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The Trophic Footprint of Humpback Whales in a Changing North Pacific

Alec Burslem[1] | Martin van Aswegen[1,2] | Andy Szabo[1,2] | Joe Roman[3] | Lars Bejder[1]

[1]Marine Mammal Research Program, Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kaneohe, Hawaii, USA | [2]Alaska Whale Foundation, Petersburg, Alaska, USA | [3]Gund Institute for Environment, University of Vermont, Burlington, Vermont, USA

Correspondence: Alec Burslem (aburslem@hawaii.edu)

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ABSTRACT

The movement of energy, nitrogen, and carbon around the earth are fundamental drivers of primary productivity and ecosystem functioning. Mobile animal taxa contribute to these movements by removing biomass in the form of plants and other animals and redistributing it via movement, excretion and ultimately death and consumption by predators and scavengers. Humpback whales (*Megaptera novaeangliae*) exhibit these processes at their extremes. Their large bodies, energy requirements and engulfment capacities, combined with a life-history strategy involving long migrations between distant feeding and breeding grounds, are expected to make them disproportionately influential on ecosystem processes relative to their population sizes. Here, we synthesise and extend recent empirical advances to estimate the total biomass required to maintain humpback whale populations at their current size. Our approach uses age-structured Monte-Carlo simulations to estimate the energetic requirements of individual whales as a function of age and life history state and scale them to population prey biomass requirements. We found that north pacific humpback whales require a total annual biomass of 1.5–5.3 million tonnes (mean = 2.6 Mt), mostly of pacific krill (85% by mass on average) not currently targeted by fisheries. Sensitivity analysis indicated that alternative calculation methods agree well in estimating energetic requirements (breathing-rate, thrust, and volume loss-metrics =2.64, 2.31, and 2.83 million tonnes/year, respectively) but volume-based estimates are extremely sensitive to common assumptions regarding reserve composition which currently lack empirical parameterisation (Sobol analysis variance contribution = 69%), highlighting reserve composition as a key target for future empirical research. Thus, as well as providing estimates of prey biomass requirements, our analysis directs future empirical work by identifying data gaps to which such estimates are sensitive, and is an important step towards forecasting how prey limitation may shape humpback whale population status and nutrient transport in changing oceans.

1 | Introduction

The movement of energy, nitrogen, and carbon around the earth are key drivers of primary productivity, carbon flux, and ecosystem functioning (Huang et al. 2024). Mobile animal taxa contribute to these movements by removing biomass in the form of plants and other animals and redistributing it via movement, excretion and ultimately death and consumption by predators and scavengers (Hoeks et al. 2020; Pringle et al. 2023; Roman et al. 2025). Unlike purely physical processes, these patterns of energy and chemical movement are mediated by animals' behavioural responses to their environment. For example, herbivores influence biomass distribution primarily through the enormous amounts they remove directly (Pringle et al. 2023), while carnivores also exert top-down influence on overall biomass distribution via removing and changing the behaviour of their herbivore and/or mesopredator prey (Hoeks et al. 2020). Conversely, the conservation and recovery of these (generally large bodied) predators require that they are consistently not limited by prey availability, as their long generation times constrain their ability to recover from perturbations to prey resources at the population level.

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Humpback whales (*Megaptera novaeangliae*) exhibit these characteristics at their extremes. Their large bodies, high energy requirements, and engulfment capacities (Goldbogen et al. 2019) and life-history strategy involving long migrations between spatially separated feeding and breeding grounds (Lennox et al. 2016) are expected to make them disproportionately influential on ecosystem processes relative to their population sizes (Roman and McCarthy 2010; Roman et al. 2025). Beyond their role as predators, whales act as nutrient transporters, enhancing primary productivity through horizontal and vertical transport of nitrogen and iron (Roman and McCarthy 2010; Lavery et al. 2010), and contribute to carbon cycling via faecal plumes (Roman and McCarthy 2010). These processes link predator biomass consumption and movement to global biogeochemical cycles.

Quantifying the biomass requirements of humpback whales is essential for understanding their ecological role as top predators, their influence on prey population dynamics, and their contributions to nutrient cycling and carbon storage. Previous studies have largely focused on regional diet composition (Moreaux et al. 2025) or feeding behaviour (Friedlaender et al. 2013), but few have attempted to scale consumption estimates to the population or ocean-basin scale (although see Savoca et al. 2021). Moreover, changing ocean conditions, shifting prey distributions, and increasing competition with fisheries underscore the importance of robust, quantitative estimates of whale energetic demands. Such information is particularly critical for ecosystem-based management and trophic modelling efforts that aim to reconcile predator requirements with fisheries production and food web stability (Estes et al. 2011). As large-bodied predators with wide-ranging habitat use and flexible foraging strategies, humpback whales exert predation pressure which is both spatially and temporally variable. Understanding the individual-level drivers of variation in consumption (e.g., reproductive state, age, migration strategy) is central to scaling from the whale- to the population- and ecosystem-levels. At the same time, integrating diverse data streams, including unoccupied aerial system (UAS; drone)-based body condition estimates (Christiansen et al. 2019), biologging (Hollers et al. 2026), and isotopic analyses (Moreaux et al. 2025), provides new opportunities to develop, refine and cross-validate prey requirement estimates.

In this study, we apply bioenergetic modelling at the ocean-basin scale to quantify the ecological footprint of humpback whales. evaluate their trophic impact in a changing ocean, and inform conservation strategies by estimating the prey stocks and densities required to support the maintenance and continued recovery of these iconic predators. In so doing, we synthesise new findings on metabolic requirements, population abundance, and behavioural partitioning to estimate the total prey biomass required annually by humpback whales in the North Pacific.

2 | Methods

2.1 | Overview

We use Leslie matrices (Leslie 1948, 1945) to model the age structure at present (assumed) stable population sizes. We then use empirically derived functions to link age to length (van Aswegen et al. 2025b) and, in turn, mass (Lockyer 1976) and total energy requirements (Gough et al. 2025; Hollers et al. 2026; van Aswegen et al. 2025a). Energy requirements are converted into biomass using representative fish:krill mixtures and empirically derived prey energy densities. Wherever available, empirical parameter estimates specific to the North Pacific were used (Table 1). Population size was based on the results of Cheeseman et al. (2024) and was age structured using Leslie matrices and age-class specific survival estimates from the published literature (Table 1). Our fecundity and growth data are conditioned on surviving animals, rates of mortality for reasons other than starvation are thought to be low in humpbacks, and here we are interested in the prey *requirements* of humpbacks, rather than biomass removed at carrying capacity. We therefore made the simplifying assumption that all whales initially survived for one full year. Length as a function of age was modelled using von Bertalanffy growth curves fitted to location and life history phase-specific empirical UAV-derived body length and putative age data (van Aswegen et al. 2025a).

Energetic requirements were calculated separately for first year calves and other life history classes. First-year calves were treated as a state variable of their mother, allowing variability in for example, maternal investment as a function of maternal age and size to inform estimated costs of calf growth and maintenance. For calves in their first year ($a = 1$) costs of growth and maintenance were averaged over the first year. For other life history phases other than calves, costs were calculated according to age-specific mass and growth rates. Energetic costs of maternal investment were then calculated by multiplying the cost of pregnancy and lactation by the fecundity coefficient. Several alternative methods of estimating and combining different energetic costs were employed.

Total energetic cost during fasting was estimated using the observed rate of volume loss which occurred on the breeding grounds (assuming negligible feeding). Estimated metabolic rates (EMR) were calculated using both breathing-rate and thrust-based methods (Gough et al. 2025; Hollers et al. 2026). Energetic costs were combined under alternative methods described below (structural uncertainty) and converted into energetic requirements by applying relevant efficiency factors (e.g., prey assimilation efficiency for all energy, milk transfer efficiency for energy used by calves, storage and mobilisation efficiency for energy used during fasting).

Estimated metabolic rates were converted into annual biomass requirements using specific energy densities for their most important prey and per-unit-mass prey intake ratios based on stable isotope analysis (Moreaux et al. 2025). Finally, energetic requirements were adjusted using empirically derived proportions of time spent on foraging grounds and time spent foraging (as opposed to e.g., resting and socialising) on foraging grounds to calculate the encounter rates necessary to meet the estimated biomass requirements under realistic foraging time budgets. For a full formal description of the simulation procedure, see the underlying R code (Digital supplement: https://doi.org/10.17605/OSF.IO/XD24A).

2.2 | Model Structure and Parameterisation

2.2.1 | Population Size and Age-Structure

Population size n was based on published mark recapture analysis specific to the North Pacific population segment (Cheeseman et al. 2024). Age structure was estimated using Leslie matrix

TABLE 1 | Input parameters for biomass requirement modelling.

Parameter	Level	Description	Value	Units	Source and study population
n	Global	Abundance	26,662 ± 4192 95% CI		(Cheeseman et al. 2024), North Pacific
i	Individual index				
Matrix population modelling					
ω	**Global**	**Maximum age**	**60–100**	**Years**	(Lagunas-Rangel 2021, R. G. Chittleborough 1965, 1959), **Global**
S_a	Global	Adult survival probability	0.979	Prob	(Ashe et al. 2013), North Pacific
S_j	Global	Juvenile survival probability	0.95	Prob	(Zerbini et al. 2010), Global
S_c	Global	First year survival probability	0.818	Prob	(Gabriele et al. 2001), North Pacific
Body size					
Males					
$L_{\infty[a>1]}$	*Individual*	Asymptotic length	12.34 SD = 0.155	m	(van Aswegen et al. 2025a), North Pacific
$L_{0[a>1]}$	*Individual*	L intercept	8.56	m	(van Aswegen et al. 2025a), North Pacific
$k_{[a>1]}$	*Individual*	Intrinsic growth coefficient	0.12 SD = 0.03	m	(van Aswegen et al. 2025a), North Pacific
Females					
$L_{\infty[a>1]}$	*Individual*	Asymptotic length	13 SD = 0.155	m	(van Aswegen et al. 2025a), North Pacific
$L_{0[a>1]}$	*Individual*	*L* intercept	8.42	m	(van Aswegen et al. 2025a), North Pacific
$k_{[a>1]}$	*Individual*	Intrinsic growth coefficient	0.15 SD = 0.04	m year^{-1}	(van Aswegen et al. 2025a), North Pacific
Calves (relative to maternal length)					
$L_{\infty[a=1]}$	*Individual*	Asymptotic length	0.74 (0.73–0.75)	m/m	(van Aswegen et al. 2025a), North Pacific
$L_{0[a=1]}$	*Individual*	L intercept	0.35 (0.34–0.35)	m/m	(van Aswegen et al. 2025a), North Pacific
$k_{[a=1]}$	*Individual*	Growth coefficient	0.007 (0.006–0.007)	m/m/day	(van Aswegen et al. 2025a), North Pacific
Life history					
a	*Individual*	Age index	$1...\omega$		
$m_{[a]}$	*Individual*	Fecundity coefficient	0.2–1	Prob.	(R. G. Chittleborough 1965), Southern Ocean
a_r	*Global*	Minimum age at first reproduction	6 ± 1.5 t (5,8)	Years	(R. G. Chittleborough 1965), Southern Ocean

(Continues)

TABLE 1 | (Continued)

Parameter	Level	Description	Value	Units	Source and study population
a_w	*Global*	Age at weaning	1	Years	(Mann 2000), Global
$\boldsymbol{P_1}$	***Global***	**Proportion of variance in fecundity attributable to structural size***	**0–0.9**		
Energetic requirements					
$\boldsymbol{\zeta_m}$	**Global**	**Milk transfer efficiency†**	**0.8–0.95**	**Prop.**	(McHuron et al. 2023), **Estimated**
ζ_d	Global	Prey digestive efficiency	0.8–0.9	Prop.	(Booth et al. 2023), Estimated
R_o	*Individual†*	Mass specific metabolic rate (BR method)	0.44 ± 0.16 SD	J/s/kg	(Hollers et al. 2026), North Pacific
R_t	*Individual*	Mass specific metabolic rate (thrust method)†	0.37 ± 0.08 SD	J/s/kg	(Hollers et al. 2026), North Pacific
R_o	*Individual*	Calf mass specific metabolic rates (BR method)†	1.61 ± 0.42 SD	J/s/kg	(Hollers et al. 2026), North Pacific
R_t	*Individual*	Calf mass specific metabolic rates (thrust method)†	1.24 ± 0.25 SD	J/s/kg	(Hollers et al. 2026), North Pacific
α	*Individual*	Volume loss intercept†	0.056197 (SE = 0.0159)	$m^3 day^{-1}$	(van Aswegen et al. 2025b), North Pacific
β	*Individual*	Effect of ML on volume loss†	−0.01262 (SE = 0.0011)	$m^3 m^{-1} day^{-1}$	(van Aswegen et al. 2025b), North Pacific
Behavioural budgets					
P_S	*Individual*	Time spent on foraging grounds	7/12	Prop	
$P_{f\|S}$	*Individual*	Time spent foraging while on the foraging grounds	0.2	%	(Miller et al. 2022), Atlantic
Physical parameters					
ρ_b	*Global*	Physical density of blubber†	985	$kg\,m^{-3}$	(van Aswegen et al. 2025a), North Pacific
Energy densities					
ζ_k	*Global*	Specific energy density of krill	3.67 ± 0.42 SD	$kJ\,kg^{-1}$	(van Aswegen et al. 2025b) and references therein, North Pacific
ζ_h	*Global*	Specific energy density of herring	5.58 ± 0.58 SD	$kJ\,kg^{-1}$	(van Aswegen et al. 2025b), North Pacific
ζ_λ	***Global***	**Specific energy density of reserves†**	**5.58 ± 0.58 SD**	**$kJ\,kg^{-1}$**	(Wright et al. 2020), **Elephant seals**
Prey split					
P_k	*Global*	Krill as a proportion of total biomass	85.3% ± 8.8% SD	%	(Moreaux et al. 2025), North Pacific

Note: Bold text indicates parameters for which empirical estimates are not available at the parvorder level, and are therefore included in the sensitivity analysis.

†Only used in volume flux calculation method.

†Only used in BR and thrust methods (see below for method descriptions).

*Varied in the sensitivity analysis but not the main simulations.

modelling and published estimates of survival probability for calves, juveniles, and adults (Table 1) and (age/size specific) fecundity rates. Initial individual age was set by sampling from the resulting probabilistic age distribution n times. Sex ratio at birth was assumed to be 1:1.

2.2.2 | Age-Specific Body Size

Body length was estimated from age using von Bertalanffy length at age curves parameterised using sex-specific parameter distributions from the published literature (van Aswegen et al. 2025a). Individual differences in growth rate were implemented using individual level Monte-Carlo sample draws of asymptomatic length (L_∞) and intrinsic growth rate (k). Length was then converted to mass using published allometric equations (Lockyer 1976).

2.2.3 | Humpback Whale Life History Parameters

For females of reproductive age, a fecundity parameter was used to describe the frequency of reproduction. Since lactation and gestation each last approximately 1 year in humpback whales, this is also the proportion of time spent in a lactating or pregnant state. This was set to 0 for males and in females was specified to be a function of age and structural length, the strength of the influence of the latter being controlled by P_l (Table 1).

2.2.4 | Costs of Humpback Whale Reproduction

Instantaneous maternal investment during pregnancy was allowed to vary as a function of time and maternal length using the empirical relationships demonstrated by van Aswegen et al. (2025b). Total cost of a pregnancy or lactation was then estimated by integrating over the full duration of the relevant life history state as a function of individual size.

2.2.5 | Diet Composition

Estimates of prey composition mass (krill vs. herring) were estimated based on stable isotope analyses conducted on skin biopsy samples collected in the North Pacific (British Columbia) during the summers of 2022–3 (Moreaux et al. 2025). A broader temporal spread may have better captured across year variability in prey composition, especially given the 'boom-and-bust' nature of herring and krill abundance and the rapid rate of isotopic turnover in skin. However, these values nonetheless represent the best data available for the North Pacific population.

2.2.6 | Energy Densities of Prey and Tissue

Energy density of prey came from published empirical measurements (van Aswegen et al. 2025a and references therein). Rather than assume that all changes in volume reflected changes in blubber of a fixed and known composition (as is commonly done), we explicitly modelled the uncertainty surrounding composition of tissue volume lost, expressed as percentages of lipid, protein, and water. Since species-specific values were not available, we based these values on empirical measurements taken from elephant seals (Wright et al. 2020). As a large marine mammal sharing many of the same salient life-history characteristics (capital breeding, fasting lactation) and ecological trade-offs as humpback whales (Boyd 2000; Champagne et al. 2012; McKnight and Boyd 2018), we expected elephants to be a closer proxy for humpback whales than similar studies of income breeding odontocetes. We specified the distribution to be centred on this empirically derived mean value, but broadened the variance such that the resulting distribution also encompassed the energy density of pure blubber.

2.2.7 | Proportional Time Budgets

In order to facilitate translation by managers of total prey requirements to prey density requirements, and comparison with previous studies, we estimated time spent on feeding grounds (P_s), and of that, the time spent actively foraging (P_{fls}) to convert total annual biomass requirements to the approximate encounter rate during foraging necessary to meet energetic requirements.

2.3 | Uncertainty and Sensitivity Analyses

2.3.1 | Parameter Uncertainty

To incorporate uncertainty around parameter values treated as global (e.g., n, ω) and to limit the influence of simulation variance, the full simulation was run 10^3 times with global parameter values drawn from appropriate distributions derived from the published literature. Parameters which were expected to exhibit biological process variability (for example, $k_{[a,i]}$) were also allowed to vary stochastically between individual whales within each simulation run. Where only 95% CIs or ranges were available, normal and gamma distributions were parameterised on the assumption that these represent 2 standard deviations.

2.3.2 | Sensitivity Analysis

A Sobol global sensitivity analysis was performed to identify the unmeasured parameters (parameters in bold, Table 1) to which model predictions were most sensitive. A parameter was considered unmeasured (bold parameters in Table 1) if it lacked an empirically derived estimate at the taxonomic level of parvorder or closer. The model was considered strongly sensitive to a parameter if the model was more sensitive to it than it was to population size n. This process formally identifies key targets for empirical research aimed at refining estimates of energetic and prey demand in humpback whales by alternative methods.

2.3.3 | Structural Uncertainty

As well as uncertainty surrounding specific parameter values, there exists structural uncertainty with respect to alternative

means of estimating metabolic requirements. Three alternative ways of estimating and assigning individual energetic requirements were therefore performed and compared: rates derived from breathing rates (hereafter BR; Gough et al. 2025 and references therein), from hydrodynamic models used to estimate thrust performance (Thrust; Gough et al. 2025 and references therein) and from fluctuations in total body volume given length (Volume flux; Christiansen et al. 2016). The breathing rate model uses observations of breathing rates from animal-borne camera tags as inputs to predictive models of gas exchange and O_2 quenching to estimate metabolic rate (Gough et al. 2025). The Thrust method uses hydrodynamic modelling of swimming performance, parameterised with empirical measurements of hydrodynamic body (e.g., tail flukes) and observed stroking rates, also from animal-borne tags, to estimate metabolic rate. Finally, the volume flux method uses repeated observations of an animal's body volume to calculate rates of energy storage tissue loss which, combined with estimates of the physical and energetic density of that tissue, are used to calculate the total energetic cost exerted over a given period (van Aswegen et al. 2025b).

Estimated metabolic rates (EMR) from BR and Thrust were available for mothers and calves on the breeding grounds while rates of tissue volume loss and gain were available for nursing females on the breeding and feeding grounds. Lipids which are mobilised and expelled as such will not be reflected in oxygen consumption beyond any metabolic costs associated with lipid mobilisation, transport and endergonic resynthesis reactions (if performed). In the case of marine mammalian milk production such costs are thought to be negligible (McHuron et al. 2023). The cost of lactation was therefore assumed to be reflected directly in tissue loss, but not in metabolic rate as estimated using thrust or breathing frequency. Thus, treating the calf as a maternal state variable, costs to the mother were estimated using each method as follows:

2.3.4 | Breathing Rate (BR) and Thrust Methods

Energetic rates of the mother and dependent calf were calculated by drawing a value from the empirically derived distribution of mass specific metabolic rates for mother and calf (Hollers et al. 2026) estimated using either the thrust method or breathing rate method as described in (Gough et al. 2025). Energetic costs of the calf (metabolic rate and growth) were uplifted to account for energetic inefficiencies of milk transfer (ζ_m). The result was then multiplied by individual fecundity (zero for males, age dependent for females) to give energetic cost of lactation (E_l) which, was then added to the cost of pregnancy (E_p; also multiplied by the fecundity coefficient) and the mother's own intrinsic energetic costs (i.e., growth [E_g] and metabolic rate [E_R]) to give total energetic requirement: E_{Total}:

$$E_{l[i]} = \frac{R_{Calf[i]} + C_{g\ calf[i]}}{\varsigma_m} \cdot m_{[i]}$$

$$E_{\text{Total}[i]} = E_{l[i]} + E_{R[i]} + E_{p[i]} \cdot m_{[i]} + E_{g[i]}$$

where cost of growth (E_g) was calculated with and without metabolic inefficiencies for the thrust and breathing rate methods, respectively, under the assumption that endothermic tissue synthesis reactions are sustained by metabolic output and are therefore represented in breathing rate.

2.3.5 | Volume Loss Method

The volume flux method uses loss or gain in total body volume to estimate energy loss (Christiansen et al. 2019; van Aswegen et al. 2025b). Total energy loss was primarily calculated using observation from animals on breeding grounds, where the lack of prey intake results in a closed system. Here, body volume loss rate could therefore be assumed to reflect total energy outlay, which was then broken down into its constituent costs in order to adjust energy expenditure for fecundity rate (m). Volume loss was therefore converted to mass loss (by multiplying by blubber density; ρ_b) and multiplied by reserve energy density (ζ_λ; with uncertainty) to calculate observed volume energy loss, E_{vo}. Total cost reflected in volume loss was partitioned to lactation (E_l) vs. baseline estimated metabolic rate (E_R) by multiplying by a proportion (P_{El}), derived from the difference in rate of volume acquisition between resting and nursing females on the foraging grounds, and energetic cost of pregnancy (E_p) was calculated separately (van Aswegen et al. 2025c):

$$E_{vo[i]} = \delta V_{[i]} \cdot \zeta_\lambda \cdot \rho_b$$

$$E_{l[i]} = E_{vo[i]} \cdot P_{El}$$

$$E_{R[i]} = E_{vo[i]} \cdot \left(1 - P_{El}\right)$$

$$E_{Total[i]} = E_{l[i]} \cdot m_{[i]} + E_{R[i]} + E_{p[i]} \cdot m_{[i]} + E_{g[i]}$$

2.3.6 | Static Versus Size-Specific Fecundity

In other capitalbreeding marine mammal species, fecundity increases as a function of size (Pirotta et al. 2025, 2024). While this phenomenon is expected to be present in humpback whales, there are, to our knowledge, no empirical studies testing this hypothesis or estimating the relevant parameters. We therefore set a parameter P_l that described the proportion of variation in fecundity which is determined by structural size, versus unstructured stochastic variability. This parameter was varied from 0 (no relationship) to 0.9 (extremely strong relationship) across the sensitivity analysis, but fixed at 0 in the main simulations for parsimony.

2.4 | Interactive Biomass Calculation Tool

Sensitivity to key parameter inputs as an interactive application was implemented using to facilitate exploration of the effects of arbitrary parameter combinations (including some measured parameters) of potential interest to managers and other stakeholders. The application allows the user to download the simulated data for exploration. To allow for rapid computation on a small server, other parameters (to which the model was not sensitive) were fixed at their mean values (Table 1). This was implemented using the shiny package and hosted as a freely available web application on the shinyapps.io platform (https://alec-burslem.shinyapps.io/HBWbiomass_requirement/).

3 | Results

3.1 | Population Size and Structure

For the present population of humpback whales in the North Pacific consisting of 26,217–27,190 (mean = 26,665) individual whales (Cheeseman et al. 2024; Table 1), the average predicted age and length structures are represented in Figure 1. Intrinsic population growth rate λ was estimated at 1.1, which is broadly consistent with the increasing population size observed over a period during which most of the studies informing the analysis were performed.

3.2 | Size and Structure of Prey Biomass Requirements

Total biomass requirement estimates ranged from 1.8–5.6 million tonnes across all Monte-Carlo simulations (i.e., including all calculation methods and sources of uncertainty; Figure 2) and were 2.64 ± 0.47, 2.31 ± 0.44 and 2.83 ± 0.65 million tonnes year^{-1} for the BR, thrust and volume loss energy demand calculation methods, respectively. The methods demonstrated surprisingly strong agreement, with the mean value for each method falling within the 95% quantiles of the other two (Figure 2). The inputs and results of all 10^3 model runs incorporating individual and global parameter uncertainty and structural uncertainty are summarised in Figure S1 (Supporting information). The average, per-individual energy requirement, broken down by age, sex, calculation method and functional components are shown in Figure 3. Estimated metabolic rate and (in females) cost of lactation dominated energetic requirements. Requirements rose rapidly during early rapid growth and the onset of sexual maturity in females before plateauing around the time of structural maturity (Figure 3).

3.3 | Sensitivity Analysis

Full sensitivity results are given in Table S1. Of the parameters included in Sobol variance-based sensitivity analysis, only reserve energy density ζ_λ (reflecting reserve composition) exerted a greater influence on the relevant model (volume loss method) than population size n. In the BR and Thrust models, the next most important source of sensitivity after n was the length-specific fecundity coefficient P_1. Sensitivity to key parameter

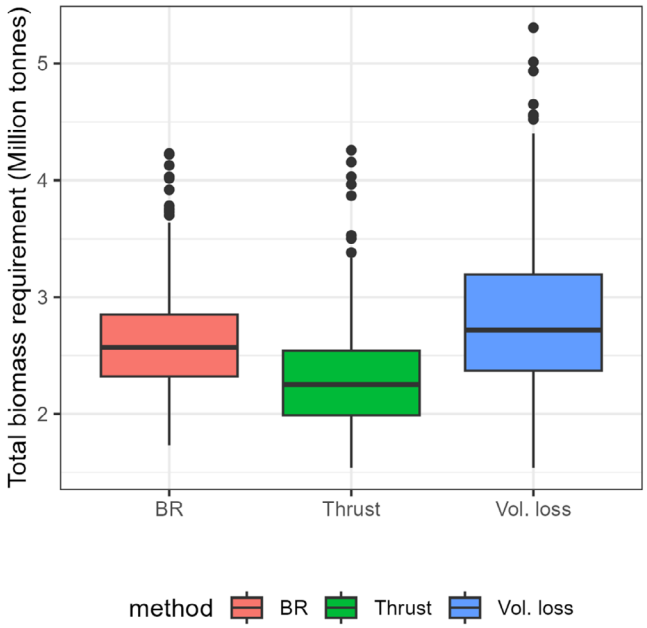

FIGURE 2 | Estimates of total biomass required by humpback whales in the North Pacific incorporating parameter and structural uncertainty. Each boxplot shows a different method of calculating energetic requirements. Red is breathing rate (BR), green is thrust power and blue is Volume loss. See 'Structural uncertainty' section for further details.

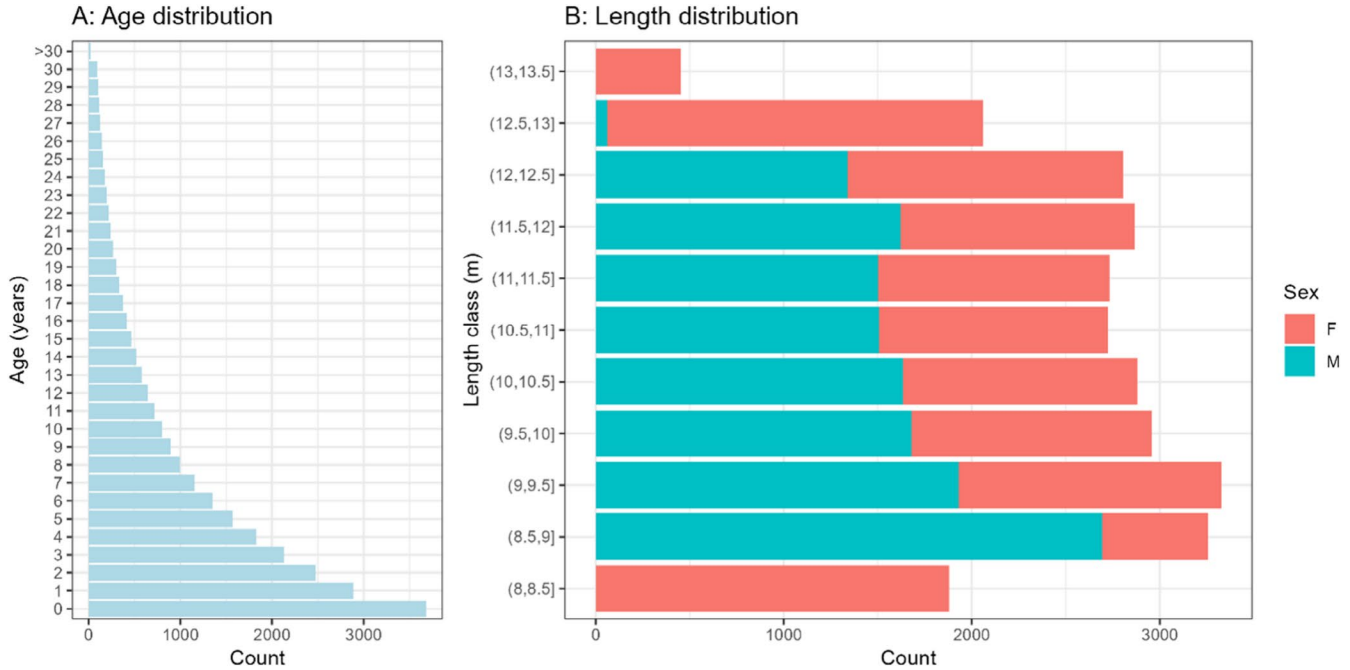

FIGURE 1 | Histograms showing mean simulated humpback whale age (panel A) and length (panel B) distribution.

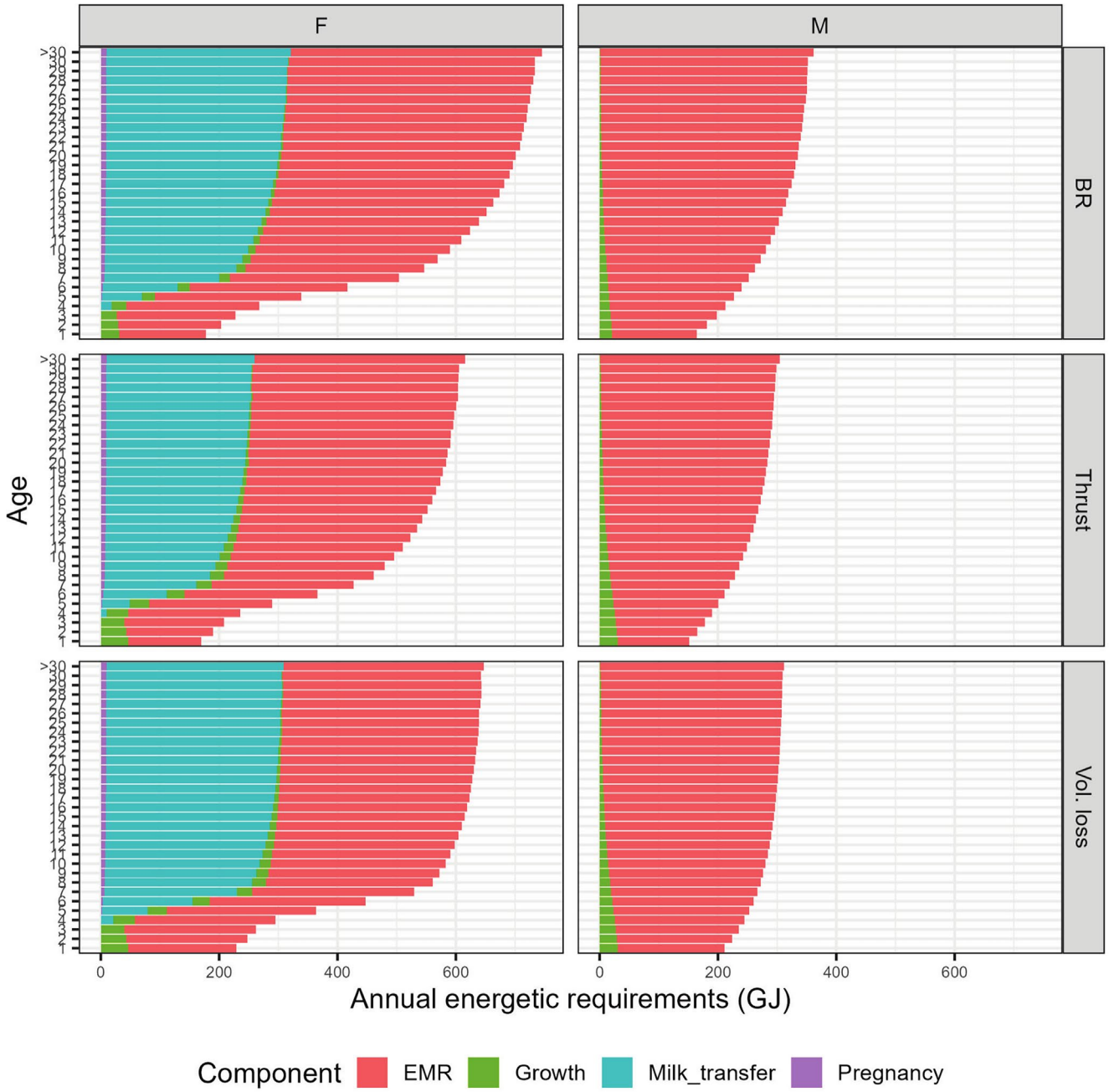

FIGURE 3 | Breakdown of energy requirements (x axis) by age (y axis), energy component (colour), sex (columns), and metabolic rate estimation method (rows; BR is breathing rate, Vol. Loss is tissue volume loss; See 'Structural uncertainty' section for further details). Age 0 (calves) are not shown as they are treated as state variables of their mothers. For further details on calving costs see 'Humpback whale life history parameters' and 'Costs of humpback whale reproduction' above.

inputs as an interactive application (e.g., Figure 4) is freely available online. The code is available via OSF, while the applications themselves are hosted at https://alec-burslem.shinyapps.io/HBWbiomass_requirement/.

4 | Discussion

4.1 | Humpback Whales May Require Less Prey Than Previously Thought

Our analysis estimates a total biomass requirement of the North Pacific humpback whale population of around 2.6 million tonnes of prey per year. To meet these annual requirements during their time on their foraging grounds, they were projected to require a prey intake rate of approximately 748 kg day^{-1} on average across all methods and life history groups. At the maximum likelihood diet composition, their diet would consist of approximately 3 million tonnes of krill and 0.6 million tonnes of herring. For comparison, the estimated North Pacific fishing stock total landings are estimated at approximately 400,000 and 60,000 tonnes of herring and krill, respectively (FAO 2026). Scaled to the global population of approximately 135,000 individuals, this would correspond to approximately 22 million tonnes year^{-1}. By comparison, the annual global biomass removal of sperm whales has been estimated at 100 million tonnes year^{-1}, which would

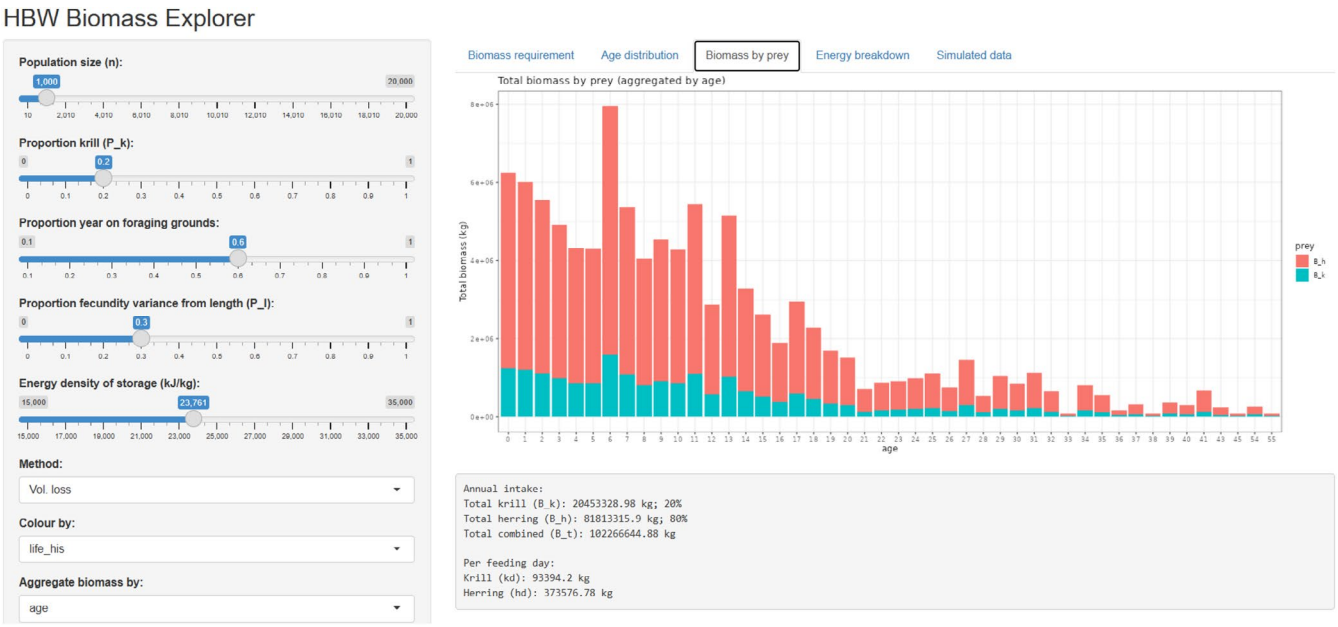

FIGURE 4 | An example page of the online sensitivity explorer showing parameter inputs and results.

similarly dwarf global fisheries (Whitehead 2018). While both estimates are necessarily very approximate they broadly agree, after accounting for the differences in population size between sperm and humpback whales (approximately 2.2:1) and energy density of prey targeted (0.6:1). We note that, while the predicted biomass requirements are extremely large, they are dominated by krill biomass not currently targeted for human consumption in the North Pacific. We note this does not preclude important indirect effects on other commercially important species for which krill may represent important prey, which our model does not consider. Models explicitly incorporating such complex ecological effects, where they can be supported by detailed empirical studies, could help to explore the implications of our results for ecosystem-fisheries interactions more fully.

Our results are of the same order of magnitude, but lower on average, than those reported by Savoca et al. (2021). Our results appear relatively robust to the choice of method for estimating energetic requirements, and Savoca et al. were able to include empirical, in situ estimates of prey concentration and engulfment volume for their prey removal analysis, suggesting there may be some systematic difference between 'top-down' and 'bottom up' approaches to estimating biomass removal in baleen whales. The source of the disparity may therefore lie in the drivers of timing, prey selection and availability and other behavioural variability in foraging, about which both we and Savoca et al. made simplifying assumptions when scaling our results. For example, Savoca et al. were estimating actual biomass removal, scaling up from inherently patchy empirical krill distribution observations, while we were scaling down from relatively stable modelled estimated metabolic rate in attempting estimate prey requirements. A combined uncertainty and sensitivity analysis investigating at what biologically plausible mechanisms may unify top-down and bottom-up predictions could help to develop testable empirical hypotheses of the drivers of humpback whale foraging behaviour with strong relevance to key contemporary conservation goals (e.g., assessing population-level vulnerability to shifts in prey availability).

Recent studies of humpback whale abundance in the North Pacific suggest that the population is currently undergoing a shift in trajectory from post-whaling recovery to a plateau, or some recent years, a contraction in population size. Recent apparent population contractions have coincided with marine heat waves on the Northern foraging grounds, suggesting prey limitation as a potential driver (Cheeseman et al. 2024). Our results suggest that the north pacific humpback whale population is not prey-limited in absolute terms at the ocean basin level. However, the population may nevertheless be at carrying capacity due to the patchy distribution of those resources and other individual-level processes, as humpback whale foraging effort is highly concentrated on relatively small foraging sites to which individual whales show high fidelity. The average female required approximately 252 t of biomass a year. Assuming that 7 months of the year are spent on the feeding grounds and that, of that time, 20% is spent in a high intensity foraging state (Miller et al. 2022), this corresponds to a required encounter and intake rate of 103 kg of biomass per hour during intensive foraging. Future studies quantifying the prey biomass encounter rate experienced by individual humpback whales during intensive foraging (e.g., using animal-attached camera or active acoustic sensors; Lawson et al. 2015) across a range of oceanographic conditions, ideally tied to downstream indicators of individual fitness, could help to elucidate the drivers of apparent recent reductions in humpback whale carrying capacity in the North Pacific.

4.2 | Life History Specific Prey Requirements Help to Elucidate the Role of Humpback Whales in Ecosystem Functioning

As highly migratory, fasting capital breeders, baleen whales can transport nutrients from highly productive temperate and

upwelling ecosystems to smaller, otherwise oligotrophic low-latitude breeding systems (Roman et al. 2025). Approximately 72% of North Pacific humpback whales breed in Hawaii, with the rest migrating to Mexico (Cheeseman et al. 2024). Humpback whales in Hawaii generally fast during the winter, whereas those in Mexico have often been observed feeding on krill (Ransome et al. 2024). By generating quantitative estimates of the total biomass of prey consumed and subsequently transported to these breeding grounds stratified by individual life history state, our analysis provides a foundation for forecasting the magnitude of potential ecosystem effects of humpback whales in the North Pacific, including impacts on nutrient cycling and breeding-ground productivity. Future studies that empirically measure nutrient enrichment of tropical waters across spatial and temporal gradients in humpback whale abundance would help ground-truth and refine predictive frameworks like those presented here.

A detailed understanding of humpback whale diet, consumption rates and energetics is essential for elucidating their ecological role as predators, providers of nutrient subsidies, and marine ecosystem engineers (e.g., Roman et al. 2014). Variation in whale diet, movement, and foraging behaviour likely modulates the magnitude and spatial distribution of these impacts. Thus, improving estimates of these parameters will therefore help refine our understanding of how whales transport nutrients both vertically through the water column and horizontally across ocean basins. Incorporating spatially explicit predictions of feeding-ground habitat use—such as those derived from GPS tag data—could further refine estimates of where nutrient transport and deposition (and, ultimately, their influence on biogeochemical processes) are likely to be concentrated.

4.3 | Model Sensitivity Identifies Reserve Composition and Length-Specific Fecundity as Key Targets for Future Research

The volume loss method offers a more parsimonious approach to estimating energy loss on the Hawaiian breeding grounds than the other two methods, as it represents a closed energetic system with no inputs, and thus a simplified set of assumptions. However, it is extremely sensitive to reserve energy density p_λ underscoring the importance of empirical work on protein sparing capacity and other drivers of compositional change underlying tissue volume flux in mysticetes. Even in highly fasting-adapted mammals, the loss of adipose tissue is accompanied by some loss of muscle and lean tissue (Atkinson and Ramsay 1995; Thiemann et al. 2006; Wright et al. 2020). While empirical studies linking tissue composition and volume in large, free-ranging cetaceans are rare, the results of Burslem et al. (2025) suggest that in sperm whales the change in total body fat percentage (estimated using tag-based densitometry) per m^3 difference in volume (at a fixed length) was only around 54% of that predicted by assuming all such differences in volume reflected changes in fixed-composition blubber volume. Capital breeding baleen whales, whose life history permits them substantial time to prepare metabolically for upcoming periods of fasting-lactation, are likely to be substantially better fasting-adapted than income breeding odontocetes such as sperm whales and therefore to demonstrate less extreme divergence from 'blubber only' predictions. However, our results indicate that energetic models are extremely sensitive to this parameter at levels of uncertainty representing plausible ranges for fasting capital breeding marine mammals and encompassing those currently used in many energetic simulation studies. Moreover, the composition of tissue mobilised on the breeding grounds has important implications for nutrient cycling. Metabolism of pure lipids results primarily in water and carbon dioxide, while mobilisation of protein rich lean tissues results in greater levels of nitrogen rich waste products such as urea (Engelking 2012). These results indicate that future empirical analysis aimed at refining predictions of energetic requirements and nutrient cycling based on volume flux should focus on gaining empirical estimates of the relationships between morphometric and compositional changes associated with nutritional state in humpback whales. Compositional and morphometric proxies of condition have been cross-validated in humpback whales using scale invariant methods (e.g length standardised surface area; Aoki et al. 2021). However, a volumetrically explicit approach (arrived at either through geometric transformation of existing scale invariant data or entirely new studies) is needed to shed light on what these proxies of condition represent in absolute energetic terms (Burslem et al. 2025).

For the thrust and BR derived methods, total uncertainty was similar to that for volume loss, but was driven largely by measured parameters. In particular, we used mean and SD values for estimated metabolic rate across all individuals. Results could be further refined and tailored to specific populations and context by incorporating additional empirically-based structure in this variance such as variation in FMR as a function of behavioural state (Hollers et al. 2026) and additional (e.g., male) life history states. Thrust and BR were also sensitive to P_l, the strength of the relationship between length and fecundity, because this parameter strongly influences the prey requirements of animals in early sexual maturity, which form a large proportion of overall requirements in the modelled population. Empirical studies linking individual body size and calving rates are thus needed to develop a full understanding of the energetic and prey requirements of humpback whales in the North Pacific and elsewhere.

Author Contributions

Alec Burslem: conceptualization (equal), formal analysis (lead), funding acquisition (equal), investigation (lead), methodology (lead), project administration (lead), software (lead), validation (lead), visualization (lead), writing – original draft (lead), writing – review and editing (lead). **Martin van Aswegen:** investigation (equal), methodology (equal), writing – review and editing (equal). **Andy Szabo:** investigation (equal), methodology (equal), writing – review and editing (equal). **Joe Roman:** investigation (equal), methodology (equal), writing – review and editing (equal). **Lars Bejder:** conceptualization (equal), funding acquisition (equal), investigation (equal), methodology (equal), project administration (equal), supervision (equal), writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors have nothing to report.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Global inputs and output of all 10,000 simulation runs incorporating parameter and structural uncertainties. **Table S1:** Results of sobel sensitivity analysis.