different whales to assess the extent to which aspects of their ecology (food availability vs. entanglements) could vary. Unfortunately, with no data available on food density and caloric values for SRWs, we were forced to use data from northern hemisphere *Calanus finmarchicus* only. Future field studies at sites where SRWs are available for research, and where it is logistically feasible, using appropriate field techniques (e.g. Cade et al. 2022) should start to remedy this data gap. The recent work of Weir & Stanworth (2020) suggests one possible field site, and further studies in the northern Patagonian gulfs (D'Agostino et al. 2018) are another possibility.

The relative importance of the uncertainties in our model quickly overwhelmed the differences associ-

ated with differently sized right whales. For entanglement-related energetic expenditure as a proportion of daily energy income, the samples for all 3 sizes of right whales were indistinguishable from each other (Figs. 1–3). Female SRWs and NARWs from 2000 are examples of right whales that were increasing in abundance, and either calving close to maximally (SRWs) or far better than NARWs now. For bioenergetic models to be informative, they should be able to detect differences between whales whose bioenergetics are implicated in their rapid decline as opposed to whales that are increasing in abundance. In comparison, entanglement-related energetic expenditure as a proportion of daily energy income was higher for the stunted NARW and more distinct from the other 3 whale classes, but their ranges still overlapped (Fig. 3C,D), even though the stunted NARW was about 20% shorter. This indicates that the effect of entanglement-related energy expenditure is more serious for shorter whales but also goes along with a higher uncertainty (Fig. 3C,D). We conclude from this that the uncertainties in our energetic model are so great that the model fails to distinguish between 3 populations of right whales that differ in ways that are important for their conservation status. Right now, the uncertainties in our models overwhelm their comparative value. However, future refinements of this and similar models are possible, when more species- and area-specific data become available, and when parameter uncertainties have been reduced.

5. CONCLUSIONS

There has been a move in ecology away from field biology, and towards more model-based work (Ríos-Saldaña et al. 2018). Our exercise in energetic modeling of right whales demonstrated that the uncertainty inherent in the field data available at present is such that the models are not as informative as we had hoped. Even though our work is only one bioenergetics model that originally aimed at examining a specific question, our approach has been used as a basis in most previous bioenergetics modeling studies. If such metabolic modeling is to inform conservation management of NARWs, then field studies are required to better quantify the hydrodynamics of NARW foraging, and to quantify the way entanglement affects foraging efficiency. Enhanced data, from more sites across the NARW range, on *Calanus* density and energy composition in the immediate vicinity of NARWs, that trigger

foraging, are also needed. As with many aspects of marine mammal bioenergetics, the metabolic rate of NARWs is unknown, which impedes the use of bioenergetics modeling to guide management decisions (McHuron et al. 2022). Until field studies are developed to better determine metabolic rates of large marine mammals in the field, all energetics models for NARWs will rely on the strong assumption that whatever value is selected for BMR has some basis in a reality but which is currently unknown.

Finally, recent correlative work (Meyer-Gutbrod et al. 2021, Pershing & Pendleton 2021) addressing the status of NARWs has a strong focus on food availability as a causal explanation for current calving failure. Our work suggests a note of caution with this focus on food availability only, while not also considering entanglements. Despite the substantial uncertainties in our models, it is clear from this work and previous studies (Moore & van der Hoop 2012, Robbins et al. 2015, van der Hoop et al. 2017a,b, Stewart et al. 2021) that entanglements can have substantial deleterious impacts on NARWs. Statistical models that can include entanglement status as a covariate for testing in model selection have proved informative (Robbins et al. 2015, Stewart et al. 2021), and further studies along those lines should be pursued as a matter of urgency.

Our original aim for this modeling project was attempting to distinguish between the relative importance of entanglement and food availability impacting the likelihood that female NARWs will calve. In this, we were unsuccessful. The energetic costs of the drag caused by entanglement can be estimated reliably (van der Hoop et al. 2014). On the other hand, our knowledge of many of the variables that are input into models of NARWs foraging, and then estimating their BMR, is, as we have shown, far less certain. We therefore cannot compare the relative influence of entanglement and food availability on the reproductive success of NARWs, and caution against any work currently purporting to do so. We also caution against over-reliance on modeling exercises that attempt to make inference on the relative energetic costs of different forms of anthropogenic impacts (e.g. Pirodda et al. 2022) or that attempt to ascribe definitively the energetic effect of some change in NARW ecology (e.g. Gavrilchuk et al. 2021). Finally, we conclude with a call for field research to better understand the feeding mechanisms of NARWs, and how entanglements can disrupt feeding; and for *in situ* studies to estimate NARW metabolic rates.

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